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Though it appears homogeneous, the ocean is a changing, and limiting, environment for the Pacific salmon.

Part II: Effect of the Ocean Environment on the High Seas Distribution of Salmon

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INTRODUCTION

To most human travellers on the high seas, ocean water appears pretty much the same from place to place. It is salty, which distinguishes it from drinking water. In the tropics, it tends to be warm and to appear deep indigo in color. As one approaches the poles, it tends to become cold and to appear gray-green if it has not solidified to ice. Outside of these features, there is little to distinguish one part from another.

To an oceanographer, the same features absorb his interest. He takes the additional steps of measuring its salinity, its temperature, and the way it absorbs and reflects light. He may go further and measure such things as the specific gases and solid substances dissolved or suspended in it and identify the living creatures that can be screened out of it. His outlook is objective, as he is secure in his thick-skinned, warm-blooded, ship-buoyed, galley-fed independence of the properties he is measuring. They interest him, but in no way are they immediately significant to his vital processes.

A salmon, thin-skinned, cold-blooded, and hungry, experiences the ocean directly, intimately, subjectively. Uninsulated, unsupported, and self-fed, its vital processes are quickly affected by changes in the properties of the ocean waters in which it is immersed.

The vital processes of living things are driven by energy derived from chemical reactions taking place within their cells. Unlike those taking place in the heated retorts of chemical laboratories, these reactions proceed at low temperatures and pressures. This happens because of enzymes, chemicals that bring the components together so aligned that reaction can proceed without a boost from a great deal of heat and pressure. Enzymes produced by living creatures are uniquely suited to functioning under the special conditions imposed by the environment on the creatures which have adapted to them.

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TEMPERATURE AND OXYGEN

Salmon, like other cold-blooded marine vertebrates, are restricted to a narrow range of temperatures within which their vital processes can function. Dissolved oxygen is also essential. Unless a salmon is within its allowable temperature range and has sufficient oxygen, it will quickly die. Given these gross limits, parts of the ocean can be readily identified in which salmon can live. Table 1 gives the tolerable and preferred ranges of ocean temperature for various species of Pacific salmon, *Oncorhynchus* spp. Within the range for each species, there is a spectrum of narrower temperature bands to which specific races of the species are adapted. It is important, therefore, in selecting stocks for transplanting, to choose races whose habitats match as closely as possible the seasonal temperature regimes of the intended receiving waters. Figures 1-3 show the distribution of surface temperatures, in both the North Atlantic and North Pacific Oceans, favorable for temperate-zone races of salmon. It might appear that surface temperature distributions present only a small part of the picture in the oceans' three dimensions. However, there are clues which lead us to suspect that the world of the salmon in the ocean is a rather thin layer close to the surface. The first of these comes from physiology: the air bladder of the salmon is open; air can be gulped in and burped out. This is the usual case with fish that do not venture too far from the surface. Fish that live at great depths and do not normally come to the surface usually have closed bladders into which gas is secreted from the blood for buoyancy control. A second clue comes from the vertical structure of ocean waters

Table 1.—Tolerable and preferred sea-surface temperatures for Pacific salmon.

Species	Tolerable Range °C	Preferred Range °C	Reference months for preferred range
Sockeye[1]	1-15	2, 3-9	May, September
Chum[1]	1-15	2, 3-11	May, September
Pink[1]	3-15	4-11	May, June
Coho[1]	5-15	7-12	May, June, July
Chinook[1]	2-13	7-10	July, August, September
Cherry[2] (masu)	5-15	7-12	March, April, May

[1]Source: Manzer, et al., 1965.
[2]Source: Tanaka, 1965.

characteristic of arctic and subarctic regions. In the North Pacific, there is a layer of water, within several hundred meters of the surface, which is colder (at 3-4°C, or 37-39°F) in the summer than the water above and below. Its significance to the distribution of salmon was first considered by Favorite (1969b) who reported that its southern limit coincided with the southern limit of salmon distribution in the central part of the ocean in the summer. I would like to suggest, since the temperature of this layer is at the lower end of the range preferred by Pacific salmon and occurs at depths where the level of dissolved oxygen is characteristically low, that the layer could serve as a summertime floor for the salmon environment in the central North Pacific Ocean. A third clue stems from the observation that practically all of the salmon caught in floating drift nets fishing at varying depths from the surface are caught within 10 meters of the surface (Fukuhara, 1953). However, this observation may be deceiving because, as Favorite pointed out, salmon sensing a net dead ahead would try to avoid it. Those sounding would be able to swim under it, those veering to the right or left would eventually swim around it, while those veering upward would tend to become enmeshed near the surface.

