MODELS OF OCEANIC MIGRATIONS OF PACIFIC SALMON AND COMMENTS ON GUIDANCE MECHANISMS[1]

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ABSTRACT

The general oceanic distribution and migratory behavior of Pacific salmon are summarized, and a model of the entire migration is developed for each of three typical stocks. The pink salmon of southeastern Alaska and British Columbia circle the Gulf of Alaska counterclockwise within an area generally bounded on the west by long. 155° W. and on the south by lat. 41° N. They travel generally "downstream" in the Alaskan Gyre and the associated currents. The pink salmon of the Karaginski district on East Kamchatka also apparently make a counterclockwise circuit of the Bering Sea and North Pacific Ocean in an area bounded approximately on the west by long. 155° E., on the south by lat. 40° N., on the east by long. 150° W., and on the north by lat. 60° N. Their migratory circuit is generally "downstream": southward in the East Kamchatka Current, eastward in the Subarctic Current, and finally westward and northward in the Alaskan Stream and the Bering Sea Gyre. The sockeye salmon of Bristol Bay make two or three counterclockwise circuits in the Bering Sea and North Pacific Ocean within an area bounded approximately on the north by lat. 60° N., on the west by long. 165° E., on the south by lat. 45° N., and on the east by long. 140° W. The number of circuits depends upon the number of winters spent by the salmon at sea. In general, they travel "downstream" in the major current systems within the area defined. The time schedule, rate of travel, and average size of the fish at various stages are described for each of the three stocks.

On the basis of this summary, we believe that the salmons' migrations could not be performed if they migrated or drifted at random, or if they depended on memorized visual or olfactory cues except for final location of the home estuary and stream. The salmon predominantly travel actively with the residual ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. Also, ocean currents produce electric potentials in a range that some fish can detect; therefore, salmon might depend for navigation on electromagnetic cues from ocean currents. Furthermore, their responses to all migratory cues must be inherited, not memorized.

The return of the salmon to its home stream, to the part of the stream where its parents spawned, or even to the hatchery where it was reared as a fry has been well documented. Clearly, it is a most unusual animal migration. Not only does the salmon return to its birthplace to spawn and die, but each successive generation appears along the coast, enters the estuary, and ascends to the spawning grounds within a few days of the same schedule.

The appearance of the salmon in coastal waters and its final ascent of the stream are only the last acts in a most remarkable series of migrations that have been studied only recently in enough detail to permit a reasonably comprehensive description. The impetus for the study developed when Canada, Japan, and the United States agreed on a convention concerning North Pacific salmon which required that the high-seas migrations of major stocks of salmon near long. 175° W. and the Aleutian Islands be learned in detail. Beginning in 1955 programs were financed to study the abundance, migration, and habits of the salmon in the central North Pacific and the Bering Sea and to learn much more about their environment. These studies have expanded to include the range of the salmon on both sides of the North Pacific, so that

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now there are available reasonably complete data on the abundance and distribution of the salmon and on their North Pacific environment (Hartt, 1962; Ridgway, Klontz, and Matsumoto, 1962; Fukuhara, Murai, LaLanne, and Sribhibhadh, 1962; Callaway, 1963; Dodimead, Favorite, and Hirano, 1963; Mosher, 1963; Favorite and Hanavan, 1963; Amos, Anas, and Pearson, 1963; Margolis, 1963; Kasahara, 1963; Manzer, Ishida, Peterson, and Hanavan, 1965; Godfrey, 1965; Mason, 1965; Tanaka, 1965; Kondo, Hirano, Nakayama, and Miyake, 1965; Hartt, 1966).

The abundance and distribution of salmon at sea are dynamic and variable. The salmon occupy almost all of the North Pacific Ocean north of about lat. 41° N. in the winter or lat. 48° N. in the summer and all of the Bering Sea south of the ice pack. They are found mostly in the upper 10 m.—far from any contact with the bottom. The maturing individuals, which are due in their spawning streams sometime between June and December, begin to move rapidly 1 to 2 months before their arrival dates and commonly maintain average speeds of 30 miles (55 km.) per day [2] for many hundreds of miles. Major numbers of several groups of salmon may, thus, pass through a particular ocean area within 3 weeks. The immature salmon, which remain in the ocean at least another year, commonly undertake extensive feeding migrations generally in a counterclockwise circular pattern that is repeated annually. The salmon of the different species are usually mixed. The mature and immature salmon of one species are sometimes mixed and sometimes segregated. The different stocks of a single species commonly vary as much in their distribution as do the different species, although in the early spring sockeye salmon (*Oncorhynchus nerka*) tend to predominate at the northern boundary of salmon waters and pink salmon (*O. gorbuscha*) at the southern.

The information on ocean migrations is as yet only fragmentary, partly because of the difficulties and expense of working in the autumn and winter and partly because of the lack of suitable gear and techniques for the study of the distribution and migrations of the young salmon after they have left the estuary. We do have enough information, however, on some important stocks to describe their migrations in considerable detail and to make some inferences to fill the gaps in our information. We shall undertake, therefore, to construct models of the ocean migrations of three typical stocks originating in diverse geographical areas: southeastern Alaska and central British Columbia pink salmon; East Kamchatka pink salmon; and Bristol Bay sockeye salmon. Substantial information is available on these stocks, and all three are large enough to have been identifiable in the ocean with reasonable certainty. Fragmentary data on other stocks and species agree with these in principle. The models will illustrate the features of the migration, the navigational problems of which we are now aware, and the kinds of position- and direction-finding information that we presume are available to the salmon.

Our discussion rejects or extends and complements the summaries and hypotheses about high-seas migrations that some authors have set forth recently. We reject the general applicability of the hypothesis about random movement of salmon suggested by Saila and Shappy (1963). We extend the hypotheses about electric navigation presented by Waterman (1959). We extend with new information the thorough review of the oceanic migrations of Pacific salmon by Neave (1964). We question and limit the applicability of sun-compass and odor-perception mechanisms hypothesized by Hasler (1966); Hasler, Horrall, Wisby, and Braemer (1958); and Hasler and Schwassmann (1960).

Perhaps our information concerning salmon migration will help to explain the mechanisms used by other aquatic species that undertake long-range oceanic migrations and about which much less is known. In the Pacific these fishes now include the albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), bluefin tuna (*Thunnus saliens*), black cod (*Anoplopoma fimbria*), and dogfish (*Squalus acanthias*); numerous species of marine mammals and turtles also are known to migrate extensively at sea.

The migrations of the salmon begin when the fry emerges from the gravel. These first few inches of migration through the gravel may well be the most hazardous of its entire life. It then moves downstream (or occasionally upstream) to sheltered waters. Coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) usually find shelter and food in rivers and streams; sockeye salmon in

[2] The miles used throughout this paper are nautical miles.

lakes; chum salmon (*O. keta*) and pink salmon in salt-water estuaries and bays. The physiological change from fresh water to salt water is highly significant, but the ecological change is not. The young salmon needs a place with food and protection from its enemies, and this it finds along the shores of lake, river, or estuary. After it reaches a length of about 5 to 8 cm. it may move to bigger waters where the feeding is better, and at a size of 10 to 15 cm. it usually seeks the open sea. This is where our story of the ocean migrations begins.

OCEAN MIGRATIONS OF PINK SALMON OF SOUTHEASTERN ALASKA AND BRITISH COLUMBIA

Of the Pacific salmons, pink salmon probably have the least complicated oceanic migrations because of their short and uniform 2-year life history. The pink salmon stocks about which we have the most comprehensive knowledge of migrations are those of southeastern Alaska and British Columbia originating between Cape Flattery, Wash. (lat. 48° N.), and Cape Spencer, Alaska (lat. 58° N.)—figure 1. Washington State pink salmon form part of these stocks in odd-numbered

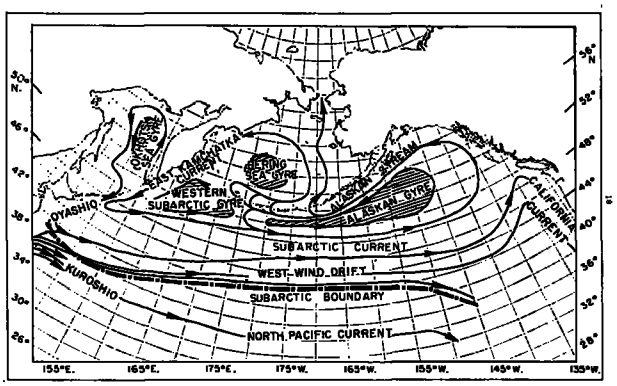

FIGURE 1.—Base map of North Pacific area and surface circulation (adapted from Dodimead et al., 1963, fig. 109).

years. Spawning takes place from mid-July to mid-October, but tends to be earlier in the more northerly areas. Fry emerge from the gravel from February through June; the peak period is in April and May (Sheridan, 1962; Neave, 1966). The fry immediately migrate downstream to salt water and then feed in schools along the shores of estuaries and bays for 2 or 3 months. As they attain a size of 5 to 6 cm., they venture farther offshore.[3] They migrate to the ocean proper in July, August, and September, at a length of 12 to 15 cm. (Gilhousen, 1962; Neave, 1966; Hartt, Dell, and Mathews, 1966).

The ocean migratory period of these stocks, typical of that of pink salmon, extends approximately from July of the year after spawning until summer or early autumn of the next year. On the basis of recent research, we can now describe or hypothesize within moderate limits of dependability the migrations of the southeastern Alaska and British Columbia pink salmon throughout essentially all stages of their 12 to 14 months at sea.

SUMMER EMBARKATION

Juvenile pink salmon enter the ocean proper at numerous points along the southeastern Alaska-British Columbia coast during July, August, and September; their abundance apparently peaks in August (Martin, see footnote 3; Hartt et al., 1966). They do not scatter randomly seaward, but turn northward and migrate along the coast in a narrow band extending about 20 miles (37 km.) offshore (Hartt et al., 1966). They continue in this manner around the northern periphery of the Gulf of Alaska and southwestward past Kodiak Island. The band widens, in the northern part of the Gulf, presumably because there the Continental Shelf is wider. Stocks other than those from southeastern Alaska and British Columbia undoubtedly join the procession off Prince William Sound, Cook Inlet, and Kodiak Island (Hartt, Smith, and Dell, 1967).

