A NEW MODEL OF OCEAN MIGRATIONS OF BRISTOL BAY SOCKEYE SALMON

ROBERT R. FRENCH AND RICHARD G. BAKKALA¹

ABSTRACT

A model is presented that describes the ocean migrations of Bristol Bay sockeye salmon from the time the fish leave the estuary until they return as adults. Bristol Bay sockeye salmon inhabit extensive areas of the ocean during various stages of their life at sea, ranging across most of the North Pacific Ocean from about long. 140°W to near long. 167°E and from near lat. 46°N to lat. 58°N in the central Bering Sea. Initially, their migration route takes the young juveniles from the eastern Bering Sea through the central and eastern Aleutian Islands passes to south of lat. 50°N where in late winter they become broadly distributed across the North Pacific Ocean. In June the immature fish start a northward movement and in summer occupy waters from lat. 50°N to the Aleutian Islands and over an east-west area from long. 160°W to 170°E; part of the population moves north into the Bering Sea. The following winter the sockeye separate into immature and maturing components. Those that will mature remain in waters north of lat. 50°N from whence they will migrate back to Bristol Bay in the spring with the major proportion entering the Bering Sea through passes east of long. 175°W. The immature fish that will remain at sea another year move south of lat. 50°N in the winter and early spring, then essentially repeat the migration they had made the previous summer. These fish as maturing fish the following winter and spring follow the same migration route as the earlier maturing group. No direct relationship was found between the distribution and migration of the sockeye and defined oceanographic features of the Subarctic Region of the North Pacific Ocean.

A model of the complete ocean migrations of sockeye salmon, *Oncorhynchus nerka*, from Bristol Bay, Alaska, was originally developed by Royce, Smith, and Hartt (1968). Their model suggested that Bristol Bay sockeye during their life at sea make two or three circuits of an elongated eastwest course extending from about long. 165°E to 140°W in the North Pacific Ocean and Bering Sea. These migrations were thought to be associated with major currents of this region—the Alaskan Stream and Subarctic Current.

Since formulation of the model by Royce et al. (1968), Bakkala (1971) studied the distribution and abundance of immature sockeye salmon in relation to ocean currents and other features of the Subarctic Region and suggested certain refinements to the earlier model. New information available through continued offshore studies combined with a review of existing tagging data has led us to propose a new model of migration of

Manuscript accepted October 1973.

FISHERY BULLETIN: VOL. 72, NO. 2, 1974.

Bristol Bay sockeye to supplement that proposed by Royce et al. (1968).

Studies of the oceanic distribution of Pacific salmon have shown sockeye salmon from Bristol Bay, Alaska, to be widely distributed in the North Pacific Ocean and Bering Sea. Tagging experiments have shown that Bristol Bay sockeye salmon range from about long, 140°W, approximately 111 km from the coast of southeastern Alaska, to near long. 167°E, approximately 463 km from the coast of Kamchatka, an east-west distance of about 3,700 km. From south to north, Bristol Bay sockeye have been identified near lat. 46°N in the northeastern Pacific Ocean to near lat. 58°N in the central Bering Sea. Notwithstanding their broad distribution and dynamic movements, the basic distribution and seasonal migrations of the sockeye are known.

In this report we examine data from tagging experiments and salmon catches in relation to environmental features to describe the distribution and migration of Bristol Bay sockeye salmon from the time they leave the estuary until they return as maturing fish. Following these discussions, a model of migrations for Bristol Bay sockeye salmon is presented.

¹Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.



LIMITS OF AREA OCCUPIED BY IMMATURE WESTERN ALASKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES LIMITS OF AREA OCCUPIED BY IMMATURE KAMCHATKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES POSSIBLE EXTENSION OF AREA OCCUPIED BY IMMATURE KAMCHATKAN SOCKEYE AS DETERMINED BY OTHER INDIRECT MEANS (SEE TEXT)

FIGURE 1.—Range and area of overlap for maturing (a) and immature (b) sockeye salmon from Asia and North America (Figures 74 and 76 of Margolis et al., 1966).

170* 160*



AREA OF OVERLAP

170

180*

160*

Numerous researchers, through tagging experiments, morphometric studies, scale studies, and analysis of parasites, have defined certain aspects of the distribution of Bristol Bay sockeye salmon (defined as those sockeye originating in the eastern Bering Sea from Unimak Island northward to the Kuskokwim River). From a comprehensive review and updating of these studies, Margolis et al. (1966) defined the limits of oceanic distribution of maturing and immature western Alaska sockeye salmon (Figure 1). Examination of recent summaries of tag returns² for 1956–69 (Figures 2 and 3) corroborates the general distribution pattern of sockeye salmon stocks from western Alaska, from other North American regions, and from Asia as described by Margolis et al. The tag returns show, however, an extension in the range of western Alaska immature sockeye salmon to west of long. 170°E (see Figure 3).

150*

Maturing Bristol Bay sockeye salmon, which had been tagged at sea primarily during April, May, and June, are shown to be distributed

²Aro, K. V., J. Arthur Thomson, and Dorothy P. Giovando. 1971. Summaries of salmon tag recoveries in North Pacific coastal and high seas areas from salmon tagging in INPFC statistical areas in the North Pacific Ocean by Canada, Japan, and the United States, 1956 to 1969. Fish. Res. Board Can., Manuscr. Rep. 1148, 641 p. (Unpubl.)