What about the other properties that oceanographers (and astute fishermen and submariners) use to distinguish ocean waters—of what significance may they be to salmon?

SALINITY

As far as its vital processes are concerned, the salt content of its environment is crucially important only during the juvenile stages of a salmon's life. Its eggs require fresh water for incubation, and the young salmon can tolerate salt water only after the kidney has developed enough that it can hold a proper balance of salts between the blood and body fluids inside and the salt water outside of the fish. With

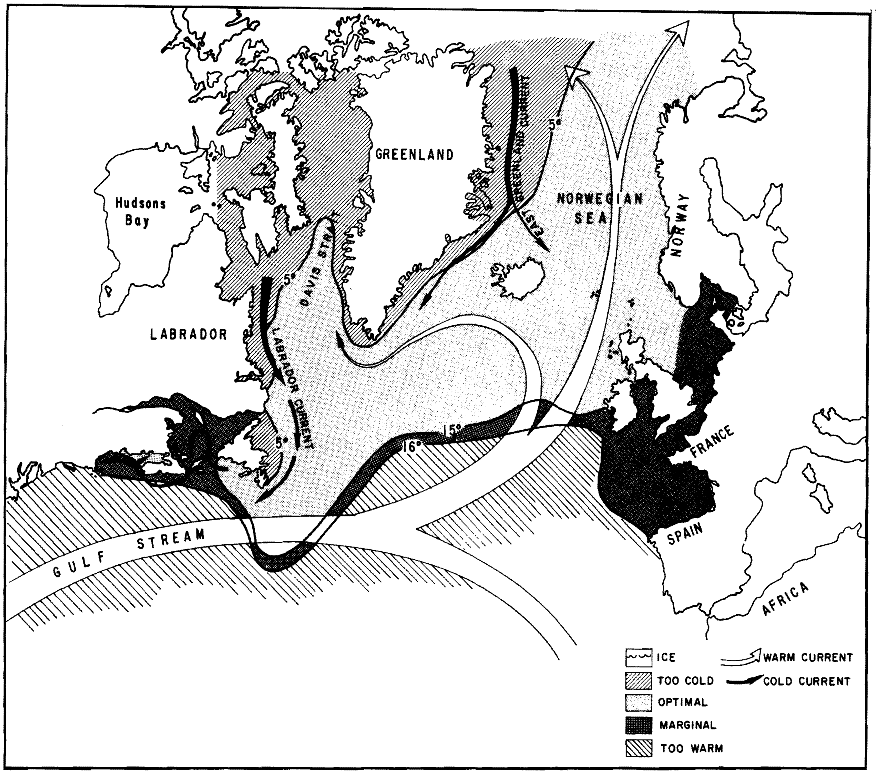

Figure 1.—North Atlantic environment for temperate zone salmon—summer sea-surface temperatures (°C). Adapted from Naumienko et al., 1968.

