SALMON OF THE NORTH PACIFIC OCEAN—PART III
A REVIEW OF THE LIFE HISTORY OF NORTH PACIFIC SALMON
4. SOCKEYE SALMON IN BRITISH COLUMBIA

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Sockeye salmon, *Oncorhynchus nerka* (Walbaum), occur naturally off the coast of British Columbia and in many of its coastal river systems, particularly those which contain lakes accessible to the sea. The more important lake nursery regions are as follows*:

1. *Columbia River drainage* (see Craddock, 1958):
   - Osoyoos Lake; formerly the Arrow Lakes.

2. *Vancouver Island*:
   - Sproat Lake and Great Central Lake (tributary to Barkley Sound), Nimpkish Lake (tributary to Johnstone Strait), and a few smaller ones.

3. *Fraser River drainage* (see International Pacific Salmon Fisheries Commission (IPSFC) Annual Report for 1943; also Schaefer, 1951):
   - Lower Fraser lakes: Pitt, Harrison, Lillooet, Tenas, Cultus, Chilliwack; formerly Cogutlam and Alouette.
   - Thompson lakes: Kamloops, Little Shuswap, Shuswap; formerly Adams.
   - Upper Fraser lakes: Seton, Anderson, Chilko, Taseko, Quesnel, Bowron; formerly Horsefly.
   - Nechako River lakes: Fraser, Francois, Stuart, Trembleur, Takla.

4. *Central coast*:
   - Long Lake at Smith Inlet and Owikeno Lake at Rivers Inlet are good sockeye producers, and there are a number of minor stocks. One of the latter that has been studied in some detail is Port John Lake, on King Island, which drains to the ocean by way of Hook-nose Creek, south of Port John.

5. *Skeena River drainage* (see Brett, 1952):
   - Upper Skeena lakes: about 15 small lakes, the largest being Bear Lake.

(c) Babine region: Babine Lake is the largest individual sockeye lake in British Columbia; sockeye are also reared in Morrison Lake which is tributary to it, and in Nikit-kwa Lake which is an expansion of its outlet stream.

(d) Bulkley region: Morice Lake, Bulkley Lake.

(6) *Nass River drainage*:
   - Meziadin and Bowser Lakes are of greatest importance.

STOCKS, RACES AND RUNS

It is now generally realized that a large percentage of the adult fish of every salmon stock must return to the stream of their birth. Only in this way can we account for the prevailing orderly return of salmon to streams in quantities more or less appropriate to the size of the available spawning or nursery areas, and independently of stream size or location. Transplantation experiments support this generalization, in that a much larger percentage of transplanted young commonly return to the site of release than would be expected on the basis of random dispersal. Homing of sockeye salmon transplants is unusually precise; they commonly return to the place of transplantation and very few (usually none) are recorded as returning elsewhere. Some recent examples are summarized in the IPSFC 1962 Annual Report.

More pertinent to an appreciation of the discreetness of stocks in nature is the accuracy of the return of native non-transplanted stocks. In British Columbia, the quantitative accuracy of homing under natural conditions was established for the Cultus Lake region by marking the whole of two successive smolt migrations. In 1933 only 17 unmarked fish of ages 4 or 5 appeared in a run of 2,864 marked sockeye of those ages; that is, 0.59% of the run was possible strays (Foerster, 1937). Even of these 17, a part or all may have been native fish accidentally left unmarked. At Hook-nose Creek possible strays amounted to only 5% to 15% of the run over a series of years, but again some or all of these might have been native fish (J. G. Hunter, unpublished).

We will use the word "stock" for each population that is substantially separated from other populations,
either in time of spawning or in place of spawning. A group of stocks is often referred to as a "run"; for example, the early Fraser run, or the Rivers Inlet run. "Race" seems usually to be used synonymously with "stock" in this context, but sometimes it refers to a group of stocks. A large lake may have several to many stocks, each spawning in a particular stream or group of streams. For example, Shuswap Lake now has four principal stocks: (1) Lower Adams River and Little River ("late Shuswap"), (2) Seymour River, (3) the early Scotch Creek fish, (4) Middle Shuswap River. Formerly it had stocks in the Anstey and the Salmon Rivers as well, while the once-large Eagle River stock is beginning to be re-established (IPSC Annual Reports). Babine Lake and tributaries may have up to 20 or more spawning stocks, grouped as follows on the basis of their time of entry into the lake: (1) Pierre Creek and about eight other streams, mainly in the southern part of the lake; (2) Morrison, Tahlo and 15-Mile Creeks; (3) Fulton River; (4) Upper and Lower Babine River; (5) several lake-spawning stocks (Brett, 1952, and recent studies). The degree of distinctness of the stocks in all lake tributaries has not yet been tested. However it is suggestive that in similar situations at Brooks and Karluk Lakes, Alaska, tagging studies have demonstrated a close to perfect tendency for adult fish captured off the mouth of each stream and distributed in many distant lake areas to distribute themselves on the same spawning grounds in the same proportions as fish marked and released directly into schools at the capture sites (Hartman and Raleigh, 1964).

The sockeye of different stocks differ in time of spawning: in particular, those which spawn on lake beaches and in lake outlets tend to spawn much later than those in tributaries, presumably because the lakes cool off later in the year. But apparently every stock has its distinctive seasonal spawning schedule.

