

# PACIFIC SALMON

LIFE HISTORIES

REFERENCE

EDITED BY C. GROOT & L. MARGOLIS

# Pacific Salmon Life Histories

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# LIFE HISTORY OF CHUM SALMON (*Oncorhynchus keta*)\*

E.O. Salo†

## INTRODUCTION

**C**HUM SALMON, *Oncorhynchus keta* (Walbaum), have the widest natural geographic distribution of all Pacific salmon species (Bakkala 1970; Fredin et al. 1977), ranging in Asia from Korea to the Arctic coast of the USSR and west to the Lena River (Laptev Sea), and in North America from Monterey, California, to the Arctic coast and east to the Mackenzie River (Beaufort Sea). Historically, they may have constituted up to 50% of the annual biomass of the seven species of Pacific salmon in the North Pacific Ocean.

Chum salmon are semelparous and anadromous. They spawn successfully in streams of various sizes, and the fry migrate directly to the sea soon after emergence. The immatures distribute themselves widely over the North Pacific Ocean, and the maturing adults return to the home streams at various ages, usually at two through five years, and in some cases at up to seven years (Bigler 1985). All die after spawning. With individuals reported to be up to 108.8 cm in length and 20.8 kg in weight (Anonymous 1928), chum is second only to chinook salmon (*O. tshawytscha*) in size. Spawning fish are characterized by the calico nuptial coloration, particularly evident in the dominant males, and the metamorphosis of the head with its prominent canine-like teeth. The eggs are comparatively large and the alevins are large and mobile.

The valid scientific name for chum salmon is

*Oncorhynchus keta* (Walbaum) (Jordan and Gilbert 1882), and the type specimen was described by Walbaum (1792) from the Kamchatka River under the name *Salmo keta*. The derivation of the word "keta" is from the language of the Nanai, who live in the Khabarovsk and Primore regions of the USSR and between the Sungari and Ussuri rivers of the People's Republic of China. This language is a sub-dialect of the Amur people, and "keta" literally means fish. Vernacular names include dog salmon and calico salmon in the United States and Canada, and there are at least nine names, varying among and within areas, in the USSR. In Japan more than ten provincial names are used for chum salmon, with the name "gila" reserved for the late run of bright silvery fish with deciduous scales.

Tchernavin (1939), Hoar (1958), and Neave (1958) assumed that the family Salmonidae had a freshwater origin and that the Pacific salmon species diverged from the trout genus *Salmo*, with the main trend in evolution towards greater adaptation to marine life. In this view, masu (*O. masou*) and coho (*O. kisutch*) salmon are closer to the ancestral form than chum and pink salmon (*O. gorbuscha*), both of which migrate to sea shortly after emergence. This hypothesis has been supported by others (Tsuyuki and Roberts 1966). Behnke (1979) concluded that the genus *Oncorhynchus* was derived from the evolutionary line leading to the subgenus *Parasalmo* after its divergence from the other *Salmo* species group. This places the various Pacific salmon and the western trout species closer to each other than either of them are to the brown trout (*Salmo trutta*) or Atlantic salmon (*S. salar*).

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Recently, the western trouts have been removed from the genus *Salmo* and placed in the genus *Oncorhynchus* (Smith and Stearly 1989).

Utter et al. (1973) and Miller and Brannon (1982) concluded that chum salmon are not as highly specialized as either pink salmon or sockeye salmon (*O. nerka*). This accounts for the chum salmon's more versatile behaviour in both freshwater and marine environments. This versatility is limited because no freshwater residents or landlocked forms have been reported; however, chum have been reared in captivity to maturity in fresh water (R.L. Burgner, Fisheries Research Institute, University of Washington, Seattle, Washington, pers. comm.).

Day (1887), Regan (1911), and Thorpe (1982), on the other hand, considered the Salmonidae to have a marine origin and that its evolutionary development has been towards greater freshwater adaptation. Thorpe (1982) argued that the occurrence of landlocked populations provides evidence of evolutionary advancement in juvenile life histories (juvenilization) and that the trend in salmonids appears to be away from dependence on the sea. In this respect, the least advanced species among the Pacific salmon would be the chum salmon and the closely related pink salmon, which both have short freshwater and extensive marine life stages. The arguments presented so far in the literature appear to favour a freshwater origin of Pacific salmon; thus, chum salmon can be considered one of the more advanced species among the Pacific salmon.

Common to virtually every region of the chum salmon's area of distribution is the occurrence of early and late returning stocks to the natal stream. Berg (1934) separated Asian chum salmon into seasonal races - summer and autumn - and classified "autumn chums" as the infraspecies *autumnalis*.

His justifications for separating autumn from summer chum salmon were (1) later entrance into spawning streams, (2) less developed reproductive products at time of entry into these streams, (3) a later spawning period, (4) larger size, and (5) greater fecundity. Although Berg's classification has been supported by other investigators (Lovetskaya 1948; Grigo 1953; Birman 1956; Hirano 1958; Sano 1966), it has not been widely used. In North America the only true summer chum salmon may be in the Yukon River, where the summer chum have the distinguishing characteristics of the Asian summer chum. From western Alaska south to British Columbia and Washington, there are runs referred to as "summer" chum, which spawn from June to early September; these chum are characterized by large body size, older age composition, and high fecundity, and are probably early autumn chum (T. Beacham, Pacific Biological Station, Nanaimo, British Columbia, Canada, pers. comm.).

In general, early-run spawners spawn in main stems of streams, while the late spawners seek out spring water that has more favourable temperatures through the winter. The timing of the runs varies from north to south, as does age at maturity and absolute (and, probably, relative) fecundity. This temporal and spatial partitioning may have originated in stocks spawning in inland streams as opposed to those spawning in coastal or island streams. In recent times, the early- and late-running stocks have adapted to rivers with appropriate characteristics, regardless of geographical location of the river basin. In this study, the summer and autumn chum runs are considered as different stocks which vary in a number of morphological, physiological, and behavioural characteristics.

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## DISTRIBUTION OF SPAWNING STOCKS

### *Range of Spawning Stocks*

On the Asian continent, spawning chum salmon range from the Naktong River in Korea and the

Nagasaki and Fukuoka prefectures of Kyushu Island of Japan (Atkinson et al. 1967) in the south, to the rivers emptying from Siberia into the Arctic Ocean as far west as the Lena River (Laptev Sea) in

## Life History of Chum Salmon

the north (Figure 1). Historically, chum salmon were also present in the Komandorskiy Islands (Smirnov 1975) and the area of present-day north-eastern China (K. Chew and L. Donaldson, School of Fisheries, University of Washington, Seattle, Washington, pers. comm.).

The southernmost mainland Asian runs of com-

mercial importance are in the Amur River. Exploitable runs exist on Sakhalin Island, the Kuril Islands, and the continental streams emptying into the Sea of Okhotsk. Chum salmon are also abundant on the Kamchatka Peninsula as well as in the Anadyr River, which flows into the Bering Sea.

On the North American continent, chum salmon

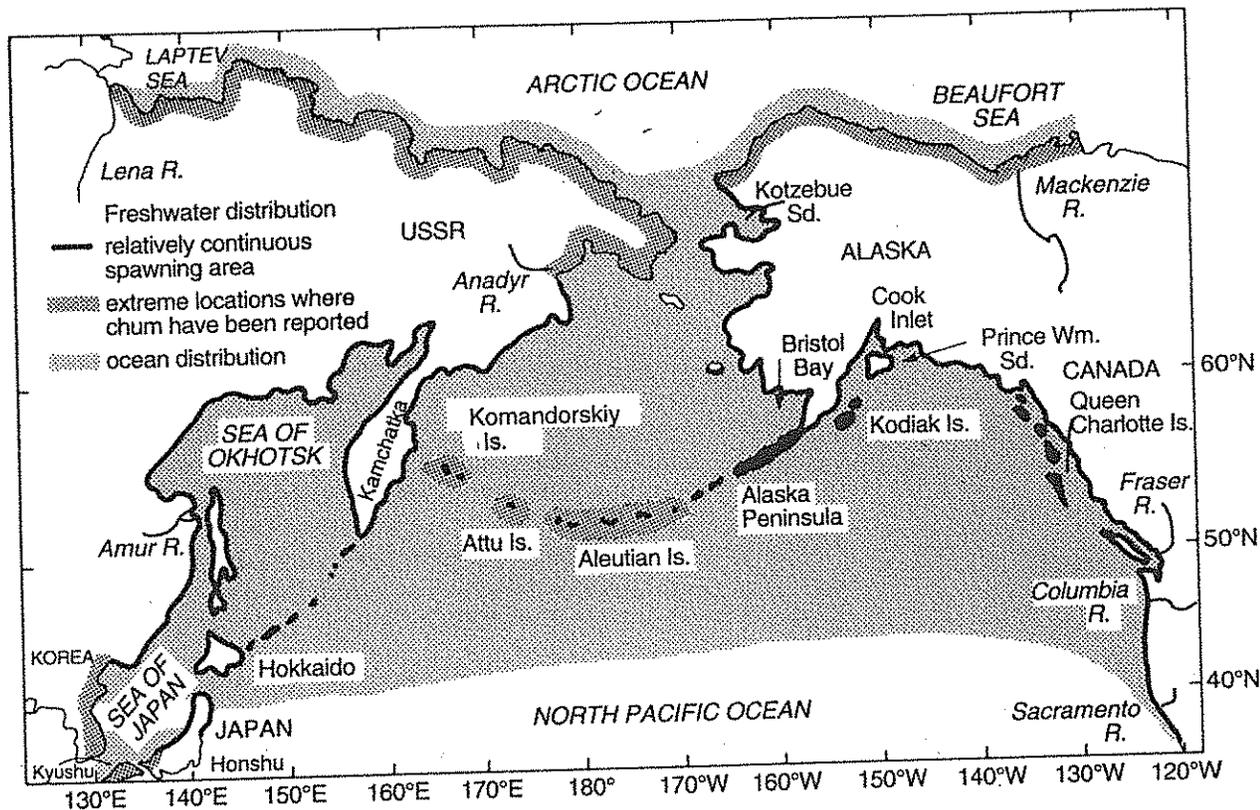


FIGURE 1

Generalized freshwater and ocean distribution of chum salmon. (From Neave et al. 1976)

range from the San Lorenzo River in Monterey, California, in the south (Scofield 1916), to Arctic coast streams in the north, as far east as the Mackenzie River system (Dymond 1940; Wynne-Edwards 1952), and west to Attu Island in the Aleutian Islands (Holmes 1982) (Figure 1). Atkinson et al. (1967) noted that chum and pink salmon occur in the Colville area (Beaufort Sea), which is approximately 71°N latitude and 152°W longitude, and that they probably also spawn in the Tunagoruk and the Usuktuk rivers, which are at approximately the same latitude as the Lena River in Asia. The northernmost large runs of commercial

importance are in Kotzebue Sound (Noatak and Kobuk rivers). Substantial runs have been reported for the Yukon River by Buklis and Barton (1984), where spawning takes place as far as 2,800 km from the sea. Runs of significant numbers occur from Kotzebue Sound to Tillamook Bay, Oregon, in streams that range greatly in size (Henry 1953, 1954). As recently as the 1940s chum salmon were abundant in the Columbia River; however, in 1982 the total run was only about 1,000 fish. Hallock and Fry (1967) reported spawning populations of chum salmon in the Sacramento River as far as 322 km upstream, but, at present, they are

only occasionally seen in northern California.

#### *Distribution and Run Timing in Asia*

There are two major groups of chum salmon in Asia: the summer chum, native to Kamchatka, the Okhotsk coast, the Amur River, and the east coast of Sakhalin; and the autumn chum, native to Japan, the west coast of Sakhalin, the southern Kuril Islands, and the Amur River. The Amur River is the only major river with both summer and autumn chum. Generally, the northern runs migrate upstream in June, July, and August, with the peak of the runs occurring progressively later farther south. The runs are principally in July and August in Kamchatka, in September and October in Sakhalin, in September through November in Hokkaido, and during October and November in Honshu.

USSR. The chum salmon runs of the Olyutorskiy and Anadyr districts begin in June and end in September in most years, and the peaks occur in July and August.

Chum salmon ascend to spawn in west Kamchatka from June to September, with peak runs occurring in July in some years and August in others. The major chum salmon streams in this region are the Bolshaya, Icha, and Kikhchik rivers (Semko 1954), all of which are in the southern half of the peninsula. Although there are about eighteen large streams on the west coast of Kamchatka, more than 80% of the chum salmon catch is from six streams from the Icha River area and southward (Sano 1966). The twelve streams north of the Icha River, which have an average stream length of 210 km, produce relatively small numbers of chum.

The migration time in the Okhotsk District is similar to that in western Kamchatka (June to September), and more than 80% of the chum salmon arrive in August. The major runs are in the Okhota and Kukhtuy rivers.

Summer chum occur in the Amur River and on the east coast of Sakhalin. Autumn chum are also present in the Amur River and along the west coast of Sakhalin, as well as in the Primore region (Sano 1966). Summer chum migrate upstream shortly after their appearance in coastal waters in July and August. Autumn chum migrate from August to early October, with about 90% of autumn fish

appearing in coastal waters during the month of September. The Amur populations are more numerous than those in other areas of this region, although the summer runs have become depressed to a level too low to support fisheries exploitation.

There are two peaks in the abundance of chum salmon in the nearshore waters of Sakhalin and the Kuril islands, one in July and August, and the other in September and October. The former group is not large and is probably destined mainly for the Amur River and the Okhotsk District, although there are a few summer chum populations in the Tym and Poronai rivers of Sakhalin. The autumn chum ascend the rivers shortly after their appearance in the nearshore waters and are considered to be related to those of northern Japan (Hirano 1953).

Japan. Historically, autumn chum occurred along the east and west coasts of Hokkaido and Honshu ranging from Chiba on the Pacific coast and Nagasaki on the Sea of Japan side. Again, the migrations of northern populations are a little earlier than southern ones, and the peak runs occur in September and October in Hokkaido and mostly October and November in areas south of Hokkaido. The existence of a late-arriving (mid-January and early February) run to various streams in Japan was also reported by Sano (1964).

#### *Distribution and Run Timing in North America*

Alaska. The large runs of chum salmon in Kotzebue Sound support the northernmost commercial chum salmon fishery and occur in two modes. The migration into the Kobuk River, which receives 25% of the run, is principally in July, and the run into the Noatak River, which produces 75% of the escapement, is in August (Bigler and Burwen 1984).

Summer chum salmon enter the Yukon River in early May, and the run overlaps with the autumn chum salmon run in June and July, although, for management purposes, 15 July is considered the end of the summer run. The autumn chum spawn from September through November in spring-fed streams and sloughs. Summer chum are more abundant, not as large, and arrive in fuller nuptial coloration than the autumn chum (Buklis 1981; Buklis and Barton 1984).

Chum salmon in the Kuskokwim River arrive in

## Life History of Chum Salmon

late August and September, and the major runs in the Togiak, Nushagak, and Kvichak rivers in Bristol Bay begin in mid- to late June, peak the first week of July, and end in late July (D. Rogers, Fisheries Research Institute, University of Washington, Seattle, Washington, pers. comm.).

Small runs of chum salmon enter numerous streams of the Alaska Peninsula in July and August, especially on the south side of the peninsula. At the same time, substantial runs occur on the north side of Kodiak Island and lesser runs on the south side. There are small runs in the Aleutian Islands chain, at least as far west as Attu Island (Holmes 1982).

In central Alaska, a substantial run of chum salmon occurs in the Susitna River and in about fifteen short streams along the northern portion of Cook Inlet (Atkinson et al. 1967). The peaks of the runs are primarily in late July. In southern Cook Inlet, the runs occur in July and August in the Kenai River and in streams north of Kachemak Bay to Resurrection Bay. Numerous runs enter Prince William Sound destined for Port Wells, the Valdez Arm, and Port Fidalgo areas, as well as the lesser arms and bays.

For chum salmon native to southeastern Alaska, the peak of nearshore abundance was established, for 1984, as the first two weeks in August (Clark and Weller 1986). The mid-point of the catches varied from 5 August in northern areas to 19 August in the south. The median of the escapements varied from late August to mid-September (Clark and Weller 1986).

Although many runs remain to be catalogued for southeastern Alaska, information on abundance and timing is available for some. In the Yakutat area, chum salmon spawn in the East River (near the mouth of the Alsek River) in October (J.H. Helle, National Marine Fisheries Service, Auke Bay, Alaska, pers. comm.). An exceptionally late and large autumn run occurs in the Chilkat River (near Haines) where unusual upwellings of warm water keep portions of the river ice-free throughout the winter (Cline 1982). This phenomenon has provided sustenance for up to 3,500 bald eagles through the winter. Runs are not numerous in the Icy Strait area except for one large run in Excursion Inlet (July and August). Smaller runs in August and September are present in the eastern part of southeastern Alaska, particularly in Stephens Pas-

sage, but more numerous and larger runs occur in the western district of southeastern Alaska. Several large runs arrive in August and September. There are numerous small runs in the Wrangell district.

Farther down the coast, many small runs spawn from July to September in the mainland streams and in the island streams all the way to the Ketchikan area (J.H. Helle, National Marine Fisheries Service, Auke Bay, Alaska, pers. comm.). Runs can be particularly strong on Prince of Wales Island where spawning occurs mainly in September and October. Recently, the runs in southeastern Alaska have been considerably enhanced by releases of large numbers of juveniles from private and public aquaculture enterprises.

**British Columbia.** In British Columbia, chum salmon spawn in over 800 streams. The most productive 58 streams produce only 50% of the total and less than 13 have large runs (Aro and Shepard 1967).

Runs in the northern part of British Columbia are earlier than those in the south. In the Queen Charlotte Islands, fisheries adjacent to the spawning grounds are in August and September, whereas chum salmon bound for streams on the northern mainland pass through the inshore fishing areas mainly in July and August. Along the central part of the British Columbia coast, peak catches are made in August, mostly in the Bella Bella and Bella Coola areas.

In the south, spawning takes place principally from October to January: October in the Chehalis area (Fraser River) and November to January in the main stem of the Fraser, Chilliwack, Vedder, and Harrison rivers. Peak spawning in streams of Johnstone Strait and the Strait of Georgia varies between early October in the northern rivers (Knight Inlet) and late December in some southern streams (Cowichan River). The peak of the catches north of Vancouver Island ranges from mid-July to mid-September, and is in October in southern British Columbia (Beacham 1984b).

**Washington and Oregon.** The pattern of broad distribution holds for the state of Washington also, although the spawning areas may be relatively farther upstream because of the comparatively numerous moderate to large rivers in the Puget

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Sound region. In the north, spawning occurs in the upper Nooksack, central and upper Skagit, Stillaguamish, Skykomish, and Snohomish rivers (Atkinson et al. 1967). Large runs occur in the Skagit River system, the Hood Canal system (where artificial propagation is the primary source), the Nisqually River system, and the Grays Harbor and Willapa Harbor areas. The spawning areas are near salt water in the coastal rivers of the Olympic Peninsula and in the smaller and shorter lowland streams of the Puget Sound area.

There are often variations in timing within the early and late autumn runs. In some Puget Sound streams a more or less distinct "middle run" may occur (Koski 1975). With runs beginning in early September and continuing in some streams as late as March, a spawning period of four to five months is common for southern Puget Sound.

Chum salmon are limited to the lower part (300

km) of the Columbia River, with more runs on the Washington than on the Oregon side. There are October runs in the Washougal, Lewis, Kalama, Cowlitz (Washington), and Sandy (Oregon) river systems. Historically, there were chum salmon in the Toutle River, but none have been seen since the eruption of Mt. St. Helens in 1980. Chum salmon spawn in the Abernathy, Elokommin, and Grays River areas on the Washington side of the Columbia River and nearby in some of the smaller Oregon streams.

Chum salmon populations in the coastal area of Oregon are small. The principal runs enter Tillamook Bay in October and November. Smaller runs of chum salmon are found south of Tillamook Bay at Netarts Bay and in the Nestucca River. Chum salmon are present in very small numbers in the Yaquina and Siuslaw Rivers, and Coos Bay.

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## SPAWNING MIGRATION

### *Homing and Straying*

The precision of homing and the degree of straying of chum are not well known and only incidental references are available. Returns of adults that were marked as juveniles indicate that the homing tendency of these fish is strong. For two seasons, Salo and Noble (1952) surveyed streams adjacent to and near Minter Creek in Washington and noted no strays, as determined from marked individuals.

For many years, chum salmon fry were released from a nearby hatchery into Walcott Slough, near Brinnon, on Hood Canal, Washington, and the adults returned, apparently unerringly, to a trapping device on the slough, where no natural run existed (Wolcott 1978). At Big Beef Creek, Washington, adult chum salmon return to a trap at the outlet of a spawning channel from which they emigrated as fry, although an alternate trap on the mainstream is available (E.O. Salo, unpublished data).

Tagging of adults near the mouths of streams may give erroneous results if the assumption is made that all fish captured are native to those

particular streams; nevertheless, for management purposes these types of studies can be valuable. By tagging mature chum salmon in Skagit Bay (Washington), Eames et al. (1981) estimated a straying rate of 14%. Hiyama et al. (1967) determined that adult chum salmon with their olfactory organs occluded showed no ability to return to their parent stream, whereas fish that were blinded did.

The strong homing tendency of mature chum salmon leads to generally uniform migration patterns from year to year and contributes to stock isolation (Beacham 1984b; Beacham et al. 1985), which, in turn, forms the basis for efficient utilization of the stream by spawning stocks. For example, in the Noatak River the stocks spawning above and below Kelly River differ electrophoretically, suggesting that they are genetically distinct (Davis and Olito 1986).

### *Rate of Migration during River Approach*

Pacific salmon characteristically go through morphological and physiological changes prior to

## Life History of Chum Salmon

spawning. Specifically, they change from a salt-water to a freshwater physiological state and from a feeding and growing to a reproductive state. Whitish and very mushy meat, called "hottchare" in Japan, is commonly observed in pre-spawning chum salmon, frequently while the salmon are still in the estuary. This deteriorating muscle condition is due to the lysing of proteins (Konagaya 1983). Also, the scales of chum salmon become embedded early in the spawning migration and the integument thickens markedly so that the skin is often marketed as "salmon leather."

The approach by chum salmon to the estuaries of their natal streams is usually fairly rapid, but varies from stream to stream. Lyamin (1949) traced the migration of tagged chum salmon as they approached and ascended the Bolshaya River and determined that they had migrated 1,200 km in 15 days (80 km/d), whereas those approaching another river had travelled only 300 km in 15 days (20 km/d). Shmidt (1947) (quoted by Lyamin 1949) reported that the "maximum speed" of travel during river approach is from 43 to 63 km/d. A travel time of 21 days is used by Anderson and Beacham (1983) for chum salmon on their migration from Johnstone Strait to the mouth of the Fraser River, a distance of 300 km.

Seven chum salmon tagged at the north end of Whidbey Island, Puget Sound, travelled at a mean time of 21 days (range 5-32 d) for distances that varied from 70 to 106 km. In the same year, 59 tagged fish were recaptured in Skagit Bay, a distance of only 15 km, and they had travelled, on the average, seven days (range 1-21 d) (Barker 1979).

Once chum salmon arrive at the mouth of their natal stream they may spend several days "milling" before ascending the stream (Hunter 1959; Koski 1975). The period of milling becomes shorter as the spawning season progresses. Eames et al. (1981) reported that some fish remained in Skagit Bay 21 days after tagging. Usually chum enter the stream when ripe and in full spawning coloration (Fiscus 1969; Koski 1975).

### *Stimuli for Stream Entry*

Once near the mouth of the stream, chum are stimulated to move upstream by an increase in stream runoff of almost any magnitude. However, late in the season, high water is not essential for a

timely ascent (Salo and Noble 1952; Hunter 1959).

The "summer" runs, whether truly summer or early autumn runs, respond to high flows caused by spring and summer snow melt, whereas the autumn runs arrive at a time when fall rains occur. Once past the tidal currents chum salmon travel upstream at a slower rate, compared to what Lyamin (1949) described as "their impetuous entry into the river."

The first chum salmon enter Japanese streams when temperatures drop to 15°C and most enter when the temperatures are 10°-12°C. The peak of migration generally occurs when the temperatures range between 7° and 11°C. Helle (1960) noted an absence of chum salmon in a glacially-fed stream in Alaska until the water cleared up, even though spawning was taking place in adjacent streams.

### *Rate of Stream Migration and Instream Orientation*

Chum salmon are large, strong swimmers and are capable of swimming in currents of moderate to high velocities. The maximum swimming speed recorded is 3.05 m/s or 67% of the maximum burst speed of 4.6 m/s (Powers and Orsborn 1985). They are not leapers and usually are reluctant to enter long-span fish ladders. Thus, they are generally found below the first barrier of any significance in a river.

In the Bolshaya River the migration rate is about 14 km/d. In the Anadyr River the first fish arrive on 3-5 July and they migrate at a rate of 40-50 km/d for a period of 10 days. This brings them to the halfway point of the river (Lyamin 1949). As they approach the spawning grounds, their speed increases.

Autumn run chum in the Yukon River migrate close to the river banks (Buklis 1981; Buklis and Barton 1984). The stocks destined for the upper Yukon and Porcupine rivers move mostly along the north bank of the Yukon River in the Galena-Ruby area between the 850 and 930 km section of the river (about halfway to the spawning grounds). The Tanana River stocks, which have a shorter distance to migrate, follow about five days later and swim mostly along the south bank.

### *Age Composition and Sex Ratio*

The age composition of the spawners often varies

## Pacific Salmon Life Histories

over the spawning season. In Big Beef Creek, a lowland stream, the early run has a higher proportion of three-year-olds than the late run (E.O. Salo, unpublished data). Henry (1954) reported that older fish appeared later in the run than younger fish at Tillamook Bay, Oregon. However, in Minter Creek, a lowland Puget Sound stream, the older chum salmon returned before the younger fish (Salo and Noble 1953). Trends similar to that at Minter Creek have been reported for Fraser River and other British Columbian (Beacham and Starr 1982; Beacham 1984a), central Alaskan (Helle 1979), and southeastern Alaskan stocks (Clark and Weller 1986). The runs in these streams are comprised of three-, four-, and five-year-old (or age 0.2, 0.3, and 0.4)<sup>1</sup> chum salmon, with four-year-olds being dominant. The five-year-olds complete their migration earlier than the more numerous four-year-old fish, which are typically well represented throughout the run. The three-year-olds return later than the five-year-olds, and the ratio of three-year-olds to four-year-olds increases to the end of the spawning run.

In general, males predominate early and females

late in the run, with the overall ratio of males to females approaching 1:1 for the entire period (Bakkala 1970). Mattson et al. (1964) reported that male to female ratios on the spawning beds of Traitors Creek, Alaska, varied from a high of 3.56:1 to a low of 1:1.34 during a single season. The ratio was generally between 1.25:1 and 1.70:1 during the early part of the run and stabilized to approximately 1:1 during the peak spawning period. In Minter Creek the ratio was 1.7:1 early in the season and equalized during the peak after which females predominated (1:1.2) (Salo and Noble 1953). Semko (1954) reported similar changes in the sex ratios within each age group in the Bolshaya River, USSR. Beacham and Starr (1982) did not observe changes in the sex ratio during the season in the Fraser River chum salmon run. However, they were sampling a mixture of stocks which may have individually exhibited this trait. Later, Beacham (1984a) pooled stocks from southern British Columbia and reported that males were more abundant than females at three and five years of age, but less abundant at four years of age.

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## SPAWNING

The spawning behaviour of chum salmon has been described by Sano and Nagasawa (1958), Tautz and Groot (1975), Duker (1977), Helle (1981), and Schroder (1973, 1982). Basically, it consists of a combination of nest-building activities by the female and courtship display by the male, leading to deposition of fertilized eggs in the nest. Immediately following egg deposition, the female fills the nest pocket with gravel and digs a new nest in front of the first one. The females are resident and usually build four to six nests in succession in one place. When all the eggs are buried they defend the redd (the combined pockets of covered eggs) until

death. The males are transitory and move from one spawning female to another. Once attracted to a female the male will use physical force to exclude rivals.

### *Nest Site Selection*

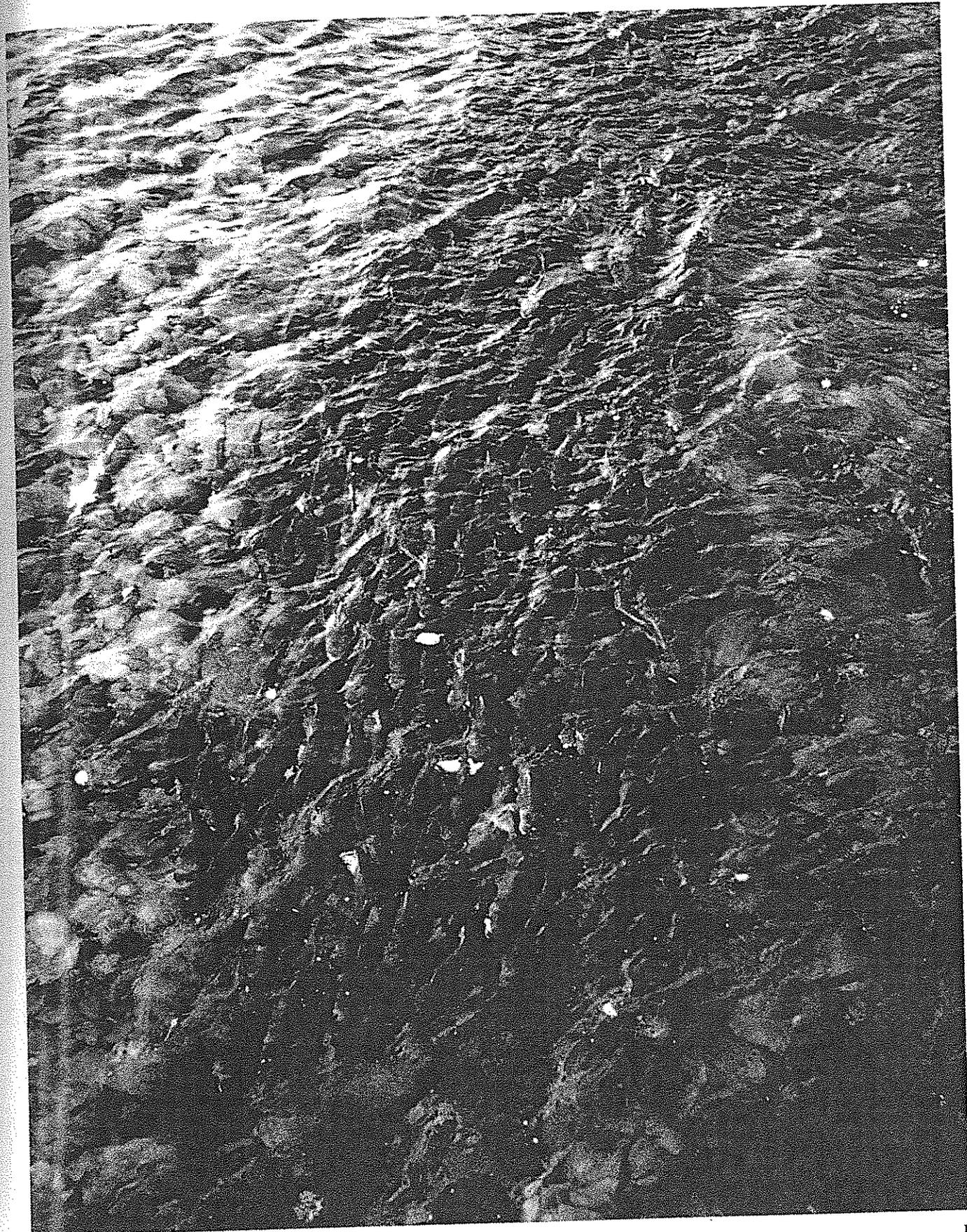
Selection of the nest site by the female involves searching for preferred hydrological and geophysical features, such as water odour, depth and velocity, gravel composition, and the presence of cover. Chum salmon prefer to spawn immediately above turbulent areas or where there is upwelling.

