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THE GEOGRAPHIC DISTRIBUTION AND ENVIRONMENTAL LIMITATIONS OF THE PACIFIC SALMON (GENUS ONCORHYNCHUS)

By FREDERICK A. DAVIDSON and SAMUEL J. HUTCHINSON

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THE GEOGRAPHIC DISTRIBUTION AND ENVIRONMENTAL LIMITATIONS OF THE PACIFIC SALMON (GENUS ONCORHYNCHUS)¹

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INTRODUCTION

There are five principal species of Pacific salmon, all of which are classified in the genus Oncorhynchus. They are chinook, or quinnat (O. tschawytscha); sockeye, or red (O. nerka); coho, or silver (O. kisutch); pink, or humpback (O. gorbuscha); and chum, or dog (O. keta). These fish are anadromous; they spend part of their lives in the sea and part in the streams. The eggs are deposited in gravel beds in the streams and lakes during the summer and fall and hatch out during the following spring months. The fry remain in fresh water for varying lengths of time, depending upon the species, but all eventually migrate to the sea where they make over 95 percent of their growth. Upon attaining maturity in the sea the adults return to the streams where they spawn and die. The studies of Gilbert (1913), Snyder (1921-24), Rich and Holmes (1928), Pritchard (1933), Davidson (1934), and Foerster (1936), on the life histories of the Pacific salmon show that they have a pronounced homing instinct and in general return to their parent streams to spawn.

The locations and depths at which the salmon feed while in the sea have not been definitely determined. Catches of chinook and coho salmon are made by the troll fishery as far as 100 miles offshore and at depths as great as 90 fathoms. Commercial and Government vessels operating in Alaskan waters have reported the presence of the salmon even farther out to sea. The continental shelf along the Pacific coast of North America averages less than 40 miles in width, thus it is evident

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that the feeding salmon frequent the waters of the open sea as well as those of the immediate coast. Bigelow and Welsh (1924), in discussing the habits of the pink salmon transplanted in the coastal streams of Maine, state that:

During their first months in salt water the fry linger near the mouths of the home streams, where they feed chiefly on copepods and other small crustaceans, or pteropods, and on insects that drift down stream with the current, and occasionally on fish fry. After they are 5 or 6 inches long they move out into deep water, and very little is known of their habits and wanderings thereafter until they reappear on the coast as adults to breed.

Since the Pacific salmon live alternately in two distinctly different environments, fresh-water and marine, their geographic distribution is influenced by the limiting factors in each environment. This study was made for the purpose of determining the geographic distribution of the salmon and gaining knowledge of the environmental limitations to their occurrence.

GEOGRAPHIC DISTRIBUTION

NATIVE

The native distribution of the Pacific salmon is confined almost entirely to the temperate and arctic waters of the North Pacific. They are found in the streams along both the North American and Asiatic coast lines within similar geographic limits. On the North American continent O'Malley (1920), Cobb (1930), and Evermann and Clark (1931), give Monterey Bay, 70 miles south of San Francisco, Calif., as the southernmost limit of their common occurrence, although a few specimens have been taken at odd times as far south as the Ventura River, Calif. From here O'Malley (1920), Gilbert (1922), and Cobb (1930), report them inhabiting the coastal streams, in varying degrees of abundance, northward along the continent to Kotzebue Sound in Bering Strait.

Dymond and Vladykov (1933) give the probable occurrence of chum salmon in the Mackenzie River of northern Canada and the definite occurrence of this species in the Lena River of northern Siberia. These rivers flow into the Arctic Ocean. From the Lena River, the northernmost point of occurrence on the Asiatic continent, they are found to a limited extent southeastward along the Arctic shores to the Chukchee Peninsula in Bering Strait. From the Anadir River just south of the Chukchee Peninsula all species, according to Caldwell (1916), Lebedev (1920), Russian Economic Monthly (1920), Baievsky (1926), and Pravdin (1932), are present in varying degrees of abundance in the coastal streams southward along the continent to the Amur River. The range of the pink and chum salmon extends farther southward to the Tumen River in northern Korea which is given by Mori (1933) as the southernmost occurrence of these salmon.

All species other than the chinook salmon, according to Jordan, Tanaka, and Snyder (1913), Tanaka (1931), Handa (1933), Oshima (1933), and Tokuhisa and Ito (1933), are found in the coastal streams of Sakhalin, Hokkaido, and Kurile Islands and the northern shore of Honshu Island. The range of the pink and chum salmon extends farther southward on Honshu Island to the Tonegawa River near Cape Inuboye on the eastern shore, and to the Omonogawa River near Akita on the western shore. A report has also been received through correspondence from Dr. Fujita of the Hokkaido Imperial University, of the limited occurrence of the chum salmon

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along the west shore of Honshu Island as far south as the Joganjigawa River. The geographic distribution of the Pacific salmon on both the North American and Asiatic continents is shown in figures 1, 2, 3, and 4.

FOREIGN

In 1872 the United States Commission of Fish and Fisheries, later the United States Bureau of Fisheries, established an egg-taking station (Baird Station, Calif.) on a tributary of the Sacramento River for the sole purpose of collecting chinook or quinnat salmon eggs for transplantation in foreign waters.² This station formed the source of supply of millions of these eggs which were shipped to the Atlantic Coast States and to countries in many parts of the world. With the development of the Pacific coast, additional egg-taking stations were established in Oregon and Washington by the Bureau of Fisheries. Following 1900, these stations furnished eggs and young of the other species of the Pacific salmon that were likewise shipped to various parts of the world for transplantation. The introduction of salmon into foreign waters was continued actively through 1930. The number, by species of eggs and young shipped, and the States and foreign countries receiving them, are given by 10-year periods in tables 1 and 2.3 Only those eggs and young that were transplanted in coastal streams for the purpose of developing natural sea-run populations are included in these tables. All transplantations in inland waters for the establishment of landlocked populations have been omitted.