Sockeye of different stocks exhibit average differences in (1) age as smolts; (2) size as smolts, even at a given age; (3) number of years spent at sea; (4) size at maturity, even at a given age (Kilik and Clemens, 1963, pp. 67–77, 96–97); (5) colour at maturity; (6) body proportions at maturity (Idler and Clemens, 1959, p. 25); (7) number of vertebrae (Foerster, MS 1940); (8) size of eggs (Robertson, 1922); (9) number of eggs per fish, at a given length or weight; (10) fat and protein content of the body at the start of migration (Idler and Clemens, 1959, pp. 14–15); (11) relative extent of fat and total energy consumption by males and by females in the process of maturation (ibid.); (12) season of upstream migration; (13) time of spawning. There are probably many other morphological and physiological differences, but no very extensive comparisons have as yet been made in British Columbia.

It is usually difficult to assess the relative importance of heredity and environment in determining the above differences. The effect of environment on certain characters is well known. There is also no question that heredity plays a large part in some cases, and perhaps in all (Ricker, 1960). For example, when eggs of one stock are transplanted to the region inhabited by another stock, the adults return from the sea at about the time that is characteristic for their parents’ home, rather than for the native fish in their adopted home.

**LINES AND CYCLES**

In southern British Columbia and southward the great majority of sockeye stocks mature mainly in their fourth year. Thus the main stream of reproduction flows from a given year to the fourth year following, so that there are four reproductive "lines"—often labelled 1901, 1902, 1903 and 1904. When one line considerably exceeds the others it is called a "dominant" line, and the resulting imbalance of population size produces a 4-year cycle of abundance and of catch. The line following the big one commonly has the next-largest population, which is sometimes called "subdominant" although it may be less than a tenth of the dominant line.

The Osoyoos Lake stock has fluctuated widely in recent years but no one line has retained superiority. With one exception, the downriver Fraser stocks have not had any cycle of abundance, certainly no very definite cycle. The exception is Cultus Lake, where the 1903 line was dominant up to 1931; during a subsequent period of experimental predator control large populations were produced in two successive lines, but these declined when the experiment ceased and in recent years the 1903 line is again coming to the fore. Most Fraser sockeye stocks above the canyon had a marked 4-year cycle, with the 1901 line being dominant, from before the start of commercial fishing up to 1917. The obstruction of Hell's Gate in 1913–14 interrupted or reduced this cycle, but in several nursery areas dominance of the 1901 line was conserved or has been restored (Stuart Lake system, Fraser Lake, Quesnel). The Shuswap Lake stocks, however, changed over and now have a strongly dominant 1902 line. The Chilko stock has also changed its dominance, and is exceptional in having a larger than ordinary subdominant line; at present (1963) the 1903 line is dominant and 1904 is subdominant, but this has shifted recently from 1904 and 1901, respectively (IPSC Annual Reports).
Various plausible suggestions have been offered as to the causes of line dominance and cycles (Foerster and Ricker, 1942; Ricker, 1950; Ward and Larkin, 1964). The most likely hypothesis involves interaction between sockeye and some of the predaceous fishes that eat them during their lake life. That is, the big years "saturate" the fish-consuming capacity of their enemies and so achieve a reduced mortality rate. This and similar effects have been named "depensation" by F. Neave. There is evidence that a depensatory situation may also exist during downstream migration or early ocean life, for Henry (1961) found that Chilko smolts survived about three times as well as expected in two years of big Shuswap runs (see also page 66). This latter provides a mechanism tending to promote synchronization of dominant lines as between different lakes, and such synchronization was in fact a conspicuous feature of the original upriver Fraser stocks.

In areas where sockeye mature in important numbers in both their fourth and fifth years, long-persisting cycles of abundance have not been observed. However, during their early commercial history both the Skeena and Rivers Inlet runs had a larger percentage of 5th-year fish than at present, and each had a marked 5-year cycle, lasting three to five generations (Milne, 1955; Godfrey, 1958). Some kind of unfavourable influence of abundant broods on subsequent ones is of course possible in these areas, no less than in the Fraser upriver lakes; current research seeks to discover its exact nature and, if possible, ameliorate its severity.

**SPAWNING, INCUBATION, HATCHING, EMERGENCE**

Spawning of sockeye in different parts of British Columbia extends from late July to early December. Peak times vary from about August 8 (Forfar Creek of the Stuart Lake area) to mid-November (Cultus Lake). In general, spawning tends to coincide with water temperatures of 3°C to 7°C so that stocks that breed in lakes or in their outlets tend to be the latest ones to spawn in a given region. There are no reports of early runs and late runs spawning regularly in the same parts of the same stream.

Spawning occurs mainly in streams, but also in some lakes, down to depths of as much as 30 meters. In most lakes the amount of lake spawning is believed to be considerably less than half of the total, but in Great Central Lake it is important, and Cultus Lake has very little else. On most sockeye spawning areas the sockeye greatly outnumber all other salmon that may be present at the same time.

The substrate used for spawning may include fine gravel, coarse gravel, and even stones 5-10 cm in diameter. Sockeye above Stephens Lake, Kispox River, spawn among rocks so large that they cannot be moved by digging, and the eggs fall into crevices (Brett, 1952).

Although no comprehensive study has been published, there may be some tendency for the average size and even the ocean age of the sockeye of different stocks to vary directly with the size of the gravel and (moveable) stones they use. For example, in the lower Fraser area large sockeye spawn in the mostly coarse gravel and stones of Morris Creek and Upper Pitt River, while the small Cultus Lake sockeye have fine delta gravel (Ricker, 1950). The rather small sockeye spawning in the Okanagan River above Osoyoos Lake also use mostly small gravel about 3 cm in diameter—the size of a golf ball (Burner, 1951).