The female explores potential nest-building sites by "nosing" with the head pointed down towards the gravel substrate. With pectoral, ventral, and anal fins fully extended, and while moving her head from side to side, she swims slowly upstream.

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<sup>1</sup> The age designation system used in this chapter is the European formulation used for Atlantic salmon and now widely employed for Pacific salmon. In this system the winters spent in fresh water and salt water are indicated and separated by a decimal point.

# Colour Plates



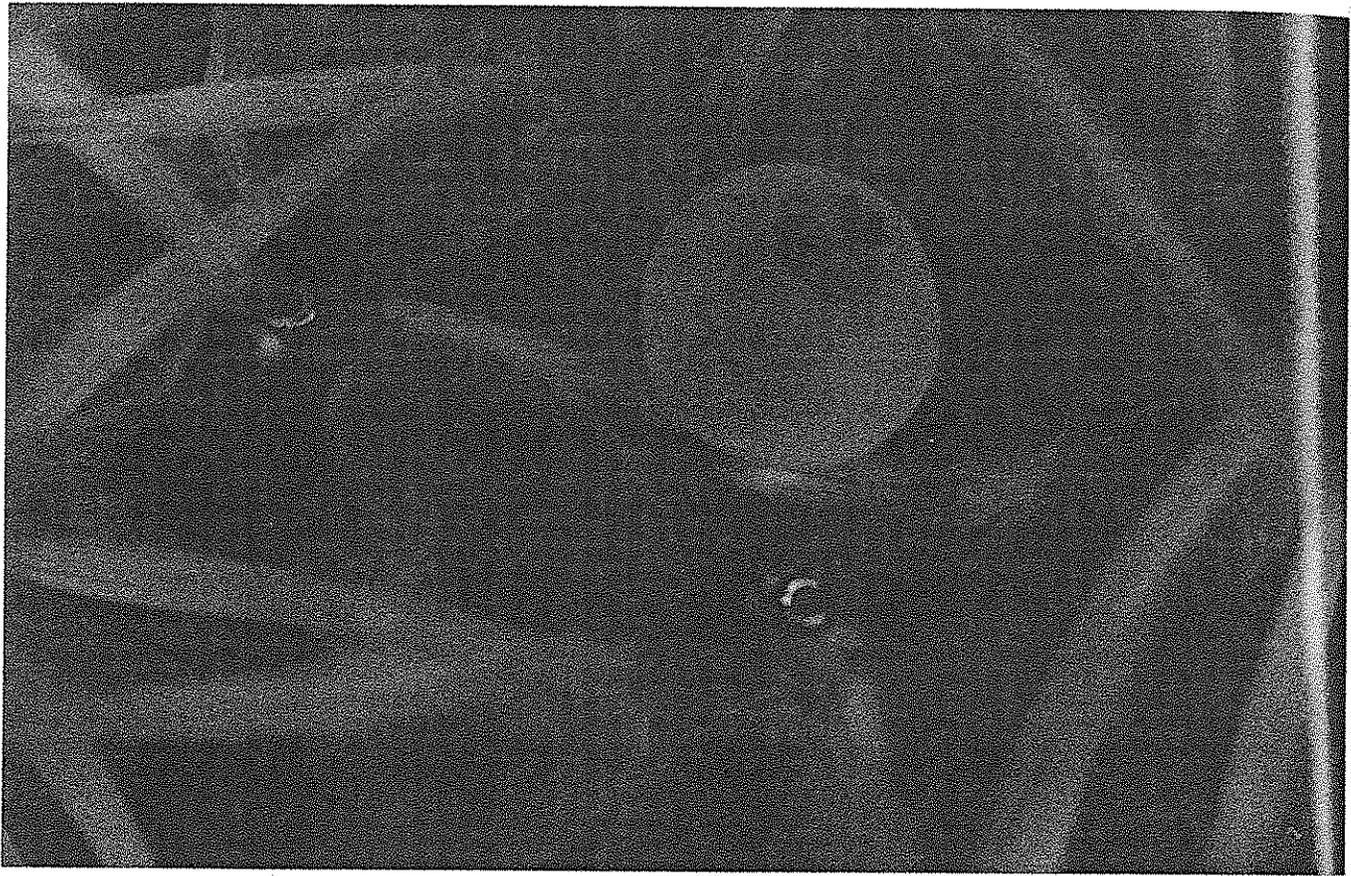
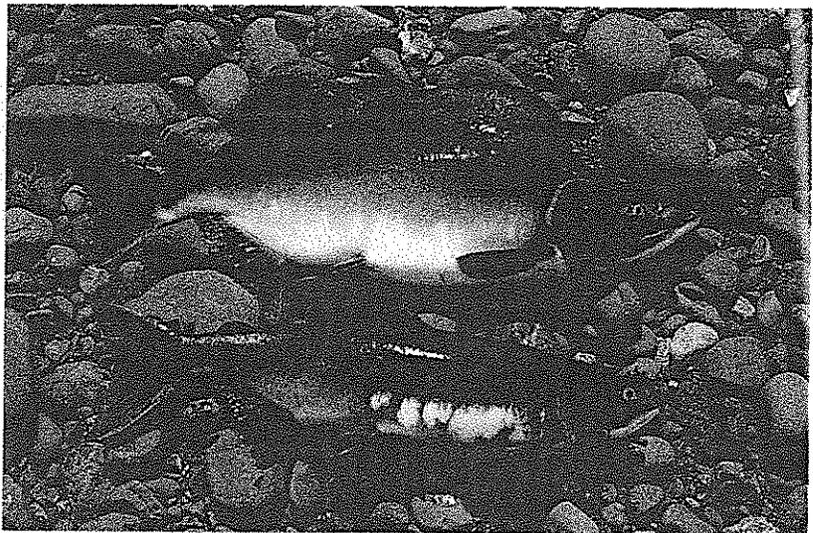
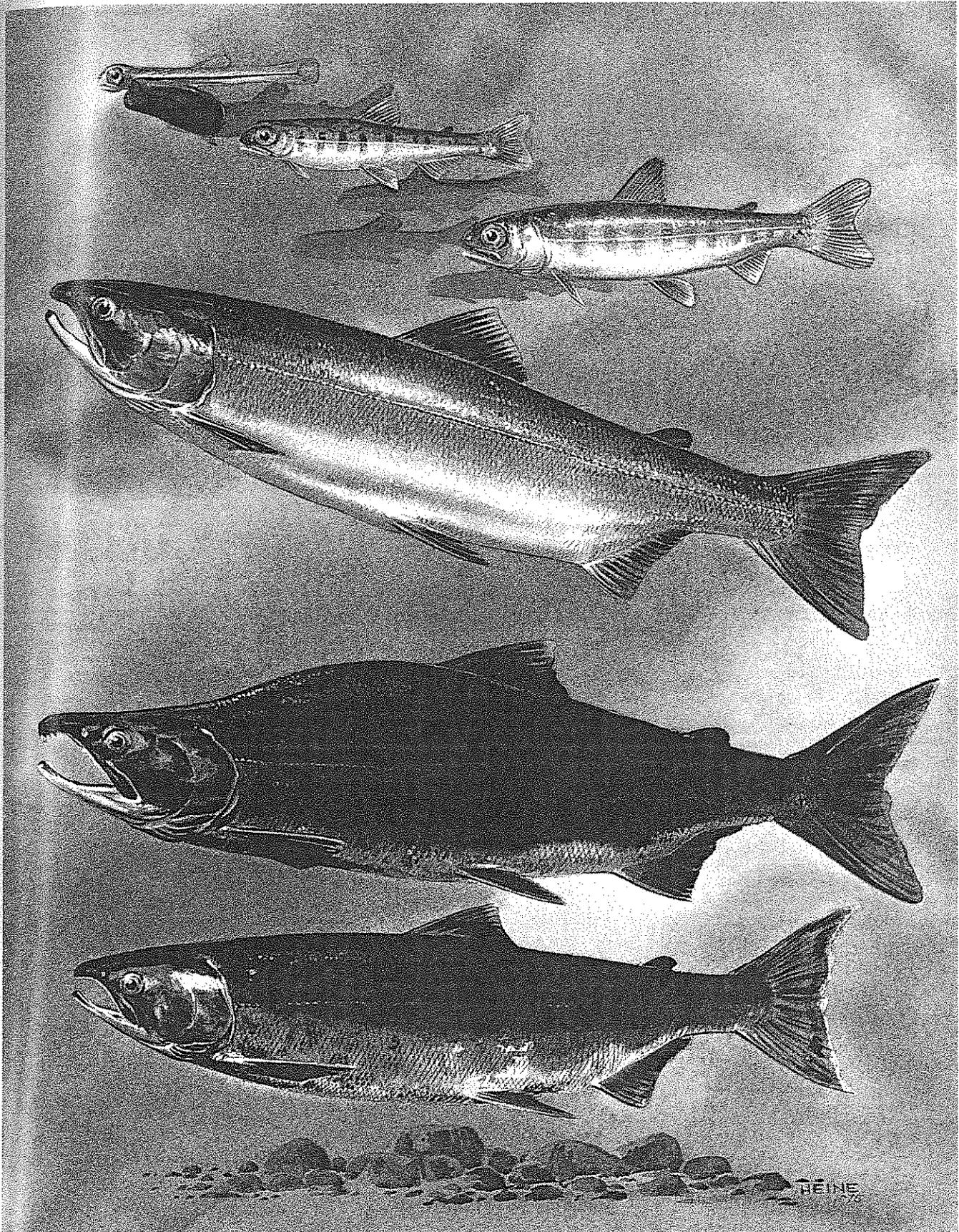


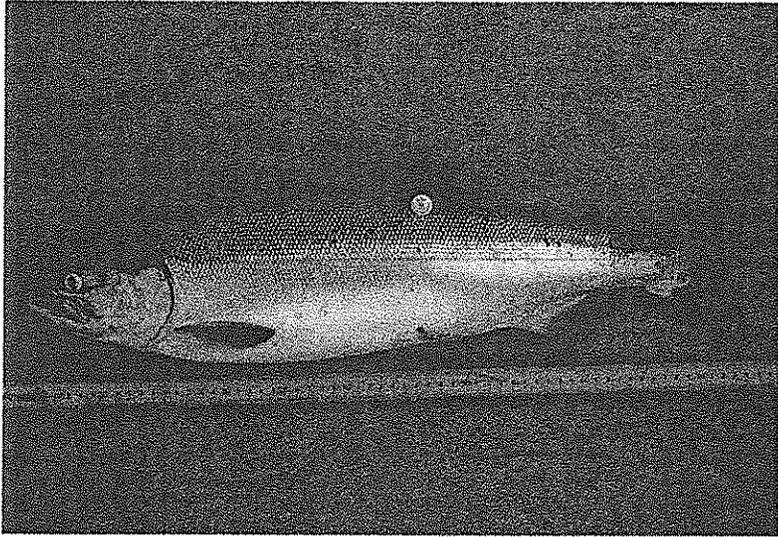
PLATE 2. Developing pink salmon eggs and hatched alevins. *Photograph by Marj Trim*

PLATE 3. Mature male and female pink salmon, British Columbia. *Photograph by J-G. Godin*

PLATE 1 (*previous page*). Pre-spawning sockeye salmon holding along the banks of the Adams River, British Columbia. *Photograph by Marj Trim*







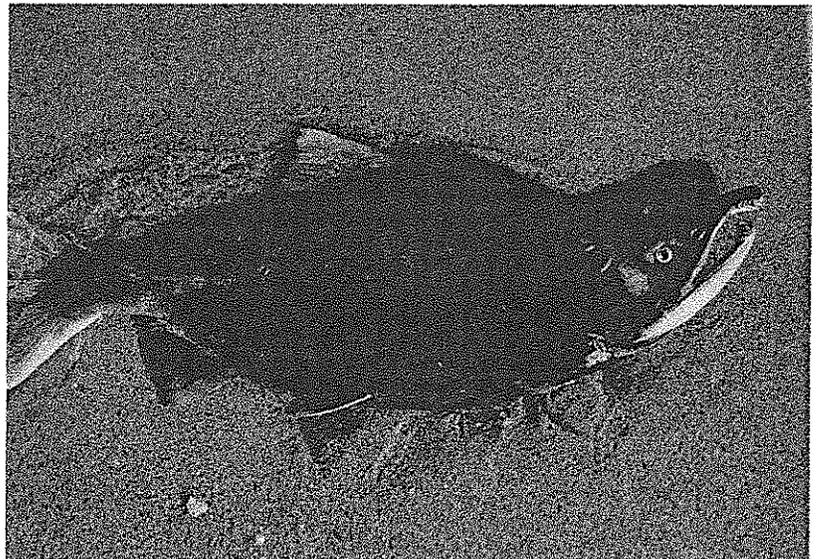
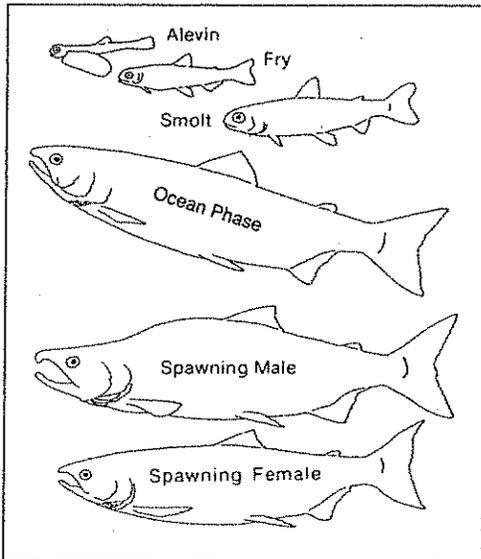
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PLATE 5. Ocean phase of sockeye salmon.  
*Photograph by K. Cooke*

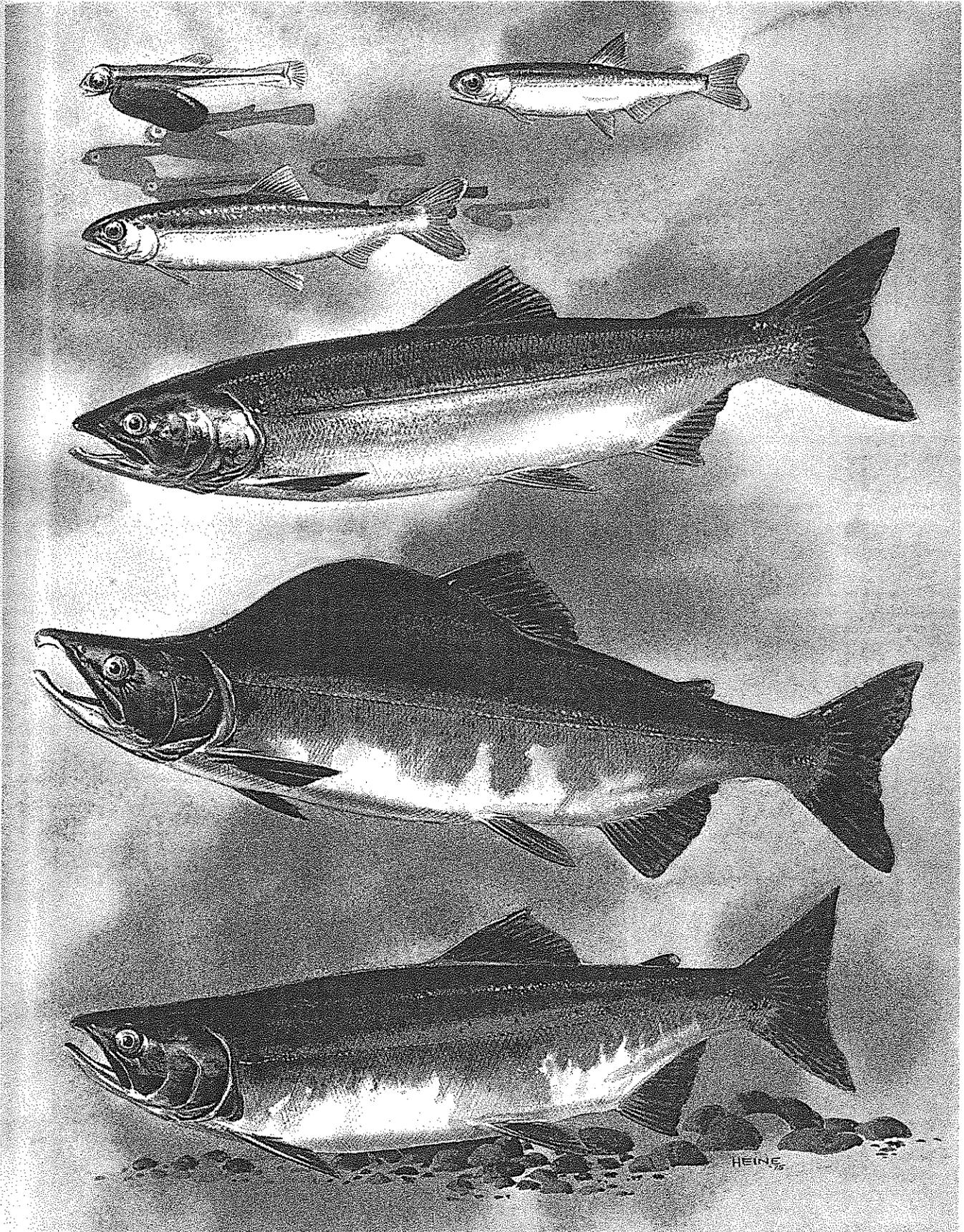
PLATE 6. Spawning sockeye salmon, Iliamna Lake, Alaska: female (top), male (bottom).  
*Photograph by Thomas C. Kline*



PLATE 4 (previous page). Sockeye salmon life history stages. *Painting by H. Heine*



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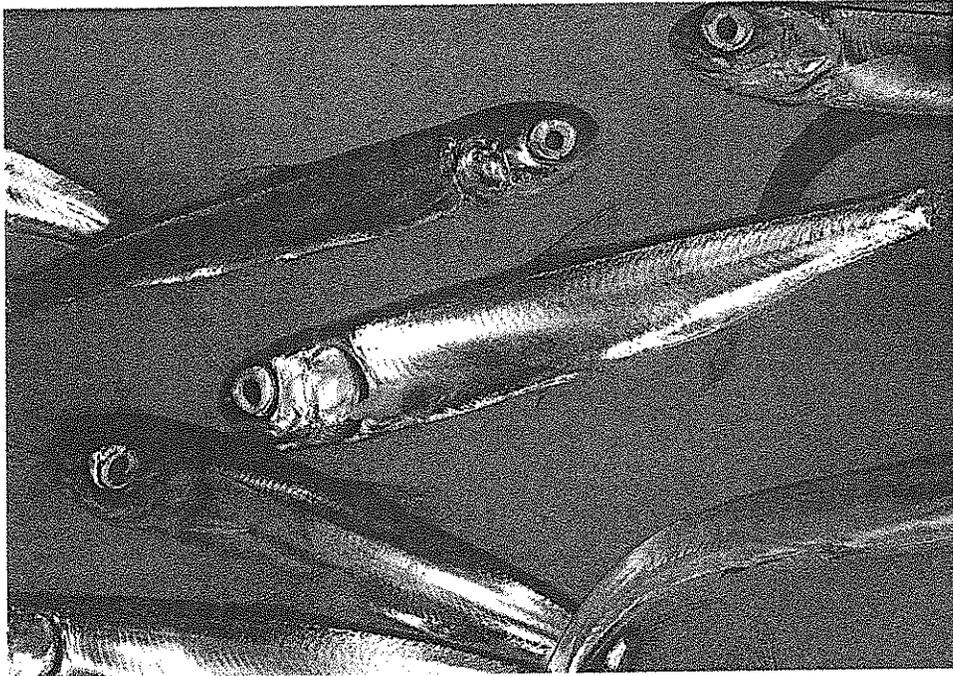


PLATE 8. Pink salmon fry shortly after emergence from the gravel. *Photograph by W.R. Heard*

PLATE 9. Albino pink salmon fry from Sashin Creek, southeastern Alaska. *Photograph by W.R. Heard*

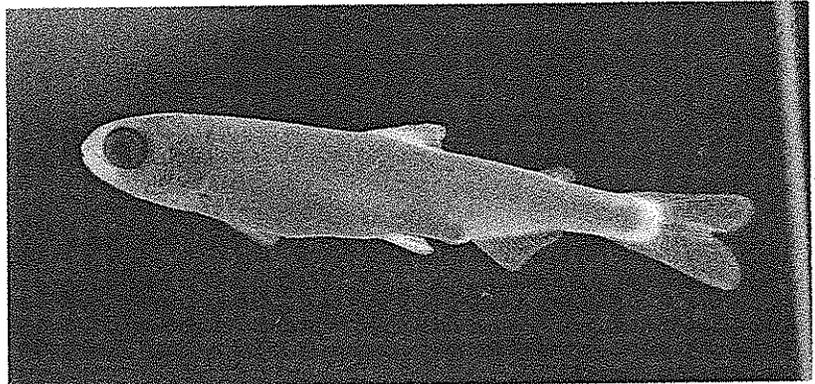
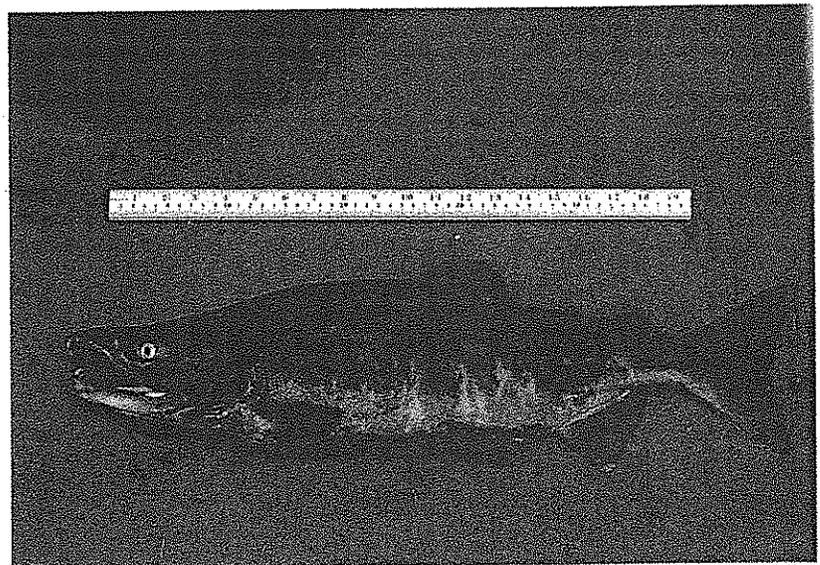
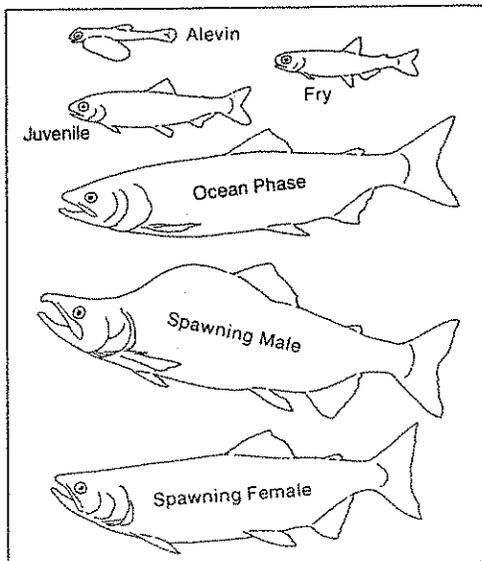
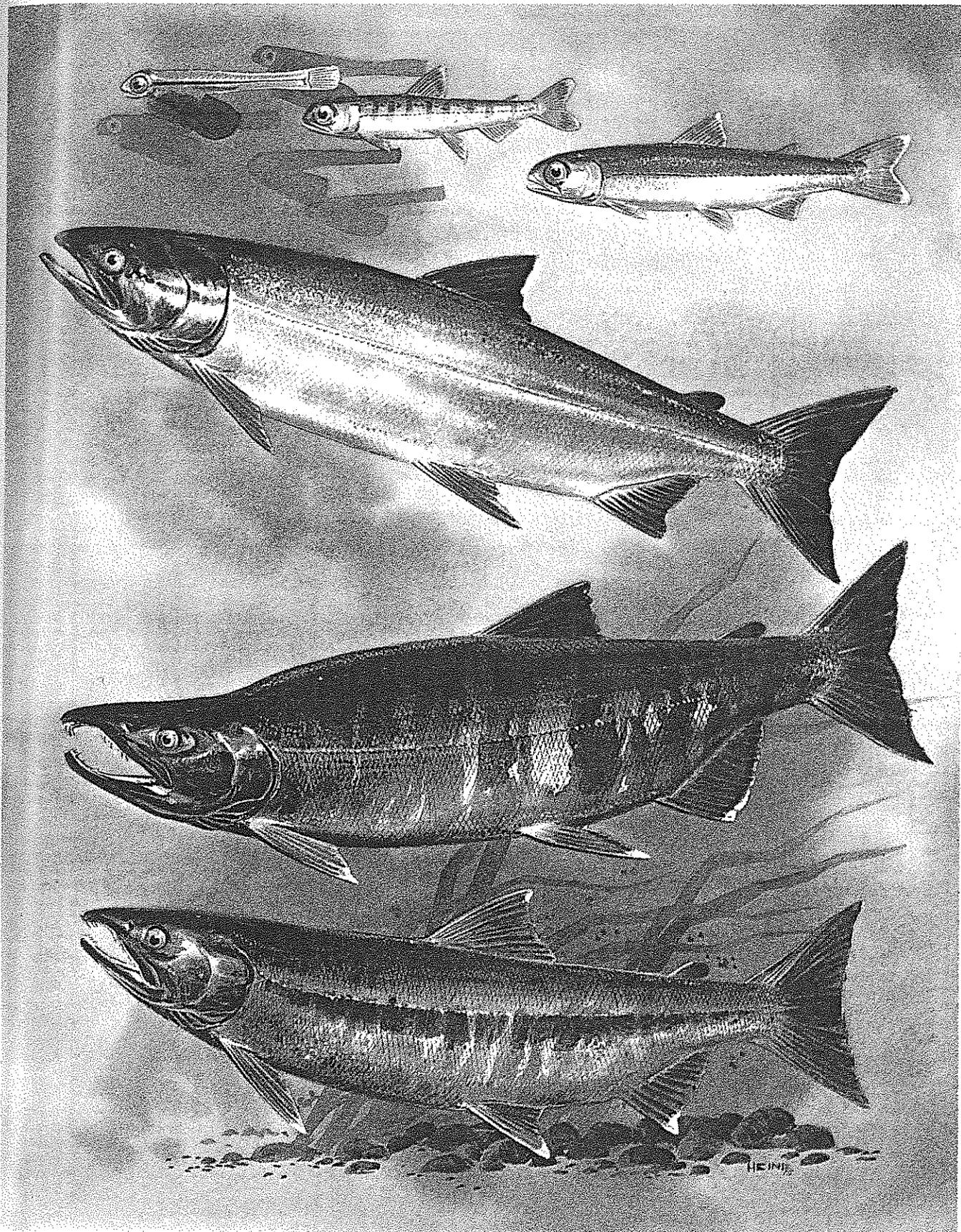
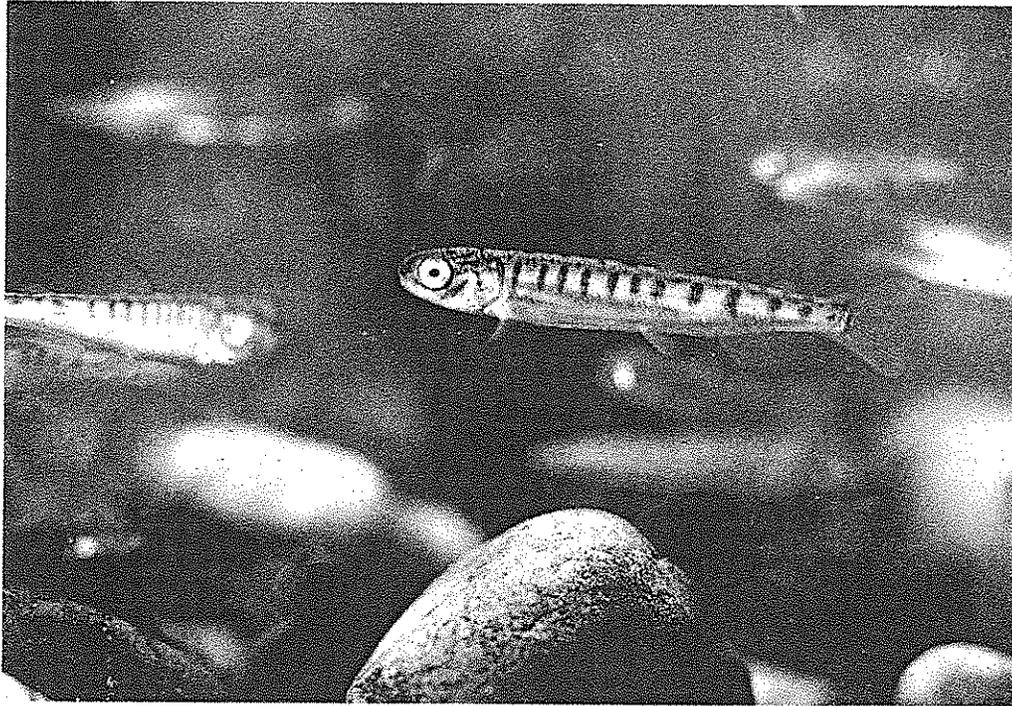