	Periods and number distributed						
Localities of distribution	ļ	1	1		1	<u> </u>	Total
_	1872-1880	1881-1890	1891-1900	1901-1910	1911-1920	19211930	
STATES							
Connecticut	1, 410, 000						1, 410, 000
Delaware	1 31,400						31, 400
Georgia	79,000		40,000				119,000
Louisiana.	43,400 215,000		3, 450, 000	100,000			43, 400 3, 765, 000
Maine.	4, 445, 000	500,000	10,000	100,000	22,500	139, 700	5, 117, 200
Maryland Massachusetts	640,000	0.0,000	400	10, 100	117, 500	100,100	768,000
Mississippi	43, 400						43, 400
		50,000	50,000	567,960	184, 710	720, 000	2, 122, 670
	2,800,000	550,000		1			3, 350, 000
			7, 007, 400	114, 240	985, 550		9, 172, 190
	1, 150, 000						1, 150, 000
		150,000	100,000		10,000		2,805,000
							340, 000
	1 200,000	300,000	304,070	50, 750	192.000		500, 000 516, 820
	1 40,000		7,000	45,000	122,000		1, 322, 000
Virginia	1, 270, 000		7,000	10,000			1, 044, 000
COUNTRIES					•		
Argentina.				1,058,000			1,058,000
	100,000	50,000					150,000
	915,000	500,000					1, 415, 000
						200,000	200,000
England	150,000						150,000
	1 355,000	300,000	395,000				1,053,000
Germany	830,000		125,000				955, 000

 TABLE 1.—Foreign distribution of Pacific salmon eggs and young
 [By 10-year periods, 1872-1930]

CHINOOK SALMON (O. tschawytscha)

² For history of establishment and early development of this station see Stone (1878).

³ For more detailed information on the data reported in these tables see United States Bureau of Fisheries reports on the propagation and distribution of food fishes (1871 to 1935).

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TABLE 1.—Foreign distribution of Pacific salmon eggs and young—Continued CHINOOK SALMON (O. tschawytscha)-Continued

	Periods and number distributed						
Localities of distribution	1872-1880	1881-1890	1891-1900	1901-1910	1911-1920	19211930	Total
COUNTRIES-continued							
Hawaii	30, 000		50,000			99, 000	129, 000 50, 000
Italy Mexico 1		50,000	50,000 50,000				50,000 100,000
Netherlands (Holland)	1, 175, 000		775, 000	1, 600, 000		400, 000	900, 000 3, 550, 000
Nicaragua ¹ Norway ²		25,000	20,000	404 000			20,000
Tasmania	20, 835, 200	2, 475, 000	12, 523, 870	494,000	1, 442, 260	1, 558, 700	494,000

No information was secured on the disposition of these shipments.
This shipment was refused in Norway and sent to one of the northern Europe countries (see Aagaard, 1930).

TABLE 2.—Foreign distribution of Pacific salmon eggs and young

[By 10-year periods, 1901-30]

SOCKEYE SALMON (O. nerka)

	Periods a	_			
Localities of distribution	1901~1910	1911-1920	1921-1930	Total	
STATE STATE		17, 500		17, 500	
COUNTRIES Argentina	397, 500	30, 700, 000		397, 500 30, 700, 000	
Chile			314,000	314,000	
Total	397, 500	30, 717, 500	314,000	31, 429, 000	

PINK SALMON (O. gorbuscha)

		1		
STATES Maryland	991, 141	27, 482, 826 15, 000	1, 722, 340 6, 350	30, 196, 307 21, 350 18, 000
New Jersey		18,000	,	18,000
New York		10,000		2,000
Total.	993, 141	27, 515, 826	1, 728, 690	30, 237, 657
	1	((-

COHO SALMON (O. kisutch)

STATES Maryland	1, 317, 387	69, 800	12,000	$^{1,\ 387,\ 187}_{12,\ 000}$
New Hampshire	315, 000 5, 000 350, 000 5, 800	8, 500 41, 875	5, 600	$\begin{array}{c} 1, 387, 187 \\ 12,000 \\ 315,000 \\ 13,500 \\ 355,600 \\ 47,675 \end{array}$
COUNTRIES Argentina Chile Total	377, 180 225, 040 2, 595, 407	120, 175	17, 600	377, 180 225, 040 2, 733, 182

In this study a transplantation has been considered successful only when it survived to the extent of producing subsequent sea-run populations with migratory and spawning habits characteristic of the species in the native distribution. In other words, the mere hatching of the eggs or rearing of the young under landlocked conditions has not been considered as indicating the successful introduction of the species.

In order to secure complete and authentic information concerning the ultimate success or failure of the attempts to introduce these salmon into foreign waters, letters requesting this information were sent to the fish commissions and scientific fishery societies of the States and countries listed in tables 1 and 2. These letters, together with the replies that were received, are on file in the office of the Bureau of Fisheries, Washington, D. C.

The history to date of the attempts to introduce the Pacific salmon in foreign waters is not very encouraging. Only 1 State and 3 countries reported the development of natural sea-run populations in their coastal streams. The others reported that negative results or, to the best of their knowledge, no natural populations had developed from the transplantations. Maine is the only State in which natural runs of salmon have been definitely established. According to Bigelow and Welsh (1924), pink-salmon fry planted in the Dennys, Medomak, St. Georges, St. Croix, Pembroke, and Penobscot Rivers survived and developed populations having characteristics similar to those in their native distribution. However, adverse sentiment of the residents in this region has greatly contributed to their present lack of abundance.

Dymond, Hart, and Pritchard (1929) report the establishment of sea-run populations of chinook salmon in the St. John River, New Brunswick, and the Port Credit River, Ontario. These salmon have been taken in the St. John River by the hundreds and vary in weight up to 8 pounds. They are also quite plentiful in the Port Credit River where fish weighing up to 30 pounds have been taken. It is assumed that the Port Credit salmon migrate to and from the sea by way of Lake Ontario and the St. Lawrence River. Other streams tributary to these waters may maintain small runs of chinooks which to date have not been identified. The streams and coastal regions of Maine, New Brunswick, and Ontario are the only foreign waters on the North American continent in which natural populations of the Pacific salmon have been established.

Transplantations of Pacific salmon have been made in both Chile and Argentina in South America. Chile reports the presence of either coho or sockeye salmon running in the San Pedro River in the southern part of the country. Legislation has been promulgated by the Chilean Government which prohibits commercial fishing for these salmon until 1940. In Argentina none of the transplantations to date, according to Marini (1936), have been successful. However, final information in Chile as well as Argentina is not available owing to the lack of adequate scientific surveys throughout the sparsely inhabited regions in which the salmon have been introduced.

All European waters stocked with Pacific salmon, according to Bottemanne (1879), Behr (1882), Aagaard (1930), and correspondence received, have been unfavorable to the survival of the species. The countries acknowledged receiving the eggs but none could cite a single instance in which adult salmon had returned from the sea to spawn. Various methods of propagation were used but none proved successful. From the many unsuccessful attempts at introducing the Pacific salmon into European waters it may be concluded that the establishment of sea-run populations in them is very improbable. However, Finland is at present importing chinook eggs with the hope of establishing natural runs of this species. The possibility of successfully introducing the Pacific salmon into the coastal waters of Norway may never be determined since the Norwegian Government has always, with thanks, declined offers to plant these salmon in their waters.

Attempts to establish natural runs of Pacific salmon in the waters of Hawaii have been unsuccessful. The eggs were hatched successfully and the young reared to the migrant stage before planting but no adults have ever returned to the streams. Although recent shipments of eggs have been made to Hawaii it is not deemed advisable to continue this practice.