The width of the band and the northerly direction of migration were determined by fishing a large, fine-meshed purse seine at various distances from shore and by facing the net in opposed directions. The seine was set in a semicircle, held open for 30 minutes, and then closed to collect fish migrating toward the opening of the seine. Catches were large when the seine was held open to the southeast and small when open northwest (Hartt et al., 1966). For example, in 1964 off southeastern Alaska, the average catch was 350 fingerlings when

[3] Martin, John W. 1964. Studies of estuarine and inshore marine ecology of juvenile pink salmon in southeastern Alaska. *In* W. J. McNeil (editor), Report of the 1964 northeast Pacific pink salmon workshop and contributed papers. U.S. Fish Wildl. Serv., Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska, Manuscript Rep. 64–5: 80–83.

the seine was open southeast and zero when it was open northwest.[4] A time-space extrapolation of the average catch (in 30 minutes in a ¼-mile-wide [0.46-km.] band) indicated that at least 750,000 juveniles migrated daily past any given line of latitude off southeastern Alaska in 1964. Thus, for the 30 to 60 days of strong migration, it is evident that major stocks of fish were involved.

The fork length of the pink salmon at this stage varies from 10 to 25 cm. The average size was significantly larger in the northern samples, presumably because of the presence of fish which had already migrated a considerable distance from southern production areas (fig. 2). The northern samples also included small fish that presumably had just entered the sea from nearby channels and bays. Mixed with the juvenile pink salmon were juvenile sockeye, chum, coho, and chinook salmons and steelhead trout (*Salmo gairdneri*), which suggests that the migratory cue at this stage is similar for all species.

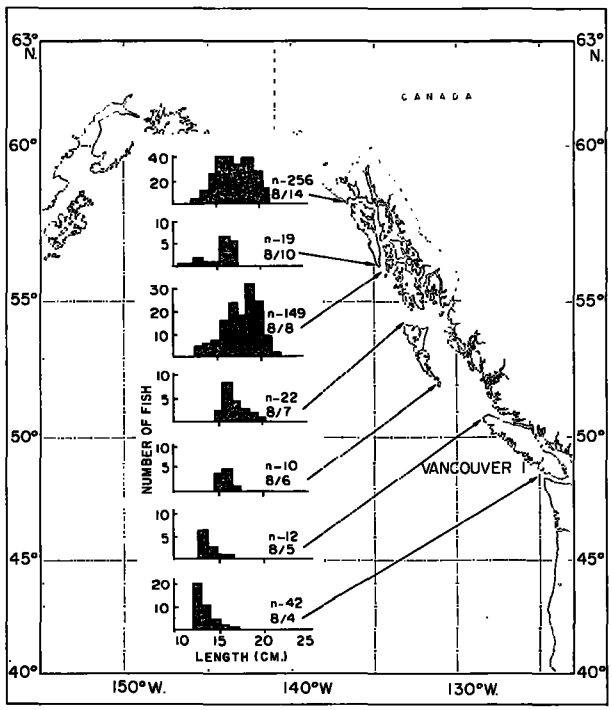

FIGURE 2.—Fork lengths of juvenile pink salmon sampled August 4–14, 1964, in eastern Gulf of Alaska.

[4] For a discussion of the validity of purse seine gear for determining directional migrations of salmon in areas of strong ocean currents, see Hartt (1966 : 8–10).

The northward migration of juvenile salmon is indicated by the purse-seine catches and tag returns. Six pink salmon were recovered a year after tagging, all in southeastern Alaska (fig. 3). All were recovered south of the point of release. If it is assumed that they entered the ocean near the point where they were recaptured as maturing fish, they must have migrated northwestward before they were tagged. The specimen tagged near lat. 59° N. by long. 138° W. had traveled about 350 miles (648 km.) by September 22, 1961, when it was tagged. Figure 3 also illustrates the locations of release and recovery for 1 sockeye salmon, 1 steelhead trout, and 58 coho salmon that were tagged as juveniles, along with the pink salmon.

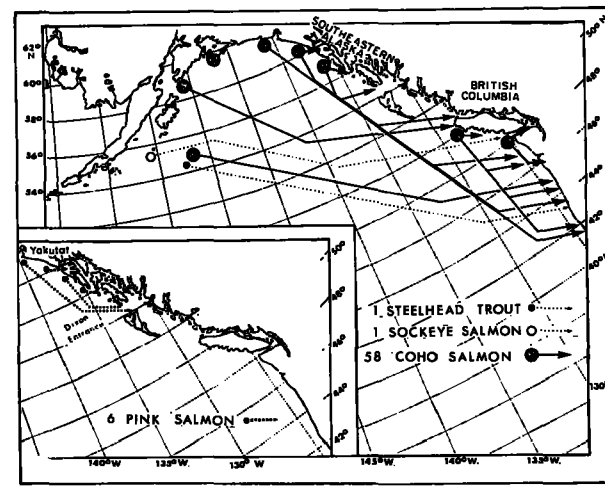

FIGURE 3.—Release and recovery diagram of salmon and steelhead trout tagged as juveniles and recovered 1 or 2 years later (all coho and pink salmon were recovered 1 year after tagging).

These fish were also recovered south of the points of release; some traveled northwestward over 1,000 miles (1,852 km.) before they were tagged.

The rate of travel of juvenile pink salmon during their first few months at sea is difficult to estimate on the basis of the few tag returns received to date, because the distances involved are relatively short and the date of ocean embarkation can only be approximated. If we assumed that the specimen tagged near Yakutat (fig. 3) on September 22 had left Dixon Entrance on August 1, and then had followed the coastline (350 miles or 648 km.), its rate of travel would be 6.6 miles (12.2 km.) per day. By the same method, if we as-

sumed that the sockeye and coho salmons and the steelhead tagged south of Kodiak Island had embarked as juveniles on May 1, then they each covered about 1,400 miles (2,593 km.), in about 4 months preceding tagging, at an average rate of 11.6 miles (21.5 km.) per day. The May 1 embarkation date is probably correct for the steelhead trout; it was fin-clipped and released in the Alsea River, Oregon, sometime in April 1958. The estimated rates of travel of the latter three juveniles are probably more accurate than the estimated rate of travel of the single pink salmon, so that 10 miles (18.5 km.) per day might be a good working estimate of rate of travel during the initial stage of their ocean migrations.

AUTUMN AND WINTER MIGRATIONS

We have much less data on the autumn and winter migrations, but the general pattern can be deduced from the substantial data on the location of juveniles in late summer and of maturing fish in early spring. By late September, most pink salmon have entered the sea, but substantial numbers still are along the coast from southeastern Alaska to Kodiak Island; juvenile migration must continue, therefore, into October and November. Neave (1964) reported 163 juvenile pink salmon in a trawl catch in Dixon Entrance (lat. 54° N.) on November 5, 1963. After the end of September, the next period for which there are data is January–February, when longlines and gill nets have been fished in recent years, although somewhat sparsely, throughout much of the Gulf of Alaska.[5] Results in 1964 indicated few, if any, pink salmon in the northern Gulf but a wide dispersion in the southern Gulf between lat. 45° and 51° N. and from about long. 133° to 156° W. (fig. 4). At this stage they average 30 cm. long (French, 1966; International North Pacific Fisheries Commission, Annual Report, 1964: 30).

Thus, between midautumn and midwinter, the young pink salmon must leave the coastal belt along the northern Gulf and migrate well to the south, where they are scattered widely in the open sea. The points at which they leave the coastal belt are unknown. They probably do not follow the Alaskan Stream very far to the west, however,

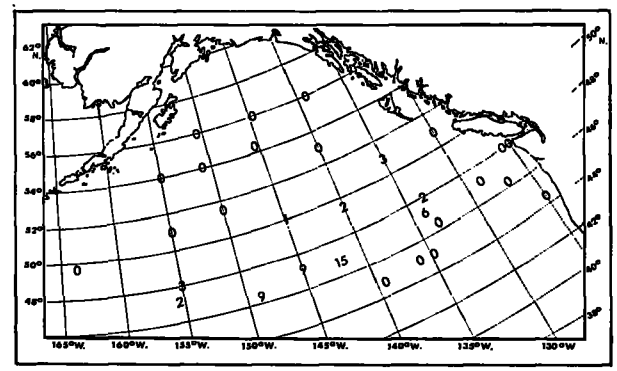

FIGURE 4.—Catch of pink salmon per longline set during winter of 1964. Canadian and United States operations January 7 to February 9 (30 sets, each using 5 to 35 skates—one skate=49 hooks).

because immature pink salmon have never been taken in the extensive seining in the summer and autumn south of the eastern Aleutian Islands. Furthermore, extensive tagging of mature pink salmon in spring and summer south of the Aleutians has yielded returns only from East Kamchatka and western Alaska; none were returned from southeastern Alaska or British Columbia nor from any other Gulf coastal areas. Thus, the stocks in question probably leave the coastal belt east of long. 160° W. Such a southward migration would place them in the eastward-flowing Subarctic Current, on a counterclockwise route back toward their embarkation points (fig. 1). The distance from the northern Gulf to the center of their winter distribution is at least 1,000 miles (1,852 km.), which, if covered in 90 days, would indicate a minimum rate of travel of 10 miles (18.5 km.) per day.

SPRING-SUMMER HOMING MIGRATIONS

The ocean migrations of the maturing pink salmon during their last spring and summer at sea are well documented by a number of years of longline and purse seine sampling throughout the Gulf from late March through mid-August (Neave, 1964; International North Pacific Fisheries Commission Annual Reports, 1961–65). In April pink salmon of the southeastern Alaska-British Columbia stocks are located mainly in the southeastern part of the Gulf east of long. 150° W. and between lat. 43° and 50° N. and are mixed with stocks from Prince William Sound, Kodiak Island, Cook Inlet, and the Alaska Peninsula. The British Colum-

[5] For convenience, *Gulf of Alaska* as used herein refers to all salmon waters east of long. 165° W., thus extending to about lat. 40° N., in conformance with the general oceanic regions described by Manzer et al. (1965).

bia stocks are farthest to the east—mainly east of long. 135° E. (Fisheries Research Board of Canada, 1962–66).