FIGURE 2.—Tagging locations $(2^{\circ} \times 5^{\circ} \text{ areas})$ for maturing sockeye salmon recovered in western Alaska, other North American areas, and Asia, 1956–69. The proportion of returns to these major land areas from each $2^{\circ} \times 5^{\circ}$ area of the ocean are shown diagrammatically by having each $2^{\circ} \times 5^{\circ}$ rectangle represent 100%. Small percentage returns could not be accurately illustrated, and in some instances percentages are exaggerated to show presence.

across most of the North Pacific Ocean and in the central and eastern Bering Sea south of lat. 60°N (Figure 2).

These tagging data also illustrate areas where Bristol Bay sockeye predominate as well as areas where they overlap with other stocks. Although tagging effort varied between some years and was far from uniform in various parts of the ocean, the return showed Bristol Bay sockeye predominating in the spring from about long. 155°W to 170°E. Their main area of overlap with other North American stocks was from about long. 140° to 160°W. With Asian sockeye, their main area of overlap was between long. 165° and 175°E.

Tag returns from immature sockeye salmon tagged primarily in the summer (late June through August) have been too few to portray their oceanic distribution in detail (Figure 3). The small numbers of tag returns are due to the poor survival associated with tagging small immature fish and the lack of widespread tagging throughout the oceanic areas inhabited by the fish. For limited data, the results show overlap of Bristol Bay sockeye with other North American stocks between about long. $145^{\circ}W$ and $175^{\circ}E$. Bristol Bay immatures predominate south of the Aleutian Islands. Total returns of tagged fish for all years indicate that in the area immediately south of Adak Island, approximately 10% of the tag returns were from other North American areas. Very few tag returns were reported from Asian streams. The returns suggest some overlap of immature fish of Asian origin with Bristol Bay fish south of the central and western Aleutian Islands, but they do not indicate areas where Asian sockeye predominate.

Recent studies by the National Marine Fisheries Service (NMFS) have been directed toward understanding the influence of the oceanic environment on distribution and migration of salmon at sea. These studies, primarily concerned with Bristol Bay sockeye salmon, should disclose the causes of change in distribution and movements of the Bristol Bay stock. They should also lead to improved forecasts of run sizes and predictions of the effect of the Japanese high-seas fishery on salmon stocks of the United States. Results of these investigations and conclusions drawn from coastal tag returns have provided information for describing the migrations of sockeye salmon through most of their life at sea.

DISTRIBUTION AND MIGRATION OF BRISTOL BAY SOCKEYE SALMON INFERRED FROM HIGH-SEAS CATCHES

The apparent relative abundance of sockeye salmon taken in gill nets, purse seines, and longlines from synoptic sampling over periods of time and large areas of the ocean furnish much information on movements and distribution of fish. This information coupled with the age composition of the catches and tagging data provides important links for formulating migration patterns of the stock.

First Year at Sea

Juveniles Age .0 (July-December)³

Juvenile salmon, age .0 fish after leaving the rivers of Bristol Bay, move southwest along the north side of the Alaska Peninsula throughout summer, but substantial numbers remain in the eastern Bering Sea until sometime after the middle of September (Hartt et al., 1967; Hartt, Dell, and Smith, 1969; Straty and Jaenicke, 1969⁴). Sampling with purse seines indicates that the juveniles do not make a rapid directional migration at this stage of life but disperse slowly toward the southwest as they move back and forth with the tides. By mid-September the juveniles are still present in large numbers east of long. 165°W extending at least 167 km offshore. The length of time that the juveniles spend in the eastern Bering Sea and their restricted distribution are probably due to the local abundance and availability of food. During this period of late summer, growth is rapid as the fish, averaging 17 to 18 cm long, feed on the abundant supply of zooplankton and larval fish (Hartt et al., 1967).

The migration routes of the juvenile sockeye

as they leave the eastern Bering Sea is unknown due to lack of sampling in fall and early winter.

Immatures Age .1 (January-June)

The small sockeye were next taken as age .1 fish (an additional year is added on 1 January regardless of state of annulus formation) in winter catches in the North Pacific Ocean at various locations; a few specimens have been taken in the south-central Bering Sea. Bakkala (1971) has summarized winter gill-net catches of age .1 fish for 1962-67 by research vessels of the Northwest Fisheries Center, NMFS. To his data we have added catches made in the winters of 1969 and 1970 (Figure 4).⁵ These data illustrate that main catches of age .1 sockeye were made near lat. 46°30'N in the central North Pacific and between lat. 48° and 51°N in the northeastern Pacific from long. 165° to 155°W. A good catch was also made near lat. 50°N at 175° and 170°W.

Relatively small numbers of fish were taken in the Bering Sea during sampling in late January and early February 1963 and near long. 170°E in February 1965. (Stations shown on long. 170°E represent stations fished as far west as long. 167°18'E.)

There were no tagging data to indicate area of origin of the age .1 fish taken in the winter. We can surmise their origin, however, on the basis of the freshwater age composition of catches, at least for some years. The largest catches of age .1 fish occurred in 1965 (10 and 16 March) near lat. 46°30'N between long. 175°E and 180°. CPUE (see footnote 5 for definition of catch per unit effort) of 16 and 13 were the largest made during the years of winter sampling. Most of these fish (78% of the catch) were age 2.1 (a salmon of age 2.1 has spent two winters in fresh water after hatching and one winter in the ocean). Later in the year in the samples taken south of Adak Island (where tag returns indicate that Bristol Bay fish predominate), the 2.1 age-group made up approximately 75% of the catch of age .1 fish. One year later this same group, now age 2.2 fish, made up about 70% of the mature age .2 fish in the 1966 run to Bristol Bay. That same year the age composition of the mature Asian sockeye

³Age designation used are those suggested by Koo (1962). The numeral preceding the dot indicates number of winters in fresh water; the numeral following the dot indicates number of winters at sea.