PLATE 10. Adult pink-chum salmon hybrid. *Photograph by W.R. Heard*

PLATE 7 (previous page). Pink salmon life history stages. *Painting by H. Heine*



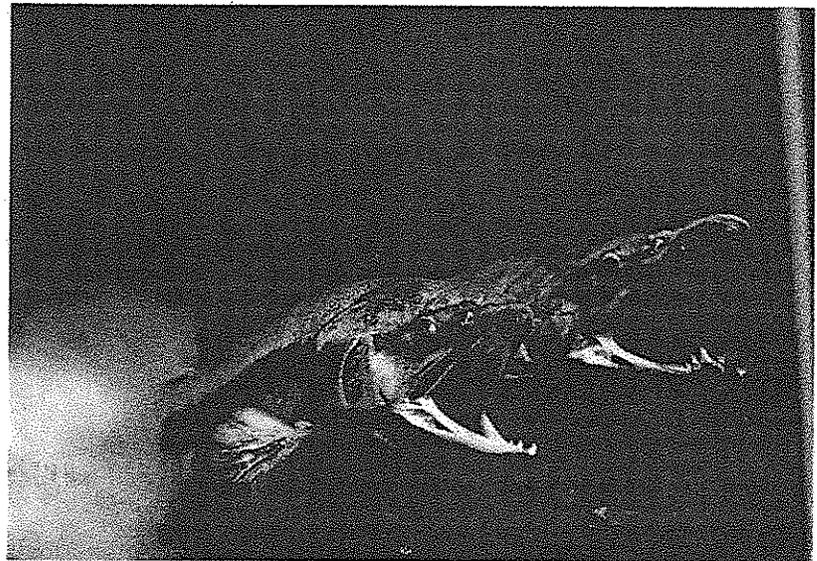




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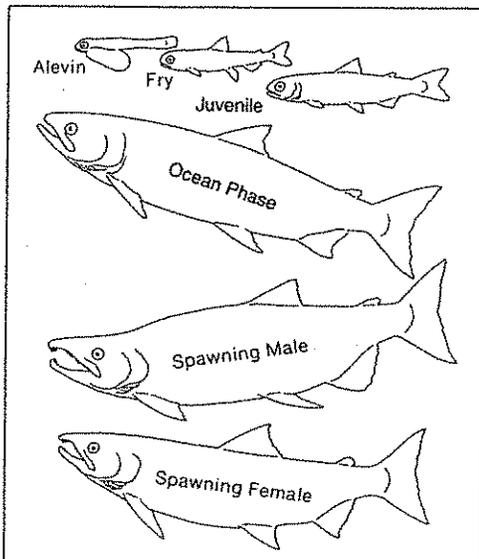
PLATE 12. Chum salmon fry. *Photograph by S.L. Schroder*

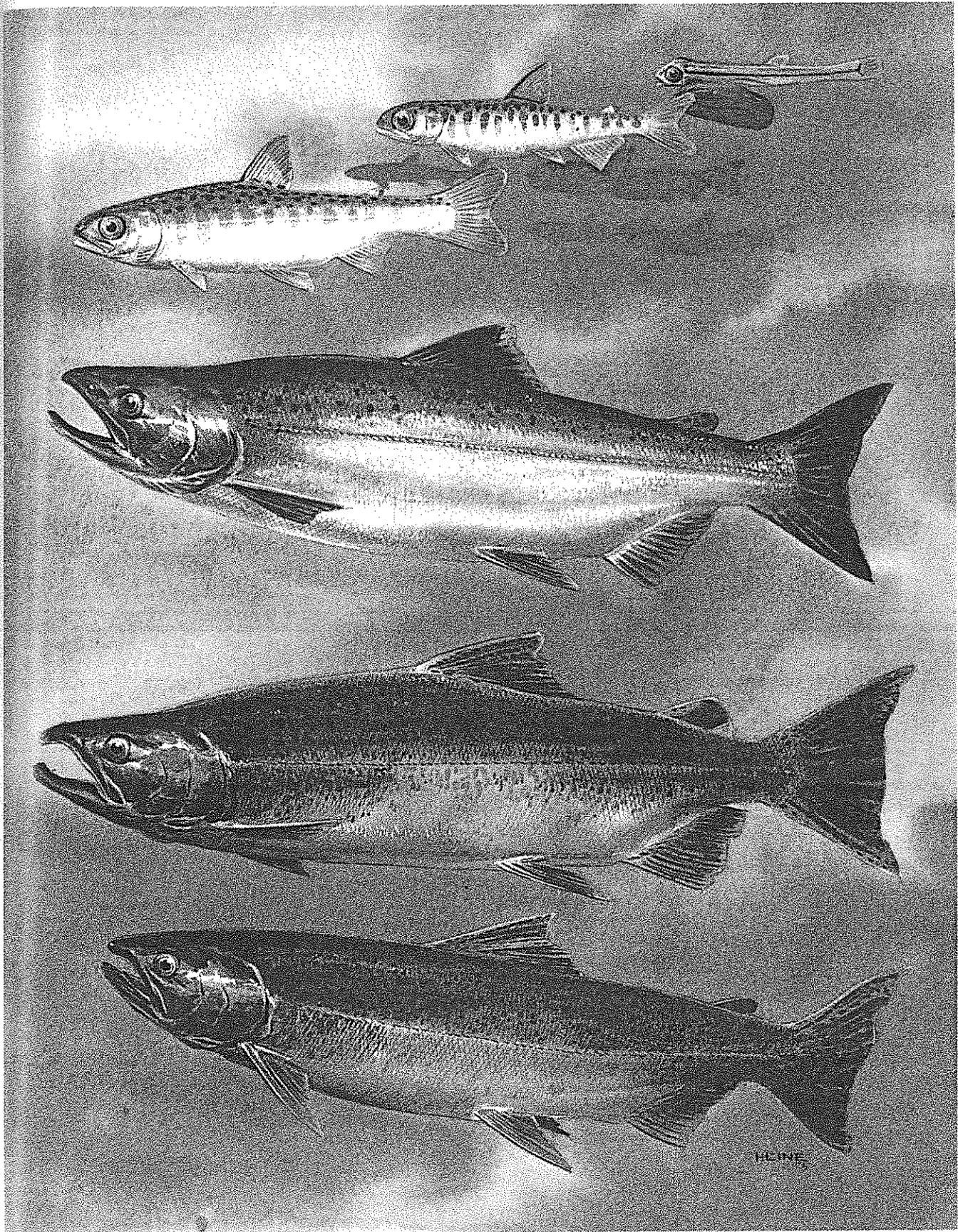
PLATE 13. Adult chum salmon during spawning act, Big Beef Creek, Washington. *Photograph by G. Duker*



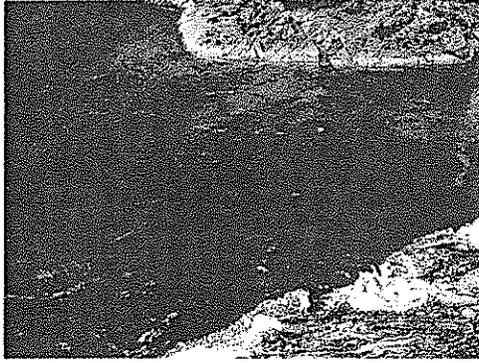
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PLATE 11 (previous page). Chum salmon life history stages. *Painting by H. Heine*









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PLATE 15. Maturing chinook salmon holding in a pool below Stamp River falls, British Columbia. *Photograph by C. Groot*

PLATE 16. Maturing chinook salmon jumping three-metre falls during upstream migration, Stamp River, British Columbia. *Photograph by Marj Trim*

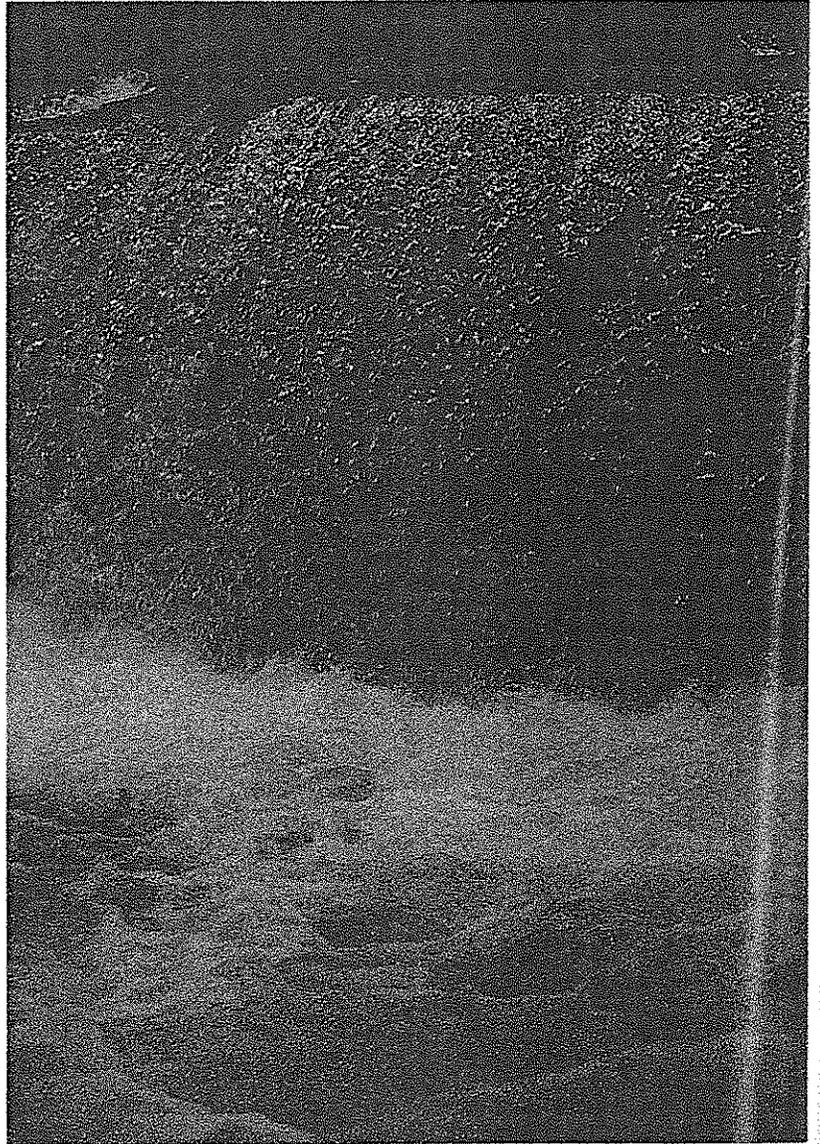
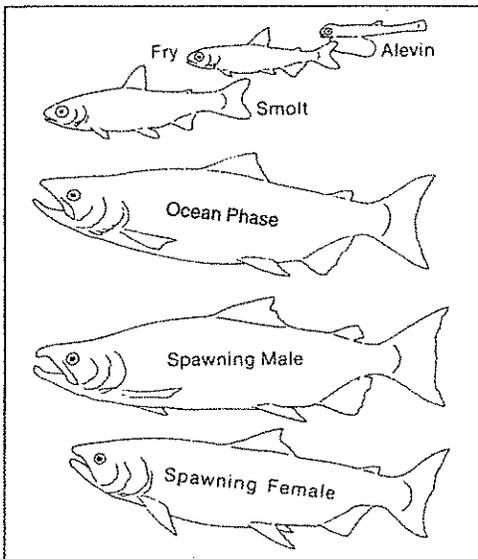
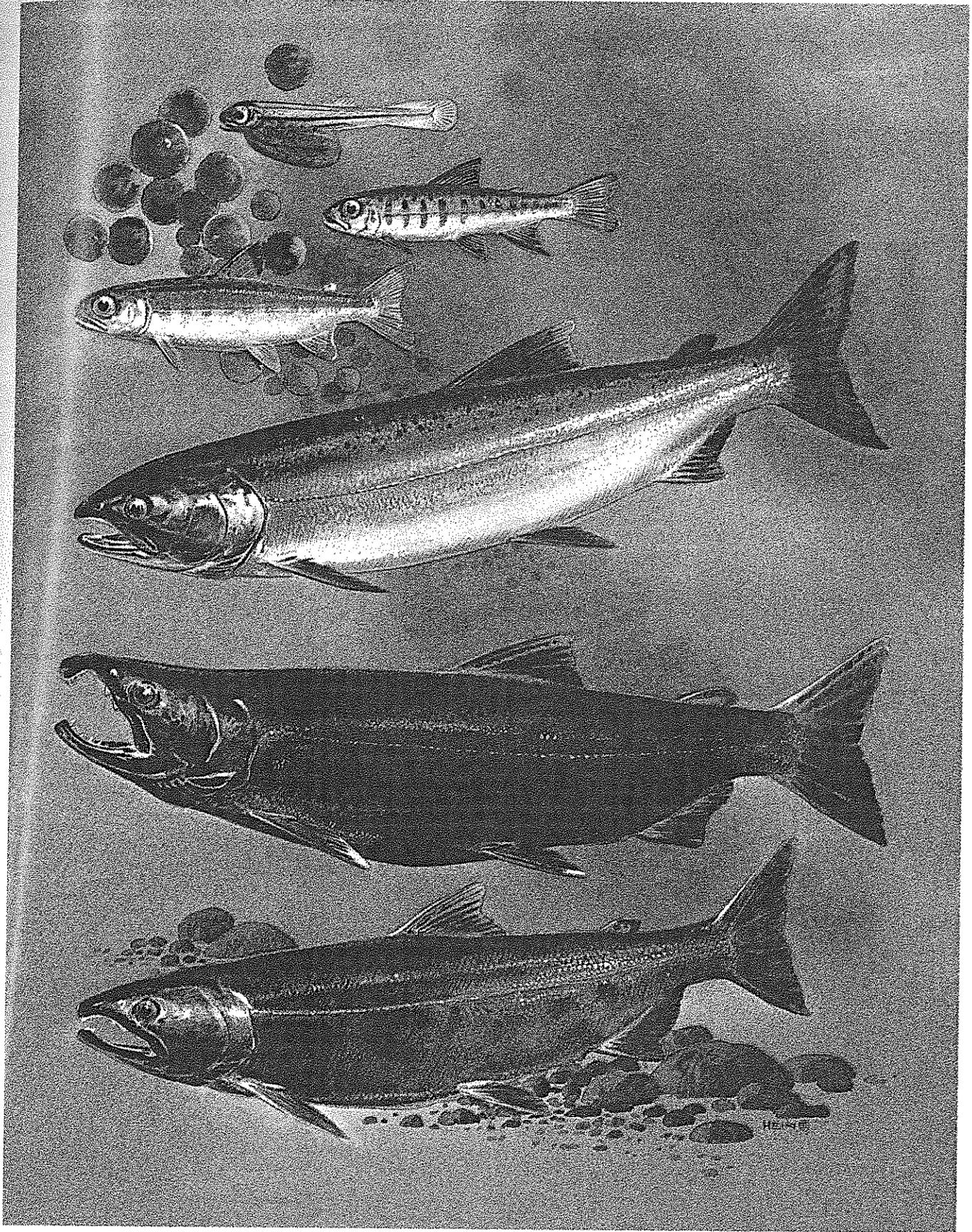


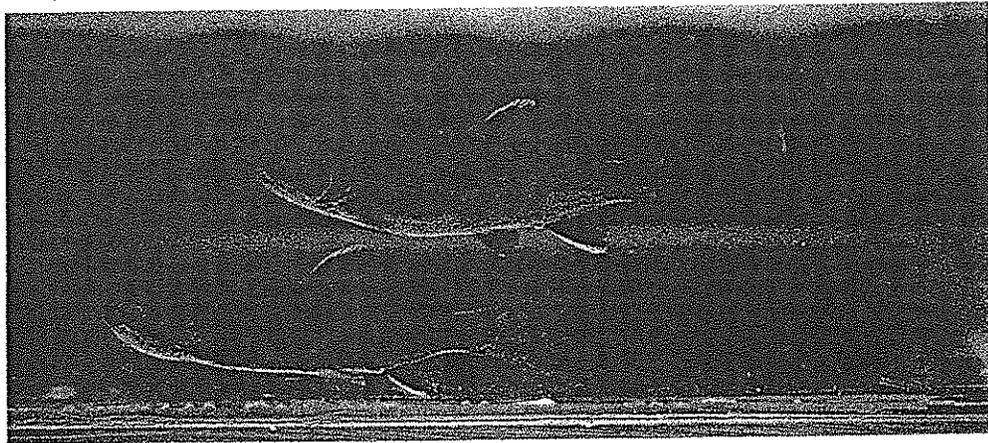
PLATE 14 (*previous page*). Chinook salmon life history stages. *Painting by H. Heine*



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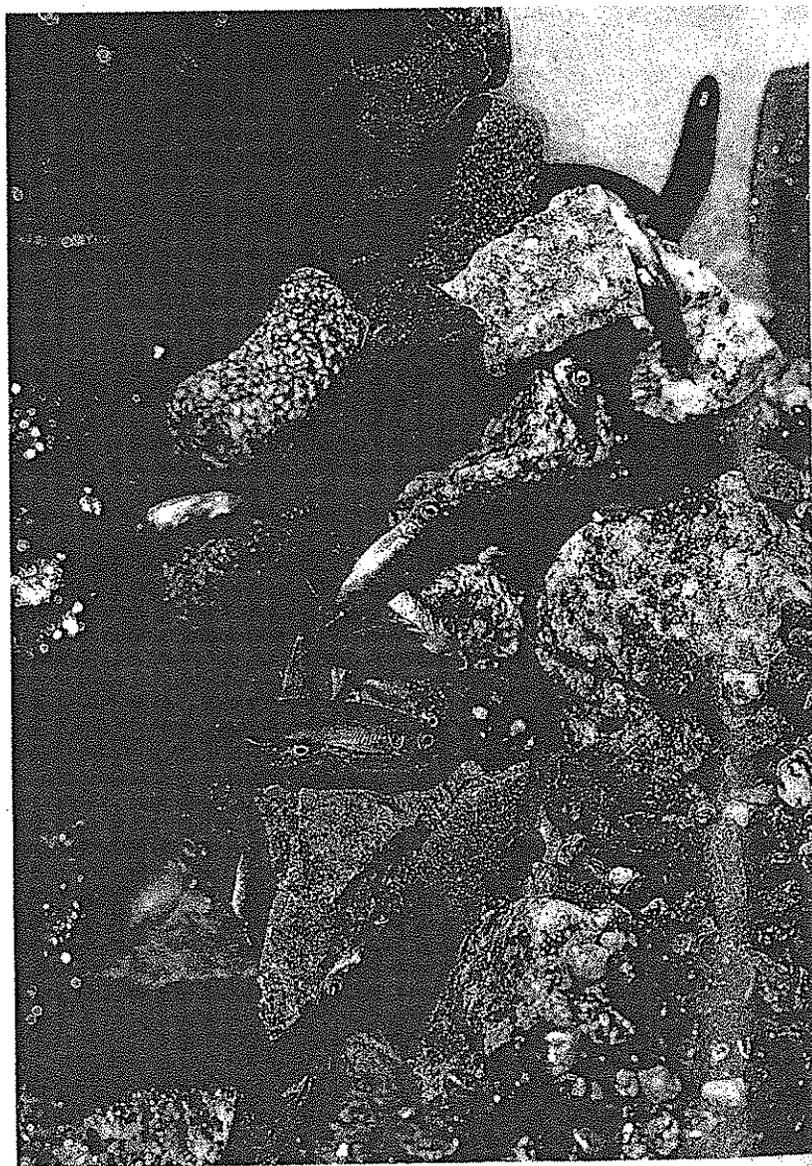




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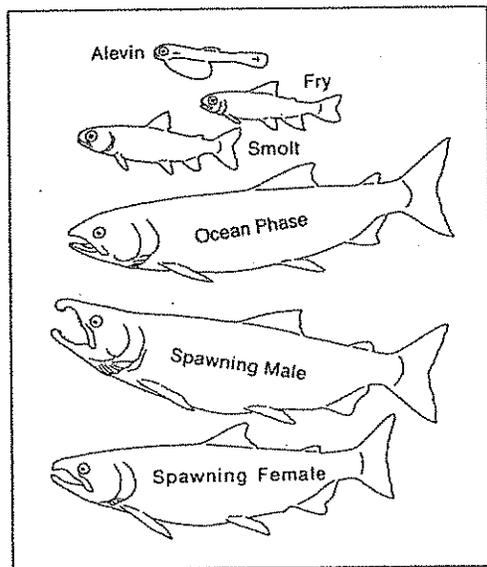
PLATE 18. Coho fry in full colour, Rosewall Creek, British Columbia. *Photograph by Marj Trim*

PLATE 19. Early coho fry in gravel bed prior to emerging, Rosewall Creek, British Columbia. *Photograph by Marj Trim*



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PLATE 17 (previous page). Coho salmon life history stages. *Painting by H. Heine*



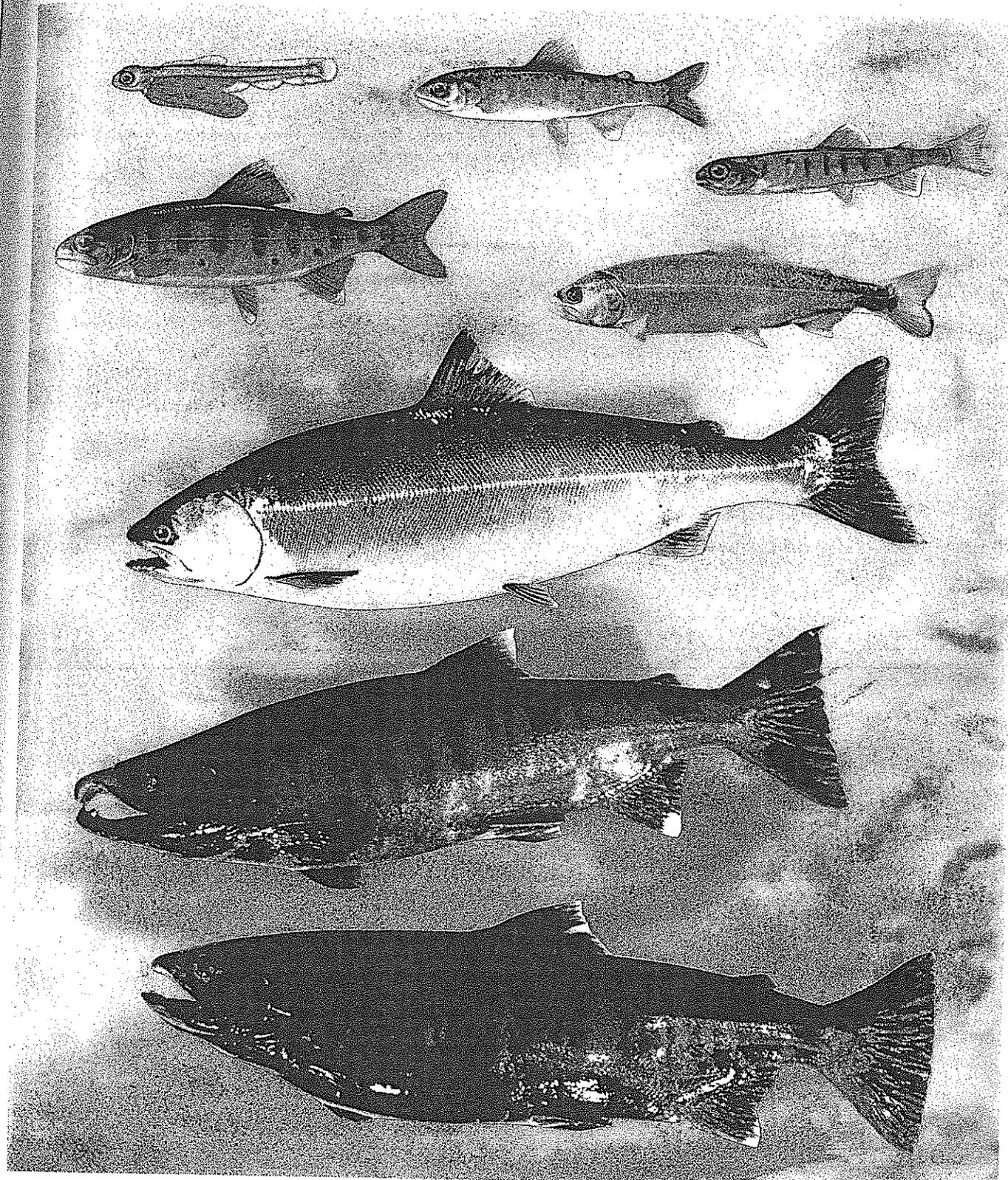


PLATE 20. Masu salmon life history stages: (left to right and top to bottom) alevin, fry, fingerling, stream-type, smolt (photograph by H. Ida), ocean phase (photograph by H. Masuda), spawning male and spawning female (photographs by H. Mayama)

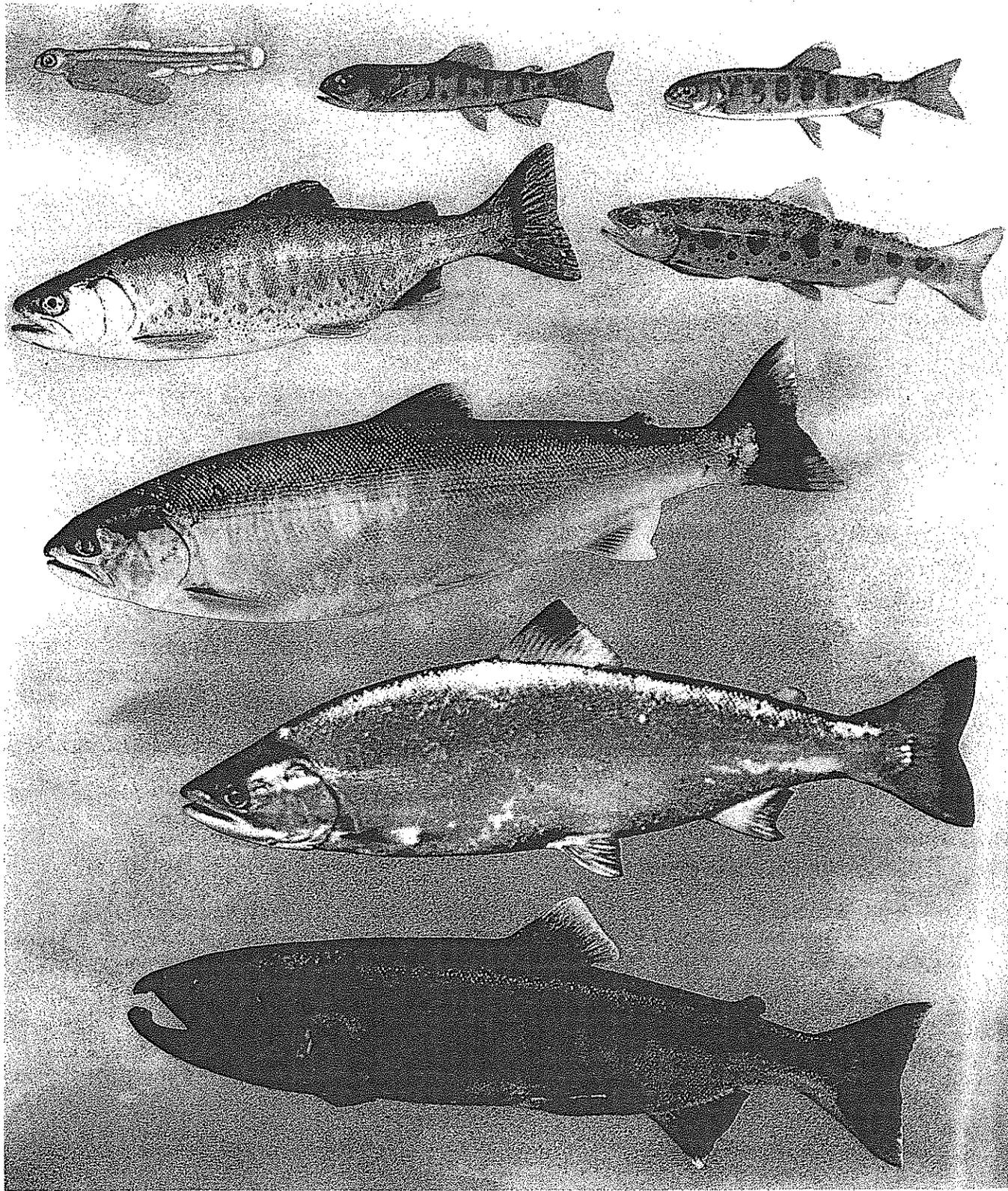


PLATE 21. Amago salmon life history stages: (left to right and top to bottom) alevin, fry, fingerling, mature stream-type (courtesy Japan Marine Products Photo Materials Association), immature stream-type, lake-type, and upstream migrating female (photographs, Freshwater Fish Protection Association), spawning male (photograph by H. Matsubara)

## Life History of Chum Salmon

After a nosing bout, she usually swims back and digs in the area just passed over (Schroder 1982). Prior to final nest site selection the female may nose and perform exploratory digging over a fairly large area. Once a suitable nest site has been located, digging movements become more concentrated into an increasingly smaller area (Tautz and Groot 1975). Much of this activity may be visually mediated (Duker 1977).