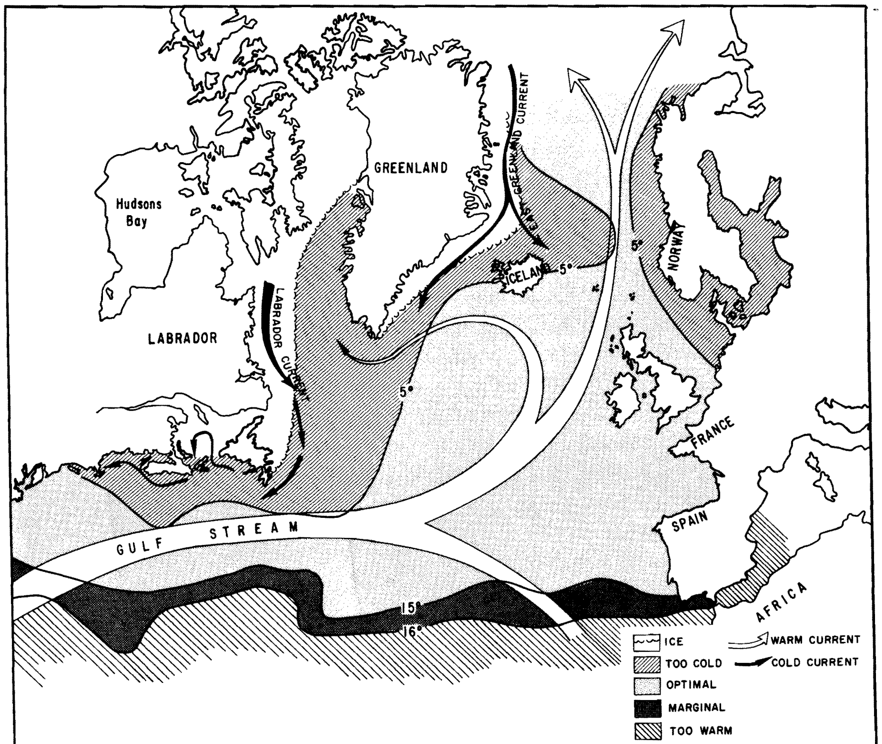

Figure 2.—North Atlantic environment for temperate zone salmon—winter sea-surface temperatures (°C). Adapted from Naumienko et al., 1968.

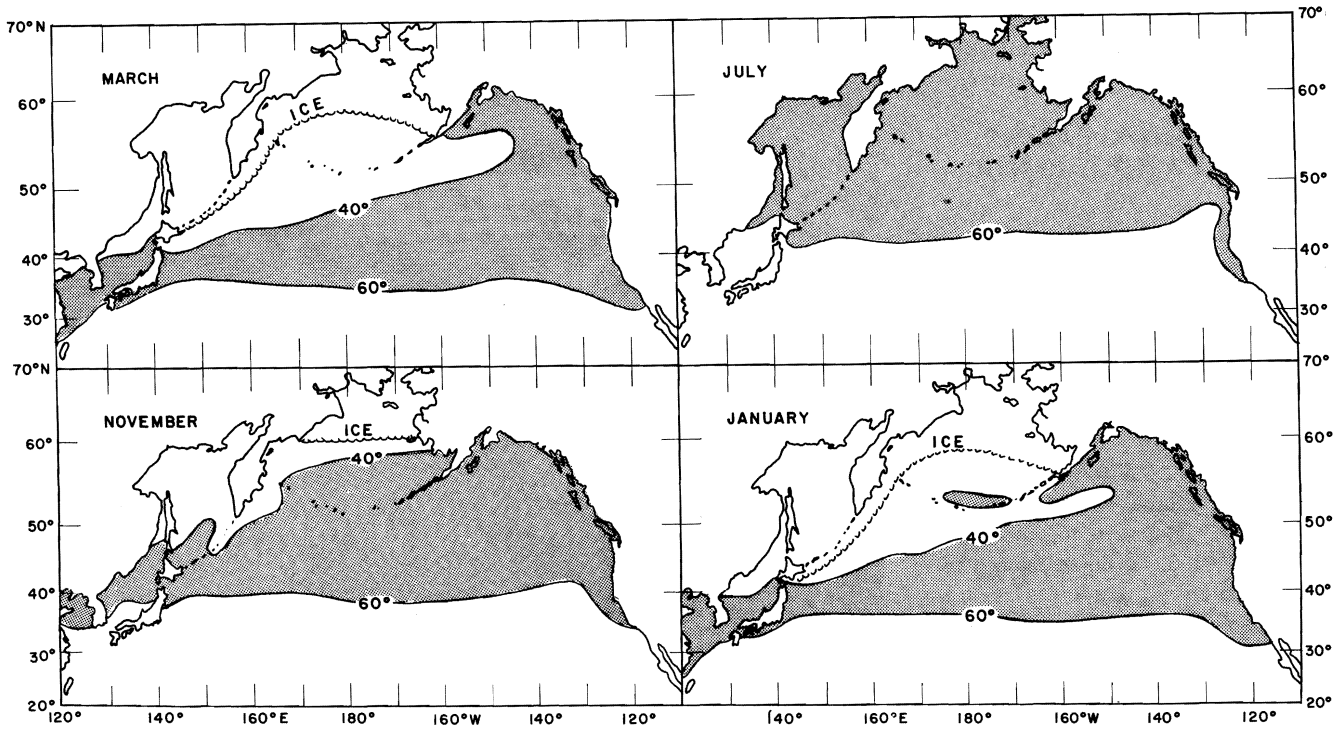

Figure 3.—North Pacific environment for temperate zone salmon—seasonal sea-surface temperature (°F). Adapted from U.S. Naval Oceanographic Office, 1969.

pink, *O. gorbuscha,* and chum salmon, *O. keta,* this occurs early and the young fry can go directly into the sea. With coho, *O. kisutch,* Atlantic, *Salmo salar,* and cherry salmon, *O. masu,* the kidney is not ready to assume this function until the fry have grown to be large fingerlings. This usually takes more than a year. In any case, by the time a salmon has migrated to the sea, salinity does not seriously affect its vital processes. This is not to say that it does not affect where the salmon goes—only that the life of the fish is not jeopardized by changes in salinity between ocean water masses. That salinity can play a powerful role as a signpost in the migration of salmon from the ocean back to their home streams has been discussed by Favorite (1969a). Also, as the primary factor controlling the density of sea water, it profoundly affects the structure and movement of ocean waters and thus, indirectly, the distribution of temperatures and the location, direction, and speed of currents.