The waters of Australia and Tasmania, according to McCulloch (1927), Tasmania Fisheries Commission (1933 and 1935), and correspondence received, have all been unfavorable to the introduction of Pacific salmon. Many attempts have been made to establish natural runs in the coastal streams but all have been unsuccessful. No particular difficulty was encountered in hatching the eggs and rearing the young to the migrant stage, see Baird (1878), but no adults ever returned from the numerous plantings in the streams. The Tasmania Fisheries Commission (1933) states that in the confined waters of the Great Lake, chinook salmon thrive and grow rapidly to support a flourishing sport fishery. Other than to maintain landlocked populations for sport fishing it is considered that attempts to stock the streams for the establishment of sea-run populations would not justify the necessary expenditure of eggs and effort.

The introduction of the Pacific salmon into the waters of New Zealand has been successful only on South Island and even there, only within definite limits. The streams in which sea-run populations have been established, and those which have been stocked consistently with salmon but which have never developed sea-run populations, are shown in figure 5. The well-defined distributional range of the salmon on South Island will be explained in the discussion on environmental limitations to their occurrence.

The many attempts to establish runs of chinook salmon in New Zealand prior to 1900 were all unsuccessful. During this period the eggs and young were divided into small consignments and distributed to many rivers throughout the colony. Following the year 1900 this practice was discontinued and only one river system, the Waitaki, was stocked. In 1905 many adult salmon returned to this river to spawn, thus establishing the first natural run of chinooks on South Island. This run survived and through natural and artificial propagation has been spread to other rivers on the island.

Although the Bureau of Fisheries records show only the shipment of chinook salmon stock to New Zealand, shipments of sockeye salmon stock were also received from another source according to W. L. Calderwood (Fishery Board for Scotland, Salmon Fisheries, 1924, No. 2) who states:

In operating with Sockeye, some curious results have appeared. Eggs were imported in 1902, and adult specimens of this fish began to appear in 1907. Dead examples were first noticed, and

these were found to have spawned and died in the usual way. A brief note in the last official yearbook states that "a number exist in Lake Ohau, having acquired a landlocked habit. These fish run up creeks at the head of the lake and spawn there every season [year] in March and April."

Hatcheries have been constructed, and each year there is an abundant egg take. The eggs are hatched and the fry used to restock the parent stream or are planted in other streams on the island. Eggs collected and eyed in New Zealand have been sent to Tasmania for transplantation. Of the four successful foreign regions in the world to develop sea-run populations, New Zealand has been the most outstanding to date. The authors wish to acknowledge the kind cooperation of A. E. Hefford, Chief Inspector of Fisheries, New Zealand, in furnishing them with complete information concerning the history of the transplantation and development of the chinook salmon in the waters of New Zealand. Pictures of the chinook salmon and the streams in which they spawn, also scenes of the sport and commercial fisheries, are shown in figures 6-9.

The sea-run populations of Pacific salmon that have been established in both Chile and New Zealand have adjusted their life cycle to the change in occurrence of the seasons in the Southern Hemisphere. The spawning migrations of these salmon occur in January, February and March which are the seasonal equivalents of July, August, and September in the Northern Hemisphere. The foreign regions into which the Pacific salmon have been introduced are shown in figures 1–4. The solid black areas indicate the regions in which the salmon have been transplanted successfully, and the dots show the regions in which transplantations failed.

ENVIRONMENTAL LIMITATIONS TO OCCURRENCE

During the first years of the introduction of the Pacific salmon into foreign waters very little was known concerning the proper methods for shipping or propagating these species. The failure of many transplantations to survive during this early period may have been due to excessive mortality in the eggs or unsuccessful rearing and planting of the young. However, with the improvement in fish-cultural methods the mortality during shipment and early propagation declined in importance so that following the year 1900 a high percentage of eggs shipped survived and the young were reared and planted successfully. This information was secured mainly through correspondence received from the various States and countries participating in this work. In view of this fact it is believed that the ultimate success or failure of these latter transplantations was dependent, to a high degree, upon the favorable or unfavorable influences existing in the foreign waters in which they were made.

NORTH PACIFIC REGION

The environmental components of the fresh-water habitats in the native distribution of the salmon, which appear to be definite limiting factors, are temperature of water and character of stream bed. The degree of tolerance to temperature is much greater for the adults than for the eggs and young. The temperatures of the streams in which the salmon have been found spawning ranged from slightly above 0° to a maximum of 21°C. This range of temperature has been determined from recording thermographs operated yearly in Alaskan streams by the Bureau of Fisheries, and from stream surveys made by the Bureau's biologists, in both the Pacific Coast States and

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Alaska. Records taken at the Bureau's hatcheries on the Pacific coast also show the range of temperature tolerated by the adult salmon. Adult salmon have also been found migrating through estuaries, and streams fed by hot springs, whose temperatures were as high as 27° C. The California Department of Public Works (1931) reports a temperature range of 16° to 26° C. in the lower reaches of the Sacramento River during the months the salmon are migrating into the river. In July and August it is not uncommon for the temperature of the lower estuary of the river to hover for days around 24° C. Although the temperature of the streams in the native range may fluctuate at a high level during the spawning period it rapidly decreases with the onset of the winter season during which time the eggs pass through the incubation period. The studies of Donaldson (1936) have shown that the eggs can withstand temperature below 4° and above 11° C. for short periods of time but that the optimum lies between these limits. The mortality was extreme in eggs maintained constantly at temperatures below 4° or above 11° C. After hatching, the optimum range of temperature in fresh water, which controls the rate of growth and survival of the young, shifts to a level of 13° to 17° C. Constant temperatures above 17° C. retarded growth and increased the mortality of the young and at 20° C. the mortality was excessive. Constant temperatures below 13° C. retarded growth and at 3° mortality was excessive. In view of the results from these studies it may be assumed that temperature in the fresh-water habitats becomes a limiting factor in the early developmental period of the salmon.

The eggs of the Pacific salmon are spawned free and, being of a higher specific gravity than water, sink to the bottom. Eggs of this type require a medium that will hold and cover them for protection and at the same time permit the free flow of wellaerated water for incubation. Such a medium is found in clean gravel beds, or in pockets among rocks, but not in mud or sand. The former conditions are invariably found in all of the native fresh-water habitats of the salmon. Spawning in the streams is usually confined to the comparatively shallow areas where the current is swift, and in the lakes to areas provided with flowing water from seepage or surface drainage. In the Pacific Coast States deforestation, agricultural developments, and mining operations have, in some areas, produced excessive erosion of the watersheds. This has always resulted in the silting of the streams and the subsequent destruction of their salmon populations. An excessive amount of silt in the water influences the normal respiration of the salmon and destroys the eggs by suffocating them with a blanket of mud. The character of the stream bed, therefore, becomes a very definite limiting factor in the distribution of the Pacific salmon.