During May and June, pink salmon shift progressively northward in the eastern half of the Gulf and by July are abundant in the northernmost areas (fig. 5). The early-run stocks then migrate toward their respective coastal destinations. Later-run fish frequently return to the southeast in August and September after having migrated northward past their area of origin (Neave, 1964). For these fish the late-season homing migration follows in reverse the coastwise route taken by the juveniles in the Alaskan Gyre and is "upstream" instead of "downstream." Returns of tagged fish to southeastern Alaska and British Columbia in 1962 (fig. 6) illustrate the spring-summer distribution and migrations of these stocks.

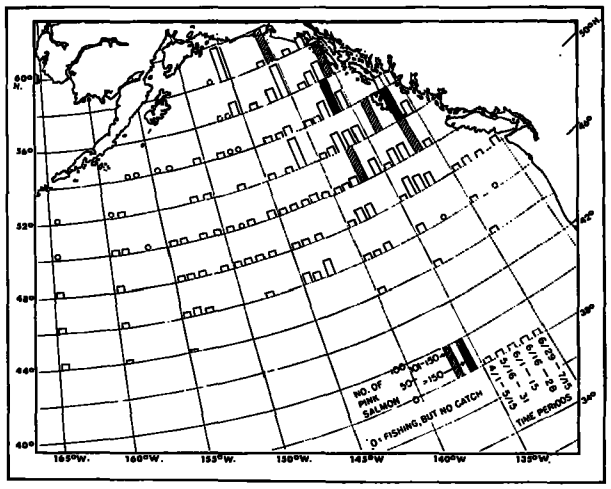

FIGURE 5.—Average catch of pink salmon per 20 skates of longline gear (49 hooks per skate) by area and by time period in 1966 (U.S. and Canadian data unpublished).

The rate of movement of the center of abundance from mid-April to mid-June appears to be about 7 miles (13 km.) per day (if movement is estimated from lat. 48° to 55° N. during the 60-day period). Rates of travel of individual tagged fish based on straight-line distances to recovery points vary from 5 to over 40 miles (9.3–74.1 km.) per day. Mean fork lengths at this stage vary from 45 to 55 cm., or even larger for late-season spawners.

The final migrations through channels and bays to the natal streams need not be reviewed in this paper except to note that coastal tagging indicates considerable "searching" or "to and fro" migrations as the numerous stocks approach their home estuaries (Noerenberg, 1959; Verhoeven, 1952).

SUMMARY

The oceanic migration of southeastern Alaska-British Columbia pink salmon is shown diagrammatically in figure 7 according to four time periods. The western limits and the southern limits are only approximate. After spending 3 to 5 months in estuaries and inner bays and channels, juvenile pink salmon enter the ocean proper in July to September at a length of 10 to 15 cm. They travel rapidly northward and westward along the coast, following the Alaskan Gyre. By late September and early October they average 20 to 22 cm. long. Their average rate of travel is about 10 to 12 miles (18.5–22.2 km.) per day. Between October and midwinter they migrate southward and in January to February are spread widely between lat. 41° and 51° N. and from long. 130° to 160° W. and have continued to migrate at least 10 miles (18.5 km.) per day. At this stage the mean length is 30 cm. In their final spring and summer, they migrate northward in the eastern Gulf from April through July, then coastward to their respective destinations; the late-spawning stocks turn back southeastward to return to their areas of origin. Mean sizes at maturity vary from 45 to 55 cm. Rates of travel in final coastward migrations are at least 10 miles (18.5 km.) per day; some individuals migrate over 45 miles (83.3 km.) per day.

OCEAN MIGRATIONS OF PINK SALMON OF EAST KAMCHATKA

Although data are fewer on the ocean migrations of East Kamchatkan pink salmon than for the southeastern Alaska-British Columbia stocks, the probable sequence of migration can be inferred and certain similarities and contrasts indicated.

The East Kamchatkan stocks (mainly the Karaginski district, fig. 8) are substantial, over 40 million adults in some odd-numbered years.[6] The spawning migration in the Karaginski region is

[6] From: "Pacific salmon catch statistics of the Union of Soviet Socialist Republics 1940–1958" (plus similar tables for individual years 1959–64), as given to the International North Pacific Fisheries Commission by the All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, unpublished.

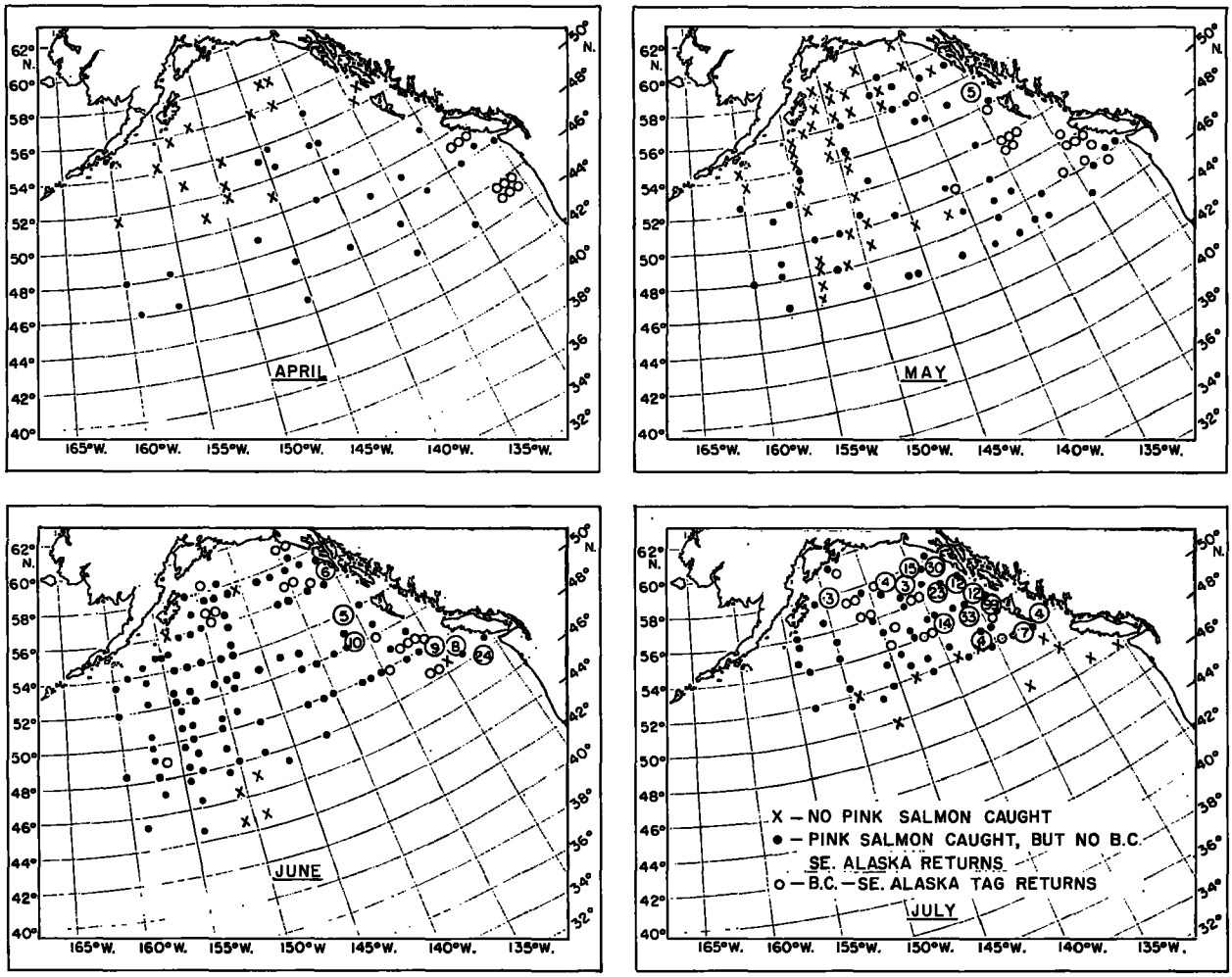

FIGURE 6.—Spring-summer distribution of southeastern Alaska-British Columbia pink salmon in the Gulf of Alaska in 1962 as shown by longline and purse seine catches and by tag returns (source: Canadian and U.S. data, International North Pacific Fisheries Commission Annual Report, 1962).

relatively brief and occurs principally in July (Kaganovskiĭ, 1949). The fry probably migrate to sea in June, but data are lacking.

If the East Kamchatkan pink salmon respond to ocean currents as do the southeastern Alaska-British Columbia stocks, then they may be expected to follow the East Kamchatka Current southwestward along the coast and then to migrate eastward with the Subarctic Current and the Westwind Drift (fig. 1). Their presence in the western Gulf of Alaska (near lat. 50° N. and long. 155° to 160° W.) in May and June has been demonstrated by tag returns (Fisheries Research Board of Canada, 1963; Hartt and Dell, 1964). Their presence south of the entire Aleutian chain from late May through early July and in the Bering Sea in June and July has also been well demonstrated by Japanese and United States tagging (Hartt, 1962; Kondo et al., 1965). Purse seining by the United States has further shown that they move very rapidly in a westward direction south of the Aleutian Islands, northward through the major passes, and northwestward in the Bering Sea. Passage south of the central Aleutians peaks sharply about June 5 to 30.

