

LIFE HISTORY OF COHO SALMON

(*Oncorhynchus kisutch*)

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INTRODUCTION

COHO SALMON were first described by Walbaum in 1792 as *Salmo kisutch*, the specific name being the vernacular for coho in Kamchatka, USSR (McPhail and Lindsey 1970). Coho (*Oncorhynchus kisutch*), one of the seven recognized species of Pacific salmon belonging to the genus *Oncorhynchus*, are widely distributed in commercially harvestable quantities throughout their natural range, from the Soviet Far East around the Bering Sea, to Alaska, and south along the North American coast to California (Hart 1973). During the 1970s the world catch of all Pacific salmon averaged just over 400 million kg annually and of this total, approximately 9% consisted of coho, with the North American catch about double the Asian catch (Fredin 1980).

The basic life history pattern for this species

begins as adult salmon migrate from the sea into streams to deposit their eggs in gravel. Each female produces several thousand eggs, which are reduced in number by a high mortality during the coho's early life history (Salo and Bayliff 1958). After spawning, the adults die. The eggs incubate during winter in the gravel, and in the spring free-swimming fry emerge. The fry take up residency in the stream for a year or more, migrate to sea as smolts, and then begin their rapid growth phase (Davidson and Hutchinson 1938). After eighteen months or more at sea, the now maturing adults travel hundreds of kilometres across ocean waters, up streams, and through lakes to return to their place of origin (Hoar 1958). Within this basic pattern there are a great many variations that have evolved in response to opportunity and selective pressures.

RELATIVE ABUNDANCE

In most areas of the North Pacific, coho occur in small numbers compared to other species of Pacific salmon and represent less than 10% of the total catch (INPFC 1979). About 1.43 million coho of Asian origin were caught per year in the Japanese high-

seas fisheries and the Soviet coastal fishery from 1925 to 1951 (Fredin 1980). Pravdin (1940) noted that catches in the early years were not a good indicator of abundance because many of the Kamchatkan fisheries were shut down before the peak of the late-running coho migration. Increased exploitation rates beginning about 1952 expanded the average annual catch in the 1952-76 period to

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about 4.64 million fish (INPFC 1979).

In North America, fishing for coho in western Alaska is considered relatively unimportant, with an annual catch of about 100,000 fish (McPhail and Lindsey 1970). Elsewhere in North America, the commercial catch of coho by American and Canadian fishermen is about 50% greater than the combined USSR-Japan catch (INPFC 1979). From 1952 to

1976 the annual catch averaged 7.46 million coho with a peak in 1986 of 10.6 million (INPFC 1979). The average annual commercial catch of coho by region (from 1920 to 1976) was: central Alaska, 0.7 million; southeastern Alaska, 1.5 million; British Columbia, 2.7 million; Washington, 1.0 million; Oregon, 0.7 million; and California (1963-76), about 330,000 (INPFC 1979).

SPAWNING POPULATIONS

Distribution

Endemic populations of coho are found throughout the North Pacific basin (Figure 1) and they are distributed widely in other cold temperate areas as a result of introductions. The genus *Oncorhynchus*

may have evolved from an ancestral *Salmo* in the Sea of Japan during the early Pleistocene (Neave 1958). Geological evidence suggests that the Sea of Japan, the Bering Sea, and the Sea of Okhotsk may have become separated during a later glacial period, thus providing for geographic isolation that

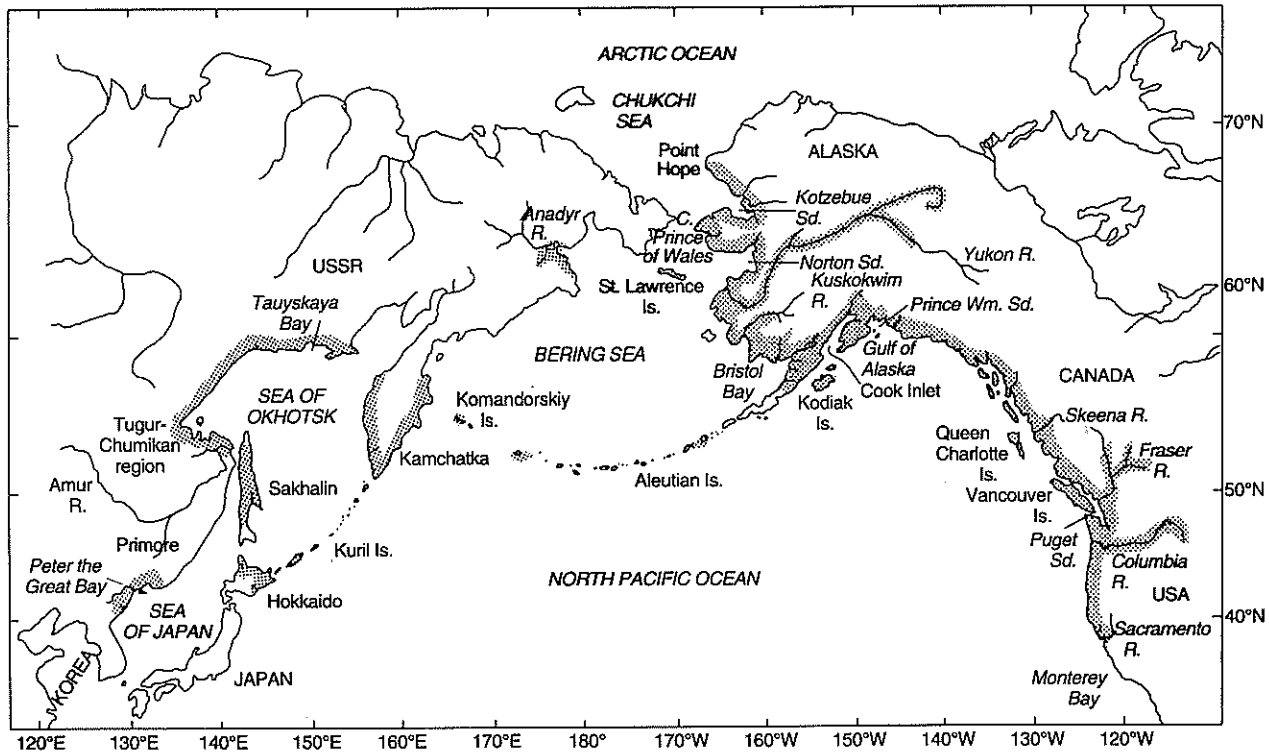


FIGURE 1
Coastal and spawning distribution of coho salmon

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led to speciation within the genus *Oncorhynchus*.

Godfrey (1965) noted that coho, like many other species, are less common in the northern and southern fringes of their distribution, and they are most abundant in the central portion of their range. On the Asian side of the Pacific Ocean, coho have been reported as far south as Chongjin on the east coast of North Korea (Matsubara 1955, as cited by Lindberg and Legeza 1965) (Figure 1).

Jordan and Snyder (1902) reported that coho were distributed in the area around Japan, from Otaru on the west coast of Hokkaido, and from Osatsubo and the Ura River. Hikita (1956) indicated that coho were rarely found in Hokkaido, but that some specimens had been examined from the Yurappu and Shokotsu rivers; however, other reports have suggested that coho were absent from both Hokkaido and the waters adjacent to Japan (FRBC 1955).

Coho occur in small numbers along the Kuril Islands chain (Iturup and Etorofu islands) (Okada 1960) and in the Naiba and Tym river systems on Sakhalin Island (Smirnov 1960; Godfrey 1965). Dvinin (1952) reported that the catch of coho from south Sakhalin was negligible. On the mainland side of the Sea of Japan, Lindberg and Legeza (1965) noted that coho are rarely found as far south as Peter the Great Bay. Berg (1948) reported that the most southerly record for Asian coho was from the Suchan River, which enters Peter the Great Bay. Coho are also uncommon on the mainland side of the Sea of Okhotsk, though they are found in the Iski River, just to the north of the mouth of the Amur River (Berg 1948). Coho are rare in the Shantarski Islands and in the Tugur-Chumikan region but they do occur in the most northern part of the Sea of Okhotsk, in the Okhota and Kukhtuy rivers (Shmidt 1950). Moreover, coho runs into Tauyskaya Bay and the Ola River were sufficient to support a commercial fishery (Shmidt 1950).

On the southwest coast of Kamchatka, the most important salmon-producing river is the Bolshaya, which yields 25%-30% of the regional catch. However, more than 90% of the production is pink salmon (*Oncorhynchus gorbusha*), with coho representing only 1.4% of the catch (Semko 1954). Pravdin (1940) noted that much of the coho run occurred after fishing terminated in early September. Other coho-producing streams on the west coast of Kamchatka include the Icha (Gri-

banov 1948) and Kikhchik (Pravdin 1940) rivers.

On the east coast of Kamchatka, the major coho producer is the Kamchatka River (Gribanov 1948). Other coho systems are the Paratunka (Popov 1933), and the Kalyger, Kyrganik, and Ozernaya rivers (Gribanov 1948). Further to the east, Berg (1948) reported that coho were uncommon in the Komandorskiy Islands. The most northerly occurring Asian coho were reported in the vicinity of the Anadyr River estuary (Andriashev 1955).

Although Asian coho have not been reported north of 65°N, North American coho have been found above latitude 68°N. In Alaska, the most northern coho population is found in the Kukpuk River near Point Hope on the Chukchi Sea (Wahle and Pearson 1987). Coho have also been found in the Singoolik, Kivalina, Wulik, Noatak, Buckland, and Inmachuk rivers, all of which enter Kotzebue Sound, Alaska. Information on coho from Point Hope to Cape Prince of Wales is sparse because they occur there in relatively small numbers and arrive in the rivers too late to be captured by the native fishermen. South of Cape Prince of Wales on the Bering Strait, coho have been identified from the Agiapuk and Kuzitrin rivers near Port Clarence and from rivers tributary to Norton Sound, such as the Snake, Nome, Fish, Swiniuk, Shaktoolik, Unalakleet, and tributaries of the Yukon River. Wahle and Pearson (1987) also reported coho from the Koozata River on St. Lawrence Island in the northern Bering Sea.

Coho are caught all along the Alaskan coast from Norton Sound to the mouth of the Kuskokwim River (INPFC 1962b). From the Yukon River south to Bristol Bay, coho commonly migrate in coastal streams and well up into the Yukon and Kuskokwim rivers (McPhail and Lindsey 1970). However, Hartt and Dell (1986) concluded that the small numbers of coho found in the eastern Bering Sea were indicative of the relatively small populations of coho that originated in the streams of Bristol Bay and vicinity. Coho are also found in the streams of Attu, Kiska, Adak, Kagalaska, Atka, and Unimak islands of the Aleutian Islands chain (Wahle and Pearson 1987) and have been stocked into five lakes along the Kenai Peninsula (Engel 1972). Throughout the northern Gulf of Alaska and southeastern Alaska, coho spawn in most coastal streams (Atkinson et al. 1967). Coho spawners have been reported in the Klukshu River (Wynne-Edwards

1947) and Village Creek (Hancock and Marshall 1984a), both tributaries of the Tatshenshini River in the Yukon Territory.

In British Columbia, coho are found in most coastal streams. In the larger rivers, including the Fraser, Skeena, Bella-Coola, Nass, and Taku rivers, they migrate some distance inland and spawn in the smaller tributaries. It was estimated by Aro and Shepard (1967) that coho spawned in 970 of the 1,500 known salmon-bearing streams in British Columbia. Coho is the most widespread of the five species of Pacific salmon and no one area of the province is the dominant producer (Milne 1964).

On the east coast of the Queen Charlotte Islands, the Tlell River (Graham Island) and Copper Creek (Moresby Island) are important coho spawning streams. In the northern mainland of British Columbia the most important coho-producing streams are the Lakelse River, a tributary of the Skeena River, and the Bella Coola/Atnarko River system.

The major individual spawning streams in southern British Columbia are the Kingcome, Kakweiken, Nimpkish, Oyster, Toba, Cowichan, San Juan, Squamish, and Chilliwack rivers (Aro and Shepard 1967). Along the west coast of Vancouver Island there are numerous small producers of coho salmon. The Somass River system, tributary to Barkley Sound, is recorded as being the most important of these rivers.

The streams of coastal Washington and Puget Sound are abundant producers of coho (Atkinson et al. 1967). Coho are found in many tributaries along the Washington side of the lower Columbia River and are known to spawn as far northeast as the Wenatchee River in the upper Columbia River basin (Wahle and Pearson 1987).

In Oregon, coho are found in many of the tributaries of the lower Columbia and Willamette rivers, as well as in most coastal streams south to the Rogue River (Atkinson et al. 1967). Wahle and Pearson (1987) observed that coho migrate south in the Willamette River as far as the McKenzie River tributary and east in the Columbia River to the Grande Ronde River, passing through southeastern Washington, southwestern Idaho, and into northeastern Oregon via the Snake River.

The distribution of coho in California has been well documented (Atkinson et al. 1967). They occur in most of the coastal streams from the California/

Oregon border south to the San Lorenzo River on Monterey Bay (Wahle and Pearson 1987). Coho are rare in the Sacramento/San Joaquin River system (Hallock and Fry 1967) and occur only in small numbers in the Klamath River (Snyder 1931) and elsewhere. High summer temperatures probably limit their freshwater distribution (Fry 1977). At sea, coho are caught consistently as far south as Monterey Bay, and two coho have been documented from Port Chamalu Bay, Baja California; one was caught 4 August 1942, and a second fish weighing 6.35 kg was caught 20 August 1963 (Messersmith 1965).

In summary, the normal distribution of coho extends from northern Japan through Kamchatka, across the Bering Sea to Alaska, and south through all coastal areas to California (Figure 1). There are, however, a number of locations to which coho eggs or fry have been transplanted in an attempt to establish a landlocked or an anadromous population outside of the North Pacific basin.

Transplants

Coho have been introduced into many areas of North America, Asia, Europe, and South America, with great success in some cases and no success in others. In North America, as early as 1873, attempts were made to introduce coho into the Great Lakes (Scott and Crossman 1973). Thousands of fry were released into Lake Erie between 1873 and 1878, and again in 1933, but although some coho up to 2.3 kg were caught in 1935, the transplant was considered unsuccessful (Scott and Crossman 1973). More recently, coho that were released into two Montana lakes (Anonymous 1951) survived to maturity but were small and had relatively few eggs (about 700 eggs per female); average weight for males was 0.43 kg and for females 0.50 kg (Beal 1955). Coho were released into Parvin Lake and the Granby Reservoir, Colorado, in 1963 (Klein and Finnell 1969). Coho fry were also planted into Lake Berryessa, Lake Almanor, Oroville Lake, and the Merle Collins Reservoir in California in the early 1970s (Wigglesworth and Rawstron 1974). In the Colorado and California releases, no natural reproduction occurred. In 1971, the province of Alberta introduced coho into Cold Lake, some of which were later recovered downstream in Pierce Lake, Saskatchewan (Scott

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and Crossman 1973). These and other small-scale introduction experiments can be best regarded as unsuccessful or inconclusive.¹

It was not until the state of Michigan began releasing coho smolts in 1966 into the Great Lakes (Lake Michigan and Lake Superior) that the potential to establish exotic or non-native coho populations was realized. Soon after the unplanned, but successful, introduction of pink salmon into Lake Superior (Kwain and Lawrie 1981), the state of Michigan released 660,000 coho smolts into Lake Michigan (Wells and McLain 1972) and 192,000 into Lake Superior (GLFC 1970). Early jack returns were very promising, so the program was escalated. In Lake Michigan the releases increased to 1.7, 1.2, and 3.3 million smolts in 1967, 1968, and 1969, respectively, with the states of Wisconsin and Illinois contributing to the smolt production in Lake Michigan. In Lake Superior the coho releases were increased from the original 192,000 (from Michigan) to 467,000, 382,000, and 656,000 during the same years, with contributions from the state of Minnesota and the province of Ontario. As the catches and escapements increased there was considerable public pressure to expand the program to the other Great Lakes. Michigan released 402,000 and 667,000 coho smolts into Lake Huron in 1968 and 1969, respectively. The states of Ohio, Pennsylvania, and New York released 111,000 and 236,000 smolts into Lake Erie in 1968 and 1969, and New York and Ontario released 41,000 and 239,000 coho into Lake Ontario in the same two years. By the end of 1977, the following number of coho smolts or fry had been released in each lake: Lake Superior, 5.23 million; Lake Michigan, 30.06 million; Lake Huron, 5.20 million; Lake Erie, 6.80 million; and Lake Ontario 4.25 million; for a total of more than 51 million coho (GLFC 1980).

The success of these transplants was phenomenal. Survival rates of fry to adults (catch plus escapement) for the early releases into Lake Michigan ranged from 19% to 32%, with the fish averaging 74 cm and 4.3 kg (GLFC 1970). In Lake Superior the survival rate for the first three plantings ranged from 2% to 24%. The lower productivity of this lake resulted in slower growth and spawners

that averaged only 1.3 kg in weight (Lawrie and Rahrer 1972). In Lake Huron the catch was equally divided between sport and commercial fisheries and totalled about 17% of the juveniles released; average weight for a mature spawner was 4.1 kg (GLFC 1970). In Lake Erie the survival was about 25% and the average weight was about 2.7 kg (Hartman 1972). Most of these fish were caught in the colder, deeper Canadian waters near Long Point, Ontario. Lake Ontario coho reached an average size of 63 cm and 2.3 kg at maturity (Scott and Crossman 1973), but the overall survival rate was low due to lamprey attacks (GLFC 1970).

Following the successful introduction of coho into the Great Lakes, other smaller lakes in the region were planted with coho. These included the Stormy and Palette lakes in Wisconsin; Hare Lake, Minnesota; and Hemlock Lake in Michigan (Engel and Magnuson 1976; McKnight and Serns 1977).

Long before the introduction of coho into the Great Lakes area, attempts had been made to establish Pacific salmon on the east coast of North America. Most of this effort took place between 1901 and 1910, and a few transplants were carried out as late as 1930. Davidson and Hutchinson (1938), in their review of the geographic and environmental limits of Pacific salmon, reported the following coho egg or fry transplants: Maine, 1.4 million; Maryland, 12,000; New Hampshire, 315,000; New York, 13,500; and to the interior states of Vermont and Pennsylvania, 47,000 and 355,000, respectively. There is no record that any of these releases produced adult salmon.