The environmental components of the marine habitats in the native distribution, which appear to be limiting factors, are ocean currents and associated temperatures and salinities (salt content). The mean directional drifts in the North Pacific from June through September are shown in figure 1. This period was selected because it is during these months that the salmon are known to be definitely migrating in the ocean. The adults are migrating from the open ocean to the streams to spawn and the young are migrating seaward from the streams. The currents in figure 1 were determined from the limits of the directional drifts during this period as given by Dall (1880), Schulz (1911), McEwen (1912), Marmer (1926), Hatai and Kokubo (1928), Uda and Okamoto (1930), Uda (1931 and 1933), Schumacher (1932), Zeusler (1934), Schott (1935), Thompson and Van Cleve (1936), and Wüst (1936). Since it is known that the salmon mature in the offshore waters and begin their spawning migration there, more emphasis was laid upon the general movements in these waters than upon the local and complex shiftings along the immediate shores.

The Japan, or Kuroshio Current; Bering Sea, or Oyashio Current; Okhotsk Sea Current, and other less perceptible currents form an intricate maze of water move-



FIGURE 1.—The geographic distribution of the Pacific salmon and the directional drifts of ocean currents during the spawning migration period of the salmon. The bars indicate the native distribution of the salmon, the solid black areas indicate the regions in which the salmon have been transplanted successfully, and the dots indicate the regions in which the transplantations were unsuccessful. The directional drifts of the ocean currents in the Northern Hemisphere are means calculated from the monthly averages of June, July, August, and September, and in the Southern Hemisphere are means calculated from the monthly averages of January, February, and March. A, Japan or Kuroshio Current and West Wind Drift; B, North Equatorial Current; C, Okhotsk Sea Current; D, Bering Sea, Oyashio or East Kamchatka Current; E, West Australian Current; F, East Australian Current; H, South Equatorial Current; J, South Pacific Current and Antarctic Drift; K, Peruvian or Humboldt Current; N, East Greenland Current; P, Labrador Current; R, Irminger Current; S, Gulf Stream or Florida Current; T, Canaries Current; U, North Equatorial Current; V, South Equatorial Current; W, Brazil Current; X, Benguela Current; Y, Falkland Current; Z, South Atlantic Current and Antarctic Drift.

ments in the North Pacific. The Japan Current has the most outstanding circulation. It is a tropical drift originating from the North Equatorial Current off the east shore of the Philippine Islands. From here it flows northward and strikes the shores of the Islands of Japan. Part is forced to the west of the islands and enters the Japan Sea. The bulk, however, closely follows the east shore of Honshu Island to Cape Inuboye just east of Tokyo. Here it is met by the Bering Sea Current of arctic origin which flows southward along the island. The southern limit of occurrence of the Pacific salmon on this shore of the island is at Cape Inuboye near the point of confluence of these currents. A similar relation exists between the distributional limits of the salmon along the shores of the Japan Sea and the confluence of the Japan and Okhotsk Sea Current. The Okhotsk Sea Current, which is of arctic nature, flows southward along the continent and is dissipated in the waters off the northern shore of Korea. The Tumen River, which marks the distributional boundary of the salmon in this region, flows into these waters. After entering the Japan Sea the Okhotsk Sea Current influences the Japan Current flowing northward along the west coast of Honshu The salmon are found on this shore of the island as far south as the Jogan-Island. jigawa River which is near the southern point of confluence of these currents. There is a definite correlation between the distribution of the salmon and the influence of ocean currents in these regions.

The Japan Current, after encountering the Bering Sea Current off the east coast of Honshu Island, takes a northeasterly course across the Pacific to form a fan-shaped divergence commonly known as the West Wind Drift. During this course it is greatly tempered. Upon nearing the coast of North America, off Vancouver Island, it divides into two branches; the northern branch forming the Alaska Current and the southern branch the California Current. According to McEwen (1912), an upwelling of cold waters along the coasts of Oregon and California influences the California Current as it flows southward. The southern distribution of the salmon on the North American continent appears to be correlated with the region dominated by this cold upwelling current.

The adult salmon are subjected to the influence of surface temperatures in the ocean during their spawning migration to the streams, for it is definitely known that they frequent the surface waters at this time. Accordingly a study was made of the mean surface temperatures from June through September in relation to the distribution The mean temperatures rather than the limits of temperature during of the salmon. this period were used owing to the continuous character of the spawning migration which in some areas extends over the entire period from June through September. The mean surface temperatures in the North Pacific during this period are given by the isotherms in figure 2. These isotherms were determined from the seasonal and monthly surface temperatures given by Dall (1880), Rosse (1881), McEwen (1912), Uda and Okamoto (1930), Uda (1931), Kokubo (1932), Zeusler (1934), and Schott (1935). Along the coasts of Japan and Korea the mean 20° C. isotherm touches the shores near the southern limits of the native range of the salmon. According to Uda and Okamoto (1930), and Uda (1931), the surface temperatures of these coastal waters range from 15° C. in June to approximately 24° in September. On the North American continent the mean 15° C. isotherm touches the shores of California below the southern limits in the distribution of the salmon. According to Schott (1935), the surface waters along the coast of California have an annual range of only 3° C.

The northern distribution of the salmon on both continents is bounded by the mean 5° C. isotherm. However, the salmon migrating to and from the Mackenzie, Lena, and other streams tributary to the Arctic Ocean may be subjected to surface temperatures only a few degrees above freezing. It is, therefore, possible that the

surface temperatures tolerated by the salmon during their spawning and seaward migrations approximate 0° C. at the minimum and are in the vicinity of 20° C. at the maximum.

Information thus far available indicates that the Pacific salmon, during their sojourn in the sea, frequent the subsurface waters to depths of 200 meters. Hence, the mean annual temperatures at 200 meters were studied in relation to the distribution of the salmon. These mean temperatures for the North Pacific are shown by the



FIGURE 2.—The geographic distribution of the Pacific salmon and the mean surface ocean temperatures during the spawning migration period of the salmon. The bars indicate the native distribution of the salmon, the solid black areas indicate the regions in which the salmon have been transplanted successfully, and the dots indicate the regions in which the transplantations were unsuccessful. The isotherms in the North Pacific Ocean give the mean surface temperatures for the period of June, July, August, and September. Those in the North Atlantic Ocean give the mean surface temperatures for the period of July, August, and September, and those in the South Atlantic and South Pacific Oceans give the mean surface temperatures for the period of January, February, and March.

isotherms in figure 3. Schott (1935) gives a review of the oceanographic studies carried on in the North Pacific and describes the subsurface temperatures in this region. The isotherms in figure 3 were taken primarily from Schott's review.