The rate of travel to the Karaginski district from the central Aleutians (about 800 miles or 1,482 km.) averages about 25 to 30 miles (46.3–55.6 km.) per day for the last 30 to 45 days at sea (Hartt, 1966). Thus, the migration is more

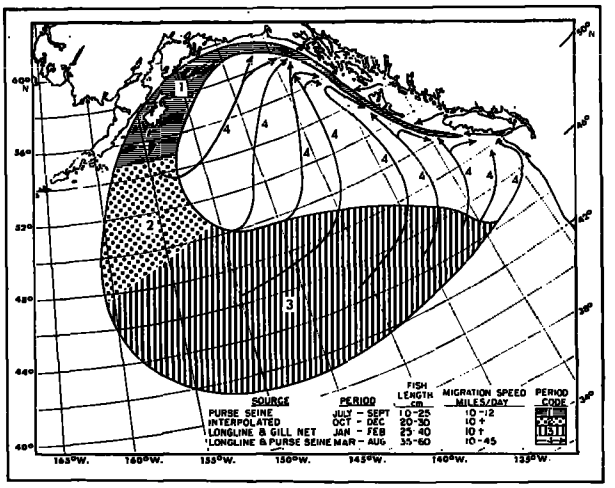

FIGURE 7.—Diagram of ocean migrations of pink salmon stocks originating in southeastern Alaska and British Columbia.

directed and rapid than that of the southeastern Alaska-British Columbia pink salmon, perhaps because the East Kamchatka stocks have a more limited time of arrival.

Recoveries of tagged pink salmon at sea suggest that the fish migrate rather directly toward their coastal destination from the point of release (fig. 8). Ishida (1960) suggested that the fish apparently follow parallel courses toward the Karaginski district from whatever point they enter the Bering Sea. Such an ability to navigate toward "home" is in agreement with Neave's thesis (1964) that to perform the observed migrations salmon at sea must maintain "bico-ordinate orientation" (i.e., oriented with respect to "home" in two components such as east-west and north-south).

The postulated migration of East Kamchatka pink salmon is diagrammed in figure 9. The first two steps—migration downstream in the East Kamchatka Current and in the Subarctic Current and Westwind Drift—are assumed (figs. 1 and 9). Direction appears to change abruptly as they depart the eastward-flowing Subarctic Current and join the westward-flowing Alaskan Stream. The influence of the Bering Sea Gyre on the migration route is unknown, but the tagging data illustrated in figure 8 indicate that migration continues rather directly through the Gyre.

A significant feature of the migration of the Karaginski pink salmon is that throughout much of their route during their last 60 to 90 days at sea they are intermingled little with other pink salmon stocks although they are extensively intermingled with sockeye and chum salmon. In the western part of their distribution they are mixed with West Kamchatka and other Sea of Okhotsk stocks, and in the eastern extreme they mix with Gulf of Alaska stocks (Hartt, 1966). In the central part of their oceanic range they are mixed only with the relatively minor Aleutian and western Alaska stocks. Tagging data indicate that their distribution is probably just as extensive in even-numbered years of low abundance as in odd-numbered years of high abundance. In addition, the abundant West Kamchatka or Gulf of Alaska stocks do not move into the central Aleutian area in years when the East Kamchatka stocks are scarce (Hartt, 1966; Kondo et al., 1965). These observations indicate that oceanic-migration patterns are independent of abundance within or between individual stocks.

OCEAN MIGRATIONS OF SOCKEYE SALMON OF BRISTOL BAY

Bristol Bay stocks are defined herein as those originating in the eastern Bering Sea between the northern side of Unimak Island and the Kuskokwim River (fig. 10); fish originating within this area migrate similarly at sea. Nearly all originate in five main river systems—Nushagak, Kvichak, Naknek, Egegik, and Ugashik—which enter at the head of Bristol Bay near lat. 58° N., long. 157° W. (fig. 10). These stocks make up the largest sockeye salmon run in the world, between 6 and 60 million mature fish per year. The annual average for 1956–65 was 23.9 million (Ossiander, 1965; Pacific Fisherman, 1966).

The life history of Bristol Bay sockeye salmon, although variable, may be described in general as follows. Spawning takes place in August and September in the vast Bristol Bay lake systems. Fry emerge mainly in June. The young fish generally spend 1 or 2 winters in fresh water and migrate to sea as 2- or 3-year-old smolts. Downstream migration is mainly in June, simultaneously with or immediately after breakup of the lake ice. Most then spend 2 or 3 years at sea so that their total age at maturity is usually 4, 5, or 6 years with various combinations of fresh-water and salt-water age. The returning run migrates through the estuaries from about June 20 through July 25, but

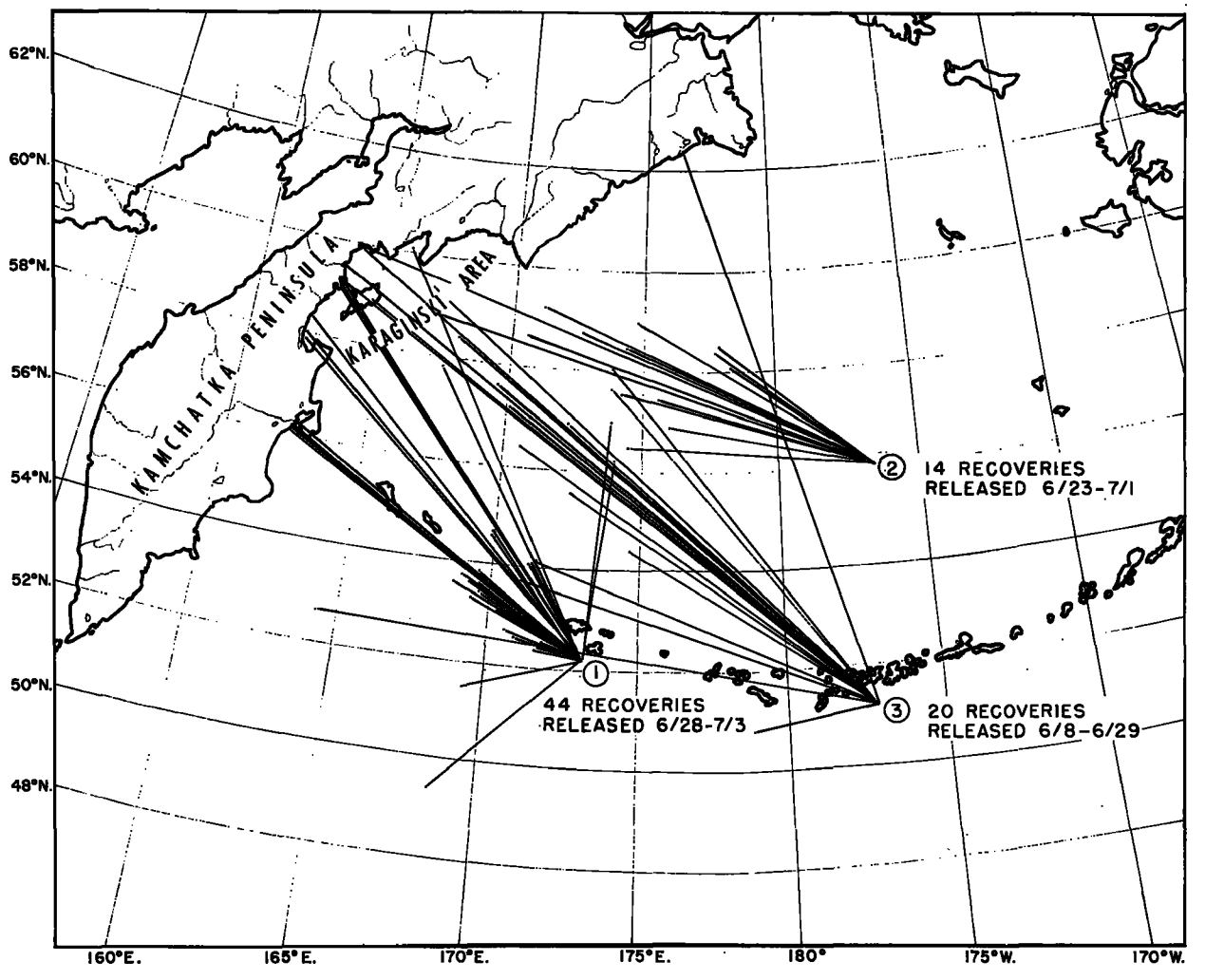

FIGURE 8.—High-seas and coastal recoveries of pink salmon tagged at three points in the North Pacific Ocean and Bering Sea in 1959.

over 80 percent of the run arrives within 9 to 22 days, and this arrival period occurs regularly between June 23 and July 18 (Royce, 1965). The peaks of the run vary only from July 2 to July 9.

The ocean migrations of the Bristol Bay sockeye salmon have been studied intensively more than 10 years (International North Pacific Fisheries Commission, 1957–66). Excellent data are available for the spring and summer periods, and some winter data are available, so that the entire migratory pattern can be inferred.

FIRST YEAR AT SEA

The smolts from the five main river systems enter the coastal waters of Bristol Bay in an intensive mass migration that peaks sharply during June. Their length at this stage typically ranges from 7 to 12 cm., varying according to river system and fresh-water age. During July, they travel at least as far westward as long. 164° W. (250 miles [463 km.] from the Naknek-Kvichak estuary) and are apparently most abundant near the Alaskan Peninsula. Observations at this stage are based on limited purse seining in 1962 and 1966 (unpublished). Purse seine catches ranged up to 1,300 fish per set. At this stage they feed heavily on euphausids and larval fish and grow rapidly; the average size of those in the westernmost samples ranged from 13 to 15 cm. in July.

After this early marine stage, data on their migrations are few until they appear a year later

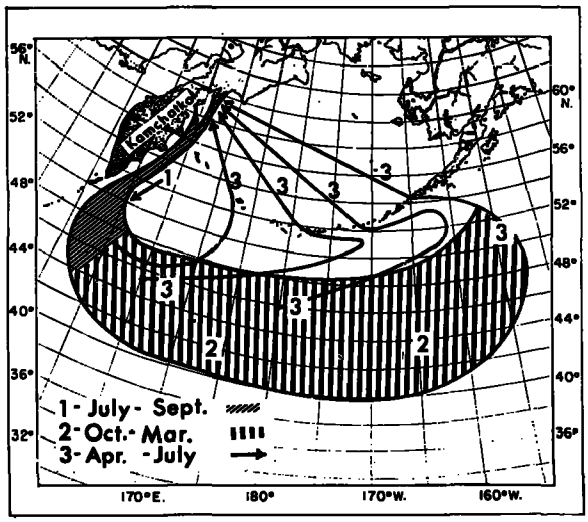

FIGURE 9.—Diagram of probable ocean migrations of pink salmon stocks originating in East Kamchatka.