⁴Straty, R. R., and H. W. Jaenicke. 1969. Estuarine ecology of sockeye salmon in Bristol Bay. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. (Unpubl. manuscr.)

⁵In this and other figures the catch per unit of effort (CPUE) of gill nets is the value of the sums of the average catch per shackle of each mesh size. A shackle is approximately 91.5 m long.

FRENCH and BAKKALA: NEW MODEL OF OCEAN MIGRATIONS



FIGURE 3.—Tagging locations $(2^{\circ} \times 5^{\circ} \text{ areas})$ for immature sockeye salmon recovered in western Alaska, other North American areas, and Asia, 1956-69. The proportion of returns to these major land areas from each $2^{\circ} \times 5^{\circ}$ area of the ocean are shown diagrammatically by having each $2^{\circ} \times 5^{\circ}$ rectangle represent 100%. Small percentage returns could not be accurately illustrated, and in some instances percentages are exaggerated to show presence.





593

TABLE 1.—Proportion of age 2.1 sockeye salmon in samples from the northeastern Pacific and south of Adak Island in 1962, 1967, and 1969 and of age 2.2 sockeye in the following year's Bristol Bay run.

	Area and time of sampling							
Year	Northeastern Pacific winter (age 2.1)			Adak Island summer	Bristol Bay in following year			
	155°W	162°W	165°W	(age 2.1)	(age 2.2)			
			···· Percer	nt				
1962	35			53	50			
1967	53	34	_	43	37			
			83	79	90			

was estimated to be about 24% age 2.2 fish (Fredin and Worlund).⁶ On the basis of age composition, therefore, we can surmise that most of the small fish taken near lat. 46°30'N in the central Aleutian area were of Bristol Bay origin and that this is one area occupied by Bristol Bay fish in winter.

In the northeastern Pacific Ocean, good catches of age .1 sockeye salmon were made in the winters of 1962, 1967, and 1969. The proportions of age 2.1 fish in these catches are shown in Table 1. Also shown are the proportions of age 2.1 fish in the catches made the following summer south of Adak Island (where Bristol Bay fish traditionally predominate as shown by tag returns) and the proportions of age 2.2 fish in the following year's run to Bristol Bay.

Catches in 1969 probably best illustrate the presence of Bristol Bay fish in the area during the winter season. Progeny of the record-size spawning run to Bristol Bay in 1965 were expected to be abundant and predominate among samples of immature fish at sea in 1969 and as age 2.2 maturing fish in returns to Bristol Bay in 1970. The 1969 winter sampling along 155°W resulted in relatively large catches of age .1 sockeye salmon in January which were composed of approximately 60% age 2.1 fish (73% in areas of largest catches near lat. 49° and 50° N) as would be expected if they originated from Bristol Bay. The few age .1 sockeye taken in more northern waters along this longitude (near lat. 52° to 55°N) were mainly age 1.1 fish (82%); they possibly originated from North American coastal areas eastward of Bristol Bay. The 1969 samples of age .1 sockeye salmon taken along long. 165° W had an even higher proportion of age 2.1 fish (83%) than samples taken along long. 155° W and compared more closely to the age composition of samples south of Adak Island in the summer (79% age 2.1) and to the age composition of maturing fish returning to Bristol Bay rivers in 1970 (90% age 2.2).

The 1967 winter sampling produced catches of age .1 sockeye salmon along long. $162^{\circ}W$ which were also similar in age composition (34% age 2.1 fish) to that of maturing fish returning to Bristol Bay in 1968 (37% age 2.2). Sampling along long. $155^{\circ}W$ in 1967 showed a somewhat different proportion of age 2.1 fish (53%) from that along long. $162^{\circ}W$. In 1962 the proportion of age 2.1 fish along long. $155^{\circ}W$ also differed substantially from that of maturing fish in Bristol Bay in 1963 (35% age 2.1 along long. $155^{\circ}W$ in winter 1962 and 50% 2.2 fish in Bristol Bay in 1963).

From the above relations, we surmise that sockeye salmon originating from Bristol Bay reach the northeastern Pacific Ocean by January and February of their first year at sea. It appears from age comparisons that they probably predominate eastward to about long. 160° W and possibly to long. 155° W in years of high abundance such as in 1969. Their range may extend even farther to the east. Catch data thus demonstrate that Bristol Bay sockeye become widely distributed across the North Pacific Ocean in their first winter at sea and probably extend from near long. 175° E to at least 155° W.

Catch data also indicated possible routes used by the young fish to move from the Bering Sea into the North Pacific Ocean. Sampling near long. 170°E in the winter of 1965 resulted in a catch of a single age .1 sockeye salmon whereas, as previously shown, large catches were made between long. 175°E and 180°. The lack of age .1 fish along long. 170°E and the evidence from age composition that fish from 175°E to 180° were of Bristol Bay origin suggest that the waters near long. 170°E may represent an area separating Asian and Bristol Bay sockeye in winter. Most Asian sockeye salmon are assumed to be located west of long. 170°E. Inasmuch as catches of age .1 fish were made in the central North Pacific Ocean from the Aleutian Islands to near lat. 45°N, it is likely that one route of the young fish from the Bering Sea is through central Aleutian Islands passes. In sampling on long. 165°, 160°, and 155°W, we caught few age ____1 sockeye north

^eFredin, R. A., and D. Worlund. Catches of sockeye salmon of Bristol Bay origin by the Japanese mothership salmon fishery, 1956-70. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, Wash. (Unpubl. manuscr.)

of about lat. 51° N compared to catches south of this latitude. It appears, therefore, that the young salmon migrate through passes between long. 169° W and 179° E (the area bordered by Umnak Island on the east and Amchitka Island on the west) and then move eastward. A possible pathway from the Bering Sea to the North Pacific may be Amchitka Pass where a branch of the Alaskan Stream in September flows northward into the Bering Sea (Favorite and Ingraham, 1972).