Ricker (1954) reported that juvenile coho had been introduced into the Ducktrap River in Maine between 1943 and 1948 and that, subsequently, a run of about one hundred adults had returned to spawn in 1952. Ricker was uncertain whether this run would be self-sustaining. The dream of establishing a self-sustaining, east-coast run of coho persists. Symons and Martin (1978) indicated that coho juveniles have been released into a New Hampshire stream since 1969 and into a Massachusetts stream since 1971. In addition, two aquaculture operations have been rearing coho in Maine. One of these sites is thought to have released, intentionally or unintentionally, some coho juveniles that strayed into Frost Fish Creek in New Brunswick in the fall of 1976. No adult coho are known to have subsequently returned to this

¹ Hasler and Farner (1942) reported on growth, age, and feeding habits of silver (silverside) salmon (*O. kisutch*) in Crater Lake, Oregon 1935-40. The present author believes this to be an error, and that, in fact, the salmon were kokanee (*O. nerka*).

creek or any other New Brunswick stream.

In the 1970s an attempt was made to introduce Washington coho into South Korean streams (R.J. Wahle, Pacific Marine Fisheries Commission, Seattle, Washington, pers. comm.). The probability of such a transplant succeeding was very low considering that the natural occurrence of coho in this area is extremely rare. Recently, there were a number of attempts to establish self-sustaining runs of coho in the Yurappu River (Ishida et al. 1975), Shibetsu River (Ishida et al. 1976; Nara et al. 1979), and the Ichani River (Umeda et al. 1981); these streams are all located on the east or southeast coast of Hokkaido. Coho eggs were supplied from the 1973-78 (excluding 1975) broods from Washington (University of Washington) and Oregon (Eagle Creek) hatcheries. These transplants appear to have been unsuccessful.

Coho transplant attempts to Europe have included shipments of eggs from British Columbia to Scotland, France, West Germany, and Cyprus, pri-

marily for experimental use or for pen rearing. None of these transplants resulted in the establishment of self-sustaining populations.

In South America, considerable effort has been made to establish coho runs for ocean ranching in Chile. Davidson and Hutchinson (1938) noted that 255,000 coho eggs had been shipped to Chile and 377,000 to Argentina, with the additional comment that "sockeye and coho (were) successfully introduced to Chile." The success of this transplant was not substantiated and, like many others, it probably failed after one or two cycles. In the last decade, large releases of coho smolts have been made in southern Chile (R.E. Noble, Union Carbide, Olympia, Washington, pers. comm.). These smolts were derived from surplus production at Washington hatcheries. Although the adult returns were small, there were sufficient numbers to justify continuation of the experiment in the hope that the transplant might succeed here as well as it did in the Great Lakes.

SPAWNING MIGRATION

Seasonal Timing

Coho begin to mature during the summer after one winter at sea and arrive at their rivers of origin during late summer and autumn. In some cases the journey is a short one along coastal routes, but in many other instances the spawning run may take one to two months and cover many hundreds of kilometres of open ocean. Successive generations of each stock appear in the estuary and ascend the spawning stream about the same time each year (Royce et al. 1968). In general, the higher the latitude, the earlier the timing (Briggs 1953). In northern Alaska and Kamchatka the migration begins in July and August (Pravdin 1940; Godfrey 1965), in British Columbia the normal timing is September/October (Fraser et al. 1983), whereas in California spawning migrations may be delayed until November/December (Shapovalov and Taft 1954).

Throughout the range of coho there are also many exceptions to the normal timing patterns.

They have been observed to leave the marine environment and enter freshwater streams as early as April, e.g., the Capilano River, British Columbia (F.K. Sandercock, unpublished data), and as late as March, e.g., the Kamchatka River (Smirnov 1960) and Waddell Creek, California (Shapovalov and Taft 1954). In one year, Foerster and Ricker (1953) observed coho in early April in Sweltzer Creek, British Columbia. For most stocks, the duration of the spawning migration appears to be three months or more. Fraser et al. (1983) reported a duration of 106 ± 21 days for Big Qualicum River coho. However, Pritchard (1943) reported that the 1942 spawning run in the Cowichan River, British Columbia, took 20-30 days, and the fish were spawned out in 30-60 days.

Coho rarely exhibit seasonal runs to single tributaries (Ricker 1972). Summer and autumn runs into the Paratunka River (USSR) have been noted, as have summer and winter runs into some Kamchatkan rivers (Gribanov 1948). In those cases where coho migrate at unusual times or over a short

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period, such behaviour appears to have evolved in response to particular flow conditions. For example, obstructions that may be passable under high discharge conditions may be insurmountable during low flows (Neave and Wickett 1953). Conversely, many early-timing runs are thought to have developed because early-entry coho could surmount obstacles during low or moderate flows but not during high flows. It can be concluded that, in such cases, these obstacles might become velocity barriers once the autumn rains begin. In California, many of the smaller coastal streams do not have sufficient flow during the summer and early autumn to breach the sand bars that are thrown up across the mouths of the streams by wave action. Fresh water entering the ocean is by seepage only, and coho cannot enter these streams until the autumn rains produce enough discharge to breach the sand barriers. This usually takes place in October/November (Briggs 1953). Holtby et al. (1984) observed that coho returning to Carnation Creek on the west coast of Vancouver Island moved into the stream on a continual basis, provided that autumn freshets were sustained. In years when freshets were infrequent, the migration was pulsed. When the initial freshet was delayed until late October, 70% of the escapement entered the stream over several days. Returning adults apparently gather at the mouths of shallow coastal streams and then move upstream on high water.

There is also a tendency for fish that migrate early to move further upstream than those that migrate later (Briggs 1953). In the Kamchatka River the early run migrates 25-30 km, whereas the late run migrates only 2-3 km up tributaries (Gribanov 1948). Mid- to late-migrating fish generally return to their natal streams in a more advanced state of maturity and closer to the onset of spawning. However, entry of coho into streams is not necessarily dependent on their state of maturity, as both ripe (mature) and green (sexually immature) fish may occur in all parts of the run (Shapovalov and Taft 1954).

If conditions (flow, temperature, etc.) in the stream are unsuitable, the fish will often mill about in the vicinity of the stream mouth, sometimes waiting weeks or even, in the case of early-timing fish, months for conditions to change. As temperatures decrease and rainfall and flow increase (Gribanov 1948), the coho will make short excursions

into the stream and then return to salt water. Coho generally begin their upstream migration when there is a large increase in flow, particularly when combined with a high tide. This was observed by Neave (1943) in the Cowichan River, British Columbia; Sumner (1953) in Sand Creek, Oregon; Shapovalov and Taft (1954) in Waddell and Scott creeks, California; and Fraser et al. (1983) in the Big Qualicum River, British Columbia. The latter authors noted that in some years there were secondary peaks in coho migration during stable or decreasing discharge periods and that migration may be related to factors other than flow. Shapovalov and Taft (1954) also observed that migration occurred on both rising and falling stream flows but not during peak floods.

Reiser and Bjornn (1979) noted that coho normally migrate when water temperature is in the range of 7.2°-15.6°C, the minimum depth is 18 cm, and the water velocity does not exceed 2.44 m/s. This pattern of migration allows coho to reach very small headwater tributaries where good spawning and rearing conditions may be found

Diel Timing

Most coho stocks actively migrate upstream during daylight hours rather than at night. Brett and MacKinnon (1954) observed that 90% of fish moving up a fishway in the Stamp River (Vancouver Island) did so between 0800 and 1830 hours, with a peak between 1400 and 1600 hours. Neave (1943) reported that when there were large numbers of coho moving, the peak migration occurred at midday; when the numbers were smaller there were two peaks, 0700-1000 and 1500-1700 hours. Artificial light had no effect on migration. Other factors, such as water turbidity, degree of sexual maturity, and size of run may influence migration fluctuations (Shapovalov and Taft 1954).

Ellis (1962) observed that, early in the season, coho migrated actively right after dawn, whereas, late in the season (September/October), they began their daily migration with low numbers moving at first light, and with progressively greater numbers moving up to 8 hours later. There was also a tendency for small groups of fish to move earlier in the day than large groups. In the Big Qualicum River, British Columbia, coho moved upstream during all daylight hours, but peak ac-

tivities occurred at dawn and sunset (Fraser et al. 1983).

Migration Behaviour

During their migration upstream, coho can frequently be seen breaking the surface or jumping clear of the water, whether there is an obstruction nearby or not. Fish holding downstream of an obstruction appear to make a number of feeble attempts to jump, as if to gauge the height or degree of difficulty in overcoming the obstacle. When they repeatedly fail to clear the obstacle, they drop back and spawn downstream in whatever sites are available. In passage through a fishway, Brett and MacKinnon (1965) noted that the fish spent a brief period of reconnoitring in each pool before moving to the next pool. Only infrequently did the fish return downstream. Vertical leaps of more than 2 m are possible.

Shapovalov (1947) noted that coho crossed over low obstructions with a characteristic rolling motion. Briggs (1953) observed coho moving across riffles where the volume of water was as low as 3.4 m³/min and the water depth only 5 cm.

Since coho are vulnerable to predation while they are migrating through shallow riffle areas, they move through these areas as quickly as possible and seek the deeper, quieter pools. They then rest in these pools before migrating further upstream. Ellis (1962) provided a detailed account of the behaviour of coho migrants in the Somass River, British Columbia. The fish were seen to move quickly through a set of rapids and into a holding pool. On entering the quiet water they then swam steadily along the deepest channel, close to the bottom. The fish held in pools for some duration, periodically jumping or wandering in schools up and down the pool. As they approached the shallow upper end of the pool, a few fish darted over the shallows and up through the next set of rapids.

Migrant Types

Milne (1950) suggested that there are probably two distinct types of coho in British Columbia. The "ocean" type primarily occupy outer coastal or offshore waters, whereas the "inshore" type remain within inside waters during their saltwater

life history phase. Taylor and McPhail (1985) also recognized two forms of the fish in their study of the body morphology of coho from the upper Columbia River to Alaska: a "coastal" form, characterized by large median fins and a deep robust body; and an "interior" form with small median fins and a more streamlined body. The characteristics of the latter type were thought to be an adaptation for the long and often arduous migrations in fresh water. In swimming tests, this type outperformed the coastal fish. However, the coastal types exhibited greater morphological variation within and between river systems, which suggests that the straying rate, and hence the gene flow, may be greater among coastal-type coho.

Rate of River Migration

Ellis (1962) reported that at river velocities of 1.0 m/s or less, coho maintained steady swimming speeds of 1.2-1.7 m/s without stopping. Migration speed is equal to swimming speed minus water velocity. Reiser and Bjornn (1979) found that the cruising speed for coho was up to 1.04 m/s, that sustained swimming ranged from 1.04 to 3.23 m/s, and that darting speeds were 3.23-6.55 m/s. Ellis (1962) observed that when stream velocities reach 1.5 m/s or more, the tendency for fish to school broke down, and the steady swimming mode was replaced by resting and darting.

Maximum non-sustainable swimming speeds up to 11 m/s have been recorded (Ellis 1962), and it has been calculated that, under a steady flow condition of 0.4 m/s, coho would be expected to migrate about 2.7 km/h (Ellis 1966). A lower rate of migration was observed by Neave (1949), who noted that coho moved 32 km upstream in two days in the Cowichan River, British Columbia. Assuming that the fish actually migrated 12 hours in each day, this represents a rate of 1.3 km/h.

Upstream Migration

Throughout their range, coho spawn in streams along the coast and in small tributaries of larger rivers (Rounsefell and Kelez 1940). Coho migrate further upstream than pink and chum (*Oncorhynchus keta*) salmon but usually not as far as sockeye (*O. nerka*) and chinook (*O. tshawytscha*). Godfrey (1965) reported that, in general, coho seldom mi-

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grate more than 240 km up large rivers to spawn. However, there are some notable exceptions. In the Kamchatka River, coho migrate over 550 km to reach some upper tributaries (Berg 1948). McPhail and Lindsey (1970) reported that coho ascend the main stem of the Yukon River almost to the Alaska/Yukon border, a distance of 1,830 km. More recent work has indicated that coho travelled about 200 km further up the Yukon River to Dawson and beyond, but the location of the spawning grounds was unknown (Ennis et al. 1982). Bryan (1973), in a biological survey of the Yukon Territory, discovered coho at Old Crow on the Porcupine River, and 350 km further upstream on the Fishing Branch River, a total migratory distance from salt water of over 2,200 km. Hancock and Marshall (1984b) reported that the heaviest concentration of spawners on the Fishing Branch River was near the Bear Cave Mountain area. In British Columbia, the long migration stocks travel about 510 km in the Skeena River; and, in the Fraser River system, they migrate 550 km in the South Thompson, 570 km in the North Thompson, and 680 km to the tributaries of the upper Fraser River. Further south, coho have been reported in the Grande Ronde River in north-eastern Oregon, a distance of approximately 800 km from the Columbia River estuary (Wahle and Pearson 1987)

Age at Time of Return

Throughout their normal range, the majority of coho mature in their third year of life, having spent about four to six months in incubation and up to fifteen months rearing in fresh water, followed by a sixteen-month growing period in sea water. Based on their scale patterns, these fish are generally designated as age 1.1 (i.e., one winter in fresh water and one winter in salt water). There are, however, many variations to this normal pattern. Some of the males mature precociously and return to spawn after only four to six months in sea water and are referred to as "jacks" (age 1.0), and others may stay in fresh water for two winters and return as age 2.1 fish.

Godfrey (1965) reported that during the period 1926-37, coho from the east coast of Kamchatka were predominantly age 2.1, whereas those from west Kamchatka matured at age 1.1. Since 1959

there has been a shift towards age 2.1 fish.

Many coho from central and southeastern Alaska also mature at age 2.1: up to 60% in the Yukon River (Gilbert 1922), and up to 93% in the Swanson River, Alaska (Engel 1968). However, the proportion may vary from year to year. For example, in Sashin Creek in southeastern Alaska, age 2.1 fish comprised 78%, 59%, 64%, and 62% of the stock in the years 1965 through 1967 and in 1969 (Crone and Bond 1976). In western Alaska, the predominant age at maturity is 1.1 (70.8%), and in the Aleutian Islands age 1.1 fish make up 60% of the stock (INPFC 1962a). Drucker (1972) observed an unusual age distribution for coho in the Karluk River on Kodiak Island, where 56.9% were age 2.1, 41.7% were age 3.1, and 1.4% were age 4.1. Late-maturing age 3.1 fish have been reported from a few other systems in Alaska but the proportion is generally less than 5%. It has been suggested that juveniles that live in Alaskan lakes during their period of freshwater residency may go to sea at an older age than those residing in rivers. However, in Oregon the growth of coho juveniles in lakes is faster than in streams. The lake rearing smolts migrate at the same age as the stream dwellers but are larger in size (A. McGie, Department of Fish and Wildlife, Corvallis, Oregon, pers. comm.).

Pritchard (1940) presented a full spectrum of ages at maturity for coho from British Columbia. He observed 0.1, 0.2, 0.3, 1.0, 1.1, 1.2, 2.0, and 2.1 age groups from scale readings but acknowledged that 97.9% of the coho examined from 6,312 fishery samples were age 1.1. Pritchard did not have the benefit of examining marked fish of known ages to validate age readings from scales, so one might question the accuracy of those observations, particularly with respect to the rarer groups. In general, there is a decrease in the number of age 2.1 fish from north to south (Gilbert 1913), with age 1.1 fish comprising 95% of the stock in British Columbia (Foerster 1955), and virtually no coho of age 2.1 occurring further south (Fry and Hughes 1954). Neave and Pritchard (1942) observed some four-year-old returns (1.2 or 2.1) from their marking experiments on coho from the Cowichan River, British Columbia, but it is possible that the delayed maturity was a result of the trauma associated with the marking.

Precocious males or "jacks," which mature mostly one year earlier than the majority of coho,

are a highly variable component of the escapement population. Fraser (1920) reported 28 age 1.0 jacks in a sample of 2,000 coho taken from the Strait of Georgia, the remainder being age 1.1. Marr (1944), in a study of Columbia River coho, observed that about 6% of the jacks were age 1.0, 84% were age 1.1, just under 10% were age 2.1, and a few were age 2.0 (the number of jacks was probably underestimated because of gillnets selectively harvesting larger fish). Neave (1949) observed a jack return to the Cowichan River of 1%-13% over several years. Wickett (1951) reported a return of only 8 jacks among 1,883 coho counted through a fence on Nile Creek, British Columbia, in a six-year period. Foerster and Ricker (1953) observed that the jack count was always greater than the return of age 1.1 fish of the same year class in Sweltzer Creek, British Columbia. In California, Murphy (1952) summarized the counts of coho jacks passing the Benbow Dam on the south fork of the Eel River over the period 1939-51. The number of jacks ranged from 6.9% to 33.8% (average 18%) for a given return year. Morgan and Henry (1959) reported that the jack return to the Ten Mile Lakes (Oregon) in 1955 represented 46% of the total return; this high percentage may be attributed to the larger average size of the smolts migrating out of the lakes (A. McGie, Department of Fish and Wildlife, Corvallis, Oregon, pers. comm.). Salo and Bayliff (1958), in their study of wild coho returns to Minter Creek (Washington), reported jack returns of 21% and 27% in two consecutive years. Andersen and Narver (1975) also observed a high rate (32%) for jack returns in a wild coho population in Carnation Creek, British Columbia.

From these and other studies of both hatchery-produced and wild coho it is obvious that the number of jacks returning to a given system is highly variable between years and between systems. It has been well demonstrated by Bilton et al. (1984) that coho that migrate earlier than average, and at a size larger than average, tend to produce a high rate of jack returns. These larger smolts represent the fast growing component of a specific brood. The jacks are known to contribute to the fertilization of naturally spawned eggs by darting in beside a full-sized male and female during the spawning process. How their genes influence the wild population is not known. During routine hatchery operations, jacks are excluded from fertilization

because it is believed that the prevalence of jacks in the subsequent return would increase, and because they are considered less productive due to their small body size.