Within each stock, the average number of eggs in female sockeye varies directly with their size, though with great individual variability. Comparing different stocks, the limited data available show pronounced differences in egg number and egg size that are not directly related to fish size. For example, Babine sockeye averaged 3,297 eggs per female (eight years of observation), the fish averaging 600 mm in fork length; whereas Cultus sockeye (six years of observation) averaged 4,094 eggs from females 20 mm shorter. Size of eggs is almost independent of fish size within a stock, in the few examples available. Comparing the different stocks that have been studied, eggs are largest in the very small Harrison River rapids sockeye—which might be related to the fact that they go to sea as fry (Robertson, 1922).

Details of spawning behaviour of sockeye in British Columbia have been studied by D. MacKinnon and G. Groot, but only summary accounts have been published to date (Fisheries Research Board of Canada (FRB) Annual Reports). In general, there is a stereotyped series of behaviour patterns by both sexes, lasting several hours, that leads to the spawning act. During this time the female digs a nest, lays 500 to 1000 eggs in it, and then covers it. Each female spawns three to five times, constructing a new nest each time; the group of nests constructed by one female is called a redd.

The eggs hatch during winter or early spring. They remain in the gravel until absorption of the yolk sac is complete and for some days or weeks thereafter. During this time they are quite active, and may move around in the interstices of the gravel. Eventually they move up out of the gravel, and begin their free life sometime during the period April to June.

A very few British Columbia stocks of sockeye move downstream to sea shortly after emerging from
the gravel. Those of the Harrison River rapids (Fraser system) were mentioned above; another such stock occurs in Gingit Creek (Nass system). Fry of most stocks move downstream out of a lake tributary into a lake. Those hatched in a lake outlet, however, mostly move upstream into the lake, sometimes stemming a fairly swift current, as at Chilko Lake. At Little River below Shuswap Lake many or most of the newly-emerged fry go downstream to Little Shuswap Lake, then swim back up to Shuswap Lake later in the spring or in early summer. At Morris Creek they first go downstream, then swim through a few hundred meters of practically slack water, then turn upstream into the Harrison River at the head of the rapids and proceed into Harrison Lake.

LAKE LIFE, GROWTH, AGE
AT MIGRATION

A very large majority of the sockeye in British Columbia enter lakes soon after emerging from the redds. In each lake the young fish disperse throughout the zone of suitable temperatures. Thus, sockeye are not found near shore in lakes with warm surface waters (e.g., Cultus, Shuswap), while they are distributed generally in lakes with cooler surface waters (e.g., Owikeno, Bear). Very small fry have been found to contain foods (ostracods and Bosmina) that suggest they live near the bottom, or in shallow water, for a few days after entering the lake. Subsequently they contain pelagic foods almost exclusively (Cyclops, Diaptomus, Daphnia, etc.). Besides plankton crustaceans, they eat a small quantity of midge pupae and even terrestrial insects in some lakes. The seasonal course of freshwater growth has been charted for two years in Cultus Lake (Ricker and Foerster, 1948). Little is known of their distribution in winter, or whether growth ceases completely during the coldest weather.

In a small lake of fairly uniform depth, such as Lakelse, young sockeye are rather evenly distributed over its open-water area. In the large Babine-Nilkitkwa system, the different parts of these lakes have variable densities of young sockeye, mainly because of the non-uniform distribution of spawning adults throughout the system. Fingerling densities were estimated as from 30 to 2,720 per acre in different parts of Babine Lake on August 21–25, 1957, and up to 5,750 per acre in Nilkitkwa (Johnson, 1958).

At Cultus and Shuswap Lakes it has been observed that in years of dominant populations the supply of sockeye salmon crustacean food organisms becomes markedly reduced, as compared with years of smaller populations (Ricker, 1937; Ward, 1957). A similar relation between numbers of sockeye and abundance of plankton has been observed at Babine Lake, both in comparing different years and in comparing different basins of the lake in the same year (Johnson, 1961). In all three lakes, sockeye of really dense populations grew to only half or less of the average individual weight of those of the smaller populations by the end of their year in the lake. However, factors other than density also affect growth rate, and there are some rather consistent differences between lakes in this respect. The range of average sizes of yearling migrant smolts in eight lakes is shown in Table I.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Length</th>
<th>Weight</th>
<th>Two-year-olds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cultus (experimental years omitted)</td>
<td>68–92</td>
<td>3.1–8.1</td>
<td>106–131</td>
</tr>
<tr>
<td>Chilko</td>
<td>70–82</td>
<td>3.3–5.1</td>
<td>101–113</td>
</tr>
<tr>
<td>Harrison</td>
<td>95–106</td>
<td>9.2</td>
<td></td>
</tr>
<tr>
<td>Shuswap (1902 line)</td>
<td>63–64</td>
<td>2.0–2.6</td>
<td></td>
</tr>
<tr>
<td>Shuswap (1903 line)</td>
<td>85</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Owikeno (1914–16)</td>
<td>59–60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Owikeno (1956)</td>
<td>61</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>Babine (mixture of several stocks)</td>
<td></td>
<td>4.8–5.7</td>
<td></td>
</tr>
<tr>
<td>Bear</td>
<td></td>
<td>7.8–9.6</td>
<td></td>
</tr>
<tr>
<td>Lakelse</td>
<td></td>
<td>4.6–6.3</td>
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</tbody>
</table>

In addition, Clutter and Whitesel (1956) tabulate observations for yearling smolts from the following runs in one year only: Francois (103 mm, 12.0 g), Horsefly (126 mm, 19.5 g), Lillooet (77 mm, 4.5 g), Stuart (95 mm, 8.4 g).