Along the coasts of Japan and Korea the mean annual 10° and 5° C. isotherms, respectively, at 200 meters, describe the subsurface temperatures of the waters at the southern distributional boundaries of the salmon. The mean annual temperatures at 200 meters on the east coast of Honshu Island, Japan, decrease from 10° to 3° C. within the comparatively short distance from Cape Inuboye to the north end of the island.

Uda and Okamoto (1930), and Uda (1931), give the monthly temperatures at 100 meters along these shores. The temperatures at 100 meters along the Korean coast do not differ appreciably from those at 200 meters and vary no more than 3° C. throughout the year. The temperatures at 100 meters along the east shore of Honshu Island average from 3° to 4° C. higher than at 200 meters and also vary no more than 3° throughout the season. In general the subsurface temperatures in this region do not fluctuate widely throughout the year.



FIGURE 3.—The geographic distribution of the Pacific salmon and the mean annual subsurface ocean temperature at 200 meters depth. The bars indicate the native distribution of the salmon, the solid black areas indicate the regions in which the salmon have been transplanted successfully, and the dots indicate the regions in which the transplantations were unsuccessful. The isotherms give the mean annual subsurface temperatures at 200 meters depth.

The southern distribution of the salmon along the North American continent falls well within the region bounded by the mean 8° C. subsurface isotherm. Here again the subsurface waters vary only 2° to 3° C. throughout the year. In the Bering Sea the mean annual temperature at 200 meters is less than 3°, and in the Arctic Ocean it is less than 0° C. Hence, if the salmon frequent the subsurface waters to depths of 200 meters, they must be tolerant to temperatures ranging from slightly below 0° at the minimum to the vicinity of 10° C. at the maximum.

Donaldson (1936) has shown that the optimum range of temperature for growth of the young salmon in fresh water is between 13° and 17° C. Furthermore, he found that mortality was excessive at constant temperatures of 20° and 3° C. In view of the temperature data given in figures 2 and 3 it is obvious that the optimum range for growth in the sea must shift to a lower level. The mean annual temperatures of the ocean waters at 200 meters throughout almost the entire distribution of the salmon do not exceed 8° and in the northern half of the range they fluctuate close to 3° C. Even if the salmon frequented only the surface waters during their sojourn in the sea they would encounter temperatures of less than 15° C. throughout the greater part of the year, for it is only during the summer that the surface waters reach this temperature



FIGURE 4.—The geographic distribution of the Pacific salmor and the mean annual surface salinities in parts per 1,000. The bars indicate the native distribution of the salmon, the solid black areas indicate the regions in which the salmon have been transplanted successfully, and the dots indicate the regions in which the transplantations were unsuccessful. The isohalines give the mean annual surface salinities in parts per 1,000.

and then only in the southern part of the range. In the northern part of the range the temperature of the surface waters at no time exceeds 10° C. Hence, the salmon must become acclimated to the colder waters of the ocean during their sojourn in them, and are able to grow and survive at lower temperatures than in fresh water.

Since the salinity of the water forms an important environmental component of marine habitats, it was likewise studied in relation to the distribution of the salmon. Although salinity data for the subsurface waters would have been more desirable it was found that only surface data were available for all of the oceanographic regions. The mean annual surface salinities in parts per thousand for the North Pacific are shown by the isohalines in figure 4. The data from which these isohalines were determined were taken from the works of Schott (1928 and 1935), Uda and Okamoto (1930), and Uda (1931).

The isohalines of 33 and 34 parts per thousand describe the mean annual salinities of the surface waters at the southern boundaries in the distribution of the salmon along the coasts of Korea and Japan. Owing to the direct contact of warm currents of high salinity with cold currents of low salinity, and the continuous shifting of these currents off the eastern coast of Honshu Island, the isohaline of 34 parts per thousand is not confined to any one district but shifts about over a broad area. Hence, the salmon frequenting the waters in this area may at times be subjected to surface salinities as high as 35 and as low as 33 parts per thousand.

The southern distributional limits of the salmon on the North American continent fall within an area whose coastal waters are characterized by mean surface salinities from 33 to 34 parts per thousand. In the northern range of the salmon the mean salinities of the surface waters do not exceed 30 parts per thousand. It is, therefore, quite possible that the salmon orient themselves in the open ocean to surface waters of salinities ranging from 30 to 35 parts per thousand.

The analysis of the marine habitats thus far has been confined mainly to the determination of the ranges in certain physical and chemical properties of the waters in the North Pacific Ocean within the limits of the native distribution of the salmon. Briefly, it was found that the occurrence of the salmon is associated with the presence of ocean currents bearing waters of low temperature and salinity. The mean surface temperatures during the spawning migration period of the salmon ranged from 0° to 20° C. The mean annual temperatures at 200 meters ranged from slightly below 0° to 10° C. and the mean annual surface salinities varied from 30 to 35 parts per thousand. Since the salmon frequent the ocean waters of these temperatures and salinities, it may be assumed that they are tolerant to them. In this analysis, however, it has not been possible to definitely determine if temperatures and salinities outside these ranges are also tolerated by the salmon or form definite limiting factors governing their The further analysis of this relationship may be found in a similar study of survival. the marine waters in the foreign regions where the salmon have been transplanted. In other words, if the foreign marine waters in which the transplantations have survived have physical and chemical properties similar to those in the native distribution of the salmon and if the foreign waters where the transplantations have failed have properties unlike those in the native distribution, fresh-water conditions being favorable to survival, then it is logical to assume that temperature and salinity values beyond the ranges of the native distribution may form limiting factors to the marine survival of the species.

SOUTH PACIFIC REGION

In discussing the foreign distribution of the Pacific salmon in this region it was pointed out that transplantations were made in Hawaii, Chile, New Zealand, Tasmania, and Australia, Natural sea-run populations developed from the transplantations in New Zealand and Chile but failed to develop from those planted in Hawaii, Tasmania, and Australia.

New Zealand is composed of two large islands, known as North Island and South Island. Some of the streams on each island were stocked with chinook salmon from the Sacramento River, Calif., but only those on South Island have developed natural sea-run populations and even here only within certain limits. The streams on both islands are shown in figure 5. The streams on South Island which support natural runs of chinooks are indicated by a solid circle, and those which have been stocked frequently from 1910 to 1929, but which have never developed natural runs, are indicated by a solid triangle. Does the explanation of this failure of the chinooks to develop natural runs in certain streams on South Island and in none of the streams on North Island lie in unfavorable conditions in the fresh-water or the marine environments?