Berg (1948) suggested that in some coho populations the jacks may not migrate to sea but may mature in fresh water. This possibility is also suggested for those stocks which undergo long fresh-water migrations, such as in the Yukon, Fraser, and Columbia rivers. It is speculated that the time involved in the downstream and upstream migration would preclude jacks from travelling much further than down to the estuary and then back to the spawning grounds.

Size at Time of Return

Size at the time of return is variable and may be influenced by sex, age, time position in the run, and perhaps other factors. Marr (1943) observed that males were generally larger than females, older fish larger than younger fish, fish in late runs larger than those in early runs, and fish in southern stocks (on the average) larger than those in northern stocks. In addition, Salo and Bayliff (1958) noted that, for a given stock (Minter Creek, Washington), the fish sampled at the peak of migration tended to be larger than both the early-returning and the late-returning fish.

Fraser et al. (1983), in a study of 2,513 coho from the Big Qualicum River, found that the average length of the three-year-olds (age 1.1) was 52.7 ± 3.2 cm (4 four-year-olds (age 2.1) had a mean length of 56.6 ± 4.7 cm) and that there was no significant difference between males and females. Andersen and Narver (1975) observed that the average length of male coho returning to Carnation Creek (British Columbia) was 58.1 cm compared to 66.9 cm for females. Engel (1968) found that the mean length of coho from Swanson River (Alaska) was 60.4 cm for males and 62.6 cm for females. Gribanov (1948) reported that Kamchatkan coho (males and females combined) ranged from 40 to 88 cm fork length but more commonly averaged 55-69 cm. He also found that males tended to be larger than females.

Over their normal distribution range, there does not appear to be any clear pattern for size. For Kamchatkan coho the average weight is 3.0-3.5 kg with a range of 1.2-6.8 kg (Gribanov 1948); for the

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Resurrection Bay area (Alaska) the average is 3.34 kg (McHenry 1981); and for southeastern Alaska, 4.8 kg (females only) (Marriott 1968). In British Columbia the average weight for coho is 4.0 kg in the Cowichan River (Neave 1949), 4.0 kg in the Big Qualicum River (F.K. Sandercock, unpublished data), 3.0 kg in the Capilano River (F.K. Sandercock, unpublished data); and 3.22 kg for all British Columbia commercial fisheries between 1952 and 1961 (Godfrey 1965). For the Columbia River the average weight was 4.5 kg (Cleaver 1951), whereas in California coho commonly weigh 3.2–5.5 kg (Fry and Hughes 1954).

Coho weighing 6.0 kg are not unusual, but any over 9.0 kg are rare. The largest coho caught to date in the Great Lakes was landed in Lake Ontario near Pulaski, New York, on 7 September 1984, and weighed 11.16 kg (G. Radonski, United States Sport Fisheries Institute, Washington, DC, pers. comm.). The largest coho on record was caught off Victoria, British Columbia, in 1947 and weighed 14.0 kg (Hart 1973).

Jacks are substantially smaller than normal adults. Foerster and Ricker (1953) reported that jacks from Sweltzer Creek (British Columbia) averaged 30 cm in length (range 27–34 cm); in Carnation Creek (British Columbia) they averaged 35.6 cm (Andersen and Narver 1975); and in the Big Qualicum River they averaged 34.2 ± 5.1 cm (Fraser et al. 1983). A total of 356 jacks sampled in Waddell Creek (California) averaged 40.9 cm in length over a nine-year period (Shapovalov and Taft 1954).

Sex Ratio

In theory, the sex ratio should be 1:1 males to females. It is assumed that, to at least the migrant stage, there is no differential mortality associated with one or the other sex. Once the fish are at sea, males or females may be subject to different rates of predation, but this seems unlikely. The greatest differential mortality is associated with the commercial and recreational fishery, which is highly selective. Because of gear restrictions and other regulations, there is a strong selection for large fish, especially females, which means more jacks can escape to the spawning grounds. Evidence for selection of females is not strong for coho salmon, but a higher rate of exploitation of large female

chinook has been demonstrated (D.E. Marshall, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.).

Foerster and Ricker (1953) noted that it is surprising that there was no constant excess of age 1.1 females over males, because the jacks (age 1.0 males) often outnumbered the age 1.1 males of the same year class. The removal of the jacks from the population must upset the original sex ratio of 1:1 found at the smolt stage.

Marr (1943) thought that the sex ratio of age 1.1 fish in the Columbia River was about 1:1 but noted that there were more males than females in the early part of the run. Sumner (1953) observed a preponderance of males in both the early and late part of the run in Sand Creek, Oregon, but as Godfrey (1965) noted, the higher proportion of males on the spawning grounds at the end of the run may simply reflect the fact that the males live longer than the females.

Some published accounts of sex ratios, especially those in the Cook Inlet area of Alaska, have indicated a greater abundance of males throughout the run. Logan (1967) observed male to female ratios ranging from 0.9:1 to 1.2:1, Engel (1968) found a ratio of 1.2:1 in Swanson River, and McHenry (1981) reported a very high ratio of 2.1:1 for Bear Creek coho. Further south, on the west coast of Vancouver Island, Andersen and Narver (1975) observed a ratio of 1.26:1 in Carnation Creek. Hunter (1949) reported a ratio of 2.07:1 for coho from Port John, British Columbia.

The results of a study by Shapovalov and Taft (1954) on California coho are more typical. They noted that there is characteristically an excess of females in the age 1.1 group, but if the 1.0 and 1.1 males are combined (for a given year class) they will outnumber the females. As an example, Salo and Bayliff (1958) showed that for age 1.1 wild coho returning to Minter Creek in two consecutive years, the females constituted 55.6% and 57.6% of the runs. If, however, the jacks were added to the 1.1 male count, then the males comprised 59.7% and 54.7% of the runs. Based on twelve years of observations, Fraser et al. (1983) noted an average of 55.7% females (range 44.6%–72.7%) among age 1.1 fish. The small sample of age 2.1 fish were 51.9% female. Similar results were reported by Berg (1948) for the Kamchatka River, USSR (55.5% females) and by Godfrey et al. (1954) for the Babine

River, British Columbia (54% females).

Overall, more coho males than females survive, because those that return to spawn as jacks are not subjected to as high a mortality rate as the adults that spend two summers at sea. Presumably, if all coho returned to the home stream at the same age, as do pink salmon, the observed average sex ratio would be 1:1.

Sexual Dimorphism

During the early freshwater and marine stages of their life history there is no apparent external phenotypic difference between male and female coho. However, with the onset of maturity the fish develop markedly different secondary sexual characteristics (Plate 17).

In male coho, the upper jaw forms an elongated hooked snout and the teeth become greatly enlarged. The hook, which turns downward, may be of sufficient size to prevent the mouth from closing. The lower jaw also elongates somewhat and may become hooked (upward) or knobbed. The dorsal area between the head and dorsal fin is projected slightly upward, thereby increasing the body depth (Briggs 1953). The colour of the spawning male is generally brighter than that of the female (Plate 17).

In females, the jaws also elongate, but the devel-

opment is much less extreme than that observed in the males (McPhail and Lindsey 1970). The dorsal projection seen on the males is absent and the colour of the females is much more subdued (Plate 17). Marr (1943) and Shapovalov and Taft (1954) found that there was a small but consistent tendency for the males of a given year class to be larger than the females.

Adult Colour

Coho captured at sea or shortly after entry into fresh water are mostly silver-coloured on their sides and ventral surfaces. The dorsal surface is a dark metallic blue and there are irregular black spots on the back and the upper lobe of the caudal fin (Hart 1973) (Plate 17).

As spawning time approaches, the males become darker, and the dorsal surface, head, and ventral surface turn bluish green. The sides of the males develop a broad red streak, which, in some populations is very bright (Carl et al. 1959). The females and jacks are not nearly as brightly coloured but appear more brassy green (Shapovalov and Taft 1954). Coho that remain in fresh water until maturity, such as those found in the Great Lakes and the "residuals" observed by Foerster and Ricker (1953), are generally a duller colour at maturity than their anadromous counterparts.

FECUNDITY

The number of eggs carried by ripe coho females varies with the region and with the size of fish. Rounsefell (1957) provided one of the first reviews of the fecundity of North American salmonids. More recently, Crone and Bond (1976) summarized the available data on fecundity of coho salmon and acknowledged that the numbers given were not strictly comparable because of the various methods used to determine egg number and because of the large variations in sample size (Table 1). There is a definite tendency for fecundity to increase from California to Alaska, and North American stocks generally have a higher number of eggs

than Asian stocks.

Apart from the correlation between egg number and latitude there is also a positive correlation between fecundity and length (Drucker 1972). Salo and Bayliff (1958) produced a regression curve for one year's data from Minter Creek of

$$y = -2596 + 84.53x$$

[where x = standard length (cm) and y = number of eggs per female]

Allen (1958) did not observe any relationship between fecundity and the time of entry of coho into fresh water. Females with high egg counts did

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TABLE 1
Some fecundities of coho salmon reported in the literature

Stock	Mean no. eggs per female	Source
Asian coho		
Kamchatka	5000	Pravdin (1940)
Kamchatka	4900	Berg (1948)
Kamchatka R.	4883 (range 2881-5974)	Gribanov (1948)
Paratunka R.	4350 (range 2800-7600)	Gribanov (1948)
N. Sakhalin	4570 (range 2995-7110)	Smirnov (1960)
North American coho		
Karluk L., AK	4706 (range 1724-6906)	Drucker (1972)
Swanson R., AK	3149-4023	Engel (1967)
Resurrection Bay, AK	3967 and 3846*	McHenry (1981)
s.e. Alaska	4510	Marriott (1968)
British Columbia		
several stocks	2699	Neave (1948)
Cultus L., BC	2300	Foerster & Ricker (1953)
Nile Cr., BC	2310	Wickett (1951)
Big Qualicum R., BC	2574 ± 549†	Fraser et al. (1983)
Minter Cr., WA	2500‡ (range 1900-3286)	Salo & Bayliff (1958)
Fall Cr., OR	1983 (N = 92)	Koski (1966)

Notes: *Mean no. for two consecutive years

†Average for 14 years

‡Average for 18 years

not have significantly smaller eggs, nor did small females have small eggs. For most stocks the average egg diameter was 4.5-6 mm (McPhail and Lindsey 1970), which is smaller than for most other Pacific salmon. The average egg diameter given for the high fecund Kamchatkan stocks is 4.5 mm (Gribanov 1948). The highly fecund Karluk Lake (Alaska) stock has eggs ranging in size from 4.91 to 6.87 mm with an average of 6.11 mm (Drucker 1972). Scott and Crossman (1973) reported that nonanadromous coho females (of west coast origin), collected in Lake Ontario, produced eggs that were 6.6-7.1 mm in diameter. Drucker (1972), in his

study of Karluk Lake (Alaska) coho, found no correlation between egg size and the length of the fish or between egg size and the number of eggs in the ovary.

The weight of the gonadal material as a percentage of total body weight is given as 11% for females (range 5%-32%) and 8% for males (range 5%-12%) by Gribanov (1948). Semko (1954), in his study of Asian coho, estimated that ovaries comprised 22.6% of the body weight. It is assumed that this percentage was determined just prior to spawning.

SPAWNING

Seasonal Timing

The spawning season for most coho populations is between November and January. However spawning timing, like that for migration, is highly vari-

able. Pravdin (1940) reported that in the Kamchatka River, 90% of the coho had deposited their eggs by December, but that spawning occurred over the period 1 September to 16 March, and in the Bolshaya River spawning occurred from

15 September to January, with a few fish spawning in February. Smirnov (1960) discussed the early and late runs of coho in the Soviet Far East and indicated that spawning occurred from 20 August to mid-March in northern Sakhalin.

In North America, coho also spawn over an extended period from October to March, with the very late spawning often occurring in the smaller, shorter streams (Rounsefell and Kelez 1940). In southeastern Alaska, spawning takes place from early October to mid-November (Crone and Bond 1976). In the Cowichan River, British Columbia, spawning occurs in the November-December period (Neave 1949), and for Oregon coastal streams the timing is generally November to February (Chapman 1965). Severe winter droughts may delay spawning until early March in Oregon coastal streams (A. McGie, Department of Fish and Wildlife, Corvallis, Oregon, pers. comm.).

For the Big Qualicum River, Fraser et al. (1983) observed that the time between the peak of migration and the peak of spawning in this short coastal stream was about 32 days. However, for populations of coho in many rivers there appears to be little correlation between the time of entry to a spawning stream and the spawning date. Early-run fish may spawn early, but many will hold for weeks or even months before spawning. Conversely, late-run fish tend to spawn soon after arrival on the grounds or following a short holding period.

A marking study was conducted at the Capilano Hatchery to determine the relationship between time of arrival and date of spawning of wild, unenhanced coho. Commencing 25 August 1971, female coho arriving at the hatchery were given a distinctive colour-coded tag to identify week of arrival. The majority of the earliest group of fish, those arriving in late August, was ready to spawn on 20 November 1971, when most of the total run was maturing. However, one female marked on 25 August was not ready to spawn until 14 February 1972. Those females that did not arrive at the hatchery until after the period when most of the population had matured were all ready for spawning by 15 January 1972 (F.K. Sandercock, unpublished data).

There appears to be a significant advantage in late spawning with regard to both interspecific and intraspecific competition. Where coho share the same spawning grounds with early migrants,

especially sockeye and chum salmon or early-timing coho, the late-running fish can often dig up eggs previously deposited in the gravel, thereby exposing these eggs to almost instant predation (Pravdin 1940). Semko (1954) observed that spawning efficiency is decreased when there is a high density of spawners on the grounds, probably not as a result of congested deposition of eggs but because previously deposited eggs were dug up and lost.

For those eggs that are not dug up, there are other hazards. Low winter flows can result in drying of the redds or may expose the eggs to freezing temperatures. Flooding may cause gravel movement and result in eggs being dislodged and swept downstream. Winter storms often cause excessive siltation that may smother eggs and inhibit inter-gravel movement of alevins (Neave and Wickett 1953).

Spawning Behaviour

When the fish reach the spawning grounds the female selects a nest site. This first site may not, however, be the only one the female uses. Once the nest site has been selected, she will defend it against other females. One or more males may attend any spawning female but they may initially be chased away from the nest by the female (Briggs 1953).

The female begins digging the nest by rolling onto either side at about a 45°-angle to the current with her head upstream and her body arched. She then commences a series of five to six violent flexes of the body and tail over the gravel on the selected site (Burner 1951). After each digging bout, the female will rest for a few minutes before digging again in the same spot. A depression is created in the stream bottom by the hydraulic suction effect of the tail, which lifts some of the gravel, silt, and sand upward from the bottom. This material is displaced downstream by the current (Briggs 1953). This digging activity may last as long as five days, during which time the female will dig several nests in succession. The males do not participate in the digging.

Although the females may be attended by several males, usually one becomes dominant, stays close to the female, and attempts to drive off other males by assuming a threatening posture and by

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nipping or biting. As already stated, the teeth become enlarged at breeding time. Damage inflicted by males on each other may result in some pre-spawning mortality. The dominant male is generally the largest of the males in attendance (Shapovalov and Taft 1954). At spawning time the female becomes aggressive towards other females and the extra males. While the female is digging the nest, the dominant male assumes a position to one side and slightly downstream of her each time she resumes her normal position over the nest. He may then move in close alongside her and make quivering movements with his head from left to right, followed by moving over her tail to the other side.

Once the nest is completed the female swims over the depression in the gravel and, while arching her body downward, pushes the anal fin down in the spaces between the stones. At this point the dominant male swims closely alongside the female, and with mouths agape, both bodies quiver, and the sperm and eggs are deposited simultaneously (McPhail and Lindsey 1970). They hold this position for two to three seconds. Accessory males, and, in many cases, jacks, rush in alongside the female or the dominant male and deposit sperm as well. The fact that the nest comprises a depression in the gravel with water flowing over it results in a back eddy of current in the nest. The eggs are nonadhesive and loose, and since they have a specific gravity greater than water they sink to the bottom (Davidson and Hutchinson 1938).

Close to the bottom of the nest the water flow is slow. This permits the sperm to make adequate contact with the eggs, ensuring a high fertilization rate. The eggs are not swept out of the nest and downstream by the current. Shapovalov and Taft (1954) estimated that at least 97% of the eggs deposited in the redd remained there and indicated that the percentage of eggs fertilized was consistently high. Semko (1954), in his study of coho spawning in the Karymaiskiy Spring, USSR, found that, of the total potential egg deposition, 72.2% were actually deposited in nests. Pravdin (1940) noted that if an average female was carrying 5,000 eggs, 1,527-3,600 eggs would be successfully deposited in the nests. By digging up a series of redds, Gribanov (1948) determined that the average number of eggs per nest ranged from 300 to 1,200, the most frequent number being 800-900.

When the spawning act is completed, the female immediately moves about 15 cm upstream of the nest and performs different digging movements. She lays her tail on the gravel and then lifts it up quickly two or three times. After each dig the female circles back into the nest before moving to the front edge of the nest again as she performs another dig. The eggs are buried in about one minute, which minimizes predation. At the same time, a depression is created for the next spawning (Briggs 1953). Successive spawnings take place in a series of nests, each slightly upstream of the earlier one. The female may spawn with other males if the previously dominant male becomes displaced (McPhail and Lindsey 1970).

Post-Spawning Behaviour

The length of time that coho remain in the vicinity of the redd after spawning was reported by Crone and Bond (1976) for several sites. During the two years of study, in Sashin Creek, Alaska, the range of survival time for females was 3-24 days, with an average of 11 and 13 days. Males survived an average of 9 days in Sashin Creek. In Drift Creek, Oregon, the males and females survived just over 13 days. In a study of coho spawners in Spring Creek, Oregon, Willis (1954) found that the average time to death after spawning was 11 days (range 4-15 d) for females, 12 days (range 4-32 d) for three-year-old males, and 15 days (range 3-57 d) for jacks. For the females and the three-year-old males, he found that a regression of the number of days in the stream from date of arrival to death indicated that early arriving fish lived about 5 days longer than late arriving fish. Because males were more abundant than females on the spawning grounds, Gribanov (1948) assumed that males must survive longer than females.