FOOD AND OCEAN CURRENTS

Within the boundaries defined by the ranges of temperature and oxygen saturation essential to the vital processes of salmon, the abundance of food and the location and direction of ocean currents must be the chief remaining determinants of salmon distribution on the high seas. From the point of view of a salmon, once a suitable environment has been established, enough food must be found, and it must be able to get back to its home stream for spawning.

The location of plankton and small fish that serve as food for salmon on the high seas is largely related to ocean circulation. Their abundance is determined by the amount of sunlight and of chemical nutrients available for the growth of the single-celled plants at the bottom of the food chain. Where wind-driven surface currents move offshore, upwelling replaces the surface waters with nutrient-rich deep water. Plankton growing in this enriched medium move with the surface currents and tend to be concentrated along the edges and in the marginal vortices that split off from the currents. What oceanographers describe as "patchiness," therefore, characterizes the distribution of plankton in the ocean. Fish such as salmon, which feed on plankton and smaller fish, will seek areas where the plankton are concentrated, much as hunters on the land will seek water holes and grazing meadows where their prey are likely to congregate. Thus, as the game trails of the forests and the plains serve the hunting cats, so are ocean currents likely to lead the predatory salmon to their sources of food. They are likely, also, to help guide the salmon back to the rivers and streams where they were spawned so that they may, in turn, spawn the next generation. Favorite (1969c, 1970) has detailed what is known about ocean circulation and the abundance of food in the North Pacific Ocean as it relates to the distribution of sockeye salmon, *O. nerka*.

TRANSPLANTING PACIFIC SALMON TO THE ATLANTIC

In Part I of this series, I noted the attempts in the USSR to establish pink salmon (from Sakhalin Island in the northeastern Pacific Ocean) in the rivers of the Murman Coast of Europe and the recent U.S. efforts in New England to develop runs of coho salmon. Rass (1965) proposed that the failure of the USSR transplants of 1956-61 to establish substantial self-sustaining runs, despite the spectacular returns of 1960, stemmed from a mismatch of the river temperatures on the Murman Coast with those of Sakhalin Island, home of the parent stock, during the period of egg incubation.

Ricker (1954) discussed the failure of Canadian efforts to transplant chinook salmon, *O. tshawytscha,* to Lake Ontario streams and to New Brunswick. Stating that " . . . the chinook is the least common salmon in the Pacific and, apart from the sockeye, the most choosy one in respect to the stream that it ascends . . . ," he felt that it was not surprising that these efforts failed. Addressing himself generally to the matter of transplanting Pacific salmon stocks, he suggested two desirable characteristics for any program of transplantation:

1. "Relatively large plantings should be made to one or a few sites, at first, so that there will be an adequate expendable surplus while the selection process is weeding out genes whose effects are in poor adjustment to the new situation . . ."
2. "Donor stocks should be carefully selected in order to match up the freshwater and marine conditions of existence of the old and the new sites as closely as possible."

Ricker was concerned primarily with the establishment of self-sustaining runs of naturally-spawning Pacific