Depending on routes followed, the migration from the eastern Bering Sea to the central North Pacific near lat. 46° N or south of the Alaska Peninsula between lat. 48° and 51° N would require migrations of from about 700 to 1,000 miles (1,300–1,850 km) and travel rates of at least 8 to 10 miles (14.8–18.5 km) per day. This rate is entirely reasonable for it has been estimated that juvenile salmon travel about 10 miles (18.5 km) per day in the Gulf of Alaska (Royce et al., 1968).

Salmon research cruises have also included oceanographic studies which have defined major oceanographic features of the Subarctic North Pacific (McAlister et al., 1970). These are permanent features of the Subarctic Region and are defined by surface and subsurface characteristics (generally between 100 and 400 m). Salmon catches have been related to these features in an attempt to determine their influence on distribution and movements of salmon. Bakkala (1971) related winter catches of age .1 sockeye salmon in 1962, 1963, 1965, and 1967 to the major water masses and indicated that the salmon were usually associated with the Oyashio Extension Area (Figure 5).

Catches in winter 1969 and 1970, however, show that the age .1 fish were not always associated with this water. The eastward-moving water between the Ridge and Transition Areas was previously separated into Oyashio and Subarctic Current Areas, but more recent terminology combines the two areas into a single feature called the Western Subarctic Intrusion (Favorite, Ingraham, and Fisk, 1972). In Figure 6 are shown four years of winter catch data and associated oceanic features in the northeastern Pacific. In 1962 and 1967, age .1 fish were associated with the Western Subarctic Intrusion. In 1969 and 1970, this water mass shifted northward (in 1970 it formed only a relatively narrow tongue stretching east of long. 160°W) but was not accompanied by a corresponding shift in distribution of the age .1 sockeye salmon. These fish remained at much the same latitudes as in the earlier years, and their winter distribution was not affected by changes in location of the specific water mass. Because this particular water mass is defined by weak eastward flow and temperature conditions between 200 and 400 m, it



FIGURE 5.—Distribution of age .1 sockeye salmon in the winters of 1962, 1963, 1965, and 1967 in relation to oceanographic features of the Subarctic Region of the North Pacific Ocean.



FIGURE 6.—Distribution of age .1 sockeye salmon from winter catches in the northeastern Pacific Ocean in relation to defined oceanographic features.

is possible that other surface conditions may have greater bearing on the distribution and movements of salmon.

Examination of surface water temperatures in relation to winter catches of age .1 sockeye (Figure 5) revealed that the largest catches were in the temperature range of 3.5° to about 5.5°C. The young fish were not generally taken in the extremes of cold or warm surface waters. This was clearly illustrated in 1965 by sampling near long. 170°E. Only a single age .1 sockeye was taken between long. 165° and 170°E in surface water temperatures of 1.8°C. No fish were caught at other stations where surface temperatures ranged from 1.6° to 2.4°C. Areas in the Bering Sea, where age .1 sockeye were caught, generally had surface temperatures of 3°C or more. The low surface water temperatures or the subsequent reduction in abundance of food forms may cause age .1 sockeye to move out of the Bering Sea and seek warmer water in the North Pacific Ocean. The highest water temperature at which age .1 fish were taken was 6.8°C.

By April and May the age .1 sockeye salmon reach their southernmost limits of distribution (Figure 7). Japanese research vessels caught relatively large numbers of age .1 sockeye in gill nets from lat. 44° to 46°N along long. 175°W illustrating their occurrence south of the central Aleutian Islands. Samples taken in 1969 were composed of about 70% age 2.1 fish, which was comparable to the age composition of age .1 sockeye salmon taken south of Adak Island that same summer in purse seines by the Fisheries Research Institute (79% age 2.1).

A few age .1 sockeye salmon were taken in early May 1968 by a Japanese research vessel along long. $175^{\circ}E$ (Figure 7). The small sample of readable scales (10 fish) was 50% age 2.1, 40% age 3.1, and 10% age 1.1. This was quite unlike the age composition of age .1 sockeye caught south of Adak Island during summer 1968 by the Fisheries Research Institute (71% age 1.1 fish), indicating that the immature sockeye along long. $175^{\circ}E$ in early May might have been Asian fish.

In the northeastern Pacific, sampling with gill nets along long. $165^{\circ}W$ in the spring of 1969 resulted in small catches of age .1 fish as far south as lat. $46^{\circ}N$, the limit of sampling. Longline fishing surveys provided some data on the distribution of age .1 sockeye salmon to the east of long. $165^{\circ}W$.

During 1964, 1965, and 1966, longline surveys by the Fisheries Research Institute (FRI) were made in the northeastern Pacific including the Gulf of Alaska to obtain salmon for tagging. Although longline gear is not considered as

FRENCH and BAKKALA: NEW MODEL OF OCEAN MIGRATIONS



FIGURE 7.-Distribution of age .1 sockeye salmon in the spring (data from 1956-61 and 1966-70).

efficient for age .1 salmon as for older age-groups, some age .1 fish were taken, and these catches at least reflected the presence of the immature fish. In April and May (Figure 8) age .1 sockeye salmon were primarily found south of lat. 52° to about 46° N and extended eastward to about 140° W.