The streams on both North Island and South Island are quite similar in origin and type. Most of the larger ones originate in mountain lakes and flow rapidly to the sea over gravelly and rocky beds, see figures 6-8. Percival (1932), in describing the streams of New Zealand, states:

The geological youthfulness of the present land-surface of New Zealand accounts for the relative absence of slowly flowing rivers such as, in other countries, give shelter to a great variety of free-swimming organisms and allow of the growth of much vegetation on the bed.

Generally speaking the rivers of New Zealand are comparable with the portions of the European rivers called by Thienemann (28) "Aschenbach" (Grayling stream), where the bed is stony and liable to flooding through the accumulation of surface water.

The streams on North Island, owing to the milder climate, are somewhat warmer than those on South Island. At Rotorua, North Island, the mean air temperature for January is 18° C. and for July is 7.5° C., while at Queenstown, South Island, the mean air temperature for January is 15.5° and for July is 3° C. Phillips (1929) reports stream temperatures on North Island, during the winter and spring, as low as 8° C., and during the fall from 12.5° to 15.5° C. Hobbs (1937) reports the mean monthly temperatures of salmon-bearing streams on South Island as ranging from 3° C. in midwinter to 16.5° C. in midsummer. Percival (1932), in discussing the presence of fish food in the streams on both islands, states that it is sufficiently abundant in most of the streams to support trout and other fresh-water fishes. In view of these facts it may be assumed that the streams on both islands provide favorable environmental conditions for the survival of the salmon during their fresh-water existence.

An examination of the environmental conditions found in the coastal waters of the islands, however, gives an altogether different picture, for North Island is almost wholly bathed by a tropical current and South Island by an Antarctic current. The directional drifts of these currents are shown in figures 1 and 5.

Hefford (1929), in discussing the reasons why runs of chinooks have not been established in the Wairau and Hokitika Rivers on South Island, and in all of the rivers on North Island, makes the following statement:

It is known that off the south-eastern coasts of South Island the water in the sea is of Antarctic origin. There is a general set or drift in a north-easterly direction of cold water from the south, and this water produces the prevailing conditions in the sea off the Otago and Canterbury coasts where the quinnat have been established for some years. The South Equatorial Drift, which sets from the eastward and impinges upon the east coast of North Island, may be said to dominate the conditions to the northward of East Cape; while between that point and Cook Strait there is a mixture of this subtropical water with water from the south. For a long time navigators have been familiar with these "sets" or surface movements of the sea, but it was not until the hydrographer of the Danish research steamer Dana had applied physical and chemical tests to the water sampled at intervals between the east coast of Auckland and the coast of Otago, in January 1929, that the significant differences in the character of the water along this line were ascertained. It seems clear from the Dana's observations that the present distribution of quinnat salmon off the New Zealand coasts coincides with the occurrence of practically unmixed Antarctic water, with its characteristic physical and chemical qualities. Not a single individual of the quinnat species has ever been



FIGURE 5.—The distribution of chinook salmon in New Zealand. The dots indicate the streams on South Island in which natural sea-run populations of these fish have been established. The triangles indicate the streams which have been stocked frequently from 1910 to 1929 with young chinooks but which have never developed natural runs. All of the streams on North Island have at some time or other been stocked with young chinooks but have also never developed natural runs. The solid arrows indicate the directional drifts of cold currents. The broken arrows indicate the directional drifts of warm currents.

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FIGURE 6.—A chinook salmon caught at mouth of the Rangitata River, Canterbury, New Zealand. The general form and markings, such as the spots on the back and fins, are typical chinook salmon color markings. Gashes on the body are due to attacks by predators, probably barracuda. New Zealand Government Publicity Photo.



FIGURE 7.—Fresh-water stream conditions as found in the Rakaia River, Canterbury, New Zealand. The clean gravel beds in the foreground and the snow-covered mountains in the background are prime factors in the fresh-water life history of the chinook salmon. New Zealand Government Publicity Photo.

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FIGURE 8.—Sport fishery at mouth of the Rangitata River, Canterbury, New Zealand. Anglers in foreground landing a chinook salmon, while others fish the surf at the mouth of the river. New Zealand Government Publicity Photo.



FIGURE 9.—Commercial fishery as carried on along the Waimakariri River, Canterbury, New Zealand. Note range in size of the chinook salmon that were netted with a small seine carried in skiff at left. New Zealand Government Publicity Photo.

GEOGRAPHIC DISTRIBUTION OF THE PACIFIC SALMON

planted in a Canterbury stream, yet the Canterbury rivers now provide the best quinnat fishing in the Dominion, the species having migrated to their mouths from the Waitaki, where the original fry were planted. The Wairau has been fairly generously stocked and yet shows no appreciable run of fish. The inference is that it is probably too far north—outside the influence of the purely Antarctic water which attracts the bulk of the species—though an odd few are known to run into the Wairau, and, in fact, into some of the southern rivers of the North Island. This season an indubitable quinnat was caught in the Tukituki River, Hawke's Bay. It does not follow that these parts are suitable for the permanent establishment of the species in abundance. The limit to which the influence of hydrographical factors pertaining to Antarctic waters extends will doubtless vary at different times, and it may be that in odd years the Cook Strait neighborhood, or even farther north, may provide suitable and congenial conditions for the quinnat salmon. But the indications afforded both by experience and by theoretical considerations seem to emphasize the probability of the fundamental relationship between the nature of the sea-water and the distribution of these salmon. There is also the case of the attempted acclimatization of the quinnat in the Hokitika River, on the west coast of the South Island. Our departmental reports show that between 1910 and 1924 the fry from over three million ova were planted in the head-waters of this river. The only apparent outcome has been a stock of lake-dwelling quinnat which has established itself in Lake Kanieri. As is well known, the west coast of the zonstorial current. Again it seems to be a case of the wrong sort of sea-water for a salmon species. Where the quinnat smolts, which have presumably entered the Tasman Sea to the number of thousands or hundreds of thousands, have disappeared to is a mystery which may never be solved. This discussion is admittedly somewhat speculative, but it seems n

The analysis of the physical and chemical properties of the coastal waters of New Zealand bears out Mr. Hefford's assumptions as to the unfavorable character of the marine waters off the north and west coasts of South Island and the entire coast of North Island. The directional drifts of the ocean currents, the mean seasonal surface temperatures, the mean annual subsurface temperatures at 200 meters, and the mean annual surface salinities are given in figures 1–4, respectively. These data were calculated in the same manner as those for the North Pacific and were taken from the studies of Buchan (1894) and Schott (1928 and 1935). Schott (1935) gives a complete summary of all the hydrographic data collected in this region.