The primary tactic used by the female is to search for an unoccupied space without fighting. Once a spawning territory is established, the female attempts to protect as much space as possible. Territorial evictions of already established females are rare events, even under relatively high (0.6 females/m<sup>2</sup>) spawner densities (Schroder 1982). Only weaker, spawned-out females are evicted.

### *Nest Construction*

In digging, the female turns her body on its side and performs a series of four to six flexures, slapping her tail on the gravel substrate. During each dig the pectoral fins are held perpendicular to the body surface and appear to function as brakes to stop her from shooting forward. After a dig, the female normally turns and swims back to the rear part of the nest. Besides turning and circling, the female also "weaves" over the nest in tight circles or figure-eight movements (Schroder 1982).

Digging is initially performed by fanning out from a downstream position of the nest to create a general impression in the gravel of several square metres. As nest construction progresses, digging occurs more and more in the center of the nest. This results in a cone-shaped hollow in the gravel of about 20–40 cm deep, with a porous layer of stones around the bottom portion.

While the female is digging, the male courts her. His principal courtship activities consist of "quivering," which is a quick approach towards the female accompanied by a high frequency low amplitude undulation of the body, and "crossing over," in which the male swims from side to side over the caudal peduncle region of the female (Tautz and Groot 1975). The first courting movement a male performs after locating a female is often a quiver.

After the nest develops a centralized depression, the female lowers her tail and mid-body and

"probes" the substrate with her anal fin extended. When contact is made with the gravel she reverses the movement and returns to the original position. She may then weave, dig, or perform another probe. As the nest nears completion the female decreases her tendency to turn and circle after each dig and increases the frequency of probes; in response, the male increases his performance of crossing-over and quivering activities (Tautz and Groot 1975). Probing and quivering usually occur in a predictable order. As soon as the female initiates a probe, the male, while quivering, approaches her from his position behind and to one side of her. After completing the probe the female comes up again and the male drifts back to his original courtship position. The angle of the probes becomes more and more pronounced as the nest develops and when it reaches about 20° the nest is complete.

Duker (1982) described a model for the pre-spawning phase of chum salmon involving orientation and species recognition, and the sensory systems utilized to locate and choose conspecific mates (Figure 2). Of the potential auditory cues available in the noisy lotic environment, only the sounds of digging by the female appear to provide information on the location of reproductively active females. Tactile cues involving physical contact in reproductive behaviour appear to be limited to the female's interaction with the gravel substrate. Visual cues, however, are important because the body coloration clearly distinguishes the species, especially the conspicuous pigment patterns found in the mouths of the spawners. Females appear to respond more actively to the external body coloration of males than do males to the coloration and configuration of females. The black and white pigmentation pattern inside the mouth is species specific, and is very evident as the courting pair gape simultaneously at spawning (Schroder 1981; Duker 1982) (Plate 13). Duker suggested that non-visual cues are perceived by both sexes during their short-range courtship interactions and that combinations of visual and non-visual cues contribute to the process of identification. He also concluded that olfaction does not play a major role in mate selection in guiding males to active female conspecifics. However, the response of chum salmon males to heterospecific females suggests that long-range olfactory cues may be

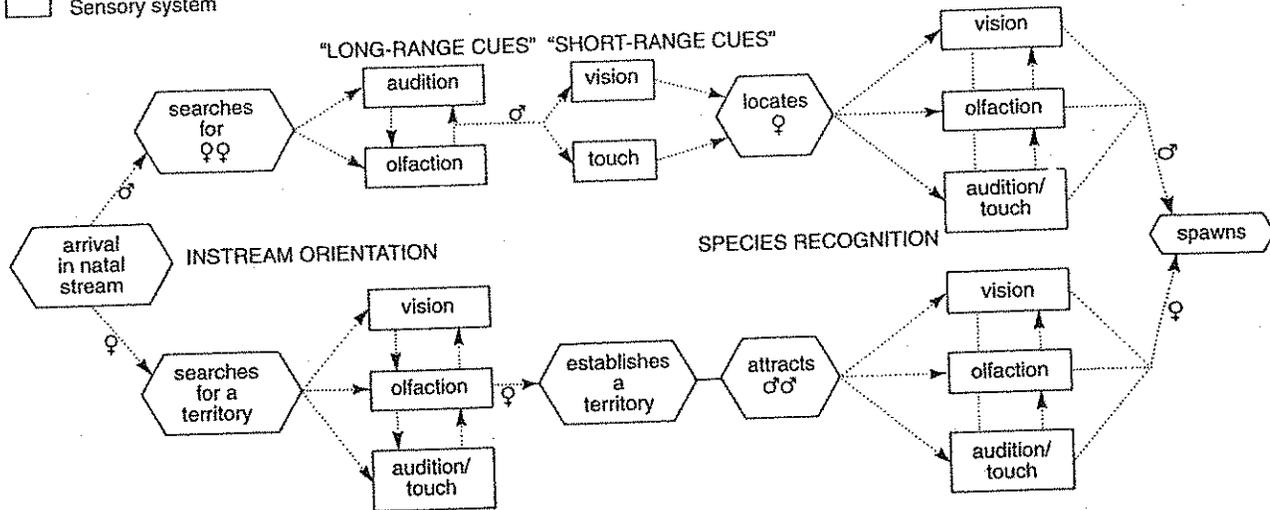
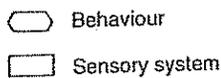


FIGURE 2

A model illustrating the behaviour of Pacific salmon and the sensory systems utilized by these fish to locate and choose conspecific mates. (From Duker 1982)

important in separating chum from coho salmon in sympatric situations.

#### *Mating and Covering of Eggs*

When the female is ready to deposit her eggs, she will move into the nest and "crouch," which looks like a probe but with mouth agape. When she starts to crouch, the male immediately moves forward and lies next to her assuming a similar posture (Plate 13). At this point the reproductive products are released with both partners vibrating their caudal peduncle and anal fin. Sometimes the female will perform several crouches in succession before releasing the eggs. In each crouch she is followed by the male. The spawning act lasts, on average, 10 seconds (Schroder 1982).

Within seconds of egg deposition, the female starts to cover the eggs with gravel. She moves upstream, turns sideways and, while laying her tail on the gravel, gently flexes her body two or three times. The first few "covering digs" do not move any gravel but drive the eggs into the gravel interstices (Tautz and Groot 1975; Schroder 1982). Subsequent digs become more vigorous as the nest pocket fills with gravel, and after 15-30 minutes, when the nest is completely closed, the female returns to normal

nest digging. This results in the construction of the second nest in front of the first one.

Schroder (1982) reported that most females (>80%) completed spawning 30-40 hours after starting their first nest in the Big Beef Creek experimental spawning channel. He also noted that about 35% of the eggs were deposited in the first nest and that the last few nests contained only one-half to one-quarter the number of eggs of the first one.

The male may stay around for a little while after mating but generally moves on to find another female in the process of nest construction. Males remain sexually active for 10-14 days. The difference in duration of sexual activity between sexes increases the likelihood of intrasexual competition, especially when the ratio of sexually-active males to sexually active females is above unity.

Male chum salmon use physical force, that is, open mouth rushes, bites, and body blocks (Figure 3), to compete with other males for spawning opportunities and, occasionally, battles occur (Schroder 1973, 1981). The ability of the male to maintain a mate, or obtain one, depends on his relative size. Large and dominant males have a greater chance of obtaining a mate, whereas small or weak males spend more time searching for po-

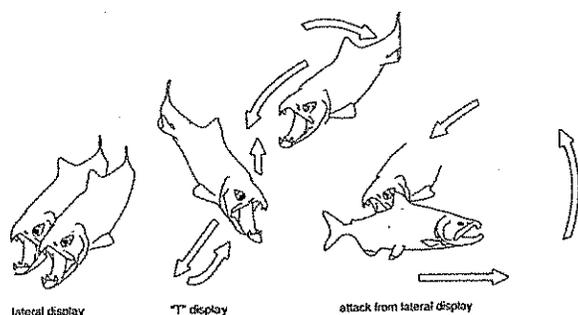


FIGURE 3

Ritualized fighting displays used by male chum salmon.  
(From Schroder 1981)

tential mates and attempt to avoid conflicts (Schroder 1982). Subdominant or satellite chum males will adopt the strategy of positioning themselves downstream from a courting pair. From this position the subdominant male continuously approaches the female and attempts to fertilize some of her eggs when she crouches with the dominant male. Schroder (1982) found that as competition for females increased, the occurrence of satellite males rose. At male-to-female ratios of less than one, the percentage of males employing the subdominant male strategy approached zero, but increased to as high as 30% when the ratio equalled three. Using electrophoretic techniques to estimate the gametic contributions of alpha (dominant) and satellite males, Schroder (1982) concluded that satellite males can make significant gametic contributions (up to 25%). He also observed from analysis of video tapes that the closer the male is to the female the more eggs he is able to fertilize. Extreme competition makes participation of some satellite males difficult because the female is obscured by competitors. Schroder (1982) also found that mate selection by males was not influenced by size of the female but by her "attractiveness" as expressed by her behaviour in terms of nosing, turning, digging, and weaving. Under extremely high spawning densities, courtship and territorial defenses break down and "mass spawning" occurs (E.O. Salo, unpublished data; D. E. Rogers, Fisheries Research Institute, University of Washington, Seattle, Washington, pers. comm.).

#### *Nest and Redd Characteristics*

Burner (1951) and Helle (1979) reported that the

average depth of chum salmon nests is 21.5 cm (range 7.5–43 cm), not including the depth of the eggs. Bruya (1981), on the other hand, found that chum salmon nests have a mean depth of 42.5 cm and that high survivals to emergence (mean 84%) resulted from egg depositions in gravel depths ranging from 20 to 50 cm. He concluded that a minimum of 30 cm is essential and a depth of 40 cm is optimal. Premature emergence of fry occurs in nests of less than 20 cm deep and rises to 80% at nest depths of 10 cm.

The size composition of gravel selected for spawning by chum salmon in Hokkaido averages 25% for gravel less than 0.5 cm in diameter, 5% for gravel from 0.6 to 3.0 cm, and 30% for gravel greater than 3.1 cm (Sano 1959). Redds of chum salmon in the tributaries of the Columbia River consisted of gravel of which 13% was larger than 15 cm, 81% was 15 cm or less, and 6% was silt and sand (Burner 1951).

Rukhlov (1969) described the spawning gravels of chum salmon of six rivers in Sakhalin in terms of silts, sand, gravel, and "shingle." He noted that the percentage of fines and sand was less in the nests than in the surrounding gravels (11.5% versus 14.7%) and that when the proportion of sand was 22% or greater, the survival of the eggs was less than 50%. Because of the predominance of pink salmon, the percentage of sand in the gravel was less in odd years. Of the six rivers, chum inhabited mainly those with significant groundwater and higher base flows.

In measurements of over a thousand redds in the state of Washington, Johnson et al. (1971) noted that, although chum salmon spawned in velocities ranging from 0.0 to 167.6 cm/s, 80% spawned in velocities between 21.3 and 83.8 cm/s, with the mean being 50.3 cm/s. The water depth over 80% of the redds ranged from 13.4 to 49.7 cm, and the distribution of the depths was highly skewed with a mean of 27.1 cm.

Water velocities selected by autumn chum in Hokkaido are from 10 to 20 cm/s (Sano and Nagasawa 1958), whereas summer chum in the My River spawn in velocities of 10–100 cm/s (Soin 1954). Water depths range from 20 to 110 cm in Hokkaido and from 30 to 100 cm in the My River. Artificial spawning channels for chum salmon are typically regulated to have flows of about 20 cm/s. Flows over Japanese-type incubation "keeper" channels,

which utilize systems of screens to retain the eggs until hatching, have flows of about 50 cm/min. Bams (1982) found that the developmental rate was increased and larger fry were produced at higher (66 cm/min) than at lower flows (33 cm/min). Chum salmon, although the second largest in size of the Pacific salmon, have adapted to spawning in waters of lesser depths and velocities than the pink salmon and some of the other species in the genus. Typically, summer chum spawn in deeper waters and higher velocities than autumn chum (Soin 1954; Sano and Nagasawa 1958).

#### *Post-Spawning Longevity and Egg Retention*

Koski (1975) defined post-spawning longevity of the chum salmon as the elapsed time in hours after they had been placed in the spawning channel at Big Beef Creek (which was very soon after arrival into the stream) until their observed death. The average longevity of females and males combined

for an early stock was 8.8 days and 10.5 days for 1968 and 1969, respectively. The late stock averaged 11.2 days and 15.2 days for the same years. Koski suggested that the colder water temperatures in 1969 may have been partly responsible for the increased longevity. The males lived longer than the females, and Koski (1975) and Schroder (1977) observed that there was no significant change in longevity with different spawning densities.

The number of eggs retained by the females after spawning vary considerably. The longer the female delays spawning and the higher the spawner density, the greater the egg retention (Schroder 1981). Although spawning generally occurs during a period of falling temperatures, prolonged cold water temperatures increase spawning time and egg retention. Spermatazoa are produced for as long as 26 days (Koski 1975), which allows males to spawn with more than one female (Smirnov 1975).

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## FECUNDITY

Fecundities of chum salmon reported in the literature are not reliable because of the uncertainty in data collection. Individual measurements may be comparable, but it is not certain how representative the samples are for the reported geographical regions and rivers of origin. This is particularly true of samples collected in commercial catches. Nevertheless, when both absolute fecundity (number of eggs/female) and relative fecundity (number of eggs/cm of length) are considered, similarities and differences among regions can be noted.

In Asia, individual absolute fecundities ranged from 909 to 7,779, and annual means ranged from 1,800 to 4,297 eggs per female. In North America, the reported fecundity of individuals ranged from 2,018 to 3,977, and annual means ranged from 2,107 to 3,629 eggs per female. Generally, the northern stocks in Asia have a higher relative fecundity than the southern stocks. This trend is apparent for both summer and autumn chum in the USSR (Ku-

likova 1972) (Table 1). These differences are masked, to some extent, when absolute fecundities are considered because of body size differences among stocks. In North America, there is a weak trend for northern stocks of autumn chum to have lower absolute and relative fecundities than the southern stocks (Table 2; Figure 4).

The reasons for the latitudinal trends are not obvious but are probably related to survival rates decreasing from south to north in Asia and north to south in North America. Information is lacking on latitudinal differences in fecundity by age and size, along with their relative survival rates.

#### *Fecundity and Stream Size*

Races in small, short streams tend to be less fecund than stocks from longer streams (Kayev 1983). Beacham (1982) reported lower fecundities for stocks on Vancouver Island and the Queen Charlotte Islands than for a few mainland stocks. Ex-

Life History of Chum Salmon

**TABLE 1**  
Length, absolute fecundity, relative fecundity, and egg diameter of female chum salmon (age 0.3), in the USSR, 1966

Location	Fork length mean (cm)	Absolute fecundity	Relative fecundity (No. egg/cm)	egg diameter (cm)
<b>Summer chum</b>				
N Anadyr R. (Bering Sea)	65.5 ± 1.10	3160 ± 191.80	48.2	.71 ± .01
Bolshaya R. (Kamchatka)	61.5 ± 0.80	2490 ± 93.53	40.5	-
Tauï R.	62.7 ± 0.65	2770 ± 85.30	45.0	-
Kukhtuy	62.2 ± 0.37	2850 ± 110.15	45.0	.75 ± .02
Iski R.	61.5 ± 0.92	2510 ± 83.00	40.8	.79 ± .02
S Amur R.	52.2 ± 0.59	2200 ± 55.20	39.8	.79 ± .02
<b>Autumn chum</b>				
N Amur R.	64.5 ± 0.71	3450 ± 716.30	53.5	.70 ± .03
Naiba R.	65.5 ± 0.93	2805 ± 67.42	42.8	.93 ± .01
Kalininka R. (W. Sakhalin)	67.3 ± 0.76	2720 ± 115.30	40.4	.90 ± .03
S Kurilka R. (S. Kuril)	69.3 ± 0.84	2600 ± 89.32	37.5	.95 ± .01

Source: Adapted from Kulikova (1972)

Notes: Rivers are listed north (N) to south (S); 100 fish sampled in each river

**TABLE 2**  
Relative fecundity (eggs/cm of fork length) of North American autumn chum salmon

Location	Eggs/cm	Sample	
		size	Source
N Yukon R. (Delta R., AK)	41.2	14	Trasky (1974)
Skeena R. (BC)	45.2	54	Beacham (1982)
Pallant Cr. (BC)	40.2	58	Beacham (1982)
Mathers Cr. (BC)	41.5	14	Beacham (1982)
Tlupana R. (BC)	41.0	26	Beacham (1982)
Little Qualicum R. (BC)	43.7	33	Beacham (1982)
Big Qualicum R. (BC)	44.1	577	Beacham (1982)
Squamish R. (BC)	43.9	61	Beacham (1982)
Fraser R. (BC)	44.9	222	Beacham and Starr (1982)
Fraser R. (Harrison R., BC)	46.9	15	Beacham (1982)
S Big Beef Cr. (WA)	46.3	-*	Koski (1975)

Notes: Locations are listed north (N) to south (S).

\*Unreported

ceptions include Big Beef Creek, which is a small stream with high fecundity levels (Koski 1975).

Beacham (1982) suggested that differences in fecundity among streams may result from high exploitation rates. Kayev (1983) found that chum salmon inhabiting short streams on the Kuril Islands, with good groundwater and favourable estuarine and marine conditions, were less fecund and had greater fry survival.

*Differences in Seasonal Runs*

In Asia, the Amur River autumn stocks are more fecund (relatively and absolutely) than summer stocks (Lovetskaya 1948; Birman 1956; Svetovidova 1961; Sano 1966; Kulikova 1972) (Tables 1 and 3; Figure 4). Early-run chum salmon at Big Beef Creek are more fecund (50 eggs/cm) than the late-run chum (46.0 eggs/cm) (Koski 1975), which is the opposite of the situation seen in the distinct seasonal races of the Amur River. Data from Andersen (1983) and Trasky (1974) showed a slight difference in relative fecundity between summer and autumn chum of the Yukon River (summer, 45.5 eggs/cm, N = 23; autumn, 41.2 eggs/cm, N = 24). Although the samples are small, the differences are similar to those presented by Koski (1975) for the early-run and late-run chum at Big Beef Creek.

*Egg Diameter*

In Asia, egg diameter increases from north to south (Table 1). Southern stocks incubate at higher temperatures, and the higher metabolic rates require a greater supply of energy; also, if the northern stocks are more fecund, egg size may be limited by egg number. However, egg diameter is correlated with female size and dependent upon spawning time (Beacham and Murray 1986; T. Beacham, Pacific Biological Station, Nanaimo, British Columbia, pers. comm.). Although the size of eggs of chum salmon has no effect on hatching time, exogenous yolk absorption ("button-up"), or emergence from the redd, larger eggs produce alevins that are longer and have greater amounts of yolk than those produced from smaller eggs. The differences are maintained through the alevin to the newly emerged fry stage (Beacham et al. 1985). Whether southern stocks encounter more potential predators than northern stocks is not known, and

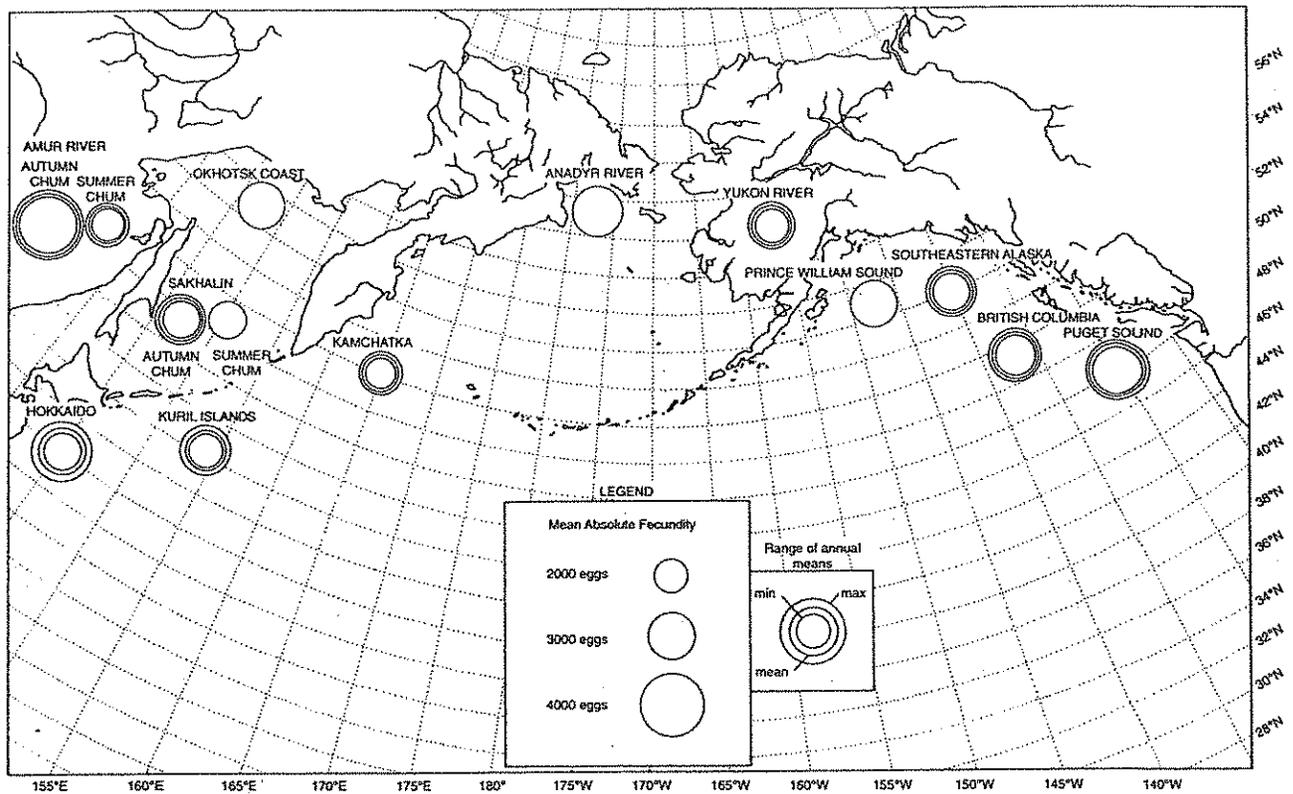


FIGURE 4

Absolute fecundity of chum salmon in Asia and North America

TABLE 3  
Relative fecundity (eggs/cm of fork length) of  
Amur River system chum salmon

Year	Summer chum			Autumn chum			
	My	Ul	Beshenaya	Angun	Kur	Khor	Bira
1946	-	-	-	-	-	46.0	56.3
1947	-	-	-	-	-	55.7	55.2
1948	-	-	-	-	-	56.7	57.1
1949	-	-	38.8	50.4	-	53.8	59.3
1950	37.2	-	40.1	52.0	61.1	-	55.4
1951	39.2	37.7	39.5	50.2	-	54.7	58.5
1952	39.5	37.5	40.0	53.3	-	52.3	57.2
1953	37.5	35.5	39.2	53.5	-	56.5	54.0
1954	39.5	39.0	39.3	-	-	-	-
1955	42.5	38.5	47.5	-	-	-	-
Average	39.6	37.7	39.5	51.7	61.1	53.7	56.5

Source: Data for summer chum from Svetovidova (1961); data for autumn chum from Birman (1956)

Note: Arrows indicate increasing distance from estuary.

whether this is related to the northern fish being smaller is also conjectural. The relationships between prey availability and predator gape are documented but these have not been related to the north-south change in fry size.

## INCUBATION AND EMERGENCE

Incubation and emergence and the "quality" and "fitness"<sup>2</sup> of the emerging fry are affected by stream flow, water temperature, dissolved oxygen, gravel composition, spawning time, spawner density, and genetic characteristics (Figure 5) (Koski 1975, 1981; Bams 1982, 1983; Beacham and Murray 1986).

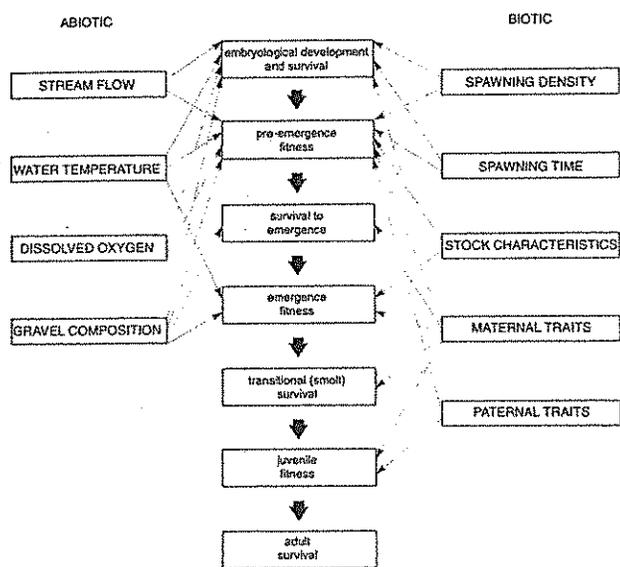


FIGURE 5

Diagram of the interrelationships of the abiotic and biotic factors in the salmonid incubation environment which affect fitness and survival. (From Koski 1975)

#### Water Temperatures and Temperature Units

The incubation time of eggs is prolonged by lower temperatures, and the time of hatching and emergence varies among stocks because of differences in the number of temperature units (TU's)<sup>3</sup> required for hatching and development. These variations may be genetically controlled, and the

differences between the temperature units required for hatching and emergence of early and late stocks result in a tendency towards similar emergence times (Koski 1975).

In many Asian and North American streams, the late-running stocks select areas with springs having water temperatures generally above 4°C. This protects the eggs from freezing and results in more or less consistent times of emergence from year to year. Nikolskii (1952) pointed out that during severe winters the redds of autumn chum near the outflow of groundwaters were less affected by freezing than redds of the summer chum in the main stream. Adaptation to intertidal spawning also allows for compensation for environmental extremes because warmer marine waters cover the spawning areas during each tidal cycle. Thorsteinson (1965) reported that a 3.2 m tidal differential caused an 8°C change in the temperature of an intertidal redd in Olsen Creek.

Low water temperatures (near or at freezing) during spawning and incubation can account for significantly high mortalities of salmonid eggs and alevins (Smirnov 1947; McNeil 1962, 1966; Levandov 1964; Sano 1967). In the state of Washington, a drop in water temperature below 2.5°C inhibits nest construction and spawning by chum salmon (Schroder 1973). Schroder et al. (1974) found significantly higher mortalities of chum salmon eggs, alevins, and fry when the eggs were incubated in water temperatures below 1.5°C during the early stage of development (before blastopore closure).

Chum salmon eggs require about 400 to 600 TU's to hatch and about 700-1,000 TU's for yolk absorption (Table 4). Values vary among stocks and among individuals within stocks. At Big Beef Creek, a range of 30 days occurred between completion of emergence of the early and late stocks in a single year, and a difference of 60 days occurred between years (Figure 6). The Susitna River (Alaska) and the Amur River autumn chum stocks have very low TU requirements (Table 4), which are stock-specific adaptations to low incubation temperatures.

2 For definitions of "quality" and "fitness" see Bams (1983) and Koski (1975, 1981). They discuss the deviation of these terms from the genetic definitions (relative reproductive success).

3 TU = the average number of degrees above 0°C during a 24-hour period.

TABLE 4  
Accumulated temperature units required for hatching and yolk absorption for chum salmon eggs

Stock	Temperature units (C°-days) to hatching		Mean temp. (C°)	Temperature units (C°-days) to yolk absorption		Mean temp. (C°)	Source
	Days	Days		Days	Days		
Amur R., USSR (autumn)	408-420	122-128	3.4 <sup>1</sup>			3.4 <sup>1</sup>	Disler (1954) <sup>5</sup>
Susitna R., AK <sup>6</sup>	292	173	1.7 <sup>2</sup>	623	284	2.2 <sup>2</sup>	Wangaard & Burger (1983)
	447	123	3.6 <sup>2</sup>	728	250	2.9 <sup>2</sup>	
	489	106	4.6 <sup>2</sup>	847	215	3.9 <sup>2</sup>	
	473	117	4.0 <sup>3</sup>	860	213	4.0 <sup>3</sup>	
BC (specific stock not reported)	510-589	52-61	9.7-9.8 <sup>3</sup>			9.7-9.8 <sup>3</sup>	Alderdice et al. (1958) <sup>5</sup>
Big Beef Cr. WA (early)				1060 <sup>4</sup>	166	-	Koski (1975)
Big Beef Cr. (late)				933 <sup>4</sup>	146	-	Koski (1975)
Skagit R., WA	453	114	4.0 <sup>2</sup>	867	155	4.7 <sup>2</sup>	Graybill et al. (1979)
	623	86	7.2 <sup>3</sup>	1124	157	7.2 <sup>3</sup>	Graybill et al. (1979)
	565	118	4.8 <sup>3</sup>	958	200	4.8 <sup>3</sup>	Graybill et al. (1979)
	509	182	2.8 <sup>3</sup>	909	325	2.8 <sup>3</sup>	Graybill et al. (1979)

Notes: 1 Water temperatures varied less than 1°C

2 Mean of variable stream water temperature

3 Constant water temperature

4 C°-days to emergence

5 Cited by Bakkala (1970)

6 Values are averages based on Appendix Table 1 of Wangaard and Burger (1983)

Although the number of TU's required for hatching and yolk absorption is generally less at low than at high temperatures (Table 4), these compensations are not sufficient to offset all the effects of temperature on development. In warm years, hatching and development is accelerated. Some compensation for annual variation in temperatures within stocks is provided for by the number of temperature units required, which is partially a function of the temperature regime experienced. Beacham and Murray (1986), working with early, middle, and late spawning Fraser River stocks, and constant temperatures of 4°, 8°, and 12°C, found that time of spawning had no effect on hatching time of alevins. Thus, development rates of eggs from fertilization to hatching provided no evidence for stock adaptation of Fraser River chum salmon to their time of spawning. On the other hand, timing of emergence of the fry within each incubation temperature was dependent on the relative timing of the stocks. Early-spawning stocks had heavier eggs, and fry from these stocks had later emergence times.