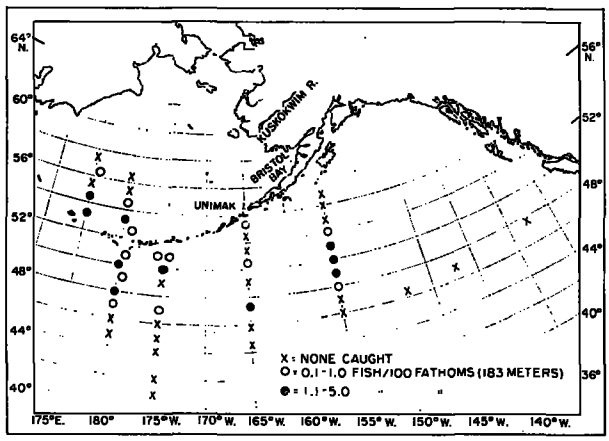

FIGURE 10.—Catches of .1-age sockeye salmon during winter gill netting in 1962 and 1963 (source: French and Mason, 1964).

as .1-age [7] immature fish of 35-cm. average length migrating westward in large numbers along the south side of the Aleutian Islands. Two items of indirect evidence, however, help fill in the first year's migration. First, the Bristol Bay sockeye salmon apparently do not migrate south of the Aleutians during their first summer; .0-age juveniles were extremely rare in the intensive purse seine sampling along the south side of the Aleutians during the summers of 1956–65 (International North Pacific Fisheries Commission, 1957–66). Second, winter sampling with gill nets (French and Mason, 1964) has shown the presence of .1-age sockeye salmon north of the western Aleutians and south of the central Aleutians during January and February (fig. 10). At this stage they average about 25 to 30 cm. long. It has not been proved that these are Bristol Bay fish, but it seems safe so to assume, because of their abundance and because tagging and other studies have shown that Bristol Bay stocks predominate in these areas in spring and summer. Thus, we may postulate that the fingerlings remain in the Bering Sea at least until autumn, and their winter distribution suggests that they reach the western Bering Sea and proceed southward into the North Pacific. The next move must be eastward in the Subarctic Current to place them in position by late spring to make the characteristic summer migration westward with the Alaskan Stream along the south side of the Aleutian Islands—a migration which has been extensively studied and described (Hartt, 1966). The postulated first year's migration is diagrammed in figure 11A as part of the schematic of their entire ocean travels. The first year's migration could be accomplished at an average rate of 10 miles (18.5 km.) per day, which is the rate indicated for the juveniles tagged near Kodiak Island in the Gulf of Alaska discussed earlier.

SECOND YEAR AT SEA

During their second summer at sea, Bristol Bay sockeye salmon are immature .1-age fish averaging 35 cm. long. They migrate westward south of the Aleutian Islands in a more or less continuous band, from late June through mid-September. The band extends offshore about 100 miles (185 km.), but the greatest abundance is usually within 30 miles (55.6 km.) (French, 1964; Hartt, 1966). The fish apparently approach from areas to the south and east and continue far westward and northwestward, as shown by tag returns from the high-seas fleet in the year of release (fig. 12). The dominance of Bristol Bay stocks is demonstrated by coastal tag returns 1 year later (fig. 12) and by the relation between age composition and abundance at sea and age composition and abundance in the Bristol Bay run 1 year later (Ossiander, 1965). Some idea of the magnitude of the

[7] Ocean age designation throughout this paper is that proposed by Koo (1962) in which the number of ocean winter annuli on the scale is preceded by a decimal point (e.g., .1-age—one winter at sea).

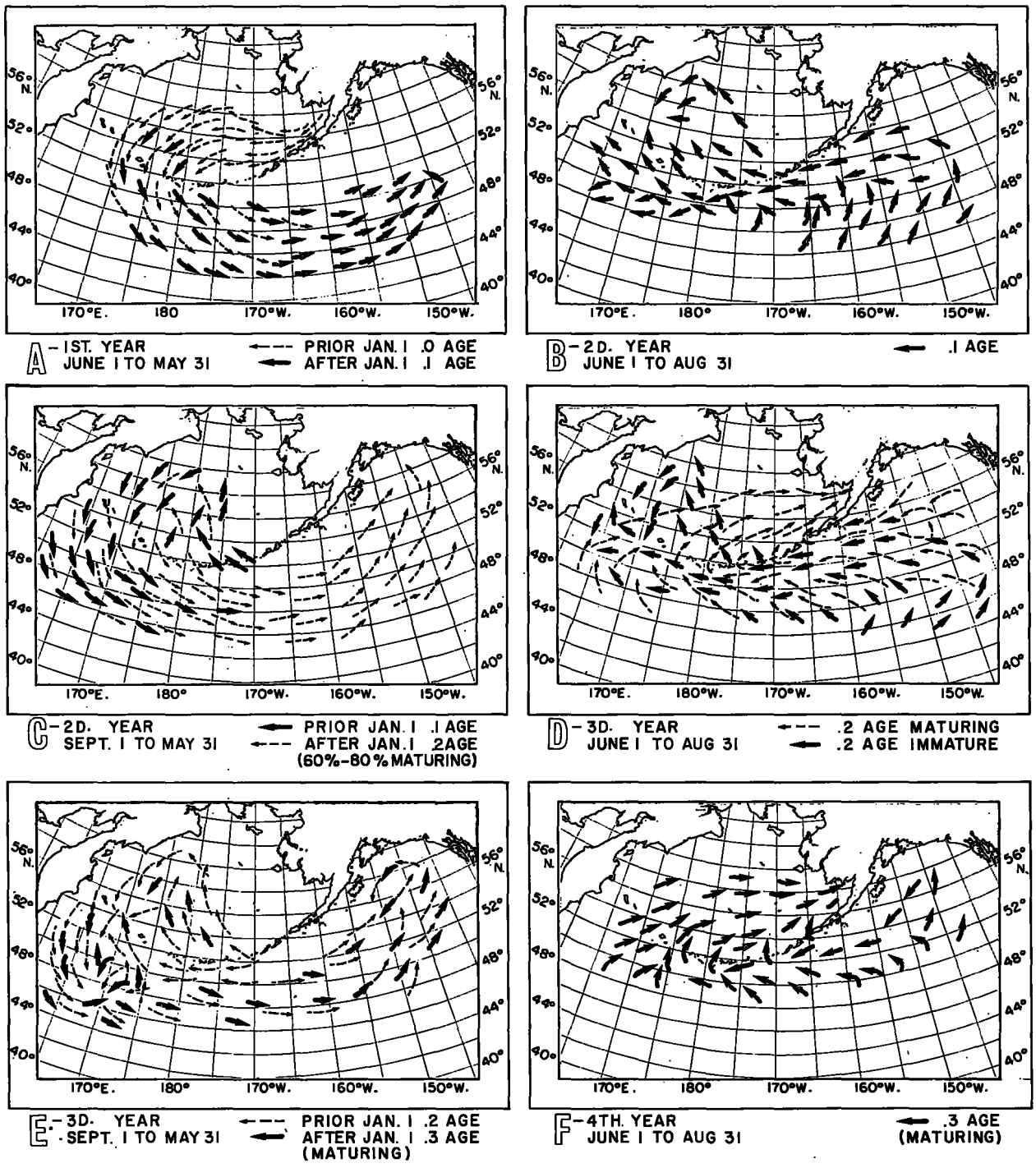

FIGURE 11.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on seine catch and tagging data through 1966; arrows indicate direction and approximate distribution.

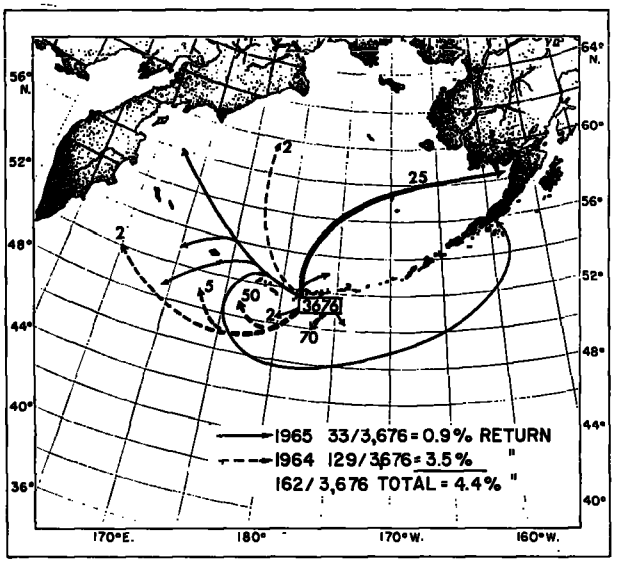

FIGURE 12.—Recovery distribution of sockeye salmon tagged as .1-age immature fish at Adak in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

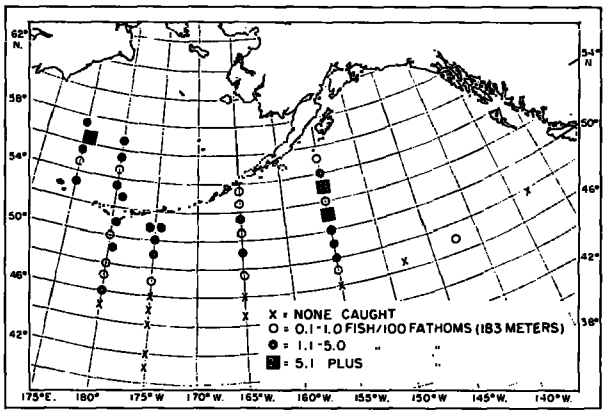

FIGURE 13.—Catches of .2-age and older sockeye salmon during winter gill netting in 1962 and 1963. (source: French and Mason, 1964).

numbers can be gained from a conservative time-space extrapolation of the average catch per 30-minute seine set; in 1964 a minimum of 0.5 million .1-age sockeye salmon per day passed westward south of Adak Island from late June through late August, or about 30 million of this age group alone. The rate of travel averaged 17 miles (31.5 km.) per day for those recovered by the Japanese fleet in 1964. Stomach examinations indicated that the fish feed actively on various crustaceans and larval fish (Dell, 1963). The probable summer migration of the .1-age immature fish is summarized in figure 11B.