Most of the age .1 sockeye salmon caught by FRI during the 3 yr of longline surveys were taken in 1964. These fish in the area of the largest catches (long. 160° to 145°W, south of lat. 52°N) were mainly age 2.1 fish (75%), the age-group which predominated among samples taken in the central Aleutian Islands area during the summer and which were likely of Bristol Bay origin, and fish which made up part of the record run of age 2.2 sockeye to Bristol Bay in 1965. Thus it appears that Bristol Bay stocks in April and May could extend eastward in the northeastern Pacific at least as far as long. 145°W.

By June the age .1 sockeye have started a northward movement along a broad east-west front and in late June have even reached the central portions of the Bering Sea (Figure 7).



FIGURE 8.—Catches of age .1 sockeye salmon in the northeastern Pacific (in numbers of fish) with longline gear, 1964–66. Data are total catches not weighted for effort.

Longline sampling also indicated northward movement of the age .1 sockeye in the northeastern Pacific (Figure 8). The sample of 11 fish caught south of Kodiak Island near long. $150^{\circ}W$ and lat. $54^{\circ}N$ were all taken in 1964 and were all age 2.1 fish; possibly these results indicate the presence of Bristol Bay immature stocks in this area in June.

Second Year at Sea

Immatures Age .1 (July-December)

In the summer, July-September, the distribution and migration of immature sockeye salmon south of the Aleutian Islands has been well documented (Hartt, 1962, 1966; French, 1964; French, Craddock, Bakkala, Dunn, and Thorson, 1967; Royce et al., 1968; Bakkala, 1971; Rothschild et al., 1971).

An example of the distribution in late July is shown in Figure 9. This typifies the distribution of immature sockeye salmon south of the Aleutians in July and August; the relative abundance of immatures is usually highest in late July or early August and at lower levels in early July and late August.

It has also been demonstrated that Bristol Bay stocks predominate south of the central Aleutian Islands by coastal tag returns 1 or 2 yr later and by the relation between age composition and abundance at sea and by the age composition and abundance in the Bristol Bay run 1 yr later (Ossiander, 1965; Rogers, 1970). Based on the limited tag returns from other areas south of the Aleutians and on the abundance of immatures in these waters, we surmise that Bristol Bay sockeye salmon predominate south of the entire Aleutian Islands chain.

Considerable evidence has been produced which indicates that migration of immature sockeye south of the Aleutian Islands in summer is predominantly westward (Hartt, 1962, 1966; Larkins, 1964; Dunn, 1969); tagging studies have indicated that this westward migration for some fish is rapid and extensive (Royce et al., 1968). This evidence implies that the total population of Bristol Bay immature sockeye salmon shifts to the west or northwest during the summer. Royce et al. (1968) describe this migration as "... they migrate westward south of the Aleutian Islands in a more or less continuous band, from late June through mid-September." This apparent movement further implies that the eastward extent of the Bristol Bay population may also shift to the west through the summer. We have not found evidence, however, that waters to the south of the eastern Aleutian Islands and Alaska Peninsula become devoid of Bristol Bay fish during the summer. Rather, it appears that the Bristol Bay population of immatures main-



FIGURE 9.—Distribution of immature sockeye salmon, 21-31 July (from Bakkala, Figure 12, 1971).



FIGURE 10.—Relative abundance of age .1 sockeye salmon along cruise tracks fished in summer 1963.

tains a broad east-west distribution throughout the summer. Definition of the eastward limit of this distribution is complicated by the intermingling of Bristol Bay and other North American stocks of immature sockeye salmon in the northeastern Pacific. Some evidence of the eastward range of Bristol Bay fish is provided by the age composition of age .1 fish sampled between long. 176° and 158°W in 1963 and 1966. In 1963 systematic sampling along long. 176° and 162°W from July to early September (Figure 10) showed that age composition of age .1 fish was very similar for the two areas as shown in Table 2. Sockeye salmon in the following year's Bristol Bay run was composed of approximately 66% age 1.2 fish and 34% age 2.2 fish or very similar to the dominant ages of age 1.1 and 2.1 fish, noted in each area the previous summer. This suggests that in the summer of 1963, Bristol Bay sockeye were distributed as far east as long. 162°W throughout the summer.

TABLE 2.—Freshwater age composition of age .1 sockeye salmon from samples along long. 162°W and 176°W in summer 1963.

Sampling			Age-group				
area	0.1	1.1	2.1	3.1	4.1		
	Percent						
176°W 162°W	0.7 1.3	65.2 67.9	31.9 27.7	2.3 3.1	0.03 0		

The age composition for the three lines fished in 1966 (Figure 11) varied considerably as illustrated in Table 3. Substantial differences were shown between samples at long. 176°W and samples to the east. The FRI purse seine samples south of Adak Island were approximately 33% age 1.1 and 67% age 2.1 fish-very similar to the age composition observed from gillnetting in this area. The following year's run to Bristol Bay, however, was composed of about 17% age 1.2 fish and 83% age 2.2 fish (Rogers, 1970). This indicates that Bristol Bay sockeye (or age-groups within the Bristol Bay stock) were distributed differently in 1966 compared to 1963. Other possibilities were that non-Bristol Bay fish made up a higher proportion of the catches in 1966 or that there were differential maturity schedules for the two major age-groups.

