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Pacific Salmon Life Histories

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LIFE HISTORY OF CHINOOK SALMON
(*Oncorhynchus tshawytscha*)

M.C. Healey*

INTRODUCTION

THE GENUS *Oncorhynchus* dates at least from the Pliocene (Smith 1975) and probably originated from a stream- or lake-dwelling *Salmo*-like fish (Neave 1958). When the modern species evolved is uncertain, but the chinook salmon (O. *tshawytscha),* and the other Pacific salmon species, may have evolved as recently as 500,000 to 1,000,000 years ago (Neave 1958). A time span of one million years is extremely short for the differentiation of seven species. Nevertheless, Neave (1958) argued that there were good geological reasons for believing that such evolution had occurred. Most important, the restriction of *Oncorhynchus* species to the North Pacific suggested that their evolution postdated the faunistic connection between Atlantic and Pacific that existed during the late Pliocene. Thus, it seems possible that the species had undergone their complete elaboration during the Pleistocene. Recent investigation of mitochondrial DNA, however, suggests that the species may be two to three million years old (Thomas et al. 1986), which would be more in keeping with their elaboration during the Pliocene.

Morphologically, the chinook is distinguished from other *Oncorhynchus* species by its large size (adults may reach a weight of 45 kg), and by having small black spots on both lobes of the caudal fin, black pigment along the base of the teeth (Plate 14), and a large number of pyloric caeca (>100) (McPhail and Lindsey 1970; Hart 1973). Chinook also differ from the other species by their variable flesh colour, from white through various shades of pink to red.

Chinook fry and parr are distinguished by having large parr marks extending well below the lateral line (Plate 14). The adipose fin is normally unpigmented in the centre, but edged with black. The anal fin is usually only slightly falcate, and the leading rays do not reach past the posterior insertion of the fin when folded against the body. The anal fin has a white leading edge, but this is not set off by a dark pigment line as it is in coho salmon. Juvenile characteristics are highly variable, however, so that proper identification often requires meristic and pyloric caeca counts.

Within the species group, the chinook is most closely related to the coho (O. *kisutch),* with which it forms one subgrouping. Sockeye (O. *nerka),* chum (O. *keta),* and pink (O. *gorbuscha)* form a second subgrouping, and masu (O. *masou)* and amago (O. *rhodurus),* supposedly the most primitive, form a third subgrouping. According to Tsuyuki et al. (1965) and Tsuyuki and Roberts (1966), the probable evolutionary order of the species is: *masou, kisutch, tshawytscha, keta, nerka, gorbuscha,* although there is some question about the ordering of *keta* and *nerka.* Tsuyuki et al. (1965) and Tsuyuki and Roberts (1966) did not recognize *rhodurus* as a separate species, but see Kato, this volume. *Oncorhynchus rhodurus* is more primitive than *O. masou.*

The chinook, like all *Oncorhynchus* species, is anadromous and semelparous (i.e., dies after

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*Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia V9R 5K6. Present address: Westwater Research Centre, University of British Columbia, Vancouver, BC V6T 1Z2 spawning once). Within this general life history strategy, however, chinook display a broad array of tactics that includes variation in age at seaward migration, variation in length of freshwater, estuarine, and oceanic residence, variation in ocean distribution and ocean migratory patterns, and variation in age and season of spawning migration.

An important objective of this chapter is to develop a conceptual model of the life history of chinook that can encompass this degree of variation. I shall argue that there must be two fundamental components of this model. The first component is racial (Healey 1983). (Here, "race" is used in the sense that Merrell (1981) used it, that is, to identify subdivisions of a population that are geographically separated to some degree and between which gene flow is reduced.) A large part of the variation in chinook life history apparently derives from the fact that the species occurs in two behavioural forms. One form, which has been designated "stream-type" (Gilbert 1913), is typical of Asian populations and of northern populations and headwater tributaries of southern populations in North America. Stream-type chinook spend one or more years as fry or parr in fresh water before migrating to sea, perform extensive offshore oceanic migrations, and return to their natal river in the spring or summer, several months prior to spawning (Figure 1). Occasionally, males of this form mature precociously without ever going to sea. The second form, which has been designated "ocean-type" ("sea-type" in Gilbert 1913), is typical of populations on the North American coast south of 56°N. Ocean-type chinook migrate to sea during their first year of life, normally within three months after emergence from the spawning gravel, spend most of their ocean life in coastal waters, and return to their natal river in the fall, a few days or weeks before spawning (Figure 1).

The second component of the life history model is tactical and encompasses variation within each race (Figure 1). This variation represents adaptation to uncertainties in juvenile survival and productivity within particular freshwater and estuarine nursery habitats. Briefly, chinook appear to have evolved a variety of juvenile and adult behaviour patterns in order to spread the risk of mortality across years and across habitats (e.g., Stearns 1976; Real 1980). By so doing, they avoid the potential disaster associated with high mortality in a particular year or habitat.

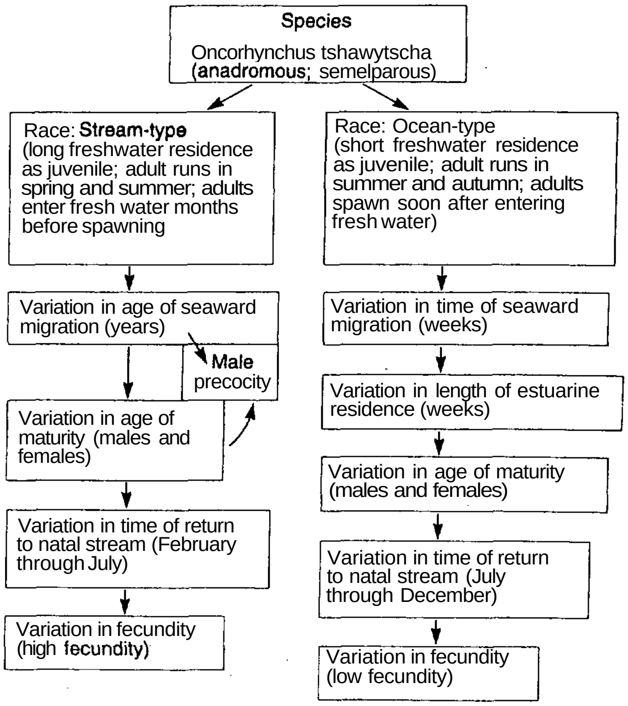


FIGURE 1

Life history structure of chinook salmon showing the division of the species into two races (ocean- and stream-type) and the range of tactical variation within each race

RELATIVE ABUNDANCE

The chinook is a valuable commercial species. Fisheries for chinook are conducted by Japan on the high seas west of 175°E in the North Pacific Ocean (west of 175°W during 1955-77) and west of

175°W in the Bering Sea by means of gillnets. The Bering Sea fishery is to be phased out by 1994. Nationals of Canada, the United States, and the USSR fish for chinook in their coastal waters and rivers. In the eastern USSR, fishing is by trap net and gillnet. In the coastal waters of the United States and Canada, fishing is by gillnet, purse seine, and troll (hook and line). Annual recorded commercial landings averaged about 23,800 t between 1970 and 1979 (INPFC 1972-82). The largest catches are along the British Columbia coast, although substantial catches are also made in southeastern Alaska, in the Japanese **mothership** fishery, and along the coasts of Washington, Oregon, and California (Figure 2). In North America the chinook is also prized as a sport fish, and approximately one million are taken each year in sport fisheries (INPFC 1972-82; Department of Fisheries and Oceans, **Vancouver,** British **Columbia,** unpublished data). Chinook are, however, the third least abundant of the Pacific salmon, with only O. *rhodurus* and *O. masou* being less abundant.

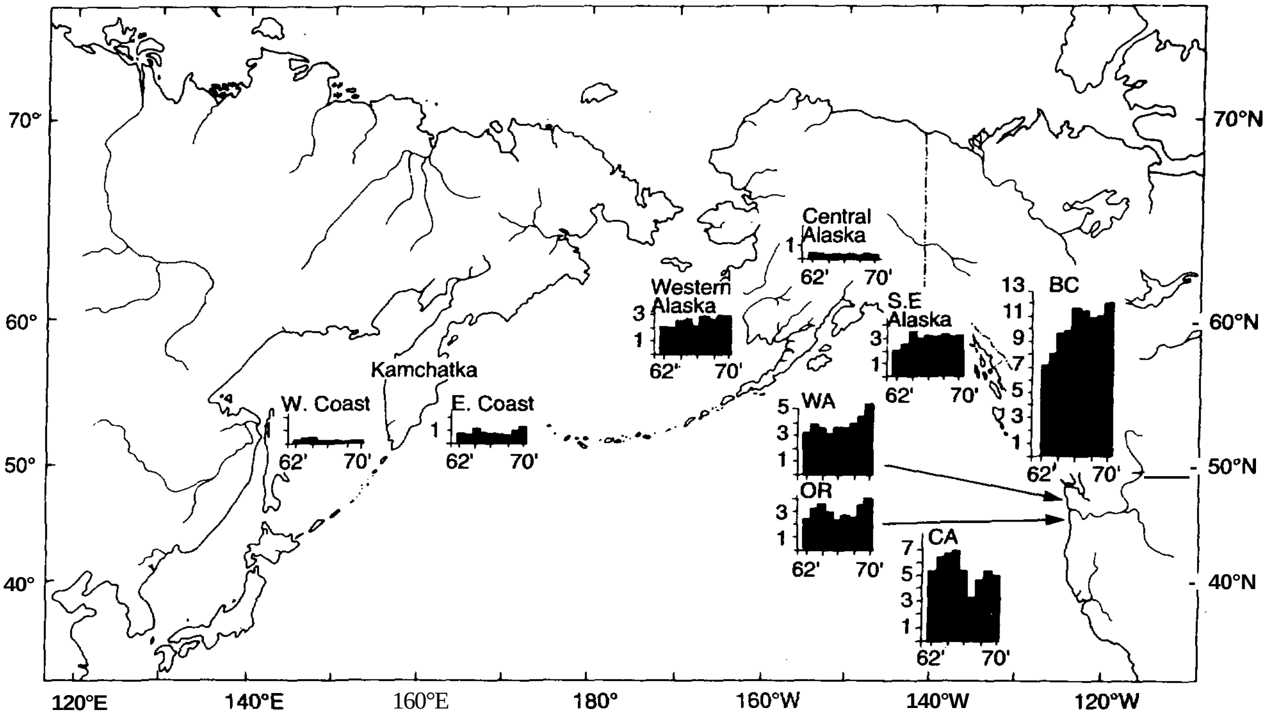


FIGURE 2

Map of the North Pacific Ocean with histograms showing the catch (hundreds of thousands of fish) of chinook in major coastal fisheries from 1962-70. (Adapted from Major et al. 1978)

SPAWNING POPULATIONS

Distribution and Abundance of Spawning Stocks

Spawning stocks of chinook are known to be distributed from northern Hokkaido to the Anadyr River on the Asian coast and from central California to Kotzebue Sound, Alaska, on the North American coast (Figure 3) (McPhail and Lindsey 1970; Major et al. 1978). Unconfirmed reports, however, suggest that chinook salmon may be distributed even further north and east on the Alaskan coast, and Hart (1973) cited an unpublished report of thirteen specimens from the Coppermine River (67°50'N, 115°00'W) in the Canadian Arctic. McLeod and O'Neil (1983) reported recovering a single specimen from the Liard River in the upper Mackenzie River drainage.

There are probably well in excess of a thousand spawning populations of chinook salmon on the North American coast (Atkinson et al. 1967; Aro and Shepard 1967) and an uncertain, but probably much lower, number on the Asian coast. Spawning occurs from near tidewater to over 3,200 km upstream in the headwaters of the Yukon River (Major et al. 1978). Individual spawning populations of chinook are relatively small, not exceeding a few tens of thousands. In British Columbia, where records have been kept on over three hundred chinook spawning populations for many decades, 80% of the populations have averaged fewer than one thousand spawners (Healey 1982a). Presumably, individual spawning populations are similarly small throughout the Chinook's range.

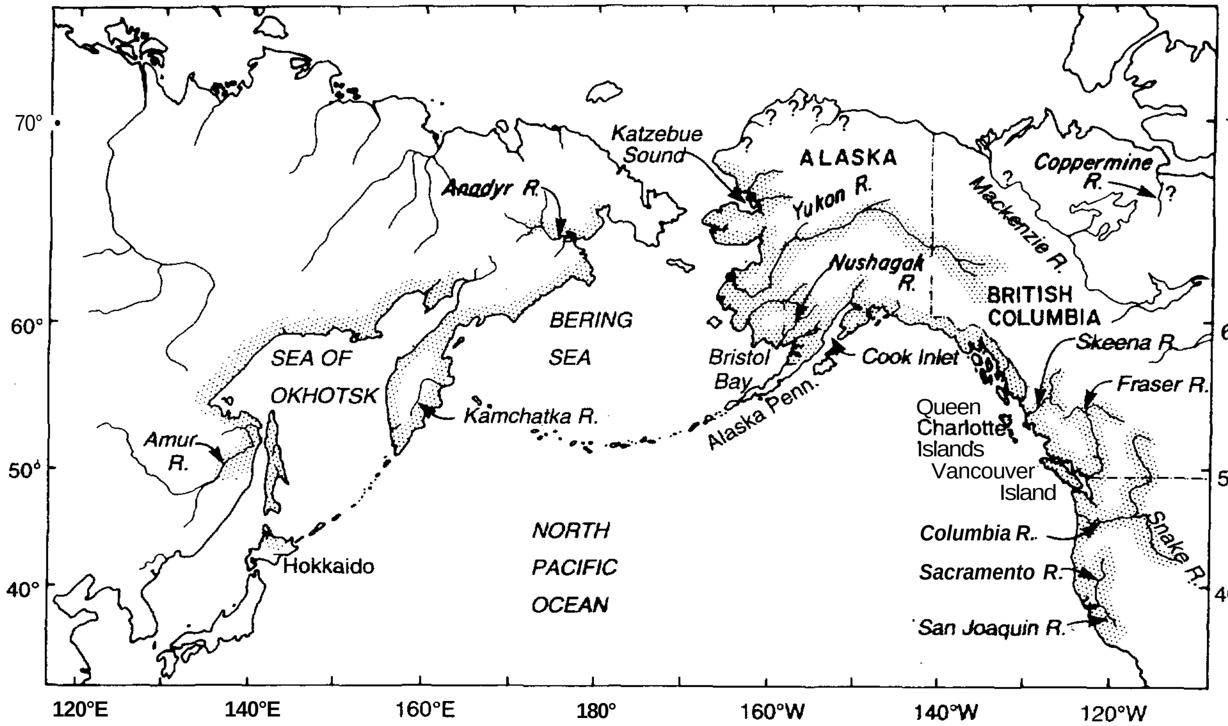


FIGURE 3

Map of the North Pacific Ocean and Bering Sea, showing the distribution of chinook spawning populations (stippled) and some of the landmarks referred to in the text. The distribution of chinook spawning populations north and east of Kotzebue Sound on the North American coast is unconfirmed (shown as question marks), except for a positive identification in the Mackenzie drainage.

The largest rivers tend to support the largest aggregate runs of chinook and also tend to have the largest individual spawning populations (Figure 4). This is not surprising, because larger rivers are likely to have more suitable spawning and rearing habitats than smaller rivers. What is somewhat surprising, however, is that major rivers at the northern and southern limits of the Chinook's range support populations as large or larger than those in major rivers near the middle of the range. The Sacramento-San Joaquin River system, at the southern limit of the range of chinook, for example, had chinook runs of a million fish or more until the early part of this century (Clark 1929). These rivers

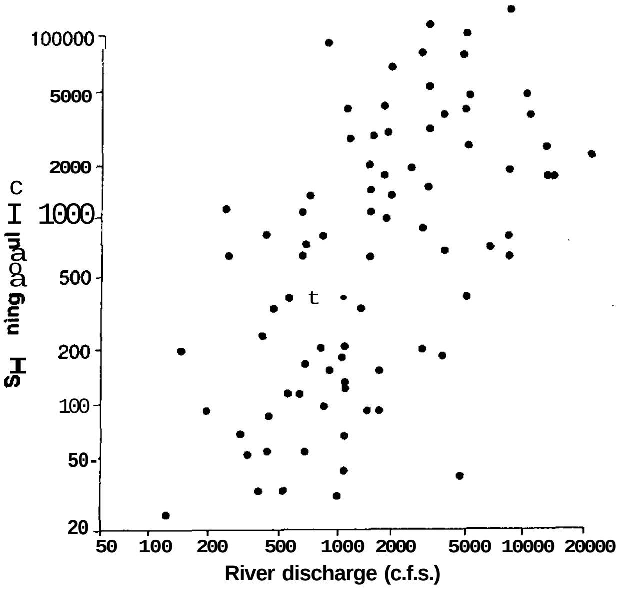


FIGURE 4

Relationship between average spawning population size (1952-76) and average river discharge for British Columbia populations of chinook salmon (both axes are on a logarithmic scale). These data are for individual spawning populations within each river system.

still have runs of several hundred thousand, even though habitat loss and water extraction have been so severe that the San Joaquin River was virtually unable to support chinook spawning, with escapement averaging less than 4,000 in the mid-1970s (Kjelson et al. 1982). Since 1980, however, escapements to the San Joaquin have recovered somewhat and escapement was 70,000 in 1985 (M. Kjelson, u.s. Fish and Wildlife Service, Stockton, California, pers. comm.). Run estimates for the Yukon and Nushagak rivers, near the northern limit of the range of chinook, are very uncertain, but catches of chinook in western Alaska and escapement estimates for these rivers indicate that runs to both rivers are probably on the order of 400,000 to 600,000 fish (Knudsen et al. 1983). By comparison, the Columbia River historically produced only about twice as many fish as the Sacramento-San Joaquin River system, and the Fraser River produced only about 200,000 chinook (Rich 1942; M.C. Healey unpublished data). Both the Columbia and Fraser rivers are near the centre of the Chinook's range on the North American coast.

Chinook have been transplanted to a variety of locations outside their normal range. Transplants to the east coast of North America have been conducted for almost a century, initially with the hope of supplementing declining Atlantic salmon (*Salmo salar*) runs, but also as a means to "control" landlocked smelt (*Osmeridae*) and alewife (*Alosa pseudoharengus)* populations (Hoover 1936; Ricker and Loftus 1968). Most transplanted populations were maintained only by artificial propagation/if they were maintained at all. Recently, however, naturally spawning populations have become established in the Laurentian Great Lakes (Carl 1982). Both artificially and naturally produced chinook are now a valuable component of the sport fisheries in Lake Michigan and its tributary streams.

Chinook from California were successfully transplanted to New Zealand around the turn of the century. The first transplants to New Zealand were in the late 1800s, and intensive stocking began in 1901. By 1907, adults were returning to New Zealand hatcheries, and by 1910 it was possible for these hatcheries to export spawn to other parts of New Zealand and Tasmania. Chinook are now widespread in rivers along the east coast of the south island and occur in some rivers on the west and north coasts. Whether this has occurred as a result of deliberate planting or natural straying is not clear (Waugh 1980).

Although the original intent of the introduction of chinook to New Zealand was to create commercially exploitable runs of fish, established runs have provided only a low sustainable yield, and little commercial harvesting of salmon has occurred. Chinook are, however, an important sport fish. Limited suitable spawning and rearing areas in New Zealand streams, together with impoundments, water extraction for irrigation, and pollution, have served to limit smolt production (Waugh 1980). Poor smolt production is presumably an important reason for the relatively low productivity of chinook in New Zealand.

Chinook have also been transplanted to southern Chile. Apparently, landlocked populations have been established there, and the hope is that marine anadromous populations will also be successful in Chile. Some returns of anadromous chinook have been reported in sea ranching operations (Lindbergh 1982).

In this chapter, I shall concentrate on chinook within their natural range. This is not to discount the possible impact of successful transplants. The introduction of chinook and other Pacific salmon to the Great Lakes, for example, almost certainly means that they will ultimately invade Atlantic Ocean drainages, with unknown consequences for local fish fauna. It is the intent here, however, to emphasize what is known about the biology of the animal in its natural habitat.

Within the natural range of chinook salmon, stream- and ocean-type spawning populations are geographically separated to a considerable degree (Healey 1983). All Asian stocks are apparently stream-type (e.g., Knudsen et al. 1983). On the North American coast, chinook spawning populations are wholly or predominantly stream-type throughout Alaska. At the Alaska-British Columbia border, however, there is a rather abrupt shift in composition. From the Nass and Skeena rivers (56°N) (Figure 3) southward, ocean-type chinook dominate all runs except, perhaps, the Yakoun River on the Queen Charlotte Islands (Table 1). Stream-type chinook make an important contribution to runs to larger rivers south of 56°N (14%-48%) but are relatively scarce in smaller rivers (0%-12% of runs). Wherever they are sympatric with ocean-type fish, stream-type fish tend to be found in headwater spawning areas and ocean-type fish in downstream spawning areas (Rich 1925; Hallock et al. 1957; Healey and Jordan 1982). The geographic separation is not complete, however, as the behavioural types are sympatric on many spawning riffles.

TABLE 1

Occurrence of stream- and ocean-type chinook in spawning runs to rivers along the west coast of North America

River system	Approximate N. latitude	% of spawning runs	
		Stream	Ocean
Alaska			
Yukon	62°30′	100	0
Cook Inlet rivers	61°30′	97-99	1-3
Taku	58°30′	100	0
Stikine	56°40′	100	0
British Columbia			
Nass	55°20′	42	58
Skeena	54°20′	48	52
Kitimat	54°00′	12	88
Yakoun	53°30′	57	43
Bella Coola	52°25′	14	86
Docee (Rivers Inlet)	51°40′	3	97
Quinsam (Campbell)	50°00′	1	99
Big Qualicum	49°25′	0	100
Fraser	49°20′	34	66
Nanaimo	49°10′	5	95
Nitinat	48°50′	1	99
Chemainus	48°50′	0	100
Cowichan	48°50′	10	90
Washington/Oregon			
Columbia	46°10′	22	78
Sixes	42°50′	12	88
California			
Klamath	41°30′	14	86
Sacramento	38°00′	10-18	82-90

Source: From Healey (1983) with additional data from Clark (1929)
Note: The rivers are ordered in descending latitude.

Timing of Spawning Runs

Chinook salmon may return to their natal river mouth during almost any month of the year (Snyder 1931; Rich 1942; Hallock et al. 1957). There are, however, typically one to three peaks of migratory activity. The timing and the number of migratory peaks varies among river systems (Figure 5). For northern river systems (Kamchatka River: Vronskiy 1972; Yukon River: Brady 1983; Cook Inlet tributaries: Yancey and Thorsteinson 1963; Nass and Skeena rivers: Department of Fisheries and Oceans, Vancouver, British Columbia, unpubl. data), a single peak of migratory activity during June appears typical, although the run may extend from April to August (Figure 5). Particular spawning populations may return later in the season, however, and this may result in two peaks of migratory activity (e.g., Kenai Peninsula: Yancey and Thorsteinson 1963).

Further south, runs tend to occur progressively later. In the Bella Coola River, an early run in late May and June is followed by *a* second, but relatively smaller, run in August (Figure *5).* In the Fraser River there are two runs of almost the same size: an early run peaking in July, and a late run peaking in September/October. The Fraser River has a third, smaller, run in August that corresponds in timing to the late run into the Bella Coola River (Figure 5) (Ball and Godfrey 1968a, 1968b; Fraser et al. 1982). A late August run domi-

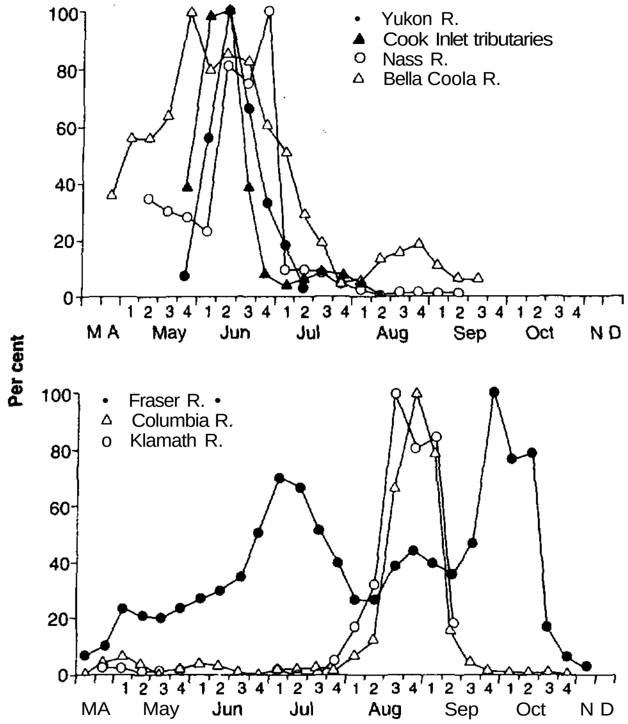


FIGURE 5

The timing of spawning runs to rivers throughout the North American range of chinook. The estimated abundance of fish during each quarter month is shown relative to the quarter monthly period with the greatest abundance of fish. Data sources are: Brady (1983) for the Yukon; Yancey and Thorsteinson (1963) for Cook Inlet tributaries; Canada Dept. of Fisheries and Oceans (unpublished data) for the Nass and Bella Coola rivers; Fraser et al. (1982) for the Fraser; Rich (1942) for the Columbia; and Snyder (1931) for the Klamath

nates chinook returns to both the Columbia and Klamath rivers. The Columbia River also has spring and summer runs, but these are numerically small relative to the late August run (Figure 5) (Rich 1942; Silliman 1950). The Klamath River has a spring run, but it, too, is relatively small (Figure 5) (Snyder 1931). Historically, the Klamath River spring run and the Columbia River summer run are believed to have been much larger, but they have since been decimated by habitat loss and overfishing.

The early run in the Fraser River may be analagous to the summer run in the Columbia River and to the spring runs in more northern rivers. The late Fraser River run appears unique in its timing, unless it is an analogue of the winter run into the Sacramento River which reaches Redding from late November through February, 350 km upstream (Slater 1963; Hallock and Fry 1967). The Sacramento River also has spring and fall runs of chinook, and a unique winter run. The winter and spring runs tend to overlap considerably in timing so that their separation is not precise during the run, but the two groups do separate on the basis of spawning area and time of spawning. Winter-run fish spawn mainly in May and June in the upper main stem of the Sacramento River. Spring-run fish, however, delay spawning until late August or September, and their spawning areas are in the upper reaches of the main stem of the Sacramento River and of the principal tributaries. The majority of chinook in the Sacramento River are fall-run fish that enter the river in September and October. These fish spawn shortly after entering the river in the middle and lower reaches (Hallock et al. 1957; Slater 1963; Hallock and Fry 1967; Kjelson et al. 1981). Thus, Chinook in the Sacramento River appear to exhibit typical stream-type (spring-run) and ocean-type (fall-run) behaviour. The winter-run fish are somewhat anomalous in that they have characteristics of both stream- and ocean-type races. They enter the river green and migrate far upstream. Spawning is delayed for some time after river entry. Young winter-run chinook, however, migrate to sea in November and December, after only four to seven months of river life. Without further information or details of the life history of these rare and interesting fish it is difficult to decide whether or not they fit the classification of stream- and ocean-type races.

Despite the wide variation in run timing within most rivers, spawning times tend to be similar among runs. Early-run fish normally delay spawning and spawn in the fall, about the same time as late-run fish. The winter run in the Sacramento River is an exception to this rule.

Detailed information on the racial composition of spawning runs is available for the Fraser and Columbia rivers (Rich 1925; Ball and Godfrey 1968a, 1968b). These data clearly demonstrate the alternation in timing of stream- and ocean-type races entering the two rivers (Figure 6). Stream-type chinook enter principally during the spring and early summer, and ocean-type chinook enter during the summer and fall. Given the fact that

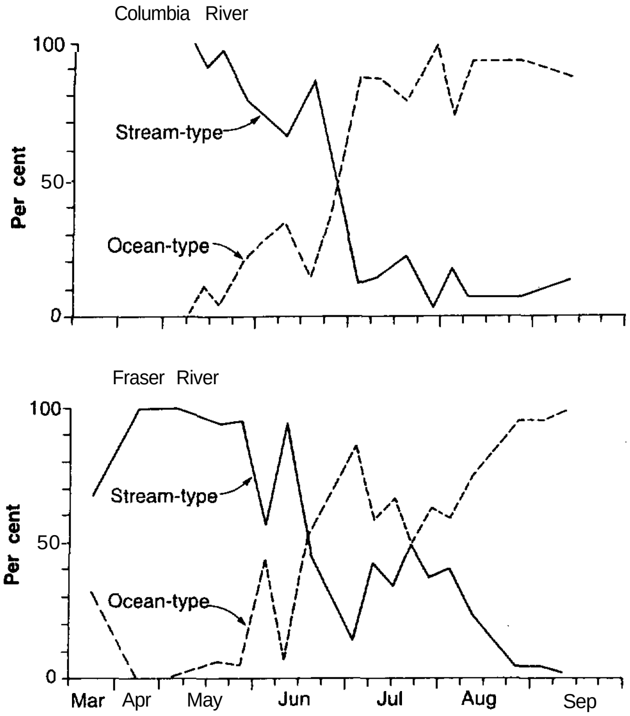


FIGURE 6

Seasonal changes in the percentage contribution of stream- and ocean-type chinook to the total run in the Columbia and Fraser rivers. (Data from Ball and Godfrey 1968a, 1968b, 1969, 1970; Rich 1942)

stream-type fish migrate to headwater tributaries of these two systems, their early entry to fresh water permits them to take advantage of peak summer flows to reach their spawning areas. Ocean-type fish, with shorter upriver migrations on average, can delay entry until after peak flows and thus take advantage of a slightly longer ocean feeding period. Stream-type fish, therefore, appear to suffer a double disadvantage. Not only do they lose feeding time in the sea, but they must also maintain their ion balance, without feeding, in the osmotically rigorous freshwater environment for several months before spawning. The adaptations required to achieve this suggest that there must be more than casual genetic separation between stream- and ocean-type chinook.

Timing of Spawning

The time at which chinook actually spawn is quite variable, ranging from May/June for some more northern populations and for the winter-run fish in the Sacramento River (Department of Fisheries and Oceans, Vancouver, British Columbia, unpublished data; Hallock et al. 1957; Slater 1963) to December/January for fall-run chinook in the Sixes and Elk rivers, Oregon (Reimers 1971; Burck and Reimers 1978), and in the Sacramento River (Hallock and Fry 1967). The trend throughout the range of chinook is to earlier spawning as one moves north (Figure 7), with northern populations tending to spawn from July to September and southern populations from November to January. Within river systems, however, individual populations may spawn at widely different times. In the Sacramento River, for example, spring-run fish spawn in August to September, fall-run fish in October to December, and winter-run fish not until May and June. Thus, there are (or were before the winter and spring runs were decimated) chinook spawning virtually every month of the year in the Sacramento River. In the Fraser River (Department of Fisheries and Oceans, Vancouver, British Columbia, unpublished data), median spawning dates for individual populations range from June to No-

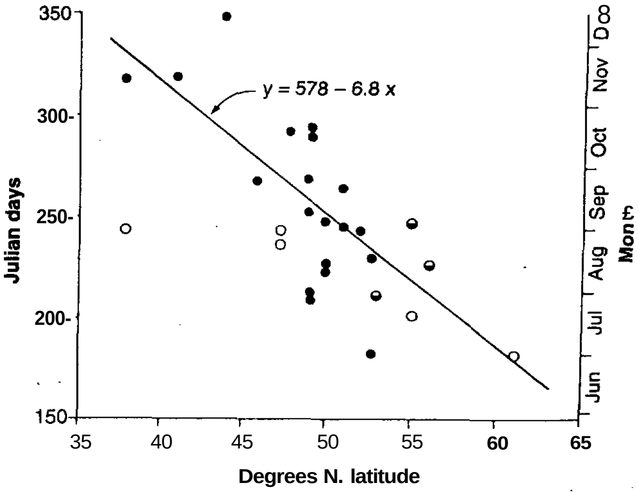


FIGURE 7

The relationship between the median spawning date and the latitude of the spawning population for stream- and ocean-type chinook. Symbols are: o = stream-type; * = ocean-type; • = mixed-type. The correlation for all data is significant (*r* - -0.755, *p* <.01). The races do not differ significantly (*p* >,05). The regression reported on the figure is the regression of Julian day on latitude.

vember, a span of six months. Spawning appears to be less protracted in northern rivers. In the Skeena River the range of median spawning dates among populations was 15 August to 25 September, and in the Kamchatka River the range among populations was 15 July to 15 August (Department of Fisheries and Oceans, Vancouver, British Columbia, unpublished data; Vronskiy 1972).

There is some suggestion that stream-type fish spawn earlier than ocean-type fish, at least in the central and southern parts of the chinook's range where the two types are sympatric. Burner (1951) noted that spring-run (stream-type) Columbia River chinook spawned in late August whereas summer- and fall-run fish (mainly ocean-type) spawned in late September. Hallock et al. (1957) also noted earlier spawning of spring-run fish, which presumably were mainly stream-type, relative to fall-run fish in the Sacramento River. Known populations of stream-type chinook in the Fraser River, however, do not obviously spawn earlier than ocean-type chinook(Department of Fisheries and Oceans, Vancouver, British Columbia, unpublished data). Northern populations, which are all stream-type, do spawn early, but this is not clearly related to race. If earlier spawning was mainly a function of race, then one would expect a discontinuity in the median date of spawning at about 56°N latitude, the latitude at which the composition of spawning populations shifts from predominantly ocean-type to predominantly stream-type. The trend to earlier spawning as one moves north is, however, continuous throughout the range of chinook, with no apparent discontinuity where population structure shifts to stream-type (Figure 7).

Redd *Characteristics*

The spawning beds chosen by chinook vary considerably in physical characteristics. Chinook will spawn in water depths from a few centimetres (Burner 1951; Vronskiy 1972) to several metres (Chapman 1943; Chapman et al. 1986). They will spawn in small tributaries two to three metres wide (Vronskiy 1972) and in the main stem of large rivers like the Columbia and Sacramento (Chapman 1943; Hallock et al. 1957).