The fact that the .1-age fish migrate past a given point for a long period indicates that they must be spread over a large area at sea. Such an extended distribution is probably characteristic of salmon in general even in their first summer, as evidenced by the long band of .0-age salmon of all species along the coast of the Gulf of Alaska described earlier. It is important to emphasize here that the .1-age immature sockeye salmon at this stage are thoroughly mixed with the .2-age immature fish that left Bristol Bay a year earlier; apparently they overtake the previous year's smolts and then follow a similar migratory path.

The winter data (figs. 10 and 13) indicate that the intermingling of the age groups takes place as early as January. In general, however, the .1-age group in figure 10 was farther south than the older fish shown in figure 13. Thus, it would appear that the migration of this age group is independent of the older fish at this early stage.

The migrations during the autumn and winter of the second year at sea can be inferred from the limited winter sampling and from the distribution and migrations observed in the following spring and summer (fig. 11C). During this period the .1-age fish add another winter mark on their scales and become .2-age fish. Some will mature in this year and migrate homeward to spawn, but others will remain at sea to mature a year later at .3-age. As illustrated in figure 13, .2-age sockeye salmon are distributed widely during the winter (January–March) in the central and western Bering Sea and in the North Pacific at most sampling stations north of lat. 45° N. As at other times of the year, Bristol Bay fish may be expected to be present in most of the samples. The data then suffer a gap until the following May, when samples taken by purse seines indicate few, if any, sockeye salmon in the Alaskan Stream south of the Aleutians. In late May and early June, however, the maturing .2-age sockeye salmon begin to appear in the catches along the entire south side of the Aleutians, and they are again migrating westward in the Alaskan Stream. The evidence, thus, indicates a southward shift during late winter and early

spring and a return migration toward the east in the Subarctic Current (fig. 1). The fish apparently repeat the winter-spring-summer round of migrations of their first year at sea (fig. 11A). Further support for this hypothesis is provided by the recovery in the Shumagin Islands area in the eastern Aleutians of .2-age sockeye salmon that had been tagged as .1-age immature fish a year earlier near Adak Island (fig. 12). The 1964 data are typical of other years' results. At Adak they had been part of the westward flow of immature fish, and at Shumagin Islands they were among maturing fish that characteristically migrate westward, many of them en route to Bristol Bay (Thorsteinson and Merrell, 1964).

THIRD YEAR AT SEA

The migrations during the third year at sea must be considered separately for one group that matures and returns to spawn at the end of its second year at sea (early in its third summer at sea), and another group that remains another full year at sea. From the numbers of .2- and .3-age fish returning in successive years, about 60 to 80 percent of the .2-age group mature and spawn. The fish of the maturing group average about 51 to 53 cm. in fork length and are thoroughly mixed with the older .3-age mature salmon. They approach the eastern Aleutian Islands area from the south and southeast in late May, migrate westward with the Alaskan Stream, northward through the Aleutian passes, and then northeastward toward their respective Bristol Bay estuaries (Hartt, 1966). The recovery distribution of sockeye salmon (mostly .2-age mature fish) tagged in the Aleutian Island area in 1960 is illustrated in figure 14. Those approaching from far to the west apparently migrate rather directly toward the Bay. Recaptures by the high-seas fleet illustrate the course through the central Aleutian area. The lack of high-seas returns from releases in the eastern Aleutians (fig. 14D) indicates that this group must have turned northward and entered the Bering Sea before reaching lat. 175° W. Migration speed is rapid during the final 30 to 60 days at sea, averaging 25 to 30 miles (46.3 to 55.6 km.) per day.

Even as late as May 1, sockeye salmon from Bristol Bay are distributed over vast areas at sea extending from 1,200 miles (2,222 km.) to the west off the Kamchatka Peninsula to 1,200 miles to the east in the central Gulf of Alaska. Figure 15 illustrates the tagging areas during the period May 1 to June 15 from which Bristol Bay recoveries were subsequently received in the year of release.

The bulk of the run passes through the Aleutian Islands area between June 1 and 20, and through the estuaries between June 23 and July 18, with the peak between July 2 and 9. Tagging has indicated a sequential correspondence between date of

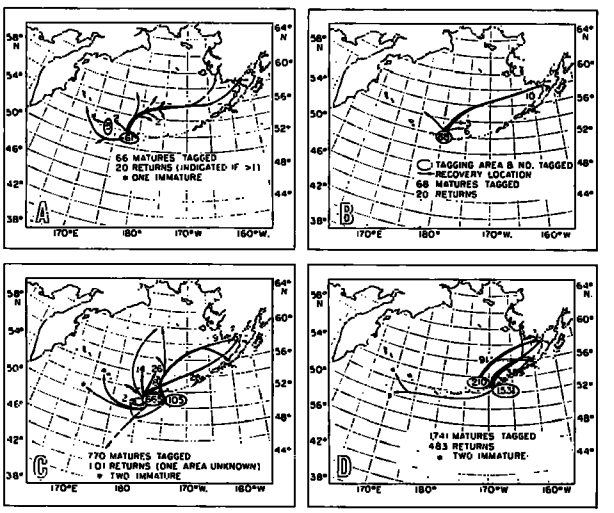

FIGURE 14.—Distribution of recoveries of sockeye salmon tagged and recovered in 1960 (U.S. tagging). Panels A, C, and D each show the results from two areas of operation; panel B shows the results from one.

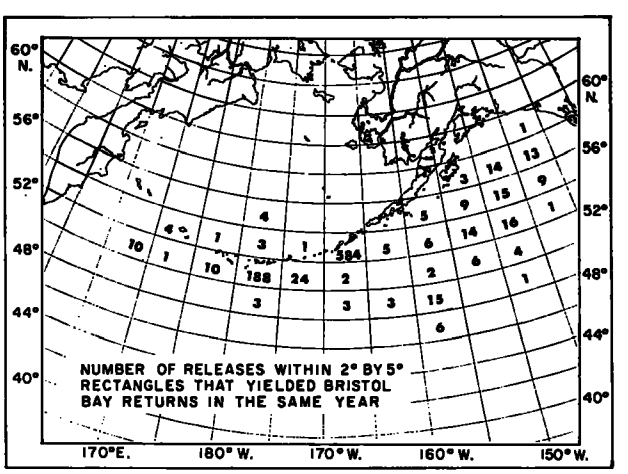

FIGURE 15.—Areas of release of sockeye salmon tagged between May 1 and June 15, and subsequently recovered in Bristol Bay in the same year between June 26 and July 24 (U.S. data 1956–65, Canadian data 1961–65, Japanese data 1958–61).

release in the Aleutians area and date of recovery in the commercial fishery and a tendency toward more rapid movement by the later migrants (Hartt, 1966). Many of the fish still feed actively on a variety of animals when within only 100 miles (185 km.) of the estuaries.

The immature .2-age fish during their third summer at sea follow a course similar to that of the .2-age mature fish except that they continue westward and northwestward in the Aleutian Islands and Bering Sea areas, rather than returning northeastward toward Bristol Bay (fig. 11D). They average 46 to 48 cm. long and are slimmer than the .2-age mature fish. Immature salmon begin to arrive in the Aleutian area just after the mature fish have passed and continue on a course similar to that described for their migrations in the previous summer as .1-age fish.

The earlier timing of the maturing group of .2-age fish indicates that they segregate from those not maturing, apparently by accelerating their speed or by taking a shorter route. As .1-age fish the previous summer they had been thoroughly mixed with the immature group, as verified by the fact that .1-age immature fish tagged in the same purse seine set frequently yield Bristol Bay returns both 1 year and 2 years later (Hartt, 1966).

The summer migrations of the .2-age immature sockeye salmon can be illustrated more completely by tag returns from U.S. tagging in 1964 (fig. 16).

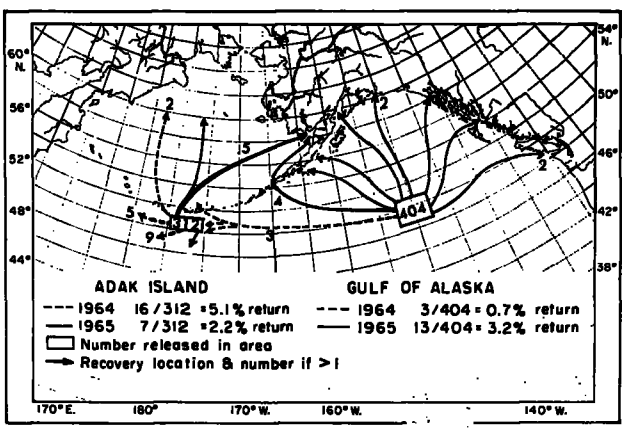

FIGURE 16.—Recovery distribution of sockeye salmon tagged as .2-age immature fish in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

In 1964, substantial numbers of .2-age immature fish were tagged in the central Aleutian area and in the central Gulf of Alaska, so that together the tag returns bring out the salient features of migration. The 312 fish tagged south of Adak Island were released between late June and mid-August and were part of the characteristic summer migration that passes westward south of the Aleutian Islands. The 16 high-seas recoveries in 1964 (late July and early August) illustrate the westward and northwestward summer migration of immature fish into the western North Pacific and Bering Sea. The high-seas returns of mature fish in 1965 were probably en route to Bristol Bay, and the five Bristol Bay coastal returns together with a lack of coastal returns from areas other than Bristol Bay illustrate that fish migrating south of the Aleutians were primarily of Bristol Bay origin. The 404 fish tagged in the central Gulf (fig. 16) were released during May 1964, at which time the enclosed area was the apparent center of abundance of .2-age immature sockeye salmon as judged by longline sampling throughout the Gulf. The four coastal returns from Bristol Bay in 1965 demonstrate the presence of this stock and the nine Gulf coastal returns indicate a mixture of all major Gulf of Alaska stocks as well. The three high-seas returns in 1964 near the central Aleutians, all in late July and early August, show that part of the group from the central Gulf entered the mass westward migration south of the Aleutians. In all probability these fish were the Bristol Bay components of the Gulf mixture, and, thus, illustrate the summer return migration from the Gulf of at least some of the Bristol Bay immature fish. The route followed by the Gulf of Alaska stocks is not known, but they apparently did not enter the migration south of the central Aleutians, since tagging in that area yielded no Gulf coastal returns. Thus, the data in figure 16 illustrate that the migratory course of different salmon stocks can be discrete even though they overlap at certain times and places, which in turn suggests inherently different responses to whatever cues may be guiding them even at the immature stage.