Although most B. C. sockeye spend only one growing season in fresh water, in a few lakes two growing seasons are more common—for example, Morice and Alastair Lakes of the Skeena system, Meziadin Lake of the Nass, and Port John Lake on the central coast. In a lake where one freshwater year is the rule, the size of the 2-year-old smolts is of course much greater than that of the yearling smolts (Table I). However, growth to the first annulus averages considerably more among yearling migrants than it does among the part of the brood that stays in the lake for a second year, although there is much overlap (Foerster, 1944; Killick and Clemens, 1963).

Comparing different stocks, there is no simple relation between first-year size and average age of migration, either inverse or direct. As shown in Table I, the Owikeno sockeye have the smallest first-year growth of any in British Columbia, but there
are very few 2-year-old smolts among them. Likewise, the 1902 line at Shuswap consistently produces very small smolts, and again there are very few second-year migrants. On the other hand, among the runs whose first-year circuli count is tabulated by Killick and Clemens (1963, p. 38), those of Taseko, Chilko and Birkenhead grow fairly slowly, and their second-year smolts are moderately numerous.

Within stocks, similarly, differences in freshwater growth rate observed to date in British Columbia bear no recognizable relation to percentage production of second-year migrants. At Cultus and Shuswap Lakes, years of very dense populations were marked by much slower than average first-year growth but did not produce a significantly greater than average percentage of second-year migrants (Ricker and Foerster, 1948; Henry, 1961). The reverse situation has been studied on Atnaquak Island in Alaska, where sockeye of a stock that produces mainly 2-year-old smolts were transplanted to a lake barren of fish. At the end of the first growing season in the new environment the fish were eight to ten times as heavy as those in their native home, but the majority nevertheless stayed for a second year in fresh water (Alaska Department of Fish and Game, 1953-1956). On the other hand, some but not all Bristol Bay sockeye are reported to have substantially increased percentages of 2-year-old smolts in years of really large populations and slow fingerling growth (personal communication from O. A. Mathisen).

It is fairly certain that hereditability plays a large role in determining age of downstream migration in at least one British Columbia stock: a large fraction of 2-year-old smolts was produced at Cultus Lake by the small year classes of 1928 and 1932, whose young made rapid first-year growth in the lake but whose parents were predominantly second-year migrants (Ricker, 1950). Of course, it is likely that in some of the lakes where growth is slow because food is scarce or temperatures are low the sockeye stock will be naturally selected for two years of lake life, so as to get its smolts to sea at a size that permits reasonable survival.

The means used by smolts to find the outlet of a lake during their seaward migration have been studied at several lakes, particularly Babine (Johnson and Groot, 1963). At least three methods of orientation are used: visual landmarks, time-compensated orientation to the day or night sky, and an unidentified mechanism or mechanisms which become apparent in the absence of these two—for example during heavy cloud cover (FRB 1963 Annual Report).

In some lakes a small part of the sea-run sockeye progeny do not migrate to sea, but become "residual" sockeye that remain in the lake. The ramifications of this situation are interesting, but they concern anadromous sockeye production only slightly (Ricker, 1938; 1959).

**FRESHWATER MORTALITY AND SURVIVAL RATES**

Table II gives the survival rates, from eggs in females to smolts in migration, obtained at three sites in British Columbia. The average for Babine Lake

<table>
<thead>
<tr>
<th>Locality</th>
<th>Cultus Lake</th>
<th>Babine Lake</th>
<th>Lakelse Lake</th>
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<tbody>
<tr>
<td>Brood</td>
<td>Survival (%)</td>
<td>Brood</td>
<td>Survival (%)</td>
</tr>
<tr>
<td>year</td>
<td></td>
<td>year</td>
<td></td>
</tr>
<tr>
<td>1925</td>
<td>1.06</td>
<td>1926</td>
<td>1.01</td>
</tr>
<tr>
<td>1926</td>
<td>1.06</td>
<td>1927</td>
<td>1.01</td>
</tr>
<tr>
<td>1930</td>
<td>3.22</td>
<td>1938</td>
<td>3.70</td>
</tr>
<tr>
<td>1931</td>
<td>2.20</td>
<td>1960</td>
<td>4.24</td>
</tr>
<tr>
<td>Average</td>
<td>1.87</td>
<td>3.77</td>
<td></td>
</tr>
<tr>
<td>Geometric mean</td>
<td>1.66</td>
<td>3.47</td>
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</tbody>
</table>

Table II. Estimates of freshwater percentage survival from eggs in females to migrant smolts, under natural conditions. Data are from Foerster (1936b, 1938a) and from unpublished data (Biological Station, Nanaimo); see also summaries of preliminary data by Parker (1962) and Ricker (1962).

exceeds that for Cultus and Lakelse. One reason, possibly, is that the good survival at Babine during 1956-57 coincided with a time of smaller than usual numbers of spawners (resulting from damage to the parents of the 1955-57 runs caused by a rock slide in 1951-52—Godfrey et al., 1954; 1956). At Port John Lake, average survival to smolt stage is about 3%, and since the great majority of the smolts have spent two years in the lake, the survival rate per month is much greater than for the lakes of Table II (J. G. Hunter, unpublished). Preliminary survival figures for Chilko Lake are larger than any of these, averaging 8% (IPSFC Annual Report for 1959).

Among the causes of freshwater mortality, important roles are played by mortality of eggs and fry in the reds and by consumption of young fish by predators in the lake. Mortality of eggs and fry in the reds has been studied quantitatively at several sites, giving average survival rates of 15% (6-Mile Creek, Babine Lake), 12% (Scully Creek and Williams Creek, Lakelse Lake), and 9% (Tally Creek, Port John Lake); the extreme range for individual years was from 3% to 19%. In the Skeena system, years of greater rainfall
favour better egg survival, as suggested by a positive correlation with the resulting catch from the year class in question (Brett, 1950).

