https://doi.org/10.17895/ices.pub.9205

B.

NORTH AMERICAN ATLANTIC SALMON

REPORTER:

A. G. HUNTSMAN

The fluctuations in fish abundance and their causes is the central fisheries problem and as such is well worthy of forming the subject of common study on the two sides of the Atlantic. Success in this co-operative effort will depend largely upon frequent comparison of results which should prove most stimulating to further endeavour.

Prof. SIEDLECKI's fine summary of knowledge concerning the European salmon for the International Council for the Exploration of the Sea (Rapp. et Proc.-Verb., Vol. 101, 1936) provides an excellent basis for an exchange of information, of which I wish to take advantage.

Statistics.

On the western side of the Atlantic the salmon occur in all of the three countries, the United States, Canada and Newfoundland. Formerly salmon were taken in the *New England States* from Cape Cod north, but they have been eliminated from virtually all the rivers, with the exception of the Penobscot in Maine. The amount taken in recent years has been in the neighbourhood of 20,000 lb. annually. Statistics have been secured periodically and more frequently in the last decade. Salmon occur in the rivers all along the *Canadian coast* and from 3,000,000 to 6,500,000 lb. are taken annually. Detailed statistics (in Reports, Fisheries, 1878 to 1916, and Fisheries Statistics 1917 to date) for the various districts have been collected quite consistently for nearly seventy years and generally throughout this period the fish have been sufficiently valuable to ensure comparative steadiness in fishing effort, in comparison with the condition for many other species of fishes. As a result the statistics can be held to have considerable biological value as representing comparative abundance.

In *Newfoundland waters* salmon occur generally, all around the island itself and on the Labrador coast all the way to Hudson strait, though rare beyond Hopedale. Statistics are available only for the last decade or so and for the most part only as totals (Annual Reports, Fisheries). Amounts have varied greatly with changing conditions, a big export trade in chilled salmon having developed since 1926. From 3,000,000 to 6,000,000 lb. have been taken annually in recent years.

Life History and Year-Classes.

The study of the relative abundance of year-classes began in relation to purely marine fishes, notably the herring and the cod, with a comparatively simple life history, passed through under comparatively uniform conditions. It is fairly obvious that the salmon requires somewhat special treatment since it spends around half its life in fresh-water streams and the other half in the sea, and since the bulk of the fish available for capture are maturing virgin fish, owing to the fact that but a small proportion survives for a second spawning. SIEDLECKI reports that the age analyses of European salmon show that the individuals bred in one year form the most important part of the population only once. While age analyses of North American salmon are as yet comparatively few (MENZIES 1925, CALDERWOOD 1927, PHELPS and BELDING 1930, HUNTSMAN 1931, LINDSAY and THOMPSON 1932, BLAIR 1935), and while they show that in quite a few places the proportions of re-spawners are higher than reported for European waters, it may be confidently affirmed that on the whole the fish born in a given year form the most abundant class only during one year. If this is true, there is no hope of assessing the relative abundance of successive year-classes merely by ascertaining their relative proportions in samples taken in successive years, which method has been so fruitful in the study of herring and cod. It will be necessary to combine the results of age analysis with the data of the fisheries.

SIEDLECKI has remarked on the uniformity in the constitution of the shoals of salmon in the south-eastern Baltic and also of the salmon in the Scottish rivers, one, or at the most, two year-classes predominating every year. It seems probable that this condition will be found to occur in general in North-American waters, and, in so far as it exists, it will be feasible to deal satisfactorily with the fisheries' statistics by themselves as being fairly indicative of year-class abundance. It will be necessary, however, to realize that a particular year-class is certain to affect by its abundance or scarcity the statistics for all the years in which it contributes to the fishermen's catches. Only by age analysis is it possible to determine the extent of such contribution and the particular year-class principally responsible for the fishermen's catch in a given season and locality.