Once the female has deposited her eggs, the attendant male leaves. The spawned-out female may continue to go through digging motions for 10 days until she dies, but nests dug after spawning is complete are shallow and nonfunctional (Burner 1951). She also may continue to guard the redd site until too weak to do so (Briggs 1953). Briggs noted that males continue their courting action until they become too weak to maintain position in the current, and then drift downstream to die.

When spawning is complete, both males and

females exhibit definite external physical deterioration in the form of frayed fins, skin loss, fungus infections, and, at times, blindness. Internally, there is a degeneration of the cardiovascular system, pituitary gland, adrenal gland, stomach, liver, and kidney (Robertson et al. 1961). Following these changes, coho, like other species of Pacific salmon, die. As Shapovalov and Taft (1954) and Sandercock (1969) have pointed out, the physical deterioration is not related to the rigours of a long journey because short and long migrant stocks, as well as non-migrant stocks, undergo the same changes and then die.

Egg Retention

During the spawning phase, coho females in most populations deposit almost all of their eggs. Published reports have indicated varying levels of egg retention, e.g., 4 eggs/female in Prairie Creek, California (Briggs 1953); 4 eggs/female (range 0-38, $N = 30$) in Fall Creek, Oregon (Koski 1966); 7-16 eggs/female in Kamchatka (Semko 1954); and an average of 60 eggs/female in Waddell Creek, California (Shapovalov and Taft 1954). Estimates of total egg deposition have largely ignored the occurrence of residual eggs, because they usually represent a small percentage of the total. However, Fraser et al. (1983) examined 401 female coho from the Big Qualicum River over a period of nine years and found the average percentage of residual eggs to be $22.0\% \pm 12.2\%$, compared to $3.5\% \pm 2.9\%$ for 290 females sampled from the adjacent Hunts Creek over a four-year period. These extremely high percentages translate into 253-941 eggs retained per Big Qualicum River female. Fraser et al. (1983) suggested that environmental factors in this river may have seriously interfered with spawning success.

Redd Characteristics

Redd sites are characterized by gravel size, water depth, and water velocity. Burner (1951) described in considerable detail the characteristics of coho salmon redds in the upper Toutle and Green River systems in Washington. The coho mostly selected small streams where the flow was 5.0-6.8 m³/min and the stream width did not exceed 1 m. About 85% of the redds occurred in areas where the sub-

strate was comprised of gravel of 15 cm diameter or smaller. In some situations there was mud or fine sand in the nest site. This material was removed during the digging process. About 10% of the redds occurred in sites where the gravel size exceeded 15 cm, and 5% were located in areas having a high proportion of mud, sand, or silt.

Coho were described by Chamberlain (1907) as being the least particular of all Pacific salmon in their choice of spawning area. They can be found in almost all coastal streams, large rivers, and remote tributaries. The redds may be located on gravel bars of smooth flowing rivers or on white-water riffles of turbulent mountain streams (Foerster 1935). On the spawning grounds, they appear to seek out sites of groundwater seepage and favour areas where the stream flow is 0.30-0.55 m/s (Gribanov 1948). In Kamchatka, water temperatures at spawning vary from 0.8° to 7.7°C, dissolved oxygen varies from 9.9 to 15.0 mg/l, and pH ranges from 6.3 to 8.6 (Gribanov 1948). California coho may spawn in water ranging from 5.6° to 13.3°C (Briggs 1953), but Davidson and Hutchinson (1938) characterized the optimum temperature for coho egg incubation as 4° to 11°C. The water may be clean or heavily silted and the substrate may vary from fine gravel to coarse rubble (Pritchard 1940). The female generally selects a redd site at the head of a riffle area where there is good circulation of oxygenated water through the gravel (Shapovalov and Taft 1954). By definition, the whole area disturbed by a female is described as a redd, whereas the sites of separate egg depositions within the redd are called nests.

For all salmon, the size of the redd is directly proportional to the size of the female, and is inversely related to the size of the gravel and the degree to which it is compacted. Where the flow rate is high (0.9-1.5 m/s), the redds are broad and oval-shaped. In a study of California coho, Briggs (1953) noted that the eggs were buried to a depth of 25 cm (range 17.8-39.1 cm) in gravel that averaged 9.4 cm in diameter (range 3.9-13.7 cm). Water velocity on the spawning ground averaged 0.58 m/s (range 0.30-0.75 m/s) and the depth of water over the redd was 15.7 cm (range 10.2-20.3 cm). In Kamchatka, Gribanov (1948) observed that coho redds averaged 134 cm in length (range 115-195 cm), 112 cm in width (range 100-135 cm), and 22 cm in depth (range 15-27 cm). The water column over the redd

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averaged 18 cm (range 4–33 cm).

From the above figures, the average redd size would be 1.5 m². Crone and Bond (1976) indicated that the average area of gravel disturbed was 2.6 m²/redd, which is similar to the average redd size of 2.8 m² observed by Burner (1951). During spawning, the redd progressively elongates with successive egg deposits as the female shifts gravel downstream to cover the eggs. The redd increases considerably in length and depth and appears to move upstream as the upper end is displaced into the "tail spill" (Burner 1951). Briggs (1953) reported that coho females often dig false nests both before and after spawning occurs. In Prairie Creek, California, only 46% of nests that were subsequently excavated contained eggs. On this basis, it is assumed that most females may dig at least three to four nests and deposit eggs in each (Godfrey 1965). Once the nest is excavated the water tends to eddy in the depression, causing it to flow slightly up-

stream and thus ensuring a safe deposition of eggs and good exposure to milt to promote a high rate of fertilization (Figure 2).

Territorial behaviour on the part of the females results in fairly regular spacing of the redds in the stream. Where coho use all parts of a spawning stream the redds will be arranged in diagonal rows across the stream. The reason for this is thought to be related to the behavioural pattern of the female; she will tolerate another female upstream or downstream of her territory but not immediately adjacent (Burner 1951).

For coho, the inter-redd space is usually about three times the size of a redd. However, the size of this space also depends on the number of spawners present, the stream bottom composition, the stream gradient, and the water velocity. A pair of spawning coho requires about 11.7 m² for redd and inter-redd space (Burner 1951).

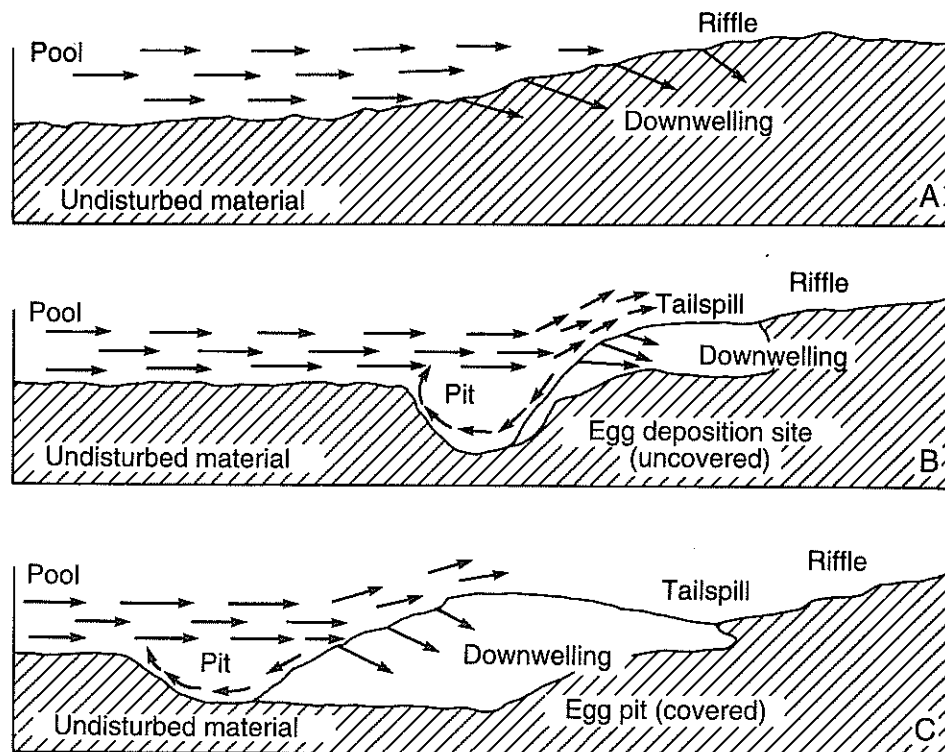


FIGURE 2

Longitudinal sections of spawning area. A: pool/riffle relationship results in percolation of water through gravel; B: excavation of nest increases flow rate through gravel and creates back eddy in pit; C: when the eggs are covered with gravel a second pit is created and water flow to the eggs is enhanced. (From Reiser and Wesche 1977)

INCUBATION, SURVIVAL, AND EMERGENCE

Incubation and Hatching

The length of time required for eggs to incubate in the gravel is largely dependent on temperature. The colder the temperature (down to almost freezing), the slower the developmental rate of the embryo and the longer the time to hatching. However, for a given temperature, there may be some variation in hatching time between eggs from different fish sampled on the same day or even between different eggs from the same fish (Shapovalov and Taft 1954). Semko (1954) observed that in Kamchatka, at an average temperature of 2.2°C (range 0.8°–3.5°C), the eggs took 137 days to hatch. Earlier work by Pravdin (1940) and Berg (1948) indicated an average time of 100–115 days for coho eggs to hatch. Gribanov (1948) found that Kamchatkan coho eggs incubating at 4.5°C hatched in 86–101 days. For North American stocks, the time to hatch is shorter than that of Asian stocks, even in the far north. McPhail and Lindsey (1970) gave a range of 42–56 days to hatching for Alaskan stocks, which is similar to the 48 days at 8.9°C and 38 days at 10.7°C for California stocks (Shapovalov and Taft 1954).

The time from hatching, through yolk absorption, to fry emergence is also dependent on temperature and, to a lesser extent, on dissolved oxygen concentration. Semko (1954) indicated that 21 days elapsed from hatching to emergence at an average temperature of 2.2°C, although as Gribanov (1948) observed, 40 days is more typical. In Kamchatka, hatching can occur from mid-January to mid-June, depending on the spawning date and incubation temperature, and emergence may occur from as early as the beginning of March to as late as the end of July.

For coho of the Big Qualicum River, Fraser et al. (1983) found that the total heat requirement for incubation in gravel (spawning to emergence) was 1036 ± 138 degree (°C) days accumulated temperature units, which is the sum of the number of degrees (°C) over zero (of the incubation water) accumulated on a daily basis. The Big Qualicum River coho eggs and alevins were in the gravel

from December until May for an average of 167 days (range 149–188 d). Further south, in three Oregon coastal streams, Koski (1966) found that the average time from egg deposition to fry emergence was 110 days (range 104–115 d).

Winter flooding and the associated silt load may reduce water circulation in the gravel to the point where oxygen levels become critical or lethal. In a study of intergravel movement of alevins, Dill (1969) found that, after hatching, the alevins moved a varying distance downward in the gravel, depending on gravel size. Where the gravel was 3.2 cm or smaller in diameter, the alevins moved down 5–10 cm. Where the gravel ranged from 3.2 to 6.3 cm in diameter, and hence there were larger intergravel spaces, the alevins moved down more than 20 cm. This downward movement would appear to be an adaptive mechanism to prevent premature emergence of alevins that are located close to the surface of the gravel bed. At this stage the larval fish have a well-defined yolk sac that is gradually absorbed. There is some indication that at the later stages of development in the gravel the alevins may initiate some exogenous feeding before the yolk sac is completely absorbed (Dill 1969).

Survival during Incubation

The percentage of eggs and alevins that survive to emergence depends on stream and streambed conditions. Winter flooding, with the disruptive effects of gravel movement, accounts for a high proportion of the loss. However, low flows, freezing of gravel, heavy silt loads, bird and insect predators, and infections, such as those by the fungus *Saprolegnia*, all take their toll. Under very harsh conditions, no eggs will survive; under average conditions, probably 15%–27% will survive to emergence (Neave 1949; Crone and Bond 1976); and under very favourable conditions 65%–85% will survive (Shapovalov and Taft 1954). Briggs (1953) examined 22 California coho redds and found that the average egg-to-fry survival was 74.3%; Koski (1966) sampled 21 coho redds in three Oregon coastal streams and found that survival

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ranged from 0% to 78% with a mean of 27.1%; and Tagart (1984) reported 0.9%–77.3% survival for 19 redds. Neave (1949) observed that the high egg-to-fry survivals achieved by coho in comparison with other salmonids was due to the selection of better spawning sites in areas of good flow stability and to less crowding. However, if the gravel bed had a high concentration (up to 50%) of fine sediment and sand (particle size <0.85 mm), survival was lower (Tagart 1984). Survival to emergence was positively correlated with gravel sizes >3.35 mm and <26.9 mm (Tagart 1984).

Emergence from Gravel

Towards the end of the incubation period, the alevins reverse their downward movement in the gravel and begin making excursions upward (Dill 1969). The alevins do not move directly upward but orient at an angle towards the current flowing over the gravel. The deeper the alevins are found in the gravel, the longer the time for emergence. At this stage of emergence, yolk sac absorption is virtually complete (Plate 19). If the gravel is heavily compacted or loaded with fine sediment and sand, the fry may not be able to get out of the gravel

(Koski 1966). Where the gravel/sand mixture was 70% sand (particle size <3.3 mm), survival to emergence was only 8% (Phillips et al. 1975). Tagart (1984) suggested that the high proportion of fines in the gravel effectively reduced the dissolved oxygen levels available and resulted in smaller emergent fry. At 30% fines, the average fry fork length was 37.5 mm; at 10% fines, the average fork length was 39.8 mm (Tagart 1984). Phillips et al. (1975) also observed that a high concentration of fines resulted in early emergence of fry that were smaller and exhibited more yolk.

Shapovalov and Taft (1954) indicated that, in California, coho started emerging from the gravel two to three weeks after hatching, but that the late developers took two to seven weeks longer. Shallow burial in clean, loose gravel, and relatively warm water temperatures all contributed to early emergence. They also found that the fry emerged primarily at night. Koski (1966) observed that the peak of emergence was about 8–10 days after the first fry emerged. Emergence from the redds he sampled continued over a period of 10–47 days with a mean of 35 days. Emergence time was prolonged in those sites having a high proportion of fine sediments.

FRESHWATER RESIDENCE

Fry Behaviour in Streams

When fry emerge from the gravel, they initially congregate in what appear to be schools (Shapovalov and Taft 1954). However, as Hoar (1951) pointed out, this is not true schooling behaviour but a milling about in an aggregation. At this stage, the fry are about 30 mm in length (Gribanov 1948). Fry that emerge first are, on average, larger than those that emerge later (Mason and Chapman 1965). Because of an early growth advantage related to their larger size and better feeding opportunities, they tend to remain larger and ultimately make up a greater proportion of the fingerling population. Small differences in size have a major effect on the outcome of an aggressive encounter

and so the larger fish maintain their dominance. Gribanov (1948) observed 30-mm fry emerging as late as 25 July in areas occupied by fry as large as 52 mm in length that had been feeding for a month or more. In cold water systems, fry emerge later in the spring and, in so doing, may avoid spring freshets and the risk of being swept downstream; but they also have a shorter growing period (Scrivener and Andersen 1982). In warm water systems, the freshets may sweep out large numbers of fry, but, for those that remain, growth is fast in the low-density environment and they reach a larger size before the winter (Scrivener and Andersen 1982).

After emergence, the fry continue to hide in gravel and under large stones during daylight

hours, but within a few days they progress to swimming close to the banks, taking advantage of any cover that is available. They congregate in quiet backwaters, side channels, and small creeks, especially in shady areas with overhanging branches (Gribanov 1948). Hoar (1958) observed that older coho fry rarely formed schools, except in quiet water, which he thought might be an adaptation to avoid stranding in pools as water levels fell. As the fry become older, they occupy areas along open shorelines and progressively move into areas of higher velocity in midstream and on the stream margins (Lister and Genoe 1970). Coho fry from small tributaries may move upstream or downstream to rear and may occupy areas not accessible to adult coho (Neave 1949). At a length of 38–45 mm (Plate 18), the fry may migrate upstream a considerable distance to reach lakes or other rearing areas (Godfrey 1965). Where they move into lakes to rear they occupy the nearshore littoral zone (Mason 1974). The majority, however, rear in streams where they set up territories. Although coho are found in both pool and riffle areas of the stream, they are best adapted to holding in pools (Hartman 1965). They do not compete well with trout for rearing space on riffles. Stein et al. (1972) observed that coho juveniles at the head of the riffles were able to defend the area against chinook fingerlings.

Territorial behaviour, coupled with the habit of settling to the bottom during darkness, provide a means by which fish may remain in one part of the stream (Allen 1969). Coho fry distribute themselves throughout the stream and, once territories are established, remain in the same locality for relatively long periods (Hoar 1958). If the area is small, an individual occupies a preferred location and defends it by repelling others. However, they do not always display classic territorial behavior (Mundie 1969). Some coho fry form groups in pools, with the large fish at the front and the smaller ones at the back. The large individuals may defend territories (i.e., space in the pool) but the smaller ones may not.

Coho tend to be more aggressive in defense of their territories where the current is fast and where most of the available food is coming from upstream. Where the current is slow or slack, the food can appear from any direction, and the fish tend to move in loose aggregates and scramble for food

(Mundie 1969). In the pool areas there is extensive cruising for food, and aggressive behaviour occurs mostly between fish near the faster water (Ruggles 1966). How aggressive the fry become depends on how many are present, their relative size, the amount of food available, and the light intensity. It would appear that when food is scarce, less time is spent on aggression. Conversely, when they are less busy feeding, they have more time for aggression (Mason and Chapman 1965; Chapman and Bjornn 1969). Coho fry are active during daylight hours and seem to tolerate a wide range of light intensities. This adapts them well to the small, shallow streams they normally occupy, where conditions of light and shade are highly variable (Hoar 1958).