Several authors have reported in some detail on the characteristics of chinook redds and spawning beds (Chapman 1943; Burner 1951; Briggs 1953; Vronskiy 1972; Neilson and Banford 1983). In addition, the expanding literature on instream flow requirements provides depth and velocity criteria for chinook spawning (Collings et al. 1972; Smith 1973; Bovee 1978). Comparison among observations by different authors is complicated by the fact that methods of measurement were different, and in some reports the methods were not given in sufficient detail to permit an assessment of comparability. The overriding impression is that, although there is good agreement among mean values for water depth and velocity in spawning beds, the range in depths and velocities that chinook find acceptable is very broad (Table 2). There is little agreement among observers about either the maximum or the minimum values for depth and velocity. For example, Burner (1951) observed chinook spawning in as little as 5 cm of water, whereas Collings et al. (1972) suggested that the minimum water depth for spawning is 30 cm. Maximum depths of spawning range over an order of magnitude, from 41 to >700 cm. Velocity minima range from 10 to 52 cm/s and maxima from 64.4 to 150.0 cm/s. There is apparently no agreement as to whether depth and velocity characteristics used in nest site selection differ between stream- and ocean-type chinook. Some authors assign greater depth and velocity preferences to stream-type and others to ocean-type chinook (Table 2).

In preparation for spawning, the female chinook digs a shallow depression in the gravel of the stream bottom by performing vigorous swimming movements on her side near the bottom. Gravel and sand thrown out of the depression accumulate in a mound, or tailspill, at the downstream margin of the depression. During the act of spawning the female deposits a group or "pocket" of eggs in the depression and then covers them with gravel. Over the course of one to several days, the female deposits four or five such egg pockets in a line running upstream, enlarging the spawning excavation in an upstream direction as she does so. The total area of excavation, including the tailspill, is here termed a "redd."

Four papers reported the size of the area of the redd excavation (Table 2). Burner (1951) observed a relatively narrow range of redd sizes in tributaries of the Columbia River, with stream-type chinook having the smaller redds. The redds of the stream-

TABLE 2
Summary of published information on water depth and velocity in chinook spawning beds, and area of the redd excavation

Source	*Type**	Water depth (cm)		Water velocity (cm/s)		Redd area (m^2)	
		Range	Mean	Range	Mean	Range	Mean
Chapman (1943)		30-460				2.4-4.0	
Burner (1951)	S	5-122	31			3.9-6.5	
Briggs (1953)	0	28-41	32	30-76			
Vronskiy (1972)	S	13-720	56t	30-150	61	*4.0-15.0‡*	
Collings et al. (1972)	S	45-52		52-68	54+		
	0	30-45		30-68			
Smith (1973)	S		31	21.7-64.4	43		
	0		38.9	18.6-80.5	49.7		
Bovee (1978)§	S	10-70	30	10-100	40		
	0	10-120	30	25-115	50		
Nelson & Banford (1983)	S			15-100	56	0.5-27.5	9.5
Chapman et al. (1986)	0	to 700		37-189	>100	2.1-44.8	17.0

Notes: *Separate values are reported for stream- and ocean-type chinook when available. S - stream-type (spring-run chinook, 0 - ocean-type (fall-run) chinook

tGeometric mean of the ranges given by Vronskiy (1972) for different tributaries

‡Maximum redd areas. These were calculated as the product of maximum and minimum length and breadth measurements given in Vronskiy (1972).

§Values taken from probability-of-use curves in Bovee's (1978) report

type fish also appeared to be in areas of coarser gravel and were often characterized by having a few large cobbles in the bottom of the excavation. Vronskiy (1972) gave only length and width measurements for stream-type chinook spawning mounds in the Kamchatka River. Maximum redd areas, inferred from the product of minimum and maximum measurements given by him, ranged from 4 to 15 m^2. Vronskiy (1972) also commented on the appearance of large cobbles in the bottom of chinook redds in the Kamchatka River but noted that in some tributaries chinook spawned in very fine gravel. Neilson and Banford (1983) reported a great range of sizes and large average size for redds of stream-type chinook in the Nechako River (British Columbia). Chapman et al. (1986) reported redd areas for the Hanford reach of the Columbia River that ranged from 2.1 to 44.8 m^2 and averaged 17.0 m^2. Neilson and Banford (1983) apparently estimated redd area as the product of maximum length and width of the redd, as I did from Vronskiy's data, whereas Burner (1951) and Chapman et al. (1986) took account of the oval shape of the redd. Thus, the measurements are not comparable, and Neilson and Banford's (1983) estimates of redd area, as well as those that I made from Vronskiy's data, will be up to twice as large as those made by Burner (1951) or Chapman et al. (1986).

Both Vronskiy (1972) and Neilson and Banford (1983) observed that the depth of the redd excavation was negatively correlated with water velocity in the spawning area. According to Vronskiy (1972), the higher mound in the tailspill of redds dug by chinook in low velocity water serves to improve subgravel irrigation of the eggs. Low velocity areas were also likely to be characterized by fine gravel that, presumably, could be dug into more easily by the fish, so that nests were deeper.

Briggs (1953) reported that chinook buried their eggs 20-36 cm deep (average 28 cm) in the gravel of two small streams in California. Vronskiy (1972) observed eggs buried from 10 to 80 cm deep in the gravel in the Kamchatka River, although he found few eggs below 50 cm. According to Vronskiy

(1972), the depth to which the eggs were buried was at least partly dependent on water flow, with the eggs being buried more deeply where flow was low. Chapman et al. (1986) found that the depth of gravel over eggs and embryos ranged from 10 to 33 cm and averaged 18.8 cm.

The range of depths and velocities within which chinook have been observed to spawn suggests that establishing meaningful minimum and maximum criteria for these factors is problematic. Although conventional wisdom states that chinook prefer deeper, faster rivers for spawning than the other *Oncorhynchus* species, measures of spawning area characteristics for other species do not confirm this wisdom (e.g., Burner 1951). Available measurements do not suggest that chinook avoid shallow water and low flows. Chinook may, however, spawn in water that is deeper and faster flowing than that used by other species because they are large enough to hold position in the faster current and to build a redd in the coarser gravel found there.

Minimum spawning depth is presumably governed by water depth needed for successful digging and spawning; however, Burner's (1951) observations suggest that this can be accomplished in as little as 5 cm of water. It is not clear why increasing depth should ever be a constraint, unless it is correlated with some other significant factor, such as velocity. Chapman (1943) observed Columbia River fall (ocean-type) chinook spawning below Kettle Falls in water 15 ft (4.6 m) deep. In one spot, as many as thirty fish appeared to be spawning together in one large redd, although he also observed numerous individual redds and some with a few fish digging together. According to Indians whom he interviewed, this sort of main stem spawning was commonplace in the Columbia River when chinook were abundant and such spawning places had been important fishing places for them. Chapman (1943) considered such spawning to be unusual, however, and stated that, in his experience, chinook normally spawned at the head of a riffle in 0.3-1.2 m of water. Chapman (1943) speculated that the spawning below Kettle Falls may have been stimulated by high subgravel flow rates below the falls.

Other authors have emphasized the importance of subgravel flow in the choice of redd sites by chinook. Vronskiy's (1972) comment about the importance of the tailspill gravel mound in stimulating subgravel flow when redds are placed in low velocity water has already been mentioned. In addition, Vronskiy (1972), like Chapman (1943), observed that most redds (95%) were located at the head of a riffle, just before the crest of the rapid. Vronskiy (1972) attributed the attractiveness of this location to the high subsurface flows that occurred there. Other spawning occurred in pools below log jams where the log jam increased the rate of subgravel flow. In the Nechako River most chinook spawn on the upstream sides of large gravel dunes oriented across the river channel, presumably to take advantage of the subgravel flow stimulated by the dune (Russell et al. 1983).

Provided the condition of good subgravel flow is met, chinook apparently will spawn in water that is shallow or deep, slow or fast, and where the gravel is coarse or fine. The requirement for good subsurface flow is consistent with the probable incubation requirements of chinook relative to the other species. Chinook have the largest eggs (Rounsefell 1957) and, thus, their eggs have a small surface-to-volume ratio compared with the other species of Pacific salmon. Their eggs should, therefore, be more sensitive to reduced oxygen levels and require a more certain rate of irrigation. Silver et al. (1963) observed that the size of chinook at hatching was dependent on water velocity in the incubation apparatus even at velocities as high as 1,350 cm/h, and on oxygen concentration even near saturation levels, at least when the incubation temperature was about 11°C.

The apparent preference of chinook for spawning areas with high subgravel flow may explain their tendency to aggregate in particular locations for spawning and to ignore other, superficially similar, areas (Vronskiy 1972). Within areas of aggregation the distribution of spawning nests is not random but, rather, tends to an even distribution (Neilson and Banford 1983). Burner (1951) suggested that each spawning pair defends an area equal to about four times the area of its redd, and he recommended that the available spawning area be divided by four times the average redd area to arrive at an estimate of the maximum spawning population that the area could support. According to Burner's (1951) estimates of redd size, stream-type chinook require about 16 m^2 and ocean-type chinook require about 24 m^2 of gravel per spawning pair.

The Chinook's apparent need for strong subsurface flow may mean that suitable chinook spawning habitat is more limited in most rivers than superficial observation might suggest, so that at high population density many chinook spawn in areas of low suitability, and their eggs consequently suffer high mortality. If this is the case, the continued high production of chinook in spite of greatly reduced spawning populations (Healey 1982a) becomes more understandable, since the apparent reduction in spawning populations will not have been accompanied by a corresponding reduction in fry production.

Length of Residence on the Redd

Chinook females in the Morice River, a tributary of the upper Skeena River drainage, spent between 4 and 18 days defending their redd after they began spawning (Neilson and Geen 1981). Chinook females in the Nechako River, a tributary of the upper Fraser drainage, spent between 6 and 25 days defending their redds (Neilson and Banford 1983). The average length of residence on the redds declined throughout the spawning period from about 14 days (early in the season) to about 5 days (late in the season) on the Morice River, and from about 15 days (early in the season) to about 4 days (late in the season) on the Nechako River. Both the Morice and Nechako river populations are mainly stream-type, although scale analysis indicates the presence of ocean-type chinook as well. As far as I am aware, these are the only measurements of residence on a redd for chinook. Apparently, no measurements exist for males, and, as Neilson and Geen (1981) pointed out, obtaining such measurements would be complicated by the fact that males are not faithful to a single redd.

FECUNDITY

The earliest measurements of fecundity in chinook salmon are those that McGregor (1922, 1923) reported for the Klamath and Sacramento rivers in California. McGregor's data indicated considerable variation in fecundity within each population but an even larger difference between populations. McGregor (1923) went so far as to propose that differences in fecundity would permit separation of Sacramento River and Klamath River chinook caught at sea. Healey and Heard (1984) summarized more recent data on the fecundity of 16 additional populations and confirmed the high intra- and interpopulation variation in chinook fecundity that McGregor (1923) had described. Fecundity of chinook females ranged from fewer than 2,000 eggs to more than 17,000 eggs. Fecundity was significantly correlated with female size in all but one of the populations examined to date. Size, however, explained only 50% or less of the variation in fecundity between individuals within a population (Figure 8). The slope of the fecundity on length relationship for chinook was also low (generally less than two in chinook compared with other fishes in which it is generally greater than three) (Healey and Heard 1984).

In several instances, fecundity had been measured for the same population over a number of years. Significant variation in average fecundity between years was evident in these populations, although the absolute interannual variation was less than that observed between years in other species (Healey and Heard 1984). The only other factor that appeared to contribute to within-population variation in fecundity was a small difference between fish of red and white flesh colours in the Fraser River population (Godfrey 1968a). Age apparently contributed nothing to variation in fecundity beyond that predicted by the difference in sizes between ages (Healey and Heard 1984).

Between-year and flesh colour variation in fecundity explained only a small additional amount of the within-population variation in fecundity, so that a great deal of individual variation remains to be explained. Healey and Heard (1984) speculated that this high variation may reflect an uncertain trade-off between egg size and egg number in the overall fitness of chinook populations. Unfortunately, there are no data on egg size in chinook sufficient to demonstrate that the more highly fecund fish within a size class also have smaller

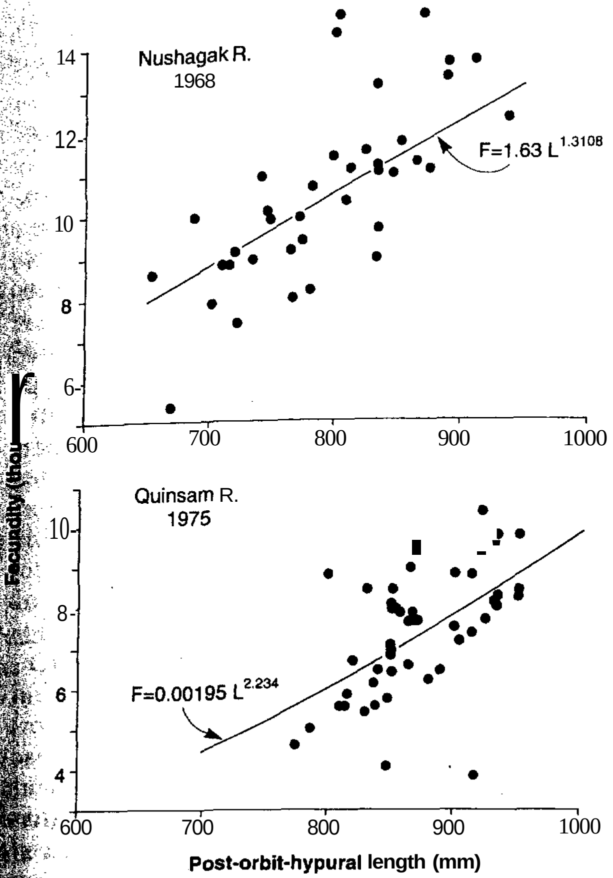


FIGURE 8

Two examples of the relationship between length and fecundity for chinook salmon. Nushagak River chinook are a stream-type race having high average fecundity, and Quinsam River chinook are an ocean-type race having low average fecundity. Although the fecundity on length regressions are significant in both instances, the amount of variation in fecundity attributable to variation in length is relatively small.

Eggs. Egg size has been shown to increase with female size in Oregon chinook stocks (Nicholas and Hankin 1988).

Fecundity, therefore, appears to be less determined by body size in chinook than in other fishes. Partly, this may be due to the unresolved trade-off tween egg size and egg number in chinook mentioned above, so that egg size varies more between chinook individuals than is usual for fishes. Also, it appears that in the trade-off between body size and fecundity among older chinook, body size was more critical, so that more energy is devoted to somatic growth and less to egg production than in other fishes (Healey and Heard 1984). More energy is devoted to individual eggs among these large fish as well (Nicholas and Hankin 1988).

Although, within populations, interannual variation in fecundity was significant, between-population variation was numerically greater (Healey and Heard 1984; Nicholas and Hankin 1988). Average fecundity at size varied approximately two-fold between populations (4,347-9,427 at 740 mm post-orbit/hypural length). In general, fecundity increased from south to north in the chinook's range, contrary to Rounsefell's (1957) conclusion based on a few samples (Figure 9). The Sacramento River population, at the southern limit of the Chinook's range, however, has an unusually high fe-

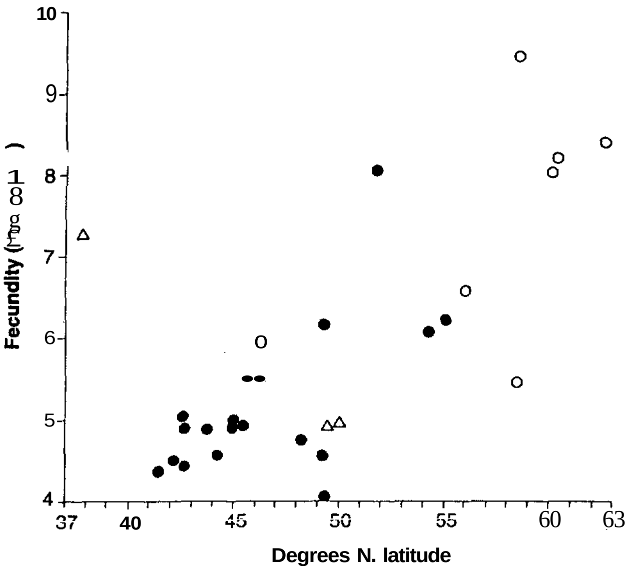


FIGURE 9

The relationship between average fecundity of chinook at 740 mm postorbit-hypural length and the latitude at which the population spawns (from data in Healey and Heard 1984; Nicholas and Hankin 1988). Symbols are: • = ocean-type populations having a common slope of fecundity on length regression; A = ocean-type populations having slopes of fecundity on length regression different from the above; o = stream-type populations having a common slope of fecundity on length regression. The overall correlation between fecundity and latitude is significant ($r = 0.663$, $p < .05$). If the populations with symbol A are left out of the regression, the relationship for ocean-type populations is also significant ($r = .642$, $p < .05$). Within the stream-type race, however, there is no relationship between latitude and fecundity.

cundity. This population, as well as three others (Quinsam River, Puntledge River, Rivers Inlet, all in British Columbia), differed from all other populations in the slope of the regression of fecundity on length (Healey and Heard 1984). Thus, it is difficult to compare the Sacramento River fish directly with most other populations. The high-fecundity populations near the northern limit of the chinook's range are all stream-type fish which spend a year in fresh water before going to sea, whereas the low-fecundity populations in the south are mainly ocean-type fish which go to sea during their first year of life. Thus, latitudinal differences in fecundity may partly reflect a racial difference between stream- and ocean-type chinook rather than a latitudinal cline. In the Columbia River, however, data are available on the fecundity of both stream- and ocean-type chinook. Although stream-type fish had a higher fecundity than ocean-type, the difference between the races was not statistically significant (Galbreath and Ridenhour 1966; Healey and Heard 1984). If the data are segregated into stream- and ocean-type life histories, there is still a latitudinal cline in fecundity within the ocean-type life history, provided the Sacramento, Puntledge, and Quinsam rivers and Rivers Inlet populations are excluded ($r = .642$, $p < .05$). The fecundity of stream-type populations alone is not significantly correlated with latitude, but, for all populations combined, the correlation is significant ($r = .663$, $p < .05$).

SPAWNING, INCUBATION, AND SURVIVAL

Egg Deposition

The fecundity of females represents only the potential for production of the next generation. This potential is subject to successive losses that, in a stable population, ultimately result in an average production of one adult female spawner for each female spawner in the parent generation. Many of these successive losses have not been documented for chinook, except in an anecdotal way. They will be listed here in order of their occurrence, together with whatever estimates of loss are available in the literature. As before, the emphasis will be on evidence of variation among populations as adaptations to local environments.

Females that die unspawned on the spawning grounds, or that do not spawn all their eggs, represent an important potential loss in egg production. Such losses are generally lumped together in estimates of unspawned egg retention, and these estimates are seldom large (Chapman et al. 1986). Vronskiy (1972) reported that egg retention was generally about 0.6% of absolute fecundity for chinook; Major and Mighell (1969) reported it to be about 0.5% for Yakima River chinook; and Shepherd (1975) reported it to be 1.3% for Morice River chinook. Paine et al.(1975), however, reported an average of 11.9% egg retention for Big Qualicum River chinook, and Shepherd (1975) reported 25% egg retention for Bear River chinook with 9 of 47 females unspawned and 20% egg retention for Babine River chinook with 30 of 230 females unspawned. Fish in these latter two rivers, however, had been subject to harassment. In 1965 about 25% of adult chinook died without spawning in a spawning channel at Priest Rapids, Washington. This mortality was apparently caused by an infection of the gills with a protozoan of the genus *Dermocystidium* (Pauley 1967).

Ovarian disease may be a cause of reduced fecundity or egg deposition. A condition termed "bad eggs" has been known for Columbia River fall (ocean-type) chinook since the early 1940s. The condition is characterized by a number of signs, including a pus-like discharge from the vent and dead white eggs, either individually or in clusters, on the surface of the ovary or near the point of attachment. The condition may be present in one or both ovaries and occurred in 2%-20% of females returning to Columbia River hatcheries (Conrad

1965). Apparently, conditions of this type are not a problem in British Columbia hatcheries or known to be a problem in wild stocks (G. Hoskins, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, pers. comm.).

Losses to eggs actually shed by females may occur in a variety of ways. Some eggs will be swept out of the redd during spawning and will be subject to heavy predation. Some eggs will not be fertilized. Some will not be buried deeply enough and will be accessible to vertebrate and invertebrate predators. Floods, siltation, freezing, desiccation, and disease can all take a toll. Poor gravel percolation or poor water quality can cause mortality of eggs. Finally, the quality of eggs laid and the embryos produced, which themselves depend on the genetic and phenotypic quality of the parents, may influence the survival of eggs. Few of these sources of egg and embryo loss have been quantified.

Opinions differ as to the quantity of eggs lost during spawning by being swept out of the redd. Vronskiy (1972) believed that there was a very high loss of eggs during spawning. He based this conclusion on the number of eggs recovered during complete excavation of redds. No more than 30% of the average fecundity of chinook females was ever recovered from a redd, and the average number of eggs recovered was about 12% of. average fecundity. Briggs (1953), however, believed that very few eggs were lost during spawning. The difference in opinion between these authors may be due to the fact that Vronskiy (1972) made his observations at a spawning area where velocity was very high, whereas Briggs (1953) conducted his investigations on small streams with lower velocity. Unpublished observations of my own, on a high-velocity riffle in the Nanaimo River, British Columbia, indicated that few eggs were lost during spawning even in fast flowing water. Both Vronskiy (1972) and Briggs (1953) commented that trout, charr, and other small fish may dart into a redd and steal a few eggs while the female is spawning, but the loss due to this kind of predation was not quantified.

Most eggs deposited in redds appear to be fertilized. Briggs (1953) reported various studies that demonstrated that between 92% and 98% of eggs were successfully fertilized. Vronskiy (1972) reported fertilization in excess of 99% for Kamchatka River chinook.

Survival during Incubation

Information on mortality of fertilized eggs and agents of mortality comes from observations made of both artificially planted eggs and natural redds. Shelton (1955) investigated the survival to hatching and emergence of eggs planted at different depths in two sizes of gravel in artificial stream channels and subjected to several rates of water percolation through the gravel. He concluded that survival to hatching was greater than 97%, regardless of planting depth in the gravel or gravel size, provided the percolation rate was at least 0.001 ft/s (0.03 cm/s). Emergence was 13% or less, however, from small gravel and when percolation was less than 0.002 ft/s (0.06 cm/s). Eighty-seven per cent of fry emerged successfully from large gravel with adequate subgravel flows.

Alderdice and Velsen (1978) reviewed the available information on rate of egg development and temperature for chinook. Upper and lower temperatures for 50% pre-hatch mortality were 16°C and 2.5°–3°C, respectively, when the incubation temperature was constant. When incubation temperature varied with the ambient temperature, development rate and survival were better at low temperatures than when incubation temperature was constantly low. Presumably, this better performance reflected the development of greater low-temperature tolerance after initial cell division. Time to 50% hatch ranged from about 159 days at 3°C to 32 days at 16°C.

Alderdice and Velsen (1978) concluded that a log inverse form of Belehradek's equation (development rate = (temperature - C) exp b/K; where C, b, and K are constants) gave the best fit to the available data on egg development in relation to temperature. Even this model, however, underestimated development rate at low temperatures. For most practical purposes a simple thermal sum model (development time = $468.7/T$; where T is the average temperature during incubation) was adequate for predicting time to hatching.

Gangmark and Bakkala (1960) recorded percolation rate, temperature, and oxygen concentration near eggs planted in Mill Creek, California. Normal temperature fluctuations were not related to egg survival/but both percolation and oxygen concentration were. Mortality of eggs increased with decreasing percolation rate, being 2.9% at 4.0 ft/h

(0.034 cm/s) and nearly 40% at 0.5 ft/h (0.0042 cm/s). Mortality also increased rapidly at dissolved oxygen concentrations below 13 ppm, averaging 3.9% at 13 ppm and 37.9% at less than 5 ppm.

The survival of eggs in undisturbed natural redds appears to be quite good. Vronskiy (1972) reported survival of 97% to hatching, and Briggs (1953) reported 90% survival to the eyed stage and 82% to hatching. Vronskiy's estimate is based on the number of live and dead eggs and alevins recovered during excavation of total redds, whereas Briggs' estimates are based on samples from redds. Both authors attempted to correct for the disintegration of dead eggs, Briggs by planting dead eggs and observing the losses over time, and Vronskiy by counting egg shells as disintegrated eggs. Despite these corrections, the estimates of survival to hatching must be taken as maximum estimates for successful redds. Neither author dealt with losses due to scouring or siltation. Briggs (1953) did, however, observe some interesting instances of high mortality in redds due to attacks by an undescribed species of oligochaete worm. This is the only description of invertebrate predation on chinook eggs buried in a redd of which I am aware, although, under the right circumstances, eggs must be available to a variety of invertebrate predators.

Stream conditions during incubation can have a dramatic effect on the survival of eggs to hatching and emergence. In a series of experiments at Mill Creek, California, Gangmark and Broad (1955) and Gangmark and Bakkala (1960) demonstrated that flooding in Mill Creek was an important cause of high mortality of chinook eggs. Apart from loss of eggs washed out of the gravel by floods, mortality was associated with low oxygen concentrations in spawning gravel (<5 ppm) and poor percolation of water through spawning gravel, with increasing mortality below percolation rates of 4.0 ft/h (0.034 cm/s).

Temperature has seldom been implicated in any significant loss of eggs during incubation. Coombs and Burrows (1957) speculated that salmon spawning in cold headwater streams with temperatures below 40°F (4.4°C) would suffer high mortality, and, at the other extreme, Slater (1963) concluded that winter-run chinook spawn would suffer high mortality in some tributaries of the Sacramento River because of high water temperature during incubation.

Chinook normally begin spawning in late summer and may begin spawning when temperatures are near 16°C, the upper temperature limit for 50% egg mortality (Alderdice and Velsen 1978). As temperatures are falling rapidly at this time of year, however, the eggs are probably not exposed to near lethal temperatures for long. Similarly, temperatures may drop below 3°C part way through the incubation period in ice-covered rivers. The impact of seasonal exposure to extreme temperatures on survival and viability of eggs and alevins has not been studied systematically, but presumably the embryos are able to survive conditions such as these, which are typical in spawning rivers.

Adequate water percolation through the spawning gravels is essential for egg and alevin survival. There is no doubt that percolation is affected by siltation and that siltation in spawning beds can cause high mortality (Shaw and Maga 1943; Wickett 1954; Shelton and Pollock 1966). There appears to have been no systematic study of the interrelation between river discharge (velocity), sediment load, and survival of chinook spawn. Of particular significance to any assessment of the probable effects of siltation on survival is Shaw and Maga's (1943) observation that siltation resulted in greatest mortality when administered early in incubation. Thus, siltation during winter freshets in coastal rivers or during summer peak discharge in snow-fed rivers may have a greater effect on the amount of suitable spawning gravel than on the survival of previously deposited spawn.

Becker et al. (1982, 1983) investigated the effects of dewatering artificial chinook redds on survival and development rate of embryos at various stages of development. Becker et al. (1982) defined stage of development in terms of accumulated thermal units during incubation and studied four stages: cleavage eggs, incubated for 56-168 Celsius degree-days (DD), embryos (249-467 DD), eleutheroembryos (553-575 DD), and pre-emergent alevins (780-814 DD). Dewatering of redds is likely to occur in regulated rivers where discharge is varied to satisfy some domestic or industrial need but could also occur in natural rivers. Alevins were most sensitive to both periodic short-term dewatering and a prolonged single dewatering, surviving at less than 4% in periodic dewaterings of one hour or a single dewatering of six hours. Eleutheroembryos were less sensitive, and cleavage eggs and embryos least sensitive. In fact, embryos apparently suffered no ill effects from daily dewaterings of up to 22 hours over a 20-day period. The development rate was also reduced in those instances in which survival was affected but not in instances when survival was good. These results seem at variance with the observation of Silver et al. (1963) that chinook embryo development is highly sensitive to any reduction in oxygen concentration or percolation rate. Since the dewatered eggs and embryos remained damp, however, they probably suffered no shortage of oxygen. Elimination of metabolic waste products may have been a problem.

Emergence

Estimating survival to emergence poses significant problems with chinook, as some fish migrate downstream as fry whereas others rear for a variable length of time in the river before migrating downstream. Counts of downstream migrants, therefore, provide only a minimum estimate of the number of fry that emerged. In Mill Creek, 85%-100% of fertilized eggs deposited in plastic mesh bags in the gravel were lost prior to emergence. These losses were associated with floods in the creek. In a channel with controlled flow, the mortality of planted eyed eggs to emergence was only 40% (Gangmark and Bakkala 1960). In Fall Creek, California, Wales and Coots (1954) and Coots (1957) found a 68%-93% mortality from egg deposition to the emergent fry stage. The 93% mortality was associated with floods. From redd excavation, Gebhards (1961) estimated that only 42% of alevins would have emerged from a single redd. Although not well documented, it appears that emergence may be a difficult time for fry.

Apparently gravel conditions can influence the success of emergence. Shelton (1955) found that only 13% of hatched alevins emerged from experimental troughs in which eggs were planted in fine gravel compared with 80%-90% emergence in troughs with coarse gravel. Emergence from fine gravel was further influenced by the depth of planting and water velocity through the gravel. Greater emergence occurred when the eggs were planted near the surface and when water velocity was low.

Major and Mighell (1969) estimated that 5.4%-16.4% of spring chinook survived to migrate as yearling smolts from the potential egg deposition in the Yakima River, Washington. In the Cowichan River, British Columbia, 9.2% and 16.5% of potential egg deposition survived to migrate as fry and fingerlings (Lister et al. 1971), whereas in the Big Qualicum River survival from potential egg deposition to fry and fingerling migrants was 0.2%-7.0% prior to flow control and 12.0%-19.8% after flow control (Lister and Walker 1966; Paine et al. 1975). M.D. Bailey (Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.) estimated that 4%-50% of potential egg deposition migrated as fry into the lower Fraser River, British Columbia, but cautioned that these estimates were based on poor data. Healey (1980b) estimated that about 12%-20% of potential eggs deposited migrated downstream as fry in the Nanaimo River, British Columbia. All these values are difficult to interpret because of uncertainty in estimates of both the potential eggs deposited and the numbers of fry produced. The values do suggest, however, that, barring serious floods, egg-to-fry survival in chinook is relatively good.

Summary of Egg-To-Fry Survival

Published estimates of the mortality rate between egg laying and fry emergence are so few and so variable that it is difficult to draw any firm generalizations (Table 3). In particular, there is little evidence that can corroborate or refute my assertions about variability among chinook populations. Under natural conditions, 30% or less of the potential eggs deposited resulted in emergent fry or fry and fingerling migrants in the systems studied (Table 3). When and how eggs die or are lost to the population is uncertain. Two features do bear some comment, however. Eggs properly buried in a redd that remains undisturbed, or which are artificially planted where subgravel percolation is good, apparently survive well. Floods, which scour the bottom or result in heavy siltation, are generally associated with high egg mortality, as is dewatering of redds (but see Becker et al. 1982, 1983). Flow control appears to result in a significant increase in average survival. These observations suggest that egg-to-fry and fingerling mortality probably occurs either at the time of spawning or as a result of

TABLE 3

Published estimates of mortality (%) of chinook to various development stages in fresh water (mean of ranges in parentheses)

River system	Eggs not spawned	Losses at spawning	Spawning to eyed stage	Spawning to alevin	Spawning to emergence	Spawning to fry/smolt	Remarks
Mill Cr. (CA)					85–100 (96)		Planted eggs, flooding channel
					40		Planted eggs, controlled flow
Fall Cr. (CA)					68-93 (85)		Natural spawning
Prairie Cr. (CA)		1.0	0–25.5 (10)	14-25(18)			Natural spawning, redd sampling
Yakima (WA)	1.0					84-95 (89)	Stream-type, weir counts of smolts
Lemhi (ID)				27	58		Emergence trap over one redd
Cowichan (BC)						84-91 (87)	Ratio of fry/smolt migrants to eggs
Nanaimo (BC)						80-88 (84)	Ratio of fry/smolt migrants to eggs
Big Qualicum (BC)	12					93-100	Before flow control
						80-88	After flow control
Skeena System							
Bear R. (BC)	25						
Morice R. (BC)	1						
Babine R. (BC)	20						
Kamchatka (USSR)	1	88		1-6 (3)			Redd sampling

Source: See text for sources

redd disturbance due to floods. Losses at the time of spawning in particular bear further investigation, in view of Vronskiy's (1972) comment that high egg losses at spawning have been observed by Russian biologists for several species of Pacific salmon, and the International Pacific Salmon Fisheries Commission's observation that losses of eggs at spawning in Adams River sockeye were heavy when the spawning stock was large (T. Gjernes, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, pers. comm.).