After they take up lake life, much of the mortality of young sockeye results from their being consumed by predaceous fishes, while an unknown percentage is eaten by diving birds (Ricker, 1941; and unpublished studies at Babine Lake). At Cultus Lake the lake survival rate of young sockeye increased abruptly following removal of the greater part of the large squawfish (*Ptychocheilus oregonensis*) and Dolly Varden char (*Salvelinus malma*) from the lake (Foerster and Ricker, 1942). Survival rate with natural propagation increased to 7.81% under predator control as compared with the previous 1.87% average (Table II), and there were comparable increases in years when other propagation methods were used.

The seasonal course of mortality from the early fry stage onward was estimated in Cultus Lake by means of a marking experiment (Foerster, 1938b): mortality was heavy during the first month, and gradually declined thereafter. The absolute rate was about 20% per month in summer but the fish in question were somewhat larger than the general lake stock. Quantitative sampling of the young fish at dusk suggested that at Lakelse Lake in 1961 the average summer mortality rate was 72% per month, but this seems unusually high. Similar studies indicated that summer mortality rates for the various basins of Babine Lake varied over a broad range (roughly 10–70% per month) and appear to be directly related to density and inversely related to the size of the fingerlings present (Johnson, unpublished).

For Lakelse the figure 20.9% was obtained for the overall survival from fry to yearling smolt stage of the 1953 year class. At Port John Lake, where a large majority of smolts spend two years in the lake, estimates of natural fry-to-smolt survival lie in the remarkably high range of 30% to 60%, and even fin-clipped fry yielded 10% smolts two years later. At Chilko Lake preliminary estimates of survival from fry to smolts (mostly yearlings) average 53% (IPSFC Annual Report for 1959).

The relation between size of spawning stock and resulting production of adult sockeye has been graphed for the dominant late Shuswap run (Ricker, 1954, from IPSFC Annual Reports), and for the Skeena system (Shepard and Withler, 1958). A similar relation between spawners and fry production has been plotted for Chilko Lake (IPSFC Annual Report for 1962). These graphs indicate the order of size of spawning escapement that will provide the greatest yield under present conditions.

**OCEAN LIFE, GROWTH, TIME SPENT AT SEA**

After reaching salt water, sockeye seem to move out into the offshore pelagic environment rather quickly. At any rate, they are not seen regularly near shore for several weeks during the summer, in the way young pink and chum salmon are. They appear in experimental pelagic gillnet catches during their second year in the ocean, especially toward autumn, being then about 25–30 cm in fork length.

In the early spring of their third year in the ocean, sockeye can be taken abundantly by gillnet or longline in the Gulf of Alaska. The relative abundance of sockeye across the Gulf has been mapped (Neave *et al.*, 1963); of course, stocks from Alaska and a few from Washington are fairly well mixed with those from British Columbia. In 1961 there was a marked concentration of sockeye near the middle of the Gulf of Alaska in April and May. Distribution changes as the season advances and the maturing fish sort themselves out and go to their respective rivers at the appropriate time for each stock involved.

Length of ocean life varies from river to river and from stock to stock within a river. The Osoyoos stock (Columbia River) has an unusually large percentage of sockeye with 1+ ocean years, including many females, although 2+ is the most common type there. All the more northern stocks have only a small percentage of fish with 1+ ocean years, and these are almost exclusively males. Killick and Clemens (1963, pp. 25–40) summarize the information for the Fraser stocks. On the Fraser as a whole, 2+ ocean years is the rule, although in Pitt Lake 3+ is most common, and three other lower-river stocks have a fairly large representation of 3+ fish. Upper Fraser stocks have very few sockeye with 3+ ocean years. In other major rivers, 2+ and 3+ ocean years both occur abundantly. At Rivers Inlet and the Skeena the two types are about equally numerous on the average, but the percentage of each type produced by any particular year class varies greatly (Godfrey, 1958). It has not yet been determined whether these variations reflect mainly (1) the varying abundance of individual stocks within the run, or (2) changes in abundance of the two ocean ages within individual stocks. J. McDonald has evidence (unpublished) that rapid growth of the Babine sockeye of 1+ ocean age is associated with a greater percentage of 2+ ocean fish among the older ages. This seems more consistent with hypothesis (2), but because of the numerous stocks that make up the Babine run, hypothesis (1) is not yet excluded. By means of a series of correlations, Godfrey (1958) demonstrated
an effect of heredity on length of time spent in the ocean (2+ or 3+ years) among Sockeye and Sockeye Inlet sockeye, but he could neither confirm nor reject a possible effect of environment.

Both hereditary and environmental influences have been definitely shown to affect the percentage production of so-called precocious male sockeye (1+ ocean years). The former has been demonstrated at Shuswap Lake, where there is a pronounced regression of the percentage of 1+ males in a given year class upon the percentage of 1+ males among the parental stock. Parental populations having 90% or more 1+ males produce progeny generations averaging about 60% 1+ males, whereas parental populations with less than 5% 1+ males average about 15% of this type among their male progeny (Ricker, 1960 from IPSFC Annual Reports). Environmental influence is suggested at Chilko, and apparently in certain other Fraser stocks also, where the relative abundance of sockeye with 1+ ocean years is related to the rate of growth of the stock during its first year at sea. For Chilko, an increase in average scale increment by 10% during the first ocean year is accompanied by an increase in the fraction of 1+ males (from about 0.5% to about 1.6% of the number of 2+ males of the same year class).