After territories are established, the fry do not rest on the bottom during daylight but orient themselves to a particular rock or log in the stream so as to occupy a small space of slow moving water. Failure to rest on the bottom at night may lead to a progressive displacement downstream (Chapman 1962). From their reference points they will make quick excursions of up to 30 cm to grab food or chase intruders but then return to take up their positions. Should they be chased out of their own territory by a larger or more aggressive individual, they will quickly settle into a new space, provided one is available. Small coho juveniles tend to be harassed, chased, and nipped by larger juveniles unless they stay near the bottom or hide under rocks or logs. By avoiding the more aggressive coho, there is much less opportunity to feed, and, consequently, the smaller individuals grow more slowly (Chapman 1962).

Habitat Utilization in Fresh Water

The abundance of coho in a stream is limited by the number of suitable territories that are available (Larkin 1977). More structurally complex streams that contain stones, logs, and bushes in the water support larger numbers of fry (Scrivener and Andersen 1982). Dill et al. (1981) found that the size of a territory was inversely related to the density of benthic food in the area and that territories were smaller where intruder pressure was high. As the fish grow, the size of their defended territory increases; for fry 49 mm in length the average territory is 0.34 m², at four months of age it is 0.79 m²,

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and at yearling size (110 mm) it is 3.7–5.5 m² (Allen 1969). McMahon (1983) reported that pools of 10–80 m³ or 50–250 m² in size were optimum for coho production, provided that there was enough streamside vegetation for shading. However, if the canopy is very dense, then the coho biomass will be reduced (Chapman and Knudsen 1980). Where coho occupy riffle areas, they tend to be uniformly distributed close to the gravel bottom and highly antagonistic. As the amount of aggression increases, so does the emigration rate (Mason and Chapman 1965).

The productive capacity of the freshwater environment for coho has been estimated by a number of investigators. Lister and Walker (1966) determined that in the Big Qualicum River, 19.1 smolts were produced per 100 m² of wetted stream area measured at low flow. For three small Oregon streams, Chapman (1965) reported a production of 18–67 smolts per 100 m² over a four-year period. Tripp and McCart (1983), in their study on outplants of hatchery coho fry into headwater streams, found that the average production was 8.4–8.5 smolts per 100 m², which is low in comparison to other estimates but may be explained by the fact that high-gradient headwater streams are not usually productive areas. In contrast, Armstrong and Argue (1977), in their assessment of some low-gradient side channels of the Cowichan River that appeared to be rich in insect fauna, found that there were 125–141 smolts produced per 100 m². Production from average coho streams probably falls between these two extremes. Foerster and Ricker (1953) reported that coho smolt production, expressed as the number of smolts produced per adult female, was seven to ten times greater from streams than from lakes.

Most coho fry move out of river systems with freshets. However, even during periods of stable flow, fry continue to migrate. The numbers of fry moving do not correlate well with the water discharge rate because the first freshet may move most fish, whereas the second freshet, a few days later, may move only the few that are still left in the stream (Hartman et al. 1982). Fish that are unable to find or to defend a territory are generally displaced downstream. If the downstream area is unoccupied, the displaced fry may take up residence. However, if fry are already occupying the space, then the new arrivals will continue to be

displaced downstream (Ruggles 1966). Displacement also occurs among larger fish due to demands for territorial space resulting from increased fish size. This displacement probably continues throughout the active growth period unless offset by mortalities (Fraser et al. 1983). Lister and Genoe (1970) found that coho progress through a series of preferred habitats: back eddies, log jams, undercuts or open bank areas, and, finally, fast water. From an evolutionary standpoint, the displacement mechanism may drive fish to explore areas that are some distance from the spawning ground, and if suitable space can be found, they will then make more effective use of the environment by being widely distributed (Allen 1969). However, in most cases, the displacement of the surplus fish is to less favourable sites, where they become vulnerable to predators or may be driven to the estuary.

Mason and Chapman (1965) noted that some coho that were larger than average, as well as smaller fish, were displaced. They suggested that rearing areas suitable for these larger fish were limited. Spring floods will also cause displacement. The preference by coho for shallow water may leave them vulnerable to sudden torrents that sweep them out of their established territory and move them downstream. Some of the coho that are displaced downstream may move back upstream, or they may migrate along the shore in low salinity water and enter other streams (Otto and McNerney 1970).

Chapman (1962), in his work on coho in Oregon, described juveniles that moved downstream between the time of emergence and October of the same year as nomads. Coho migrating downstream from November onward were defined as smolts. In addition to factors such as size, level of aggressive behaviour, and food availability, there may be an innate tendency on the part of nomads to migrate. The fact that some coho fry migrate downstream early in the spring, even when rearing space is available, would support this suggestion.

From the study of scales, it has been concluded that coho that enter the sea in the first spring or summer of life do not generally survive to the adult stage (Crone and Bond 1976). However, Crone and Bond (1976) found that, under experimental conditions, fry could survive salinities as high as 29 ppt. provided that they had been accli-

mated to lower salinities for 35 days. These authors also noted that the scale patterns developed by fry that reared in salt water were indistinguishable from those of smolts that had spent a year in fresh water. This is contrary to the general observation that fry displaced into salt water do not contribute to production. Underyearling coho are poorly equipped physiologically to survive early emigration into salt water, however, the type of estuary may have a substantial bearing on their ability to survive (Otto 1971). Kennedy et al. (1976) observed that coho fry put into salt water died prematurely and that non-smolted fingerlings either died immediately or grew slowly and then subsequently reverted to their parr condition and died. Weisbart (1968) showed that salinity tolerance was not a function of age but of size. Coho fry up to 5-6 cm in length and five months of age do not survive in sea water. The threshold size for survival seems to be about 7-8 cm.

Although underyearling coho smolts are extremely rare in nature, they are readily produced under hatchery conditions of abundant food, favourable growing temperatures, and proper photoperiod exposure (Brannon et al. 1982; Clarke 1988).

Feeding in Fresh Water

Coho juveniles are highly dependent on visual cues for locating and capturing food (Hoar 1958). Coho rarely feed on non-moving food or off the bottom in streams, preferring to pick off food in suspension or on the surface. At times they dart quickly to the surface and snap at floating particles, some of which are food, but others may be bits of wood, conifer needles, etc. Following these darting movements, coho quickly return to their original position (Shapovalov and Taft 1954). During daylight hours and the morning and evening twilight periods, coho can often be seen jumping clear of the water surface to capture insects flying nearby. During darkness, feeding activity ceases.

Because coho normally occupy the slower moving sections of a stream, this allows the capture of food with the minimum expenditure of energy (Mundie 1969). The most productive coho areas are small streams rather than large rivers, because small streams have the highest proportion of marginal slack water to midstream area. Insect mate-

rial found in the midstream drift of large streams is generally unavailable to juvenile coho and is lost from production. The wider the stream, the greater the loss of food. Mundie (1969) found that juvenile coho in British Columbia streams were highly dependent on drifting organic material consisting primarily of stream and terrestrial insects. He observed that 38 fish, 3.0-3.5 cm in length and collected through April-May, had consumed 337 different food items. A sample of 30 fish collected in July contained over 900 items. Almost half of the food consisted of chironomids in various stages of development.

Chapman (1965) demonstrated that, in Oregon streams, there was a positive correlation between the amount of terrestrial insect material found in coho stomachs and the extent to which the stream was overgrown with vegetation. In the smallest, most densely shaded stream, terrestrial insects comprised 40% (dry weight) of the food consumed. Where the streams were more open, the percentage was reduced to 21%-29%. The most productive streams are those with alternating pools and riffles about equal in area. A pool to riffle ratio of 1:1 provides optimum food and cover conditions for juvenile coho (Ruggles 1966). Invertebrate food production is maximized in the riffle area and the pool is the optimum environment for coho holding and feeding (Mundie 1969). In Kamchatka, Gribanov (1948) found that the principal food of river-dwelling juvenile coho was adult insects and, only secondarily, insect larvae. In the Paratunka River, coho consumed chironomids, stoneflies, and, occasionally, crustaceans (Pravdin 1940).

Mason (1974) found that, in British Columbia, juvenile coho food could be divided into 21 categories. The most important category was adult winged dipterans, which comprised 80% of the food items eaten. Less than 11% of the lake-dwelling coho population had zooplankton in their stomachs, and this food item represented only 5% of the volume. Zorbidi (1977) observed that coho of Lake Azabache, USSR, at a size of 6.3-7.6 cm, fed primarily on terrestrial insects and chironomids and did not appear to eat zooplankton. In Cultus Lake, British Columbia, young sockeye fry were the principal food item for coho juveniles. Other fish and insects were less consistently a part of the diet of the Cultus Lake coho (Ricker 1941; Foerster and Ricker 1953).

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At the yearling stage, coho may become predatory, supplementing their insect diet with the fry of their own or other species (Gribanov 1948). Pritchard (1936) found that yearling coho in British Columbia ate large numbers of pink salmon fry and small numbers of chum and coho fry. Hunter (1959) estimated that coho smolts consumed 1.5–2.0 pink or chum fry per day. Shapovalov and Taft (1954) reported that, in California, steelhead and coho fry were not subject to yearling coho predation, because they emerged from the gravel after the coho smolts had migrated to sea. However, large numbers of chinook fry were taken by coho outmigrants. Chamberlain (1907) and Zorbidi (1977) both reported that larger coho (12.3–13.7 cm) fed on threespine (*Gasterosteus aculeatus*) and ninespine (*Pungitius pungitius*) sticklebacks, in addition to terrestrial insects and aquatic insect larvae.

Fingerling Behaviour in Streams

By late summer and early autumn, as water temperatures begin to decline, juvenile coho feeding activity decreases, and the fish move into the deeper pools of the stream, especially those with overhanging logs (Hartman 1965; Scott and Crossman 1973; Bustard and Narver 1975a). At this time, the number of coho in the stream may be reduced substantially, but those systems with good winter habitat lose fewer juvenile coho (Tschaplinski and Hartman 1983). With the onset of fall freshets, the resident coho undergo high rates of redistribution (Scarlett and Cederholm 1984). The fish spend more time hiding under the cover of logs, exposed tree roots, and undercut banks. Skeesick (1970) reported that coho moved upstream into side creeks that remained clear and stable during the winter. These fish were larger than residents of the side creeks, and this difference in size was maintained over the winter (the average size of the mainstream and side creek coho in the spring was 101 cm and 86 cm, respectively). Tripp and McCart (1983) also observed that juvenile coho would move 200–400 m upstream to enter small tributary streams to overwinter. The distance moved appeared to be governed by the flow rate of the tributary stream. When the discharge was high, the flow could be detected further downstream. Groundwater seepage into these smaller tributaries

is thought to be the main attractant. By seeking cover and entering side channels, the fish avoid being swept out of the stream during winter freshets, and they also avoid some predators at a time when their swimming ability is reduced because of a lowered metabolic rate (Hartman 1965; Bustard and Narver 1975a). Brett et al. (1958) demonstrated that the cruising speed of underyearling coho was reduced from 30 cm/s at 20°C to 6 cm/s at just above 0°C.

In some rivers, the fish moved a considerable distance downstream before entering tributaries. In the Clearwater River, Washington, marked coho moved as far as 38 km downstream from summer rearing areas before entering tributaries (Scarlett and Cederholm 1984). The timing of the movement was always in response to freshets and the associated high water velocities, turbidity, and gravel movement. Coho streams with the best over-wintering habitat were those with spring-fed ponds adjacent to the mainstream (Peterson 1980) or protected, slow flowing side channels that may only be wetted in winter (Narver 1978). In unstable coastal systems, coho production may be limited by the lack of side channels and small tributaries to provide protection against winter freshets (Cederholm and Scarlett 1981). Beaver ponds create additional habitat used by coho, both in winter to avoid freshets, and in summer to avoid the stranding caused by low flows (Bryant 1984). However, there may be disadvantages for small coho in these pond-like environments for they become more susceptible to cutthroat trout (*Oncorhynchus clarki*) predation (Peterson 1980). For larger coho, migrating out of the mainstream into tributaries and sloughs may result in a high survival rate, e.g., over 67% in Carnation Creek, British Columbia (Tschaplinski and Hartman 1983).

In December, coho are no longer found on the riffles (Ruggles 1966). Narver (1978) observed that juvenile coho moved into areas with water depths over 45 cm and lower velocities (15 cm/s) when temperatures declined below 7°C. He also found that as temperatures in the stream approached 2°C, the coho moved closer to cover provided by logs, tree roots, undercut banks, etc. Coho also preferred side pools with cover to pools without cover, and clean rubble to silted rubble (Bustard and Narver 1975b). Coho that congregate in the deep pools of the stream form dense groups, and

the level of aggression is low. No displacement occurs as subordinate fish are driven back but not out of the group (Hartman 1965). Coho that occupy lakes during the summer migrate out of the lake into inlet streams to overwinter (Gribanov 1948). However, in the Tenmile Lakes, Oregon, coho juveniles moved into the lakes following the fall freshets and reared there until the following spring (A. McGie, Department of Fish and Wildlife, Corvallis, Oregon, pers. comm.). In the spring, there is a strong movement of juvenile coho back to the main stream (Tschaplinski and Hartman 1983).

Growth of Fry and Fingerlings

With moderate water temperatures and an abundant food supply, coho fry will grow from 30 mm at emergence in March to 60-70 mm in September, to 80-95 mm by March of their second year, and to 100-130 mm by May (Rounsefell and Kelez 1940). Mason (1974) described two growth phases for coho of Great Central Lake, British Columbia. From April to mid-June, coho increased in length from 37 mm to 62 mm; in summer the growth slowed; and by October the coho averaged 72 mm in length. By the following April the coho were 90-130 mm in length, which reflects a second spurt of growth in the early spring following the period of no growth in midwinter.

During the winter months, feeding virtually ceases and growth stops. Low winter temperatures are a major cause of growth reduction, but winter floods and turbid water conditions also restrict feeding opportunities. Noggle (1977) observed that coho terminated feeding when sediment concentrations exceeded 300 mg/l (with some variation depending on the type of sediment), but that they did not abandon their territory even when sediment loads approached 4,000 mg/l. Where side channels are fed by groundwater, temperatures may be such that coho continue to feed and grow during the winter (G.F. Hartman, Department of Fisheries and Oceans, Nanaimo, British Columbia, pers. comm.). By March, when temperatures are on the rise, the fish again commence a period of rapid growth. Increasing temperatures and an abundance of insect food stimulate the resumption of feeding. The pre-smolts complete their final growth phase before

starting on their seaward migration (Shapovalov and Taft 1954).

Fry and Fingerling Survival

During their life history stage in freshwater streams, two physical factors play a large role in coho survival: water discharge rate and temperature. Work by Neave (1948, 1949), Smoker (1953), and others has clearly demonstrated a correlation between summer flows and the catch of adult coho salmon two years later. Low summer flows reduce potential rearing areas (less wetted area), cause stranding in isolated pools, and increase vulnerability to predators (Cederholm and Scarlett 1981). High winter flows in typical coastal streams can be particularly hostile to fish 45-70 mm in size (Narver 1978). Coho fry production has been shown to be a function of the stability of winter flows (Lister and Walker 1966). McKernan et al. (1950) stated that winter flooding only had a significant impact when the flow was over 50% greater than the average flood. Extreme floods are almost invariably detrimental. When a flood commences, there is a greater abundance of food available as stream insects are dislodged from the gravel, but this disruption results in a loss of food production in the longer term, as the food sources are destroyed (Mundie 1969).

With low summer flows and high ambient air temperatures, the water temperature can approach or exceed the upper lethal temperature of 25°C for juvenile coho. Brett (1952) found that exposure to temperatures in excess of 25°C or a quick rise in temperature from less than 20°C to 25°C resulted in a high mortality rate. Prolonged exposure to water temperatures close to 0°C was tolerated by coho, but a sharp drop in temperature from 5°C to almost 0°C resulted in mortality. Brett (1952) also observed that juvenile coho preferred a temperature range of 12°-14°C, which is close to optimum for maximum growth efficiency.

Godfrey (1965) summarized the fry-to-smolt survival for two British Columbia streams, one Washington stream, and one California stream. He found that the published values for survival ranged from 0.70% to 9.65% with the average in the range of 1.27%-1.71%. Neave and Wickett (1953) estimated survival from egg to smolt for British Columbia coho to be 1%-2%. Most of the mortality

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takes place in the first summer. Based on fry outplants, Tripp and McCart (1983) concluded that summer mortality of coho fry was density-independent. In the following spring, the mortality rate was higher than during the winter period, but the mortality was still less than one-third that of the previous summer (Crone and Bond 1976). Survival for the fry-to-smolt stage was estimated by Fraser et al. (1983) at 7.3% for the Big Qualicum River. Drucker (1972) noted that the long period of freshwater residency probably resulted in a higher freshwater mortality but contributed to a lower marine mortality because smolts were larger when they went to sea. Mace (1983) estimated a 2%–4% loss to avian predators after the smolts reached the Big Qualicum River estuary. Because of the relatively low survival rates from fry to smolt, it is obvious that the freshwater environment plays a major role in the fluctuation of coho abundance.

Freshwater Predators

Predation is a major component of the mortality suffered by juvenile coho, but predator species and effect varies with stream system and geographical area. Fry and smolts are subject to predation by a wide variety of predators, especially when coho are aggregated in pools and side channels, or in years when the egg-to-fry survival is high and the fry are very abundant. Larkin (1977) indicated that rainbow trout (*Oncorhynchus mykiss*), cutthroat trout, Dolly Varden charr (*Salvelinus malma*), squawfish (*Ptychocheilus oregonensis*), and Rocky Mountain whitefish (*Prosopium williamsoni*) are all important predators of juvenile coho. Godfrey (1965) suggested that cutthroat trout were the main predators of coho fry in British Columbia, but Chapman (1965), in his studies of Oregon coho populations, found that cutthroat trout were not significant in coho fry mortality because only occasional fry were taken, even when they were abundant. Patten (1977) reported that torrent sculpins (*Cottus rhotheus*) were important predators of coho from the time of emergence at a size of 30 mm until the coho were 45 mm; fry larger than this were rarely taken by sculpins. Logan (1968) found that 31% of the Dolly Varden charr stomachs examined from an Alaskan coastal stream contained coho juveniles. Shapovalov and Taft (1954) observed that predatory fish were responsible for most of

the coho loss in California, but that garter snakes (*Thamnophis sirtalis*) were also able to capture coho fry, especially in pools that were drying up.