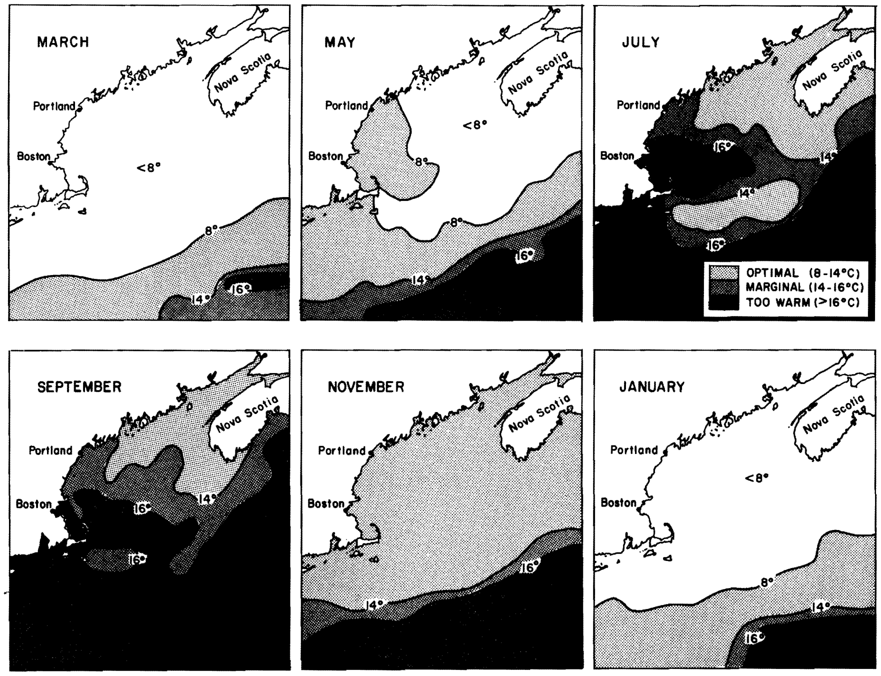

Figure 4.—Sea-surface temperatures in the Gulf of Maine suitable for Pacific Salmon (°C). Adapted from Colton and Stoddard, 1972.

Figure 5.—Boundary between cold Labrador-type water (lighter color) and the warmer Gulf Stream influenced water (darker color, below) in November. Salmon would be confined to the lighter colored cool waters at this time. This photograph, taken from the NOAA-2 satellite, corresponds generally to the November temperature structure indicated in Figure 4.

salmon, as were the 1956-61 USSR experiments on the Murman Coast. To do this, the matching of environmental requirements of donor stocks with appropriate conditions in the receiving waters is critical. However, the urgency for precise matching of environmental conditions can be somewhat relaxed if some of these conditions can be controlled artificially. This can be done readily for the freshwater phase by using hatcheries for egg incubation and the rearing of fry.

Recent success in New Hampshire in establishing coho salmon runs into Great Bay partly stems from that state's willingness to accept the necessity of hatchery rearing to accommodate to the freshwater requirements of the imported Washington stocks. The conditions for ocean survival, however, still had to be met. In this, New Hampshire has been fortunate, in contrast to Rhode Island and Connecticut. These states failed in attempts to establish runs of coho salmon from Oregon and Washington into Block Island and Long Island Sounds although they used much the same hatchery techniques for incubation and rearing as employed in New Hampshire. The seasonal sea-surface temperature structure of the Gulf of Maine (Figures 4 and 5) suggests an explanation for these contrasting results. In the summer and early fall, a temperature front extends eastward from Cape Cod to the Gulf Stream. Temperatures in excess of 16°C (61°F) occur south of the front which would block the return of fall-spawning coho salmon to rivers and streams south and west of the Cape. North of the Cape, however, there would be little to prevent their moving into estuaries from the cool offshore waters in the late summer and early fall as a prelude to their fall spawning migration. The seasonal, surface-temperature structure of the Gulf of Maine, and of Nantucket, Vineyard, Block Island, and Long Island Sounds is such that the thermal barrier moves to the south and offshore in the late fall and winter and does not start to build up again off Cape Cod until early summer. An isothermal band favorable for temperate-zone races of salmon (8-14°C, or 46-57°F) moves from the open sea south of Long Island in the late winter, progressing gradually northward with the advancing seasons, until it becomes compressed along the Maine coast and into the Bay of Fundy by late summer. By the fall, it begins to spread to the south, eventually returning to its wintertime position offshore, south of Long Island. This suggests that Pacific salmon, planted in New England, would be found in ocean waters off the coast of Maine and in the Bay of Fundy in the summer, where they should be accessible to both sport and commercial fishermen. They would tend to move with the southward spread of 8-14°C water and, if chosen from stocks appropriately selected for the timing of their migrations back to fresh water, would appear off their home streams when the 8-14°C band was in a favorable position offshore.

From the foregoing, it seems likely that the early fall-running coho salmon was a poor choice for establishing runs of Pacific salmon in Rhode Island and Connecticut. A late fall-running stock might have had better success. It also appears that spring-running stocks of chinook salmon, cherry salmon and steelhead trout, *Salmo gairdnerii*, should be able to migrate from the ocean into streams flowing into Block Island and Long Island Sounds.

Systems for introducing appropriately selected stocks of Pacific salmon thereby generating new sport and commercial fisheries on the coast of New England will be proposed in the concluding paper in this series.

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