The abrupt change in the life of the salmon at the smolt stage that is involved in descent to the sea, and the comparatively very rapid growth in the sea make it desirable to define two types of year-classes. In addition to the usual one based upon the year of birth, which may be distinctively designated the birth year-class, there seems a need for some purposes of referring the fish to the year of descent to the sea as smolt. This I will designate the smolt year-class. Grilse will thus all belong to the smolt year-class of the preceding year, small salmon to that of the second preceding year and big salmon to that of the third preceding year.

Populations versus Races.

The year-classes of salmon that are most abundant vary with the locality, each local population tending to be characterized by having particular age-groups in about the same relative proportions year after year. Following the classical work of HEINCKE on the herring, local peculiarities in the various species of fishes have commonly been considered to be racial. However, proof has been lacking that the peculiarities were racial rather than the effect of the environment on each generation. Evidence is accumulating that the characters considered racial may be produced directly by the environment, whether they be body proportions, numbers of vertebrae, type of growth-rate or seasonal behaviour in spawning or migrating. Owing to their at least moderately precise relation to particular rivers, the populations of salmon have to a greater extent than those of purely marine species, such as herring and cod, the necessary isolation to develop geographical races. Nevertheless there is evidence that mixing can readily occur since kelts from one river have been shown to enter other rivers and even traverse the entire range of the species from the bay of Fundy to northern Labrador.

For North American rivers the salmon exhibit differences similar to those for European rivers, upon which SIEDLECKI following MENZIES relies as evidence "that in every river exists a special race". In Canadian waters the greatest difference is shown between the rivers at the head of the bay of Fundy and those of Chaleur bay, particularly the Cascapedia. Those of the former locality have two-year smolts and practically all, females as well as males, spawn as grilse; those of the latter have a very considerable proportion of three and four-year smolts and spawn as two-sea-year and three-sea-year salmon, grilse being usually few and practically all males. Also the former enter the river only very late, while the latter enter at the beginning of the season. The greater value of large fish that run early, coupled with a belief in races, caused the Canadian government to incur heavy expense in breeding from such fish. To test the value of such procedure an experiment was begun in 1932 and completed in 1936, in which fry from Chaleur bay salmon (early-running large fish) were planted in East Apple river in the middle of the head of the bay of Fundy, where the salmon run only late and are practically all small. They were carefully followed through their life history and compared with the local fish (Ann. Rep. Biol. Board, 1932—1936) and quite failed to show any appreciable difference from the local fish either in time spent in fresh water, in time spent in salt water, in season of return to river, or in size at maturity. So far as it goes, this experiment, planned as a crucial one, has negatived the theory of races.

On the other hand, differences between the local populations are seen more and more clearly as related to the character of the environment. Similarly to the British, Norwegian and Swedish salmon, the river life of Newfoundland and Labrador salmon is somewhat progressively longer going northward (LINDSAY and THOMPSON), as is also that of New Brunswick and Gaspé salmon (CALDERWOOD; PHELPS and BELDING; HUNTSMAN). Similarly there is progressively slower sea growth of the Newfoundland and Labrador salmon going from south to north (LINDSAY and THOMPSON). Also evidence is accumulating that the number of years spent in the sea before return varies inversely with the temperature of the sea and with the ease of return. The prevailing south-west winds of summer concentrate the surface water at the heads of the bay of Fundy and of the large bays of the south coast of Newfoundland, giving a high sea temperature and taking the fish to the coast near the river mouths, thus making return easy. These are the districts where the salmon return predominantly as grilse.

North American salmon return to the rivers in one locality or another in all months of the year. Season of return is seemingly dependent upon the temperature of the sea being sufficiently high and upon the occurrence of satisfactory freshets in the rivers. The western part of the outer coast of Nova Scotia alone has salmon entering the rivers during the winter months, this in correspondence with the occurrence of the highest sea temperatures in winter. The Saint John river of New Brunswick has an extensive varied watershed, with a large discharge, and its salmon enter in all months, except the three with the lowest temperatures in the sea (bay of Fundy). The Apple river at the head of the bay of Fundy, with lower winter and higher summer sea temperatures, and with small discharge from spring to fall, has its salmon entering only in the fall near spawning time.