Dippers (*Cinclus mexicanus*), robins (*Turdus migratorius*), crows (*Corvus brachyrhynchos*), herons (*Ardea herodias*), and fish-eating ducks (e.g., *Mergus merganser*) all consume significant numbers of coho. Wood (1984), in his study of the foraging behaviour and dispersion of common mergansers (*M. merganser*), found that 40-g coho smolts were selected over 2-g coho fry and suggested that the difference in capture frequency could be explained by the difference in conspicuousness due to size. He further observed that, as density of smolts increased, or the amount of cover decreased, the rate of capture by mergansers increased. However, coho smolts, having once been exposed to merganser attacks, were less likely to be captured in subsequent attacks. During the winter months, the avian predation rate is much lower, partly because the migratory species may have departed to southern wintering areas, and also because the coho are hiding. In many streams the presence of an ice cover over the stream makes them less vulnerable (Crone and Bond 1976). Mammals such as mink (*Mustela vison*) and otter (*Lutra canadensis*) prey heavily on over-wintering juveniles and migrating smolts. Predators tend to take a fixed number of prey so that the proportion of prey taken increases as the number of prey decreases. In those situations where salmon fry are reduced to small numbers, the predators can eliminate them entirely (Larkin 1977).

Juvenile Colour

In the alevin stage, young coho have silver- or gold-coloured bodies and large vertically oval blobs of dark brown pigment (parr marks) in a row along the lateral line (Plates 17 and 19). The lateral line bisects most of the parr marks, and the pale area between the parr marks is greater than the width of a parr mark (Scott and Crossman 1973). The back and sides are often cinnamon-yellow and the fins are tinged with orange. Once the fish reach a size of 10–14 cm, the long, narrow, dark brown parr marks along the side (usually 11 per side) are distinctive, the rest of the body is a dull gold colour, and the fins are varying tones of orange (Gribanov 1948) (Plates 17 and 18). The anal fin has a

white leading edge, which is followed by a parallel, narrow black stripe (Hart 1973). Stein et al. (1972) described the same white-black striping on the dorsal fin of juvenile coho from the Sixes River, Oregon. As the juveniles approach the migratory smolt stage, the parr marks become less evident and the overall colour of the fish is lighter and more

silvery (Plate 17). The fin colours fade from orange to pale yellow, although the tail may retain some of the orange coloration. By the time the smolts reach the estuary, the change to a silvery coloration is almost complete on the sides and bottom, and the dorsals are blue-black.

RESIDUALS

Foerster and Ricker (1953) reported on the occurrence in Cultus Lake, British Columbia, of what they termed "residuals." These are coho that spend their entire life in fresh water. Foerster and Ricker demonstrated that these residuals were derived from anadromous parents and were not produced by a self-sustaining resident population. They thought that the number of residuals was at least equal to, or possibly several times greater than, the number of outmigrant smolts. Because of an unexplained high rate of mortality in their third year, the reproductive potential of the residual population was low, and few survived to maturity. The largest residuals that were sampled ranged from 46.5 to 59.5 cm and had a maximum weight of 2.4 kg. The residuals matured at the same age as the anadromous component and included jacks (age 1.0) and a 1:1 sex ratio among age 2.0 males and females. The colour at maturation of the resid-

uals was more subdued than that of the anadromous fish. Schmidt (1950) reported that lacustrine forms of coho had been collected in the lakes of the middle Okhota River in the Soviet Far East and that they matured at a size of 30-35 cm. These, like the residuals studied by Foerster and Ricker (1953), were not landlocked. Foerster and Ricker indicated that, up until 1953 at least, there were no documented self-sustaining populations of "landlocked" coho. Later, Rounsefell (1958) reported that a dwarfed landlocked coho population had been found in Becharof Lake in the Egegik River system of Bristol Bay, Alaska. Subsequently, it has been confirmed that the Great Lakes coho, though not strictly landlocked, do spend their entire lives in fresh water and have established self-sustaining populations. There is no evidence of residual coho in streams.

SMOLT MIGRATION

Seasonal Timing

The migration of coho downstream towards the sea begins in spring. Factors that tend to affect the time of migration include: the size of the fish, flow conditions, water temperature, dissolved oxygen levels, day length, and the availability of food (Shapovalov and Taft 1954).

In the more southerly part of the distribution range for coho, the outmigration begins early. In

California, the outmigration of smolts over 10 cm in length occurred as early as mid-March, increased substantially through April, and peaked about mid-May (Shapovalov and Taft 1954). Chapman (1965) reported that smolts migrated in Oregon between early February and May. In Minter Creek, Washington, the smolt migration occurred between 15 April and 1 June, with the peak in May (Salo and Bayliff 1958). In southern British Columbia, Fraser et al. (1983) reported that, over a fifteen-

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year period in the Big Qualicum River, the migration duration averaged 119 ± 28 days and that the midpoint of the migration occurred on 26 May ± 5 days. Andersen and Narver (1975) found that the midpoint for two-year-old smolts migrating out of Carnation Creek on the west coast of Vancouver Island was reached on 9 May. In northern British Columbia, at Lakelse Lake, the coho outmigration in 1952 took place between 13 May and 14 June (Foerster 1952). In 1981, in the Resurrection Bay area of Alaska, the smolt migration began 28 May, reached its midpoint (50% migration) on 19 June, and ended on 3 September (McHenry 1981).

The smolt migration out of Karluk Lake on Kodiak Island began in mid-May and ended in early July; these are smolts that had resided in the lake one to four years before migrating (Drucker 1972). Drucker observed that, in general, the higher the latitude the later the migration, with about a one-month separation between outmigration peaks of coho from California compared to those from the Gulf of Alaska. In the Soviet Union, Pravdin (1940) found that smolts from the Paratunka River on Kamchatka migrated from June to October, but the main migration occurred between 1 August and 25 September. Churikov (1975), working in northeastern Sakhalin, reported that a net was set in the Bogataya River on 24 May and fished continuously. The first smolt was caught 26 June and catches continued until 5 August. The peak of the migration was between 13–22 July. Scott and Crossman (1973) observed a springtime migration pattern for coho smolts moving downstream to enter the Great Lakes. The fish migrated between late March and June and arrived at the stream mouths between April and August, with the peak in late May.

Tripp and McCart (1983) reported that the main peak of migration for coho coincided with a time of maximum stream discharge and then declined. However, a second peak of migration occurred at a time of decreasing flows but increasing temperature. In some cases, the smolt migration occurred after the spring flood (Churikov 1975). For a single river system there are year-to-year variations in the timing of smolt migration that are related to environmental factors. In years with low flows and higher temperatures, the outmigration is earlier (Shapovalov and Taft 1954). Coho migration in Alaska usually occurs when temperatures are in the range of 5.0° – 13.3°C (Drucker 1972) and, in the

USSR, at 9.0° – 12.0°C (Churikov 1975). In Bear Creek, Alaska, McHenry (1981) found that the migration started when water temperatures were 2.5°C , peaked at 8.1°C , and ended at 9.7°C . Few coho migrated before the temperature reached 3.9°C . In another Alaskan study, Logan (1967) found that most coho migrated when temperatures were 6.7° – 11.1°C , with the peak on 11 June at a temperature of 8.0°C .

Most smolts migrate to sea after spending just over one year rearing in fresh water. In the more southerly part of their range, where temperatures and food availability are better, coho reach migrant size in about fifteen months. However, in areas where conditions are less conducive to growth, they may require an additional one or two years to reach this size.

Diel Timing

As indicated earlier, the bulk of the seaward migration takes place at night. Meehan and Siniff (1962) found that on the Taku River (British Columbia) the peak migration occurred daily between 2300 h and 0300 h. Mace (1983) reported that coho smolts were rarely seen descending the Big Qualicum River in daylight, and that they appeared in the transition zone between the river and estuary only in the late afternoon and evening.

Outmigrant fry exhibit quite the opposite behaviour from that of fish that take up residence in the stream. McDonald (1960) showed that with the onset of darkness, the fry moved up to the surface and were distributed across the stream and swam or drifted with the current. Downstream fry movement started at about 2100 hours and concluded at 0400 hours, with a peak migration between midnight and 0100 hours.

Migration Behaviour

Fish that have spent a year or more in the stream, and are about to undergo the physiological changes associated with smoltification, begin by defending their territories less vigorously and by forming aggregations. They rise to the surface at night and begin moving downstream (Hoar 1951). The migrating fish move downstream in schools of 10–50 smolts, and fish of a similar size seem to school together (Shapovalov and Taft 1954). The

fish approach falls or rapids, where there is a steep gradient, tail-first, with their heads into the current. They dart forward a few times, each time coming closer to the edge. When they finally go over falls, some turn and head downstream as they are falling. After one is swept over the falls, several others in the school generally follow.

Age at Time of Migration

Throughout a large part of their range in North America coho typically spend one winter in fresh water after emergence from the gravel and migrate downstream as yearling (age 1.) smolts. In some river systems, coho may stay two, three, or even four winters in fresh water before migrating to sea as two- (age 2.), three- (age 3.), or four-year-old (age 4.) smolts, respectively. However, the proportion of these older coho smolts in most freshwater systems is generally low.

In California, Shapovalov and Taft (1954) found no two-year-old coho smolts in their sampling in Waddell and Scott creeks. In British Columbia, Pritchard (1940) examined the scales of 6,312 commercially caught coho and found that the incidence of fish that had migrated to sea as two-year-old smolts was 0.9%; Foerster (1955) estimated a 1% occurrence of two-year-olds; Armstrong and Argue (1977) observed a 2.4% incidence of two-year-old coho smolts in the Cowichan River; and Fraser et al. (1983) reported an average occurrence of 1.6% two-year-olds in the Big Qualicum River for five years sampled during the 1964-73 period, and 7.1% (for 1973) in the Little Qualicum River. An atypical example for British Columbia is the coho stock of Carnation Creek on the west coast of Vancouver Island; in one year (1974) the incidence of two-year-old smolts was 58.4%, and the average of the three previous years was still high at 46.0% (Andersen and Narver 1975). The occurrence of a high proportion of two-year-olds is much more common in the north. For example, the Taku River had a 54% incidence of two-year-olds (Meehan and Siniff 1962); in Hood Bay Creek (Alaska) in 1968 and 1969, respectively, 50% and 45% were two-year-olds, 7% and 5% were three-year-olds, and the balance were one-year-olds (Armstrong 1970); and among Karluk Lake coho, 44%-51% were two-year-olds, 42%-49% were three-year olds, and 1.5%-6% were four-year-olds in the years 1956, 1965, and 1968 (Drucker 1972). However, McHenry (1981)

found that the coho smolts coming out of Bear Creek in the northern Gulf of Alaska area were only 27.1% two-year-olds and 0.1% three-year-olds.

In Kamchatka the majority of the coho go to sea as two-year-olds and some as three-year-olds (Gribanov 1948).

Smolt Size

The size of coho smolts is fairly consistent over the geographical range of the species. Gribanov (1948) observed that a fork length of 10 cm seemed to be a threshold for smoltification. Shapovalov and Taft (1954) found that coho from Waddell Creek, California, migrated at an average length of 11.5 cm (range 7.5-16.5 cm). Coho smolts from Sand Creek, Oregon, averaged 10.6 cm (range 3.3-19.3 cm) over a three-year period (Sumner 1953). In Washington, Minter Creek smolts were 9.5-10.6 cm (Salo and Bayliff 1958), and in British Columbia, Foerster and Ricker (1953) observed that Cultus Lake smolts were 11-12 cm, with a few large two-year-old smolts at 26.1 cm. Yearling smolts from Carnation Creek were only 7.4-7.9 cm, whereas the two-year-olds were 9.9-10.3 cm (Andersen and Narver 1975); and Cowichan River yearling smolts were 8.8-9.8 cm, and the two-year-olds were 9.8-10.5 cm (Armstrong and Argue 1977). Fraser et al. (1983), in summarizing fifteen years of Big Qualicum data, found that the long-term average smolt size was 9.85 ± 5.8 cm and that these fish weighed 11.18 ± 2.44 g (11 years of data). Alaskan smolts sampled by Logan (1967) were 10.4-15.4 cm, the smaller fish being yearlings, and the larger fish two-year-olds. McHenry (1981) sampled larger yearling smolts from the Resurrection Bay area that averaged 12.2 cm (18 g) and two-year-olds that were 13.5 cm (24 g).

Coho smolts in the eastern USSR also tend to be larger. Pravdin (1940) examined smolts from the Paratunka River that averaged 11 cm as yearlings and 11-15 cm as two-year-olds. Berg (1948) described Kamchatkan coho smolts averaging 13-14 cm in length, and Churikov (1975), working on the Bogataya River, Sakhalin Island, captured smolts averaging 12.3 cm in length, with an average weight of 25.1 g (range 15-34 g).

Growth is obviously very rapid once the smolts reach the estuary, because fish sampled in near-shore areas ranged in size from 14 to 22 cm (Rounsefell and Kelez 1940; Berg 1948; Fisher et al. 1984).

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Estuarine Predators

After the smolts reach the estuary they are vulnerable to predation by many of the same predators (cutthroat trout, Dolly Varden charr, herons (*Ardea herodias*), mergansers (*Mergus merganser*), and mink (*Mustela vison*)) that they faced during their freshwater rearing and migration stages. They are also eaten by a variety of new predators. The new ones include dogfish (*Squalus acanthias*), lamprey (*Lampetra* sp.), and sharks (e.g., *Lamna ditropis*) (Larkin 1977); avian predators such as Bonaparte's

gulls (*Larus philadelphia*), glaucous-winged gulls (*L. glaucescens*), arctic loons (*Gavia arctica*), and mergansers (Mace 1983); and at least fifteen species of marine mammals (mainly seals (e.g., *Phoca vitulina*), sea lions (*Eumetopias jubatus* and *Zalophus californianus*), and killer whales (*Orcinus orca*)) that consume coho in the lower reaches of rivers, in estuaries, and in nearshore waters (Fiscus 1980). However, for most mammals, salmon constitute only a small proportion of the diet. Other fish, such as the daggertooth (*Anotopterus pharao*), may be important predators in offshore waters (Hartt 1980).

OCEAN LIFE

Fish in their First and Second Ocean Year

One of the first reports of coho smolt behaviour on entering sea water was given by Chamberlain (1907), who concluded that the smolts stayed in the nearshore areas close to their home streams for several months before migrating further. He thought that coho from a particular stream continued to school together. Gribanov (1948) found that migrant Kamchatkan coho first occupied the quiet marine inshore areas, away from the surf zone, and swam in the top layers in discrete schools of 20-30 fish. He concluded that if the smolts remained in areas adjacent to shore during their first summer and winter, it was unlikely that they would undertake a long migration in the second summer before returning to their home stream. Churikov (1975) reported that Asian coho smolts spent only a brief period in estuaries before moving along the shoreline.

Shapovalov and Taft (1954) suggested that California coho remained close to the shoreline after migrating to sea from Waddell Creek, and that they probably stayed there for a few months before beginning to disperse. Recoveries of marked fish at that time indicated that they remained within 150 km of shore, which, in California, is out to the edge of the continental shelf. Milne (1964) noted that the location of the main coho fishing grounds off the coast of British Columbia indicated that the feeding areas were over the continental shelf within sight of land and at depths of less than 90 m. Most

coho salmon that were caught for tagging in their first ocean year in the Gulf of Alaska were close to shore, but some were also taken up to 150 km offshore (Godfrey 1965).

Smolts entering the sea from California to British Columbia tend to move northward along the coast. Some reach the coastal waters of central Alaska by late summer. During seining for juvenile salmonids in nearshore and offshore waters, Fisher et al. (1984) found that almost all of the coded-wire tagged coho that had been released from coastal Oregon were recovered further north than Oregon. However, tagged fish from the Columbia River were found both north and south of the Columbia River estuary.

After about twelve months at sea, coho gradually migrate southward along the coast, but some appear to follow a counter-clockwise circuit in the Gulf of Alaska. Royce et al. (1968) reported that coho do not drift, but actively migrate in a circular pattern with the currents. In the open ocean, coho were thought to occupy the area from the surface to a depth of 30 m. There was no evidence of particular stocks schooling together and, in fact, single net sets in some cases contained several salmonid species of different ages (Royce et al. 1968).

Some of the Washington and British Columbia stocks migrate only short distances to good feeding areas and remain there until they approach maturity (Godfrey et al. 1975). Healey (1980), in his study of juvenile salmon in the Strait of Georgia,

observed that after coho smolts had entered salt water, they dispersed quickly throughout the strait. The number that remained in the strait to rear to maturity varied from year to year and probably was dependent on smolt density and feeding conditions. Healey suggested that fish that found themselves in poor feeding areas moved to outside waters, whereas those in good feeding areas remained.

Hartt (1980) reported on the results of coho tagging studies conducted along the west coast of North America. Samples were taken from the Juan de Fuca Strait, Washington, to Bristol Bay, Alaska. Coho were found in nearshore and offshore areas. The coho migration out of Puget Sound and the Strait of Georgia took place later in the summer than for other salmon species. Once in outside waters the coho moved rapidly northwest and south along the coast during their first summer. Juvenile coho from California, coastal Oregon, and the Columbia River make up a significant proportion of the coho stocks that follow the coastal belt northward during the summer months, as far as the northeastern section of the Gulf of Alaska (Hartt and Dell 1986). Hartt (1980) also found that some coho followed a counter-clockwise circular route across the open Gulf of Alaska during the first fall and winter. Dahlberg (1982) reported that a coded-wire tagged coho smolt released at Toledo Harbour in southeastern Alaska was later recaptured as a four-year-old at 55°N, 143°W, about 1,600 km west of Baranof Island, Alaska.