In summary, differences in TU's required for emergence of fry vary within stocks depending on

temperature regimes (weather) and among stocks depending on long-range temperature characteristics (climate) of the incubation environment. Generally, there is a tendency towards a common time for emergence and migration.

#### *Dissolved Oxygen*

A number of authors (Wickett 1954; Coble 1961; Phillips and Campbell 1962; McNeil 1966) have shown that the survival of salmonid eggs and alevins is directly related to the intragravel dissolved oxygen content. Wickett (1954) calculated that the lethal level (minimum) for chum salmon is 1.67 mg/l. Koski (1975) found that the survival rate decreased rapidly when the concentration of oxygen dropped below 2 mg/l. Alderdice et al. (1958) conducted experiments on the survival of various-aged chum salmon eggs after seven days of exposure to low dissolved oxygen levels and found that (1) eggs were most sensitive to hypoxia between 100 and 200 C degree-days, and compensated for reduced oxygen availability by reducing the oxygen demand and rate of development (increase in TU requirements); (2) very low oxygen levels at

## Life History of Chum Salmon

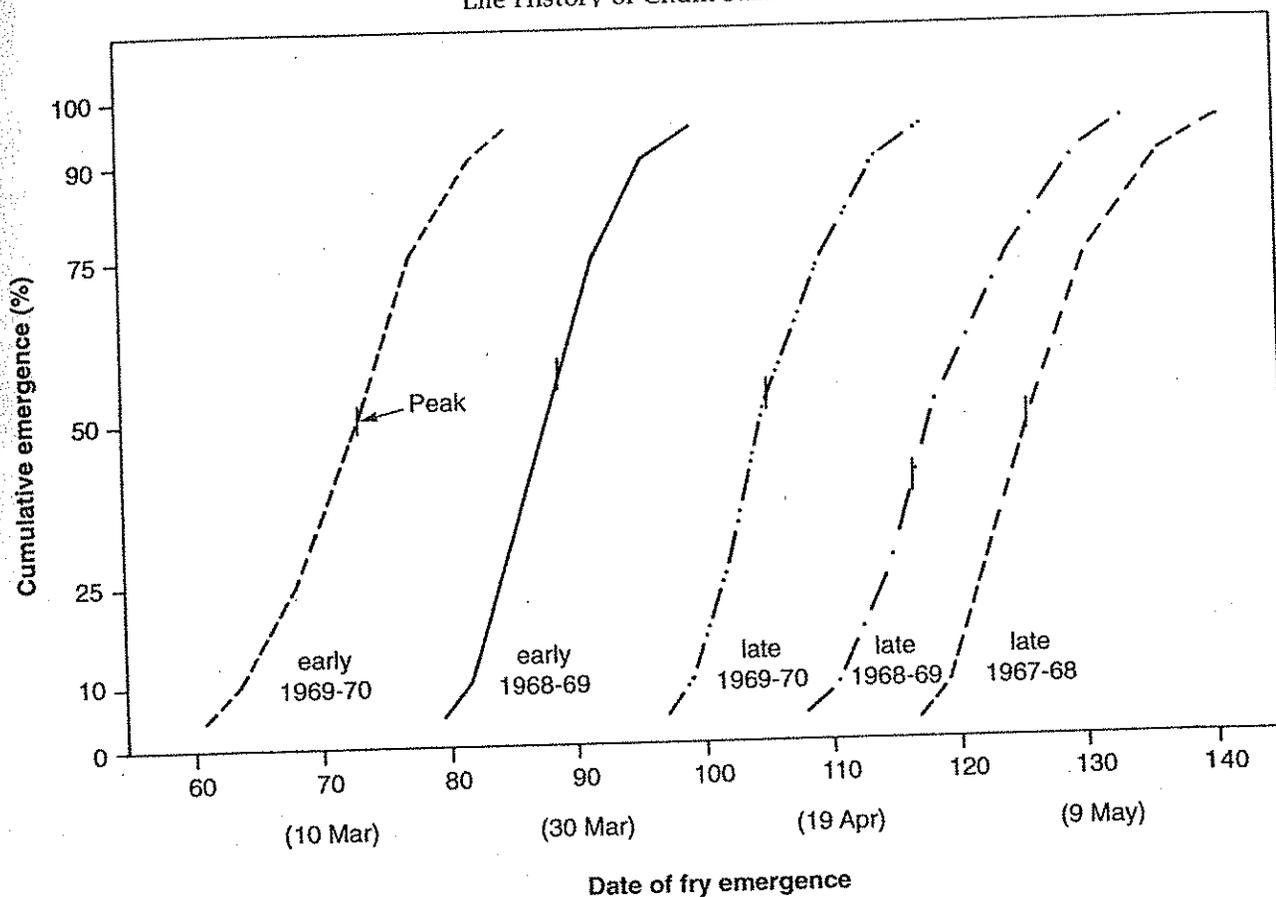


FIGURE 6

Annual variation in the timing of fry emergence for early and late stocks of chum salmon from the Big Beef Creek channels (Julian calendar and the calendar year date are given). (From Koski 1975)

early incubation stages cause monstrosities; (3) estimated median lethal levels rose slowly from fertilization to hatching; and (4) oxygen consumption per egg rose from fertilization to hatching, although the consumption per gram of larval tissue declined from a high at about the time of blastopore closure. Under experimental conditions, the incipient median lethal level for dissolved oxygen rose with development from approximately 0.4 ppm in early development to 1.0-1.4 ppm prior to hatching. The calculated critical oxygen levels varied from 0.72 ppm at 4 C degree-days to 7.1 ppm at 452 C degree-days. Fast and Stober (1984) corroborated the increasing oxygen requirements for developing salmon embryos and determined that chum salmon have lower oxygen requirements than either coho salmon or steel-

head (*O. mykiss*), reflecting a lower metabolic demand.

Koski (1975) found no significant differences in the size of chum salmon fry emerging from redds with prolonged minimum dissolved oxygen concentrations (less than 6.0 mg/l). Alderdice et al. (1958) reported that eggs subjected to low dissolved oxygen levels just prior to hatching, hatch prematurely at a rate dependent on the degree of hypoxia, and Koski (1975) noted that the number of days to initial emergence was greater at prolonged low dissolved oxygen concentrations (less than 3.0 mg/l).

Bams and Lam (1983) concluded that deteriorating water quality in a Japanese-style keeper channel (upstream to downstream) measurably reduced larval development rate, growth rate, and

yolk conversion efficiency. The main effective factor was low dissolved oxygen which stimulated the pre-emergence of fry during unfavourable conditions.

#### Condition Factor, Egg Size, and Fry Size

The coefficient of condition,  $K_D$  ( $=10 \cdot \sqrt[3]{\text{Weight}(\text{mg})/\text{Length}(\text{mm})}$ ), was developed by Bams (1970) as a comparative index of the condition of salmon alevins and fry. Bams reported a  $K_D$  of 1.92 at tissue resorption for chum from Hooknose Creek, British Columbia. The  $K_D$  at this stage for Big Beef Creek chum fry was 1.89 for those incubated in 10 cm of gravel, and 1.83 for those incubated in deeper gravel (Bruya 1981). Although there are differences among stocks (Abbasov and Polyakov 1978; Koski 1981; Beacham and Murray 1986), Bruya (1981) felt that the difference between Bams' results and his were due to the effects of preservation in formalin. Incubation environments with low oxygen can produce alevins with high indices of development ( $K_D$  factors) (Alderdice et al. 1958). Also, large eggs produce alevins with higher  $K_D$  values than do smaller eggs, so the actual factor of development is affected by the size of the egg (Beacham and Murray 1986). Late-spawning Fraser River stocks have smaller eggs and shorter times from fertilization to fry emergence than early-spawning stocks (Beacham and Murray 1986).

The need to optimize the development of eggs and alevins in a biologically efficient manner has been recognized by a number of investigators (Disler 1953; Brannon 1965; Bams 1967, 1969; Poon 1970; Emadi 1973; Mathews and Senn 1975; McNeil and Bailey 1975). The results of these studies are being applied in chum salmon hatcheries in the Soviet Union, Japan, and North America.

Chum salmon alevins incubated on unaltered screen substrates at production levels of 8,000 eggs per tray in water with and without sediment were found to be significantly smaller, by as much as 0.1 g/fry in weight and 4.9 mm in length, than fry incubated on artificial substrates (B. Snyder, Big Beef Creek Fish Research Station, University of Washington, Seattle, Washington, pers. comm.). Also, at the time of "ponding" of the former fry, they were less developed and had a higher condition coefficient ( $K_D$ ) than fry incubated on artificial substrates.

#### Gravel Composition and Spawner Density

Sediment affects the survival of salmonids in at least three ways: (1) direct suffocation of eggs and alevins, (2) reduced intragravel water flow and dissolved oxygen content, and (3) a physical barrier to emergence (Koski 1966, 1975; Gibbons and Salo 1973; Iwamoto et al. 1978). Using substrates with four different levels of intragravel sediments, Koski (1966, 1975) determined the rates of survival to emergence in experimental channels. The survival to emergence was highest (63%) in gravel containing 11%-30% sand. For each 1.0% increase in sand there was a 1.26% decrease in survival to emergence (Koski 1981) (Figure 7). Koski assumed that the amount of fines in the spawning gravel is, in essence, an index of the "living space" available for the developing eggs and alevins, reflecting the

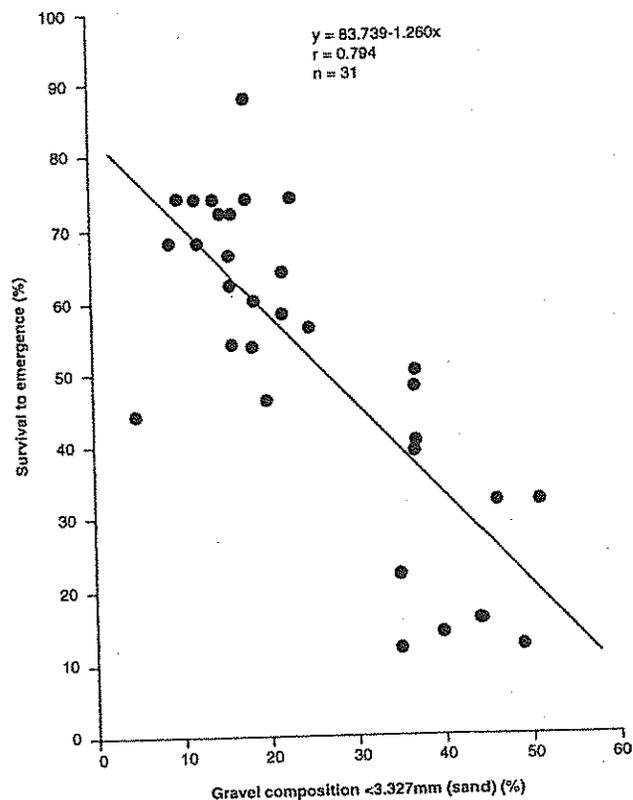


FIGURE 7

Relationship between the percentage of sand (fines <3.327 mm,  $\geq 0.105$  mm) in the gravel and the rate of survival to emergence of chum salmon (1968 and 1969). (From Koski 1975)

percentage of voids within the gravel.

In an experiment in the incubation channels at Robertson Creek, British Columbia, Dill and Northcote (1970) determined that the survival of chum salmon from planting of eggs to emergence of fry was higher in large gravel (5.1-10.2 cm) than in small gravel (1.0-3.8 cm). Gravel size, depth of egg burial (20.3 and 30.5 cm), or density of eggs (50 and 100) had no effect on the condition coefficient or timing of emergence.

Using survival from egg deposition to downstream migration of the fry as a criterion, Schroder (1973) determined that the optimum spawning density of chum salmon in controlled flow channels of Big Beef Creek was 1.7 m<sup>2</sup>/female (0.6 females/m<sup>2</sup>). Thorsteinson (1965) found that the optimum density of spawners in the intertidal areas of Olsen Creek, Alaska, was between 2 and 3 females/m<sup>2</sup>, with no increase in successful egg deposition at five or more females per square metre.

#### *Effects of Salt Water and Other Water Quality Factors*

Bailey (1964) and Thorsteinson (1965) determined that chum salmon spawning in the intertidal areas of Prince William Sound, Alaska, was widespread and that the intertidal spawners were discrete stocks with an extended spawning period. Although chum rarely spawn in the lower intertidal areas where the pink salmon spawn, significant changes in temperature, salinity, and dissolved oxygen do occur with each rise and fall of the tide. Survival of the eggs and alevins decreases from the upper to the lower areas. Hashimoto (1971) concluded that treatment with a salt solution lowered the incubation rate of chum eggs and increased the occurrence of dead eggs and abnormal hatching. Although the period from fertilization to the beginning of hatching was reduced, the number of days from the first hatching until the last hatching increased. In eggs that hatched prematurely, the chorion was digested by the hatching enzyme when the moisture in the perivitelline liquid was dehydrated.

Land uplift and subsidence associated with the large earthquake in Alaska in March 1964 caused major ecological changes in the intertidal areas of Prince William Sound. The effects of these changes

in land level on behaviour and survival of intertidal spawning chum salmon are discussed by Thorsteinson et al. (1971).

#### *Relationships of Eggs and Fry with Benthic Fauna*

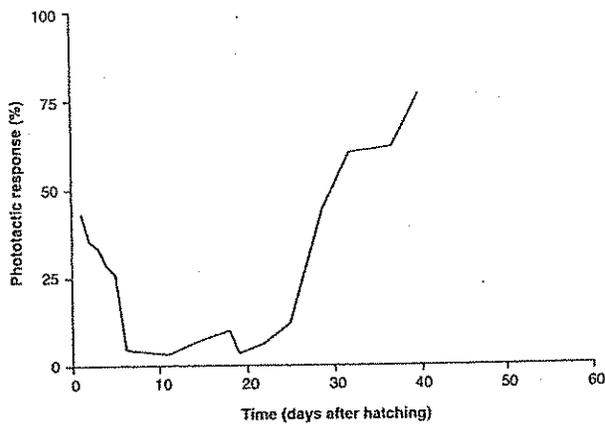
Nicola (1968) discussed a case of potential mutualism between the normal predaceous stonefly nymphs of the genus *Alloperla* and developing chum salmon embryos in the Harris River, Alaska. Analyses of the numbers of missing and dead embryos in relation to the numbers of stonefly nymphs in containers of buried eggs supported the hypothesis that stonefly nymphs are scavengers and not predators. Nicola noted that fungus was not found in any of the containers. Because of the biological oxygen demand, the removal of dead eggs was probably beneficial. The absence of saprophytes, along with the disappearance of eggs, was also noted by Vibert (1956).

#### *Behaviour of Alevins in the Gravel Environment*

Under conditions of adequate velocity, dissolved oxygen, and darkness, alevins move downward through the gravel substrate. Fast and Stober (1984) showed that chum alevins made more successful migrations through 20 cm of gravel than either coho or chinook alevins. The head/body thickness ratio allowed chum alevins (71.5 mg) on the day after hatching to pass through a number 7 sieve (2.80 mm mesh size). This adaptation allows the relatively large egg and alevin to use gravels with small interstitial spaces. The factor of robustness became evident when steelhead alevins, which are smaller than chum fry, migrated through number 7 and number 8 (2.36 mm) meshes, but in fewer numbers than the chum fry.

Fast and Stober (1984) also showed that chum alevins are photonegative from day 6 to 25 after hatching. After this time there is a rapid reversal to photopositive behaviour corresponding with the onset of emergence (Figure 8). The early photonegative behaviour is believed to be an adaptation for predator avoidance by keeping the alevins in the relative safety of the gravel until they have developed sufficiently to survive upon emergence.

Disler (1953) reported that alevins of autumn chum in the Amur River feed prior to yolk absorption; however, it is not known whether this con-



**FIGURE 8**

Photobehaviour of chum salmon alevins from hatching to yolk absorption. Each data point represents the mean percentage of 30 alevins in the light compartment of four separate light-dark choice tests. (From Fast and Stober 1984)

tributes to the growth of the alevins or if it is important in the development of their feeding behaviour.

## DOWNSTREAM MIGRATION OF CHUM SALMON FRY

### *General Pattern of Downstream Migration*

Chum salmon fry (Plate 12) typically emerge during nighttime hours and promptly migrate downstream to estuarine waters where they linger until they make the transition to waters of higher salinity. In the shorter rivers the migration is over in about 30 days, whereas in the longer rivers the migration is prolonged. Migration timing varies from early spring to midsummer by latitude, length of stream, timing of spawning of parental stocks, and interactions with other species, particularly pink salmon.

The movement downstream generally starts in the early nighttime hours and ceases during the middle of the night. In the early morning hours there is some aggregation or schooling leading to minimal to moderate downstream movement until broad daylight. As the lengths of the streams and their flows increase, variations (some of which are extreme) of the typical patterns occur. Migration during daylight hours, in well-lit areas, is not un-

common in some of the Asian and northern North American streams. Deviations from nocturnal migrations also occur with increased turbidity of the stream. Regardless of the variations in migration patterns, for most of their lives chum salmon are obligatory ocean dwellers (Hoar 1958).

The migration of chum fry has been described variously as either a displacement by the current after loss of orientation during darkness (Neave 1955) or as an active migration downriver where the fry are oriented with respect to the river flow (Hoar 1958). Combinations of the two have also been reported. The problem is that responses of migratory fry in the field are commonly quite different from those in test streams (Neave 1955). The migration-by-displacement principle received support from Kobayashi and Ishikawa (1964). Others (Semko 1954; Kostarev 1970; Iwata 1982a, 1982b) described active migrations, often with lingering and feeding, particularly among the larger fry. Chum salmon probably combine the elements of displacement and active swimming, and the

behaviour varies with the relative strength of the orienting factors, such as current, temperature, and visual reference points (Hoar 1958).

#### *Seasonal and Diel Timing*

In both Asia and North America the seasonal migration of chum fry is progressively earlier from north to south with the duration of the migration tending to be longer in the southern streams. Migrations in larger rivers are generally of longer duration than those in shorter streams.

The migration in Kamchatka is from early April through June with the peak in late April and early May (Semko 1954), whereas in the Okhotsk area the migration is from May to July with the peak in late June (Volobuyev 1984). In Hokkaido the migration lasts from March to June depending upon the river, with the peaks varying from April to late May (Kobayashi and Ishikawa 1964; Kobayashi et al. 1965; Sano 1966; Kobayashi and Kurohagi 1968).

A pronounced north to south pattern is evident in North America. Chum fry migration in the Yukon and Noatak River systems is from ice break-up in late spring until autumn, with the principal outmigration in June and July (Martin et al. 1986). The Noatak River has a less-defined peak than the Yukon River (Merritt and Raymond 1983). Farther south, in Olsen Creek (Prince William Sound) and the Taku River, the migrations are in May and June with peaks in mid-May and early May, respectively (Kirkwood 1962; Meehan and Siniff 1962). In the Skeena River system, the chum fry migration extends from mid-March to mid-April (McDonald 1960), and in Hooknose Creek the peak of migration occurs in late April and early May (Hunter 1959).

Fraser River chum fry move downstream from February to June (Todd 1966) with the majority migrating between mid-March and the end of April (Beacham and Starr 1982). In the Nooksack and Skagit rivers (Washington) the migrations are from April to June (Tyler and Bevan 1964; Davis 1981). In Minter Creek (southern Puget Sound), the migration extends from late January to late April (Salo and Noble 1954). At Big Beef Creek the migration lasts from February to June and has two peaks, in April and May (Koski 1975). The Satsop and Humptulips rivers, which empty into Grays Harbor, Washington, have migrations that peak

in late April (Brix 1981).

Although the diel migrations of chum fry are typically described as nocturnal, there are some extreme variations from this nighttime pattern. The literature is not representative enough by region to establish "norms" and their variations.

Nocturnal migrations have been described by Volobuyev (1984) for the Okhotsk region, by Kobayashi and Ishikawa (1964) for the Ishikari River (Hokkaido), by Hunter (1959) for Hooknose Creek (British Columbia), by Davis (1981) for the Skagit River (Washington), by Koski (1975) for Big Beef Creek (Washington), and by E.O. Salo and C.H. Ellis (unpublished data, Washington Department of Fisheries) for Minter Creek (Washington). Diurnal and nocturnal migrations have been recorded by Rosly (1972) for the Amur River, by Kostarev (1970) for the Ulkhan River, by Semko (1954) for the Karymaiskiy Spring areas (West Kamchatka), by Meehan and Siniff (1962) for the Taku River, by McDonald (1960) for the Kispiox River (British Columbia), and by Todd (1966) for the Fraser River.

Following their initial emergence and movement, chum fry prefer well-lit areas, and more than 50% of them are often found in exposed locations. However, when the light intensity exceeds 500 foot candles they seek deeper, less illuminated areas. Some chum fry can be found at nearly all natural light intensities (Hoar 1958). On the other hand, Kobayashi (1960) noted, as did C.H. Ellis and E.O. Salo (unpublished data), that active nocturnal migrations were terminated by bright moonlight.

Kostarev (1970) found that the main body (66%) of fry on the Ulkhan River migrated on clear, cloudless days; whereas on days of variable cloudiness, 33.9% migrated; and on cloudy days, only 0.1% showed definite seaward movement. Peak migration occurred during morning hours with good illumination and high water temperatures. On bright days the migrating fry stayed close to the surface, whereas during evening hours or cloud cover conditions the fry were in deeper water. There was no definite peak on cloudy days, although the main body of fry still migrated during early morning hours.

McDonald (1960) reported that, in general, chum salmon fry migration in the Skeena River takes place nocturnally where the migration distances are short, but that some daylight movement occurs where travel distances are longer. The time of max-

imum migration of chum fry in the lower Fraser River happens during the early afternoon at the beginning of the season and becomes progressively earlier in the day as the season advances (Todd 1966).

#### *Behaviour during Migration*

Chum fry do not school as strongly as pink and sockeye fry. Their schools are not compact and if left undisturbed for some time, the individuals tend to scatter. Chum fry apparently lack a pronounced hiding behaviour whether schooled or not. When one individual approaches another the mutual recognition is generally evident. This can take the form of either attraction or agonistic behaviour. Vestigial territorial behaviour may be observed in relatively constricted areas (Newman 1956; Hoar 1958). Older chum fry near the end of their downstream migration feed more and school less if left undisturbed.

According to Hoar (1958), chum fry respond consistently and positively to currents at all times of the day. He noted that at 0600 h, 70% were in the current; at 1200 h, 50%; and in the evening (1800–2000 h), about 40%. In general, they respond to changes in flow by heading into the current as long as they can maintain their position.

The chum fry of the Karymaiskiy Spring areas, western Kamchatka, migrate to sea shortly after emergence but move slowly in the currents and tarry on the spawning grounds, some reaches of the river, at log jams, and in flooded valley areas (Semko 1954). Also, they feed intensively in fresh water. Most of the fry in the Ulkhan River migrate in a narrow band in the main channel of the river, but some that are in the shoals orient head-upstream and those in calm waters swim head-downstream (Kostarev 1970).

In the streams of Hokkaido, chum fry move seaward in small schools facing upstream, staying near shore, and avoiding strong currents. They migrate actively when the stream temperature rises to about 15°C and leave the coastal area when the temperature exceeds 17°C (Mihara 1958).

In the Fraser River, chum are generally distributed across the entire river throughout the season. As the season progresses, more fry tend to migrate near the surface in the top metre of water. This change in migratory behaviour was not as pro-

nounced in even years (1962 and 1964) as in odd years (1963 and 1965), when pink fry were not present (Todd 1966). Hunter (1959) and K.L. Fresh and S.L. Schroder (Washington Department of Fisheries, Olympia, Washington, pers. comm.) found that in a smaller stream the chum migrated in the stronger currents in the middle of the stream, and Kobayashi and Ishikawa (1964) observed, in a Japanese stream, that most of the movement of fry was close to the bank and was not affected by current velocity.

The larger the river, the greater are the influences of variation in flow, turbidity, and temperature within and between years. Rosly (1972) found that fingerlings in the Amur River were in better condition due to increased feeding opportunities during years of low flows than during years of high flows. This relationship was reflected in the catches of autumn chum four years later with higher survival resulting from low flow years.

In the Otsuchi River, Iwata (1982a) observed that upon release at about 1 g, chum fry formed schools within 3–5 minutes, and when in slow moving water of less than 20–30 cm/s, they started to move downstream along the bank with their heads directed seaward. However, in currents of 30–80 cm/s their heads were oriented upstream and they were displaced by water flow. In shallow, rapid flows (80–120 cm/s) their position became random due to strong turbulence. Thus, the fry showed either positive or negative rheotaxis dependent upon the flow.

While migrating, chum fry are attracted by shade or darkness of waterweed communities (Figure 9). When the density of fish becomes high in the shaded areas they continue to move downstream. When the fish reach sea water they respond strongly to the mixed water and either turn back to fresh water or swim in the upper layer of lower salinity.

#### *Feeding*

It is not clear to what extent chum fry feed as they migrate down the larger rivers because only a few cases have been documented.

Chum fry in the Ulkhan River begin feeding early as "they spend a long time gaining weight in the spawning beds" (Kostarev 1970). Lingering as late as June, their basic food consists of the larvae

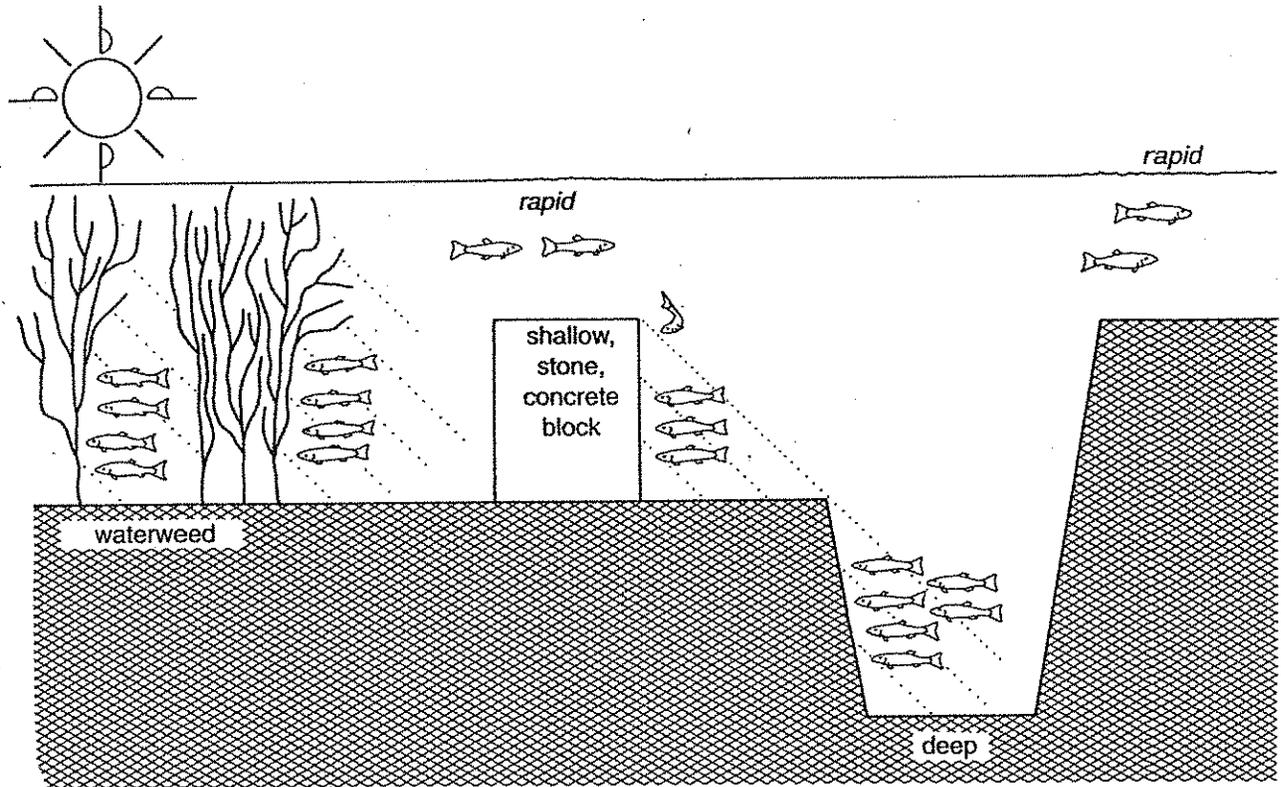


FIGURE 9

Schematic representation of chum salmon fry in fresh water showing areas of lingering in the shade (negative phototaxis). Fry migrated downstream in flatbottom, sunny areas. The fish in the rapids exhibit negative rheotaxis. (From Iwata 1982a)

and chrysalis of chironomids, mayfly larvae, *Trichoptera*, and other insects. The chum salmon migrating downstream in the rivers of the Sea of Okhotsk coast of Sakhalin and in the Lovetskaya River, Sea of Japan, feed much more intensively than pink salmon, and the intensity of their feeding increases towards the end of the downstream movement; the feeding spectrum also appears to be broader than that of the pink salmon (Frolenko 1970). The staples in the freshwater diet are benthic chironomids, and *Ephemeroptera* and *Plecoptera* larvae.

The chum fry released from the Chitose River hatchery in Hokkaido gradually increase in size as they migrate downstream. Their growth rate is low in March and April, the time of the normal migration (Kobayashi and Ishikawa 1964), and increases in May and June for both the fry from late or early releases that are already in the lower reaches of the

river. Chironomids are the most abundant of the benthic invertebrates in their diet. Similar findings were reported by Mayama (1976) on the Anabetsu River. According to Kobayashi and Abe (1977), cited by Iwata (1982a), a small number of fry released from a hatchery were observed feeding in a river 1.5 months after release. Kaeriyama (1986) documented feeding and growth of the "river type" of chum fry. Delayed migrations of actively feeding fry have been observed in several Washington streams (Salo and Noble 1954; Tyler and Bevan 1964).

Downstream migrating chum salmon in the Yukon River range in size from 29 to 107 mm, with the majority being less than 70 mm. Differences in time of emergence were cited by Martin et al. (1986) as contributing to the variance; however, this implies that some of the groups feed in the river.

Kobayashi (1960) noted that feeding accelerated after sunset when light intensity is reduced to about zero lux during both active and passive downstream migration. Daytime feeding could be induced by artificially supplying food. The growth rate of fry that fed during the night was greater than that of fry fed during daytime (also reported by S. Schroder and K. Fresh, Washington Department of Fisheries, Olympia, Washington, pers. comm.). Other reports of chum salmon feeding in fresh water are in Baggerman (1960), Sparrow (1968), and Bailey et al. (1975).