Periodic Scarcity and smolt Year-Classes.

An angler (GRISWOLD, 1929) was the first to notice a scarcity occurring every nine years in the salmon of the Grand Cascapedia and Restigouche rivers, and as well in the commercial catches of Quebec and New Brunswick. PHELPS and BELDING (1931) confirmed this for the Restigouche angling catch in a very thorough analysis, finding the period to be nine or ten years. Independently HUNTSMAN (1931) discovered it as occurring generally in the commercial catches and as far back as statistics have been collected. The average length of the period was determined as 9·6 years in close agreement with a periodicity in abundance of various fur-bearing animals (snowshoe rabbit, lynx, marten etc.) of the interior of Canada. The ruffed grouse (*Bonasa*) of the interior shows a similar period.

GRISWOLD, following an idea advanced by OTTO PETTERSSON, has attributed the scarcity to a nine-year tidal cycle, but no sufficiently good agreement is seen with either tidal or sun-spot cycles. The years of greatest scarcity of salmon were found to vary in somewhat orderly fashion with the district, the head of the bay of Fundy, the main part of New Brunswick and the Gaspé peninsula in order from south to north having the scarcity progressively later with yearly intervals. For this and another reason I placed the "action of the unknown factor in the river period several years before its effect is apparent in the catches."

If we relate life history to year of occurrence of the scarcity, the matter will be more clear. The scarcity varies in degree and in distinctness from period to period, as well as from one district to another. The most pronounced scarcity was about 1880. In Figure 1 are given the courses of the commercial catches through that time of scarcity in two portions of each of the three districts mentioned above and the scarcity is brought into relation with the life history of the local salmon of each district, the principal birth year-classes (B) and smolt year-classes (S) involved in the scarcity being shown. From south to north the mid-years of scarcity are 1879, 1880 ($1880^1/_2$) and 1881; the corresponding smolt year-classes are 1878, 1878 and 1878—9; and the corresponding birth year-classes are 1876, 1875—6 and 1874—6. The year of scarcity is progressively later, the smolt year-class coincides or possibly becomes later, while the birth year-class rather definitely becomes earlier. Any common cause will then operate between birth and the smolt stage, that is, in the river life, and nearer the smolt stage. The unknown factor can best be considered as acting upon a particular smolt year-class, previous to its descent to the sea.

Study of the river life has revealed the chief mortality of the larger parr as due to fish-eating birds (belted kingfisher and American merganser), which nest and rear their young along the salmon streams (WHITE, 1936, 1937). These birds are largely unable to secure food when the streams are swollen and murky, as in rainy weather. I have accordingly explored the possibility of dry summers being responsible for increased mortality of the large parr (of the smolt year-classes related to the times of salmon scarcity) by restricting their habitat and exposing them to attack by birds. The last scarcity