The migrations of the .2-age immature sockeye salmon during the remainder of their third year at sea are apparently a repetition of those in their second year, i.e., westward or northwestward into

the western North Pacific and Bering Sea during summer and fall, and then southward and eastward in the Subarctic Current in winter and spring (fig. 11E). During summer and fall they are mixed with the .1-age group of the next younger generation, and in winter they are joined by the newest generation of juveniles coming from Bristol Bay as discussed earlier. Finally, at the end of their third year and the beginning of their fourth summer, they again migrate westward in the Alaska Stream, northward through the Aleutian passes and northeastward to Bristol Bay. As .3-age mature fish they average 57 to 59 cm. in fork length and are accompanied by that part of the new .2-age group that is maturing in the same year. Their final migration is shown diagrammatically in figure 11F.

SUMMARY

A review of the entire ocean migration of Bristol Bay sockeye salmon as summarized in figure 17 indicates that they make two or three circuits of an elongated east-west course extending from about long. 165° E. to 140° W. The diagram is simplified and idealized, but it takes into account the major seasonal migrations and shifts in abundance shown by available catch and tagging data. The change in age is shown for convenience as occurring only at the western extremity of the migration, but undoubtedly each age group is distributed over a considerable part of the migratory path at the time the winter annuli are formed.

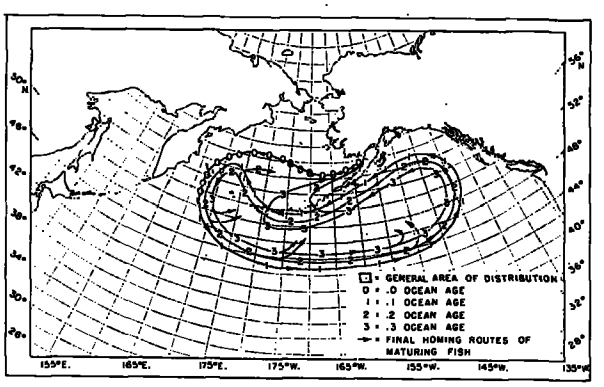

FIGURE 17.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on U.S. seine catch data, and on Canadian, Japanese, and U.S. tagging data through 1966.

COMMON CHARACTERISTICS OF SALMON MIGRATIONS

We have described the principal features of the migration of three of the major stocks of salmon in the North Pacific. We have postulated migrations and behavior that seem to us to be necessary if the salmon are to migrate to where they have been found, even though our information has some significant gaps. Many of the features of the migrations and behavior of these stocks are characteristic of most salmon stocks; we will summarize them in this section before we turn to a discussion of possible direction-finding or position-finding mechanisms.

The first outstanding feature is that each individual performs the migration once with no possibility of learning from a parent and with a poor chance of spawning successfully to perpetuate the race if it becomes lost or departs from the required time schedule. Clearly the navigational system is an entirely inherited series of responses to stimuli.

Second, the salmon migrate near the surface of the ocean, mostly in the upper 10 m. The success of the Japanese high-seas fishery, which uses surface gill nets (about 5 m. deep), and the research fishing experience with gill nets and longlines indicate that the salmon are typically caught near the surface. A few salmon (mostly chum salmon) have been taken by gill nets set at depths of 30 to 70 m. (International North Pacific Fisheries Commission, Annual Report, 1960: 26), but the latter depth seems to be near the depth limit. In coastal waters, coho salmon are often taken by trollers at a depth of 10 to 20 m. and chinook salmon between 20 and 30 m. (Milne, 1955).

The third outstanding feature is the long distance traveled. The pink salmon from southeastern Alaska or British Columbia and from the Karaginski district cover 3,000 miles (5,556 km.) or more in 12 to 15 months. Some of the pink salmon from the Karaginski district travel more than 4,000 miles (7,408 km.). Even greater distances are traveled by chum salmon which return to Hokkaido from south of Kodiak and chinook salmon which return to the Columbia River from south of the central Aleutian Islands. Further, the salmon that spend more than 1 year at sea, such as the chum and sockeye salmon, may well undertake an annual feeding migration in excess of 2,000 miles (3,704 km.). Our information about such migra-

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tions for immature fish is scanty, but the circumstantial evidence certainly indicates that the Bristol Bay sockeye salmon undertake substantial feeding migrations during their second and third summers at sea before they return to the home stream.

Fourth, much of the migration is not to and fro, but circular. The circuit which is closed only upon return home appears to consist of a single loop in the pink salmon from southeastern Alaska-British Columbia and Kamchatka and multiple loops in the Bristol Bay sockeye salmon. In none of these cases does it appear to be possible for the salmon to use memorized stimuli that could be followed back in reverse order.

During these long migrations the races that have been studied extensively occupy a distinctive but very large part of the ocean. Thus, the ranges of the various stocks of the several species overlap to an enormous extent. For example, tagged salmon have returned to Bristol Bay and also to the Fraser River from a group caught in a single set of the net in the northwestern part of the Gulf of Alaska. The salmon of the several species tagged near Adak Island, Alaska, have been recovered from nearly the western, northern, and eastern extremities of the range of Pacific salmon.

We believe that particular stocks of salmon have no tendency to school as a group in the ocean. We reinforce this assertion by the observation that usually we capture salmon of different species, age groups, and sizes on single sets of gear except when close to a destination of maturing salmon where a single stock may predominate. Even in such areas with a dominating single stock, the numbers caught per seine set are much more uniform over considerable areas and on successive days than would be true if the salmon were in separate, compact schools as are herring, for example.

Perhaps the most startling evidence of the individual behavior of salmon is indicated by the distribution of the mature Bristol Bay sockeye salmon in May and early June, 4 to 10 weeks before they arrive in Bristol Bay (fig. 15). At this time they are spread over some 2,000 miles (3,704 km.) of ocean in an east-west direction and some must migrate to Bristol Bay from as far as 1,200 miles (2,222 km.) away, either directly or in a dogleg to circumnavigate the Alaskan Peninsula. Within this range no evidence has appeared of segregation of the runs to the individual Bristol Bay rivers.

The salmon appear to be nearly continuous travelers. Many of them average about 10 miles (18.5 km.) per day while immature. When maturing, they commonly travel an average of 25 to 30 miles (46.3–55.6 km.) a day and occasionally may average more than 45 miles (83.3 km.) daily over long distances.

These speeds are clearly faster than most ocean currents that may carry the fish. The directional catches of the purse seine in many parts of the ocean for both mature and immature fish indicate clearly that the salmon exceed the speed of the current. The migration is positive, not a passive drifting.

These long migrations terminate on a remarkably consistent schedule. The migration of the Bristol Bay sockeye salmon past Adak Island (about 900 miles [1,667 km.] from home) is completed in about the same length of time and in about the same sequence of individuals as the migration through the fishing areas in Bristol Bay (Hartt, 1966). The runs in Bristol Bay in 1956–65 peaked on the average date of July 5, and the earliest and latest peaks were July 2 and July 9 (Royce, 1965). Eighty percent of the run in the same years arrived in 9 to 22 days. Other runs of salmon in more southerly latitudes commonly occur over greater periods of time, but we believe this spread is usually due to different schedules of the several populations that make up these runs. It appears to be common for a single interbreeding population to keep a schedule that varies from the average by only a few days.

The arrival of the salmon is less variable than the seasonal change in the weather. For example, average water temperatures at Weather Station P, located at lat. 50° N., long. 145° W. in the central Gulf of Alaska, show an average monthly increase of 2.2° C. from May to July (Bureau of Commercial Fisheries, 1957–65), but the range of attained mean monthly temperatures for 1957–65 shows that the May mean varied from 6.1° to 7.8° C., the June mean from 7.8° to 10.6° C., and the July mean from 10.6° to 13.3° C. If the timing of salmon migrations were governed by certain critical temperatures in the waters through which they are distributed, then the arrival date would vary by about 2 weeks around a mean.

The routes followed during the migrations seem unrelated to land or continental shelves. Sometimes a considerable concentration of salmon appears in passes and near points, but the normal migratory routes seem to be across open water, even where, as in the approaches to inner Bristol Bay, it would be convenient to follow close to the shore.

The remarkable directness of the final migration in the open sea is illustrated by the Karaginski district pink salmon that migrate through the area of the Japanese high-seas fishery. When the fish have been tagged and released from different points along a north-south line, the recaptures show the tendency to proceed rather directly toward their destination (fig. 8). Obviously, their migration is not random as suggested by Saila and Shappy (1963).

Many of the migration routes traverse different ocean domains. The Karaginski pink salmon, for example, within 2 months apparently travel from the eastwardly flowing central Subarctic Current across the Alaskan Gyre, across the westerly flowing Alaskan Stream, and through the Bering Sea Gyre in the western Subarctic Domain (see Dodimead et al., 1963:167). Bristol Bay sockeye salmon regularly occupy the Alaskan Gyre and the western Subarctic Gyre in late spring and migrate through the Bering Sea Gyre on the homeward migration. Such routes clearly take the salmon through parts of the ocean far removed from any recent mixing with home-stream waters, and we conclude, as does Neave (1964), that the olfactory sense cannot provide a significant source of guidance information except at the end of the route.

Much of this migration takes place through and during some of the most prolonged and violent ocean storms in the world. The weather of the Aleutians area (U.S. Department of Commerce, 1955: 343) is characterized by persistently overcast skies, high winds, and violent storms. No other oceanic area in the world is recognized as having worse weather in general than that of the Aleutian Islands—clear weather over large areas is rare. Even in the milder summer periods, the sky is obscured by fog, mist, haze, or clouds most of the time. In the outer parts of Bristol Bay (U.S. Department of Commerce, 1955: 631) the average weather in June (the month when most salmon are homeward bound) is 44 percent fog, mist, or haze, and mean cloud cover is 8/10. In the central Gulf of Alaska (U.S. Department of Commerce, 1955: 619) the average June weather is 25 percent fog, mist, or haze; the mean cloud cover is 9/10. Our own experience with several years of vessel operation in this area indicates that it is impossible to navigate by celestial observations alone, and we suggest that salmon have far too little opportunity to observe the direction of either the sun or the polarization of light to keep the kind of schedule that they manage.