MARINE MORTALITY AND SURVIVAL

Estimates of marine mortality commonly include freshwater mortality during downstream migration of smolts, and sometimes the normal mortality during upstream migration of such adults as escape the fishery. That is, survival rate is measured as the ratio of enumerated adults (catch plus fish reaching the nursery lake) to the number of smolts estimated at the time they leave the lake. To date there have been no quantitative estimates of losses during the downstream migration of smolts, although predation has been observed during this period. Table III gives estimates of marine survival, in this inclusive sense.

One of the more important factors affecting survival rate after leaving the lake is the size of the smolts. This was demonstrated for Cultus Lake sockeye by Foerster (1954); Ricker (1962, fig. 1) summarized available information for three British Columbia stocks and three from elsewhere. The average increase in survival rate between smolts 7 cm in fork length and those 14 cm is from about 4% to 30%. In British Columbia, few stocks have smolts that average more than 10 cm in length and at that size the average survival rate is about 15%.

At Chilko Lake there is not much variation in size of smolts from year to year, and no relation of survival to smolt size has yet been demonstrated there. However, Henry (1961, p. 72) obtained a good correlation between first-year ocean growth (as indicated by number of scale circuli) and percentage survival over six years of observation, omitting two other years for reasons described below. An 11% increase in number of circuli corresponded to a 220% increase in survival, from 5% to 16%. It seems unlikely that so small a difference in growth, as such, could cause so large an increase in survival, although the growth figures are for the survivors only, and those that died might have been more affected by the difference in growth rate. Henry suggests that the primary relationship may be between survival and food available at the very beginning of ocean life, so that a deficiency of food for a few weeks could cause serious mortality.

<table>
<thead>
<tr>
<th>Babine Lake</th>
<th>Chilko Lake</th>
<th>Cultus Lake</th>
<th>Port John Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smolt year</td>
<td>Survival (%)</td>
<td>Smolt year</td>
<td>Survival (%)</td>
</tr>
<tr>
<td>1958</td>
<td>2.60</td>
<td>1951</td>
<td>18.26</td>
</tr>
<tr>
<td>1959</td>
<td>6.43</td>
<td>1952</td>
<td>15.21</td>
</tr>
<tr>
<td>1960</td>
<td>1.03</td>
<td>1953</td>
<td>6.03</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>1954</td>
<td>7.09</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>1955</td>
<td>6.63</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>1956</td>
<td>20.80</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>1957</td>
<td>15.10</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>3.35</strong></td>
<td><strong>12.73</strong></td>
<td><strong>7.31</strong></td>
</tr>
<tr>
<td><strong>Geometric mean</strong></td>
<td><strong>2.58</strong></td>
<td><strong>11.40</strong></td>
<td><strong>7.31</strong></td>
</tr>
</tbody>
</table>
but still have only a rather small effect on the total first-year growth of the survivors.

The Shuswap Lake sockeye of the 1902 line have in recent years produced some very large adult runs from spawning populations of only moderately large size. The best of these was the brood year 1954, when about 2.1 million spawners produced 19 million adult fish which is about 0.5% overall survival from potential egg deposition to returning adult. Because there is no estimate of the number of smolts, there is no direct information on whether this represents exceptionally good lake survival or exceptionally good sea survival, or both. However, Henry (1961) found that the Chilko Lake smolts (see Table III) which migrated downstream in 1952 and 1956—two dominant years at Shuswap—had exceptionally good survival, being respectively 2.5 and 3.6 times what was expected on the basis of their first-year ocean growth.

Finally, there has been a relation between marine survival of Chilko smolts and Fraser River discharge "at the time the migrants enter the estuary" (IPSC Annual Report for 1961, fig. 2A), such that increasing the discharge by 65% was accompanied by an increase in survival from about 4% to 18%. Thus, marine survival of the Chilko stock has been related to three things: discharge, early sea growth, and size of the Shuswap stock. There is, however, considerable correlation among these three factors in the series available to date, and only further study can reveal to what degree each plays an active role.

No studies have yet been made of downstream and marine mortality among sockeye stocks that customarily go to sea as fry; at Harrison River, at least, such fry are larger than is usual for sockeye. Attempts have been made to send fry to sea artificially. At Hooknose Creek newly-emerged fry were released directly above the brackish estuary of the creek in several years. Very few adults survived and returned to the same stream—far fewer than survived from the same number of fry which were allowed to spend the customary time in a lake before going to sea (J. G. Hunter, unpublished).

INSHORE AND UPSTREAM MIGRATION

Maturing sockeye appear in coastal waters from about May and the runs continue into October. Largest catches are made in July through September. Each stock of sockeye has its own characteristic time of appearance. In southern British Columbia the earliest are those to lakes tributary to Alberni Inlet (Barkley Sound). These come into fresh water mostly in the latter half of May or early June, enter the lakes and remain there until spawning time in the fall. On the Fraser, the now extinct Alouette Lake run was of this early type (Foerster, 1931). Today the earliest Fraser runs go far upriver, to Forfar Creek and adjacent streams in the Stuart Lake system, the peak of their migration in the central San Juan Islands area being about July 8. These are followed in succession by Bowron (July 18), Horseshy (July 26), Upper Pitt River (July 30), Chilko (August 2), Raft River (August 2), Seymour River (August 3), Stellako (August 4), Birkenhead (August 10), Weaver Creek (August 16), Lower Adams River (August 22) and Cultus Lake (August 24)—as shown by scale identification (Henry, 1961), by tagging adult sockeye (Killick, 1955; Verhoeven and Davidoff, 1962), and by fin-clipping the smolts (Foerster, 1936; 1937). This timing is also summarized by Killick and Clemens (1963, pp. 3, 72) for Sooke, where the order differs slightly.