The directional drifts of the ocean currents shown in figures 1 and 5 were calculated for the months of January, February, and March, which cover the spawning migration period of the Pacific salmon in this region. The South Pacific Current and the Antarctic Drift, which are so closely related that they may be considered as one current, carry waters of low temperatures and salinity. South of New Zealand a portion of this combined current divides. Part flows northward along the west coast of South Island and merges with a branch of the warm East Australian Current near the central coast of the island. Natural runs of California chinooks have been established only in the streams along this coast south of the point of confluence of these The remainder flows northward along the east shores of South Island to currents. Cook Strait where it is met by counter drifts from the warm South Equatorial Current. Natural runs of California chinooks have also been established only in the streams along this coast south of the point of confluence of the cold and warm currents. This shows a relationship between ocean drifts and the occurrence of natural runs of salmon similar to that found along the coasts of Korea and Japan.

The mean surface and subsurface temperatures, and mean surface salinities, given in figures 2, 3, and 4, all show that the coastal waters of North Island are warmer and more saline than those of South Island. The mean 15° C. surface and 10° C. subsurface isotherms and mean 35 parts per thousand surface isotherms all touch the shores of South Island near the upper limits of the range in which the salmon have established natural runs. Similar mean temperatures are also found in the coastal waters near the native limits of occurrence of these salmon in California. Hence, from these observations in New Zealand, it may be assumed that the California chinooks react unfavorably to temperatures beyond the ranges found in their native habitats, but that they tolerate surface salinities of higher values up to 35 parts per thousand which is the maximum found throughout the entire native range of the Pacific salmon.

Further demonstration of the unfavorable influence of coastal waters of high temperature and salinity on the marine survival of these salmon may be found in the failure of the attempts to introduce them into the streams of Hawaii, Australia, and Tasmania. The upper reaches of the streams in these countries have been favorable to the introduction of trout, whose fresh-water requirements are similar to those of the salmon. In fact, the salmon eggs shipped to these countries, according to correspondence received, Baird (1878), McCulloch (1927), and Tasmania Fisheries Commission (1933 and 1935), were hatched without considerable loss and the young reared successfully to the stage of seaward migration. Landlocked populations of chinooks have been established in the Great Lake of Tasmania but no adults have ever returned from the plantings in the rivers, although chinook eggs were also imported from New Zealand for stocking them. No adults have ever returned from the many plantings of salmon made in the rivers of Australia and Hawaii.

The mean directional drifts in figure 1 show that Hawaii, Australia, and Tasmania are completely surrounded by currents of tropical origin during the spawning and seaward migration periods of the salmon. Schott (1935) shows that this same condition also prevails throughout most of the year. The mean isotherms and isohalines given in figures 2, 3, and 4, show that in general the surface and subsurface temperatures and surface salinities of the coastal waters of these countries exceed the values found in the native marine habitats of the salmon. The mean surface temperature during the spawning migration period appears to be an exception in the case of Tasmania. This may indicate that all marine conditions must be favorable before survival of the salmon is possible.

The attempts to introduce sockeye and coho salmon from Washington and Oregon into the waters of southern Chile have been successful. The coastal streams of southern Chile are similar in origin and character to the streams of southeastern The climates of the two regions are also quite similar, being characterized Alaska. by heavy rainfall and comparatively mild temperature. The hydrographic conditions of the waters along the southern coast of Chile (see figs. 1-4) are also similar to those in the native marine habitats of these salmon. The returns, thus far, of adult salmon have been reported only in the most southern streams in which transplantations were made. This does not mean, however, that other streams in the region are not suitable for the establishment of natural runs, but merely that no returns have as yet been reported in them. It is for this reason that areas of both success and failure have been indicated on the distributional charts in figures 1-4. The successful transplantation of sockeye or coho salmon in Chile supports the conclusion that environmental conditions in both the marine and fresh waters of a foreign region must be similar to those in the native habitats of the salmon before successful introduction may be expected.

NORTH ATLANTIC REGION

Many attempts have been made to introduce the Pacific salmon into the streams along the eastern coast of North America and the countries of northern Europe (see tables 1 and 2). Of these many transplantations all but those in the streams of Maine, New Brunswick, and Ontario were failures. The origin and character of the streams and lakes along the North American coast, north of the State of Maryland, indicate that they originally provided the physical requirements essential to the freshwater survival of these salmon. Kendall (1935) states that the original range of the Atlantic salmon (Salmo salar), which has fresh-water requirements similar to those of the Pacific salmon, probably extended from Delaware to Labrador. The establishment of natural runs of Pacific salmon in Maine, New Brunswick, and Ontario, as well as the development of landlocked populations in lakes throughout this region, gives further evidence of the suitability of these fresh waters for the introduction of these salmon.

Many of the streams in this region have been gradually altered, through the introduction of power dams and pollution, so that at present they may not provide the essential requirements for the fresh-water survival of the salmon. However, these hazards were not so serious from 1872 to 1900, during which time the majority of the transplantations of Pacific salmon were made (see tables 1 and 2). Mather (1887) states that natural runs failed to develop from the transplantations of chinook salmon in the Hudson River but that the runs of Atlantic salmon in the river could be greatly improved through the introduction of eggs and young from other coastal streams. Since the Pacific and Atlantic salmon have similar fresh-water requirements, the indications are that the Hudson River, in 1887, provided the essential fresh-water The failure of these salmon to develop natural runs in conditions for both species. the coastal streams from Maryland to the Gulf of Maine cannot be wholly attributed to the presence of unfavorable conditions in them. In fact, the streams of Maine would still support natural runs of Alaska pink salmon had they not been destroyed through adverse sentiment. The consistent lack of returns from plantings made in the coastal streams of Virginia, North Carolina, South Carolina, Georgia, and especially in the warm and muddy streams of Louisiana and Mississippi, may be in part attributed to their unsuitability for the fresh-water existence of the salmon.

The millions of California chinook eggs sent to the countries of northern Europe, according to Baird (1878), Bottemanne (1879), Behr (1882), Aagaard (1930), and correspondence received, were all hatched with little loss and the young reared successfully to the stage of seaward migration. Many of the young were also reared to the adult stage in natural or artificial ponds in France, Germany, and Holland. In France these landlocked fish were spawned artifically for propagation in inland waters. The rivers and lakes of northern Europe in which the chinooks were reared and liberated have in the past supported large populations of trout and Atlantic salmon, see Kendall (1935), all of which have fresh-water requirements similar to those of the chinooks. In fact, many of these rivers and lakes still support populations of Atlantic species. With the exception of artificial barriers and hazards introduced in these rivers through the progress of civilization, they all provide the essential conditions necessary for the fresh-water survival of the Pacific salmon. The warm silt-bearing streams of southern Europe, in which efforts were made to establish natural runs of chinooks, do not provide the conditions essential to the survival of these fish. It is not surprising that the transplantations in these streams were unsuccessful. However, the failure of the chinooks to develop natural runs in the rivers of northern Europe cannot be logically attributed to this cause.