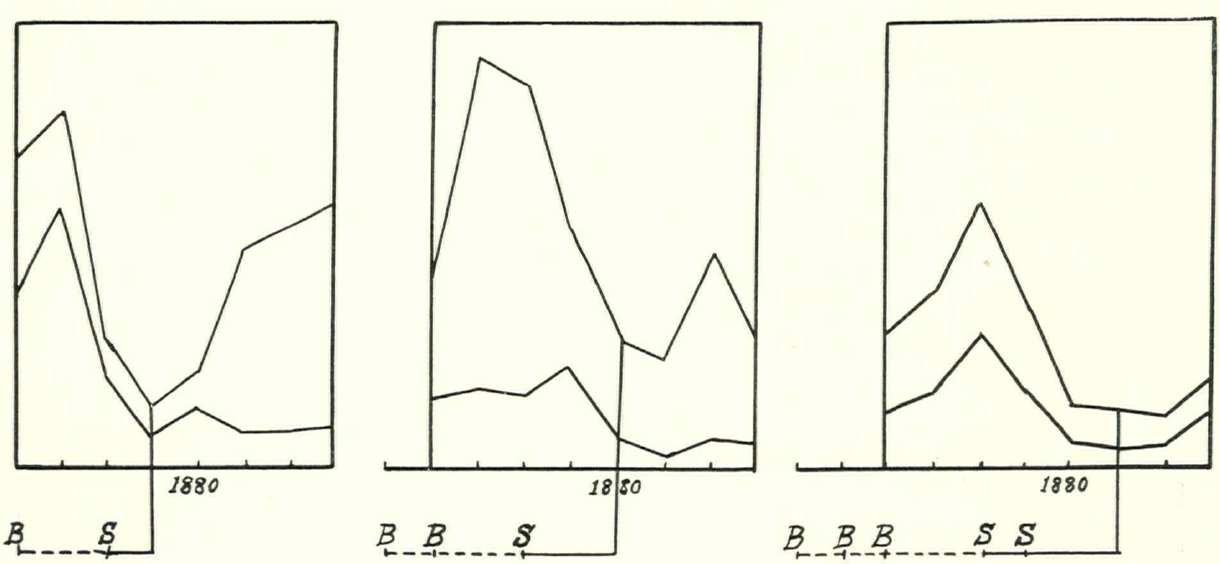

Fig. 1. Courses of salmon fisheries from 1876 to 1883. Left: head of bay of Fundy, Minas basin above and Petitcodise river below. Middle: eastern New Brunswick, Richibucto river below and Miramichi river above. Right: Gaspé peninsula, Bonaventure county above and Gaspé county below. Life histories of local salmon indicated for year-classes involved in mid-year of scarcity; B, birth year-class and S, smolt year-class.

affected chiefly the 1926 and 1927 smolt year-classes and in correspondence with this the summers of 1923 to 1926 prove to have been dry, as shown by both rainfall and river discharge records. Pronounced scarcity of salmon is thus seen to follow with the proper interval, a succession of dry summers.

The records of neither rainfall nor river discharge are sufficiently comprehensive to give a very adequate basis for relating dry summers to salmon scarcity. Nevertheless, a fairly good correlation is evident in Figure 2, which gives the courses of the Miramichi salmon fishery for the past sixty-eight years and of the summer rainfall at Chatham near the mouth of the river, whose watershed is broad and of rather uniform slope. It is indicated how the most pronounced times of scarcity, 1880—81, 1919—20 and 1928—9, were preceded at the proper interval by periods of four successive dry summers.

It may be seen in Figure 2 that there are short periods of one to three dry summers intervening between those which cause the periodic scarcity of salmon. When most definite, which was around 1900, they made the periodic scarcity less evident, tending to produce intervening scarcities.

It is to be noted that, while no successive scarcities at nine- or ten-year intervals are to be seen in SIEDLECKI's Diagram 3 of the salmon fishery results of seven European countries over a thirteen-year period, there is some evidence of scarcities of salmon in the Wye, as well as for the British and Norwegian fisheries in general during the last twenty years (HUTTON 1934) and in the Tyne for a fifty-year period (STORROW 1932), corresponding to the most pronounced ones for Canadian waters. A common primary factor (movements of air masses?) probably acts, though in somewhat different fashion, on both sides of the Atlantic.

Dominance of Year-Classes.