In the Skeena River gillnet fishery, the runs to Alastair and Lakelse Lakes are the earliest of any size, and reach their peaks in late June. These are followed by runs to Morice Lake, and to streams tributary to Babine (July), and Babine Lake outlet (early August). Rivers Inlet runs enter fresh water during August.

Because of variable lengths of upstream migration and variable times spent by the fish in lakes before maturity, times of entry of sockeye into fresh water are only loosely correlated with times of spawning, although a positive correlation does exist.

Although modal time of upstream migration is reasonably constant for each race, there is some variation from year to year, some of which seems to have a systematic pattern. Gilhousen (1960, p. 26) found that in the dominant 1902 line of the late Shuswap race the peak times tend to be later in years of large populations, the difference between the largest and smallest observed being about 15 days. He also notes that successive generations of a given line tend to be alternately later and earlier, by a matter of five days or so, in the late Shuswap and Chilko stocks at least.

Not much is known in detail about the routes by which sockeye approach the coast and enter their home rivers. Sockeye tagged in southern Alaska have been taken in the Nass and Skeena fisheries, and the fraction of these stocks taken in Alaska apparently varies from year to year (Shepard et al., 1962). It has long been known that the majority of sockeye of the Fraser River runs enter the Strait of Georgia by way of the Strait of Juan de Fuca, but that some, usually less than 10%, come in through Johnstone Strait. In 1958 an exceptionally large fraction of the run passed through Johnstone Strait, amount-
ing to at least 23\%, more likely 37\% (Gilhousen, 1960). In the same year ocean temperatures within 100 miles of the coast were exceptionally warm (Tully et al., 1960). Similar unusually large percentages appear to have come through Johnstone Strait at times about 11 years apart (Gilhousen, 1960, p. 20). Another characteristic of the migration of the dominant line of late Shuswap sockeye is a variable period of delay off the mouth of the Fraser River. However, a long delay seems to be the exception rather than the rule among sockeye stocks.

On their journey upstream some sockeye stocks may encounter unfavourably high temperatures. In the upper Fraser River these have occurred several times, causing direct mortality in the river or spawning failure after reaching the spawning grounds (IPSFC Annual Report for 1961, p. 18). Columbia River sockeye also may suffer mortality on the way up the river (Sylvester, 1938).

The detailed behaviour of adult sockeye when moving upriver and passing moderate obstacles has been studied and photographed by Ellis (1962). Sustained swimming capacity in migration, for sockeye of the Great Central Lake run, has been determined as about 0.9 meters per second at 18°C to 20°C, but of course much greater speeds are attained in short bursts (unpublished data of J. R. Brett and colleagues). Other studies have defined the energy required to maintain this activity (as well as the analogous performance of fingerlings and smolts).

After reaching a lake, sockeye of some stocks spend up to three or four months in the lake before spawning. Some mortality occurs during this time, but its magnitude is difficult to estimate. Over several years at Port John Lake, 20–30\% of the adults that were counted into the lake did not enter the tributary spawning streams (lake spawning is negligible here). However, it is difficult to know how much of this loss is truly natural mortality. Many fish that escape the fishery carry net marks, and these marks have been shown to reduce their viability.

Physical obstacles to upstream migration may be natural or artificial, temporary or permanent. Natural changes in land elevation and river base-levels, within the last few thousand years, have cut off sockeye runs to such lakes as Kootenay in the Columbia drainage, Ootsa and Stave in the Fraser drainage. In these lakes kokanee persist as a reminder of the former sockeye populations. Artificial obstacles include the dams which have exterminated the runs to Coquitlam, Alouette and the two Arrow Lakes.

Temporary or incomplete barriers to migration have had serious effects on certain stocks. Best known are the Fraser River obstructions, particularly rock dumped into Hell's Gate in 1913 and early 1914, which blocked a very large percentage of sockeye ascending in those years and reduced the dominant 1901 line to inconsiderable proportions. Although much of the rock was removed early in 1915, the Gate remained a difficult spot for fish to navigate, especially at intermediate water levels (Thompson, 1945). Fishways were opened for use in 1943–46, which made the passage very much easier at this spot (Jackson, 1950). Another major sockeye obstruction resulted from a natural rock slide on the Babine River in 1951. It blocked about two-thirds of the sockeye ascending that river in 1951 and 1952, following which the rock was successfully removed (Godfrey et al., 1954; 1956). At an earlier period, a dam at the outlet of Quesnel Lake caused serious mortality before a satisfactory fishway was built. A number of natural waterfalls and rapids in various British Columbia rivers that were partial or seasonal obstacles to sockeye migration have also been improved by construction of fishways (Clay, 1961).

CHANGES IN ABUNDANCE

Although Columbia River sockeye have never been commercially harvested in Canada, three Canadian lakes used to contribute substantially to the runs on that river. Of these, the Upper and Lower Arrow Lakes lost their stocks when the Grand Coulee dam was built. Osoyoos Lake still contains a moderate run, and an artificial spawning channel helps to support it.

Among sockeye stocks at least partly harvested in British Columbia, the largest are those of the Fraser River. This system contains about 70\% of the area of the province's available lake nurseries, and the yield from it is shared with the United States on an almost 50/50 basis. The Fraser catches (4-year average) were high and fairly steady from the 1890's to 1916, following which they collapsed mainly as a result of the rock slides at Hell's Gate in 1913–14. Some stocks began to recover during the late 1920's and 1930's, and recovery was accelerated in the late 1940's after fishways were built at Hell's Gate and elsewhere, and special fishing closures protected the most depleted stocks. In 1951–54, total annual sockeye production in "Conventional waters" averaged 32.4 million pounds (Canada, 16.2 million), or almost 50\% of the level of the early years of the century. Since then, although the average catch has declined somewhat, there have been substantial

1 Ed. note: 1937 convention between Canada and the United States for the protection, preservation and extension of the sockeye and pink (since 1961) salmon fisheries in the Fraser River system.
increases in spawning runs in critical regions, setting the stage for new advances.