Many coho, however, do not take a long migratory route around the Gulf of Alaska but spend their entire marine life in inshore waters (Hartt and Dell 1986). The distribution of juveniles in their first summer in the Gulf of Alaska does not overlap with that of immature salmon that are a year or more older, which may serve to reduce feeding competition. By remaining in inshore areas, coho avoid pelagic predators in the open ocean. Coho that were tagged in the northern Gulf of Alaska, in the vicinity of Kodiak Island, were recovered in almost all areas from Alaska to Oregon. However, coho that were tagged further south, from southeastern Alaska to Cape Flattery, resulted in few Alaskan recoveries (Hartt 1980). As early as 1929 and 1930, Pritchard (1934) found that maturing coho tagged along the north and central coasts of British Columbia were recovered south or east of

their release site. He found that the distances travelled between release and recapture sites were much less for coho than for chinook, and he concluded that coho stocks were mostly local.

Clemens (1930) reported that coho tagged in Queen Charlotte Strait were recovered to the south. Fish that were caught and tagged in one area comprised a variety of stocks. There was no evidence from marking studies that fish captured from one school were all headed for a specific area or spawning stream. Coho that were captured and marked along the north coast, and that were subsequently recovered in the Strait of Georgia, used both the Juan de Fuca and Johnstone Strait entrances.

Foerster (1955) summarized coho tagging experiments between 1925 and 1951 and found that coho moved in all directions towards small streams along the coast. He also noted that coho migrated shorter distances and at a slower rate than chinook and concluded that these differences were due to the coho's greater wandering during feeding activity. All tagged coho were recovered in the same year as they were marked and released, whereas chinook tags were recovered over two or more years. Coho tagged in both Alaska and Oregon were recovered in the Fraser River, British Columbia.

Movement and Distribution at Sea

Godfrey (1965) was one of the first to summarize all known data on ocean distribution of coho salmon over the broad expanse of the North Pacific. He noted that, until the 1950s, it was generally believed that coho did not undertake extensive ocean migrations. Not until after the mid-1950s was there any systematic sampling in the offshore areas. One coho tagged in the northern Gulf of Alaska area in September was later recovered in Depoe Bay, Oregon, a distance of 2,200 km (Godfrey 1965). Godfrey (1965) also noted that North American coho have not been found in large numbers in offshore waters and that they probably wintered in areas well to the south of the Gulf of Alaska.

Asian coho are generally found in the southern part of the western Pacific Ocean in spring and early summer, and north of latitude 45°N by mid to late summer (Godfrey 1965). Semko (1958) indi-

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cated that most Kamchatkan coho were feeding 1,600-1,800 km southeast of Kamchatka between 165°-173°E and 45°-50°N. He also found that the number of coho in the Bering Sea was insignificant. Godfrey et al. (1975) reported that Asian coho, in their first ocean year, migrated progressively southward from the Kamchatkan peninsula to at least 40°N as water temperatures declined. Of the five species of Pacific salmon common to both North America and Asia, coho have exhibited a preference for the highest minimum ocean temperatures (at 5°-5.9°C) and are not generally found in waters cooler than 7°C (Manzer et al. 1965). As temperatures increase during the summer months, coho move progressively northward throughout the North Pacific Ocean and into the Bering Sea (Figure 3). The following spring, they again move north over a broad expanse from Hokkaido and the Kuril Islands on the west and from as far east as 175°W (Godfrey et al. 1975). With the onset of maturity in mid-July and August, coho that are in waters north of 52°N, near Kamchatka, head for east Kamchatka, while those south of 52°N move towards west Kamchatka, the northern coast of the Sea of Okhotsk, and the east coast of Sakhalin (Kondo et al. 1965).

North American salmon, of all five species, and steelhead intermingle with Asian salmon south of 46°N in the North Pacific Ocean (INPFC 1985). Initial evidence for intermingling of Asian and North American coho stocks came from a 1959 tagging program conducted by Japan. At that time, 225 coho were tagged directly south of Adak Island in the Aleutian Islands (about 176°W); later, eight were recaptured in western Alaska and two in eastern Kamchatka, each having travelled about 1,800 km (Godfrey 1965). More recent studies have shown that coho from western Kamchatka and areas in the northern Sea of Okhotsk occur south of 46°N and between 175°E and 175°W (INPFC 1983); western and central Alaskan coho are also present in this same area (INPFC 1985). In 1983, observers on Japanese research vessels noted that coho were distributed south of 45°N, between 170°E and 180° in May; by June they had moved north to 46°N; and by July they had moved to 51°N between 162°E and 176°W (FAJ 1984). Two coho that were tagged and released in the vicinity of 51°30'N, 177°00'W were subsequently recovered (one each) in southeastern Kamchatka and Bristol

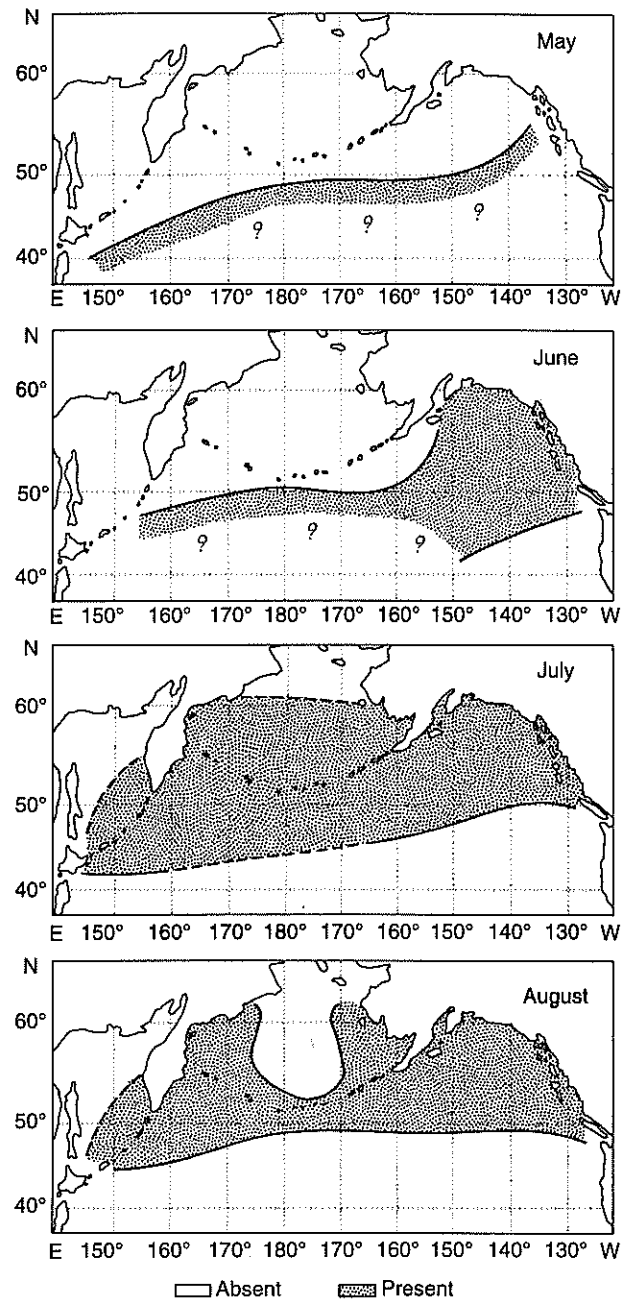


FIGURE 3

Occurrence of coho salmon in the North Pacific Ocean, May through August. (From Manzer et al. 1965)

Bay (NWAFC 1984). The eastern known limit for Asian coho is about 177°W (at 45°N) for coho recovered in both southeastern and southwestern Kamchatka (NWAFC 1984); the western known limit

for North American coho was demarcated by a fish that was tagged and released (June 1983) at 177°33'E (44°30'N) and later recovered (August 1983) in the Mulchatna River, Bristol Bay, Alaska (INPFC 1985).

Alaskan coho from streams that are tributary to the eastern Bering Sea follow a migration route that is similar to Asian coho. When temperatures decline in late summer, immature coho migrate south to the Aleutian Islands (40°N), and some move into the Gulf of Alaska. When temperatures begin to increase in spring, coho commence a northward migration back to their home streams. Coho stocks in the Gulf of Alaska are characteristically highly mixed and are derived from a wide variety of streams from Alaska to as far south as Oregon (Godfrey et al. 1975; Hartt and Dell 1986).

Direction-Finding during Migration

Some of the mechanisms that operate in salmon orientation during migration are understood, but the comprehensive details of the migration mechanisms that direct the fish from smolt to spawning adult are not known. It is not clear how salmon are able to migrate over the great distances they cover and return to their natal streams. During the salmon's ocean life "some awareness of position in relation to the place of origin is maintained" (Neave 1964). Neave (1964) suggested that fish might have an internal clock that records both local and home stream time so that a change in latitude would be detected by a change in day length, and a change in longitude would be indicated by the shift in time at which daylight begins and ends. Royce et al. (1968), in their review of ocean migration of Pacific salmon, noted that salmon of different species and different stages of maturity are often mixed in the feeding areas and that there is no strong tendency to school by group. In fact, the different stocks of coho show as much difference in their distribution as do different species. Royce et al. (1968) thought that the navigation system of salmonids was an inherited series of responses to stimuli because an individual makes the migration circuit only once and must find its way back to the home stream at the right time. They concluded that, because the circuit may be made only once, it was not simply a matter of following the cues in the reverse order. The routes

followed are often in the open ocean away from the shoreline, and, in many cases, even beyond the continental shelf.

Ocean temperature gradients are thought to be unlikely as a major guiding mechanism because seasonal variations would potentially disrupt the timing of the return to spawn by two or more weeks (Royce et al. 1968). Celestial navigation has been considered and rejected because during much of the migration period the skies of the North Pacific Ocean are overcast (Royce et al. 1968). Olfactory cues in the open ocean are highly unlikely (Royce et al. 1968). Ocean currents would not seem to be important as the fish are known to migrate actively against, with, and across current patterns, and they do not simply drift with the flow (Royce et al. 1968). It is known that ocean currents generate small electrical potentials across the current (0.1–0.5 microvolts per cm). If fish can detect these potentials, it may provide them with directional cues. It is thought that a sensor associated with the lateral line of the fish may make it possible to use these electromagnetic phenomena for navigation (Royce et al. 1968).

Burgner (1980) suggested that salmon migrating over long distances in the ocean must be relying on an inherited response to guidance stimuli. Presumably, the migration pattern exhibited by a particular stock has evolved to optimize fish growth and survival. Other cues cited by Burgner (1980) are polarized light, photoperiod, pheromones, and electrical and magnetic fields. Although there are a variety of possible open-ocean migration cues, the fish may use a combination of mechanisms, or they may migrate by some means as yet unrecognized. However, after the fish reach the vicinity of their home stream, the guidance mechanism is clearly olfaction (Wisby and Hasler 1954).

Rate of Travel

The speed at which fish travel in the marine environment has only been measured indirectly. Clemens (1930) reported the recovery of two coho that had been tagged at Sooke on the southwest coast of Vancouver Island. One fish was recovered the next day at a distance of 55 km, and a second fish was recovered 11 days later in the Fraser River, having covered a minimum distance of 150 km.

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Godfrey (1965) stated that the rate of migration was difficult to judge, but it was known that a few individuals had averaged at least 48 km/d and that a slow rate may be the result of feeding diversions. Jensen (1953) and Allen (1966) estimated a rate of 9.2–13.0 km/d for fish moving from the central Washington coast to the Seattle area. An even slower rate of 6 km/d was reported by Parker and Kirkness (1951), who found that coho marked and released in Alaska had travelled an average of 215 km over a 36-day period. Van Hyning (1951) marked and recaptured coho that were feeding off the Oregon coast and found that they had moved only 3 km/d (range 0–17 km/d). Using some selected recoveries and assuming a fairly direct path between tagging and recovery locations, Godfrey et al. (1975) suggested an average migration rate of just under 30 km/d. Royce et al. (1968) stated that salmon could maintain a rate of 55 km/d over long distances.

Ocean Food Habits

On first entry to salt water, juvenile coho feed mostly on marine invertebrates, but as they grow larger they become more piscivorous (Shapovalov and Taft 1954). A number of studies have shown that coho, during their estuarine and early marine life stages, are important predators on chum and pink salmon fry (Parker 1971; Slaney et al. 1985). In her study of stomach contents of juvenile coho of both wild and hatchery origin from Yaquina Bay, Oregon, Myers (1978) found that coho captured in beach areas had eaten primarily anchovy (*Engraulis mordax*), surf smelt (*Hypomesus pretiosus*), and sand lance (*Ammodytes hexapterus*). In the channel areas, hatchery coho fed primarily on crangonid shrimp and megalopa larvae of Dungeness crab (*Cancer magister*), whereas wild coho concentrated on juvenile surf smelt. Levy and Levings (1978) found that coho smolts in the estuary of the Squamish River, British Columbia, were feeding on unidentified fish, as well as *Anisogammarus* and *Neomysis*. In the Strait of Georgia, Healey (1978) sampled coho that had a mean monthly (May–October 1976) fork length of 11.6–28.1 cm. Examination of stomach contents of these coho and of coho of a similar size caught in 1975 revealed that herring (*Clupea harengus*), sand lance, and unidentified fish remains accounted for 34.6% and 29.0% of

the contents (by volume) over the two years and that amphipods accounted for 26.7% and 40.5%. Crab megalops were important in 1975 and made up 26.2% of the diet. Overall, the stomach contents as a percentage of body weight ranged from 0.40% to 1.51%. More recently, Healey (1980) noted that the amount and type of food in juvenile coho stomachs was a function of its availability and that there was a positive correlation between the abundance of juveniles and the amount of food in their stomachs. The fish are obviously attracted to good feeding areas and will remain there as long as the food is in sufficient supply.

Chamberlain (1907), sampling adult coho taken from the northern Gulf of Alaska, found that they had eaten sand lance, sticklebacks (*Gasterosteus aculeatus*), small herring, and the occasional flatfish, cottid, and salmonid. Marine invertebrates, including amphipods, isopods, and crab larvae, were also included in the diet. Pritchard and Tester (1943, 1944) found that coho consumed a wide variety of food items, but that herring and sand lance were the most important components of the diet. Pritchard and Tester (1943, 1944) also found that coho ate sardines (*Sardinops sagax*), anchovies, capelin (*Mallotus villosus*), rockfish (scorpaenids), sable fish (*Anoplopoma fimbria*), lanternfish (myctophids), Pacific saury (*Cololabis saira*), hake (*Merluccius productus*), walleye pollock (*Theragra chalcogrammus*), and other coho salmon. Among the invertebrates eaten by coho, they found euphausiids, squid (*Loligo opalescens*), goose barnacles (*Pollicipes polymerus*), and jellyfish, although the last three items were observed in one year only. The diet of adult coho salmon is very similar to that of chinook, except that invertebrates make up about one-fifth of the diet in coho, and less than 3% in chinook. In some situations, coho may feed more heavily on fish than do other salmonids (FRBC 1955).

On the Oregon coast, 97% of the stomachs of the troll-caught coho contained larvae of the Pacific crab (*C. magister*) (Anonymous 1949). Heg and Van Hyning (1951) found that maturing coho in their second summer at sea consumed herring, anchovies, smelt, euphausiids, and crab larvae (especially *C. magister*), and in some areas, squid. The diet of Washington coastal coho was similar to that of Oregon fish but included sardines and rockfish, with anchovies and smelts occurring rarely (Silliman 1941).

On the British Columbia coast a number of studies have been undertaken to determine the nature of adult coho diets. Herring was found to be the dominant food item for coho off the southwest coast of Vancouver Island (FRBC 1955). Foerster (1955) observed sand lance, sardines, and herring in coho stomachs. Chatham Sound coho stomachs contained mostly herring larvae and sand lance (Manzer 1969).

It was noted earlier that "outside" stocks of coho from the west coast of Vancouver Island were generally larger than "inside" stocks from the east coast of the island. Prakash and Milne (1958) found that the food of coho from the west coast of Vancouver Island consisted primarily of fish, with crustaceans forming a minor part of the diet. On the east coast of the island, fish were less important, and amphipods made up the bulk of the diet. They also noted that, on average, an "inside" fish contained only half the volume of food as an "outside" west coast fish, which was probably relative to the differences in growth. The diet differences reflect different feeding conditions and food availability. In British Columbia waters, coho are opportunistic feeders and show considerable plasticity in what they eat (Prakash 1962).

Senter (1940) noted that the coho of southeastern Alaska fed on a mixture of herring, smelts, and candlefish (*Thaleichthys pacificus*), and that maturing females seemed to have more food in their stomachs than males. Additional items found in the stomachs of coho from the Gulf of Alaska included copepods and chaetognaths (Manzer and Neave 1958, 1959).

Churikov (1975) reported that juvenile coho stomachs sampled in Kamchatkan estuaries contained 69.4% gammarids and 27% winged insects, the balance being made up of miscellaneous food items. Andrievskaya (1968) found that maturing coho in the Sea of Okhotsk consumed young walleye pollock, sand lance, and other fish; and that coho over 25 cm in length on the Bering Sea side of Kamchatka ate young greenlings (hexagrammids), whereas coho sampled more than 150 km offshore were found to contain 90.8% amphipods (primarily *Parathemisto japonica*), with the balance made up of fish. Gribanov (1948) observed that Asian coho continued to feed on fish and invertebrates up to the time they entered their native rivers.

It has been determined by sonar observations

and the position of fish in gillnets that salmon feed as individuals. The schools disperse for feeding and then later regroup (Burgner 1980). Before feeding on prey fish, a solitary salmon circles a concentration of prey. Suddenly, it attacks the prey, which surface and churn the area into a froth of bubbles, then quickly disperse. The feeding coho will circle and attack once again when the forage fish have regrouped (Grinols and Gill 1968).

Various estimates have been made of the quantity of food taken by adult coho. LeBrasseur (1966) observed that when coho consumed euphausiids, squid, and fish, the stomach contents were equivalent to about 1% of body weight. He also noted, as did Chapman (1936), that a high proportion of coho sampled had empty stomachs. How the fish are captured during sampling, e.g., hook and line, or gillnet set overnight, will have a strong bearing on what will be found in the stomach. The fish may be caught before they have begun feeding for the day and may have digested all the food captured previously. Coho also frequently egest food from their stomachs when caught.

As a further comment on coho being opportunistic feeders, it is interesting to note that, in the Great Lakes, adult coho feed on rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*), both of which are abundant in this environment. This may be one of the keys to the success of this introduced exotic (Scott and Crossman 1973).