#### Smoltification

The physiological changes associated with smoltification are not as clearly defined in chum salmon as in species with longer freshwater residence. Iwata (1982b) noted that fry weighing from 0.4 to 1.8 g had a plasma sodium ( $\text{Na}^+$ ) concentration of 130-140 mmol/l. Upon reaching the estuarine area (salinity 2-25 ppt), the  $\text{Na}^+$  level increased slightly to 150-160 mmol/l. The osmoregulatory ability of chum fry decreased gradually when they were reared for an extended period in fresh water.

Chum salmon achieve maximum ATPase activities at sizes 48-55 mm (0.9-1.2 g). After introduction into brackish water and, later, sea water,  $\text{Na}^+$ - $\text{K}^+$  ATPase specific activities increase rapidly after a short period of decline (3-24 hours) (H. Fuss, Washington Department of Fisheries, Olympia, Washington, pers. comm.). The increase is greatest in fish smaller than 45 mm. The basal levels in the larger fish are higher prior to introduction into brackish water.

Although there has been considerable research on the predation of chum fry in fresh water, the impact on total survival is not clear. Hunter (1959) found that during the course of a 2.6 km journey to sea, chum and pink fry mortalities averaged 45% (ranging from 22.6% to 85.5%, 1948-57). Other quantitative estimates of chum salmon losses due to predation vary in magnitude and are indicative of sampling differences (Table 5). In a series of experiments with Big Beef Creek chum salmon, Beall (1972) found that coho yearlings selected smaller chum fry and that the predation rate decreased as the size of the fry increased. Sculpins, on the other hand, were random in their selection of prey by size. No selection of chum fry (by either length or weight) by coho salmon or rainbow trout (*O. mykiss*) was found in a subsequent study at Big Beef Creek (Fresh and Schroder 1987). Chum fry with some yolk reserves appeared to be more vulnerable, however. Significant predation by coho and trout was limited to larger individuals, and predation by sculpins was insignificant. Fresh and Schroder (1987) concluded that satiation of predators can be reached in small streams by controlled release of fry. In Japan, Hiyama et al. (1972) released small (36 mm) and large (50 mm) chum fry into a small coastal river where, previously, losses were estimated to be 50%. Although the fate of all chum fry in their three-day experiment was not described, a greater percentage of the larger chum juveniles was recovered at a weir 3 km downstream.

TABLE 5  
Estimates of freshwater mortality by predation for chum salmon

Location	Major predator species	Time period of estimate	Estimate (%)		Source
			Mean	Range	
Nile Cr. BC	-	Annual	47	35-62	Neave (1953)
Karymaiskiy Sp., USSR	Coho, charr	Annual	37	2-68	Semko (1954)
Hooknose Cr., BC	Coho, cottids	One week	58	33-85	Hunter (1959)
Big Beef Cr., WA	Coho, trout	48 hours	22	5-60	Fresh & Schroder (1987)
Big Beef Cr.*	Coho, cottids	24 h +	47-56†		Beall (1972)
Hooknose Cr.‡	Coho, cottids	Annual	45	23-85	Hunter (1959)

Source: \*In a test aquarium and test stream gauntlet

†47% for those incubated in gravel, 56% for those incubated in open troughs

‡Includes pink salmon

*Chum-Pink Salmon Interactions*

Chum fry change their vertical distribution in the water column during downstream migration in years when pink salmon fry are present (Todd 1966). Semko (1954) noted that in 1944 (pink salmon present), 41.5% of the chum fry migrated in the light and 58.5% in the dark; whereas in 1945 (pink salmon absent), 1.2% migrated in the light

and 98.8% in the dark. Somewhat the same pattern was repeated in 1946 when 29.2% migrated in the light and 70.8% in the dark, whereas in 1947, 1.8% migrated in the light and 98.2% in the dark. Thus, chum fry show a greater tendency to migrate during daylight hours in years when pink fry are present in the river system than when they are absent.

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EARLY SEA LIFE

Chum salmon are second only to chinook salmon in dependence upon estuaries, and they may choose either the upper or lower estuaries, depending on the relative productivity of each. This selective use of habitats of differing salinities is made possible by the euryhaline tolerance of the fry (Kubo 1953; Baggerman 1960; Congleton et al. 1982).

*Time of Entry into Sea Water*

The timing of entry of juvenile chum salmon into sea water is commonly correlated with the warming of the nearshore waters and the accompanying plankton blooms. A model of optimal annual mean time of downstream migration and entry into the estuary, maximizing early-marine survival was developed by Walters et al. (1978). The model included parameters of (1) production of zooplankton, (2) the rations and growth of young salmon, (3) survival related to body size, and (4) timing of arrival of fry into the ocean. The predicted optimal mean time for saltwater entrance coincided closely with the known peak abundance of chum fry in the Fraser River estuary.

The median date of downstream migration and entry into sea water is directly related to latitude, with a variance from 31 March at 46°N to as late as 20 June at 57°N - 59°N (Godin 1982). The migrations occur from May to June in western Alaska and from April to June in southeastern Alaska. In Oregon, Washington, and southern British Columbia, migrations occur from February through May,

and are earlier to the south. Variations in time of entry into estuaries, which can affect early marine survival, are caused by fluctuations in weather and stream runoff patterns.

Outmigrations from North American and mainland Asian streams are correlated in a broad sense with the warming of nearshore waters (March through June). In Honshu and Hokkaido, seaward movements occur earlier (March - May) and peak in late April, apparently as an adaptation to avoid the approaching warm (14°C) Tsushima Current (Irie 1985). Usually the juveniles have moved offshore by mid-June (Figures 10 and 11).

Martin et al. (1986) found that juvenile chum salmon of the Yukon River did not utilize the nearshore habitat of the delta because the outmigrants were widely distributed and occurred more frequently in the offshore waters than in the coastal habitats. The fish were dispersed by the large river plume, and the smaller fry (36.8-43.8 mm), which Martin et al. (1986) surmised to be summer-run stock, were particularly vulnerable to dispersion.

The behaviour patterns at entry and during estuarine residency appear to be consistent among the more typical North American estuaries (Healey 1982a). The young chum salmon spend up to three weeks rearing in the estuaries of the Fraser and Nanaimo rivers and occupy tidal creeks and sloughs high in the delta area (Healey 1982a). Their movements in and out of the estuary are correlated with the tides (Congleton et al. 1982). In Hood Canal, Washington, the initial distribution of the juveniles is widespread after entry into salt water,

TABLE 7 (continued)

Location	Years	Age composition (%)					Source
		0.1	0.2	0.3	0.4	0.5	
<b>Washington</b>							
<b>Puget Sd.</b>							
Bellingham	1910	0	53.5	44.8	1.7	0	Gilbert (1922)
Admiralty Inlet	1935	0	38.2	52.9	8.9	0	Rounsefell & Kelez (1938)
North Sd.	1957-68	0	26.1	72.8	1.1	0	Pratt (1974)
	1969-83	0	19.7	72.4	7.9	0	Ames (pers. comm.)*
<b>Hood Canal</b>							
	1963-70	0	57.1	42.2	0.7	0	Ames (pers. comm.)*
	1971-83	0	36.2	61.1	2.7	0	Ames (pers. comm.)*
	1965-76†	0	35.7	62.3	2.0	0	Wolcott (1978)
<b>South Sd.</b>							
	1962-70	0	60.3	39.2	0.5	0	Ames (pers. comm.)*
	1971-83	0	40.9	56.8	2.3	0	Ames (pers. comm.)*
Bellingham-Samish bays	1957-67	0	33.1	64.3	2.6	0	Pratt (1974)
Skagit Bay	1954-70	0	29.8	67.9	2.3	0	Pratt (1974)
Everett	1963-70	0	22.9	75.1	2.0	0	Pratt (1974)
<b>Admiralty Inlet, Point</b>							
No Point	1961-70	0	50.2	49.1	0.7	0	Pratt (1974)
Seattle	1962-70	0	60.0	39.4	0.6	0	Pratt (1974)
Minter Cr.	1938-55	0	49.1	49.3	1.6	0	Salo (unpubl. data)
Grays Harbor	1969-82	0	36.2	62.3	1.5	0	wdf (pers. comm.)‡
Columbia R.	1914	0	70.5	28.7	0.8	0	Marr (1943)
<b>Oregon</b>							
<b>Tillamook Bay</b>							
	1947-61	0	52.7	46.4	0.9	0	Oakley (1966)
	1947-49	0	10.2	89.2	0.6	0	Henry (1954)

Notes: \*J. Ames, Washington Department of Fisheries, Olympia, WA

†Late run fish only, mid-October and later

‡Washington Department of Fisheries, Olympia, WA

A few chum stocks show an alternation of dominance between three- and four-year-olds (four-year-olds and five-year-olds in some Asian stocks) that may be related to the presence of dominant year classes of pink salmon (see section on chum-pink salmon interactions). The mean age at maturity is negatively correlated with growth during the second year of marine life but not with growth in the first year (Helle 1979) and is also negatively correlated with abundance of the brood (Helle 1979; Beacham and Starr 1982).

The relationships of growth and brood abundance to mean age at maturity indicate that the environment and competition can override the genetic factors that control age at maturity. Alternatively, genetics may control the "basic" rate of growth and thresholds of size with maturity. Helle's (1979) correlation with growth during the second year suggests that this may be the time that determines whether a fish returns as a three-year-old. Although Helle (1979) did not correlate the return of four-year-olds with third year growth

or the return of five-year-olds with fourth year growth, his data provide some evidence that growth during the third or fourth year can influence age at maturity. For example, about 58% of the Olsen Creek 1956 brood returned as three-year-olds. In an average brood year, 15% of the males and 9% of the females are three-year-olds. The 1956 brood experienced a warm first year (1957) and their second marine year was the El Niño year of 1958 which led to good growth. In 1960, no five-year-old fish returned, and this is the only year with no five-year-olds recorded. Four-year-olds were dominant (nearly 100%). It is possible that good conditions in 1958 (the third year of life for these potential five-year-old fish) may have led to their maturing early in 1959 as four-year-olds. Data are not adequate to determine whether the second year at sea is the pivotal year for all age groups at all times or whether the penultimate year can be an important determinant, or if perhaps it is dependent on both environment and genetics.

Life History of Chum Salmon

*Size at Maturity and Age Composition*

Within its range, the average size of chum salmon (all ages combined) increases from north to south

in both Asia and North America (Table 8, Figure 22). Fish in southern areas have a longer growing period and mature at a younger age than northern populations. Also, within age groups there is an

**TABLE 8**  
Average weights of chum salmon from Asia and North America

Location	Years	Mean weight (kg)	Range of annual means	Source
<b>ASIA</b>				
<b>USSR</b>				
Anadyr R.		3.2		Kaganovsky (1933)
Kamchatka				
N.E. coast	1965-69	3.74	(3.21-4.04)	INPFC (1979)
East coast	1958-69	3.65	(3.22-4.07)	INPFC (1979)
s.w. coast	1958-69	3.52	(2.97-4.26)	INPFC (1979)
n.w. coast	1958-69	3.45	(3.05-4.61)	INPFC (1979)
Sea of Okhotsk				
Northern coast	1960-69	3.61	(3.20-4.31)	INPFC (1979)
Okhotsk coast	1958-69	3.52	(3.01-4.01)	INPFC (1979)
Amur R.				
Summer chum	1958-69	2.52	(2.31-2.79)	INPFC (1979)
Autumn chum	1958-69	4.37	(3.83-5.06)	INPFC (1979)
Sakhalin				
West coast	1963-69	3.47	(3.33-3.76)	INPFC (1979)
East coast	1963-69	3.41	(2.86-3.72)	INPFC (1979)
Kuril Is.	1955-67	4.04	(3.68-4.50)	Ivankov & Andreyev (1971)
<b>Japan</b>				
Coastal	1962-76	3.19	(2.96-3.44)	INPFC (1979)
<b>NORTH AMERICA</b>				
Alaska	1960-76			
Arctic, Yukon, & Kuskokwim rivers		3.17	(2.77-3.63)	INPFC (1979)
Bristol Bay		3.01	(2.68-3.40)	INPFC (1979)
Alaska Pen. & Aleutian Is.		3.10	(2.63-3.36)	INPFC (1979)
Chignik		3.34	(2.95-3.99)	INPFC (1979)
Kodiak Is.		3.67	(3.08-4.97)	INPFC (1979)
Cook Inlet, Resurrection Bay		3.41	(2.99-3.95)	INPFC (1979)
Prince Wm. Sd. & Copper and Bering rivers		3.73	(3.00-4.45)	INPFC (1979)
Southeastern		4.27	(3.76-4.94)	INPFC (1979)
British Columbia	1951-75			
Northern (areas 1-10)		5.30	(4.29-6.43)	Ricker (1980)
Southern (areas 11-27)		5.00	(4.20-5.71)	Ricker (1980)
Fraser R. (area 29)		5.32	(4.40-6.07)	Ricker (1980)
Washington				
Puget Sd.	1960-70	4.47	(3.98-4.97)	Pratt (1974)
Willapa Harbor*	1968-81	4.87	(4.15-5.59)	
Coastal and Grays Harbor*	1968-81	5.33	(4.90-6.00)	
Columbia R.	1938-76	5.58	(4.90-6.40)	INPFC (1979)

Note: \*Calculated from pound and numbers data in "1981 Fisheries Statistical Report," Washington Department of Fisheries, Olympia, WA (net fishery only)

## Pacific Salmon Life Histories

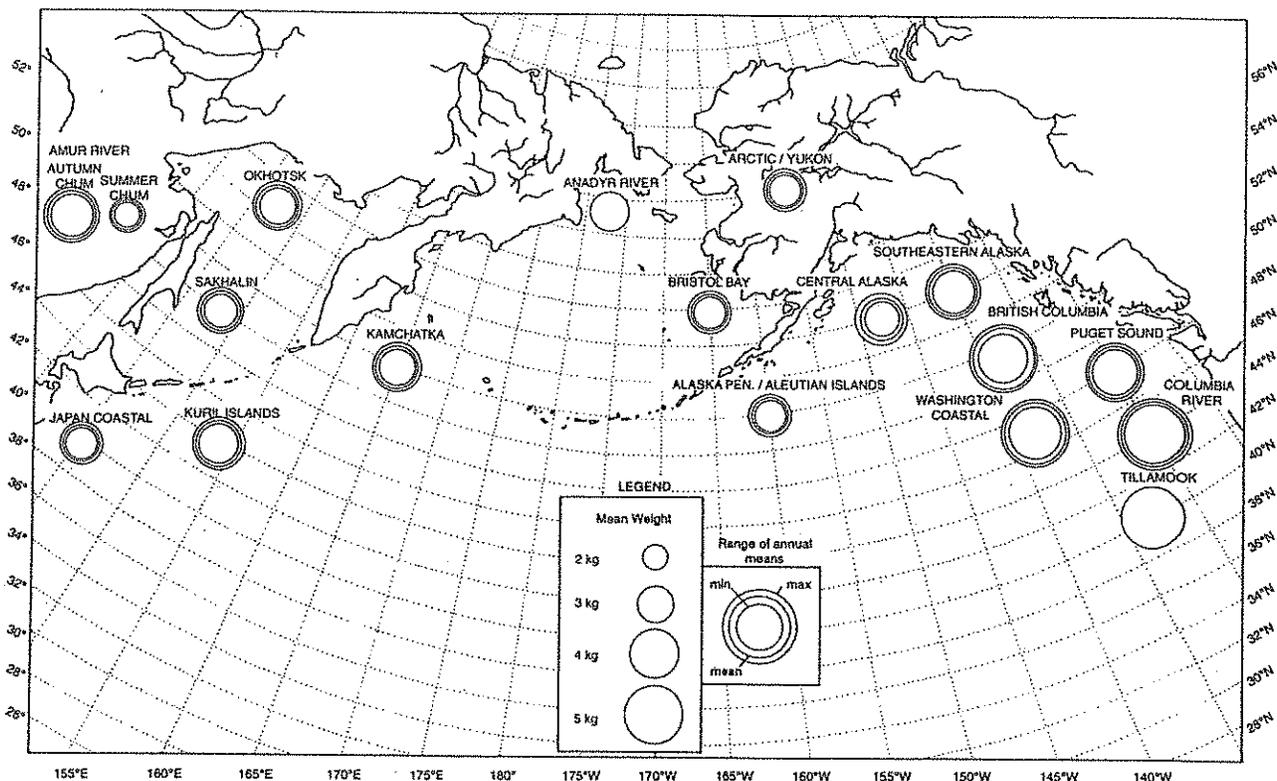


FIGURE 22  
Mean weight of chum salmon

increase in size from north to south (see age 0.3 chum in Table 9). The Asian fish are generally older (Figure 23) and smaller than the North American stocks (Figure 22) at a given latitude. Considerable spatial and temporal variability in size within regions is superimposed upon this broad latitudinal trend. For fish of a given age and sex, Ricker (1980) found no significant differences in size of chum salmon from northern and southern British Columbia, although the overall size tended to be larger but more variable in northern British Columbia (Table 9). The generally decreasing trend in mean weight from north to south was attributed to the relatively greater number of age 0.2 chum salmon in southern catches. In Alaska, the average weight of chum salmon is less than in British Columbia, and generally increases from north to south (Table 9). A notable exception in this trend are chum salmon from Kotzebue Sound, which exceed the size of chum salmon from Olsen Creek (Helle 1984). Interestingly, the returns to Kotzebue Sound comprise a relatively greater proportion of

younger fish as compared to other northern Alaskan areas (Table 7). This reversion to younger maturing fish in the far north was also mentioned by M.L. Frey (College of Fisheries, University of Washington, Seattle, Washington, pers. comm.) (see also Figure 23). In Puget Sound, age 0.3 chum salmon from northern areas tend to be larger than age 0.3 chum from southern areas (Pratt 1974) (Table 9). Fish harvested in northern Puget Sound are primarily from Fraser River stocks, and are predominantly age 0.3. In southern harvest areas, age composition is less stable, with age 0.3 chum dominant in some years, and age 0.2 chum in other years. There has been a consistently greater proportion of younger fish in southern Puget Sound since the early 1960s (Table 7).

Considerable temporal variability in chum salmon size is also evident within localized regions. A general decrease in the size of British Columbia chum salmon at a given age, along with a general decrease in ocean temperature between 1951-75 was reported by Ricker (1980). More re-

TABLE 9  
Mean length and weight of age 0.3 chum salmon at maturity from Asia and North America

Location	Years	Fork length (cm)			Weight (kg)			Source
		female	male	both	female	male	both	
<b>ASIA</b>								
<b>USSR</b>								
Anadyr R.				60.2				Ostroumov (1967)
Kamchatka								
East coast	1959	59.8	63.5		2.83	3.49		Sano (1966)
s.w. coast	1959	61.7	65.2		2.79	3.29		Sano (1966)
Bolshaya R.	1932-49			61.3			2.88	Semko (1954)
	1951-60			62.1			2.90	Petrova (1964)
n.w. coast	1959	63.0	68.3		2.93	3.74		Sano (1966)
Okhotsk	1959	59.1	62.6		2.70	3.26		Sano (1966)
				62.3				Kostarev (1967)
Amur R.								
Summer chum	1959	55.5	57.7		2.21	2.57		Sano (1966)
				59.0				Lovetskaya (1948)
Autumn chum	1959	66.1	69.4		3.40	4.16		Sano (1966)
	1925-49			66.8				(?)
				67.3				Lovetskaya (1948)
Sakhalin	1959	64.7	64.9		3.28	3.68		Sano (1966)
Kuril Is.	1967	71.5	74.4	73.3	4.02	4.14	4.09	Ivankov & Andreyev (1971)
<b>Japan</b>								
<b>Hokkaido</b>								
Nemuro district	1959	70.3	73.1		3.78	3.97		Sano (1966)
Okhotsk coast	1959	69.1	70.7		3.99	4.45		Sano (1966)
Pacific coast	1959	73.3	76.7		4.49	5.62		Sano (1966)
s.w. coast	1958	77.6	77.2		5.37	5.52		Sano (1966)
Japan Sea coast	1959	68.7	70.4		4.13	4.26		Sano (1966)
<b>Honshu</b>								
Pacific coast	1959	75.7	76.4		4.55	5.18		Sano (1966)
Sea of Japan	1959	73.9	75.9		4.79	5.24		Sano (1966)
<b>NORTH AMERICA</b>								
<b>Alaska</b>								
Kotzebue Sd.	1962-65*	64.3	70.0					Regnart et al. (1966)
Yukon R.	1920	62.0	67.1					Gilbert (1922)
	1962-65*	60.3	66.8					Regnart et al. (1966)
Alaska Pen.	1951-57*	63.6	69.3					Thorsteinson et al. (1963)
Kodiak Is.	1948-57*	65.7	71.3					Thorsteinson et al. (1963)
Prince Wm. Sd.	1952-58	67.2	71.9					Thorsteinson et al. (1963)
Olsen Cr.	1959-78†	66.3	71.1					Helle (1979)
<b>s.e. Alaska</b>								
Traitors Cove	1961*	70.8	76.6					Mattson & Hobart (1962)
	1963*	72.1	77.0					Mattson et al. (1964)
East R.	1963*	67.1	72.2					Mattson et al. (1964)
Yakutat	1961*	62.0	72.3					Mattson & Hobart (1962)
Lynn Canal	1961*	71.1	74.8					Mattson & Hobart (1962)
Icy St.	1961*	67.4	72.6					Mattson & Hobart (1962)
Portland Canal	1961*	73.4	78.8					Mattson & Hobart (1962)
<b>British Columbia†</b>								
<b>Northern</b>								
Nass (area 3)	1957-72	73.2	76.8					Ricker (1980)
Skeena (area 4)	1957-72	74.5	78.1					Ricker (1980)

(continued on next page)

TABLE 9 (continued)

Location	Years	Fork length (cm)			Weight (kg)			Source
		female	male	both	female	male	both	
Ogden-Principe (area 5)	1957-72	74.2	77.8					Ricker (1980)
Whale Channel (area 6)	1946			70.3				Ricker (1980)
	1948			68.9			4.57	Ricker (1980)
Bella Bella (area 7)	1958-72	74.7	78.7					Ricker (1980)
	1947			68.9			4.16	Ricker (1980)
Bella Coola (area 8)	1958-72	73.2	74.2					Ricker (1980)
	1946			78.9				Ricker (1980)
	1947			71.6				Ricker (1980)
	1948			73.9			5.66	Ricker (1980)
Rivers Inlet (area 9)	1958-72	75.9	78.8					Ricker (1980)
	1946			74.9				Ricker (1980)
	1947			74.6			5.25	Ricker (1980)
	1958-70	74.5	78.3					Ricker (1980)
Smith Inlet (area 10)	1959-70	74.6	78.0					Ricker (1980)
Southern								
Upper Johnstone Str. (area 12)	1945			70.4			4.61	Ricker (1980)
	1948			69.4			4.07	Ricker (1980)
	1950			72.5				Ricker (1980)
	1953			77.6				Ricker (1980)
Lower Johnstone St. (area 13)	1958-72	74.8	76.5					Ricker (1980)
	1945			69.8			4.61	Ricker (1980)
	1950			72.6				Ricker (1980)
	1958-72	74.8	76.0					Ricker (1980)
St. of Georgia (areas 14-18)								
Nanaimo (area 17)	1916	70.8	74.9		5.14	5.88		Ricker (1980)
	1917	73.1	76.3		5.33	6.09		Ricker (1980)
Little Qualicum (area 17)	1917	76.3	73.4		5.53	6.28		Ricker (1980)
	1978	73.3						Beacham (1982)
Chemainus (area 18)	1917	73.1	74.6		4.77	5.25		Ricker (1980)
	1978	72.3						Beacham (1982)
Areas 14-18	1960-72	75.8	76.3					Ricker (1980)
Juan de Fuca St. (area 20)	1946			73.0				Ricker (1980)
	1948			73.9			5.34	Ricker (1980)
	1958-72	72.9	74.7					Ricker (1980)
	West Vancouver Is. (areas 23-26)							
Barkley Sd. (area 23)	1946			70.3				Ricker (1980)
Areas 23-26	1959-63	73.5	74.3					Ricker (1980)
Fraser R. (area 29)	1950			73.3				Ricker (1980)
	1957-72	75.4	77.2					Ricker (1980)
Washington (Puget Sd.)								
Northern Sd.	1964			78.3				Pratt (1974)
	1970			75.7				Pratt (1974)
Bellingham	1910	70.4	76.0					Bakkala (1970)
Southern Sd.	1964			72.9				Pratt (1974)
	1970			70.9				Pratt (1974)
Big Beef Cr.								
Early Run	1968-69	69.8	77.5					Koski (1975)
	1969-70	69.8	76.6					Koski (1975)
Late Run	1968-69	72.1	77.2					Koski (1975)
	1969-70	71.2	76.9					Koski (1975)
Discovery Bay to Tacoma	1963-66	71.2	74.3					Pratt (1974)
	1970	69.6	72.4		4.43	4.97		Pratt (1974)
Columbia R.	1914	74.8	80.6					Marr (1943)

(continued on next page)

TABLE 9 (continued)

Location	Years	Fork length (cm)			Weight (kg)			Source
		female	male	both	female	male	both	
<b>Oregon</b>								
Tillamook Bay	1947	73.2	79.7		4.76	5.63		Henry (1954)
	1949	70.9	76.9		4.67	5.86		Henry (1954)
	1959	72.1	80.0					Bakkala (1970)

Notes: \*Mid-eye-fork of tail length (MEFT) converted to tip of snout-fork of tail length (TSFT) using the following equations (developed from equations of Helle 1979):

$$\text{♀ TSFT} = 7.9948 + 1.0706 \text{ MEFT}$$

$$\text{♂ TSFT} = 132.8937 + .9285 \text{ MEFT}$$

†Mid-eye-hypural length (MEHP) converted to tip of snouth-fork of tail length using the regression equations of Helle (1979):

$$\text{♀ TSFT} = 49.148 + 1.123 \text{ MEHP} (r^2 = .91)$$

$$\text{♂ TSFT} = 132.669 + 1.038 \text{ MEHP} (r^2 = .94)$$

‡Post-orbital-hypural length converted to tip of snout-fork length by using a factor of 1.25 (Ricker 1980). Number in parentheses indicates British Columbia statistical areas.

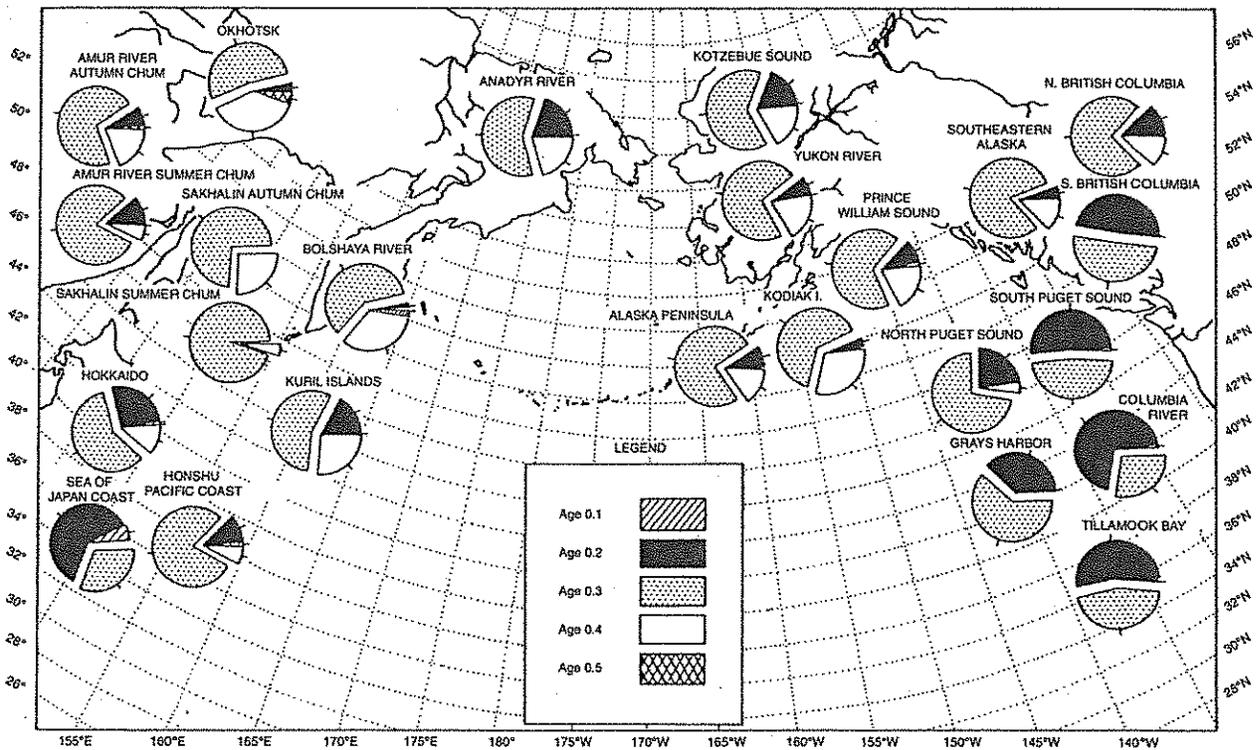


FIGURE 23  
Age composition of chum salmon at maturity

cently, small increases in the mean weight of chum salmon from British Columbia (all ages combined) were noted, possibly due in part to selection by gillnets, which remove more of the smaller fish (Ricker 1984). Selective removal of smaller fish tends to increase progeny size within an age group, but also favours survival of older ages, which have slower growth rates (Ricker 1984).

Similarly, a decrease in the average length of age 0.3 chum for Puget Sound was evident for fish sampled in 1964 and 1970 (Pratt 1974). Pratt also noted that reduced average weights during odd years suggested competition for food between chum and pink salmon during the pre-maturation period for years that coincide with returning pinks.