The Skeena River sockeye pack declined gradually from the time of World War I, until during the 1930's when it was about 60% of the original average level of seven million pounds a year. There was some recovery following reduction of rate of utilization in the 1940's, so that 75% of the early 5-year average level of catch was taken in 1951-54. Following this the effects of the 1952 rock slide became apparent, which had seriously reduced spawning for two years. Although these effects have now been overcome, Canadian catch-plus-escapement has not yet exceeded the 1951-54 level. Recent data (Shepard et al., 1962) indicate that considerable numbers of sockeye bound for the Skeena (and Nass) may be intercepted by fishing gear in Alaska in some years.

The Rivers Inlet run is fished by Canadian nets only. Its catch today equals that of the Skeena, and has averaged about five million pounds a year since early in the century. Most of the smaller runs are not known to have exhibited important trends in abundance; their present combined average yield is eight million pounds a year.

Efforts have been made for many years to refill the niche once occupied by certain extinct stocks of the upper Fraser, by transplanting eyed eggs from other streams. The task is a difficult one, but there have been some successes, while in other areas the issue is still in doubt. The recent experiments are summarized in the 1962 Annual Report of the International Pacific Salmon Fisheries Commission (pp. 23-25).

PREDICTION OF ABUNDANCE AND SIZE OF SOCKEYE

Predictions of the abundance of individual sockeye stocks can be made by several methods: (1) from the size of the catch in parental years; (2) from estimates of parental spawning stocks and spawning conditions; (3) from estimates of the numbers and the size of smolts in the seaward migrations that will contribute to the run being predicted; (4) from the abundance of maturing 3rd-year fish (usually estimated on the spawning grounds) plus the observed ratio of 3rd-year to older fish for the stock in question; (5) from surveys made on the high seas prior to inshore migration.

The order of the above listing is, in general, that of increasing reliability. This is because sources of variation in survival rate are successively eliminated the closer one gets to the time of appearance of the fish in coastal waters. However, method No. 5, which should be best from this point of view, presents considerable technical difficulty because of mixture of stocks, and it is still under development. In method No. 4 much of the variability in even the ocean survival rate is eliminated, but it is not everywhere useful either because of difficulty in estimating the numbers of the 3rd-year fish, or because of unresolved year-to-year variation in the ratio of 3rd-year to older fish. Part of the variation is associated with early growth rate in the sea and an adjustment for this can sometimes be made (IPSFC Annual Report for 1961, fig. 28). With method No. 3 accuracy can be improved in the special circumstances of the Chilko stock (and possibly other Fraser stocks) by taking into consideration the abundance of the Shuswap stock of the year in question—as described above. Likewise, method No. 2 can be improved on the Fraser by applying the observed relation between marine survival and river discharge.

Predictions for a particular year, made by methods 1-4, are most accurate in areas where the great majority of fish mature at a single age, notably the Fraser River. In the stocks of central and northern British Columbia there is much variation between broods in respect to time spent at sea, and this introduces an added variable into any prediction equation. Ocean age is usually either 2+ or 3+ years, and up to 70% or more of the returning adults from a given smolt migration may be in the one category or in the other, in different years. Some success to date has been achieved with the Babine stocks in predicting relative return after 2+ and 3+ ocean years from the length of the fish of 1+ ocean years from the same year class; the larger the latter the ratio of 2+ to 3+ years among the older adults (J. McDonald, unpublished). Unfortunately, at Babine the fraction of 1+ fish produced by a given smolt migration is quite variable, and hence of little value for predicting the total size of its year class, so forecasts of the abundance of these runs are not yet very precise.

Longline fishing carried out systematically in the early part of the year may provide a basis for predicting the abundance of runs returning to spawn later in the year. Attempts are underway to correlate the total abundance of maturing sockeye in the eastern North Pacific each year with information on distribution and relative abundance in the ocean from longlining in April and May. The age and detailed growth history of the ocean-caught fish is indicated on their scales, and since these differ in various ways from stock to stock, there is a prospect of predicting the abundance of at least some of the larger stocks in Canada and the United States (Bilton and Shepard, 1963). There is also partial geographical separation
of the runs to different major rivers. However, the method has not yet been fully standardized or adequately tested.

Prediction of the individual size of the sockeye in a given year can also be of value. Early-season sampling at sea can probably give information concerning the size of the fish to be expected in most of the major stocks, though details have not yet been worked out.

Failing this, or supplementing this, it has been found (Killick and Clemens, 1963, p. 107) that the deviations from long-term mean size of each of the various Fraser River sockeye races tends to be consistent within a given year, so that after some fish of the first stocks have been taken and measured, the size of the fish in the remaining stocks can be accurately predicted for that season.

This method cannot be used over any wider geographical area, however. Killick and Clemens found only minor and non-significant agreement in fish size between the Fraser and three more northern British Columbia sockeye runs ($r = 0.03-0.23$). There is a significant correlation between sizes of sockeye of the Nass and Skeena Rivers ($r = 0.487$), and between those of the Skeena River and Rivers Inlet ($r = 0.567$), but neither of these is large enough to be useful for prediction and in any event there is not enough difference in timing of these runs to make such a prediction of practical value.

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