Major and Mighell's (1969) observations on spring chinook deserve comment, as their estimates of survival from egg deposition to smolt migrants are comparable to estimates of survival from egg deposition to fry and underyearling smolt migrants for fall chinook in other systems. It is tempting to assert that this is an example of the dichotomy between stream- and ocean-type chinook. There are, however, a number of possible sources of error in the data on which these estimates were based. Major and Mighell (1969) estimated potential egg deposition by counting redds and multiplying by the average fecundity of females in the Columbia River. In my view, this procedure is liable to give a biased estimate of potential eggs deposited because false redds may be counted as true redds, because redds may be missed, or because the fecundity of local stocks differs from that of the general population. The apparent high survival of spring chinook from egg to smolt may, therefore, be fortuitous. Egg-to-migrant survival was negatively correlated with redd count and potential egg deposition in the Yakima River, even excepting an unusual mortality of eggs in the upper Yakima River due to low flows in 1957 (Figure 10). Such a relationship is consistent with the notion that redd counts may have been inaccurate, so that variations in survival were more a reflection of error in redd counts than real variation in survival. It is also consistent, however, with

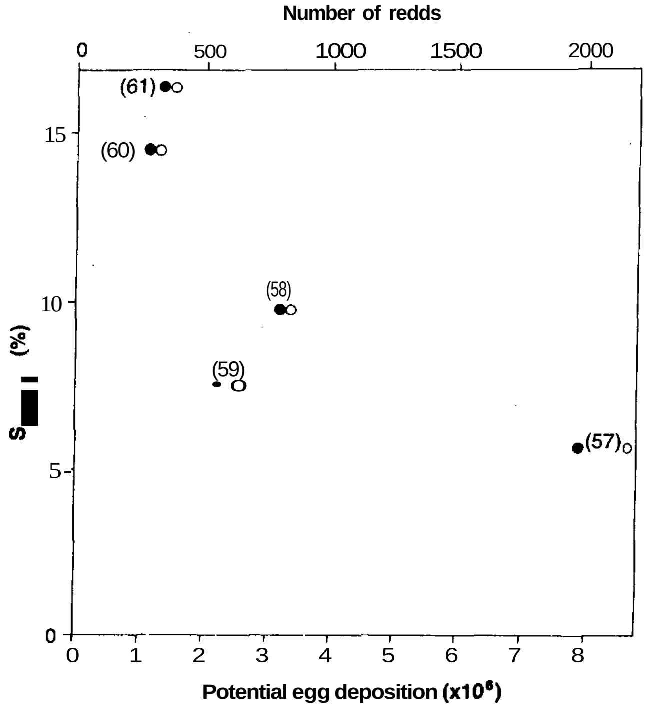


FIGURE 10
The relationship between the number of spring chinook redds counted and estimated **egg-to-smolt** survival (●), and between potential egg deposition and egg-to-smolt survival (o) for the Yakima River, Washington. Brood years are in brackets. (Data from Major and **Mighell** 1969)

the possibility suggested earlier that good redd sites are few in most rivers, and that fry and smolt production may be more related to the amount of good spawning area than to the number of spawners. A third possibility is that yearling smolt production is independent of spawner density over a wide range of spawner densities. Lister and Walker (1966) noted a rather small variance in underyearling smolt production compared with fry production in the Big Qualicum River and speculated that rearing habitat was a limiting factor in smolt production.

FRESHWATER RESIDENCE AND DOWNSTREAM MIGRATION

Fry Migrations

Factors controlling the emergence of chinook fry from the spawning beds **are not** well studied. According to Reimers (1971), most emergence is at night, although up to 20% of fry emerged during the day in his experimental troughs. Emergence was reduced during a full moon. In **Reimers'** (1971) experiments, emergence peaked just after alevins reached maximum weight.

Upon emergence, fry swim, or are displaced, downstream. Thomas et al. (1969) found that fall chinook fry go through a period of reduced swimming ability just before the time of complete yolk absorption, and that this coincided with the time of peak downstream migration. They hypothesized that reduced swimming ability was the cause of downstream migration.

Downstream movement of fry occurs mainly at night, although small numbers may move during the day. Peak nightly catches of downstream migrants may occur before (Reimers 1971), at (Lister et al. 1971), or after midnight (Mains and Smith 1964). Differences in time of peak catch most likely reflect the distance of trapping sites below the main spawning area rather than differences in time of emergence from the gravel. Reimers (1971) also observed that downstream movement was inhibited by bright moonlight, so that, on moonlit nights, peak trap catch was shifted from before to after midnight.

Once started downstream, chinook fry may continue migrating downstream to the river estuary, or may stop migrating and take up residence in the stream for a period of time ranging from a few weeks to a year or more. What determines whether fry will hold and rear in the river, or migrate downstream to the estuary, is unknown. Kjelson et al. (1981) observed that peak catches of chinook fry in the Sacramento-San Joaquin delta often followed flow increases associated with storm runoff. They speculated that flow surges influence the numbers of fry that migrate from upper river spawning grounds to the delta. Healey (1980b) also observed that downstream movement of fry was correlated with river flow in the Nanaimo River. Reimers (1968) and Lister and Walker (1966), however, speculated that social interaction or density-dependent mechanisms may cause fry to be displaced downstream. Reimers (1968) observed lateral displays, chasing, nipping, fighting, fleeing, submission, and redirected aggression among juvenile fall chinook in stream tanks, where the agonistic behaviour of one or a few dominant fish apparently stimulated the downstream movement of subordinate fish. These same behaviours, with the exception of nipping and redirected aggression, also occurred in natural stream populations of chinook. Lister and Walker (1966) observed that, in the Big Qualicum River, fry migrants varied almost 100-fold in abundance between years, whereas fingerling migrants varied only about ten-fold in abundance. They concluded that available freshwater rearing area limited the number of fry that could reside in the river, and that the rest were displaced downstream. A similar conclusion could be drawn from Major and Mighell's (1969) observations on production of stream-type smolts in the Yakima River.

River discharge and intraspecific interaction may both play a role in stimulating downstream movement of chinook fry. Other factors, however, may also be important. Stein et al. (1972) observed that juvenile coho apparently were dominant to chinook and grew faster in sympatric groupings in stream troughs. Chinook were able to grow as rapidly as coho, however, when alone in the troughs. Stein et al. (1972) speculated that interaction with coho may influence the downstream movement of chinook. Recently, Taylor and Larkin (1986) demonstrated that stream-type chinook fry showed stronger positive rheotaxis and were more aggressive towards conspecifics and coho fry than were ocean-type chinook fry. Taylor (1988) confirmed for other stocks that stream-type chinook were more aggressive but not that they had stronger rheotaxis than ocean-type chinook. These behaviour patterns are consistent with the expected length of river residence of the two races and suggest that river residency and its associated behaviour patterns may be inherited.

Lister and Genoe (1970) reported habitat segregation among juvenile chinook and coho in the Big Qualicum River, as did Chapman and Bjornn (1969) and Everest and Chapman (1972) for chinook and steelhead *(Oncorhynchus mykiss)* in headwater tributaries of the Snake River, and Murphy et al. (1989) for chinook and coho in the Taku River. Everest and Chapman (1972) found that underyearling chinook in summer occurred over all substrate types, at all depths, and in water of all velocities (up to 1.2 m/s) studied, but that abundance generally declined with increasing substrate particle size, increasing depth, and increasing water velocity. In these studies, chinook were larger and emerged earlier than the associated coho and steelhead of the same brood year. Since the larger, older fish chose higher velocity habitats, there may have been little competition for space between the species. Habitat segregation in these studies seemed to be a mechanism for reducing competition rather than a result of competition.

A large downstream movement of chinook fry immediately after emergence is typical of most populations (e.g., Lister and Walker 1966; Bjornn 1971; Reimers 1971; Healey 1980b; Kjelson et al. 1982). The downstream migration of stream- and ocean-type chinook fry, when spawning grounds are well upstream, is probably a dispersal mechanism that helps distribute fry among the suitable rearing habitats. In the case of ocean-type populations that spawn close to tidewater, downstream migrant fry may be swept to the river estuary in a few hours. It has been hypothesized that migrant fry swept to the estuary represent those that are surplus to the carrying capacity of rearing habitat in the river (Lister and Genoe 1970). Often these fry represent the majority of the emergent population, however, and it seems doubtful that such a waste of reproductive potential would be adaptive (Figure 11). Furthermore, it is now known that estuaries provide important nursery habitat for recently emerged chinook fry (Northcote 1976; Healey 1980b, 1982b; Levy and Northcote 1982). Downstream migration of fry in the lower Nanaimo River, British Columbia, for example, appears not to be a consequence of limited rearing habitat in the river. In some years, few chinook remained to rear in the lower river after the fry migration, yet large numbers of fry consistently reared in the river estuary (Healey *1980b;* Healey and Jordan 1982). It seems probable that the Nanaimo River estuary is the preferred rearing habitat for at least part of the Nanaimo River chinook population rather than a final refuge for displaced fry. Chinook in the Nitinat River, British Columbia, also migrate to the estuary in large numbers as fry, and most of the underyearling smolts from both the Nitinat and Nanaimo rivers are produced in the estuary rather than in the river (Healey 1982a). Similarly, large numbers of ocean-type fry migrate seaward in the Sacramento River, the Cowichan River (Figure 11), and the Fraser River (M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.) and rear in the river estuaries (Kjelson et al. 1981, 1982; Healey 1982a; Levy and Northcote 1982). It should be noted that the principal rearing areas in the Sacramento-San Joaquin and Fraser River estuaries are essentially fresh water whereas rearing areas in Vancouver Island estuaries range up to 20 ppm salinity.

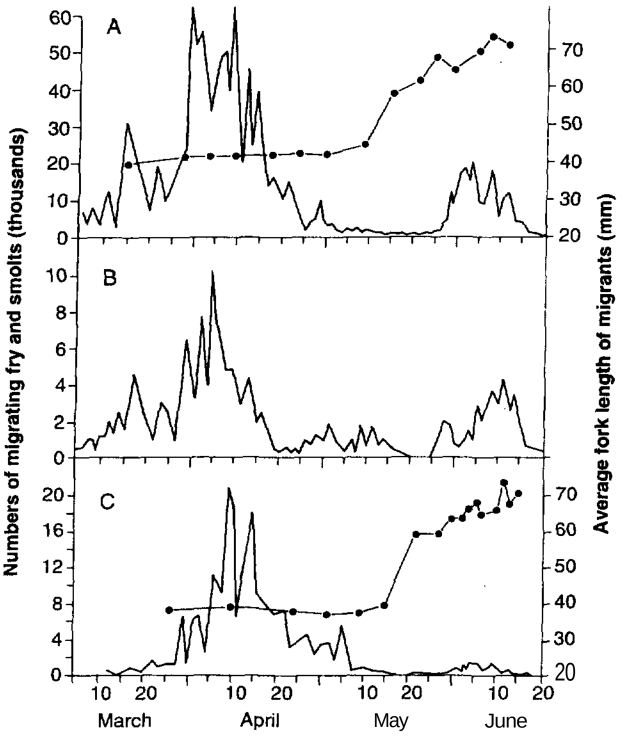


FIGURE 11

The temporal pattern in abundance of fry and underyearling smolts migrating seaward in three Vancouver Island rivers. *A* - Cowichan River, 1967; *B* - Big Qualicum River, 1967; *C* = Nanaimo River, 1980. Average fork length of migrants in the Cowichan and Nanaimo rivers is shown and demonstrates the rapid switch from fry (35-40 mm) to smolt (60-70 mm) migrants in late May.

In the Nanaimo River there are three geographically separated spawning areas, and fry from the two most downstream areas drift down to the estuary. Many fry from the middle spawning area, however, rear in the river and migrate to sea after six to eight weeks, and fry from the upper spawning area may spend up to a year in the river before migrating to sea (Healey and Jordan 1982). Analysis of polymorphic enzyme systems and body morphology suggested that the fry from the three spawning areas were genetically distinct and may be programmed to migrate seaward at different ages (Carl and Healey 1984). Clarke et al. (1989) found that stream-type chinook required a period of short day length before they would adapt to and grow well in sea water, whereas ocean-type chinook did not. From these and the observations of Taylor and Larkin (1986) and Taylor (1988), it appears that the downstream movement of fry after emergence may not be totally involuntary and that length of river residency may be dependent upon the fish's genotype. It is reasonable that stream- and ocean-type chinook would differ in this regard since length of freshwater residence is an important distinguishing characteristic for these races.

Downstream movement of fry is normally most intense between February and May (Figures 11 and 12), being earlier in more southern populations. Rich (1920), for example, observed a few fry as early as December in the lower Columbia River and in October and November in the Sacramento River. The timing of peak downstream migration

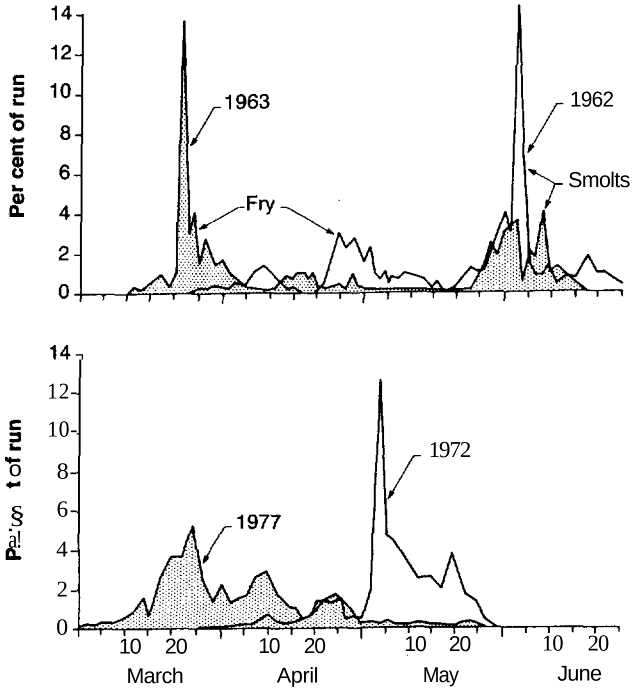


FIGURE 12
Examples of variation in downstream run timing of ocean-type chinook in the Big Qualicum River *(A)* and the Fraser River (*B*). Only fry migrants are shown for the Fraser, but both fry and smolt migrants are shown for the Big Qualicum. Note that large variation in fry migration timing is not paralleled by variation in smolt migration timing in the Big Qualicum.

can vary substantially from year to year in the same system. Time of peak downstream movement varied from the fourth week of March to the fourth week of April in the Big Qualicum River (Lister and Walker 1966), and from mid-March to early May near the mouth of the Fraser River between 1964 and 1977 (M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.) (Figure 12). The beginning and end of the run appear to vary less from year to year, so that, when the run peaks early, the temporal pattern has a negative skew, and when the run peaks late, the temporal pattern has a positive skew.

In addition to annual variation in the peak of the run, there is tremendous day-to-day variation in the abundance of downstream migrants (e.g., M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.; Healey and Jordan 1982). The causes of both annual and daily variation in run are not well understood. As noted earlier, Kjelson et al. (1981) speculated that downstream migration in the Sacramento River was stimulated by high discharge. Mains and Smith (1964) also suggested that peaks in downstream movement of chinook at Central Ferry on the Snake River were triggered by freshets. The greatest movement of chinook at this trapping location was at river temperatures between 4.5° and 13°C, but there appeared to be no relationship between migration and temperature. At Byer's Landing on the Columbia River, Mains and Smith (1964) found no relationship between the migration of chinook and either discharge or temperature. At Byer's Landing, temperatures ranged from 4.5° to 15.5°C during the run. In the Nanaimo River, daily variation in the downstream run of chinook fry was positively correlated with discharge while the run was increasing in 1975 and 1976, but not while the run was decreasing; yet variation in discharge was comparable over both the increasing and decreasing portions of the run. Greatest fry migration occurred at river temperatures of 6.0°-9.0°C in 1975 and 8.0°-11.0°C in 1976, but variation in the downstream run was not correlated with temperature in either year (Healey 1980b). Irving (1986) found that simulated freshets in experimental stream channels increased the numbers of fry moving downstream, provided water velocity at peak flows exceeded 25 cm/s.

In larger rivers, chinook fry migrate more at the edges of the river than in the high velocity water near the centre of the channel (Figure 13) and, when the river is deeper than about 3 m, they prefer the surface (Mains and Smith 1964; M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.; Healey and Jordan 1982). These observations provide further support for my earlier suggestion that downstream movement of fry is not simply *a* passive displacement controlled by water velocity, but that some active behaviour of the fry helps direct the migration.

Habitat Utilization in Fresh Water

The process by which chinook take up residence in a stream is not well studied. Reimers (1971) observed that, on the first night after emergence, virtually all fry drifted downstream in a stream

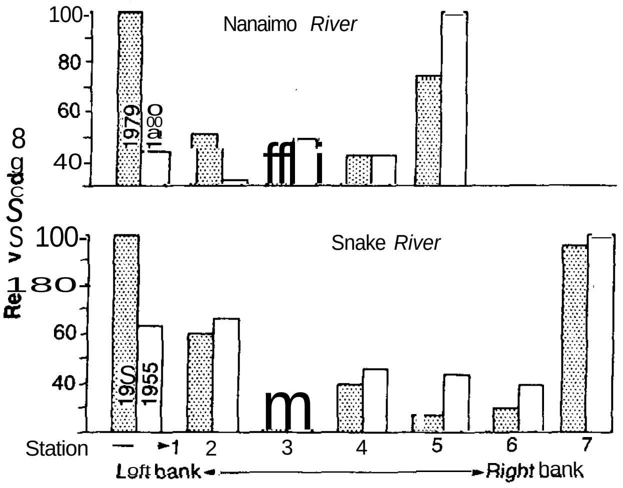


FIGURE 13

Lateral distribution of downstream migrating chinook fry in the Nanaimo and Snake rivers showing the tendency of the fry to concentrate near the river banks. Numbers of fry-per-unit-volume of water at each station across the river is shown as a percentage of the station with the greatest fry-per-unit-volume. For both rivers, stations were distributed with equal spacing from bank to bank.

trough. On each succeeding night, however, fry that were moved back upstream in the trough showed a stronger and stronger tendency to hold position in the trough. These observations suggest that stream residence develops over a number of days and that fry could be displaced quite far downstream before taking up residence. The tendency for all fry to drift downstream on the first night after emergence may partially explain why few fry were found rearing in the lower reaches of the Nanaimo River, where spawning occurs only a few kilometres from the estuary. This explanation is unsatisfactory, however, as fry were also observed drifting into the lower river from more upstream spawning areas, and presumably these could have occupied habitat in the lower river if they had been so inclined. Resident fry were relatively abundant in suitable habitat near the upstream spawning areas. Carl and Healey (1984) demonstrated that fry that migrated to the Nanaimo River estuary were genetically and morphologically different from those that reared in the river. Furthermore, Taylor and Larkin (1986) and Taylor (1988) showed that stream-type chinook fry displayed greater inter- and intraspecific aggression than ocean-type fry and that some stream-type stocks also displayed stronger positive rheotaxis. The behavioural mechanisms for holding position in the river after emergence thus appear to be better developed in some types of chinook fry than in others.

Lister and Genoe (1970) studied habitat segregation among juvenile fall (ocean-type) chinook and coho in the Big Qualicum River during the spring of 1967, when flow in the river was held constant at about 5.8 m^3/s. They examined three sites along the river, and each site was subdivided into two or three habitat types which differed in velocity, depth, and distance from shore. Chinook emerged during March and April, whereas coho emerged during May. Thus, chinook arrived in the study areas at least six weeks earlier than coho. Chinook were larger than coho at the time of emergence and, because they emerged earlier, grew even larger before the coho fry appeared in the study sites. Smaller fry of both species inhabited marginal areas of the river, particularly back eddies, behind fallen trees, undercut tree roots, or other areas of bank cover. As they grew larger, both species moved away from shore into midstream and higher velocity areas. Although the correlation between size of fish captured and velocity of sampling site within species was weak, chinook were always larger and more abundant than coho in high velocity subareas. Thus, there was important habitat segregation between chinook and coho in the Big Qualicum River, and this was mainly a consequence of the larger size and earlier emergence of the chinook salmon.

Chapman and- Bjornn (1969) and Everest and Chapman (1972) reported qualitatively very similar observations on habitat segregation between stream-type chinook and steelhead in the Snake River. Juvenile chinook were most abundant where substrate particle size was small, velocity was low, and depth was shallow, but were found in small numbers in virtually every habitat investigated. Fish size was positively correlated with water velocity and depth for both species, but the species differed in size owing to differences in emergence timing and fry size between the species.

Murphy et al. (1989) sampled various habitat types in the lower Taku River for chinook, coho, and riverine sockeye. They found that chinook were mainly in riverine habitat and seldom in beaver ponds or off-channel sloughs. Velocity and turbidity were the principal factors associated with chinook distributions. Chinook were rare in still water or where velocity was greater than 30 cm/s. There was little overlap in chinook habitat with that of coho or sockeye. Thus, habitat segregation appears to provide *a* mechanism for reducing competition between cohabiting chinook and other stream salmonids, and the pattern of segregation is similar for stream- and ocean-type races.

The movement of fish offshore and into faster water represents a shift from predominantly sandy substrate to predominantly boulder and rubble substrate. Chapman and Bjornn (1969) suggested that chinook prefer finer substrates than steelhead of comparable size, but both species showed a strong preference for the rubble type of habitat. Any interpretation of substrate preferences is confounded by velocity preference, however, and needs further investigation.

Edmundson et al. (1968) reported limited day-to-day movement of young chinook in a stream aquarium, suggesting strong fidelity to a particular site. Reimers (1968) reported that juvenile chinook in the Sixes River were primarily solitary animals and displayed aggressive behaviour towards other chinook, suggesting the existence of defended areas in the stream, at least during the day. Chapman and his co-workers (Don Chapman Consultants 1989) observed temporary defence of feeding territories by chinook in the evening. As with habitat preferences, these observations need to be substantiated in other rivers and other situations.

Day and night distributions of chinook in streams may be quite different. Edmundson et al. (1968) and Don Chapman Consultants (1989) found that at night chinook moved inshore to quiet water over sandy substrates or into pools and that most settled to the bottom. With returning daylight, these fish returned to occupy the same riffle and glide areas that they had occupied on the previous day.

Fingerling Migrants

Fish that elect to hold in the river after emergence may migrate seaward almost any time of year. In the southern half of the Chinook's range, many stream dwellers migrate seaward as fingerlings between April and June of their first year of life (Healey 1980b, 1982b; Kjelson et al. 1981/1982) (Figure 11). Although following close on the heels of the fry migration, fingerling migrants are readily distinguished by their larger size. In all the rivers studied, a sharp change in size of fish accompanies the change from fry to fingerling migrants (Figure 11). Fry migrants normally range from 30 to 45 mm in fork length, although they have been recorded as small as 20 mm and as large as 55 mm (Mains and Smith 1964; Lister et al. 1971; Healey et al. 1977). Many fry migrants still have visible yolk and few have begun feeding, although those above 44 mm fork length may have some food in their stomachs. Fingerling migrants, on the other hand, normally range from 50 to 120 mm in fork length, and all have been actively feeding for some time (Mains and Smith 1964; Lister et al. 1971; M.C. Healey unpublished data).

The factors stimulating downstream movement of underyearling chinook are not known. Although it is well documented that June is a month of very active downstream migration for fingerlings, they are known to migrate downstream at other times of the year as well. The main fingerling migration tends to be earlier in the southernmost parts of the Chinook's range (Kjelson et al. 1981) and is influenced by the presence of populations with unique spawning times (e.g., Slater 1963). In some Columbia River tributaries, juvenile chinook were found to be resident as late as October but were gone in November (Reimers and Loeffel 1967). Bjornn (1971) observed downstream movement of stream-type chinook fingerlings in the Lemhi River (Idaho) during the fall months. He proposed that this migration represented a redistribution of fish to more suitable wintering habitat. Fingerling migration is known to occur through August in the Fraser River (Northcote 1976; M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.) but is generally observed to be complete by the end of June in most other rivers sampled (Lister and Walker 1966; Lister et al. 1971; Healey and Jordan 1982). Reimers and Loeffel (1967) were able to relate extended residence in Columbia River tributaries to slow growth, and suggested that size was an important variable in determining when fish will move downstream. Nevertheless, downstream migrant fingerlings vary substantially in size, both within and between rivers (Table 4), so that some factor other than size must also play a role. Furthermore, it is known that chinook may move out of tributaries and into a river main stem, or simply relocate downstream with the approach of winter (Bell 1958; Chapman and Bjornn 1969; Park 1969). Presumably, as Bjornn (1971) suggested, suitable summer habitat may not be suitable winter habitat. The disappearance of chinook from some Columbia River tributaries in October or November (Reimers and Loeffel 1967), therefore, probably indicates relocation to an instream wintering area rather than seaward migration.

Fingerlings migrate downstream throughout the day, but the majority migrate at night (Mains and Smith 1964; Lister et al. 1971). In the Columbia and Snake rivers, fingerlings apparently preferred the shoreline during migration (Mains and Smith 1964). In the lower Fraser River and in the Nanaimo River, however, most fingerlings migrated in the fastest water near the centre of the river (M.D. Bailey, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.; Healey and Jordan 1982).

The rate of downstream migration of chinook fingerlings appears to be both time-and size-dependent and may also be related to river discharge and the location of the chinooks in the river. Cramer and Lichatowich (1978) observed that migrating spring chinook fingerlings in the Rogue River, Oregon, travelled downstream only about 0.3-5.0 km/d in the upper reaches of the river but travelled 6.1-24.0 km/d in the lower reaches during June-September. Rates of downstream migration in the Rogue River were also related to fish size and time of year. Larger chinook travelled downstream faster, and the rate of migration increased with the season. In 1975, a year of low and stable river flow, the rate of downstream migration was negatively correlated with discharge, whereas in 1976, when flows were higher and more variable, the rate of migration was positively correlated with discharge. Cramer and Lichatowich (1978) interpreted the negative correlation in 1975 to reflect a reduction in rearing habitat as discharge dropped and interpreted the positive correlation in 1976 to reflect a direct effect of discharge on the migration rate at higher discharge.

TABLE 4

Fork length (mm) of age 0.0 and 1.0 riverine smolts in various rivers and years

River	Year	Fork length		Source
		Mean	Range	
Age 0.0				
Sixes (OR)	1969	62.0	40-91	Reimers (1971)
Nitinat (BC)	1980	52.7	44-67.5	Healey (unpubl. data)
Cowichan (BC)	1966	77.3	63-98	Lister et al. (1971)
	1967	72.1	60-91	″
	1978	63.8	57-75	Healey (unpubl. data)
Nanaimo (BC)	1979	68.8	52-84	Healey & Jordan (1982)
	1980	63.5	49-76	″
Big Qualicum (BC)	1972	66.5		Paine et al. (1975)
Age 1.0				
Yakima (WA)	1959	125.5	105-170	Major & Mighell (1969)
	1960	124.6	105-170	″
	1961	127.0	105-170	″
	1962	134.0	90-170	″
	1963	132.6	90-160	″
Snake (OR)	1954	101.0	55-147	Mains & Smiths (1964)
	1955	101.0	55-147	″
	1957	68.4	45-105	Bell (1985)
	1958	67.9	50-95	″
Upper Columbia (OR)	1955	84.2	55-140	Mains & Smith (1964)
Taku (BC, AK)	1961	73.3	45-110	Meehan & Siniff (1962)
Crooked Cr. (AK)	1961	93.5	90-140	Waite (1979)

Growth of Fingerlings

Direct estimates of the growth of juvenile chinook in fresh water exist only for the Sacramento River (Kjelson et al. 1982). Inferences about growth in other river systems can be made from seasonal changes in the size of resident chinook or from the size of downstream migrants. These estimates must be viewed with caution, however, as the length of freshwater residence is not known precisely for either the downstream migrant fish or for those captured during river residence.

Tagged chinook fry in the upper Sacramento River grew an average of 0.33 mm/d over a period of 72 days. Fry that had migrated to the freshwater Sacramento-San Joaquin delta, however, grew significantly more quickly, averaging 0.53-0.86 mm/d in two years of observation (Kjelson et al. 1982). Chinook that migrated seaward as fingerling smolts in June of their first year of life averaged 52.7-77.3 mm fork length in four Vancouver Island rivers and one Oregon river (Table 4). Assuming that the length of river residence is indicated by the difference in run timing between the fry and fingerling smolt migrants, these fish spent an average of about 60 days in the river before migrating to sea. Growth rates thus ranged from a low of 0.21 mm/d in the Nitinat River in 1980 to a high of 0.62 mm/d in the Cowichan River in 1966. These rates are comparable with those based on tagged fish in the Sacramento River and delta.

Yearling Smolts

Stream-type chinook do not migrate to sea during their first year of life but delay migration until the spring following their emergence from the gravel and, in northern rivers, sometimes for an additional year as well (Healey 1983). As noted earlier, stream-type chinook characteristically return to their natal river in spring. Apparent exceptions to this pattern occur in some Oregon rivers, such as the Rogue, where spring-run adults produce underyearling smolts (Cramer and Lichatowich 1978; Nicholas and Hankin 1988). Chinook that overwinter in the larger rivers often move out of the tributary streams and into the river main stem, where they occupy deep pools or crevices between boulders and rubble during the winter. In the Nanaimo River, two lakes along the river main stem are also used as overwintering areas. A fall redistribution of fish, presumably from preferred summer habitat to preferred winter habitat, has been observed in some systems (Reimers and Loeffel 1967; Chapman and Bjornn 1969; Bjornn 1971; Carl and Healey 1984; Don Chapman Consultants 1989). Bjornn (1971) found that the number of downstream migrants in an experimental stream trough in the fall was related to the presence of suitable substrata for overwintering in the experimental stream trough.

Yearling smolts normally migrate seaward in the early spring, sometimes preceding the main migrations of fry and fingerlings and sometimes intermixed with them. In the Brownlee-Oxbow section of the Snake River, yearling smolts migrated downstream from April to June with peak numbers in May (Bell 1958). Bell also captured a few downstream migrant fry, mainly in May. In the Yakima River, Washington, yearling smolts migrated mainly in April and May, with the time of peak movement ranging from the third week of April to the second week of May (Major and Mighell 1969). Underyearling smolts were not abundant in the Yakima River until June. In the Taku River, yearling smolts migrated seaward from April to June, with peak movement in early May (Meehan and Siniff 1962). There were no underyearling migrants in the Taku River. The main period of yearling smolt outmigration from the Kasilof River on the Kenai Peninsula, however, was July (Waite 1979).

Bell (1958) related the peak in migration of yearling smolts to spring floods and increasing temperatures. As with the underyearling migration, however, there has been no systematic study of the factors triggering migration. Yearling migrants do appear to be less nocturnal than underyearlings. Meehan and Siniff (1962) could find no significant difference in the abundance of migrants between day and night in the Taku River, although, on average, more smolts moved at night. Major and Mighell (1969) also observed greater movement of yearling smolts during the night, but Bell (1958) found that the greatest movement was during the daylight hours.

Raymond (1968) found that the rate of downstream migration of yearling smolts in the Columbia and Snake rivers was positively correlated with discharge, but that rates of travel through free-flowing and impounded sections of these rivers were similar. At low discharge, the rate of migration was 21 km/d, whereas at moderate discharge it was 37 km/d. These rates of migration are considerably faster than those of underyearling smolts observed by Cramer and Lichatowich (1978). The rapid migration of smolts through impoundments on the Columbia River indicates that yearling smolts undertake a directed migration that is independent of river flows.

Growth of Yearling Smolts

Yearling smolts vary greatly in size. In the Yakima River, they ranged from 100 to 160 mm in fork length, and the average increased from 124.6 mm to 134.0 mm between 1959 and 1962 (Table 4). These sizes suggest an average growth rate of 0.25 mm/d, but the increase in size over time is perplexing. Major and Mighell (1969) could not explain the apparent increase in smolt size, but suggested that it could be due to differential growth of separate tributary spawning populations coupled with the differential contribution of these populations to the smolt run. This explanation is highly speculative.

Rich (1920) presented data for the Columbia River that suggest a growth rate of about 0.20 mm/d for spring chinook during the period March - September. During this period, the fish increased in length from 40.0 to 74.5 mm. Mains and Smith (1964) observed that yearling smolts in the Columbia River averaged about 84.2 mm fork length in 1955, for an annual growth rate of about 0.12 mm/d. In the Snake River, by comparison, Mains and Smith (1964) found yearling smolts to be about 101 mm in 1954 and 1955. Thus, growth in the Snake River was close to 0.17 mm/d. Bell (1958), on the other hand, found yearling smolts in the Snake River to be only about 68 mm fork length (growth = 0.077 mm/d) in May 1957 and 1958. In April 1958, however, Bell (1958) observed a second, larger size mode at 100-104 mm among the smolts captured in the Snake River. Fish in the larger mode were equivalent in size to those captured by Mains and Smith (1964). During May and June, 1958, Bell observed only one size mode, but the position of the mode changed from 70-74 mm in May to 85-89 mm in June. The modes in May tod June appear to be a continuation of the smaller April mode, with appropriate growth during each month of about 0.33 mm/d.

In the Taku River the size range for yearling smolts was 50-105 mm with a mean of 73.3 mm (Meehan and Siniff 1962). Thus, in the Taku River the average growth rate was only about 0.09 mm/d. Loftus and Lenon (1977) recorded mid-eye to fork lengths of chinook smolts in the Salcha River (a tributary in the upper Yukon River drainage, Alaska) to be 55-86 mm with a mean of 73 mm. These smolts were slightly larger than those in the Taku River when the difference in length measurements was taken into account. In Crooked Creek, on the Kenai Peninsula, Alaska, yearling smolts averaged 93.5 mm fork length (Waite 1979). As these smolts did not emigrate until late July, however, they had the benefit of spring growth in the year of migration. Assuming their river residence time was about 430 days, the growth of Crooked Creek smolts averaged 0.124 mm/d.

In the Snake River, therefore, the average annual growth for smolts in the smaller mode was comparable to the growth in the Taku and Salcha rivers, whereas the fish in the larger mode had grown at a rate more comparable to that in the Yakima River. Smolts captured in the Columbia River and Crooked Creek were intermediate in size and growth rate.

The existence of two distinct size groups of fish in the same run (e.g., the Snake River) suggests that there may be important differences in microhabitat affecting chinook growth in rivers. If the increase in size of fish in the smaller mode in the Snake River represents growth, then the rate of growth during the spring months was 0.33 mm/d. Rich (1920) observed growth of 0.20 mm/d in the Columbia River. All these rates are slower than the growth rate observed for underyearling smolts.

Major and Mighell (1969) observed that, within the same year, the average size of yearling smolts migrating downstream in the Yakima River decreased with time, and suggested that the larger fish migrated first. Bell (1958), on the other hand, observed that the larger fish of one group of yearling smolts were caught later in the season in the Snake River, and Mains and Smith (1964) observed no systematic change in smolt size with time. These apparently conflicting results may simply reflect the unresolvable interactions of differences in stock growth and microhabitat as well as opportunities for spring growth during and prior to migration.