#### *Relationship between Abundance and Size of Adults*

Although there are no studies that provide direct evidence of density-dependent growth in chum salmon, there are several reports indicating lesser growth during years of greater abundance. Soviet authors have cited relationships between abundance of chum salmon stocks and size of adults (Birman 1951, 1960; Semko 1954; Petrova 1964); however, none of these studies are conclusive. Conversely, Helle (1979) found no correlation between mean length and abundance during year of return or brood year, but he did find a higher mean age at maturity from abundant year classes (also reported by Beacham and Starr 1982). A high mean age at maturity is related to slow growth during the second year of ocean life and, although difficult to demonstrate, density-dependent factors may be the linking mechanism. In the six-year period between 1979 and 1984 the adult chum salmon (0.3 in age) returning to the Ohkawa River (Honshu) showed a decrease in length (Y. Ishida, Far Seas Fish Research Laboratory, Shimizu, Japan, pers. comm.). Also, the numbers of fish returning as four-year-olds that showed slow growth as two- and three-year-olds is increasing. This decrease in length may be due to density dependency associated with the massive releases from Japanese hatcheries. Ricker (1980) found a positive correlation between mean weight and catch for the major areas of British Columbia; however, he concluded that this positive correlation may be an artifact

caused by variable year-class strength.

Density-dependent growth is difficult to show for chum salmon because the final year in the ocean is so important in determining the final size of the adults (Ricker 1964; Helle 1979). Therefore, comparisons of the size of adults produced by different year classes may not be an accurate index of density-dependent growth. Rather, they may reflect the interactions of genetically-determined size thresholds and environmental differences encountered during the final year of life. Also, density-independent factors (weather) will determine the carrying capacity of the marine environment for chum salmon. For this reason, an index of competition, such as abundance of fish, may not accurately express the differences in intensity of competition among years.

Little is known about the carrying capacity of the North Pacific Ocean or even the density of prey and the optimal ration for chum salmon. Neave (1961) calculated that the maximum density of chum salmon was about 180 kg/km<sup>2</sup> during the late 1930s when chum salmon were very abundant. It is not known whether densities of this magnitude can lead to slower growth.

Density dependence may not always be reflected in the size of returning adult chum salmon, as mortality may increase in years when chum salmon are abundant because of higher predation rates resulting from slower growth. Beacham and Starr (1982) showed a negative relationship between survival of chum salmon and total abundance of pink and chum salmon fry. They also showed an inverse relationship between the return/spawner ratio and the abundance of chum salmon of the previous brood year, suggesting competition between adjacent year classes. Helle (1979) found no relationship between survival and brood abundance; however, Helle's "survival" was based on return/spawner ratios, which incorporated freshwater mortality. Also, it is difficult to compare results when the effects of the fishery (size of catch) are not clear.

#### *Survival*

Chum salmon experience differential losses during each stage of their life history. The magnitude of survival is a reflection of complex interactions between biota and environment at each stage.

## Life History of Chum Salmon

The survival of chum salmon eggs from spawning to emergence varies widely among streams and can vary by factors as high as twenty from year to year in a particular stream (Table 10). Parker (1962) reported a range of 1%-22% survival over fourteen years in Hooknose Creek, British Columbia, which was attributed to radical changes

in flow (scouring and freezing). Higher survivals with less variability are obtained from controlled streams, as in the Big Qualicum River, where survival to emergence averaged 11.2% prior to flow stabilization and 24.9% after stabilization (Table 10). Egg-to-fry survival was further improved to 74% when a spawning channel was built.

**TABLE 10**  
Survival of chum salmon in early stages of development in natural and artificial environments

Location	No. of years sampled	Method of measuring survival	Survival <sup>1</sup>		Source
			Range (%)	Mean (%)	
<b>Natural stream environment</b>					
Disappearance Cr. AK	2	-	8.7-16.9	12.8	Wright (1964)
Big Qualicum R., BC	4	Downstream migrant fry counts	5.0-17.0	11.2	Lister & Walker (1966) <sup>2</sup>
Nile Cr., BC	4	Downstream migrant fry counts	0.1- 7.0	1.5	Wickett (1952) <sup>2</sup>
Hooknose Cr., BC	14	Downstream migrant fry counts	1.0-22.0	8.5	Parker (1962) <sup>2</sup>
Karymaiskiy Sp., Bolshaya R., USSR	7	Downstream migrant fry counts	0.7- 4.2	2.4	Semko (1954) <sup>2</sup>
Khor R., USSR	-	Examination of redds at hatching	25.0-30.0	-	Levanidov (1964)
Five tributaries of the Amur R., USSR	7	-	2.0-12.0	-	Levanidov (1964) <sup>2</sup>
Iski R. (Amur Trib.), USSR					
1940		Examination of redds	54.3-85.9 <sup>3</sup>	71.6 <sup>3</sup>	Smirnov (1947) <sup>4</sup>
1941			3.3-17.3	6.8 <sup>3</sup>	
Memu R., Japan	3	Downstream migrant fry counts	16.2-34.4	27.6	Nagasawa & Sano (1961) <sup>2</sup>
<b>Controlled stream environment</b>					
Abernathy Cr. spawning channel, WA	1	Downstream migrant fry counts	-	82.1	Bur. Commer. Fish. <sup>5</sup>
Jones Cr. spawning channel, BC	1	Downstream migrant fry counts	-	30.0	Trade News (1956) <sup>2</sup>
Nile Cr. (natural stream protected from floods), BC	4	Downstream migrant fry counts	3.4-11.8	7.5	Wickett (1952) <sup>2</sup>
Big Qualicum R. (natural stream with controlled flow), BC	2	Downstream migrant fry counts	24.5-25.2	24.9	Lister & Walker (1966) <sup>2</sup>
Big Qualicum R. spawning channel, BC	6	Downstream migrant fry counts	64.2-85.7	74.0	Paine (1974)
Big Beef Cr., WA	3	Downstream migrant fry counts	25.6-57.9 <sup>6</sup>	-	Koski (1975)

Source: Adapted from Bakkala (1970)

Notes: 1 Percentage survival calculated from potential egg deposition

2 Cited in Bakkala (1970)

3 Ranges and means of several areas in the Iski River

4 Cited in Sano (1966)

5 Bakkala (1970)

6 Survival range was 7.2%-88.4% in individual experimental units.

The survival of fry to maturity also varies among regions and between years, with the average reported survival ranging from 0.3% to 3.2% for wild chum salmon, whereas hatchery-produced chum have an even greater variance (Table 11). The survival of chum salmon from the Fraser River and

Puget Sound frequently varies on an odd- and even-year basis (see section on chum-pink salmon interactions). However, most of the variability in marine survival is related to ocean conditions (e.g., temperature, cloud cover, and salinity). Blackburn (1985) reported a negative correlation be-

TABLE 11  
Survival of chum salmon from egg to fry and fry to adult under natural and hatchery conditions

Location	Date	Freshwater survival (egg to fry)		Marine survival (fry to adult)		Source
		Mean (%)	Range (%)	Mean (%)	Range (%)	
<b>Natural streams</b>						
USSR						
Five tributaries of the Amur R.						
Summer chum	1955-58, 1960	6.1	1.3-13.1	2.5 <sup>2</sup>	1.5-3.2 <sup>2</sup>	Levanidov (1964) <sup>1</sup>
British Columbia						
Fraser River	1961-79	14.2	5.7-35.4	1.2 <sup>2,4,5</sup>	0.3-2.7 <sup>2,5</sup>	Beacham & Starr (1982)
Hooknose Cr.		7.8	-	2.8 <sup>2</sup>	-	Parker (1962) <sup>1</sup>
Washington						
Minter Cr.	1938-54 (N = 10)	9.1	2.8-16.9	1.9 <sup>3</sup>	1.4-2.4 <sup>3</sup>	Salo (unpub. data)
Big Beef Cr. (spawning channel)	1967-69 (broods)	-	25.6-58.9	-	0.5-2.6 <sup>3</sup>	Koski (1975)
Walcott Slough	1916-18	-	-	0.8 <sup>6</sup>	-	Wolcott (1978)
<b>Hatchery production</b>						
Japan						
Hokkaido	1962-77	80	-	2.0 <sup>2</sup>	0.5-2.7 <sup>2</sup>	Hiroi (1985)
Honshu	1962-77	80	-	1.0 <sup>2</sup>	0.3-2.5 <sup>2</sup>	Hiroi (1985)
USSR						
s.w. Sakhalin	1964-78	-	-	0.3 <sup>2</sup>	0.1-0.7 <sup>2</sup>	Roukhlov (1982)
s.e. Sakhalin	1964-78	-	-	0.3 <sup>2</sup>	0.01-1.8 <sup>2</sup>	Roukhlov (1982)
U.S.						
Alaska						
Washington						
Hood Canal	1916-69	-	-	0.34 <sup>7</sup>	0.25-0.43	Wolcott (1978)
Hood Canal		-	-	-	0.50-2.70 <sup>8</sup>	
Hood Canal	1966-71	-	-	-	0.96-3.0	Wolcott (1978)

Notes: 1 Cited by or calculated from values in Bakkala (1970)

2 Does not include fishing mortality

3 Includes fishing mortality

4 Survival varies on odd and even cycle

5 1961-74

6 Minimum estimate

7 Unfed fry

8 Fed fry

tween salinity (indexed by rainfall or river discharge) during the first summer of ocean residence and marine survival for seven stocks of chum in Washington and British Columbia.

The marine survival rate of hatchery-produced chum salmon in Japan has recently increased to over 2% due to artificial feeding of the fry before release. Similar and even greater rates have been obtained in North American hatcheries, but not as consistently. Reportedly, hatchery-reared chum salmon from the Soviet Union have a lower survival rate (Table 11), although these data are incomplete.

Most of the mortality suffered by chum salmon in the marine environment occurs within the first few months of life. Parker (1962) suggested a survival of 5.4% for the first five months of marine life. Bax (1983a), in separate sequential experiments, estimated average daily rates of mortality to be between 31% and 46% over a two- and four-day period, respectively. Later, Whitmus (1985), working in the same area of Hood Canal (Washington), estimated the survival of one marked group to be 42% over a two-day period. He also found the emigration and the survival rate to be size-dependent. The rates estimated by Bax (1983a) and Whit-

## Life History of Chum Salmon

mus (1985) are an order of magnitude higher than those estimated for pink salmon over a 40-day period subsequent to saltwater entry (Parker 1968).

Healey (1982b) also determined that the mortality of juvenile salmon during early sea life is probably size-dependent. Significant mortality by size occurred in the time period that the fish were

laying down scale circuli numbers 2-4 and was size-selective over the size range 45-55 mm fork length. Chum salmon lay down the first scales at about 40 mm and they are completely scaled by the time they reach 50 mm. Although no particular mortality could be identified, the size range corresponded with the size at which the chum salmon moved from shallow water to the pelagic habitat.

## ABUNDANCE

### *Productivity of the North Pacific Ocean*

The annual catch of North Pacific Ocean chum salmon from 1925 through 1981 averaged over 41 million fish (range 18-83 million). In this period the mean Asian catch was 26.5 million and the North American mean was 11.5 million (Figure 24). In the thirty-year period after 1952 the mean annual harvest of chum salmon was 24.9 million for Japan, 6.9 million for the USSR, and 2.4 million for Canada (Figures 25 and 26).

The catch trends by area for North America and Asia are shown in Figure 27. The ratio of Asian to North American chum, based on catches since

1930, has been as high as 3.5:1 in 1936 and as low as nearly 1:1 in 1952-53. However, over the years, Asian fish have constituted the bulk of the production. The decade with the greatest total catch of chum salmon was 1934-43, with an annual average of 57.5 million fish (Figure 24). If the fish had an average weight of 3.66 kg, the average catch would have been 210,600 t. The peak year was 1936, when 83 million fish weighing 304,000 t were harvested. If one assumes a catch to escapement ratio of 3:1, the production would have been 111 million mature fish or 407,000 t. If the catch to escapement ratio was 2:1, the annual production would have been 126 million mature fish or 462,000 t.

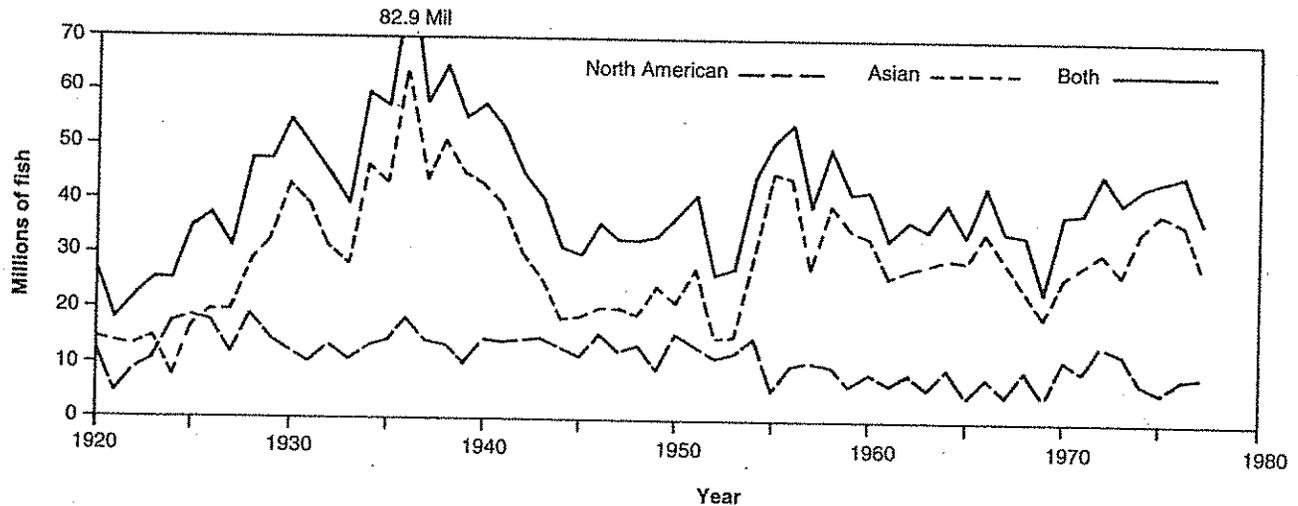


FIGURE 24

Total catch of chum salmon of Asian and North American origins by commercial fisheries of the USSR, Japan, U.S., and Canada, in millions of fish, 1920-77

Pacific Salmon Life Histories

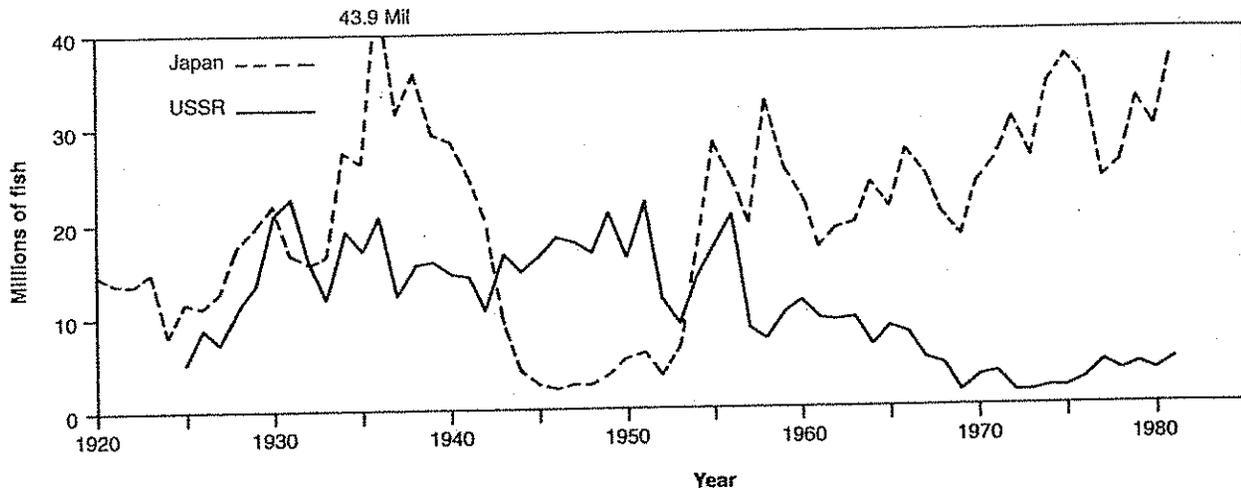


FIGURE 25

Catch of chum salmon by commercial fisheries of Japan and the USSR, in millions of fish, 1920-81

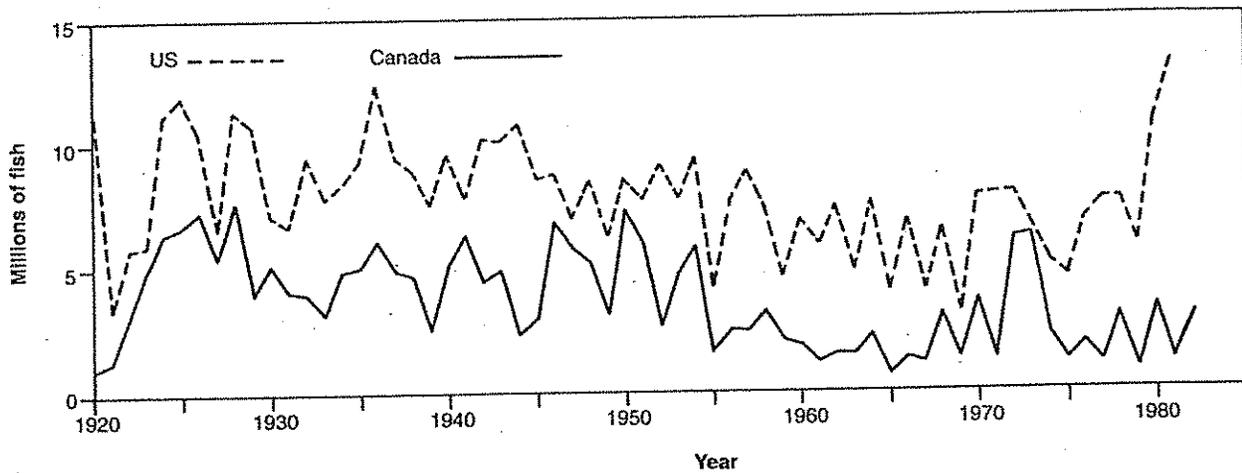


FIGURE 26

Catch of chum salmon by commercial fisheries of the u.s. and Canada, in millions of fish, 1920-81

G. Grette (Pentec Environmental, Edmonds, Washington, pers. comm.) estimated the age composition for the maturing chum for 1936 by using the age composition for Asian and North American chum salmon separately and then estimating the average numbers in each age group by incorporating a factor based on the proportion of chum salmon produced on each continent. The number of immature fish was determined by working backwards from the catch and age composition of the maturing stock and by multiplying by the inverse

of the survival rate. Using the estimated age composition for the catch and for a production of 126 million mature fish, the total biomass (immature and mature) of chum salmon supported by the North Pacific Ocean was estimated to be between 860,000 and 1,300,000 t. The biomass estimates vary with assumptions on survival rates and growth from time of entry into the ocean to the time of maturity (ages 0.2, 0.3, and 0.4). Then, by using the available data on the age and size at maturity for the Asian and North American stocks, the total

## Life History of Chum Salmon

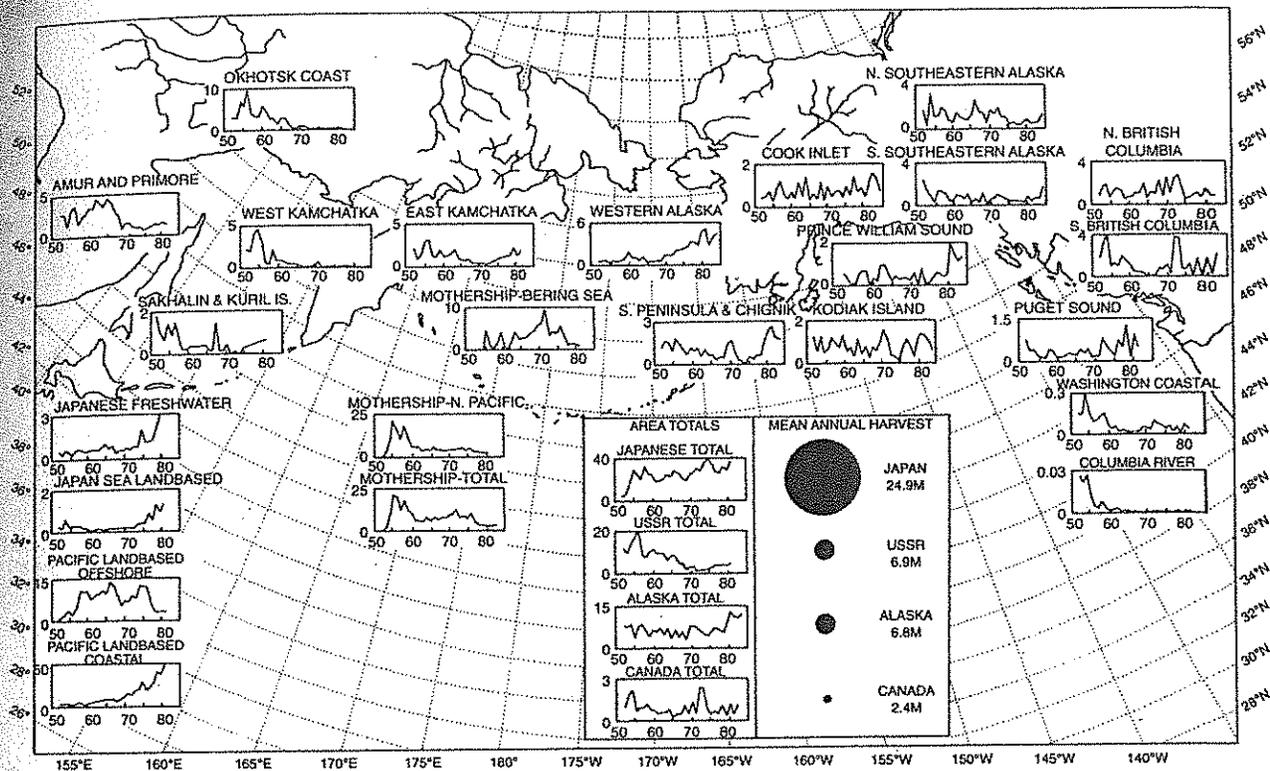


FIGURE 27

Commercial harvest of chum salmon, 1952-84, in millions of fish, and mean annual catch by Japan, USSR, Alaska, and Canada

annual biomass was calculated to be 1,300,000 t (Table 12). If the catch to escapement ratio was 1:1 the total biomass would be 1,600,000 t and the harvest of mature fish would be 604,000 t.

Neave (1961) estimated the annual biomass of chum salmon for the years 1936-39 to be 510,000 t for the mature fish, and 845,000 t for the immatures, for a total of 1,355,000 t. This is about equal to the lower estimate calculated above using a 2:1 catch ratio. According to Neave (1961), chum salmon contributed 47% of the total biomass of the six species of Pacific salmon.

### Asian Catch

Japan caught the major portion of Asian salmon from 1933 to 1942 (average annual catch 28.4 million versus 15.1 million for the USSR), although the production at this time was primarily from the Asian mainland (Figure 27). The catch by Japan dropped dramatically during the war and imme-

diately postwar years, 1943-53. After the resumption of distant-water fishing, the Japanese catch of chum salmon averaged 22.8 million from 1955 to 1969. During this period the USSR catch averaged 9.1 million but plummeted to 1.5 million in 1969 (Figure 27). In the 1970s the Japanese developed a massive and very successful hatchery program, and the nearshore and terminal catch rose to over 48 million fish (152,600 t) in 1985, while the far seas catch diminished from 6 million fish in 1965 to 2.5 million fish in 1981, primarily due to international restraints (Figure 27). Correspondingly, the coastal sea catch rose from 16.4 to 34 million fish in the same period.

Birman (1960) developed a relationship for the long-term fluctuations in abundance of Amur River autumn chum salmon, pink salmon, and south Sakhalin herring (*Clupea harengus pallasi*). Relating the warming and cooling of the waters in the Asiatic region of the Kuroshio Current to the abundance of the three species of fishes, he con-

TABLE 12  
Number and biomass of chum salmon in the North Pacific Ocean in 1936,  
assuming a 2:1 ratio of catch to escapement

Year class	Millions of fish	Total tonnes	Mature 3-y-olds		Mature 4-y-olds		Mature 5-y-olds		Age in 1936
			(millions of fish)	(tonnes)	(millions of fish)	(tonnes)	(millions of fish)	(tonnes)	
1931	27.72	127 512					27.72	127 512	5 (22%)†
1932	114.51	400 786			81.90	286 650	32.61	114 135	4 (65%)†
1933	153.49	414 423	16.38	44 226	96.351	260 145	40.76	110 052	3 (13%)†
1934	190.66	285 990	19.27	28 905	120.44	180 660	50.95	76 425	2
1935	238.33	71 499	24.09	7 227	150.55	45 165	63.69	19 107	1
Total annual biomass = 1 300 210 tonnes									
Total mature stock = 458 388 tonnes									

Source: Calculated by G. Grette, Pentec Environmental, Edmonds, WA

Notes:

\*Proportion surviving; partly based on Parker (1962); size based on Ricker (1964).  $\log w = -2.22 + 3.2 \log L$  and using  $\bar{w} = 3.6$  and 13:65:22 age ratio

†Age composition of maturing stock

cluded that, synchronously, chum salmon and herring thrived during the warmer years and pink salmon were more abundant during the colder years.

Earlier, Birman (1957) had correlated the cyclic rise and fall in abundance of chum salmon and herring with the eleven-year cycle of sunspot activity which, in turn, he associated with warm and cool climatic periods. Wolcott (1978) also compared cyclic sunspot activities to the marine survival rates of Walcott Slough chum salmon and concluded that the relationship was strong. Others, however, felt that the reductions were due to overfishing as well as to natural causes. The catches of chum salmon in 1961-65 in the continental Okhotsk region, as well as those from western and eastern Kamchatka, were produced by the 1955-60 year classes. Kostarev (1982) stated that "in spite of the favorable conditions for natural production (in these winter periods), it was impossible to compensate for the significant spawner deficiency in these periods."

#### North American Catch

The u.s. catch, predominantly Alaskan, averaged

about 8.7 million fish between 1920 and 1951, while the Canadian catch averaged about 4.7 million fish (Figure 27). In the decade 1955-65 the Canadian, Washington, and Oregon catches dropped significantly, indicating extremely poor marine survival rates (Figures 27 and 28). This was very noticeable at Minter Creek, Washington, where records were kept of wild outmigrant juveniles as well as the hatchery contribution for the 1950-61 year classes. No unusual freshwater influences were detected during this period. The period 1950-55 was characterized by falling temperatures and low sunspot activity (Wolcott 1978). This was followed by a decade of warmer than normal northeastern Pacific Ocean temperatures (Chelton 1984). During this period, the central Alaskan stocks showed a definite odd-even year relationship (Figure 29). From 1975 to 1984, again a period of relatively warm ocean temperatures, the western and central Alaskan stocks thrived. Catches increased without significant changes in escapement (Bigler 1985). Confounding the analysis, to some extent, was the resurgence of the Japanese mothership fishery from 1955 to 1960.

## Life History of Chum Salmon

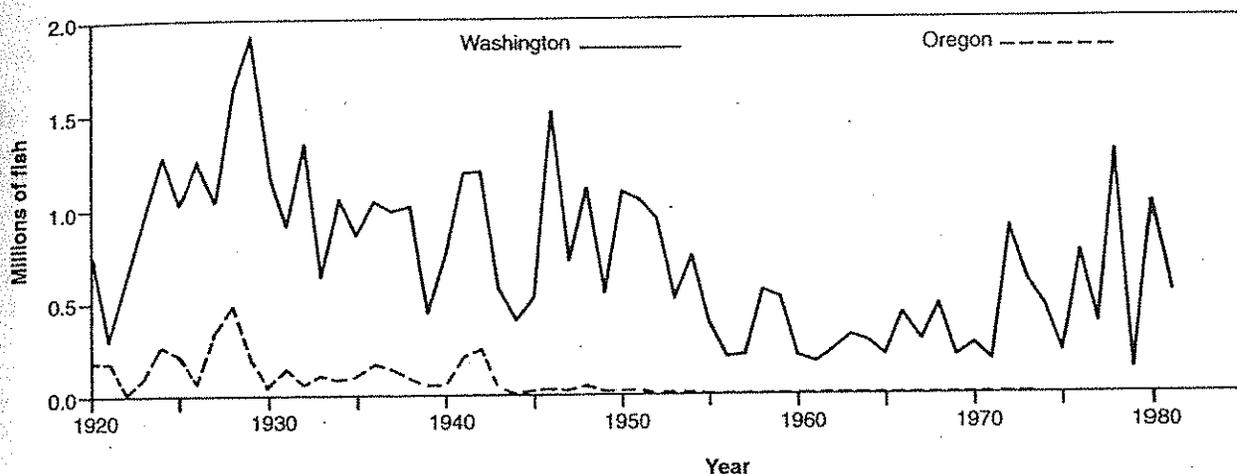


FIGURE 28

Catch of chum salmon by commercial fisheries in the states of Washington and Oregon, in millions of fish, 1920-81

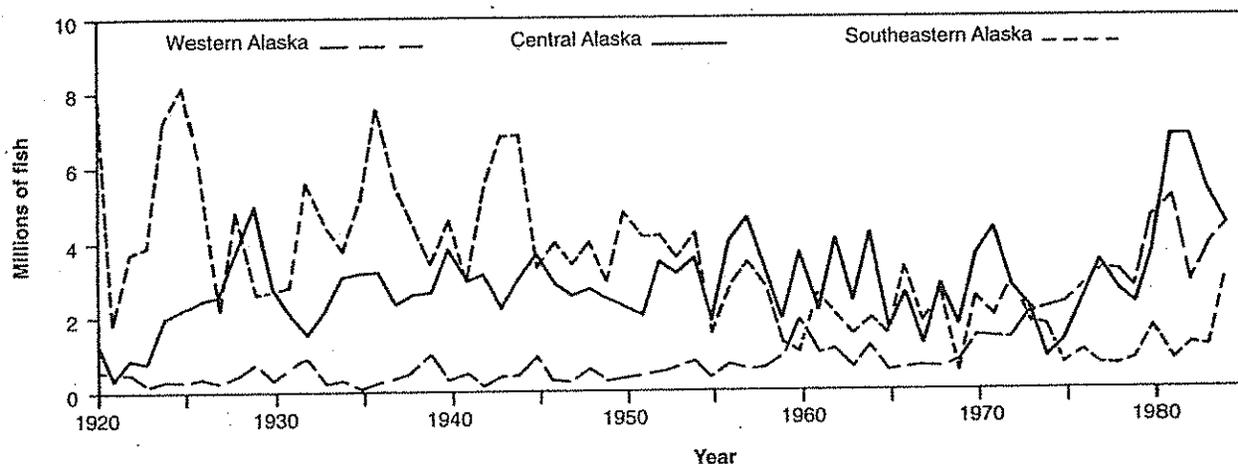


FIGURE 29

Catch of chum salmon by commercial fisheries in Alaska, in millions of fish, 1920-84

### *The Japanese Hatchery Program*

Other than fisheries, perhaps the greatest human influence on the status of chum salmon stocks has been the phenomenal concentration of hatcheries on Hokkaido and Honshu where 262 rivers are managed almost entirely by artificial propagation. Before 1966, the fry were released without supplemental feeding, and the rate of return averaged about 1%. The larger the fry, the sooner they migrate offshore, avoiding the warm currents (Figures 10 and 11). Since feeding of the fry became an established practice in the late 1960s, the rate of

return has been consistently about 2% and, on occasion, nearly 3% (Figure 30) (Shirahata 1985).