Although age composition of the samples did not clearly demonstrate the predominance of Bristol Bay sockeye in the northeastern Pacific in 1966, it seems likely that a large proportion of the fish taken in this area as well as south of the Aleutian Islands generally were of Bristol Bay origin. This assumption is based on the relative high abundance of sockeye shown by catches south of the Alaska Peninsula and Aleutian Islands, in view of the relative size of the Bristol Bay stock compared to other North American stocks and the evidence from tagging studies on immatures (see Figure 3).



FIGURE 11.—Relative abundance of age .1 sockeye salmon along cruise track fished in summer 1966.



FIGURE 12.—Distribution and abundance of age .1 sockeye salmon in July 1967, 1968, and 1969 as shown by catches of Japanese research vessels.

TABLE 3.—Freshwater age composition of age .1 sockeye salmon from samples along long. 158°W, 167°W, and 176°W in summer 1966.

Sampling			Age-group		
area	0.1	1.1	2.1	3.1	4.1
			Percent		
176°₩	0.1	29.6	68.5	1.8	0
167°W	0.6	52.7	43.7	3.0	0
158°W	0	68.1	29.5	2.4	0.10

Further evidence that a considerable proportion of the Bristol Bay immature sockeye salmon remain in the northeastern Pacific Ocean through the summer is indicated by catch data from research vessels fishing simultaneously along various longitudes in July and August (Bakkala, 1971). These data (Figures 10 and 11) showing peaks in relative abundance followed by a decline in abundance in two or three areas at similar time periods indicated that the major proportion of immatures from the eastern areas did not migrate westward and move through the area south of the central Aleutian Islands at a later time period.

Royce et al. (1968) suggested that many age

.1 sockeye salmon from Bristol Bay migrate northward into the Bering Sea in late summer. The fact that some Bristol Bay sockeye occupy waters of the western Bering Sea has been established by the recapture of 5 sockeye in Bristol Bay tagged as immatures in the Bering Sea west of 180°. Recent catch data indicate that the abundance of Bristol Bay immatures in the Bering Sea varies depending upon the abundance of the stock and perhaps on other factors. Machidori $(1970)^7$ reported on catches of age .1 sockeye salmon in the Bering Sea during research cruises in 1967, 1968, and 1969. His data are shown in Figures 12, 13, and 14 as converted from tans (one tan of gill net is 50 m long) to CPUE in equivalent shackles of gear. Although fishing effort was not equal in all areas in July, August, and September, the data suggested lack of substantial numbers of salmon in the Bering Sea east of long. 175°E in July, but show large catches in August indicating a movement of

⁷Machidori, S. 1970. On summer distribution of immature sockeye salmon in the northwestern North Pacific and its adjacent waters. [In Japanese] Fish. Agency Jap., Tokyo (Int. North Pac. Fish. Comm. Doc. 1311), 59 p. (Transl., 15 p.)



FIGURE 13.—Distribution and abundance of age .1 sockeye salmon in August 1967, 1968, and 1969 as shown by catches of Japanese research vessels.

immatures into the Bering Sea in August. In 1969 catches were much larger in August from long. 172°30' to 177°30'E than in 1967 or 1968, suggesting the presence of large numbers of age .1 fish that were progeny of the 1965 record run to Bristol Bay. Evidence from age composition of these catches (mainly age 2.1 fish) also indicated that they were predominantly Bristol Bay fish as originally suggested by Machidori. The location of these fish in the central and western Bering Sea indicates that routes of travel from the North Pacific to the Bering Sea were through passes west of Adak Island. Large numbers of age .1 fish, probably of Asian origin, were taken in the Bering Sea west of long. 175°E in September (Figure 14), but sampling did not extend far enough eastward to determine if Bristol Bay fish still remained in the Bering Sea.

From the above analysis we conclude that some proportion of the age .1 fish from Bristol Bay inhabit the central and western Bering Sea in August and that their abundance in the Bering Sea varies with the abundance of the total stock.

Although some of the Bristol Bay immatures move north into the western Bering Sea, the large numbers of immatures remaining south of the Aleutians indicate that many of the Bristol Bay sockeye remain in the North Pacific Ocean and maintain a broad east-west distribution throughout the summer. At the time large catches of age .1 sockeye were taken in the Bering Sea -from 12 to 30 August 1969-large catches were also being made south of Adak Island from 1 to 15 August (French, Bakkala, Dunn, and Sutherland, 1971). Catches by Japanese and United States research vessels in August 1970 better illustrate this point (Figure 15). The relative abundance of age .1 sockeye was generally higher throughout the area south of the Aleutian Islands than it was at stations fished in the Bering



FIGURE 14.—Distribution and abundance of age .1 sockeye salmon in September 1967, 1968, and 1969 as shown by catches of Japanese research vessels.



FIGURE 15.—Distribution and abundance of age .1 sockeye salmon in August 1970 as shown by catches of United States and Japanese research vessels.

Sea; the CPUE averaged about four times higher in the North Pacific than in the Bering Sea (sets with no catch were disregarded).

Further evidence of fish remaining in the North Pacific Ocean is provided by tag recoveries in 1964, as reported by Bakkala (1971). His summary of FRI tagging experiments (Figures 16 and 17) shows that immature sockeye, mainly age .1 (129) but including 16 age .2 fish, were recaptured in the North Pacific from 1 to 43 days after tagging. Recovery locations indicated that direction of movement from the tagging site was diverse and that recaptures were made to the south, southwest, west, and north. Four immature sockeye salmon were recaptured in the Bering Sea near lat. 60°N, apparent further evidence of movement of some Bristol Bay immatures into the western Bering Sea.