POSSIBLE GUIDANCE MECHANISMS

Little can be said about the physiology of salmon which specifically explains how they navigate during transoceanic migrations, because the necessary experiments have not been performed. If certain generalizations are made, however, some interesting possibilities emerge from the migration data just presented and from the literature of fish physiology as a whole.

Two of the preceding generalizations from the tagging and seining data seem particularly significant. First, the most common direction of travel follows the various North Pacific currents. Second, salmon in the open sea do not drift with the current, but actively swim with it. We, therefore, conclude that the migrations of salmon on the high seas are actively directional in a way which somehow relates to the ocean currents. Directional cues for animal orientation have included celestial bodies, water movement, olfactory stimuli, and electrical or magnetic fields. Let us examine whether any of these are compatible with our data on salmon migrations.

SUN ORIENTATION

The sun, a prominent object by which some terrestrial animals navigate, could similarly serve salmon on the high seas. Indeed, certain lake fish have such an orienting mechanism (Hasler and Schwassmann, 1960). Also, some arthropods orient to the plane of polarization of sunlight (Ivanoff and Waterman, 1958). Arthropods and fish both require good visibility of the sun, however, because both become disoriented when clouds obscure the sun (Waterman, 1959; Hasler et al., 1958). Salmon, on the other hand, migrate at night as well as during the day and through regions where clouds obscure the sun almost continuously.

Furthermore, small lakes have only minimal amounts of wave action to complicate a fish's view of the sun, but marine fish must view the sun through a water surface which is never completely calm. Also, lake fish can migrate in straight lines; salmon migrate along circular as well as straight routes. This circumstantial evidence casts doubt on sun orientation as a primary navigational mechanism for Pacific salmon.

Although the cloudy weather of the North Pacific severely limits the possible use of sun orientation by salmon, use of the sun cannot be entirely eliminated from consideration. An oceanic bird, the slenderbilled shearwater (*Puffinus tenuirostris*), which makes an annual circum-Pacific, transequatorial migration, travels near the Aleutian Islands at about the same time that some salmon there begin their final homeward migration. The slenderbilled shearwater appears to use sun orientation as its primary navigational cue (Serventy, 1963), even though a related shearwater becomes disoriented during overcast conditions (Matthews, 1964). Despite such evidence on possible use of the sun, a simpler hypothesis to explain navigation by salmon on the high seas seems preferable.

ORIENTATION TO WATER MOVEMENT

Fish in rivers and streams are very sensitive to current direction and usually orient upstream to maintain position. Salmon smolts often show an active downstream orientation during their seaward migration. Optical, tactile, and lateral-line senses all seem to be involved in these rheotropisms, but the need for some kind of stationary reference point, such as a shore or the stream bottom, makes this an unlikely mechanism for use on the high seas where reference points are very distant. Direct detection of water movement also seems unlikely because of the very large size of the water bodies and, therefore, the correspondingly slight velocity gradients. A gradient does exist, however, and the sensitivity of fish to velocity gradients in the absence of other cues appears untested; it cannot be entirely excluded as a possible navigational mechanism.

Salmon are perhaps capable of detecting the interfaces between moving bodies of water either through sensing of chemical differences between two bodies of water or by detecting the water turbulence at the interface. This navigational cue would lead to a great deal of random swimming, however, while the fish searches for these margins and would tend to concentrate fish near the margins of ocean currents; neither behavior is characteristic of salmon migration. Salmon are relatively evenly distributed across the ocean currents and the migration routes appear well defined and "purposive," often converging on the spawning streams from several directions.

ELECTRICAL POTENTIALS AVAILABLE FOR ORIENTATION

Because sea water is an electrical conductor moving through the earth's magnetic field, the production of an electrical voltage can be expected. Oceanographers have recognized the electrical potential of sea water for some time. Stommel (1954) found potential differences of 0.2 to 2.6 v. across long distances in the Atlantic Ocean among several submarine cables. Similar voltages were observed between Florida and Cuba. Snyder (1966), in describing the underwater search for the atomic submarine *Thresher*, reported a voltage of about 140 mv. (millivolts) between towed electrodes, one on the surface and one in about 2,440 m. of water. Hughes (1962) attempted to use these voltages to measure ocean currents by towing electrodes, spaced 46 m. apart, behind a ship. He found voltages of 3 to 5 mv. when the ship crossed the current and a reversal of polarity when the ship traveled in the reverse direction. Voltage was nil when the ship moved either with or against the current. The voltages per knot of current varied considerably in shallow water but consistency was greater in deep water.

The electrical gradient that might be available for navigational use, therefore, is about 0.1 to 0.5 μv. (microvolts)/cm. Because these voltages are directly related to the current and are polarized with respect to its direction, electrical cues seem to be a possible navigational device for salmon on the high seas. Magnetic sensitivity has been shown for several animals, but the receptor organ is unknown. Presumably, detection occurs as a result of a voltage induced within the receptor (Brown, Barnwell, and Webb, 1964). The basic question, therefore, is whether fish can detect minute voltages.

ELECTRICAL SENSITIVITY OF FISH

At present no information appears to be available on the electrical sensitivity of salmonids. Even though experiments in the electrical guidance of salmon smolts migrating downstream have been large and intensive, this work seems not to have included any examination of possible electroreceptor organs. Certain other fish, however, which have electric organs as well as electrical receptors have been investigated extensively.

One group of electric fish includes the electric eel. Hagiwara, Szabo, and Enger (1965a) described the physiological properties of electroreceptors in the electric eel, *Electrophorus*. Two types of electroreceptors reside in the lateral line. Some of them respond only to electrical stimuli, but others are mechanically and electrically sensitive. The threshold of the "pure" electroreceptors to imposed square pulses was 2 to 30 mv./cm. and the discrimination threshold was 1.5 to 5 mv./cm. Since the electric eel's low-voltage pulses that it uses for electrolocation are still relatively high voltages—20 to 50 v.—Hagiwara et al. (1965a) suggested that the response of the mechanoreceptors to these electric signals may be only incidental and not biologically significant. Because salmon hardly experience signals of this magnitude, however, more useful interpretations can be gained from information on a group of weakly electric fish.

Members of several genera of the weakly electric gymnotid eels have electric organs that produce electrical pulses of about 30 mv. at 40 to 600 per second. Lissmann (1951) recorded such signals from *Gymnarchus* and played back the fish's own signals through a pair of electrodes in the water at a distance from the fish. At a strength of about 30 μv. the fish responded to the signals by immediately attacking the electrodes. Lissmann and Machin (1958) performed behavioral experiments with *Gymnarchus* which indicated that the fish discriminated changes in the electrical field of 0.02 μv./cm.

In contrast, the sensitivity of individual receptors is much less than that indicated by behavioral experiments. Hagiwara and Morita (1963), who recorded electrical activity from individual neurons of the lateral-line nerve in two other gymnotids, *Staetogenes* and *Gymnotus*, found a threshold for an imposed electrical field of about 10 mv./cm. along the long axis and a discrimination threshold of 0.1 to 1 mv./cm. Hagiwara et al. (1965b) found that the electroreceptors of *Sternarchus* responded phasically and tonically to stimuli. The rate of response was highest in the presence of a metal conductor and lowest in the presence of a plastic plate over the receptor. When an electrical field was applied between head and tail, response rate changed for different polarities. At the site of greatest electrical sensitivity they found only one kind of sensory organ. The organ included several cells grouped around a single opening on the lateral line and innervated by a single sensory nerve fiber.

Enger and Szabo (1965), who recorded electrical activity in the medulla of several gymnotids, concluded that tonic responses can yield information to the fish about the presence and position of objects within the electric field and that phasic responses give information on movement, direction of movement, the size of an object, and the position of the front edge of that object. Dijkgraaf (1963) described the electrical sensitivity of the gymnotid group as about 0.05 μv./cm. or 0.05 μamps. (microamperes). Machin (1962) concluded that such small signals could be distinguished from background "noise" if about 40,000 receptors were involved and that this was a reasonable number of electroreceptors which might occur in the lateral-line system. Thus, it appears reasonable to conclude that at least some fish possess electroreceptors of adequate sensitivity to detect and determine the polarity of electrical voltages of the magnitude produced by ocean currents.

PREDICTION OF ELECTRICAL SENSITIVITY FOR SALMON

As indicated above, no investigations are known concerning the electrical sensitivity of adult salmon or of the presence of receptor organs in the lateral line of salmon which might be electrically sensitive. In his recent review of lateral-line function, however, Dijkgraaf (1963) came to several conclusions that might apply to salmon. His first suggestion was that the basic electroreceptor organ is a modified mechanoreceptor which has achieved maximal response to electrical stimuli. Secondly, because electrical receptors occur in the lateral line of several widely separated groups of fish, he suggested that they may have evolved

independently several times. It would appear that any fish that has lateral-line organs possessing even secondary electrical sensitivity could develop an electronavigation system relatively easily and quickly. For example, the galvanotropism of the catfish *Parasilurus* (Abe, 1935) seems to be such a development. Although we have no physiological information to confirm electronavigation on the high seas for salmon, the circumstantial evidence described above indicates that it should be included among the more likely sensory mechanisms that salmon may use during their travels.

CONCLUSIONS ON GUIDANCE MECHANISMS

We believe that the salmons' migration cannot be performed if they migrate or drift at random, or if they depend on any memorized visual or olfactory cues at any time except during the final location of the home estuary and stream. We note that the salmon predominantly travel actively with the ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. We note also that ocean currents produce electric potentials in a range which some fish can detect. We suggest, therefore, that salmon may depend on electromagnetic cues from ocean currents. We suggest further that their response to all migatory cues is inherited, not memorized.

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