Summary of Freshwater Residence and Downstream Migration

Although there is some variation in timing, all populations of chinook appear to display similar migratory behaviour. At the time of emergence, there is an extensive downstream dispersal of fry, although some fry apparently are able to take up residence in the natal river at the spawning site. For populations that spawn close to tidewater, this downstream dispersal carries the fry to estuarine nursery areas, whereas in others it serves principally to distribute the fry among suitable freshwater nursery areas. Later in the spring, there appears to be a second dispersal that carries some populations to the sea or simply redistributes the population within the river system, presumably to more suitable summer rearing areas. For those populations that remain a year in fresh water there is a third late fall redistribution to suitable overwintering habitat, usually from the tributaries to the river main stem. Finally, in the spring there is a migration of yearling smolts to sea.

During the late spring and fall redistributions in fresh water, the population tends to shift into deeper water and to move seaward. These changes in habitat are consistent with the shorter term habitat changes observed by Lister and Walker (1966) and Chapman and Bjornn (1969), in which chinook moved into deeper, faster water as they grew in size. The redistributions may punctuate developmental stages as well as achieve more efficient utilization of freshwater nursery habitat. The tendency for redistribution to carry the fish downstream may be coincidental. Such a movement pattern may also be adaptive, however, by shortening the length of spring migration for yearling smolts, particularly for headwater spawning populations in larger rivers.

MORTALITY AND ITS CAUSES DURING FRESHWATER RESIDENCE

Rates of survival from fry to fingerling migrant stage and from fry to yearling migrant are unknown, with the exception of some recent data from the Sacramento River. Based on the ocean returns of chinook from the same brood year - marked and released as both fry and smolts in the Sacramento River at Red Bluff and in the Sacramento-San Joaquin River delta - survival from fry to smolt ranged from 3% to 34% for the 1980-82 year classes (M. Kjelson, u.s. Fish and Wildlife Service, Stockton, California, pers. comm.). Evidence from these and other releases of tagged fish in the Sacramento River system suggest that fry that rear in the upper river experience a higher survival to smolting than fry that rear in the delta (Kjelson et al. 1982; Brown 1986). Survival of smolts passing through the Sacramento-San Joaquin River delta was highly correlated with discharge of the Sacramento River.

Major and Mighell (1969) estimated that 5.4%-16.4% of potential egg deposition survived to migrate as yearling smolts in the Yakima River. Assuming even a high average egg-to-fry survival rate (30%), fry-to-smolt survival would have to have been about 30% to account for these rates. This seems too high a rate of survival to be generally true in other populations.

Even though estimates of fry and fingerling mortality rates are nonexistent, except for the Sacramento system, mortality is presumed to be heavy in all rivers. Mortality rates of 70%-90% among fry and fingerlings are recorded for other species of Pacific salmon (Foerster and Ricker 1941; Hunter 1959; Parker 1965), and, as these are similar to the losses of chinook observed in the Sacramento River system, it seems reasonable to suppose that chinook in other rivers suffer similar losses. Healey (1980b, 1982b, and unpublished data) could account for only about 30% or less of downstream migrant chinook fry in the estuaries of the Nanaimo and Nitinat rivers, suggesting that mortality was high during this stage of the Chinook's life.

Predators are commonly implicated as the principal agent of mortality among fry and fingerlings of chinook and other species, and heavy losses due to predators have been documented in some instances (Foerster and Ricker 1941; Hunter 1959). Patten (1971), however, was only able to infer sculpin predation of 1%-4% among chinook fingerlings released from a hatchery in the Elokomin River, Washington, during 1962 and 1963. Most important predators were the prickly sculpin (*Cottus asper)* and the torrent sculpin (C *rhotheus*). Less important were the reticulate sculpin (C. *bairdi)* and the coast range sculpin (C. *aleuticus)*. However, the release of fingerlings occurred during a single night in 1962 (1.5 million) and during three nights in 1963 (2.5 million), so that the young chinook were available to the predators for only a brief period. Had the releases extended over two to three weeks, as in a natural fingerling migration, losses to predators might have approached 0.5 million (Patten 1971). Also, the large size of the fingerlings relative to the sculpins probably reduced the efficiency of sculpin predation. Although other quantitative estimates of the rate of predation on chinook are lacking, various authors have reported juvenile chinook in the stomachs of predatory fishes (Clemens and Munro 1934; Thompson 1959a, 1959b).

Other fish are generally considered to be the most important predators of juvenile salmon, but invertebrate predators have occasionally been observed to kill or injure juvenile salmon. Eisler and Simon (1961), for example, observed that *Hydra oligactus* caused high mortality among recently hatched chinook alevins in hatchery troughs. Exposure of alevins to 400 hydra in 500 ml of water for only five minutes was sufficient to cause mortality as high as 80%. Dead alevins showed symptoms comparable to white spot disease. Coho alevins exposed to as few as 20 hydra in 500 ml for several days suffered high mortality. Mortality of this magnitude due to hydra may be confined to hatcheries. Novotny and Mahnken (1971) observed a marine isopod, *Rocinella belliceps pugettensis,* attacking fry and fingerlings of chum, coho, and pink salmon in aquaria and in the field at night in Puget Sound. The isopod normally attached to the young fish on the side behind the dorsal fin. Young salmon so attacked would swim in a darting, erratic, and twisting manner, presumably attempting to dislodge the isopod. Even if the isopod attacks were not fatal, the erratic swimming of the fry could attract other predators.

Since the behaviour during comparable life history stages of populations which reside for different lengths of time in fresh water is essentially the same, it seems likely that they are exposed to similar patterns of instream mortality during these stages. The existence of different lengths of stream residence, however, suggests that, at least in the past, there must have been a survival advantage to protracted stream residence in some situations and not in others. The nature of that advantage is not immediately apparent, particularly in situations such as those encountered in the Nanaimo River, where different behaviour patterns coexist in a relatively small river system.

FOOD HABITS IN FRESH WATER

The principal foods of chinook while rearing in fresh water appear to be larval and adult insects. Kjelson et al. (1982) found Cladocera, Diptera, Copepoda, and Homoptera to be the dominant foods of chinook fry in freshwater regions of the Sacramento-San Joaquin River delta. Chapman and Quistdorff (1938) found dipteran larvae, beetle larvae, stonefly nymphs, and leaf hoppers to be the roost abundant diet items of young chinook (43-152 mm standard length) in tributaries of the Columbia River. Clemens (1934) found that young chinook in Shuswap Lake fed primarily on terrestrial insects, small crustaceans (mainly Cladocera), and chironomid larvae, pupae, and adults. Herrmann (1970) found young chinook in the lower Chehalis River feeding principally on crustaceans such as *Corophium,* and on immature and mature insects. The presence of *Corophium* in the diet of these fish suggests that they had been feeding in estuarine waters. Rutter (1902) found young chinook in the Sacramento River feeding mainly on larval and pupal insects. Loftus and Lenon (1977) found Diptera, Plecoptera, and Ephemeroptera to be the most important components of the diet of chinook smolts in the Salcha River, Alaska. In a more detailed study of the diet of chinook in fresh water, Becker (1973) found that insects constituted over 95% of their diet in all seasons. Adult Chironomidae were by far the most important dietary group, comprising 58%-63% of the diet. Following these, in order of importance, were: larval chironomids (17%-18%), Trichoptera adults (3%-5%), Notonectidae (3%-5%), and Collembola (1%-5%). Some seasonal variation was apparent, with Diptera declining in importance from 99% to 70% between March and May, then increasing again to 85% by July. Notonectids were most important in May, Trichoptera in June and July, and Collembola in April and May. In contrast to these results, Craddock et al. (1976) found crustacean zooplankton, especially Cladocera, to be important in the diet of chinook during July-August in the lower Columbia River. Insects predominated at other times of the year.

The importance of insects in the diet of chinook in fresh water indicates that chinook feed in the water column or at the surface on drifting food. Their basic diet is similar to that of coho, steelhead, and other stream-dwelling salmonids (Mundie 1969; Chapman and Bjornn 1969). Whether there is competition for food resources among the cohabiting species is not known; however, any such competition is presumably reduced by the habitat segregation among species described earlier.

UTILIZATION OF ESTUARINE HABITATS

Fry Migrants

Many of the fry of ocean-type chinook that migrate downstream immediately after emerging from the spawning beds take up residence in the river estuary and rear there to smolt size. Recently emerged chinook fry are known to rear in the Sacramento and Columbia River estuaries (Rich 1920; Kjelson et al. 1981, 1982), in the Skagit River estuary (Congleton et al. 1981), in the Fraser River estuary (Dunford 1975; Goodman 1975; Levy and Northcote 1981; 1982; Levings 1982; Gordon and Levings 1984), the Nanaimo River estuary, the Campbell River estuary and other estuaries on the east coast of Vancouver Island (Healey 1980b, 1982b; Levings et al. 1986), and the Nitinat and Somass River estuaries on the west coast of Vancouver Island (Birtwell 1978;Healey 1982b).

In some instances, the salinity of the estuarine rearing habitat is low (e.g., Sacramento River: Kjelson et al. 1982; Fraser River: Levy and Northcote 1981, 1982) or is unknown, but observations on the Cowichan, Nanaimo, Courtenay, Campbell, and Nitinat River estuaries demonstrated that chinook fry will rear where salinity is commonly 15-20 ppm or more (Healey 1980b, 1982b; Levings et al. 1986). Thus, estuary rearing may be considered qualitatively different from rearing in the river channel further upstream. Although many chinook fry appear unable to survive immediate transfer to 30 ppm salinity, they are clearly able to survive transfer to 20 ppm or less, and osmoregulatory capability develops quickly in fry exposed to intermediate salinities (Weisbart 1968; Wagner et al. 1969; Clarke and Shelbourn 1985). I have transferred chinook fry directly from downstream migrant traps on the Nanaimo River into sea water of 32 ppm in the laboratory with no apparent short-term ill effects or retardation of growth compared with controls maintained in fresh water and brackish water of 15 ppm (M.C. Healey, unpublished data). Some chinook fry, therefore, appear to be able to tolerate immediate transfer to high salinity.

Rich (1920) reported observing chinook fry in the Columbia River estuary as early as December, and earlier still, in October and November, in the

Sacramento River estuary. During March and April, fry were abundant in the Columbia River estuary. Rich did not measure salinity at the capture sites but did observe that the smallest fry appeared to avoid brackish water and were consistently associated with freshwater inflows to the estuary. Without associated data on downstream migration of fry or estimates of relative abundance, little can be concluded from Rich's (1920) observations other than that healthy fry were present in the estuary. It is worth noting, however, that on the basis of a few samples collected irregularly from the Columbia, Sacramento, and other rivers, Rich (1920) hypothesized much of what we now know to be true about the early life history of chinook salmon.

More recently, Kjelson et al. (1981, 1982) have provided much more detailed observations on the Sacramento-San Joaquin River estuary. Fry arrive at the river delta mainly from January to March and reside there for about two months before migrating seaward. Most rearing occurs in freshwater habitats in the upper delta area, and the fry do not move into brackish water until they smoltify. Levy and Northcote (1981, 1982) described similar behaviour of chinook fry in freshwater marsh areas of the Fraser River delta. Fry migration to the delta was later in the Fraser River, however, it occurred predominantly in April and May.

Observations on a number of Vancouver Island estuaries and on the Fraser River estuary (Healey 1980b, 1982b; Levy and Northcote 1981, 1982; Levings 1982) showed that these estuaries were not only important nursery areas for chinook, but also that the distribution of chinook changed seasonally and tidally. At high tide, the young chinook were scattered along the edges of the marshes at the highest points reached by the tide. As the tide receded, the young chinook retreated into tidal channels and creeks that dissect the marsh areas and retain water at low tide. With the incoming tide, the chinook again dispersed along the edges of the marshes. On the Fraser River, Levy and Northcote (1982) found that chinook were among the last fish to vacate tidal channels in the marsh when the channels dried up at low tide.

The twice-daily pattern of migration from low-tide refuges to the marsh areas and back again was continued throughout the period of residence of fry in the estuaries. As the season progressed, however, the major concentration of young fish moved seaward through the delta area in Vancouver Island estuaries. This is partly due to the fact that larger fish appear to prefer deeper water, and that larger fish are able to osmoregulate in higher salinities. The redistribution of fish may, however, also be associated with increasing temperatures in shallow tidal channels, particularly at low tide. Healey (1980b) found that fry moved away from sampling stations where temperatures exceeded 20°-21°C. This seasonal, seaward movement was not apparent in the Fraser River estuary (Levy and Northcote 1981). Kjelson et al. (1982) reported that, in freshwater rearing areas of the Sacramento-San Joaquin River delta, fry distribution changed from day to night and with fish size. Fry were concentrated near shore in shallow water during the day but tended to move offshore at night. Larger fish also tended to be further offshore than smaller fry. During the day fry were concentrated in the upper 3 m of the water column but became more randomly distributed in the water column at night.

Fry remain in the estuarine nursery areas until they are about 70 mm fork length, after which they disperse to nearby marine areas. In the Fraser River estuary, peak abundance of fry in channels through the marsh was April and May. Juveniles were still abundant in major arms of the river in June (Dunford 1975; Goodman 1975; Levy et al. 1979). Most were gone from the river arms by July but remained abundant over the sand flats at the delta front (Roberts and Sturgeon banks) throughout August (Goodman 1975; Gordon and Levings 1984). In the Nanaimo River estuary and other Vancouver Island estuaries, fry were most abundant in April-June, but the time of peak abundance varied from year to year in accordance with changes in the timing of the downstream run of chinook fry (Healey 1980b, 1982b). Sasaki (1966) observed that young chinook salmon were most abundant in the Sacramento-San Joaquin River delta during April-June, similar to the timing observed in more northern deltas. However, Kjelson et al. (1981, 1982) observed that fry were most abundant in February and March in the Sacramento-San Joaquin River system, and that these were replaced by smolts from upriver in April to June.

The proportion of downstream migrant fry that find a place to rear in the estuary is not well known. For both the Nanaimo and Nitinat River systems on Vancouver Island, only 30% or less of the estimated downstream migrants could be accounted for in the estuary. The fate of the remaining 70% is unknown, but it was unlikely that they reared elsewhere, despite their apparent ability to survive and grow in habitats with high salinity. Thorough sampling of other potential nursery areas in the vicinity of the Nanaimo River in 1976 and 1977 failed to reveal any significant numbers of chinook fry outside the estuary in April and early May (Healey 1980b, 1982b). Levy and Northcote (1981) estimated that the population of young chinook in the Ladner marsh complex of the Fraser River was approximately 305,000 during mid-May, 1979. Taking account of the fact that the Ladner marsh represented less than one-half the marsh area of the Fraser River delta, that some other important habitats had not been taken into consideration, and that the delta population would probably turn over several times owing to the arrival of new downstream migrants and the emigration seaward of fish which had completed their rearing in the delta, Levy and Northcote (1981) speculated that several millions of chinook probably reared in the delta. The population accounted for in the Fraser River delta is, nevertheless, small relative to the estimated 64 million chinook fry that migrated through the lower Fraser River during March-June 1979. The fate of the many millions of Fraser River chinook fry that do not rear in the delta is unknown. Thus, it appears that there may be high mortality of downstream migrant fry shortly after they complete their downstream migration. The agents of this mortality are unknown.

The residence time of cohorts of fry in estuarine habitats has been approximated by mark and recapture studies in the Nanaimo, Nitinat, Fraser, Skagit, and Sacramento-San Joaquin River estuaries (Healey 1980b; 1982b; Congleton et al. 1981; Levy and Northcote 1982; Kjelson et al. 1982). On the Nanaimo River estuary, recovery of marked fry suggested a maximum residence time of about 60 days. The average length of residence of fry, based on recaptures of marked fry and on rate of growth and maximum sizes of chinook in the inner estuary, was about 20-25 days (Healey 1980b). Residence times in Nitinat Lake were similar to those in the Nanaimo River estuary, the average in 1979 being about 21 days and in 1980 about 17 days. Levy and Northcote (1982) and Congleton et al. (1981) investigated residence in tidal channels through marshes and found much shorter residence times, about 8 days in the Fraser River marshes and about 3 days in a single channel of the Skagit River marsh. The relatively short residence times observed by Levy and Northcote (1982) and by Congleton et al. (1981) may reflect the limited area sampled relative to the range of habitat available to fry. In both instances, movement between tidal channels in the marsh (observed by Levy and Northcote 1982) and movement of cohorts of fry seaward with time (and thus out of the marsh but not out of the estuary) (Healey 1980b) may have contributed to shorter residence time estimates in these studies. The maximum residence time of chinook fry in the Sacramento-San Joaquin River delta was 64 days in 1980 and 52 days in 1981 (Kjelson et al. 1982). All the residence times so far calculated include the combined effects of migration and mortality.

Levy and Northcote (1981) investigated the relationship between occurrence and abundance of chinook fry in various marsh habitats according to the physical characteristics of the habitat. Chinook abundance was significantly correlated with twelve of twenty-two habitat characteristics. In a multiple regression analysis, however, only two characteristics (area of low tide refugia and elevation of tidal channel banks) explained significant amounts of variation in chinook catch. A large number of correlations among the habitat characteristics may have confounded the analysis, but the results suggest that young chinook prefer tidal channels with low banks and many subtidal refugia. Chinook, and associated fish species, also tended to be associated with larger tidal channels.

Fingerling and Yearling Migrants

The apparent movement of fry migrants away from the Nanaimo and Nitinat River estuaries in late May and June coincided with the downstream migration of fingerling smolts, so that the fingerling smolts took over the habitat vacated by the fry. In estuaries on the Oregon coast there appear to be few fry migrants, and the first chinook to enter these estuaries are fingerling smolts. (Reimers 1971; Reimers et al. 1979; Myers 1980; Myers and

Horton 1982). In the Sacramento-San Joaquin River estuary, as in the Vancouver Island estuaries, fingerling smolts replaced the fry in estuarine nursery areas (Kjelson et al. 1982). The fingerling smolts tend to occupy deeper water in the estuary and to remain there for varying periods. In the Nanaimo and Nitinat River estuaries, fingerling smolts were abundant during June and July but began to decline in abundance about mid-July and were rare after August, although a few occurred year-round in the outer estuary of the Nanaimo and other rivers (Healey 1982b) (Figure 14). In Oregon coastal estuaries, fingerling smolts appear to reside much longer-well into October (Reimers 1971; Myers 1980; Myers and Horton 1982; Nicholas and Hankin 1988) (Figure 14). The period of greatest abundance of fingerling smolts tends, however, to be June to August in Oregon estuaries. In the Sacramento-San Joaquin River estuary, fingerling smolts were most abundant from April to

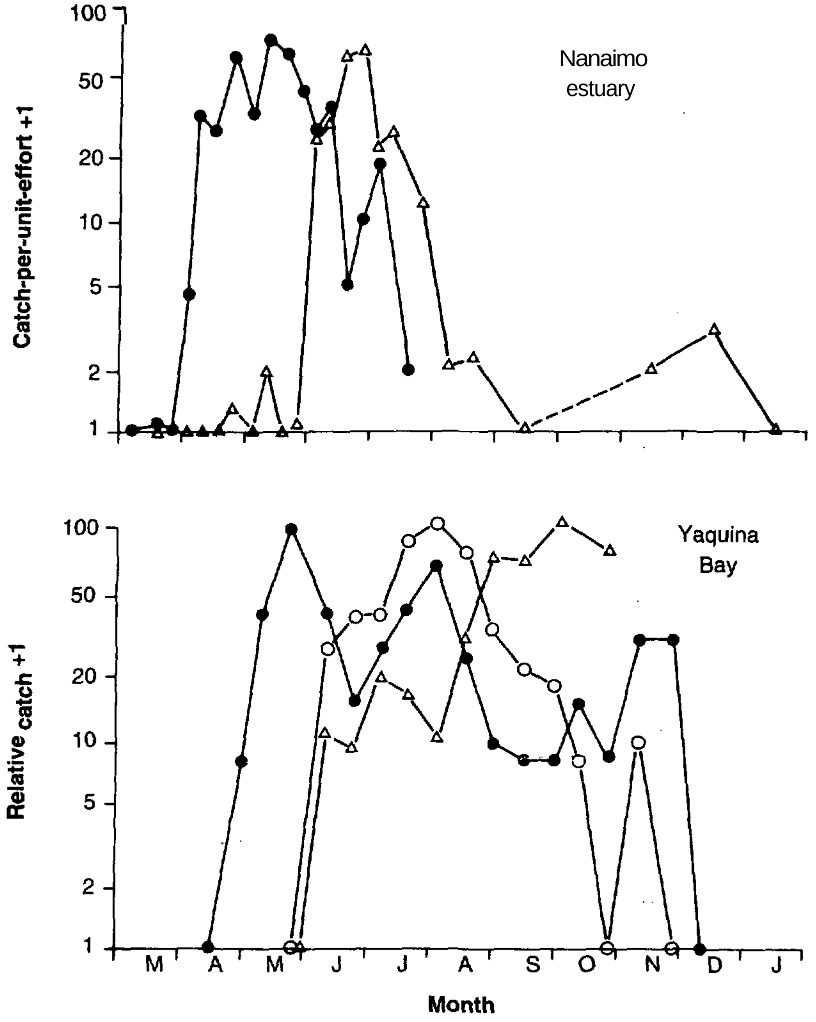


FIGURE 14

Abundance of juvenile chinook at various locations in the Nanaimo and Yaquina estuaries during March to January. Symbols are: • - inner estuary beaches; o = outer estuary beaches; A = outer estuary deep water. Note the different scales on the ordinates. (Adapted from Healey 1982b and Myers 1980) mid-June but were scarce during summer months, apparently because of high water temperature in the delta and bays (Kjelson et *al.* 1982). There was a small secondary peak in smolt abundance in the fall, representing fish that had remained in cooler water upstream over the summer (Kjelson et al. 1982). It is possible that estuaries along the open coast from Washington to California provide important sheltered habitat for young fall chinook during the summer and autumn, provided temperatures in these esturies do not get too high. Sheltered habitat is much more common along the British Columbia coast, and there may be less stimulus for young chinook to remain in British Columbia river estuaries.

Chinook that migrate to sea as yearling smolts often do so together with the emergent fry and they, too, spend some time in the estuary of their natal stream. While the fry are concentrated in the delta area, yearling smolts occupy the delta front, so that there is no spatial conflict between the two life history types in the estuary. Not all downstream migrant yearlings remain in the estuary and some disperse to other nearshore areas adjacent to the river mouth. Also, it appears that the length of residence of yearling smolts in the estuary is relatively brief, as is their residence in sheltered coastal waters in general (Healey 1980b, 1982b, 1983; Levy and Northcote 1981).

Food Habits in Estuaries

The food habits of chinook in estuaries are documented for a number of British Columbia estuaries (Dunford 1975; Goodman 1975; Birtwell 1978; Sibert and Kask 1978; Fedorenko et al. 1979; Levy et al. 1979; Northcote et al. 1979; Healey 1980b, 1982b; Levy and Northcote 1981; Levings 1982), a number of Oregon estuaries (Reimers et al. 1978; Myers 1980; Bottom 1984), and the Sacramento-San Joaquin River estuary (Sasaki 1966; Kjelson et al. 1982). Diets vary considerably from estuary to estuary and from place to place within an estuary. Dunford (1975), Northcote et al. (1979), Levy et al. (1979), and Levy and Northcote (1981) reported that chironomid larvae and pupae were the most important diet items of ocean-type chinook in tidal channels throughout the Fraser River marshes. Of secondary importance were *Daphnia, Eogammarus, Corophium,* and *Neomysis*. Diets of chinook from the north arm of the Fraser River tended to be more restricted, with greater emphasis on *Neomysis*. Chinook captured in the main river channels or over Roberts and Sturgeon banks at the delta front were larger than those found in tidal channels; and juvenile herring, sticklebacks, and other small fish, as well as cumaceans, insects, and *Neomysis* were important in their diet (Dunford 1975; Goodman 1975; Northcote et al. 1979; Levy and Northcote 1981; Levings 1982). Yearling smolts (stream-type) were larger still and fed heavily on chum fry, as well as on *Eogammarus, Neomysis, Corophium,* and chironomids. Northcote et al. (1979) noted that chinook fry less than 50 mm long in the Fraser River marshes demonstrated an intermediate to long path food web dominated by benthic detritivores, but with significant input from other pathways such as herbiverous zooplankton and terrestrial insects. Larger chinook characteristically had long path food webs with multiple dietary compartments, including benthic detritivores, zooplankton, and fish.

Chinook fry (ocean-type) in the Nitinat River estuary fed mainly on adult insects, gammarids, crab larvae, and Cladocera, whereas those in the intertidal zone of the Nanaimo River estuary fed mainly on crab larvae, mysids, adult insects, and harpacticoid copepods. As was observed in the Fraser River estuary, chinook that had moved into deeper water in the Nanaimo River estuary began to feed heavily on fish (Healey 1980b). Insects and amphipods were the preferred diet items of ocean-type chinook in the Somass River estuary, except in some heavily industrialized areas where a paucity of other fauna resulted in chinook feeding on oligochaetes (Birtwell 1978).

Research on a number of Oregon estuaries has shown that benthic amphipods, particularly *Corophium* spp., and aquatic insects are the dominant food of juvenile fall chinook (Reimers et al. 1978; Bottom 1984). By contrast, Myers (1980) found that fishes, especially Engraulidae, Osmeridae, and Clupeidae, dominated the diet of juvenile wild chinook in the Yaquina estuary, Oregon.

Insects and Crustacea dominated the diet of young chinook in the Sacramento-San Joaquin River delta (Sasaki 1966; Kjelson et al. 1982). Sasaki (1966) found that chironomid larvae were important in the upstream areas of the delta, whereas *Neomysis* and *Corophium* were important in the lower delta. By contrast, Kjelson et al. (1982) found Cladocera, Copepoda, and Diptera were the most important foods in the upper and lower estuary and that amphipods and mysids constituted only a small percentage of the diet.

Seasonal changes in diet are typical, and presumably reflect seasonal changes in the abundance of prey organisms. In the Nitinat River estuary, chinook diet was dominated by insects and *Eogammarus* during April. Towards the end of April, however, larval herring became important and remained so until the end of June. About mid-May crab larvae began to comprise an important part of the diet and continued to be important until the end of June. Cladocera were not important until late May and were a significant diet item until late June (Figure 15).

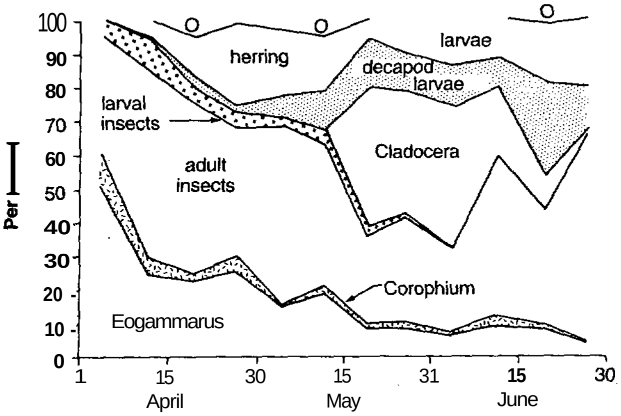


FIGURE 15

Seasonal changes in the diet of juvenile chinook in Nitinat Lake. At top of figure, *O* refers to other diet items. (From Healey 1982b)

Most studies of chinook diet are based on samples taken during daylight hours. Studies of the Sixes River estuary, however, indicate that juvenile chinook feed actively at night (Bottom 1984). Their principal foods in this estuary were the amphipods *Corophium* and *Eogammarus,* which are inactive during the day but migrate into the water column at night.

Sibert and Kask (1978) compared the diets of chinook among the Fraser, Cowichan, Nanaimo, and Campbell River estuaries, and found little correlation among the diets of fish from comparable physiographic regions of different estuaries or among the diets of fish from different physiographic regions of the same estuary. The same, or closely related organisms did tend to show up consistently in the diets, however, although their numerical contribution to diet varied widely between estuaries.

Chinook generally cohabit with other salmonids in estuaries, in particular with chum salmon. Although they often eat the same organisms, the correlation between their diets was weak in the Fraser and Nanaimo River estuaries (Dunford 1975; Sibert and Kask 1978). The diet of chinook also correlated poorly with the diet of cohabiting coho in the Nanaimo River estuary (Sibert and Kask 1978). The diet of chinook was, in fact, more similar to the diet of some non-salmonids in these estuaries (e.g., herring, *Clupea pallasi;* stickleback, *Gasterosteus aculeatus;* shiner perch, *Cymatogaster aggregata;* and sand lance, *Ammodytes hexapterus)* (Sibert and Kask 1978). Myers (1980), on the other hand, found that there was often considerable overlap in the diets of wild chinook and hatchery coho in Yaquina Bay, Oregon.

In general, chinook appear to be opportunistic feeders in estuaries. Comparison of their diet with that of other similar-sized salmonids in the same area suggests that chinook prefer slightly larger organisms and that larval and adult insects, as well as amphipods of various sorts, are their preferred prey in the intertidal regions of most estuaries. Dunford (1975) found that chinook were more efficient predators of chironomid larvae than chum and were able to capture and eat *Neomysis* that chum could not capture. In a mixed assemblage of Cladocera, chironomid larvae, and *Neomysis,* chinook fed preferentially on chironomids and Cladocera. As the chinook become larger and begin to inhabit deeper water, their dietary preference appears to shift to larval and juvenile fishes.

Growth in Estuaries

In the Columbia River estuary, young fall chinook (ocean-type) increased in length from 38 mm in April to 113 mm in October, an average daily increase of 0.44 mm, assuming that these fish were from the same cohort (Rich 1920). Chinook in the Sacramento River estuary increased in length by 0.48 mm/d between March and July, again assuming the same cohort was being sampled (Rich 1920). The probability that these samples were from the same cohort is rather small, however, as young chinook probably do not spend such a long time in the estuary, and their departure from estuaries appears to be size-related. Also, the "alternation" of different juvenile life history types in the estuary makes it unlikely that these growth estimates relate to a single behavioural type. The fish captured later are likely to have reared in the river for some weeks or months. These estimates of growth rate in estuaries must, therefore, be considered minimum estimates. Kjelson et al. (1982) estimated growth rates of fry tagged with coded-wire tags in the Sacramento-San Joaquin River estuary to be 0.86 mm/d in 1980 and 0.53 mm/d in 1981. These rates of growth are faster than those based on unmarked fry.

During 1978 and 1979, young-of-the-year chinook in the Fraser River estuary increased from 40 to 60-68 mm fork length between March and July (Levy and Northcote 1981). Their increase in length was slow until mid-May, rapid from mid-May until the end of June, and then slow again during July. From mid-May until the end of June they increased an average of 0.56 mm/d in 1978 and 0.39 mm/d in 1979.

The slow increase in length of chinook fry in the Fraser River estuary from March to mid-May was almost certainly due to the continued addition of recently emerged fry to the estuary population, since the main period of downstream migration of fry was from mid-March to mid-May in both years (Levy and Northcote 1981). The apparent slow growth of chinook in July may have been due to movement of larger chinook away from the beaches and into deeper water. Levy and Northcote (1982) observed that young chinook captured by purse seine in deep water in an old river channel on the Fraser River foreshore were significantly larger than those captured by beach seine along the margins of the channel. As noted earlier, Kjelson et al. (1982) observed a similar distribution of chinook in relation to size in the Sacramento-San Joaquin River estuary.

Reimers (1971) observed the growth rate of young fall chinook in the Sixes River estuary both by sampling the general population and by observing changes in the length of marked cohorts. Both sources of data gave similar results. Growth in the estuary from late April to early June was rapid. During this period, chinook increased in average length from 48 to 79 mm, an average of 0.9 mm/d. From June to August, growth in the estuary was poor, and the fish increased only 6 mm or 0.07 mm/d during this period. From September to November, growth was again rapid, averaging about 0.5 mm/d. Reimers (1971) hypothesized that poor growth during the June-to-August period was due to the large population of chinook in the estuary at this time, and that the increased rate of growth in September to November resulted from both a reduction in population size and better utilization of the whole estuary. By means of otolith microstructure, Neilson et al. (1985) confirmed that individual fish show a rapid growth until June in the Sixes River estuary, after which their growth slowed down. Neilson et al. (1985) suggested that the decline in growth rate after June resulted from a combination of high temperatures in the estuary that reduced growth efficiency and competition for food. Neilson and Geen (1986) also noted that chinook that entered the estuary at a large size remained large relative to members of the same cohort throughout their first year of ocean life.

The rate of growth of marked fry in the Nanaimo River estuary averaged 1.32 mm/d (4%-5% body weight/d) (Figure 16). From average length data for the general population, however, the rate of increase in length during April to June was only about 0.5 mm/d (Healey 1980b), or less than half the rate indicated by marked fish. Other estuaries on the east coast of Vancouver Island showed rates of growth based on average length data from 0.22mm/d in the Cowichan River estuary to 0.61 mm/d in the Courtenay River estuary (M.C. Healey, unpublished data) and 0.46-0.55 mm/d in the Campbell River estuary (Levings et al. 1986). Presumably, these are underestimates of the true growth rate in these estuaries. Average length in the general population of chinook in the Nitinat River estuary increased about 0.33 mm/d during the years 1975-77 (Fedorenko et al. 1979). In 1979, however, fish from a marked cohort increased about 0.62 mm/d (3% body weight/d) (Figure 16). Measurements based on increases in average length of the general population in estuaries, therefore, appear to underestimate the true growth rate by a factor of about two. The exception to this is Reimers' (1971) data for the Sixes River. Variation in growth rate among estuaries is also on the order of two times, as is evident from data of the Na-

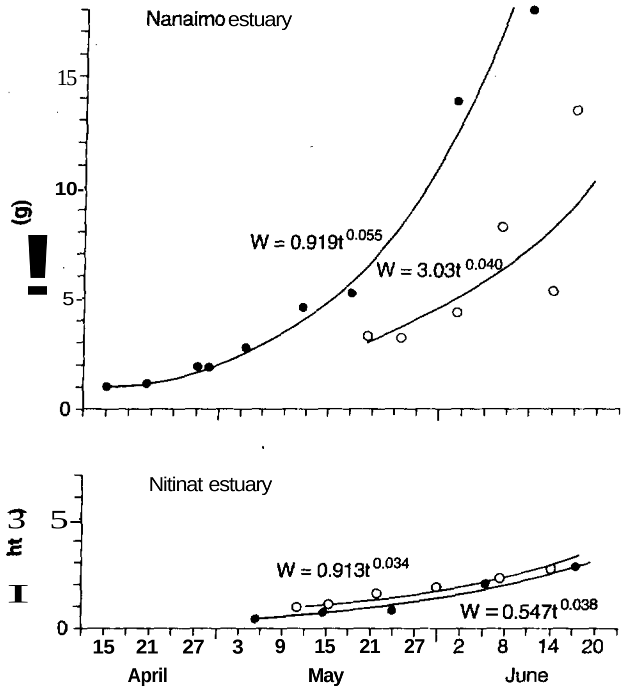


FIGURE 16

Growth of marked cohorts of chinook fry in the Nanaimo and Nitinat River estuaries. Closed and open circles refer to different tagged groups of fry. Regressions are the regression of log weight (W) on days (t) following marking.

naimo and Nitinat River estuaries. The available evidence suggests that variation in growth rates between estuaries and between years within an estuary is correlated with food supply (Healey 1982b; Neilson et al. 1985).