Since for salmon each birth year-class dominates the catch for only one year, the dominance of one year-class over others is to be seen only by comparing the catches for successive years. As the direct effect of a dominant year-class is so short, interest in it

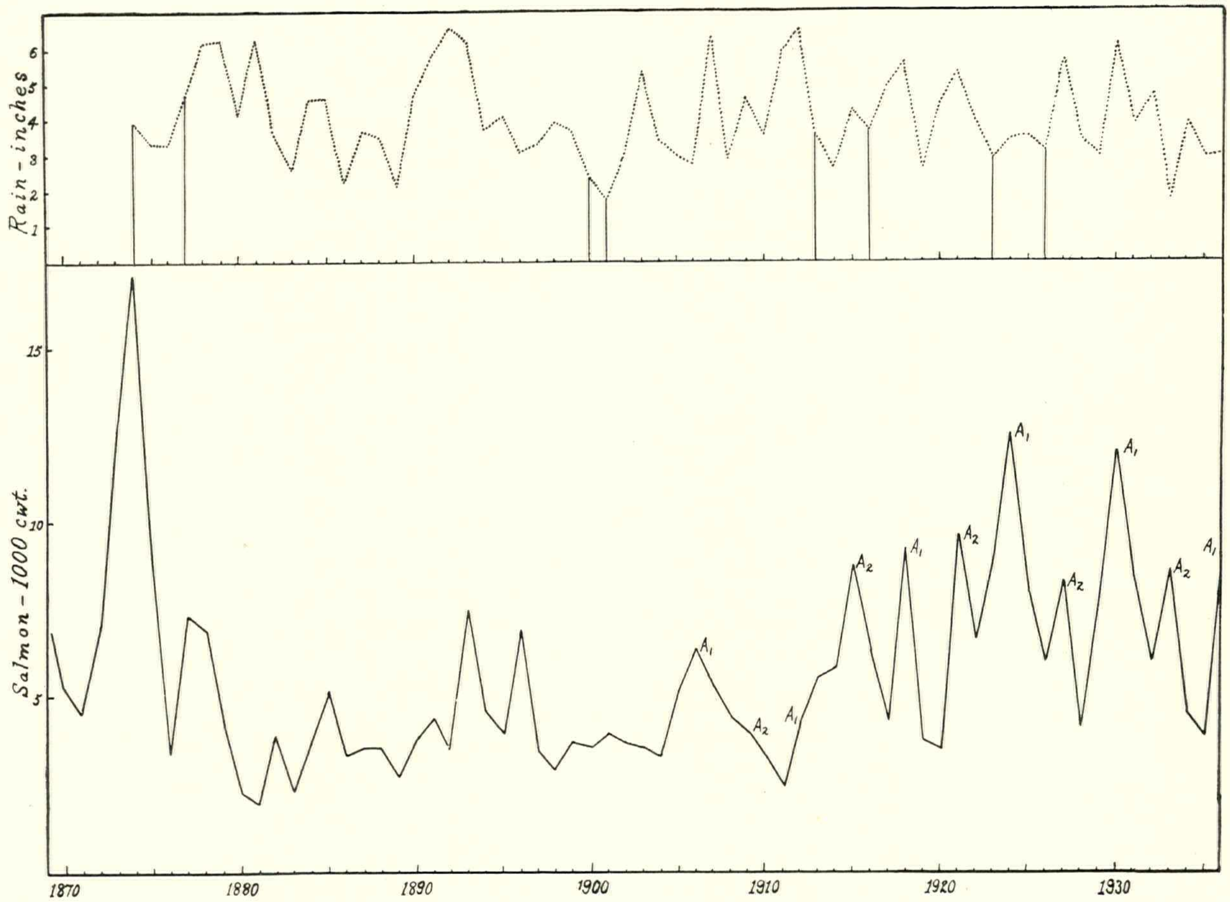

Fig. 2. Course of Miramichi salmon fishery from 1870 to 1936. Mean rainfall for July—August at Chatham from 1874 to 1936.

will lie chiefly in knowing its cause or in following its indirect effect in producing as offspring another dominant year-class. An outstanding example of such effect was the Pacific sockeye salmon (*Oncorhynchus nerka*) of the Fraser river, which continued to be extremely abundant every four years (the length of life of the majority of the fish) for a considerable period until a rockslide in 1914 prevented them from ascending the river.