Because tag recoveries were dependent on the location and effort of the Japanese mothership fleet, the degree of movement to certain areas, as illustrated in Figure 16, may not have been



FIGURE 16.—Recovery locations for immature sockeye salmon tagged near Adak Island from 16 June to 24 July 1964 and recovered in the North Pacific Ocean from 12 July to 9 August 1964 (data from Fisheries Research Institute, 1964).

accurately reflected. Effort was concentrated south of the Aleutian Islands (near, west, and southwest of the release location) and in the Bering Sea near lat. $60^{\circ}N$ (Figure 17). Movement of tagged fish to the east could not be detected, and movement north and northwest in the area between the Aleutian Islands and lat. $58^{\circ}N$ would have a low probability of being detected compared to movement in the North Pacific Ocean. A substantial portion of the recoveries occurred in the North Pacific Ocean over an extended period; 36% of the recoveries were taken 10 to 19 days after tagging, 19% 20 to 29 days after tagging, and 4% 30 or more days after tagging. These recoveries indicated that substantial numbers of the releases remained in the North Pacific Ocean.



FIGURE 17.—Fishing effort and tag recoveries per unit of effort by the Japanese mothership fleet in 2° by 5° areas and for the period of 21 July to 10 August (data from Fisheries Agency of Japan, 1966 and Fisheries Research Institute, 1964).

There is some doubt about the true proportion of immature sockeye salmon remaining in the North Pacific Ocean in comparison to those moving to the Bering Sea. The rates of return from the highseas fleet was 3.5% of age .1 fish and 5.1% of age .2 fish, rather low rates considering the total fishing effort, although the small age .1 fish even with tags affixed may not be vulnerable to the fishery with its large-mesh gill nets. By way of comparison tag returns of 8.9% were made on the high seas of maturing fish from tagging experiments in the central and western Aleutian Islands area in 1960 (Hartt, 1966).

Because of the dynamic nature of the ocean migration of salmon (the rate of travel of those recovered in 1964 ranged from 2 to 50 nautical miles per day and averaged 17 nautical miles per day), it is possible that the fish recovered in the North Pacific Ocean after an extended period had migrated extensively and reentered the fishing area south of the Aleutian Islands. We do not know if the immature salmon make such a migration in the summer. It is known, however, that immature sockeye salmon become more widely distributed in the Bering Sea in August compared to their distribution in July (see Machidori, footnote 7), a pattern which might argue against the possibility of a return migration to the North Pacific Ocean in July or even by early August.

In relation to oceanographic features, the age .1 fish in summer were found primarily in the Ridge Area water south of the Alaska Peninsula and eastern Aleutian Islands but were located in both the Ridge Area and the Alaskan Stream south of the central and western Aleutian Islands (Bakkala, 1971). Ridge Area waters in summer were also found to have greater concentrations of food organisms than other water areas of the Subarctic Pacific Region (McAlister et al., 1969, 1970).

In summary, the evidence from distribution studies indicates that movements of Bristol Bay immatures in June are northward from areas they occupy in spring to waters they occupy in summer-generally between lat. 50°N and the Aleutian Islands and Alaska Peninsula. The majority of Bristol Bay fish appears to remain in these waters through the summer, but some smaller proportion continues northward or northwestward into the Bering Sea. Thus, the distribution of immatures is seen to shift northward from spring to summer but not extensively on an east-west plane.

Conflicting with this hypothesis of summer distribution is other evidence which has indicated that migrations in the North Pacific are predominantly and continuously westward throughout the summer (Royce et al., 1968), implying that the population of Bristol Bay immatures is displaced to the west during the summer and leaves waters of the northeastern Pacific Ocean. Direct evidence of immature sockeye salmon migrating long distances across the North Pacific from the northeast Pacific is provided by tag recoveries on the high seas of age .2 immature fish. Three immature sockeye salmon were tagged in the northeast Pacific near long. 145°W in May and recovered in the central Aleutian Islands area in July and August of the same year. Similarly, two immature sockeye tagged south of Unalaska Island in late June were recovered in the western Aleutian Islands area, one near 171°E in late July and one near 173°E in early August of the same year. Such long migrations across the North Pacific have not been demonstrated by the age .1 fish. The apparent contradiction of the two lines of evidence cannot satisfactorily be resolved at

present. It may be that the Bristol Bay population of immatures actually shifts to the west in the summer but to a limited degree, or the movements of the fish are not constant from year to year. Our inability to readily identify stocks of sockeye at sea and the limited sampling make such movements difficult to detect. Another possibility is that migrations are not as directional as some evidence would imply but rather more variable; a yet undetected recirculation (or eastward movement) of immatures may also be occurring to maintain a broad east-west distribution of immatures throughout the summer.

Information on the distribution and movements of age :1 fish in the fall and early winter is limited. The only catch data available are from south of the western Aleutian Islands (Figure 18). Age .1 fish were still abundant in this area in October and November. It is unknown whether these sockeye had remained in the North Pacific Ocean through the summer and fall or were, at least in part, fish that had returned from the Bering Sea.

Immature and Maturing Age .2 (January-June)

During their second winter at sea, the sockeye (now age .2 fish) either remain in the northern part of the North Pacific Ocean or move into southern areas depending on their maturation schedule (if they mature as age .2 fish the following summer or not). Generally most age .2 sockeye mature; the percentage maturing has been estimated as ranging from 60 to 80% each year (Royce et al., 1968). Separation of the immature age .2 fish is evident at least by midwinter. Catch data from winter cruises show a partial separation of the two groups of age .2 sockeye in most areas fished (Figures 19 and 20). This may represent the period when the immature component of the age .2 group are in the process of separating from the maturing group by moving south, leaving the matures in the more northerly waters.