Considering the limited information available on rates of growth of young chinook, particularly their growth in fresh water, no substantial comparisons between freshwater and estuarine growth can be made. Kjelson et al. (1982), however, demonstrated by means of fry tagged both in the river and the estuary that fry grew more rapidly in the estuary. In many other instances, growth of chinook that rear in the river during their first spring appears slower than growth of those that migrate to the estuary. Reimers (1971) and Rich (1920) inferred this from the closer spacing of circuli on the scales of fish that had reared in the river, and suggested that circulus spacing could be used to distinguish between fish that reared to smolt size m the river and those that reared in the estuary. Reimers (1971) proposed that up to five, and Schluchter and Lichatowich (1977) proposed that up to seven, different juvenile life history patterns involving different periods of river and estuarine residence could be distinguished from patterns of scale growth in the Sixes River and the Rogue River, Oregon. These patterns of scale growth were presumed to reflect differences in growth rate between fry residing in the river and in the estuary. In other instances, there appears to be no substantial difference in growth between fish that rear to fingerling smolt size in the river and fish that rear in the estuary (Vancouver Island estuaries, M.C. Healey 1980b, 1982b; M.C. Healey, unpublished data). Fish from these systems that reared in the estuary and fish that reared in the river did not differ in the spacing of circuli on their scales.

Apparently egg size may influence rate of growth, at least in hatchery fry with abundant food. Fowler (1972) found that fry from large eggs were larger at hatching and maintained that advantage over 10-12 weeks after hatching. Rombough (1985) found that larger eggs produced alevins with greater maximum weight, but also that it took the alevins from larger eggs longer to reach their maximum weight after fertilization, compared with alevins from smaller eggs. Such variations in growth rate could have important implications for mortality if the larger fry outgrow potential predators more quickly. In Fowler's (1972) experiments, however, the more rapidly growing fry from larger eggs also had a higher mortality rate from unspecified causes. Thus, the advantage of faster growth may be offset by other unknown disadvantages associated with larger eggs.

Healey (1982b) estimated the production and food requirements of chinook and other salmon species in the Nanaimo and Nitinat River estuaries. Chinook were second to chum in production in the inner Nanaimo River estuary, producing about 200 kg during the spring and early summer, compared with 1,750 kg for chum. In the Nitinat River estuary, however, chinook dominated juvenile salmon production, contributing 774 kg of an estimated total production of 1,137 kg. These levels of production are small relative to the area of the two estuaries, being about 0.031 g/m^2 in the Nanaimo River estuary and 0.025 g/m^2 in the Nitinat River estuary. Food resources required to support this production were 0.093 g/m^2 in the Nanaimo River estuary, consisting of mainly benthic foods but including about 30% insects; and 0.078 g/m^2 in the Nitinat River estuary, of which about 40% were benthic organisms, 40% insects, and 20% plankton (Healey 1982b). The standing crops of food organisms in these estuaries appeared sufficient to support considerably greater production. Growth of chinook in the Nitinat River estuary was, however, considerably less than growth in the Nanaimo River estuary, and this was correlated with lower standing crops of food organisms in the Nitinat River estuary. Also, there was a positive correlation between abundance and growth rate in the Nanaimo River estuary and the fullness of chinook stomachs, suggesting that growth and production were positively related to food supply in this estuary (Healey 1982b).

Differences among stream- and ocean-type races are evident in their utilization of estuarine habitats. Ocean-type fish make extensive use of estuarine habitat, whereas stream-type fish spend little time in the estuary of their natal stream. Among the ocean-type races there is a further dichotomy between those that migrate to the estuary as fry in March or April and remain there until about June and those that migrate as fingerlings in May or June and remain until August or later. This dichotomy becomes blurred in Oregon, where a variety of juvenile behaviour patterns has been identified (Reimers 1971; Schluchter and Lichatowich 1977; Nicholas and Hankin 1988) but is apparent again further south in the Sacramento-San Joaquin River estuary (Kjelson et al. 1981, 1982). The period of estuarine occupancy by ocean-type chinook varies regionally, being greatest in the open coast estuaries of Washington to California, and least in the sheltered coastal estuaries of British Columbia. Estuaries apparently provide a rich feeding habitat for the smaller fry and fingerling migrants, and growth in estuarine habitats, although variable, is relatively rapid. Why stream-type chinook do not spend more time in estuarine habitats is not immediately apparent. The tendency for chinook to become piscivorous, however, as soon as their size permits, and the particular oceanic migratory pattern of stream-type chinook (Healey 1983), may preclude a longer estuarine residence.

OCEAN LIFE

The distribution, seasonal abundance, and migratory behaviour of first ocean-year chinook salmon are described by Healey (1976, 1980a, 1980b) for the Strait of Georgia (British Columbia), by Miller et al. (1983) and Fisher et al. (1983, 1984) for the waters off the coasts of Washington and Oregon, and by Hartt (1980), Healey (1983), and Hartt and Dell (1986) for coastal and offshore waters from the Columbia River to the Bering Sea. The sampling device in all these studies was a small-mesh purse seine, so that the results pertain only to the surface waters (about 20 m deep).

Information on the distribution and migratory habits of older chinook derive from a wide variety of sources. Sampling of commercial troll catches from southeastern Alaska to California has provided information on the general coastal distribution of chinook and their distribution by age and race (Fry and Hughes 1951; Parker and Kirkness 1956; Milne 1964; Ball and Godfrey 1968a, 1968b, 1969, 1970; Wright et al. 1972; Argue and Marshall 1976; Nicholas and Hankin 1988). Sampling the catch of the Japanese mothership and land based gillnet fisheries has provided information on the distribution of chinook in the western North Pacific Ocean. (Geographic distribution of these fisheries is shown in Figures 19 and 20.)

Research cruises by Canadian, u.s., and Japanese vessels have provided more extensive information on chinook salmon distribution throughout the North Pacific Ocean. Gear employed in research cruises included floating longlines and gillnets (Major et al. 1978). As with the seine sampling for first ocean-year chinook, samples taken on the high seas by gillnet and longline relate mainly to the surface waters. Chinook are probably underrepresented in these samples because of their tendency to be distributed deeper in the water column than the other species of Pacific salmon (Milne 1955; Taylor 1969; Argue 1970). Despite potential sampling biases and difficulties in comparing among gear types, the observations of all authors are consistent in that they indicate a major difference in the distribution and migratory behaviour of stream- and ocean-type chinook during their ocean life.

More specific information on the distribution of particular stocks or groups of stocks of chinook is derived from tagging and recapture. Immature and maturing salmon have been tagged in both coastal and high-seas fisheries, and tagged fish have been recaptured from a few weeks to several years after tagging (Kondo et al. 1965; Hartt 1966; Godfrey 1968b; Aro et al. 1971; Aro 1972, 1974). Comparatively few fish tagged in the ocean have been recaptured after a sufficient length of time, however, to permit a precise determination of migratory routes and timing. Considerably more detailed information is available from tagging of hatchery-produced smolts and noting their recovery in coastal troll and net fisheries (e.g., Cleaver 1969; Wahle and Vreeland 1977; Dahlberg 1982; Wertheimer and Dahlberg 1983, 1984; Dahlberg and Fowler 1985; Dahlberg et al. 1986; Nicholas and Hankin 1988). A wealth of this kind of information has been produced over the past decade as a result of the extensive application of coded-wire tagging in hatchery evaluation (Jefferts et al. 1963). Most of these data, however, remain completely unanalysed. Furthermore, the question of whether the behaviour of hatchery fish is comparable with that of wild stocks remains unresolved, although Healey and Groot (1987) found that wild and hatchery chinook from the east and west coasts of Vancouver Island had similar oceanic distributions.

Fish in their First Ocean Year

Observations in the Strait of Georgia indicated that, in these sheltered waters, young chinook began to disperse seaward from their natal estuary shortly after completing their downstream migration. Apparently, the first to do so were the stream-type smolts. In the Nanaimo River estuary, stream-type smolts were rarely captured in the inner estuary but were common in the outer estuary and in other nearshore sampling stations in the vicinity of Nanaimo in June and July of 1975 and 1976, but were rare after July (Healey 1980b) (Figure 17).

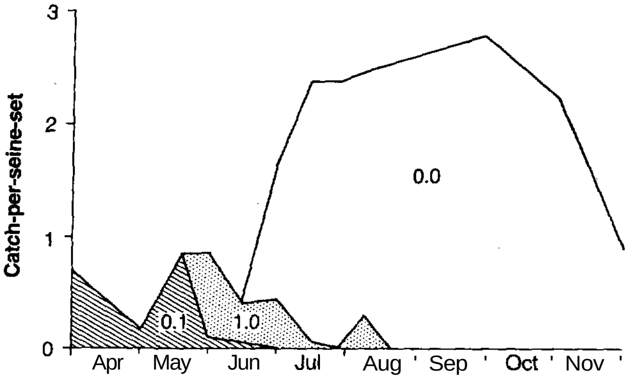


FIGURE 17

Seasonal occurrence of 0.0, 1.0, and 0.1-aged chinook in purse seine catches near Nanaimo, BC, during 1975-77. (From Healey 1980a)

Sampling from May to October, 1976, throughout the Gulf Islands (along the southeast coast of Vancouver Island) confirmed this seasonal pattern of abundance of stream-type smolts outside the Nanaimo area (Healey 1980a). As stream-type juveniles declined in abundance in the sheltered waters of the Strait of Georgia, ocean-type juveniles increased in abundance. In the Nanaimo area, ocean-type juveniles were about five times as abundant in purse seine samples as stream-type juveniles, and ocean-type fish remained abundant from July until November (Figure 17). Seine net catches were lower during the winter, but some chinook were present in surface waters and available to the seine throughout the year (Healey 1980b). In the Gulf Islands region of the Strait of Georgia, young chinook were rather constant in abundance from May to October, 1976. Samples taken throughout the Strait of Georgia in August to September, 1975 and 1976, revealed that chinook were most abundant in the region of the Fraser River plume and less abundant elsewhere. This distribution was much more pronounced in 1975 than 1976 (Healey 1980a).

The general conclusion from these observations was that stream-type chinook in their first ocean year are common in the surface waters of the Strait of Georgia only in the spring and early summer, but that ocean-type chinook in their first ocean year are abundant throughout the summer and autumn, and some remain in the surface waters of the strait throughout their first ocean year. There was no indication of an outmigration of young ocean-type chinook from the Strait of Georgia before November in 1976. Seine samples taken by the Snoquomish Indian band in Puget Sound in October and November, 1976, indicated an abundance of chinook in their first ocean year that was similar to that in the Strait of Georgia (Hartt and Dell 1986).

The estuaries along the open coasts of Washington, Oregon, and California afford the only sheltered water habitat in these regions. Here young ocean-type chinook remain in estuaries considerably longer than was observed in British Columbia estuaries (Reimers 1971; Myers 1980; Myers and Horton 1982) (Figure 14), although stream- and ocean-type chinook also occur in coastal waters outside the estuaries during the summer (Miller et al. 1983; Fisher et al. 1983, 1984). These observations suggest that the affinity of young ocean-type chinook for sheltered waters is general throughout the range of chinook, but that there is also some offshore movement of these fish.

Off the coasts of Washington and Oregon, Miller et al. (1983) found young chinook in abundance during sampling from 27 May to 7 June, 1980. Catches were greatest off the Columbia River mouth, north of this river, and in seine sets made within 20 km of shore. Catches of chinook in their first ocean year declined in July, presumably owing to high surface water temperatures at this time, and catches increased again in August-September when surface temperatures were lower. In the August-September sampling, young chinook were distributed about equally north and south of the Columbia River mouth but were still most abundant close to shore. Significantly, young spring chinook (stream-type) from Columbia River hatcheries were present only in the May-June samples, and then only in the northernmost sampling transects, indicating a rapid migration of these fish north from the river mouth. In 1982 and 1983 Fisher et al. (1983, 1984) sampled an area similar to that sampled by Miller et al. (1983) in 1980 and captured similar numbers of young chinook. During 1982, chinook were most common in samples taken in May and June but were rare in September. During 1983, catches were highest in May and September but were low in June. There was no clear trend in abundance from south to north in these samples; sometimes young chinook were more abundant south of the Columbia River and sometimes north. Nor was there any clear evidence from the samples of Fisher et al. (1983, 1984) that young chinook were more abundant close to the coast.

Miller et al. (1983) compared catches in seine sets held open towards the north or south. In May-June, 80% of chinook were captured in sets held open towards the south, indicating a significant northward dispersal at this time. During July and August-September sampling, however, the direction of the set had no effect on catch. These data indicated a northward dispersal of ocean-type chinook immediately on entry into the sea, but also indicated that movements were not directed throughout most of the summer. This is reminiscent of the summer residency of young ocean-type chinook in the Strait of Georgia.

Hartt (1980) and Hartt and Dell (1986) reported on an extensive series of samples taken by purse seine along the coast of North America from the Columbia River to Bristol Bay, throughout the Gulf of Alaska, along the Aleutian Islands chain, and into the central Bering Sea. Hartt and his co-workers made a total of 3,073 sets during the 15-year period, 1956-70, mostly during the summer months, but extending from April to October. The sampling was concentrated in coastal waters (Figure 18), with offshore seining principally in the spring and early summer. Most young chinook were caught near the coast, and catches overall were greatest from the Columbia River to southeastern Alaska. Smaller catches were made in central Alaska, along the Aleutian chain to Adak Island, and in Bristol Bay. No chinook in their first ocean year were captured in the central Gulf of Alaska or in the central Bering Sea. Greatest catches were in the June-August period, and there was an indication, although catches in all areas were small, that chinook appeared in the catches later in the north than in the south.

An important feature of Hartt's catches was that, by far, the majority of chinook were stream-type (245/253 or 97%)(Healey 1983). Of the eight ocean-type fish captured, six were captured off

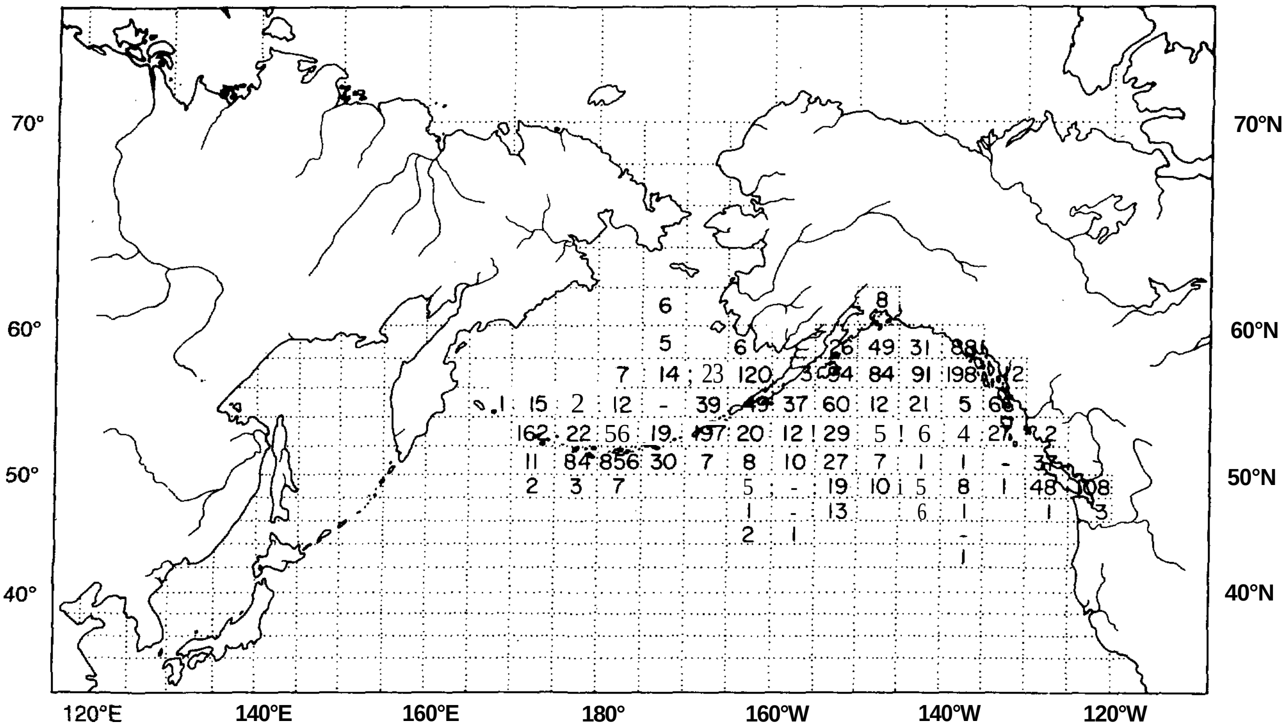


FIGURE 18

Numbers of small-mesh purse seine sets made by Hartt and his co-workers (Hartt and Dell 1986) between 1956 and 1970 in 2° x 5° geographic areas. These areas are the standard statistical recording areas of the International North Pacific Fisheries Commission (INPFC).

Cape Flattery and two off southeastern Alaska. Thus, it appeared that juvenile chinook in their first ocean year, living along the outer coast, at least from Cape Flattery and northward, were predominantly stream-type fish, whereas those in sheltered inside waters were predominantly ocean-type. The samples collected by Miller et al. (1983) and Fisher et al. (1983, 1984) suggest that ocean-type chinook were more common along the open coast south of Cape Flattery.

Fish in their Second and Subsequent Ocean Years

With the exception of organized coastal fisheries and the Japanese mothership and landbased fisheries (Figure 19 and 20), comparatively few chinook have been captured in the open ocean, but the distribution of captures has been very widespread (Figure 19). Chinook almost certainly occur further offshore south of 46°N on the North American coast than is currently indicated, probably even south of 40°N, considering the continued high production of chinook from Californian rivers. Sampling, however, has not been adequate to demonstrate this.

Manzer et al. (1965) reported on the freshwater ages of 847 chinook captured in the Japanese mothership fishery between 175°E and 175°W. These fish were all stream-type. The majority were probably of Asian and Alaskan origin, although recent returns of coded-wire tagged chinook showed that fish from British Columbia, Washington, and Oregon migrate as far west as 160°W-175°W longitude (Dahlberg 1982; Wertheimer and Dahlberg 1983, 1984; Dahlberg and Fowler 1985; Dahlberg et al. 1986). It is possible, therefore, that some of the fish in the sample reported by Manzer et al. (1965) originated from populations south of the Alaskan Panhandle. If so, none was an ocean-type fish. More recent sampling of the Japanese high-seas fisheries (Knudsen et al. 1983; Myers et al. 1984) revealed a similarly low contribution of

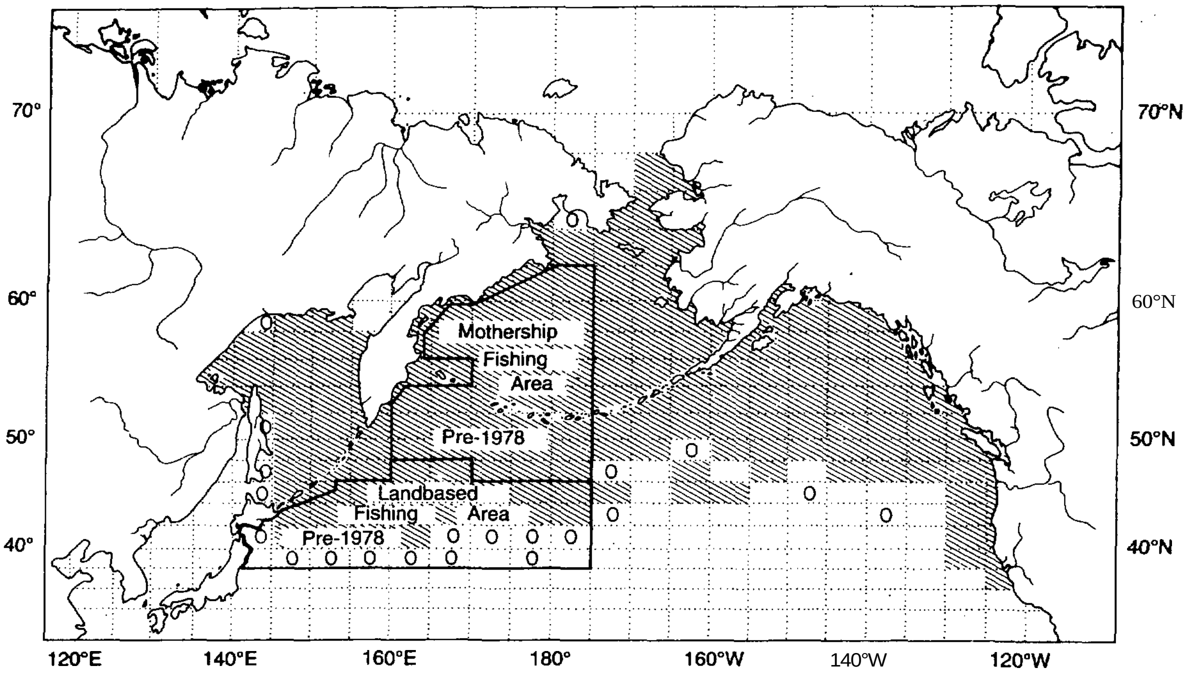


FIGURE 19
Known distribution of chinook in the North Pacific Ocean and Bering Sea based on captures in high-seas and coastal sampling (shaded 2° × 5° INPFC statistical areas). Areas in which sampling occurred but no chinook were captured are shown (0). The Japanese mothership and landbased fishing areas prior to 1978 are shown.

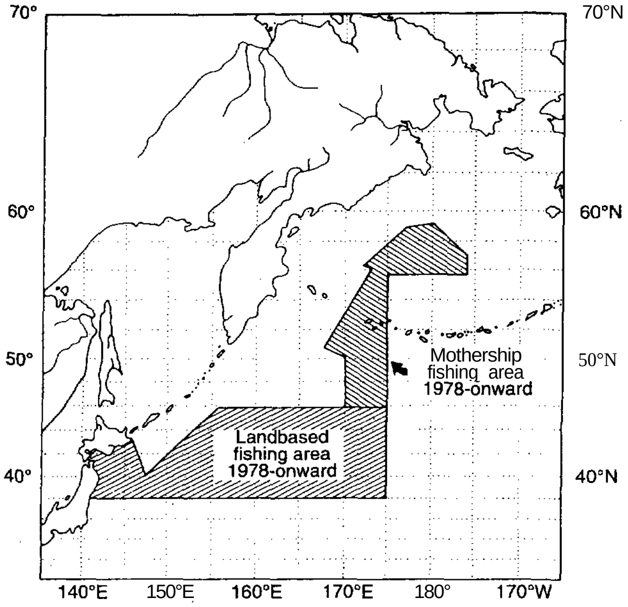


FIGURE 20
Japanese mothership and landbased fishing areas following renegotiation of agreements in 1978, which were in effect until 1986

ocean-type fish, although there are no absolute criteria for distinguishing age 0. and age 1. fish, and there was some disagreement between Japanese and u.s. ageing of the fish reported by Knudsen et al. (1983). The u.s. ageing team found some ocean-type fish (68/2779) and the Japanese team, none.

Further east, ocean-type fish do make a contribution to the high-seas population. Of 80 chinook captured by Canadian research vessels fishing with longlines north of 45°N and east of 170°W during 1961-67, 52 (65%) were stream-type and 26 (35%) were ocean-type (Healey 1983). These fish were almost certainly of North American origin, and were probably mainly from southeastern Alaska and rivers to the south. Since stream-type chinook appear to comprise no more than 25% of all spawning populations from the Sacramento River to southeastern Alaska, the percentage of stream-type fish in the Canadian research vessel catch on the high seas was significantly greater than expected, if stream- and ocean-type chinook have similar ocean distributions ($X^2 = 68.3$; $p <$ .001). The high percentage of stream-type fish in this sample was not a consequence of the fish being captured mainly in the northern Gulf of Alaska, as the catch was equally distributed north and south of 49°N. Furthermore, of the 28 ocean-type fish captured, 14 were captured north of 49°N, and 14 south of this latitude. Thus, there was no evidence of a higher proportion of ocean-type fish in the southern half of the sampling area, as would be expected if ocean-type fish were well distributed offshore, but they were concentrated in more southerly areas, in keeping with the distribution of their spawning populations (Healey 1983). It appears, therefore, that stream-type fish constitute a high proportion of the high-seas population regardless of latitude, although the proportion is lower in the eastern than in the central and western North Pacific Ocean.

Chinook are abundant in coastal waters along the coast of North America from southeastern Alaska to California throughout their ocean lives. In these coastal waters, the representation of stream- and ocean-type races is the opposite of that observed on the high seas, and ocean-type fish predominate (Healey 1983).

The proportion of stream-type chinook in the commercial troll fisheries of Alaska, British Columbia, and Washington in recent years has ranged from 3% to 4% in the Strait of Georgia to 25% in the Queen Charlotte Islands area of British Columbia (Table 5). The proportion off Washington and off southeastern Alaska was similar at 15%–16%. In recent years, therefore, stream-type fish have made up a relatively small proportion of the ocean troll catch, generally less than 20%, and significantly less than one would expect from the proportion of stream-type fish in the regional spawning populations.

There is evidence that stream-type chinook may, historically, have constituted a greater percentage of the coastal troll catch than they do at present. In the Strait of Georgia, stream-type fish were 28% of the catch during 1911-20 and declined to 3%-4% by 1961-70 (Table 5). Off the west coast of Vancouver Island, stream-type fish were 20% of the catch during 1921-30, declined to 3.9% during 1961-70, and increased to 9.0% during 1981-85 (Table 5). Off Washington and Oregon, stream-type chinook constituted more than 20% of the catch before 1950 but only 15% of the catch after 1960 (Table 5). These changes must be interpreted cautiously, however, as scale interpretation and fishing patterns may have changed over the years. For example, stream-type fish were a high percentage of the recent net catch in major river estuaries of British Columbia (Table 5) and, as noted earlier, maturing stream-type chinook return to the estuary of their spawning river early in the year. If historic troll fisheries were nearer river mouths, or were concentrated earlier in the year, then their catch of stream-type fish might naturally have been higher. On the other hand, habitat modification, particularly damming of the Columbia and

TABLE 5

Stream-type chinook (as a percentage) in coastal troll catch and river mouth gillnet catch during several decades

Fishery	Data source*	1911-20	1921-30	1941-50	1951-60	1961-70	1971-80	1981-85
S.E. Alaska troll	1				15.7			
North BC troll	2		23.0		5.6	20.6		25.0
Central BC troll	2					9.3		12.0
Van. Is. troll	2		20.0	12.4	10.9	3.9		9.0
Georgia St. troll	2	28.0	17.5		6.5	3.4		
Wash./Oreg. troll	3		22.0	28.4	34.4	15.3	12.8	
Fraser R. net	4					42.8	28.1	
Skeena R. net	4					48.1		
Nass R. net	4					46.2		

Notes: *1 Parker & Kirkness (1956)
2 Milne (1964); Ball & Godfrey (1968a, 1968b, 1969, 1970); Healey (1986)
3 Wright et al. (1972); Rich (1925); Van Hyning (1951)
4 Godfrey (1968a); Ball & Godfrey (1968a, 1968b); Fraser et al. (1982); Ginetz (1976)

Sacramento rivers, but also water extraction for irrigation and hydraulic mining (Kjelson et al. 1981, 1982), have probably had a much greater effect on stream-type chinook than ocean-type, owing to their longer upriver migrations and longer river residence, both as adults and as young. It is, therefore, quite conceivable that stream-type chinook were relatively more abundant a few decades ago. The possibility that the changes in percentage of stream-type fish in the troll catches represent a real reduction in the numbers of stream-type fish is further supported by the observation that spring and summer spawning runs (mainly stream-type fish) have declined drastically in several rivers in the southern half of the Chinook's range (Snyder 1931; Rich 1942) and by the fact that the older maturing stream-type chinook are less able to support an intensive fishery than younger maturing ocean-type chinook (Hankin and Healey 1986).

The information on distribution of races indicates that stream-type chinook move offshore early in their ocean life, whereas ocean-type chinook remain in sheltered coastal waters. Stream-type fish maintain a more offshore distribution throughout their ocean life than do ocean-type. Although ocean-type fish are captured offshore in the eastern half of the North Pacific Ocean, they are much less common there than stream-type fish, whereas the reverse is true close to the coast. Since only stream-type chinook occur in western Alaska and in Asia, it is not surprising that catches in the western North Pacific Ocean are virtually all stream-type. Stream-type chinook are also common in river mouth fisheries of British Columbia (Table 5) and in early season catches in the Fraser and Columbia rivers (Figure 6). These observations suggest that maturing stream-type fish move rather quickly through the coastal troll fisheries to the river estuaries and so are available for only a relatively short time to the troll fisheries. Healey and Groot (1987) noted that maturing chinook returning to their native river travelled more than 45 km/d, or close to their optimal cruising speed, on a direct course towards the river. They appear to remain in the river estuaries for some time, however, and while there are vulnerable to the river mouth gillnet fisheries.

Ocean Distribution in Relation to Temperature

High-seas catches of chinook by research vessels generally have been too small to permit analysis of chinook distribution in relation to ocean temperature except for catches by Japanese research vessels in the western North Pacific Ocean. There, during 1962-70, chinook were encountered at temperatures ranging from 1° to 15°C (Major et al. 1978). There was no evidence for a preferred temperature within this range, except that, in April and May, relatively fewer chinook were encountered at temperatures below about 5°C. These data refer, of course, to Asian and Alaskan stream-type chinook. This may mean that chinook are indifferent to temperature over this range. The data may not be *a* true reflection of temperature selection (or lack thereof) by chinook, however, as the samples of fish and temperature measurements came only from surface waters. As will be demonstrated later, chinook are not concentrated at the surface. Surface catches may, therefore, not be representative of temperature selection occurring at depth.

Vertical Distribution of Chinook

Information on the depth distribution of chinook comes primarily from two sources, neither of which distinguished between stream- and ocean-type fish. Sampling was also conducted only during daylight hours. Taylor (1969) reported the depth of capture of immature chinook off the east and west coasts of Vancouver Island during survey cruises for Pacific herring. Most samples came from the west coast of the island, and these will be emphasized here. Chinook were captured in trawls fishing deeper than 60 fm (110 m), but most fish were captured above 40 fm (73 m) (Table 6). Chinook were not concentrated near the surface but were most abundant in the 30-40 fm (57-73 m) stratum. Chinook captured in trawls in the Strait of Georgia were more abundant near the surface, with most (51/53) captured between 10 and 20 fm (20-37 m) (Table 6). Argue (1970) reported a more extensive set of data based on troll sampling in Juan de Fuca Strait. Argue's (1970) samples only extended to 55 m, and most chinook (54%) were captured in the 48-55 m stratum (Table 6). Possibly, catches would have been as large at even greater depth. Both young chinook (younger than .2) and maturing chinook (older than .2) were captured more frequently at shallower depths than were older immature chinook (Table 6). There appeared

TABLE 6

Depth distribution of chinook (as a percentage of catch) captured off the west (W) and east (E) coasts of Vancouver Island during herring surveys (Taylor 1969), and in Juan de Fuca Strait during a troll fishery investigation (Argue 1970)

Depth		Taylor 1969		Argue 1970*				
		All ages		Immature				Maturing
fm	(m)	*N* = 194 W	*N* = 53 E	All ages *N* = 150	0.0+1.0 *N* = 50	0.1 *N* = 76	0.2 *N* = 71	*N* = 19
0-5	(0-9)	23	2	3	2	10	0	11
6-10	(11-18)			3	7	8	6	17
11-15	(20-27)	7	96	7	14	21	21	44
16-20	(29-37)			17	21	29	10	18
21-25	(38-46)	7	2	16	32	16	25	0
26-30	(48-55)			54	24	14	38	10
31-35	(57-64)	46						
36-40	(66-73)							
41-45	(72-82)	6						
46-50	(84-91)							
>50	(>91)	10						

Note: *Argue's data are segregated by age and maturity

to be a seasonal change in depth distribution, with the average depth of capture dropping from 33 m in June and July to 41 m in August-October (Figure 21). Taylor (1969) did not indicate the freshwater ages of the fish captured. The fish in Argue's samples, however, were virtually all ocean-type.