Ocean Growth

Crone and Bond (1976) found that coho smolts that entered the sea as yearlings ranged in length from 79 mm to 120 mm; those that migrated as three-year-olds were 91 mm to 139 mm, and the four- and five-year-olds were 151 mm and 175 mm, respectively. The latter two unusual age groups were from fish sampled from the Karluk system in Alaska (Drucker 1972).

Coho grow very rapidly after they reach the marine environment. Hartt (1980) reported that the average fork length of smolts that had moved beyond the estuary was 150–270 mm. During their first year at sea, growth was estimated at 1.23 to 1.50 mm per day. For example, fish tagged off southeastern Alaska and the Queen Charlotte Islands grew from an average size of 253 mm in July to 290 mm in August and to 311 mm in September

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(Godfrey et al. 1975). In April and May these fish would have been 60–70 mm. Mathews and Buckley (1976) and Healey (1980) reported growth rates of 1.1 mm/d for coho during their first six months in salt water (for a size range of 100–280 mm), with a daily increase in weight of about 2% per day. Healey (1980) calculated that the length-weight relationship for Strait of Georgia juvenile coho was: $W = 1.62 \times 10^{-6} L^{3.42}$, where W = weight in g and L = body length in mm. Phillips and Barraclough (1978) developed a length-weight relationship for Strait of Georgia coho sampled from Saanich Inlet (1966–1975) as: $\text{Log}_{10} W = 3.309 \text{Log}_{10} L - 5.576$, or $W = 2.655 \times 10^{-6} L^{3.309}$.

Clemens (1930) sampled coho from the Strait of Georgia that were entering their second year in salt water. For fish caught April through June, he noted the following progression in average size: 1–15 April, 0.91–1.14 kg; 16–30 April, 1.14–1.35 kg; 1–15 May, 1.35–1.60 kg; 16–31 May, 1.60–1.92 kg; and 1–15 June, 1.92–2.14 kg. By 15 September the fish had reached an average length of 61 cm and a weight of 2.95 kg. He concluded that the growth during the spring months was about 0.45 kg per month and by summer had decreased to half this rate. Milne (1950) and Prakash and Milne (1958) compared the growth rate of coho found in the Strait of Georgia with that of coho from the west coast of Vancouver Island. They observed that fish of the same age from west coast waters were 0.9–1.9 kg heavier than fish from the Strait of Georgia and that both groups doubled their weight between June and September. They attributed this difference to better feeding conditions in west coast waters that may have been a result of higher nutrient levels and more favourable ocean temperatures. Godfrey (1965) reported that coho caught off the west coast of Vancouver Island in June had a fork length of 54.6–58.8 cm, and 64.4–69.8 cm by September. The average weight for commercially caught coho was 3.22 kg. Ricker (1976) concluded that the growth rate of coho in their final year of life was from 0.6 to 2.5 kg in inside waters (Puget Sound, Strait of Georgia) and 0.8 to 4.0 kg in outside areas. These weights are lower than the average of 4.30 kg (2.33–6.76 kg) reported earlier by Rounsefell and Kelez (1940). Shapovalov and Taft (1954) found that coho from Waddell Creek, California, entered the sea at 10–15 cm fork length and returned 16 months later at 62 cm.

Gribanov (1948), in a study of Asian coho, observed that this species grew faster than all other species of salmon except pink salmon. Most coho measured were 55–69 cm, with a range of 40–88 cm in fork length. The usual weight for Kamchatkan coho was 3.0–3.5 kg, with extremes of 1.2–6.8 kg.

Smolt-to-Adult Survival

Various estimates of survival from the smolt to the adult stage have been made. Shapovalov and Taft (1954) observed survivals ranging from 0.98% to 7.72%, with a mean of 4.95%, and suggested that the bulk of the mortality occurred during the first year at sea. Part of the difficulty in making these and other estimates was the necessity of clipping off different combinations of fins. Later it was shown that fin marking resulted in additional mortality, the severity of which depended on which fins were removed.

Foerster (1955) summarized some earlier estimates that had been made on survival rates. For coho from Nile Creek on the east coast of Vancouver Island, the estimates for three different brood years were 3.2%, 4.9%, and 9.9%; for coho from Port John (British Columbia) the rates for a series of four brood years were 7.0%, 7.2%, 3.8%, and 19.1%; for Cultus Lake coho the return rate was 8.1% for marked coho. In a detailed study of Puget Sound hatchery coho, Mathews and Buckley (1976) estimated that, after the first six months at sea, 13% of the smolts survived; after twelve months, survival was down to 9%. Of fish that survived to catchable size, approximately half would be taken in the commercial and recreational fisheries. The numbers that returned to the home stream were about 4% of the smolts that had migrated to sea. This compares to an average survival rate of 3.8% (range 0.9%–9.4%) observed for ten brood returns to Minter Creek (Washington) (Salo and Bayliff 1958), and 5% (range 1.0%–7.7%) for four broods of Waddell Creek (California) coho (Shapovalov and Taft 1954). The smolt-to-adult survival rate for Big Qualicum (British Columbia) coho was much higher at 10.8% (range 5.4%–15.5%) over a 15-year period (Fraser et al. 1983). Ricker (1976) estimated that the mean monthly instantaneous rate of oceanic mortality for coho was 0.013 during the final year of life.

In the early 1970s it was thought that the maxi-

imum smolt-to-adult survival (catch plus escape-ment) was about 20%-25%. However, Bilton et al. (1982) showed clearly that, under optimum conditions of size and time of release, survivals in excess of 40% can be anticipated. From this experiment, maximum adult production (43.5%) was achieved

by releasing 25.1-g coho smolts on 22 June (1975). Smolts released at earlier or later dates, and at larger and smaller sizes, did not survive as well. Bilton et al. (1982) also observed that smolts released in April at a size of >20 g produced the largest number of jacks.

HOMING AND STRAYING

All anadromous salmonids deposit their eggs in freshwater gravel beds for incubation. The resultant fry, which live in fresh water for varying lengths of time, move downstream to the marine environment as smolts. After a growth period in the sea, fish nearing maturity return or "home back" to their parental stream to spawn. Fish that do not return to their home stream or release site and that spawn in other streams and tributaries are considered to be strays. A return to the parental spawning ground provides a mechanism for enhancing survival by the repeat usage of good sites. Ricker (1972) noted that homing has the further advantage of getting the approximate number of spawners back to a spawning ground or rearing area that can accommodate them. Homing can potentially be a disadvantage if fish return to areas that have marginal spawning areas or poor rearing conditions.

Straying can also be a survival mechanism in that it may protect against the loss of an entire stock due to some environmental catastrophe in the home stream (e.g., the volcanic eruption of Mt. St. Helens, Washington, in 1983). If there is no straying, areas that lack spawners due to poor conditions or restricted access will not become recolonized if conditions become more suitable. Fish are also able to extend their normal ranges through straying.

The cues used by salmon to move from offshore feeding areas to the vicinity of their home stream are not fully understood, but once they reach the point of leaving the estuary and entering fresh water they appear to rely primarily on olfaction.

Harden Jones (1968) developed a hypothesis of sequential imprinting for home-stream detection which states that "young salmon may undergo a

series of imprinting processes corresponding to each major change of environment made in fresh water; gravel bed, lake outlet, tributary river, main river. It could be important that the sequence in which these imprints are made should correspond exactly to the reverse sequence of stimuli that the upstream migrant receives on the way home." Thus, distinctive home-stream odours could enable fish to migrate back to their incubation site.

Wisby and Hasler (1954) were the first to demonstrate that fish with their olfactory pits plugged were unable to identify their home stream. Fish with olfactory occlusion continued to migrate upstream, but their choice of direction at critical junctions appeared to be random. Brett and MacKinnon (1954) demonstrated that coho and chinook salmon detect odours at low concentrations. Fish migrating upstream are known to exhibit an avoidance reaction to the presence of mammals by moving back downstream. Odours from the skin of (predatory) mammals or human hands at dilution rates of greater than 1 ppm were sufficient to displace coho downstream. Brett and Groot (1963) reported that, although salmon were highly sensitive to olfactory cues, other cues, such as vision and the sensitivity of the acoustico-lateralis system, are also probably used for successful homing. Groves et al. (1967) demonstrated that in chinook, olfaction was far more important for homing than was vision. Some fish had their olfactory systems experimentally blocked and others were blinded. Of the latter group, at least half of the fish were able to home correctly using olfaction (or other senses). However, when the olfactory system was blocked, fewer than one-tenth of the fish were able to find their home stream.

If the Harden Jones (1968) hypothesis is correct

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and olfactory stimuli are imprinted by fish during development, then presumably, by following olfactory cues, the adult fish will get back to the spawning area and the gravel in which it incubated as an egg. In many cases, however, egg-to-fry-to-smolt development is not a simple sequence. In Chilliwack Lake, British Columbia, wild coho juveniles (under-yearlings) were tagged and released in the lake in the fall. In the following spring these marked smolts were found in small tributaries of the lower river below the lake, presumably having over-wintered there. As returning adults, all marked fish were recovered in the main river above the lake and none in the lower river tributaries (B.C. Pearce, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.). In Alaska, coho that were marked while rearing in a small tributary of the Berners River were found spawning the next year in another tributary where conditions were better (Gray et al. 1978). It can be concluded that coho juveniles may rear a long distance from where they emerge as fry but are obviously imprinted with the memory of their natal spawning ground. Imprinting must occur initially in the earliest life history stages. If juveniles are captured or incubated and reared in a hatchery, and then transported for release elsewhere, the adults will return to the point of release. In cases where the point of release is upstream in the same river system in which they were incubated and/or reared, many adults will not bypass the lower site to reach the release point (Lister et al. 1981).

The question of the time required for imprinting has been explored using a large number of hatchery coho. In some cases, the exposure of coho smolts to a specific water source, like spring water, for 36-48 hours has been sufficient to assure a high degree of homing success. Jensen and Duncan (1971) reported on a study that involved transporting marked coho smolts 250 km downstream from the Wenatchee River, Washington, to below Ice Harbour Dam on the Snake River. Both of these rivers are major tributaries to the Columbia River. Several groups of smolts were held up to 48 hours in a spring water source and then released between March and May. By September, jacks were returning to the release site, and the following year jacks (from a second release group) and three-year-old fish returned to this specific water source. This

source was flowing at less than 0.76 m³/min into the Snake River, which was running at many thousands of m³/min. This, and other examples of very specific homing can be cited, but there are also numerous studies of marked coho that indicate persistent low levels of straying.

Taft and Shapovalov (1938) reported that wild coho were marked (multiple fin clip) and released in Waddell Creek (California). When they returned as adults, approximately 20% of the recoveries were made in Scott Creek, which enters the Pacific Ocean about 8 km south of Waddell Creek. Lister et al. (1981) discussed two experiments on marked wild coho in which coded-wire tags were used rather than the less reliable multiple fin marks. These fish were tagged as smolts and later recovered as adults on the spawning grounds. In two tributaries (13 km apart) of the Squamish River (British Columbia), one of 27 tagged adult coho (3.7%) had strayed between tributaries. In the Cowichan and Koksilah rivers, which enter Cowichan Bay (British Columbia) about 2 km apart, two of 150 tagged adults (1.3%) were from fish that had strayed between systems. Shapovalov and Taft (1954) observed that the rate of straying from a given stream is fairly constant for a given year class but may vary considerably from year class to year class. They hypothesized that the "conditions existing at the time of the migration to the ocean determine the amount of straying that will take place one and two seasons later." Just what these conditions are was not stated, but it was noted that there was a tendency towards (1) a positive correlation between the number of outmigrants and the amount of straying, and (2) a negative correlation between the average size and the number of strays.

A recent study of recoveries of coded-wire tagged coho on the east coast of Vancouver Island indicated that the straying rate for hatchery-released fish (0%-5%) was less than that for wild coho stocks (0.7%), but most straying rates were in the range of 0.1% (M. Labelle, Resource Ecology/Resource Management Science, University of British Columbia, Vancouver, British Columbia, pers. comm.). Fish that were recovered in other than their home streams were found to have strayed, on average, about 12 km. M. Labelle also observed that those stocks that had been manipulated in some way - for example, eggs collected from a particular brood stock, transported to a different

incubation and rearing site, and then returned to their native stream for release as fry or smolts - had the highest subsequent straying rates. Deterioration of stream conditions, such as low flows, was also seen to increase the straying rate up to 50%. The furthest stray recorded by M. Labelle was a Quinsam River coho that was recovered in the Quatse River about 190 km to the northwest.

One interesting aspect of the straying question is whether a fish, once having strayed, can sort out the error and find its way to its home stream. In California, Taft and Shapovalov (1938) observed that a steelhead released from Scott Creek returned as an adult to Waddell Creek and was captured at a fence site 2.5 km from salt water, where it was again marked and released. It was subsequently recaptured in its home stream. Similarly, coho marked as juveniles before release from the Capilano Hatchery near Vancouver, British Columbia, were recovered in the Seymour River as adults, about 8 km to the east and 20 km from salt water. These fish (which had previously been marked by an adipose fin clip and a coded-wire tag) were tagged with an external (Petersen disc) tag, and about a week later several of them entered the Capilano Hatchery, a distance of at least 33 km. They had backed out of the Seymour River, reentered salt water, proceeded west to the mouth of the Capilano River, and then migrated up river to the hatchery. There, the coded-wire tags were removed and read to confirm that they were, in fact, fish of Capilano Hatchery origin. Had those fish been killed and examined in the Seymour River, it would have been assumed that they were strays that were about to spawn there. Thus, many records of strays may only indicate that, at the time of capture, the fish was in the wrong place and that,

given the opportunity, it may have retraced its route and returned to its home stream (E.T. Stone, Department of Fisheries and Oceans, Vancouver, British Columbia, pers. comm.).

The occurrence of long-distance straying became more evident with the use of coded-wire tags, which proved more reliable than multiple fin marks. Between 1974 and 1980, a total of 70 jacks and 64 adult coho bearing coded-wire tags were recovered at four enhancement sites from which they were not released. On the east coast of Vancouver Island, coho from five release sites (two south and three north) strayed into the Big Qualicum Hatchery. Coho from the Big Qualicum and Puntledge hatcheries entered the Quinsam Hatchery to the north. In the lower mainland of British Columbia, strays occurred in both directions between the Seymour and Capilano rivers, with the majority (by virtue of the numbers released) straying from the Capilano River to the Seymour River. For longer distance strays, a coho from each of the following release sites strayed north into the Big Qualicum Hatchery: Chilliwack Hatchery in the Fraser River valley, British Columbia; Lummi Bay near Blaine, Washington; and the Salmon River, a tributary of the Queets River in northern Washington. Another fish from Lummi Bay entered the Capilano Hatchery (F.K. Sandercock, unpubl. data).

The extensive use of coded-wire tags in recent years has demonstrated beyond doubt that the majority of coho that are native to a particular stream return to that same stream at maturity. In situations in which the survival rate is high or the spawner capacity of the stream is approached, straying may occur into adjacent streams.

CONCLUDING REMARKS

In summary, coho are widely distributed over much of the North Pacific basin and have been successfully transplanted to more non-endemic locations than any of the other species of Pacific salmon. Coho have often been described as "op-

portunistic," a term which is especially appropriate in describing their choice of spawning sites. Their success as a species may be partly attributed to their utilization of a myriad of small coastal streams and to their aggressiveness and apparent

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determination to reach the small headwater creeks and tributaries of larger rivers to spawn.

In many cases, they overcome difficult obstructions to reach areas inaccessible to other salmon and then share these locations with only migrant steelhead or perhaps resident cutthroat trout. These small headwater streams generally provide cool, clear, well-oxygenated water, with stable flows that are ideal for incubation and subsequent rearing.

Groundwater seepage in these small streams moderates the high temperatures in summer as well as the near-freezing temperatures in winter, thus sustaining a much more stable environment. Aquatic insect production, a prime source of food for juvenile coho, is often rich in small streams and is further supplemented by terrestrial insects that fall into the water from streamside vegetation. Almost anything of an appropriate size that is moving in or on the water column can be considered as food for coho.

Most coho mortality occurs during the rearing stage in fresh water, where the juveniles may be exposed to winter and spring freshets, summer droughts, or simply lack of rearing space. However, by remaining in these streams for a year or more before migrating to sea, juvenile coho avoid the high mortality rate associated with entry, as fry, into sea water, such as is experienced by chum and pink salmon. Once the coho smolts migrate to sea, the survival rate is high.

To take advantage of this high survival rate in the marine environment, coho have been incubated, reared, and released from hatcheries for almost a hundred years. Coho can be readily adapted to the hatchery environment and are potentially the easiest of all the Pacific salmon to domesticate. In fact, the burgeoning fish-farm industry in western North America initially concentrated on coho salmon, partly because of availability of a surplus of coho eggs from hatcheries.

Coho smolts, produced either in the wild or in a hatchery environment, often survive to adults at three or four times (sometimes 10-20 times) the rate of other salmon species. Of all salmon caught commercially in the North Pacific basin, coho make up only a small percentage, which probably reflects on the total amount of freshwater rearing space available.

Coho are taken commercially, as incidental catch in seine and gillnet fisheries (river traps in Asia), and in the directed troll fishery. For trollers, the prized species is chinook, but whatever the coho lack in size, compared to chinook, they make up for in quantity.

The recreational fishery on the Pacific side of North America is highly oriented towards chinook and coho salmon. Although most sportsmen would rather catch a chinook because of the larger size, it is often the coho that fills the bag because of their abundance, their availability in nearshore waters, and their willingness to take the angler's lure. When the coho return to the estuaries and rivers they may be further harvested in the Native food fisheries.

Because spawning stocks of coho are so widespread, it becomes virtually impossible to determine escapement populations and, hence, total stock size. The problem of estimating how many there are is made even more difficult by the fact that adult coho can be found returning to their natal stream in almost every month of the year.

The diversity in life history strategies exhibited by the large number of coho stocks in the North Pacific is reflected in the broad range of migration and spawning timing, the multitude of suitable freshwater habitats, the variety of foods consumed in both fresh water and salt water, and the various strategies followed in ocean rearing. It is this adaptability that would seem to assure the continued survival of this valuable species.

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