The number of chum fry released annually from 1982 to 1985 was over 2 billion (300 t), and adult returns in 1984, 1985, and 1986 exceeded 40 million fish (Table 13), for a greater than 2% survival from time of release. The mean survival for fish released from 1976 to 1980 was 2.6%. To put these numbers in perspective in the calculations of the biomass of chum salmon in the North Pacific Ocean as indicated in Table 12, the combined estimate of fry emanating from Asia and North America was 4 billion in 1936.

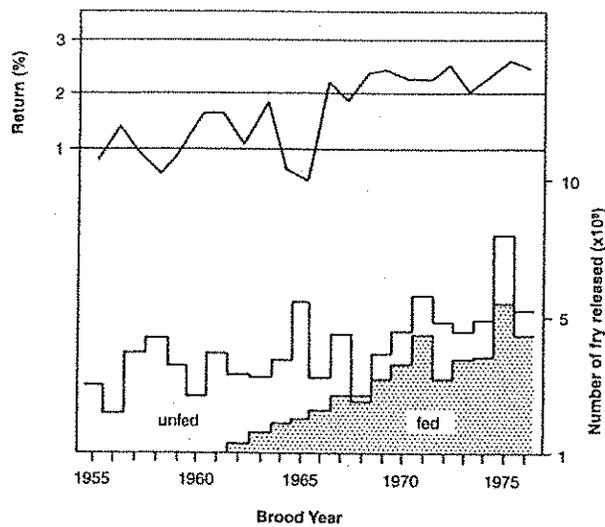


FIGURE 30

Chum salmon fry released from Hokkaido sea ranches, 1955-76, and return (%) related to fed and unfed fry. (From Mahnken et al. 1986)

TABLE 13  
Annual returns of adult chum salmon to Hokkaido and Honshu, 1966-86

Year	Total (Thousands)
1966	4 442
1967	5 012
1968	2 513
1969	4 620
1970	5 851
1971	8 548
1972	7 884
1973	9 175
1974	10 772
1975	17 686
1976	10 419
1977	12 559
1978	16 208
1979	24 028
1980	22 418
1981	29 904
1984	37 928
1985	48 086
1986	48 014

Source: From Hiroi (1985) for the years 1966-81; for the years 1984-86, Hiroi (pers. comm.)

## CYCLES AND CHUM-PINK SALMON INTERACTION

Some chum salmon stocks exhibit definite and quite regular even- and odd-year variations in behaviour, age at maturity, size, marine survival, and abundance (Rounsefell and Kelez 1938; Smirnov 1947; Lovetskaya 1948; Noble 1955). These patterns appear to be related to the presence of pink salmon which have strong biennial cycles of abundance. In years when pink salmon juveniles are abundant, the feeding rates of juvenile chum salmon are lower and growth rates are less (Ivanov and Andreyev 1971). As mentioned earlier, the diets of chum salmon may also change. These variations probably result from interspecific competition and from responses that evolved to minimize this competition. Gallagher (1979) suggested that Gause's "exclusion principle," which states that two species cannot occupy the same

niche at the same time, is the proper paradigm in which to consider the chum-pink salmon interaction. No matter what the proximal causes may be in the observed cycles in chum salmon stocks, competition must still be viewed as the ultimate cause.

The effects of chum-pink salmon competition vary with the life history phase of the fish and the environment in which it occurs. Chum and pink salmon often spawn in the same reaches of the river, and the possibility exists for density-dependent effects on the deposited eggs resulting from redd superimposition. During years when spawners of both species are abundant, the effects can be both positive and negative. Excessive movement of the gravel can be detrimental. On the other hand, as noted earlier, during years of pink

salmon dominance the spawning gravels are cleaner. The deterioration of large numbers of salmon carcasses can cause oxygen deficiencies, as can large clumps of dead and dying eggs. However, density-independent factors associated with weather and climate (e.g., stream flow, scouring, freezing) are very important in determining egg-to-fry survival in these species. More frequently than not, these factors override the density-dependent effects in fresh water and control survival to the fry stage. Variations in temporal and spatial behaviour of downstream migrants can occur in a cyclic pattern, as noted earlier.

Recent research indicates that there are density-dependent effects in the marine environment for some salmonid stocks (Peterman 1978; Rogers 1980; Beacham and Starr 1982; McGie 1984). For chum and pink salmon, direct and indirect evidence indicates that density-dependent effects are present in the early marine environment (Birman 1960). In the southern Kuril Islands, feeding rates of chum and pink salmon juveniles were lower in years when juveniles were abundant (Ivankov and Shershnev 1967, 1968; both cited by Ivankov and Andreyev 1971). Chum fry in the Strait of Georgia near the Fraser River estuary were found to be larger in years when pink salmon were not present (Phillips and Barraclough 1978; cited by Beacham and Starr 1982). Survival of chum fry to adulthood varies with environmental conditions, but for some stocks an even-odd year pattern is evident. Fraser River chum salmon have a higher survival rate during even "non-pink" years than during "pink" years (Figure 31). A similar pattern of survival is present for chum salmon from Hoodspout Hatchery at Hood Canal, Washington (Gallagher 1979). The period of life history at which these patterns are formed is not clear, but it is probably during the early stages at age 0.0 to 0.1.

The possibility also exists for chum-pink salmon competition to occur later in their marine life. Beacham and Starr (1982) suggested that marine survival of chum salmon is influenced by the abundance of adjacent year classes. Such competition would occur in the ocean, not the nearshore or estuarine environment. Also, some chum salmon stocks that do not compete with pink salmon in the early marine environment show odd and even cycles. In Tillamook Bay, Oregon, chum salmon stocks show an alternating age at maturity, yet no

pink salmon are present in this area. The same patterns are evident for Willapa Harbor and Grays Harbor on the coast of Washington (S.L. Schroder, Washington Department of Fisheries, Olympia, Washington, pers. comm.).

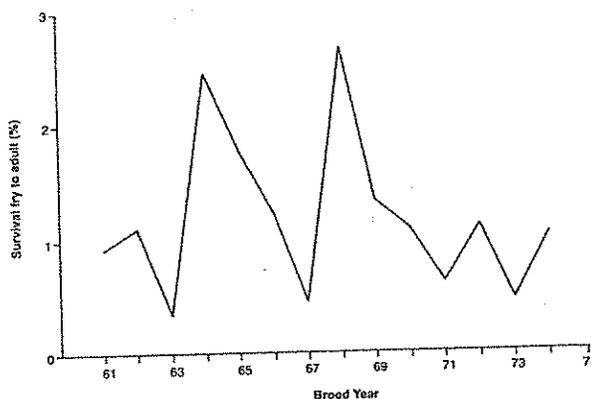


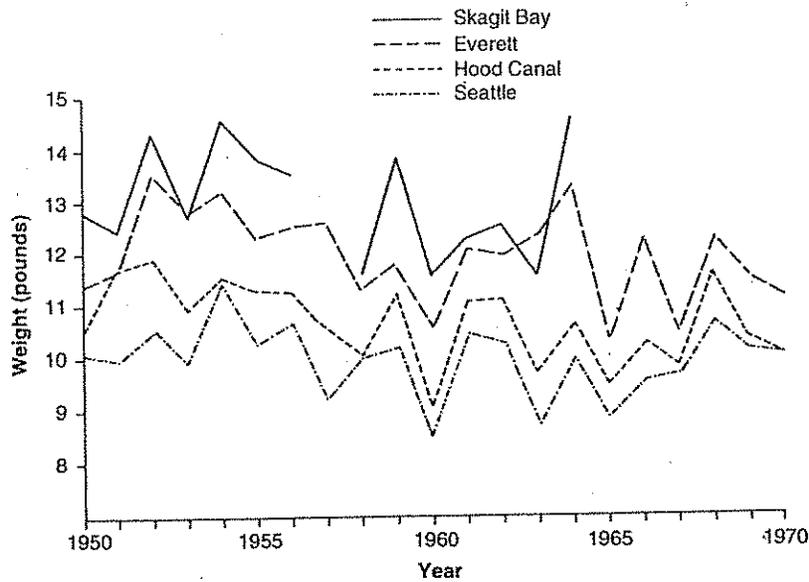
FIGURE 31

Percentage survival from fry to adult for Fraser River chum salmon for brood years 1961-74.  
(Data from Beacham and Starr 1982)

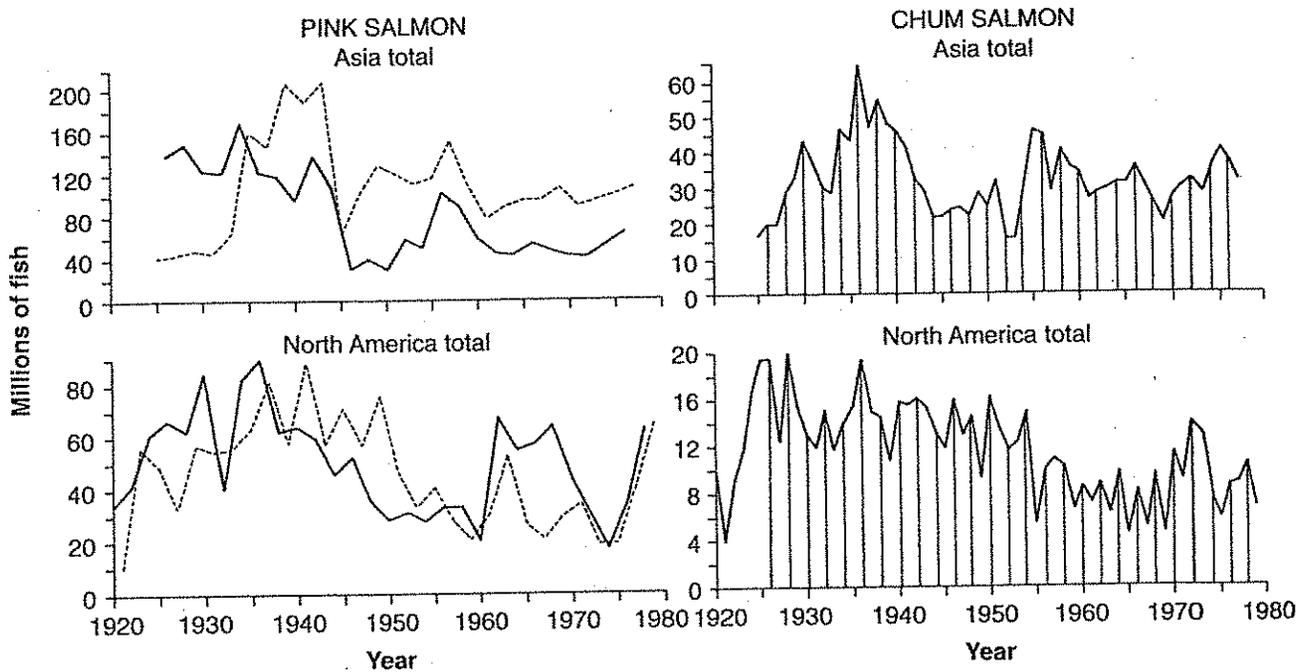
Andrievskaya (1966) reported an even-odd cycle shift in the diet of maturing chum salmon in western Kamchatka. In even years (low pink salmon abundance), chum and pink salmon ate similar prey, but during odd years (high pink salmon abundance), the chum diet consisted of prey of lower nutritional quality. Pratt (1974) reported that Puget Sound chum salmon were smaller during odd "pink" years than during even "non-pink" years (Figure 32). It is possible that Puget Sound chum salmon compete with pinks in a way similar to that reported by Andrievskaya (1966).

The catch of chum salmon in the northeast Pacific Ocean exhibits a distinct even-odd year relationship with higher catches during even years (Figure 33). Also, North American pink salmon stocks show an alteration of dominant cycles, changing in roughly ten- to fifteen-year periods (Figure 33). Near the time of these changes, there are indications of breaks in the odd-even chum salmon patterns, although they are not precise or regular (1954-58 for chum salmon, 1954-62 for pink salmon).

Pink salmon are present nearly exclusively in odd years in the streams of Puget Sound and tribu-



**FIGURE 32**  
Average purse seine chum weights from selected areas in Puget Sound, 1950-70. (From Pratt 1974)



**FIGURE 33**  
Total Asian (1920-77) and North American (1925-79) pink and chum salmon catches. For pink salmon graphs, odd-year data are plotted by the dotted line and even-year data are plotted by the solid line. (Adapted from Asian and North American pink and chum salmon catch statistics, 1980; Proceedings of Pink and Chum Salmon Workshop of 1979; and C.K. Harris, Fisheries Research Institute, University of Washington, Seattle, wa, pers. comm.)

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taries of the Fraser River. In this region, chum salmon are more abundant in even years than during odd years (Gallagher 1979). This biennial cycling of chum salmon is manifested in two underlying cycles: 1) survival from fry to adult is higher for even-year than for odd-year broods; and 2) regular alternations occur in age at maturity between even- and odd-year broods (Gallagher 1979). For Puget Sound stocks, odd-year broods return in roughly a 50:50 ratio of three-year-olds to four-year-olds (Figure 34). Three-year-olds comprise about 35% of even-year broods while four-year-olds make up about 65%. A similar pattern exists for Fraser River stocks, although the values vary slightly (Figure 35) (Gallagher 1979; based on data from Bilton 1973). The net result of these alternations is that chum salmon put more reproductive effort into even "non-pink" years than into "odd-pink" years. Gallagher (1979) concluded that these alternations represent a genetic adaptation which allows chum salmon to minimize competition with pink salmon in the early marine environment. This tendency for odd-year brood chum salmon to return at a younger age is even more noteworthy because, due to competition, they are smaller juveniles and, therefore, might be expected

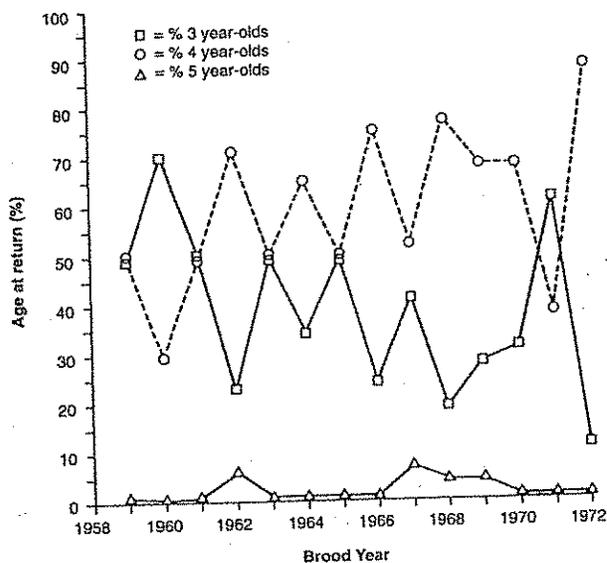


FIGURE 34

Age at return of the total chum salmon brood to Puget Sound as a percentage of three-, four-, and five-year-olds, 1959-72. (From Gallagher 1979)

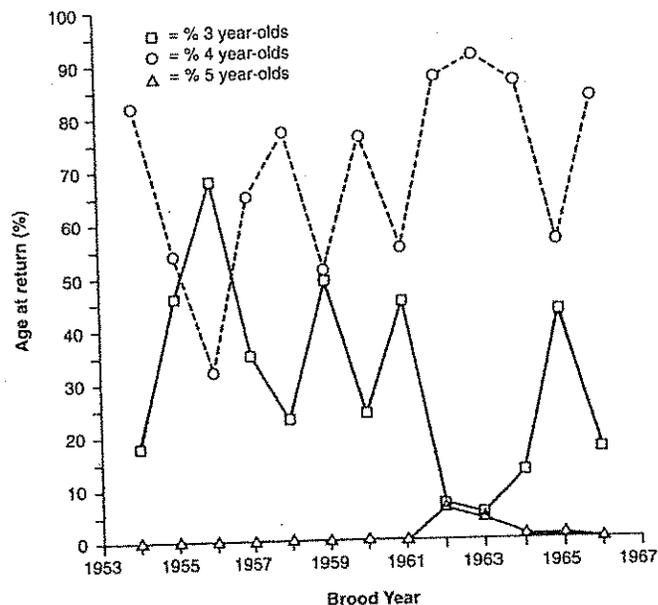


FIGURE 35

Age at return of the total chum salmon brood to the Fraser River, BC, as a percentage of three-, four-, and five-year-olds, 1954-66. (From Bilton 1973, cited in Gallagher 1979)

to return older as more time is needed to reach critical size at maturity.

Smoker (1984) developed a model of the chum-pink salmon interaction based on an adaptation of the Ricker curve to two interacting stocks. He concluded that environmental influences alone could not account for the type of fluctuations in abundance and age at maturity of Puget Sound chum salmon stocks and that a fairly strong genetic mechanism must also be present.

Fluctuations in age at maturity also occur in some stocks which coexist with both even- and odd-year pinks. Chum in Olsen Creek, Alaska, show a more complicated pattern than do Puget Sound stocks, although this pattern appears to agree with Gallagher's conclusion that more reproductive effort is concentrated into odd years which coincide with the subdominant pink year (Gallagher 1979). A regular pattern exists in age at maturity for Bolshaya River chum (Table 14). However, in this region (western Kamchatka), the dominant pink cycles periodically alternate between odd and even cycles; and the presence of a regular pattern in Bolshaya River chum cannot be easily

TABLE 14  
Age composition of Bolshaya River chum salmon  
for brood years 1937-46

Brood year	Catch from brood*	Age composition (%)			
		0.2	0.3	0.4	0.5
1937	462 000	0.4	62.8	36.4	0.4
1938	25 000	19.3	68.9	11.8	0
1939	259 000	4.6	26.8	67.6	1.1
1940	129 000	1.5	84.2	10.1	4.2
1941	1 115 000	2.6	33.8	63.7	0
1942	257 000	1.0	89.9	1.8	7.2
1943	1 703 000	9.0	17.3	71.7	2.0
1944	294 000	0.3	60.8	38.9	0
1945	1 342 000	0.9	60.2	35.3	3.6
1946	360 000	1.0	29.7	69.2	- †

Source: Adapted from Sano (1966); based on data from Semko (1954)

Notes: \*Values rounded to nearest 1,000; includes only catches in the Bolshaya River area

†Data unavailable, percentage was assumed to be zero

explained by a genetic model because there does not appear to be time for adaptation to the alternating pink cycles. Table 14 indicates that even-year broods produce fewer chum than odd-year broods (assuming uniform escapement) in the Bolshaya River. Based on this, we might expect the effect of selection to be an increase in spawning effort in the odd brood years at the expense of even brood years. However, the opposite is true. The population is putting more effort into low-survival even broods than into high-survival odd broods. However, the even broods do coincide with the subdominant pink salmon cycle, which conforms to Gallagher's postulate of competitive exclusion between pink and chum salmon. Consequently, the apparent differential mortality appears to be acting in the opposite direction to produce this effect. Also, the pattern of age alteration appears to break down in the 1945 and 1946 brood years and assumes a direction in agreement with selective pressure.

Other stocks show odd-even variations in age at return, but often the data are presented in terms of catch year (Table 15). These data defy analysis without data on the relative strength of the year classes.

Available data limit the determination of the relative contributions of genetics and environment

to these fluctuations in age at maturity. Gallagher (1979) noted reversals in these alternatives which occurred simultaneously in Puget Sound, Fraser River, and Olsen Creek stocks. This strongly suggests an effect of the environment interacting with or overriding heredity. Such genetic control must be very malleable and sensitive to be influenced by environmental conditions and by density-dependent interactions in the ocean.

Gallagher (1979) and Smoker (1984) considered the early marine environment to be the most important site of chum-pink salmon competition in Puget Sound chum stocks. Limiting the scope of competition to this life history phase leads to two implicit assumptions for Puget Sound stocks: (1) local chum stocks compete with local pink stocks; and (2) odd-brood chum salmon compete with pink salmon, whereas even-brood chum salmon do not. But Puget Sound chum salmon mature at three or four years of age and pink salmon mature after two years. Because of this age overlap, a Puget Sound chum salmon from an even brood year could compete with a Puget Sound pink salmon in the North Pacific Ocean. More likely is the possibility of competition with pink salmon or chum salmon from other areas. The paths of migration of chum and pink salmon and their ocean distribution provide an opportunity for chum-pink and chum-chum competition among distant stocks.

Table 16 provides a theoretical model for considering the possibilities for competition (intraspecific or interspecific) for Puget Sound chum salmon stocks. The model assumes effects of competition to be density-dependent and to result in slowed growth. Competition in the home stream is limited to redd superimposition and egg retention. The effects of reduced growth depend on the life stages during which it occurs. Slow growth during the first year of life may lead to increased mortality. During the first year, Puget Sound chum salmon interact with local chum and pink salmon and with regional stocks as they migrate northward up the British Columbia coast. From the end of their first year to the end of their penultimate year, as they feed in the North Pacific Ocean, they will interact with pink and chum salmon from Washington, Canada, and, to some extent, with those from Alaska and Asia. During this time, density-dependent growth influences age at maturity and may

TABLE 15  
Yearly variation in age composition of chum salmon populations

Area and year	No. of fish sampled	Age composition (%)				Source
		0.2	0.3	0.4	0.5	
<b>NORTH AMERICA</b>						
<b>Alaska</b>						
Kotzebue Sd.						Regnart et al. (1966)
1962	68	7.3	63.3	28.0	1.4	"
1963	255	32.6	47.4	18.8	1.2	"
1964	463	55.7	42.5	1.8	0	"
1965	480	2.7	92.3	5.0	0	"
<b>Yukon R.</b>						
1961	97	4.1	75.3	20.6	0	Regnart et al. (1966)
1962	915	1.9	69.3	28.8	0	"
1963	650	6.0	83.3	10.2	0.5	"
1964	268	33.2	63.0	3.7	0	"
1965	486	0.2	97.3	2.5	0	"
<b>Prince Wm. Sd.</b>						
1952	187	23.5	47.1	29.4	0	Thorsteinson et al. (1963)
1953	819	8.4	76.4	15.1	0	"
1954	100	45.0	45.0	10.0	0	"
1955	55	10.9	81.8	7.3	0	"
1956	617	11.0	86.2	2.8	0	"
1957	218	6.9	72.0	21.1	0	"
1958	141	15.6	76.6	7.8	0	"
<b>British Columbia</b>						
<b>Nootka</b>						
1933	160	14.4	24.4	59.4	1.8	Pritchard (1943)
1934	124	16.9	73.3	9.0	0.8	"
1935	186	17.2	44.6	36.6	1.6	"
1941	518	9.1	50.6	39.6	0.7	"
<b>Oregon</b>						
<b>Tillamook Bay</b>						
1947	65	32.3	66.2	1.5	0	Oakley (1966)
1949	287	4.9	94.7	0.4	0	"
1950	481	76.2	22.5	1.3	0	"
1959	310	51.2	48.0	0.8	0	"
1960	92	68.2	30.8	1.0	0	"
1961	123	83.4	16.0	0.6	0	"
<b>ASIA</b>						
<b>Sea of Okhotsk coast</b>						
1957	-	1.4	63.1	9.8	25.7	Kondo et al. (1965)
1958	-	6.8	25.2	68.0	0	"
1959	-	1.9	86.0	9.5	2.6	"
1960	-	0.3	42.1	57.0	0.6	"
1961	-	1.2	32.9	63.0	2.8	"
<b>West Kamchatka coast</b>						
1957	-	0	68.2	23.0	8.8	Kondo et al. (1965)
1958	-	19.0	58.6	22.4	0	"
1959	-	0.6	91.7	7.7	0	"
1960	-	0.2	59.8	39.7	0.3	"
1961	-	0	37.6	59.2	3.1	"
<b>East Kamchatka coast</b>						
1957	-	5.0	72.5	21.5	1.0	Kondo et al. (1965)
1958	-	9.0	75.6	15.4	0	"
1959	-	0.8	83.7	13.7	1.8	"
1960	-	1.0	41.4	54.8	2.8	"
1961	-	0.8	51.1	44.7	3.4	"

Source: From Bakkala (1970)

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TABLE 16  
Theoretical location and effect of competition (chum/chum and chum/pink) for Puget Sound  
chum salmon stocks

Stock/effect	Location of Competition					
	Home stream	Nearshore estuary	BC coast	North Pacific	BC coast	Puget Sound
	First year →			End of first year to end of penultimate year	Final year →	
Local stocks	+	+	minimal*	0	minimal*	+
Major effect of competition	↓Survival to migrant fry†	↓Survival to adult	↓Survival to adult	-	↓Size at return‡	↓Size at return‡
Regional stocks (WA, OR, BC)	0	0	+	minimal*	+	0
Major effect of competition	-	-	↓Survival to adult	↓Age of maturation‡	↓Size at return‡	-
North Pacific stocks	0	0	0	+	0	0
Major effect of competition	-	-	-	↓Age of maturation‡	-	-

Notes: ↑ = increased effect, ↓ = decreased effect; + = competition, 0 = no competition

\*The magnitude of effect will depend on the size of the local stock compared to the size of the regional stocks or size of regional stock compared to size of North Pacific stock.

†Effect only for chums on chums or chums on pinks, not pinks on chums, because pinks spawn before chums. Effect is due to redd superimposition and egg retention.

‡Survival to adult may also decrease due to predation.

influence survival. To define these interactions, further studies similar to Peterman's (1984) approach to sockeye salmon interactions are needed.

G. Grette (Pentec Environmental, Edmonds, Washington, pers. comm.) hypothesized that as Asian, Canadian, Washington, and southeastern Alaskan chum salmon have a moderate overlap of feeding grounds, and as competition is not strategically advantageous, a pattern of avoidance has developed. Both Asian and southern North American stocks are influenced by pink salmon, so competition at that time is minimized by conserving reproductive energies to off-year cycles. This temporal avoidance is not evident for western Alaskan dominant even-year chum salmon, which may be present in large numbers as age 0.1 fish in the same feeding areas as are northern even-year pink salmon. The adaptations in these instances may be limited to a shift in age at maturity to put more reproductive effort into the "off-years."

Interactions between chum and pink salmon are evident, and interactions between chum, pink, and

sockeye salmon are implied. The partitioning of the oceanic feeding areas among the various age groups of chum and sockeye salmon, along with the variable input of odd- and even-year pink salmon, suggests that the dynamics and plasticity of the chum and sockeye salmon are "fitted in" the rigid, structured life history of the pink salmon. Perhaps it is necessary for one of the three species to be structured. It is increasingly apparent that the occurrence of odd- and even-year cycles has been brought about by oceanic phenomena. Concurrently, the suggested eleven-year periodicity of sunspots and the resultant cooling and warming of the oceans superimposes environmental effects that override the genetic mechanisms affecting odd- and even-year behaviour.

## CONCLUDING REMARKS

In spite of our inability to define precisely the patterns of evolution of the salmonids, more specifically, the species in the genus *Oncorhynchus*, the different adaptive features and degrees of specialization of the seven species of salmon are quite evident. Whether *O. keta* is the most primitive in a genealogical line or whether it evolved as a species between the sockeye-pink salmon and the chinook-coho salmon is presently not clear.<sup>7</sup> However, we can identify the remarkable adaptations of the chum salmon, which, in total, constitute an effective strategy for survival.

Chum salmon have maintained subtle but complex patterns of diversity in behaviour that have led to accommodation to a wide spectrum of environmental conditions. This has resulted in the chum salmon having the widest geographical distribution of the Pacific salmon and, prior to the influences of harvest, probably the greatest biomass of any of the salmon species in the Pacific Ocean. The adaptations that brought about these successes include: an ability to spawn successfully in streams of various sizes in a number of systems; the separation of runs by time and space, maintained by well-developed homing and migratory behaviour, thus making for efficient utilization of stream and ocean pasturage; exhibition of broad

patterns of phototaxis and rheotaxis; retention of some aggressive but vestigial territorial behaviour as fry in fresh water, whether schooled or separated as individuals; the ability to feed in fresh water (perhaps as long as a year) when necessary or advantageous (otherwise their residence in fresh water is short); alteration of patterns of diel outmigration from streams with large numbers of pink and chum salmon outmigrants; the loss of (or never attaining) obligatory schooling, or the maintenance of loose schools which break up when advantageous; the alteration of diet on the high seas during intense competition with pink salmon or with chum salmon cohorts; the maturation and return as adults of cohorts (and siblings) at various ages, thus increasing fecundity by increased size, and distributing the gene pool over several years; a genetic adaptation to alter the age at return to increase spawning potential to coincide with the subdominant pink salmon cycles; indications of spatial and temporal (odd-even year) partitioning of ocean feeding areas as strategies to minimize intra- and interspecific competition; and the maintenance of a broad and plastic genetic base which can be overridden by environmental factors when strategically advantageous.

Under certain conditions the chum salmon has proven to be a highly successful animal for artificial propagation (aquaculture), and, in recent times, the number of chum salmon in the North Pacific has reached historic proportions.

<sup>7</sup> Smith and Stearley (1989) indicated that chum salmon lie between the coho-chinook and pink-sockeye groupings on a phylogenetic tree of the salmonids. (Editors)

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