Ocean *Distribution in Relation to Area of Origin*

There are two sources of information on oceanic distribution of chinook in relation to area of origin: tagging studies and analysis of scale patterns. Tagging studies include both the tagging of immature and maturing chinook in the ocean with subsequent recapture in the ocean or on the spawning beds, and the tagging of hatchery smolts at the time of seaward migration with subsequent recapture in the ocean. Scale pattern analysis attempts to determine the area of origin of chinook captured on the high seas from characteristic features of their scales. Neither source of information gives a

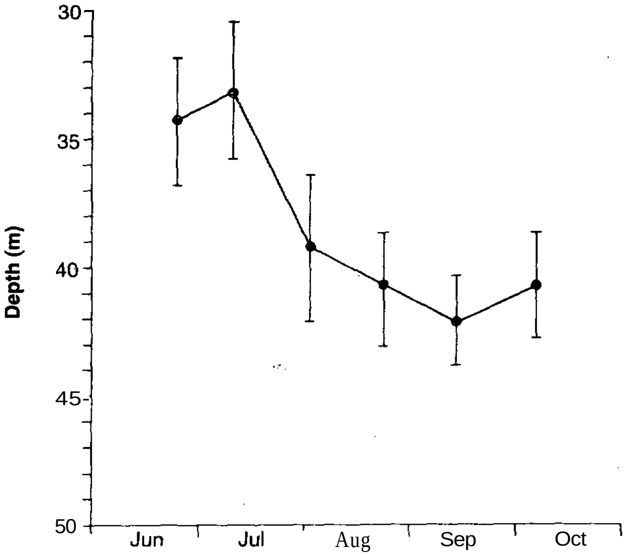


FIGURE 21

Seasonal changes in the average depth of capture of chinook in Juan de Fuca Strait. Bars show two standard errors around mean. (Data from Argue 1970) very satisfactory picture of the ocean distribution of the many stocks of chinook salmon. The majority of ocean tagging of chinook has been conducted along the Pacific coast of North America from southeastern Alaska to California. Godfrey (1968b) summarized data from ocean tagging in this area during the period 1924-64. In addition, a few tags have been recovered from chinook tagged during high-seas fishing operations in the northern North Pacific Ocean and the Bering Sea (Major et al. 1978; Knudsen et al. 1983). The ocean distribution of chinook tagged as smolts and recaptured in coastal fisheries has been described by Cleaver (1969), Wahle and Vreeland (1977), Wahle et al. (1981), and Healey and Groot (1987):

A total of *21,566* chinook salmon were tagged in coastal waters during the 1924-64 period, and recaptures numbered 2,418 (Godfrey 1968b). Recoveries of tags came from recreational and commercial fisheries and from spawning ground surveys. Because of unequal sampling and recovery effort, the tag returns provide only a general indication of the stock composition in various regions of the coast. Some important generalizations are, however, possible. Most recaptures were made either in the area of tagging or to the south, except for the tagging off California, where it was only possible to recover tags in the area of tagging or to the north (Figure 22). When tagging was conducted in inside sheltered waters, most recaptures came from the area of tagging or immediately adjacent areas. When tagging was conducted in more open waters, however, such as off the west coast of southeastern Alaska or off the west coast of Vancouver Island, recaptures were more widely distributed geographically (Figure 22). Fish tagged off southeastern Alaska were recaptured as far south as Oregon coastal streams, whereas fish tagged off California were recaptured as far north as the Washington coast. These data suggest a northward dispersal of juveniles along the coast, followed by a southward homing migration of maturing adults. The more limited dispersal of fish tagged in inside waters is, however, perplexing. It may indicate the presence of "resident" stocks that do not undergo long-distance migrations. It may also be a reflection of a greater number of stream-type chinook in the groups tagged in outside waters, coupled with the apparent longer migrations of this race. Recent analysis of tag returns from hatchery and wild

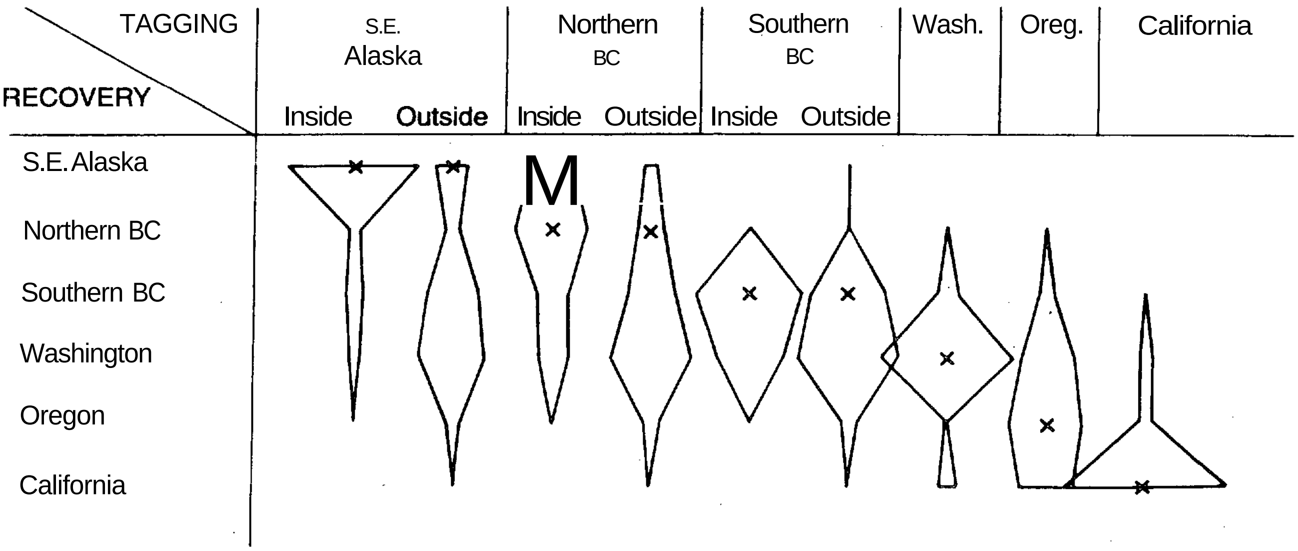


FIGURE 22
The distribution of recaptures from chinook tagged as immatures in coastal waters from southeastern Alaska to California. Tagging location in each diagram is marked *(x)*. Proportion of recaptures in each region is indicated by the width of the diagram at that point. Inside and outside tagging areas for some regions refer to inside or outside coastal island chains.

chinook stocks on the east and west sides of Vancouver Island (Healey and Groot 1987) indicate that "inside" ocean-type stocks have a more restricted migration than "outside" ocean-type stocks.

Coastal Oregon stocks of chinook show diverse ocean migration patterns that do not correspond to the general northward migrating behaviour on other parts of the North American coast. Stocks that spawn in rivers on the central and northern parts of the Oregon coast (from the Elk River north) show the typical northward migration as immatures, and these stocks contribute to fisheries from Oregon to Alaska. Stocks that spawn in rivers on the southern part of the Oregon coast (from the Rogue River south), by contrast, disperse mainly south and contribute to fisheries off Oregon and northern California. One stock, the Umpqua River spring-run chinook, disperse both north and south from their natal river and are harvested from northern California to Alaska (Nicholas and Hankin 1988).

The distribution of particular stocks by age is revealed by returns of fish tagged from hatchery releases. Releases from Columbia River hatcheries dispersed mainly north of the Columbia River, although some were also captured south of the river mouth (Figure 23) (Cleaver 1969). Fish aged two years were caught mainly off the Washington coast; fish aged three years, off Washington and southern British Columbia; fish aged four years, off Washington and southern British Columbia but with a few returns from northern British Columbia and southeastern Alaska; and fish aged five years, mainly from southern British Columbia, but extending into northern British Columbia and southeastern Alaska (Figure 23). Chinook from the Robertson Creek Hatchery on the west coast of Vancouver Island also dispersed mainly north as they became older, but there was somewhat greater southward dispersal than was apparent for the Columbia River fish. Robertson Creek fish were clearly distributed further north than Columbia River fish (Figure 23). Robertson Creek fish, however, also dispersed further north than Big Qualicum River fish from eastern Vancouver Island (Healey and Groot 1987). It appears that there may, in some instances, be considerable differences in the ocean distribution of stocks from the same geographic area.

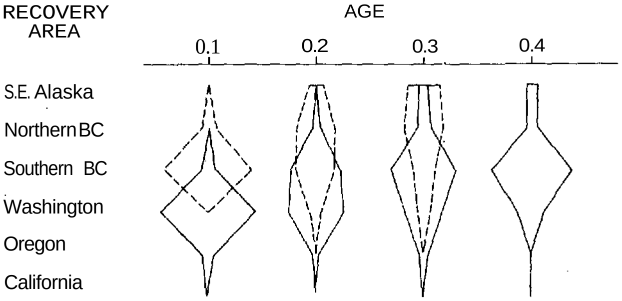


FIGURE 23
Distribution of recaptures by age for ocean-type chinook from Columbia River hatcheries (solid lines) and Robertson Creek, BC (dashed lines). Proportion of recaptures in each region is indicated by the width of the diagram.

Wahle and Vreeland (1977) and Wahle et al. (1981) described the ocean distribution of fall (ocean-type) and spring (stream-type) chinook from various Columbia River hatcheries by means of recaptures in coastal fisheries. Fall chinook were recaptured mainly in British Columbia and Washington fisheries and, secondarily, in Columbia River estuary fisheries. Except for the Kalama Hatchery (Washington) release, there were no recoveries of fall chinook from southeastern Alaska and relatively few recoveries from south of the Columbia River (Figure 24). There were some interesting, and perhaps significant, differences in the contribution of different hatchery stocks to the different fisheries. For example, the proportion recovered in British Columbia fisheries ranged from 12% to 50%, and the proportion recovered in the Columbia River estuary ranged from 2% to 26% (Figure 24). Spring chinook, in general, had a wider distribution than fall chinook. For example, up to 20% were recaptured in southeastern Alaska, and all stocks contributed to the Alaskan catch. More spring chinook tended to be caught south of the Columbia River and in the river estuary as well. As with the fall chinook stocks, there were interesting differences in the apparent ocean distribution among spring chinook hatchery stocks.

To a large extent, the distribution of tag recoveries of various stocks has been determined by the location of intensive fisheries for chinook. This is clearly revealed by the recent recovery of tags from chinook captured incidentally in foreign trawl fisheries within the United States 200-mile conserva-

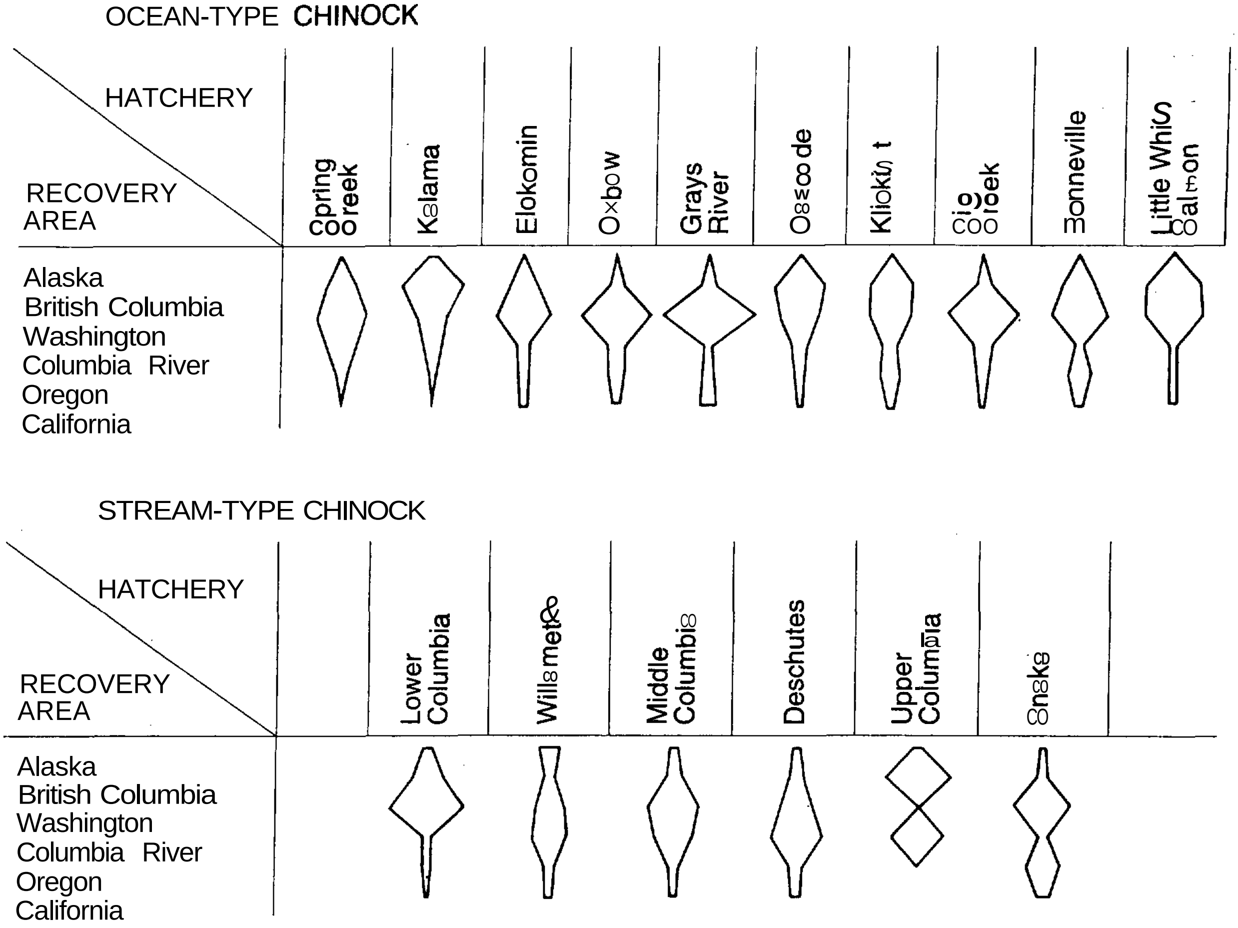


FIGURE 24

Distribution of recaptures of chinook from ten Columbia River hatcheries producing ocean-type chinook and six hatcheries producing stream-type chinook. Proportion of recaptures in each region is indicated by the width of the diagram.

tion zone in Alaska (Dahlberg 1982; Wertheimer and Dahlberg 1983, 1984; Dahlberg and Fowler 1985; Dahlberg et al. 1986). Approximately 60,000 chinook have been examined by United States observers aboard foreign trawlers fishing mainly south of the Alaska Peninsula and in the southeastern Bering Sea, and these have yielded a total of 244 tagged chinook that originated from rivers ranging from central Alaska to California. The distribution of recaptures extends from northern southeastern Alaska westward through central Alaska, along the Alaska Peninsula and Aleutian Islands to about 175°W, and northward into the southeastern Bering Sea (Figure 25).

Of the recaptured chinook, 70 were from stocks in southeastern and central Alaska, 75 from stocks in British Columbia, 43 from stocks in Washington, 54 from stocks in Oregon, and one each from stocks in California and Idaho. The recaptures of Alaskan stream-type chinook in these coastal trawl fisheries provide evidence that at least some fish from northern stream-type stocks remain close to the coast for one to two years following their seaward migration, similar to the behaviour of ocean-type chinook from further south. The recaptures of chinook from stocks in British Columbia and further south represent definite range extensions for these stocks. Most of the recaptures were of ocean-

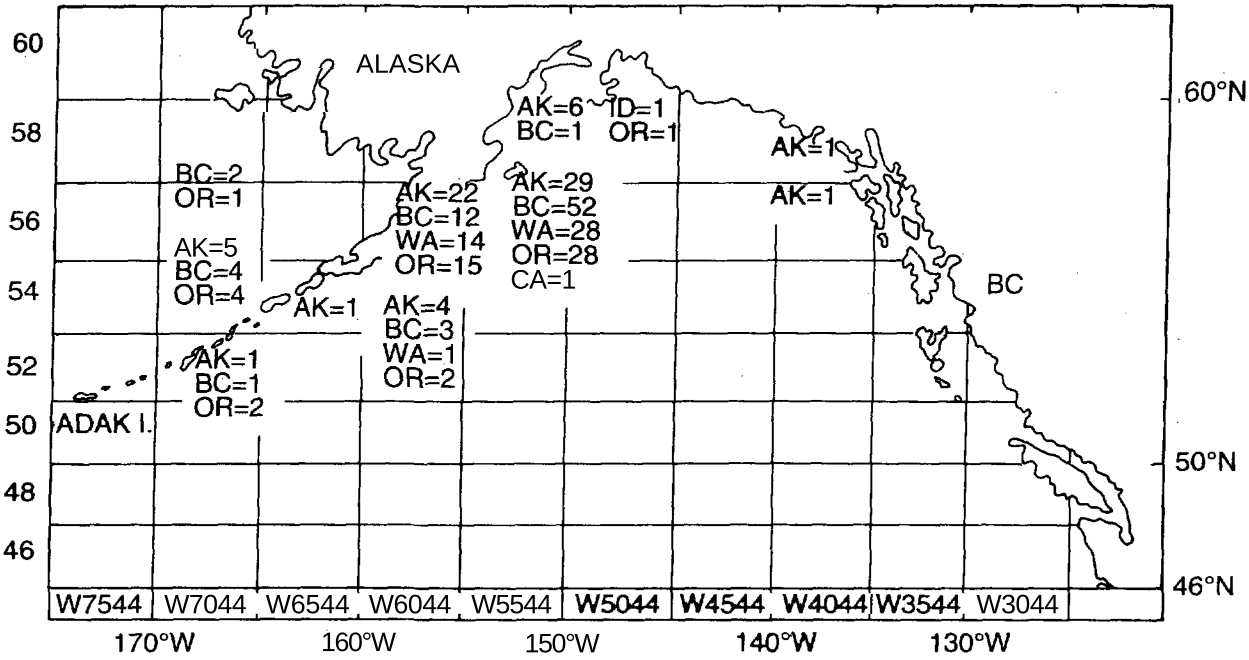


FIGURE 25

Numbers of tagged chinook from different coastal origins recovered as by-catch in the foreign trawl fleet fishing within the u.s. 200-mile zone off Alaska. Catches are shown within INPFC statistical areas.

type chinook, and the previous maximum extent of their range along the coast had been determined from recaptures in the troll fisheries of southeastern Alaska. These new recaptures extend the range of these stocks westward along the coast to nearly 175°W and, for British Columbian and Oregon chinook, northward into the Bering Sea (Figure 25).

Although the recaptures from incidental catch of chinook in foreign trawl fisheries indicate significant range extensions for numerous stocks of chinook, the incidence of tagged chinook among those landed is very low (0.4% overall, 0.3% if only ocean-type stocks are considered), indicating that only a small proportion of these stocks travels so far west and north. Furthermore, these recaptures, together with a single return to the Columbia River from chinook tagged south of Adak Island, appear to define the probable western limit of stocks from south of the Alaskan Panhandle at about 180°, because examination of almost 53,000 chinook captured in the Japanese mothership fishery operating within the United States 200-mile conservation zone west of 175°E produced no tagged chinook. Nor did examination of over 20,000 chinook captured by Japanese research vessels fishing in the northern North Pacific Ocean and Bering Sea produce any tagged chinook (Dahlberg 1982; Wertheimer and Dahlberg 1983, 1984; Dahlberg and Fowler 1985; Dahlberg et al. 1986).

The information presented to this point refers only to coastal distribution of particular stocks of chinook salmon. Information on the open ocean distribution is much more sketchy and speculative, as most of it is not based on tag returns from fish of known origin.

Approximately 2,099 chinook older than age 1. have been tagged and released on the high seas west of 150° W and in the Bering Sea between 1956 and 1984 (C. Harrison, Fisheries Research Institute, University of Washington, Seattle, Washington, pers. comm.). Thirty-three of these have been recaptured (Figure 26), and these recaptures provide some information on the ocean migrations of stream-type chinook. Recaptures up to 1972 were discussed by Major et al. (1978).

Twenty-one fish tagged in the central Bering Sea were recaptured within the Bering Sea and its coastal areas (Figure 26). Five had moved towards the west (northwest to southwest) from the

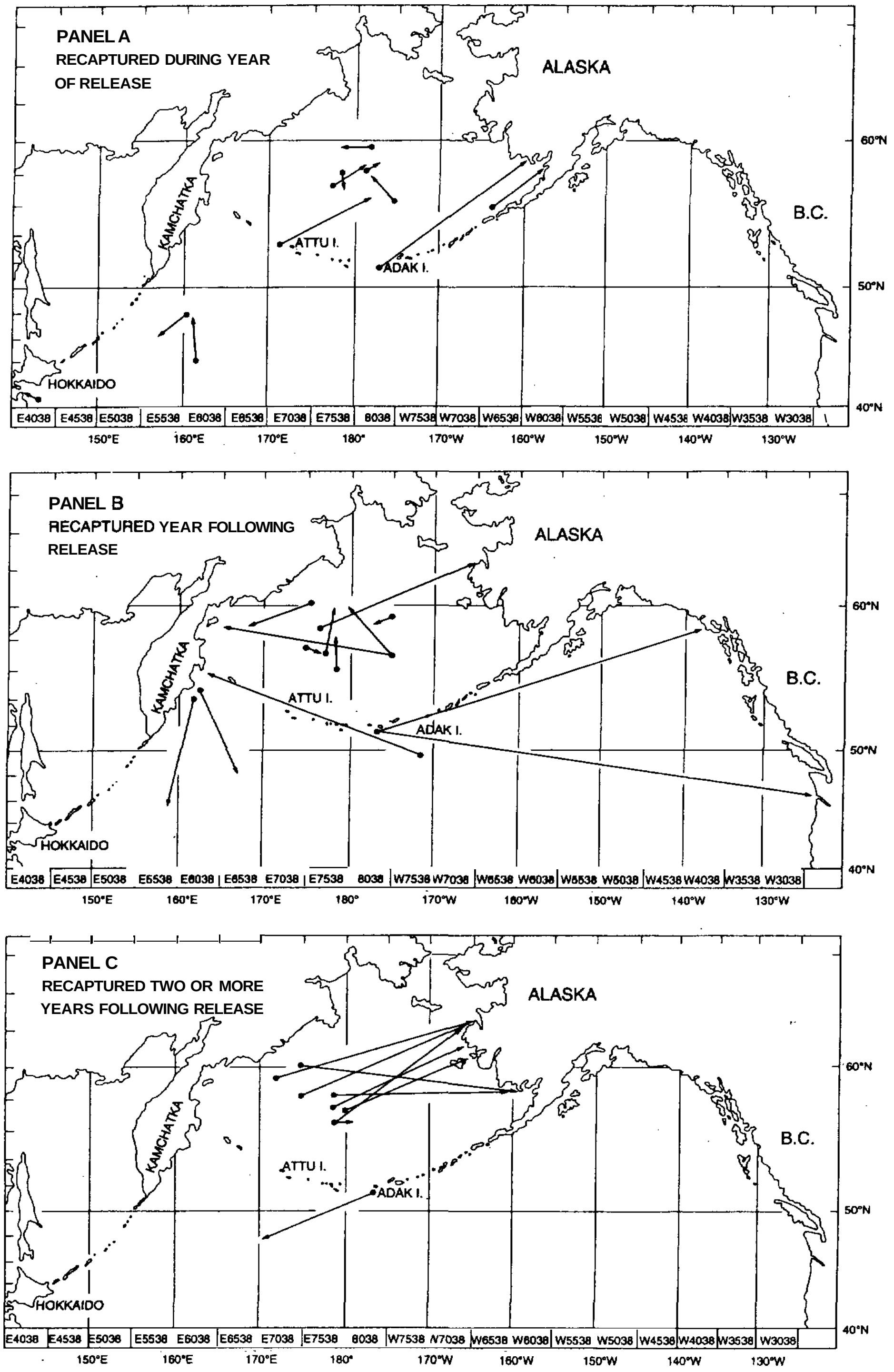


FIGURE *26*

The location of tagging (●) and recapture (→) of chinook tagged on the high seas in the central Bering Sea, in the N.W. Pacific, and south of Adak Island in the Aleutian chain. *Panel A,* chinook recaptured in the year of tagging. *Panel B,* chinook recaptured one year after tagging. *Panel C,* chinook recaptured two or more years after tagging point of release, and three a moderate distance north or northeast. Three of these were immature at the time of recapture and the other four were of undetermined maturity. Eight had moved east to river mouths in western Alaska, and these were all mature at the time of recapture, most being recaptured two years after tagging. The remaining five fish were recaptured only a short distance from their point of tagging. Scant as these results are, they suggest a north and westward movement of immatures and an eastward movement of matures, at least of those bound for western Alaskan rivers.

Of five chinook tagged and recaptured in the western North Pacific Ocean, three were recaptured south or southwest, one north, and one west of their tagging sites (Figure 26). Their maturity at the time of recapture was not determined. Four fish tagged south of Adak Island in the Aleutian chain were recaptured, three as maturing fish and one of undetermined maturity (Figure 26). Of the maturing fish, one was recaptured in Bristol Bay, one in southeastern Alaska, and one at the Columbia River mouth. The fourth fish was recaptured southwest of Adak Island. One other fish tagged south of the Aleutians was recaptured off the east coast of Kamchatka one year later. These returns reveal only that chinook from the northern North Pacific Ocean are from diverse origins and that fish from the Columbia River may migrate as far west as Adak Island.

The costliness, and the limitations, of ocean tagging have led investigators, particularly those in the United States, to explore other techniques for identifying the origin of chinook captured on the high seas. One of these techniques is the estimation of stock composition by discriminant analysis of scale measurements.

The earliest attempts to classify high-seas catches of chinook by this technique were described by Major et al. (1978). In these early studies only western Alaskan and Asian stock groupings were recognized. The analysis was expanded by Knudsen et al. (1983) and Myers et al. (1984) to Include classification of central Alaskan, southeastern Alaskan/British Columbian, and Washington/Oregon/Californian stock groupings. The Washington/Oregon/Californian stock grouping was eliminated from further consideration by these authors when they found that it made an insignificant contribution to high-seas catches. Most recently, Ito et al. (1985, 1986) and Myers (1986) have investigated how altering the proportion of the different Asian stocks used as known standards in developing the discriminant functions affects the classification of unknown samples from the Japanese mothership and landbased fisheries. Myers et al. (1987) summarized findings from recent u.s. analyses.

The results of these analyses are controversial, particularly when they are used to estimate numbers of fish of different origins landed by a particular fishery. Before presenting some of the results of these analyses, the most important criticisms of the methodology will be summarized. There can be no doubt that the quantitative results of the discriminant function analysis are sensitive to the composition of the standards used to develop the discriminant functions, and to assumptions about which stocks or stock groupings contribute to the catch in any high-seas fishery. Because the analysis is sensitive to these factors, it is my view that it is inappropriate at this time to use the discriminant function analysis to estimate stock composition quantitatively. It is also my view, however, that the analyses are sufficiently consistent, particularly with respect to mixing proportions of some stocks, to provide a reasonable basis for speculation about qualitative features of the high-seas distribution of chinook.

There are numerous technical difficulties involved in applying discriminant function analysis of scale features to the analysis of a sample of scales from fish of unknown origin. A set of scales appropriate for such an analysis must be compiled from known populations. Features of the scales that are unambiguous in terms of their measurement, and that differ between populations but are reasonably consistent within populations, must be discovered if classification by discriminant function analysis is to be successful. The scales of unknown origin that are to be classified must be comparable with those used to develop the original discriminant functions and must comprise an unknown mixture of only those stocks for which discriminant functions have been calculated. Failure to meet these and other technical requirements in the data can result in errors in classification of unknown seriousness. Myers et al. (1984) and Myers (1986) report rather careful screening of the data to minimize the possibility of such errors, such as ensuring that the scales used in the analysis were from the preferred area of the body, and that the discriminant functions were brood year specific. It is virtually impossible, however, to eliminate all such sources of error.

An important potential source of error in the classification of an unknown mixture of scales is the presence of scales from stocks not included in the standards used to develop the discriminant functions. Such scales will be classified into one or more of the stocks specified in the analysis and, if abundant, could greatly bias the estimate of stock composition.

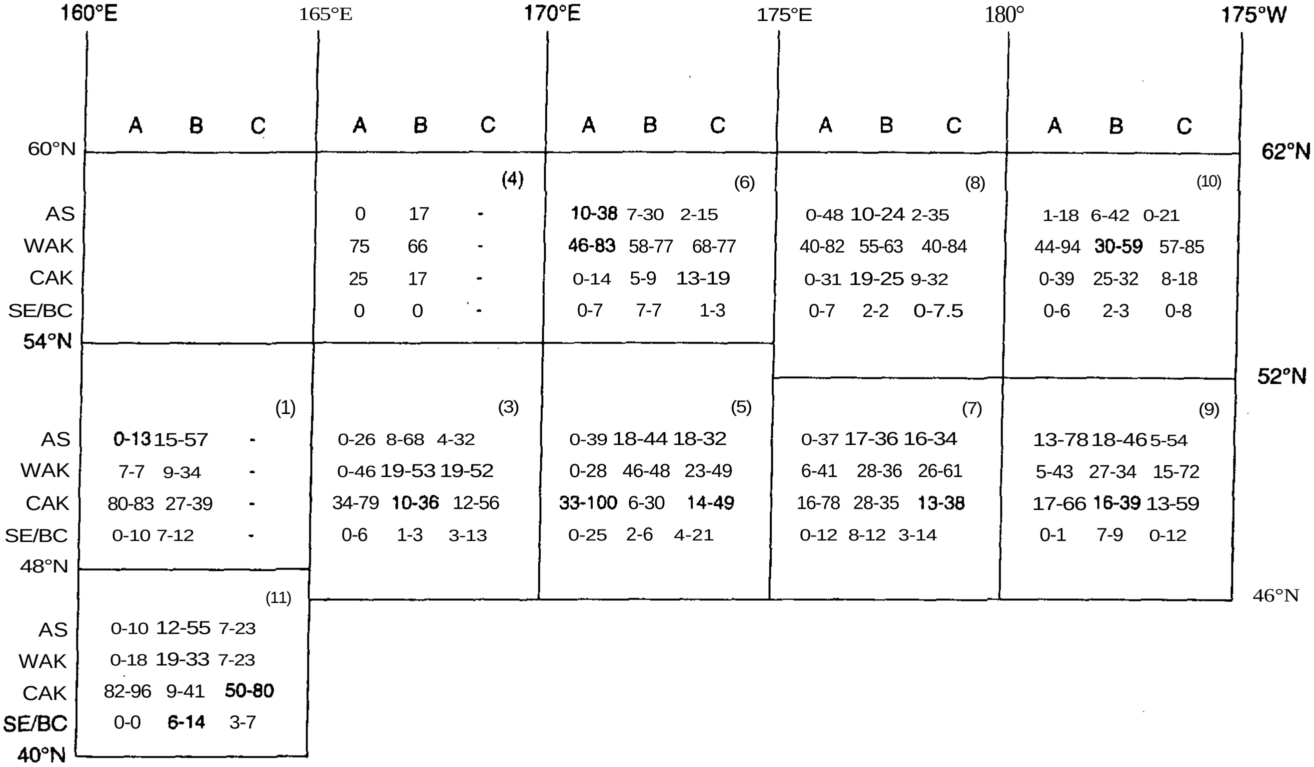
The success in classifying the scales of known origin from which the discriminant functions were calculated provides one indicator of the magnitude of error that might occur in classifying a sample of unknown scales. It should be remembered, however, that there may be greater error in the classification of individual scales than in the estimate of overall stock composition.

The overall success in classifying fish of known origin by the discriminant functions developed from those fish ranged from 69.4% to 79.7% in the studies reported by Myers et al. (1984) and Myers (1986), and was 60.9% in the study reported by Ito et al. (1985). Although these are reasonably high rates of successful classification, there is still room for considerable error in quantitative estimation of stock composition. For individual stock groupings, the success in classifying known samples ranged from 58.5% to 95.5% for the Asian grouping, from 64.6% to 89.9% for the western Alaskan grouping, from 47.0% to 67.7% for the central Alaskan grouping, and from 70.5% to 83.5% for the southeastern Alaskan/British Columbian grouping (Myers et al. 1984, Ito et al. 1985; Myers 1986). The central Alaskan stock grouping was the grouping most likely to be misclassified in all analyses, and these fish tended to be misclassified as belonging either to the southeastern Alaskan/British Columbian or Asian stock groupings rather than to the western Alaskan grouping (Myers et al. 1984; Ito et al. 1985, 1986; Myers 1986). The directions and degree of misclassification of central Alaskan scales depended to a considerable extent on the stock proportions in scales used for the Asian standard (Myers 1986).

Considering the potential sources of bias and error it is not surprising that the quantitative estimates of stock composition produced by different analyses differ considerably. In Figure 27 the estimates from recent publications of stock composition of immature chinook captured in July in subareas of the Japanese mothership fishery are shown (Myers et al. 1984; Ito et al. 1986; Myers 1986). Despite the quantitative disagreement in the results of different analyses, there appears to be considerable qualitative agreement.

In the Bering Sea, all the analyses agree that western Alaskan (including the Canadian Yukon) chinook are the most abundant stock grouping. Next in abundance are Asian and central Alaskan chinook, which are each about half as abundant as western Alaskan chinook. The southeastern Alaskan/British Columbian stock grouping is rare in the Bering Sea (Figure 27).