Figures 1-4, inclusive, give hydrographic data for the North Atlantic Ocean similar to those given for the other oceanographic regions. These data were calculated in the same manner as in the other regions and were taken from the works of Rathbun (1882), Townsend (1901), Nansen (1913), Bigelow (1917 and 1933), Sandström (1918), Bjerkan (1919), Huntsman (1921), Dawson (1922), Schott (1926), Zeusler (1926), Smith (1928), Church (1932, 1934, and 1936), Helland-Hansen (1933), and Parr (1933). The mean directional drifts in figure 1 show the general movements of the North Atlantic waters from June through September, the period during which the spawning migration of the salmon occurs in this zone. Three major currents dominate the waters of the North Atlantic; namely, the Gulf Stream or Florida Current, the Labrador Current, and the East Greenland Current.

The North Equatorial Current, banking up the waters in the Caribbean Sea and the Gulf of Mexico, gives rise to a strong current, the Gulf Stream, which flows out of the gulf through the straits between Florida, Cuba, and the Bahamas. This current follows the coast line of Florida and Southeastern United States until it reaches Cape Hatteras. Here it turns more to the eastward toward the banks of Newfoundland, thus allowing a cold current from the north to bathe the shores of Canada and the United States as far south as Cape Hatteras. However, the influence of this cold current is not appreciably effective south of Cape Cod. South of the banks of Newfoundland the Labrador Current meets the Gulf Stream. This cold current has only a minor influence on the Gulf Stream as it continues eastward toward the coast of Europe.

The cold current which bathes the Northeastern shore of the United States is not a continuation of the Labrador Current, but originates in the Gulf of St. Lawrence. As it leaves the gulf it turns southward and effectively carries waters of low temperature and salinity to the shores as far south as Cape Cod. It is interesting to note at this point that the Pacific salmon have not developed natural runs in the coastal streams south of Cape Cod. Here again, as in the North and South Pacific regions, the occurrence of natural runs of these salmon is associated with the presence of ocean drifts bearing waters of low temperature and salinity.

As the Gulf Stream follows its eastward drift toward the coast of Europe it branches into a number of lesser currents whose warm waters greatly temper the areas influenced by them (see fig. 1). The major branch passes to the northward of the Faeroes and flows toward and along the coast of Norway, where it divides and sends branches to Spitsbergen and the Barent Sea. A portion of the Gulf Stream also flows around Scotland and enters the North Sea. Other branches penetrate the English Channel and bathe the shores of France, Spain, and Portugal.

The North Sea, which averages considerably less than 200 meters in depth, is readily influenced by the warm and saline waters of the Gulf Stream. The Baltic Sea, being likewise very shallow, warms rapidly in the summer months, and the waters flowing from it during this period fluctuate around 17° C. Furthermore, all of the fish in the Baltic Sea area migrating to and from the open ocean must pass through the warm and saline waters of the North Sea. The failure of the California chinook salmon to develop sea-run populations in the streams tributary to these seas is consistent with their failure to develop natural populations under similar conditions in the South Pacific region.

The mean temperatures and salinities of the coastal waters in the areas of the North Atlantic (see figs. 2, 3, and 4), where the Alaska and California salmon have failed to establish natural runs, are beyond the ranges of temperature and salinity found in the native marine habitats of these salmon. The areas in which they have been successfully established all have coastal waters with temperatures and salinities similar to those in the native marine habitats of the salmon. In other words, the reactions of the Pacific salmon to both fresh-water and marine environmental conditions in the North Atlantic are consistent with their reaction to similar conditions in the South Atlantic and South Pacific regions.

SOUTH ATLANTIC REGION

The only attempts to introduce the Pacific salmon into the South Atlantic region have been those made in the waters of southern Argentina, which have apparently failed. The streams of Argentina, with the possible exception of those in southern Patagonia, receive a great deal of drainage from plateaus and are essentially alluviumbearing streams with sandy and mud bottoms. Since it is known that the Pacific salmon do not spawn in sandy- or mud-bottomed streams, nor could the eggs survive under such conditions even if so spawned, it is not surprising that sea-run populations have failed to develop from the transplantations in these streams. Marini (1936) also reports unfavorable high temperatures in some streams in which the salmon were transplanted. Complete surveys have not as yet been made of all the streams in Patagonia in which the salmon have been introduced. There may still be streams in the southern extremity of this province that will support natural runs which are at present unknown.

The mean directional drifts of the currents, the mean seasonal surface temperatures, the mean annual subsurface temperatures (200 meters), and the mean annual surface salinities for the South Atlantic, are given in figures 1–4, inclusive. These data were taken from the oceanographical studies of Buchan (1894), Schott (1926), and Church (1934). The hydrographic conditions of the coastal waters of Patagonia, as given in these figures, are in every case similar to those found in the native marine habitats of the salmon. Hence, it appears that the failure of the attempts to introduce these salmon in Argentina lies in the unfavorable environmental conditions in its fresh waters.

SUMMARY

The native distribution of the Pacific salmon (genus Oncorhynchus) is confined almost entirely to the temperate waters of the North Pacific. They are found in varying degrees of abundance along the North American coast from Monterey Bay, Calif., to Kotzebue Sound, Bering Sea, and along the Asiatic coast from the Anadir River, Siberia, to the Tumen River, Korea, and Cape Inuboye, Honshu Island, Japan. They also occur in isolated streams along the Arctic coast. From 1872 to 1930, millions of eggs and young of Pacific salmon from California, Oregon, Washington, and Alaska were shipped to the Atlantic Coast States and foreign countries for the purpose of establishing natural runs in their coastal streams. Transplantations were made in Hawaii, Australia, Tasmania, New Zealand, Chile, Argentina, Eastern United States, Eastern Canada, England, Ireland, France, Holland, Germany, Finland, and Italy. Of these many transplantations only those in New Zealand, Chile, the State of Maine, and the provinces of New Brunswick and Ontario have developed natural populations of these salmon with characteristics similar to those in their native distribution.

The environmental components, as considered in this study of the foreign streams and lakes and coastal waters in which these salmon have developed natural runs, have in every case been similar to the components of the waters frequented by the salmon in their native range. On the other hand the environmental components of the foreign waters in which these salmon have failed to develop natural runs have differed from those of the waters native to the salmon. The failures of the transplantations in some areas have been due to the lack of suitable fresh-water conditions; in others, to the lack of suitable marine conditions, while some areas provided neither fresh water nor marine conditions favorable to the introduction of the salmon.

Owing to the dependence of the Pacific salmon on particular environmental conditions, as shown in this study, there are no oceanographic regions in the world that can support populations of these fish as great as those supported by the North Pacific region.

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