SIEDLECKI finds evidence of good salmon years following each other at six-year intervals in most of the European countries studied. The Canadian statistics (HUNTSMAN, 1931) show cycles of from four to eight years in different districts in agreement with the length of life of the majority of the local fish or of the oldest to be in significant numbers. These lines of dominant generations or year-classes derived

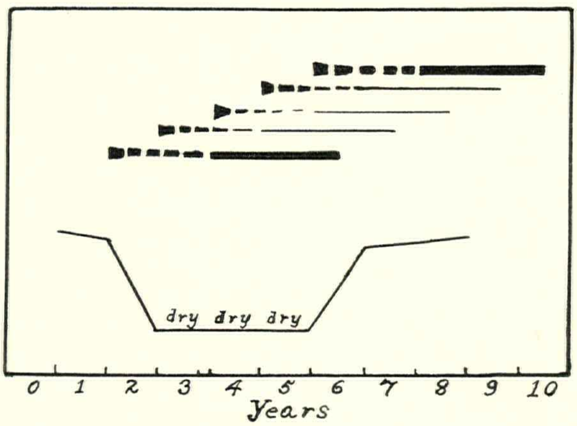

Fig. 3. Effect of three successive dry years on the numbers of salmon in successive year-classes. River life shown as an interrupted line, sea life as a continued line.

successively from each other were recognised as continuing for longer or shorter periods, depending upon the mathematical relationship between the length of each generation and the length (9·6 years) of the period between successive scarcities. These scarcities were seen each as favouring a particular birth year-class in definite relation to the unfavourable effect upon the given smolt year-class that was scarce in the adult stage. In the simplest example, the five-year cycle of the Saint John river, dominance was found to be transferred every twenty-five years from one line of generations to that immediately preceding it as the result of the favourable influence of the scarcity factor being so transferred in that time ($5 \times 5 = 25$; $9{\cdot}6 \times 2^1/_2 = 24$, that is one year less). For other cycles the relationship was more complicated and its effects less clear.

Now that a cause is seen for the periodic scarcity, the way in which it produces an unfavourable effect upon one year-class and a favourable effect upon another can be shown. Figure 3 shows how a succession of three dry summers may reduce the stock of successive year-classes, supposing that each at birth is equally abundant. The smolt year-class immediately following the end of the dry period shows the most pronounced adverse effect. The birth year-class immediately following the dry period will be the first to be quite free from the latter's influence and for two-year smolts is definitely the one favoured. Three-year smolts, however, may be sufficiently favoured by having their last two river years without drought, to maintain, or perhaps acquire, dominance.

Maintenance of dominance seems definitely effected by the dominant year-class keeping down the numbers of the following year-classes, particularly during river life. In experiments and in nature. salmon parr have been found to eat fry. An exceptionally distinct instance of rather long continued dominance of lines of generations is to be seen in the Miramichi during the period from 1915 to the present (Figure 2). The reason in part seems to be that the prevalent smolt age (three years) is exactly half the full age (six years) at spawning of the main part of the fish. Two lines of dominant generations are thus able to alternate without interfering with each other. That designated A_1, has been throughout more successful than the other, A_2, and of each there have been already four generations, without any indication of the condition disappearing. Its origin may be referred to the two very dry seasons of 1900 and 1901, which acted over the whole Miramichi watershed in favouring the birth year-class of 1901, as shown by the large catch of salmon in 1906. Such synchronization of all parts of the river system is necessary if the phenomenon is to be apparent. The force that produces it can also destroy it, and the dry periods of 1905—6 and 1908—9, coming at the wrong time in the cycle, at least prevented dominance of year-class 1904 in 1909 and of year-class 1907 in 1912. However, beginning with 1910, every third year has been relatively dry, which has been the right time in the cycle to ensure its maintenance. Thus rainfall is seen to be the outstanding influence in determining fluctuations in the abundance of Atlantic salmon in Canadian waters.