In the western North Pacific Ocean, the greatest disagreement is over the relative contribution of central Alaskan and Asian stock groupings; the analyses of Myers et al. (1984) and Myers (1986) suggest that central Alaskan chinook often dominate in this area, whereas the analyses of Ito et al. (1985, 1986) suggest that Asian chinook dominate (Figure 27). This disagreement is not, as yet, technically resolvable. The very high percentage of central Alaskan chinook in the western North Pacific Ocean suggested by Myers et al. (1984) (sometimes as high as 100%) seems inconsistent with the apparent abundance of this species in spawning escapements in central Alaska. Myers et al. (1987), however, suggested that chinook may be more abundant in central Alaska than previously thought. Comparison of measured characteristics suggests similarity between Asian and central Alaskan scales in a number of features. It seems possible that there may be considerable misclassification of Asian scales as central Alaskan and vice versa, depending on the scale characters and the stocks used to calculate the discriminant functions. Leaving aside the relative contributions of Asian and central Alaskan chinook, all the analyses suggest that the chinook population of the western North Pacific Ocean is comprised mainly of stocks from Asia, western Alaska, and central Alaska, and that each of these stocks makes a substantial contribution to the population. Southeastern Alaskan/British Columbian chinook, although perhaps slightly more abundant than in the Bering Sea, still constitute only a small per-



Subdivision	Stock	A	B	C
(1)	AS	0-13	15-57	-
(1)	WAK	7-7	9-34	-
(1)	CAK	80-83	27-39	-
(1)	SE/BC	0-10	7-12	-
(3)	AS	0-26	8-68	4-32
(3)	WAK	0-46	19-53	19-52
(3)	CAK	34-79	10-36	12-56
(3)	SE/BC	0-6	1-3	3-13
(4)	AS	0	17	-
(4)	WAK	75	66	-
(4)	CAK	25	17	-
(4)	SE/BC	0	0	-
(5)	AS	0-39	18-44	18-32
(5)	WAK	0-28	46-48	23-49
(5)	CAK	33-100	6-30	14-49
(5)	SE/BC	0-25	2-6	4-21
(6)	AS	10-38	7-30	2-15
(6)	WAK	46-83	58-77	68-77
(6)	CAK	0-14	5-9	13-19
(6)	SE/BC	0-7	7-7	1-3
(7)	AS	0-37	17-36	16-34
(7)	WAK	6-41	28-36	26-61
(7)	CAK	16-78	28-35	13-38
(7)	SE/BC	0-12	8-12	3-14
(8)	AS	0-48	10-24	2-35
(8)	WAK	40-82	55-63	40-84
(8)	CAK	0-31	19-25	9-32
(8)	SE/BC	0-7	2-2	0-7.5
(9)	AS	13-78	18-46	5-54
(9)	WAK	5-43	27-34	15-72
(9)	CAK	17-66	16-39	13-59
(9)	SE/BC	0-1	7-9	0-12
(10)	AS	1-18	6-42	0-21
(10)	WAK	44-94	30-59	57-85
(10)	CAK	0-39	25-32	8-18
(10)	SE/BC	0-6	2-3	0-8
(11)	AS	0-10	12-55	7-23
(11)	WAK	0-18	19-33	7-23
(11)	CAK	82-96	9-41	50-80
(11)	SE/BC	0-0	6-14	3-7

FIGURE 27

Estimates by various authors of stock composition of chinook captured in subdivisions of the Japanese mothership fishery based on discriminant function analysis of scale characteristics showing variation in results. AS = Asia, WAK - Western Alaska, CAK - Central Alaska, SE/BC - southeastern Alaska/BC. The numbers (1)-(11) represent subdivisions of the Japanese mothership fishing area. *A* = estimates of stock composition from Myers et al.'s (1984) discriminant analysis of scale characters; range of values for brood years 1971-77. B - estimates of stock composition from Ito et al.'s (1985, 1986) discriminant analysis of scale characters; range of values for different assumptions about Asian stock origins; brood year 1970. *C* - estimates of stock composition from Myers's (1986) discriminant analysis of scale characters; range of values for different assumptions about Asian stock origins; brood years 1973, 1974, and 1976

centage of the population in the western North Pacific Ocean (Figure 27).

Summary of Ocean Distribution of Chinook

Despite the many extensive and intensive investigations that have been conducted, our understanding of the ocean migratory and distribution patterns of chinook is still very sketchy. Information on the distribution of ocean-type populations has been derived almost exclusively from the intensive ocean troll fisheries off Oregon, Washington, and British Columbia. Nevertheless, the relatively small number of recaptures of southern British Columbian and Columbia River chinook in southeastern Alaska, where there is an active troll fishery, suggests that most ocean-type chinook do not disperse more than about 1,000 km from their natal river. Some go much further, of course, as revealed by the recaptures from south of the Aleutian chain and in the southeastern Bering Sea. All recaptures to date are from near the coast, and the dispersal of ocean-type populations offshore is revealed only in catches by Canadian research vessels fishing in the eastern North Pacific Ocean. The low catches of chinook in this part of the North Pacific Ocean, and the low proportion of ocean-type chinook among the few that were cap-

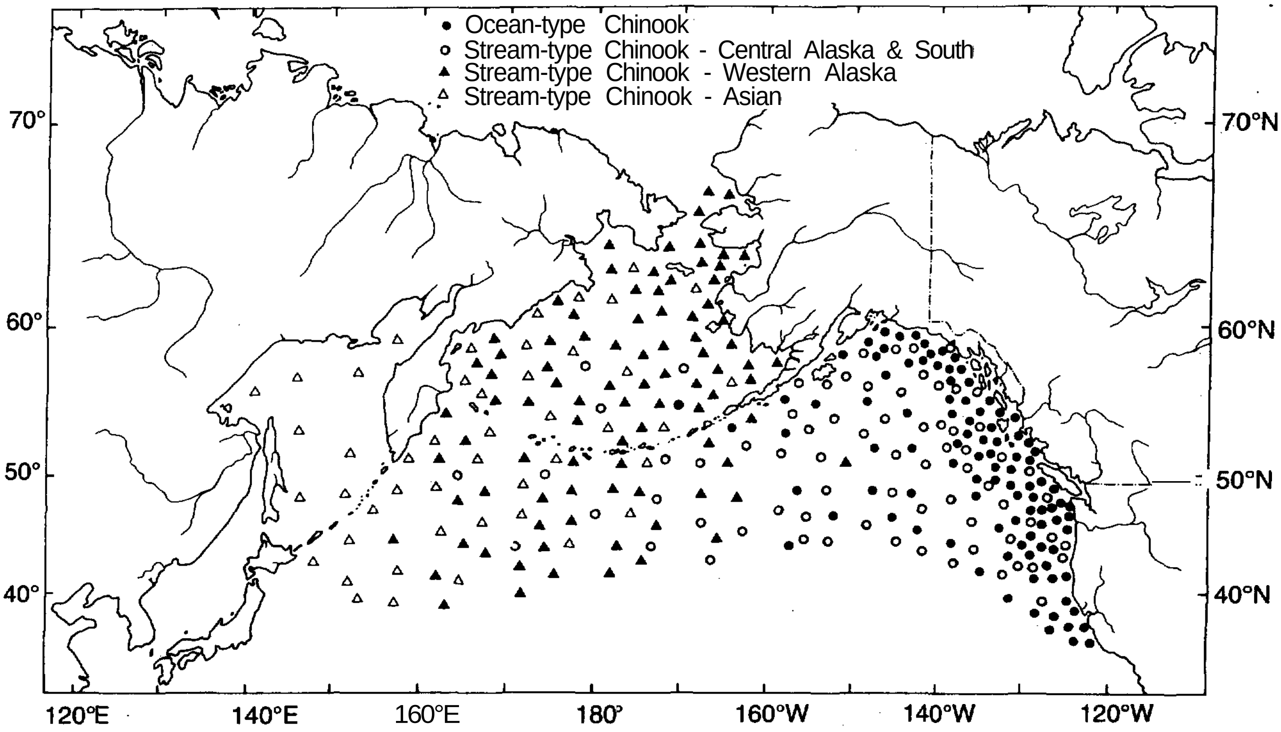


FIGURE 28

The likely ocean distributions and relative abundance in different parts of the North Pacific Ocean and Bering Sea of ocean- and stream-type chinook from various regions of the North American and Asian coasts. Stream-type chinook from western Alaska include Canadian Yukon River chinook. See text for details regarding the basis of these distributions and difficulties with the data.

tured, suggests that ocean-type chinook do not often wander far from shore (Figure 28) or that they are found at greater depths than those fished by the research vessel gear.

The dispersal of stream-type chinook appears to be much broader, as revealed by their contribution to both coastal and high-seas catches. Recaptures of tagged stream-type chinook from the Columbia River in coastal troll fisheries show greater dispersal of this race, both north and south of the river mouth, than of ocean-type populations. The high contribution of stream-type fish to the high-seas catches throughout the North Pacific Ocean and Bering Sea further indicates much greater offshore dispersal of this race (Figure 28).

The high-seas distribution of stream-type chinook from different regions of the North American coast and Asia is a matter of considerable debate. Nevertheless, I believe a few speculations may be made about such distributions, with the understanding that these will be subject to modification as more information becomes available.

Asian chinook are probably distributed throughout the Bering Sea but are also probably concentrated west of 180°. In the northern North Pacific Ocean they appear to be distributed at least as far east as 175°W, and probably further, and to be relatively more abundant in the western North Pacific Ocean than in the Bering Sea. The southern limit of their distribution is not known but is at least 40°N latitude and perhaps further south (Figure 28).

Western Alaskan chinook (including Candian Yukon chinook) are also distributed throughout the Bering Sea. Chinook are probably much more abundant in western Alaska than in Asia, so that chinook from western Alaska tend to dominate Bering Sea catches, even in the western half of the sea. Alaskan chinook are, nevertheless, probably relatively more abundant in the eastern and central than in the western Bering Sea. Western Alaskan chinook apparently also migrate south of the Aleutian chain into the North Pacific Ocean. The limits of their distribution there are not known, but they may occur as far westward as 160°E, and probably extend considerably east of 175°W. Western Alaskan chinook may also be distributed as far south as 40°N (Figure 28). I believe that western Alaskan chinook will ultimately be shown to have a very wide distribution in the western North Pacific Ocean, but they are probably no more abundant than Asian chinook in these waters (Knudsen et al. 1983; Myers et al. 1984) (Figure 27).

Central Alaskan chinook are also probably widely distributed in the central and western North Pacific Ocean and Bering Sea (Figure 28). As I noted earlier, the relative abundance of central Alaskan chinook in these waters is controversial. I suspect that they will ultimately be shown to be less abundant than Asian chinook in the Bering Sea and western North Pacific Ocean.

Southeastern Alaskan/British Columbian chinook appear to be relatively rare in both the Bering Sea and the western North Pacific Ocean, at least on the basis of scale analysis (Figure 27). Since virtually all chinook captured in the Bering Sea and western North Pacific Ocean are stream-type, any fish of the southeastern Alaskan/British Columbian stock grouping captured there must have been of the stream-type race. The southeastern Alaskan/British Columbian chinook, as well as those from Washington, Oregon, and California, are probably distributed mainly in the eastern North Pacific with the greatest concentrations over the continental shelf waters along the North American coast (Healey 1983).

Ocean Food Habits

Most data on food habits of chinook in the ocean are from samples taken in the commercial fishery and, therefore, relate to larger fish. Healey (1980a), however, reported on the diets of chinook of 10-30 cm fork length captured in the Strait of Georgia in late summer, 1975 and 1976. Small fish, particularly herring, pelagic amphipods, and crab megalopa made up between 70% and 92% of the diet, with fish being the largest single contributor at 28%-63% of the diet. Adult insects were also important in the diet of chinook captured in 1976 but not in 1975. There was evidence for regional variation in diet within the Strait of Georgia in that fish composed about 79% of stomach contents in the Gulf Islands region but only 37% in the Fraser River plume and central region of the Strait of Georgia. Pelagic amphipods were relatively unimportant in the Gulf Islands region but constituted 24% of stomach contents in the Fraser River plume and 14% of stomach contents in the central Strait of Georgia. Crab megalopa increased in importance from 11.5% of stomach contents in the Gulf Islands region to 46.4% of stomach contents in the central Strait of Georgia. Insect adults were only important in the Fraser River plume.

For larger chinook, diet information is available from southeastern Alaska south to the California coast. The data span a number of years and times of year and thus provide evidence for regional, annual, and seasonal changes in diet. Techniques of data collection and analysis have not been consistent among investigators, however, so that quantitative comparisons must be viewed with caution.

Reid (1961) described the diet of chinook captured in the troll fishery off southeastern Alaska in 1957 and 1958. Stomachs were sampled from mid-June to mid-September. The volume of stomach contents was measured, and organisms were identified taxonomically and counted. Thirteen different taxa were identified in the stomachs, but by far the most important diet item was herring (60%-68% of volume). There were some indications of differences in diet between years. For example, squid were about ten times as common in the diet in 1958 as in 1957, whereas fishes other than herring were much more important in 1957. There was also an indication that squid were more important in sheltered inside waters than in the more open water fishing areas. The importance of herring relative to other foods was related to size of chinook, increasing from less than 20% of diet for chinook less than 64 cm to more than 60% for chinook more than 100 cm in length.

Pritchard and Tester (1944) and Prakash (1962) described the diet of chinook salmon in British Columbian waters. In both studies, samples were collected from the commercial fisheries. Pritchard and Tester (1944) sampled from the whole coast during 1939-1941, whereas Prakash (1962) sampled only the west coast of Vancouver Island, the Juan de Fuca Strait, and the Fraser River estuary. Contribution of various taxonomic groupings to diet was estimated as a percentage of the total stomach volume in both studies.

Pritchard and Tester (1944) recorded 21 different taxonomic groupings in the diet of chinook during the three years of sampling. Fish of various sorts, but especially herring and sand lance (*Ammodytes hexapterus*), dominated the diet. Invertebrate taxa never exceeded 6% of the diet. Some between-year variation in diet was evident, most notably in the absence of pilchards (*Sardinops caerulea*) from the diet in 1939 and their relative importance in 1940 and 1941. This change appeared correlated with the strength of the pilchard stocks in southern British Columbia. Regional variation in diet was also apparent but chiefly in the alternation in relative importance of sand lance, herring, and pilchards. Off the northwest coast of the Queen Charlotte Islands, for example, herring and sand lance were almost equal in importance and pilchards were unimportant. On the northern mainland coast, herring were relatively important only in 1939 and were replaced by pilchards in 1940 and 1941. Off the northwest coast of Vancouver Island, sand lance predominated, constituting about 70% of the diet. Various invertebrates were also sometimes important in this region. On the southwest coast of Vancouver Island, herring predominated together with pilchards in 1940 and 1941. In 1939, sticklebacks were important (presumably replacing pilchards). In the northern Strait of Georgia, herring was the dominant food; and in the southern Strait of Georgia, pilchards were dominant. These regional differences in diet are unlikely to reflect patterns of dietary preference among regions. Rather, they probably reflect the relative abundance of potential prey between regions and years. Pritchard and Tester (1944) were of the opinion that chinook were largely opportunistic feeders. Apart from the Chinook's apparent preference for fish as prey, this interpretation is probably correct.

Prakash (1962) found herring to be the most important diet item of chinook off southern Vancouver Island (72.5% of the diet). Larger herring were taken off the west coast of the Island than off the east coast (13-23 cm compared with 5-10 cm). As Reid (1961) noted in Alaska, large chinook tended to have a higher percentage of herring in their diets than did small chinook. Consequently, stomach samples from the west coast of Vancouver Island, which were from larger chinook, indicated a higher proportion of herring in the diet than stomach samples from the east coast of the island. Invertebrate food organisms (mainly euphausiids) dominated the diet of chinook from the east coast of Vancouver Island in May and June, but otherwise there was no evidence for significant seasonal changes in diet.

Robinson et al. (1982) reported on the stomach contents of 27 chinook captured in the Qualicum River area of the Strait of Georgia during April and May, 1981. They ranged from 29 to 72 cm in length. Their principal diet items were chum salmon fry, larval herring, sand lance, euphausiids, and adult herring. This is a rare instance in which predation by chinook upon the juveniles of another salmon species has been documented.

Silliman (1941) reported on the diet of chinook captured by trolling off the coasts of Washington and Vancouver Island in 1938. Stomach contents were measured gravimetrically. Herring dominated the diet of chinook captured off Vancouver Island (Pritchard and Tester 1944; Prakash 1962), but euphausiids dominated off Westport, Washington (43% of the diet). Fish of various sorts still made up most of the diet in the Westport area, but no one species overshadowed the rest.

Heg and Van Hyning (1951) described the diet of chinook captured by trolling off the Oregon coast in 1948-50 and of chinook captured by sports fishermen in 1950. Clupeids and clupeid remains dominated the diet, and anchovies (*Engraulis mordax*) were the most important single species. Invertebrates (predominantly euphausiids) constituted only 4%-5% of the diet.

Merkel (1957) reported on the diets of chinook captured in the ocean sport troll fishery off San Francisco. Sampling extended from February to November, and samples were adequate to permit monthly comparisons of diet as well as comparison by size of fish and location of capture. Northern anchovy (29.1%) and various juvenile rockfishes (22.5%) were the most important diet items, although euphausiids (14.9%) and herring (12.7%) also contributed significantly. Seasonal variations in diet were dramatic. Anchovies dominated the diet from August to November, rockfishes during June and July, and herring in February and March.

During April and May, invertebrate foods, especially euphausiids but including squid and crab megalopa, were dominant. The importance of invertebrate foods in April and May, but also to some extent in June, is reminiscent of Prakash's (1962) observation that invertebrates dominated the diet of chinook off southeastern Vancouver Island in May and June.

Diet was also related to location of capture (Merkel 1957). In water shallower than 20 fm (38 m), anchovies dominated (91%-92% of diet). In water deeper than 20 fm (38 m), rockfishes dominated (71%-74%); but a wider variety of organisms occurred in stomachs, and herring and euphausiids were significant diet items. Anchovies were less than 5% of the diet of chinook taken over deep water and rockfishes less than 1% of the diet of chinook taken in shallow water. *As* other authors have observed, small chinook fed more heavily on invertebrates than large chinook. Chinook less than 25 in. (63 cm) long captured near the Farallon Islands (California) had 85% invertebrates in their stomachs, whereas chinook more than 25 in. (63 cm) long had only 52% invertebrates in their stomachs.

Viewed together, the coastwide data on chinook diet suggest some regional trends (Figure 29). In general, the importance of herring and sand lance increases from south to north, whereas the importance of rockfishes and anchovies decreases. These trends probably reflect the relative abundance of the prey along the coast. Pilchards were important in the central parts of the chinook's range prior to the collapse of the pilchard stocks. More recent observations suggest that pilchards are not important in the diet of chinook at present, but that anchovies are more important further north than is indicated by the historic data. Euphausiids are important from time to time, and there is no clear geographic trend for their importance. Other prey items are incidental. The importance of fish in the diet of chinook is apparent in virtually all studies and, in fact, chinook appear to be the *Oncorhynchus* species most dependent on fish as food (Healey 1976).

Not only are seasonal and regional variations in diet composition apparent but so are seasonal and regional variations in feeding intensity. Healey (1982c) found that the weight of stomach contents of first ocean-year chinook in the Strait of Georgia ranged from 0.4%-1.73% of body weight between regions and years of sampling. Stomach contents tended to be highest in areas where catch was highest, suggesting that the young chinook were congregating in good feeding areas. For commercial-sized fish, Prakash (1962) found that stomach contents were greater off the west coast of Vancouver Island than off the east coast during May to September, and that contents tended to be greatest in August (Figure 30). The percentage of stomachs with food was uniformly high (greater than 80%) among troll-caught fish, except for samples from the west coast of Vancouver Island and the Juan de Fuca Strait in September. Chinook sampled from the Fraser River gillnet fishery had little in their stomachs, and the percentage of stomachs with food declined from about 50% in July to 0% in October. Stomach contents of chinook captured off the west coast of Vancouver Island and coastal Washington during April-October 1938 ranged from 0.1 to 63.7 g/fish (Silliman 1941). Contents increased during the sampling period off the west coast of Vancouver Island but decreased off the coast of Washington (Figure 30). Silliman (1941) found a significant relationship between salmon troll catch and the weight of fish in the diet of chinook. He interpreted this to reflect the relative attractiveness of troll lures, which mimic prey fishes, during periods when the chinook were feeding on fish. Finally, Merkel (1957) observed that stomach contents of chinook off California were least in spring and fall and greatest in early summer (Figure 30).

Although highly variable, the data on stomach contents suggest that chinook feed most actively in spring and summer. They also suggest that the best feeding periods are during July and August off southwest British Columbia but earlier, during April to June, from Washington to California. These differences in seasonal feeding patterns may, in turn, reflect the differences in diet along the coast described earlier (e.g., the greater importance of anchovy and rockfishes south of Washington and the greater importance of herring and sand lance north of Washington).

Ocean Growth

Healey (1980a) and Miller et al. (1983) provided data on the growth of chinook salmon during their

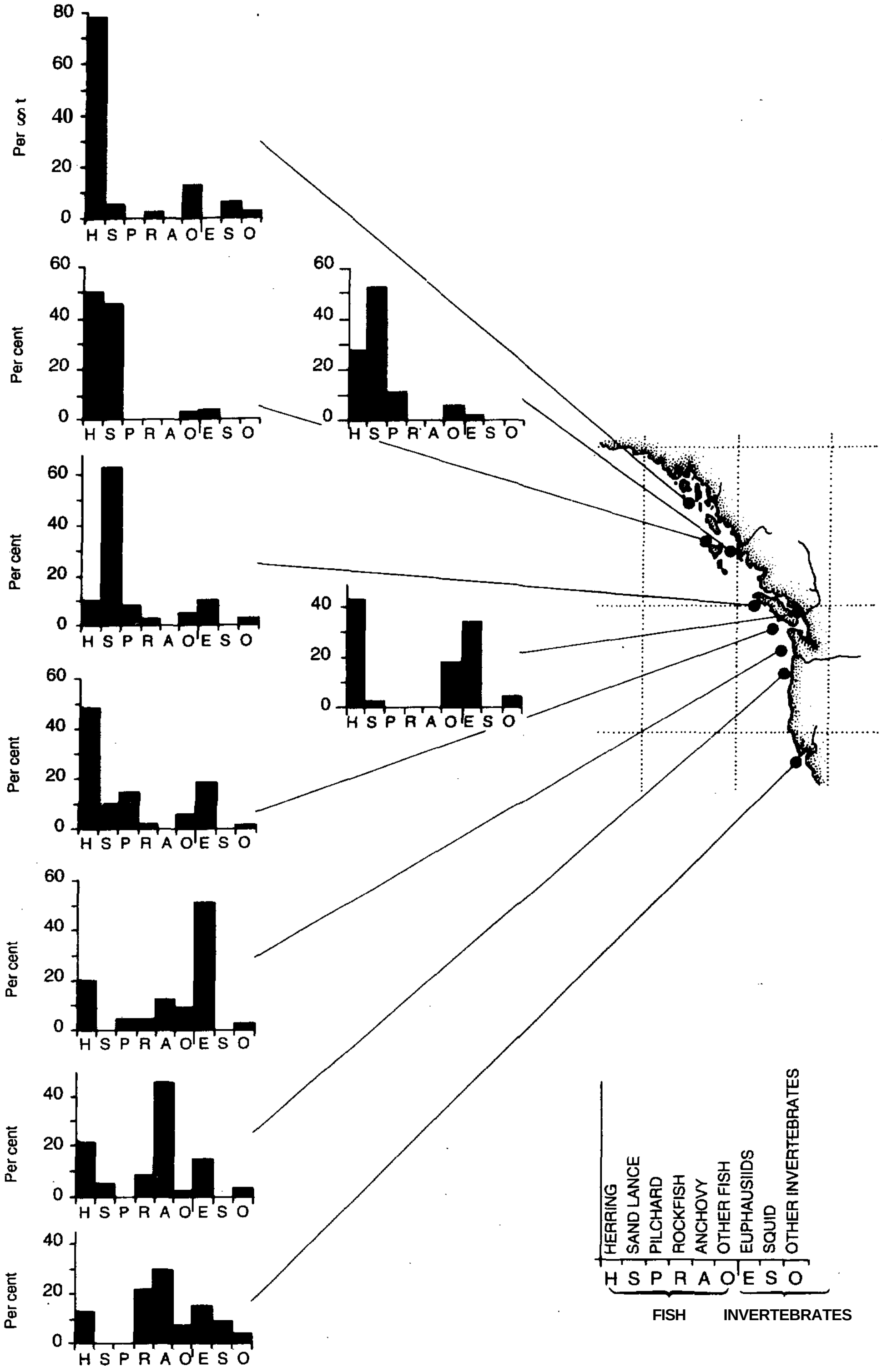


FIGURE 29
Diet composition of chinook from southeastern Alaska to California

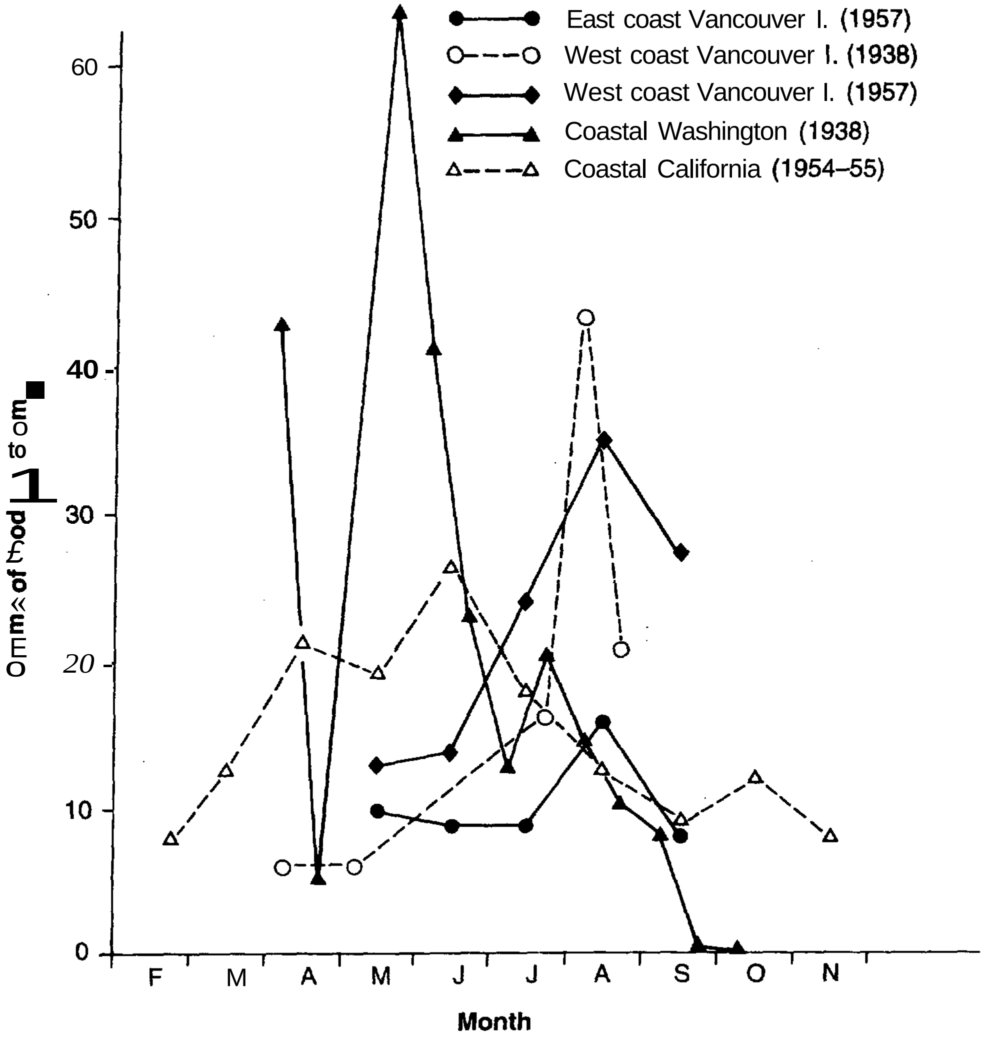


FIGURE 30

Seasonal changes in the weight of stomach contents" of chinook captured off Vancouver Island, Washington, and California

first summer at sea. For chinook in the Strait of Georgia in 1976, modal size groups increased in length by 0.75-0.85 mm/d. Chinook captured off the Washington/Oregon coast in May-September 1980 increased in length by 1.74 mm/d. These data must be interpreted cautiously, as there is little likelihood that the same cohort of chinook was sampled throughout the time series of sampling in either study. In particular, the increase in length of chinook off the Washington/Oregon coast seems high. By comparison, chinook sampled by Fisher et al. (1984) in the same area showed little increase in mean length (0.3 mm/d).

Loeffel and Wendler (1969) summarized the known information on growth of chinook at sea based on time series of samples from a single location and on back-calculations from scales. Figure 31, adapted from their report, represents a composite picture of growth of stream- and ocean-type races. The data suggest a definite seasonal pattern of growth in both races, with rapid summer growth and slow winter growth. Faster growing fish mature at a younger age as is clearly shown by the back-calculated lengths of fish that matured at

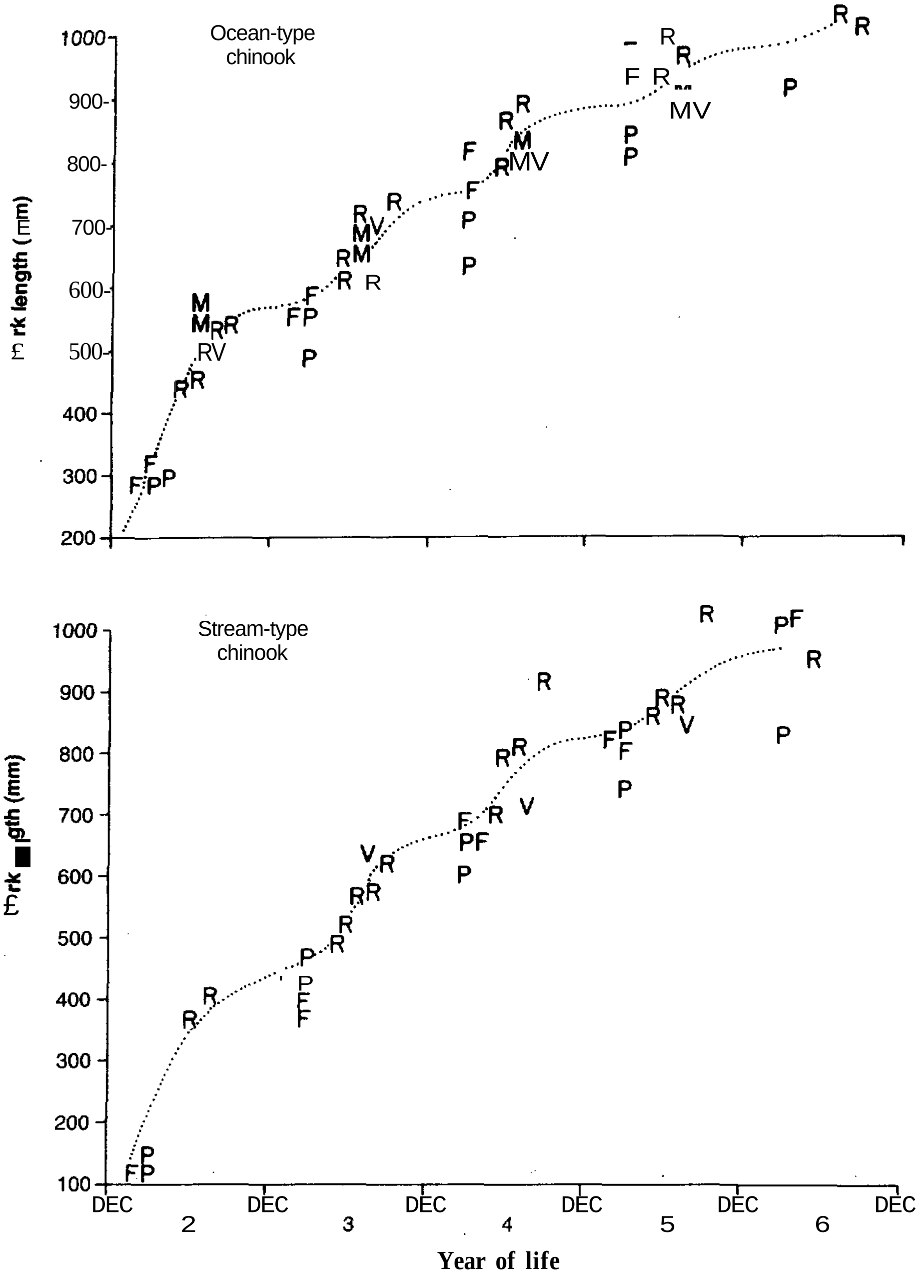


FIGURE 31

Growth curves (fork length at age) for ocean- and stream-type chinook. Letters refer to data from different sources. (Adapted from Loeffel and Wendler 1969)

different ages (Figure 32). Grachev (1967) observed the same pattern in Kamchatka River chinook, and Neilson and Geen (1986) observed that age at maturity was negatively correlated with the size of chinook at the end of their first year in the ocean. The apparent seasonality of growth (Figure 31) may be accentuated, therefore, by the disappearance from the ocean population each summer and autumn of the larger members of each age class that are returning to fresh water to spawn. Ocean-type chinook are larger than stream-type chinook at every calendar age. This is because the stream-

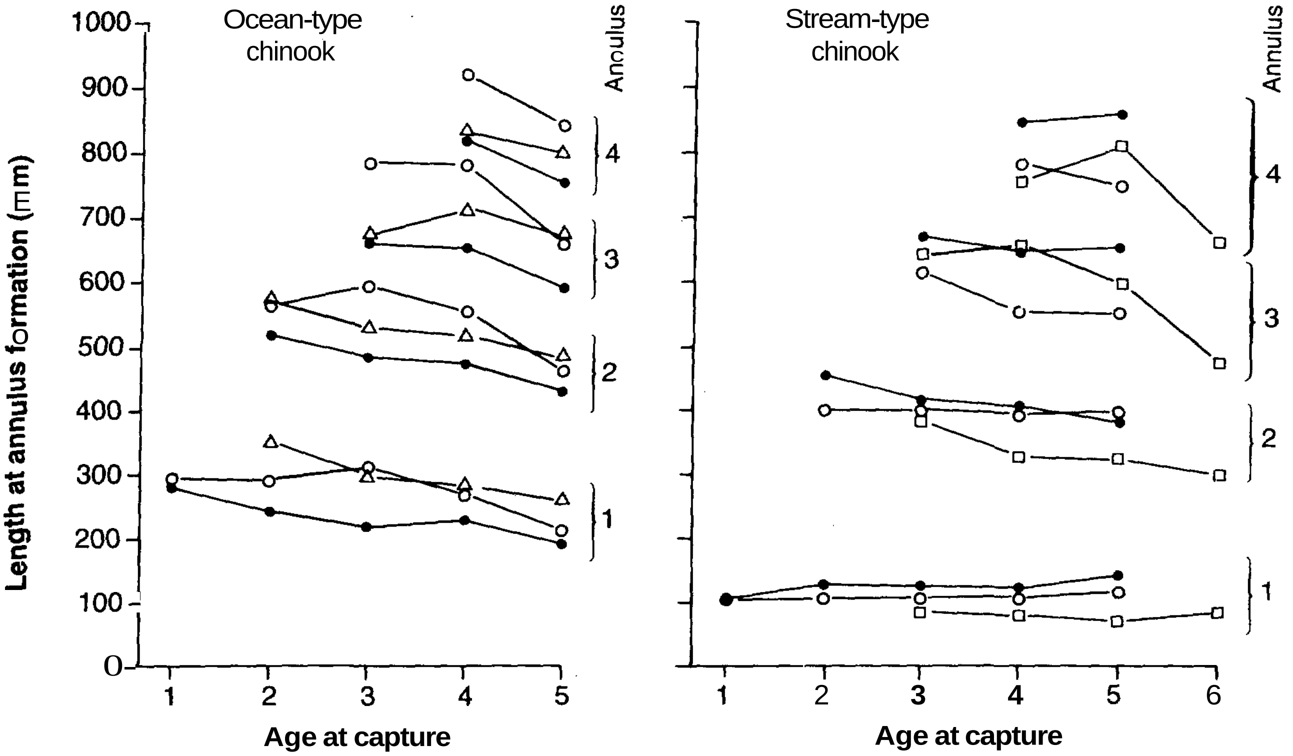


FIGURE 32
Length at annulus formation for ocean- and stream-type chinook which mature at different ages. Data from southeastern Alaska (●), Strait of Georgia (o), west coast of Vancouver Island (A), and the Fraser River (□)

type fish grow more slowly than ocean-type during their first year of life. Rates of growth of the two races during ocean life are similar (Figure 31).

Taken at face value, the available data suggest that, for North American populations, length at age is greater in the south than in the north (Figure 33). The data are a little difficult to interpret, however, as the Alaskan samples were from the ocean troll fishery and include many immature fish, of which some would be from Fraser River, Columbia River, and other, more southern stocks (Figures 22-24) (Parker and Kirkness 1956). Size at age of Kamchatka River chinook was similar to chinook caught off southeastern Alaska (Grachev 1967), whereas on the basis of latitude I would have expected them to be more similar to Yukon River chinook. Also, the growth rates of fish aged two to six years are similar for all areas sampled (0.35-0.57 mm/d). In fact, the Columbia and Sacramento River populations of both races had the slowest growth rate over the ages two to six years. The differences in size between regions are entirely due to differences in size at age 0.1 in ocean-type chinook or age 1.1 in stream-type chinook. Conceivably, the differences in size at these ages could be due to differences among investigators in interpretation of annuli. Chinook are notoriously difficult to age from scales (Godfrey et al. 1968). Conversely, it is possible that growth during the first ocean year differs dramatically along the coast. The apparently greater growth of first ocean-year fish off the Columbia River, compared with those in the Strait of Georgia (see earlier), is consistent with this explanation.

Grachev (1967) reported back-calculated growth increments for Kamchatka River chinook spanning 23 brood years, from 1933 to 1955. The most complete samples were of males representing ages 1.2, 1.3, and 1.4. Mean lengths in the year of migration varied from 58.3 to 70.4 cm for fish aged 1.2, and from 72.7 to 88.5 cm for fish aged 1.3. Total length was most closely correlated with the length incre-

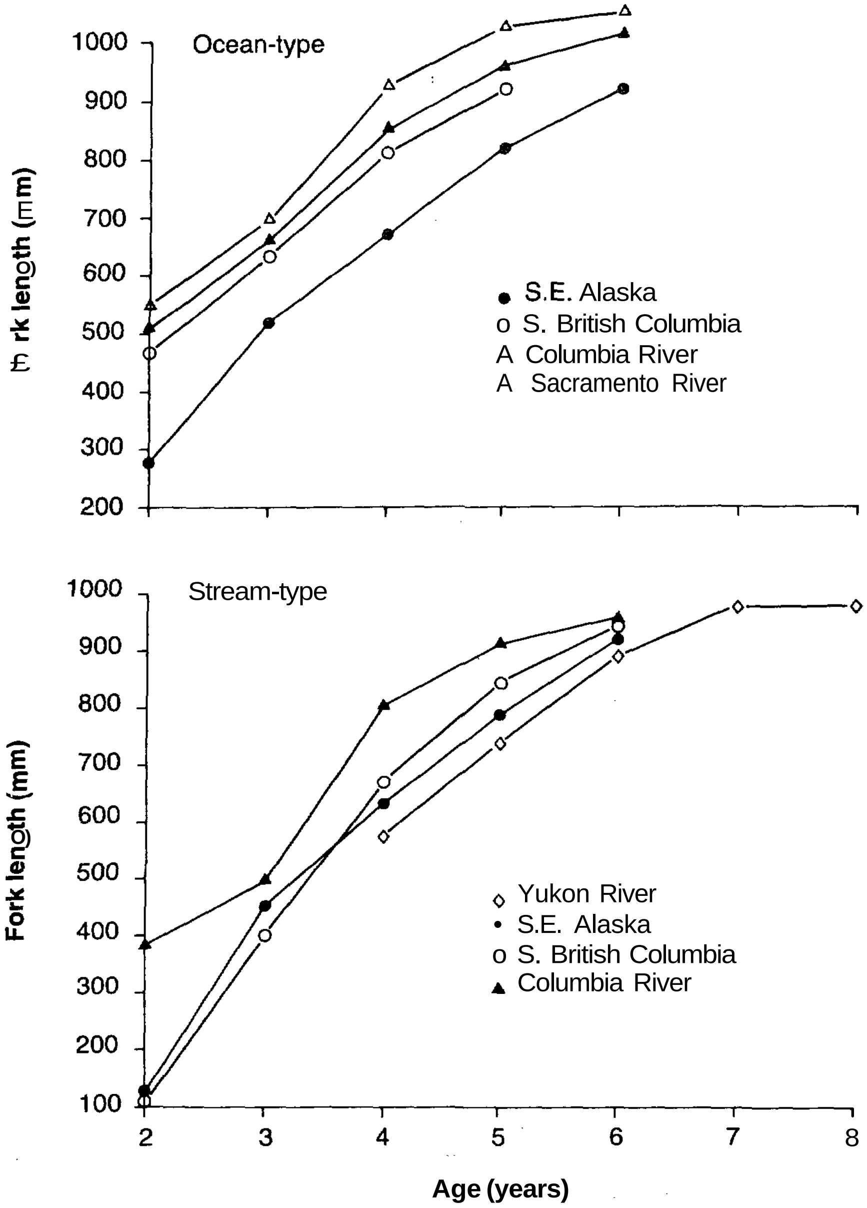


FIGURE 33

Length at age for chinook captured in the southeastern Alaska troll fishery and rivermouth fisheries in southern BC and the Columbia and Sacramento rivers

ment laid down during the final ocean year, suggesting that feeding conditions during this last year at sea were most important in determining final adult size of each age class.

All of the above analyses of growth are incomplete and superficial because they do not take fully into account the complex interrelationships among growth, migration, and maturation in chinook. Samples taken in ocean fisheries consist of representatives of numerous spawning stocks. The younger fish in a sample will be mainly from nearby spawning populations and the older fish, mainly from distant spawning populations. For chinook older than the age of first maturity, those remaining at sea will be the smaller, slower growing component of any spawning stock. Samples taken on the spawning grounds suffer from the opposite problem. The spawning fish in the younger age groups will be the faster growing members of the age class. Any model of growth for chinook must take account of these phenomena. Current data are inadequate for the task. More recent tag recovery data may prove sufficient, but these data are as yet largely unanalysed.

MATURATION AND RETURN TO SPAWN

As was the case with growth rate, estimating age-specific rates of maturity in chinook is *a* complex problem. Again, current data are inadequate for the task. Three approaches have been taken to date:

1 The proportion of each age class in samples captured at sea that will mature in the year of capture is determined from gonad/body weight ratios or egg size (Rich 1925; Borque and Pitre 1972; Wright and Bernhard 1972; Ito et al. 1974; Baranski 1979).

2 Maturity schedules are estimated from tag returns (Parker and Kirkness 1956; Cleaver 1969).

3 Maturity schedules are inferred from the age composition of spawning runs (various authors, but see Godfrey 1968a; Loeffel and Wendler 1969; Hankin and Healey 1986).

Mature chinook captured on the spawning grounds range from 0.1 to 0.5 in age for ocean-type stocks and from 1.0 to 2.5 for stream-type stocks. Not all populations have all ages, however, and most populations are dominated by a few age classes. Two examples of age-frequency curves will suffice to illustrate the differences between systems, races, and sexes (Figure 34). In the Yukon River (Brady 1983), which has only stream-type chinook, six-year-old fish of both sexes predominate in the spawning run. Males dominate the younger ages (ages 4 and 5), however, and females the older ages (ages 7 and 8). In the Fraser River, which has both stream- and ocean-type fish (Godfrey 1968a), four-year-old fish predominate in the run, and this is the most abundant age class for male and female ocean-type and male stream-type chinook. Female stream-type fish were most abundant at age 5. For both races, males were more common among the younger fish, and females among the older fish.

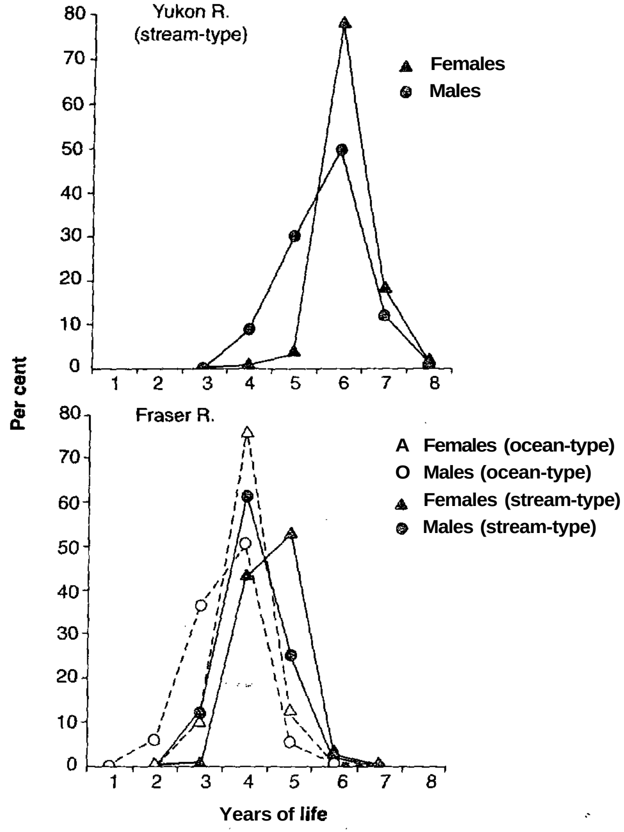


FIGURE 34

Composition by age (as a percentage) of spawning runs to the Yukon and Fraser rivers for ocean- and stream-type chinook

The average age of mature male ocean-type chinook ranged from 3.02 to 3.88 years in river systems for which comparative data exist, and from 3.98 to 4.32 years for mature female ocean-type chinook (Table 7, see table for references). For stream-type chinook, the range was from 3.69 to 5.64 years for males and from 4.39 to 6.12 years for females (Table 7). Thus, males mature at a younger average age than females, regardless of race. The difference in age between males and females was small in some instances (0.1 y) but in other instances it was large (1.3 y) (Table 7). From the Sacramento River (37°45'N) to the Nass River (55°00'N) there was no consistent trend in the age of maturity among sexes and races. There was a weak positive correlation between age and latitude for stream-type females and a weak negative correlation between age and latitude for ocean-type males, but neither correlation was significant. North of the Nass River, however, and in Kamchatka, chinook appear to mature about a year older, on average (Table 7). Thus, the stream-type races, at least on a geographic scale, have a longer generation time than the ocean-type, presumably owing to their longer freshwater residence.

The standard deviation of age at maturity for males ranged from 0.601 to 1.058, with no consistent geographic or racial trend. For females, the standard deviation of age at maturity ranged from 0.206 to 0.698, again with no consistent racial or geographic trend. The variation in male age of return was, therefore, consistently larger than the variance in female age of return. This trend is reflected in the high percentage of females returning to spawn at a single age, compared with males (Figure 34).

The age composition of spawning runs provides a measure of the ages over which chinook mature but gives only a rough indication of age-specific maturation rates. These latter rates depend not only on a knowledge of the number of mature fish in each age group but also on the number of immatures. Such data are provided by sampling populations at sea and assessing the proportion of maturing fish in each age class, and by analysing tag returns to estimate both mortality and maturity rates.

On the basis of tag returns from Columbia River hatchery chinook, Cleaver (1969) estimated maturation rates at various ages for the 1922 brood year, 1954-55 brood years, and the 1961 brood year. Rates of maturation ranged from 1% to 5% for chinook in their second year, from 18% to 35% for chinook in their third year, from 61% to 96% for chinook in their fourth year, and were 100% for chinook in their fifth year (Table 8). There was evidence for a greater proportion of mature fish among the youngest age groups in recent years.

On the basis of tag returns from ocean tagging off southeastern Alaska, Parker and Kirkness (1956)

TABLE 7

Mean age (years) and standard deviation of age for mature stream- and ocean-type chinook from rivers throughout the geographic range of the species

River	N. Latitude	Race	Mean age		Standard deviation		Source
			Male	Female	Male	Female	
Sacramento	37°45′	Ocean	4.18		0.779		Clark (1929)
Klamath	41°30′	Stream	4.40	4.60	0.764	0.592	Snyder (1931)
		Ocean	3.88	3.98	0.618	0.458	
Columbia	46°15′	Stream	3.98	4.39	0.667	0.547	Rich (1925)
		Ocean	3.55	4.29	1.058	0.698	
Fraser	49°15′	Stream	4.13	4.56	0.601	0.563	Godfrey (1968a)
		Ocean	3.59	4.00	0.732	0.206	
Skeena	54°15′	Stream	4.13	4.56	0.677	0.485	Godfrey (1968a)
		Ocean	3.47	4.19	0.827	0.441	
Nass	55°00′	Stream	3.69	4.82	0.876	0.405	Godfrey (1968a)
		Ocean	3.02	4.32	0.745	0.476	
Taku	58°30′	Stream	5.29		0.539		Kissner (1973)
Yukon	62°31′	Stream	5.64	6.12	0.803	0.425	McBride et al. (1983)
Kamchatka	56°00′	Stream	5.39		0.618		Vronskiy (1972)

Note: Sexes not distinguished in Sacramento, Taku, and Kamchatka rivers

TABLE 8
Age-specific maturity schedules (proportion maturing at age) for male and female ocean-type chinook as calculated by various authors for various times and locations

			Age				
Location	Year(s)	Sex	2	3	4	5	Source
Columbia R.*	1922	male/female	0,009	0.181	0.754	1.000	Cleaver (1969)
	1954-55	male/female	0.050	0.350	0.610	–	
	1961	male/female	0.009	0.338	0.959	1.000	
Wash. coast†	1972	male	0.300	0.700	0.990	1.000	Wright & Bernhard (1972)
		female	0.030	0.490	0.990	1.000	
Puget Sd.†	1975-77	male	0.120	0.480	0.950	-	Baranski (1979)
		female	0.030	0.240	0.950	–	
Vancouver Is.†	1967-70	male	0.360	0.440	0.700	–	Borque & Pitre (1972)
		female	0.020	0.120	0.630	–	
S.E. Alaska*	1950-52	male/female	–	0.320	0.545	0.905	Parker & Kirkness (1956)
Columbia R.‡	1919	female (S)§	0.000	0.000	0.770	0.960	Rich (1925)
		female (O)§	0.000	0.150	0.870	1.000	

Notes: *Results based on tag recaptures
†Results based on ocean sampling and maturity indices
‡Results based on analysis of egg size
§S - stream-type; O - ocean-type

estimated maturity rates for chinook aged three to five years that were similar to, but slightly lower than, Cleaver's (1969) estimates for 1954-55 brood year Columbia River chinook.

Unfortunately, the tag-return data analysed by Parker and Kirkness (1956) and Cleaver (1969) do not permit separate estimates of maturity rate for males and females. Estimates based on maturity indices for fish captured in the ocean do, however, permit separate estimates of maturity by sex. These estimates are consistent with the maturation pattern established from spawning runs in that males show a greater proportion maturing at a younger age than do females (Table 8). Maturity rates of 12%-36% were observed among males in their second year of life, as were maturity rates of 0%-3% for females in their second year and 0%-49% for females in their third year. Although two-year-old jack males are common in some populations, maturity rates of 12%-36% for this age group, as a general proposition, are unlikely, as that would mean two-year-old males would be a dominant age group among mature males in spawning runs to most rivers rather than a minor component (Figure 34). Similarly, two-year-old mature females are virtually unknown, and three-year-old mature females are uncommon in spawning runs except in a few Oregon stocks (Nicholas and Hankin 1988); yet the maturity rate estimates from gonad size indices (Wright and Bernhard 1972; Borque and Pitre 1972; Baranski 1979) suggest that two-year-old mature females should be relatively common and that three-year-old mature females should be a dominant component of spawning runs. Rich's (1925) estimates of female age-specific maturity rates, which are based on egg size rather than gonad size, seem much more appropriate, as they indicate no maturation of two-year-old females, 15% maturation among three-year-old ocean-type females, and high rates of maturation among four- and five-year-old females of both ocean- and stream-type races. Also, the patterns of maturity among stream- and ocean-type females described by Rich (1925) are consistent with the pattern observed in spawning runs (Figure 34). Even Rich's (1925) estimates, however, produce run age-composition estimates that include too many young fish in comparison with observed run compositions. Clearly, there is some fundamental problem with the commonly used indices of maturity for fish captured in the ocean, or the samples that have been analysed to date are not representative of the general maturity schedules for chinook. One possible factor contributing to the apparent high proportion of maturing fish in the ocean samples off southwest Vancouver Island, Washington, and in Puget Sound may be the observation by Ito et al. (1974) and Major et al. (1978) that maturing fish constitute a higher proportion of the nearshore catch of chinook. However, this alone is not a sufficient explanation for the high proportion of maturing fish in the younger age groups, particularly the observed numbers of maturing two- and three-year-old females.

Although most chinook do not mature until they have spent at least one summer at sea, a few male chinook may mature without migrating to sea (Rutter 1902; Rich 1920; Burck 1967). Such males may mature at the end of their first summer or, more commonly, after their second summer in fresh water. It is generally the largest males in any sample that show evidence of maturity (Rich 1920). This phenomenon is documented for the Columbia and Sacramento rivers, but probably occurs elsewhere as well. The proportion of stream-dwelling males that become mature is unknown, but Rich (1920) noted that 10%-12% of males in the McCloud River, California, which were stream-resident, matured precociously.

Precocious maturation of males is associated with stream-resident populations in headwater tributaries, suggesting that it is a characteristic of stream-type chinook. It is not known whether precocious males contribute to reproduction, although J.W. Mullan (u.s. Fish and Wildlife Service, Leavenworth, Washington, pers. comm.) suggests that they do. They cannot always do so, however, as some mature outside the normal spawning time for sea-run fish. Nor is it known for sure whether precocious males die after maturing. Rich (1920) claimed that at least some recovered, but Burck (1967) found that, of 259 specimens of mature precocious males that he held in a downstream migrant trap, all died. J.W. Mullan (u.s. Fish and Wildlife Service, Leavenworth, Washington, pers. comm.) suggests that most precocial age 0. males survive whereas most precocial 1. males die.

MORTALITY IN THE OCEAN

Estimates of natural and fishing mortality of chinook are derived from several sources. Parker and Kirkness (1956) were apparently the first to attempt such an estimate. Their estimate, based on recaptures of fish tagged off southeastern Alaska, was 34.1% annual mortality for all age classes.

Cleaver (1969) estimated probable values of natural mortality and maturity from recaptures of tagged 1961-brood chinook released from several Columbia River hatcheries. Unfortunately, maturity and mortality are confounded in the data so that it was not possible to estimate either uniquely. According to Cleaver (1969), the most realistic solution to the joint estimate of maturity and mortality occurred when instantaneous annual natural mortality was 0.45 (36% annual mortality). This is very close to the value obtained by Parker and Kirkness (1956).

Henry (1978) explored the mortality and maturity schedules for 1961 and 1962 brood year Columbia River hatchery chinook. His analysis differed from Cleaver's (1969) in that he assumed a fixed maturity schedule and calculated age-specific mortality rates. Henry's (1978) estimates suggested some differences in natural mortality between brood years and much higher natural mortality during the first ocean year than during later ocean years. Although these results are intuitively reasonable, the differences in mortality between brood years could be an artifact of the assumption that maturity was fixed. There seems to be no greater reason for assuming a fixed maturity schedule than for assuming a fixed mortality schedule.

Ricker (1976) reviewed all published approaches to estimating the natural mortality rate of Pacific salmon at sea/discussed their strengths and weaknesses, and assessed their biases. The published estimates of natural mortality for chinook, according to Ricker (1976), are likely to be too large, both because of tag loss and mortality of tagged fish, and because they do not take full account of mortality due to catch and release in some fisheries. This latter uncontrolled mortality source is particularly important for chinook, most of which are captured as immature fish in hook-and-line fisheries, and for which there are size limits that forbid landing small fish. At this point in time, it is impossible to state what is the real natural mortality rate of chinook salmon in the ocean. In all probability, the value is considerably less than 35% per year, probably closer to the value of 20% per year estimated to be a reasonable average for sockeye (Ricker 1976). It is also probable that age-specific mortality declines with age in chinook so that most ocean mortality occurs during the first year or two of ocean life.

The available data are too scanty to determine whether ocean mortality schedules differ among populations. In addition, all of these data refer to the ocean-type race so that no interracial comparison may be made. Parker (1962) argued that it was logical to suppose that causes of mortality (especially predators) were more concentrated in the coastal zone, so that one would expect greater mortality among salmon during their residence in coastal waters. Parker (1962) further argued that smaller salmon should be more vulnerable to predators and should, therefore, suffer greater mortality than larger salmon. If these arguments hold, then ocean mortality of ocean-type chinook should be greater than that of stream-type chinook because stream-type chinook enter the ocean at a large size and move offshore quickly, whereas ocean-type chinook enter the ocean at a small size and spend most of their ocean life in coastal waters. Even if their natural mortality rates do not differ substantially, I would expect fishing mortality to be lower for the stream-type race, at least for stream-type populations on the North American coast south of central Alaska. These populations appear not to contribute substantially to the Japanese high-seas fishery and, because they are distributed further offshore than ocean-type chinook, they do not contribute heavily to the intensive coastal troll fishery (Healey 1983).

HOMING AND STRAYING

Fish that survive to mature and return to fresh water to spawn must select a spawning stream, ascend it (Plate 15), and then select an appropriate spawning riffle. Upstream migration of mature chinook apparently occurs mainly during daylight hours (Plate 16), at least for the ocean-type race (Neave 1943). A few fish, however, do migrate upstream at night.

Salmon, in general, have well-developed homing behaviour, apparently returning to their natal stream to spawn with considerable fidelity. The choice of spawning river, tributary, and even riffle appears to be guided by long-term memory of specific odours. Groves et al. (1968) demonstrated the apparent importance of olfaction for chinook returning to the Spring Creek Hatchery on the Columbia River. They took chinook that had already returned to the hatchery, occluded their olfactory or visual senses, and released the treated (and untreated control fish) twenty or more kilometres downstream and upstream from the hatchery. The results of the study are summarized in Table 9. About 49% of control fish returned to Spring Creek from downstream releases and 37% from upstream releases. This difference was not statistically significant. About 23% of chinook with their vision destroyed found their way back to Spring Creek, significantly fewer than the control fish ($X^2 = 28.7$; $p < .001$). Only 6 of 193 (3%) chinook with their nasal sacs plugged, however, returned to Spring Creek, significantly less than either the controls ($X^2 = 101.8$; $p < .001$) or chinook with their vision destroyed ($X^2 = 46.1$; $p < .01$). Chinook with both vision and olfaction occluded were hardly recaptured at all, but two still found their way back to Spring Creek. The implication of these results is

TABLE 9

Chinook captured at Spring Creek, tagged, and relased upstream and downstream from Spring Creek, and recaptured at Spring Creek, other Columbia River hatcheries, and in river sport and domestic fisheries

	Treatment			
	Control	Olfactory occlusion	Visual occlusion	Olfactory and visual occlusion
Number released downstream	192	152	192	150
Number recaptured at:				
Spring Creek	94	6	46	2
Other hatcheries	45	27	51	1
Fisheries	1	16	0	15
Number released upstream	49	41	49	41
Number recaptured at:				
Spring Creek	18	0	10	0
Other hatcheries	8	1	4	3
Fisheries	1	2	2	3

Source: From Groves et al. (1968)

that both olfaction and vision are important in selection of home stream, but that olfaction is by far the more important sense. In a related study, Hara et al. (1965) demonstrated an electrophysiological response of the olfactory bulb of chinook to infusion with home-stream water, implying recognition of home-stream odour. The interpretation of electrophysiological results has been cast into doubt, however, by Bodznick (1975) who could find no correlation between the electrophysiological response and the actual migratory behaviour of sockeye salmon.

Quite a large number of the fish released by Groves et al. (1968) were recovered at hatcheries other than Spring Creek, even among the control fish. These cannot be regarded as true strays, however, as most of the hatcheries were operating weirs, and once the fish had entered a hatchery stream, they could not get out. Thus, the fish were unable to correct any mistakes in homing. Similarly, the fish originally selected for the study had been "trapped" by a weir at Spring Creek, and some may not really have been Spring Creek fish.

More representative data on straying are provided by Rich and Holmes (1928) and McIsaac and Quinn (1988), who reported on the return of adults, which had been tagged as fingerlings, to various Columbia River hatcheries and tributaries. None of the fish investigated by Rich and Holmes (1928) was released into a tributary from which its parents had come, whereas Mclsaac & Quinn (1988) investigated return rates for transplanted and resident fish. Although all recoveries were made within the Columbia River, Rich and Holmes (1928) found that stream-type chinook showed rather poor fidelity to their particular release tributary. Ocean-type chinook, on the other hand, showed very strong fidelity to their release site. Mclsaac and Quinn (1988) found that chinook from an upriver population transplanted to the Bonneville Hatchery returned poorly to the hatchery and that many recaptures came from well upstream. Control fish, by contrast, homed faithfully. Rich and Holmes (1928) suggested that their results implied a contribution of both heredity and learning to homing behaviour, but also that the suitability of the release tributary for chinook was important. It may also be the case that the time of imprinting to home-stream odour of stream-type chinook is different from that of ocean-type. Since stream-type fish undergo several in-stream migrations during their freshwater life, imprinting to the home stream may occur very early, whereas ocean-type fish may delay imprinting until just before ocean migration. Thus, stream-type fish reared for several weeks in a hatchery before being released into a tributary may not imprint to the tributary. McIssac and Quinn's (1988) results, however, suggest much more strongly that heredity is important.

Detailed information on straying of ocean-type chinook is given by Quinn and Fresh (1984) for fish from the Cowlitz River Hatchery on the Columbia River drainage. These authors found that home-stream fidelity among four brood years of chinook averaged 98.6%, and that most strays were from spawning areas close to the Cowlitz River. Ten chinook, however, were recovered from spawning areas in Puget Sound and the Juan de Fuca Strait. Such long-distance strays, although few in number, could have important consequences for the genetic composition of regional spawning populations. In contrast to the results for the Cowlitz River, Uremovich (1977) reported considerable straying of Elk River hatchery chinook into the adjacent Sixes River.

Among the categories of chinook returning to the Cowlitz River, older chinook strayed more than younger chinook, and males that had spent only one summer at sea were the most faithful of all. These males also returned to the river later in the season than older age classes. The proportion of strays varied among brood years, and the amount of straying appeared to be related to brood year success. Higher straying was observed among brood years with the poorest overall returns, suggesting that conditions that were poor for survival were also poor for home-stream fidelity (Quinn and Fresh 1984). Such a behaviour pattern could be coincidental. It could also be a mechanism to provide for wide distribution of spawners during poor survival years. Uremovich (1977) also reported variation in straying between years but offered no explanation.

CONCLUDING REMARKS

This completes my summary of life history observations on chinook. Throughout, I have highlighted the degree of variation among chinook populations, and, in particular, the important differences between the stream- and ocean-type races. In my view, there is a sufficient basis for separating the species into these two races. As was outlined in Figure 1, the races are distinguished by fundamental ecological differences in (1) the geographic distribution of their spawning populations; (2) the duration of their freshwater residence as juveniles prior to seaward migration and as adults prior to spawning; (3) their oceanic distribution and dispersal; and (4) timing of their spawning migrations. There is also evidence for genetic segregation between these life history types (Healey 1983; Carl and Healey 1984), for morphological differences between juveniles (Carl and Healey 1984), and for the inheritance of migratory timing (Rich and Holmes 1928).

Assuming that there are two races of chinook salmon, one must then ask how these could arise and how they could persist when the races are sympatric. If it were only the case that stream-type chinook occurred in the headwater tributaries of the larger rivers, then one might presume that stream-dwelling behaviour had arisen independently in each river and was maintained through disruptive selection (Merrell 1981). The environmental heterogeneity producing ocean- and stream-type juvenile life history patterns could be related to a critical time of arrival in the ocean, such as that suggested by Walters et al. (1978) for pink and chum fry from the Fraser River. If such a critical time period existed, it could render seaward migration from the headwaters impractical during the first summer because the length of time required for the young fish to grow to smolt size and traverse the river would bring them to sea at a bad time. The spring and summer redistribution migrations of stream-type chinook within the river system correspond in timing with the spring and summer seaward migrations of ocean-type chinook. These within-river dispersals of the stream-type race could be the remnants of the seaward migratory behaviour of the ocean-type race, and suggest that one type may be derived from the other. Some stream-type populations may, in fact, have arisen through disruptive selection in ocean-type populations. In many instances, the different ocean distributions of stream- and ocean-type chinook, their different migratory behaviour while at sea, and the particular geographic distribution of their spawning populations argue against such an explanation for the origin of stream-type chinook. Recent information on genetic differentiation among populations of chinook, however, does not always reveal patterns consistent with a segregation into stream- and ocean-type races (Gharrett et al. 1987; Utter et al. 1989; Winans 1989).

An alternative explanation is that stream-type chinook developed (or persisted) in the Bering refugium, or on the Asian coast, during the last glaciation, whereas ocean-type chinook developed (or persisted) south of the glaciation on the North American coast. With the retreat of the ice, both races could have expanded to occupy their present distributions. Gharrett et al. (1987) suggested that the genetic composition of chinook populations supports this interpretation. For this explanation to hold, however, selection gradients or reproductive isolating mechanisms must be sufficient to prevent introgression in the natural populations, at least where they are sympatric. It is also necessary to postulate some barrier preventing significant invasion of the ocean-type race north of 56°N. Conditions in the freshwater environment might provide such a barrier if, for example, riverine and estuarine productivity and temperature were too low to permit chinook to reach a critical size for smolting during their first summer. Riverine temperatures, at least during the summer growing season, however, appear adequate for good growth (Healey 1983). Although I am confident that the explanation for the absence of ocean-type chinook north of 56°N lies in the trade-off between survival and growth for small chinook in the river versus in the ocean, the precise mechanism preventing northward invasion of ocean- type chinook is not apparent.

These possible explanations, and others, for the existence of stream- and ocean-type chinook need to be critically tested, and they offer an opportunity for fruitful research into the evolution of Pacific salmon. There is no doubt, however, that Pacific salmon have the capability to adapt quickly to new opportunities. The recent appearance in the Great Lakes of spring-spawning chinook, which must have developed from the fall-spawning introduced race, attests to this (Kwain and Thomas 1984), as does the development of even-year runs among pink salmon from a single odd-year release into the Great Lakes (Kwain and Chappel 1978).

Segregating the species into stream- and ocean-type races accounts for only a small part of the interpopulation variation in chinook. There is also considerable interpopulation (within race) and intrapopulation variation that requires explanation (Healey and Heard 1984). Interpopulation variation includes (1) differences in the proportion of the population migrating seaward at different ages (fry or fingerlings for ocean-type chinook, one- or two-year-old smolts for stream-type); (2) differences in the proportion maturing at each reproductive age; (3) differences in growth; and (4) differences in fecundity. Intrapopulation variation involves the same population attributes and leads to a variety of life history tactics within any population. Variation in length of riverine and estuarine residence has attracted considerable attention and has been interpreted as reflecting life history adaptation (Rich 1925; Reimers 1971; Healey 1980b, 1982b; Levy and Northcote 1981). Differences in the relative length of riverine and estuarine residence by chinook in the Sixes River, Oregon, led Reimers (1971) to postulate five life history types of chinook in that system. From analysis of adult scales, Reimers (1971) concluded that only one of these life history types contributed most to the spawning population in the Sixes River. Healey (1980b, 1982b) recognized two distinct behaviour patterns among ocean-type chinook in Vancouver Island rivers: migration to the river estuary immediately after fry emergence in the spring, and migration to the estuary four to six weeks after emergence.

The existence of this degree of variation indicates considerable plasticity in the species. Whether this plasticity is a consequence of genetic polymorphism, or is largely environmentally induced, remains to be demonstrated. Carl and Healey (1984), however, found genetic differences between fry and fingerling migrants in the Nanaimo River on Vancouver Island, suggesting a genetic basis for the two behaviour patterns of ocean-type chinook recognized by Healey (1980b, 1982b).

Despite the apparent biological and ecological plasticity of the species, the possibility that many populations may be specifically adapted to local conditions cannot be discounted on the basis of present evidence. Such adaptation could have produced unique gene pools in some instances through the fixation of successful mutations. Given the intrapopulation variability of chinook, however, it seems more likely that local adaptations are due to the development of effective gene combinations rather than to fixation of mutations. Furthermore, it suggests that chinook should be able to adapt rapidly to new situations. The success of hatcheries in producing chinook on the Pacific coast, and the success of chinook transplants to New Zealand, Chile, and the Great Lakes testify to the adaptability of the species.

The extent of intrapopulation variation further suggests a degree of "bet hedging" in the life history strategy of the chinook salmon (Stearns 1976). Such a tactic may be very appropriate for a species like chinook, which occurs in many small, possibly locally adapted, spawning populations. Having a variety of life history tactics would serve to spread the risk of mortality across a number of habitats and thus reduce the probability of complete failure of a year class. Indeed, this strategy may partly explain why chinook have been able to persist in the face of continued heavy fishing pressure and, in some systems, significant habitat modification.

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