By spring, separation of immature and maturing age .2 sockeye is much more pronounced (French, Bakkala, Osako, and Ito, 1971). It was shown that in the northeastern Pacific Ocean immature sockeye were not taken north of about lat. 49° in April and only appeared in catches in this area in late May and June. Maturing sockeye, however, were taken throughout the area from lat. 49° to 54° N. In the western and central Aleutian area along long. 175°E and 175°W, immatures were primarily south of lat. 48°N, and matures were caught mainly north of this latitude in May.

On the basis of the winter and spring catch data, we surmise that in winter, age .2 immature sockeye start migrating to southern waters and by spring become well separated from the maturing fish. Maturing sockeye tend to remain in northern waters throughout the winter and spring. They are found primarily in Ridge Area water and waters of the Western Subarctic Intrusion Area (Bakkala and French, 1971).

Most of the maturing Bristol Bay population probably shifts eastward in Ridge or Western Subarctic Intrusion Area waters during the fall or winter. Evidence of eastward movement is provided by comparing results of sampling south of Adak Island in summer 1969 with those from south of the Aleutians in spring 1970 (Figure 21). On the basis of age composition, magnitude of catches, and historical tagging data from this area, we conclude that the large numbers of sockeye taken near long. 176°W in July and August were primarily Bristol Bay fish; some of these sockeye undoubtedly moved even farther west, and others were probably already to the west of Adak Island. In spring 1970, sampling demonstrated that most maturing sockeye were east of long. 175°W indicating that many of the fish located west of long. 175°W in the previous summer had returned east of long. 175°W by spring.

The location of concentrations of Bristol Bay sockeye in spring (which is influenced by the extent of their eastward movement in fall or winter) determines the main migration routes taken to reach Bristol Bay; probably the largest part of the population is located east of long. 175°W, and the main migration is through passes east of long. 175°W. This conclusion was also indicated by Kondo et al. (1965). (We do not know the relative abundance or distribution of Bristol Bay sockeye that may be in the Bering Sea in late winter or early spring prior to the time of migration.) The intrusion of the Western Subarctic Gyre or northward shift of the Western Subarctic Current may affect the westward distribution of Bristol Bay sockeye or the eastward distribution of Asian sockeye in some years. For example, the percentage of Bristol Bay fish in catches by the Japanese mothership fleet in the area where Asian and Bristol Bay sockeye salmon



FIGURE 18.—Distribution of immature sockeye salmon in the fall in relation to oceanographic features of the Subarctic Region of the North Pacific Ocean (from Bakkala, Figure 48, 1971).



FIGURE 19.—Distribution of immature age .2 sockeys salmon in winter (data from 1962-70 with the exception of 1964, 1966, and 1968).

intermingle (long. 170° to 175°E, lat. 46° to 52°N) was estimated to be 5.8% in 1967 and 49.4%in 1968 (Fredin and Worlund⁶). In spring 1967, cold water (2°C) from the Western Subarctic Domain intruded well east of long. 170°E at lat. 47°N, whereas in 1968 the cold water was farther west than in 1967 (French et al., 1971). This change in the environment may have limited the westward distribution of Bristol Bay fish and in turn the catch of Bristol Bay sockeye by the Japanese in 1967.

Tagging data indicate that salmon west of long. 170°W in April and May will pass through Aleutian Islands passes west of Adak Island; fish east of long. 170°W will pass through Aleutian passes east of long. 175°W. In Figure 22,



FIGURE 20.—Distribution of maturing age .2 sockeye salmon in winter (data from 1962-70 with the exception of 1964, 1966, and 1968).



FIGURE 21.—Fishing stations and relative abundance of immature sockeye salmon during summer 1969 near Adak Island (shown above station line) and maturing sockeye salmon in spring 1970 (shown below stations).

recoveries of tagged salmon by the mothership fishery (which were made only west of long. 175°W) show a marked decline in recoveries for tagging locations east of long. 175°W. For tagging locations east of long. 170°W, recoveries were almost all from Bristol Bay and only a very few recoveries were made in the mothership fishery. Thus, primary routes to Bristol Bay for the salmon located east of long. 170°W must have been through Aleutian Islands passes east of long. 175°W (primarily Amukta Pass).

Routes of maturing sockeye salmon moving eastward in the Bering Sea may be variable and over a broad front. Largest catches by the

Japanese mothership fleet between long, 180° and 175°W in the Bering Sea in June occur from the Aleutian Islands to lat. 56°N, and fairly good catches may extend to lat. 58°N (Peterson, 1971). U.S. research vessels have made large catches of maturing sockeye salmon in June near the Pribilof Islands-which indicate migrations far north of the Aleutian Islands. The entry of most sockeye into Bristol Bay, however, is apparently off the southern coast of the bay. Gill-net sampling near Bristol Bay, before the fishing season, between long. 165° and 160°W indicated that the largest concentration of sockeye salmon was about 40 miles (74 km) from the Alaska Peninsula (French, Craddock, and Dunn, 1967). Paulus (1968)⁸ reported the largest catches in this area to be from 40 to 60 miles (74 to 111 km) offshore.

Third Year at Sea

Most age .2 sockeye that do not mature after their second year at sea remain an additional year in the ocean and then return to Bristol Bay to spawn as age .3 fish. A few fish will stay at sea still another year to return as age .4 fish, but they make up a very small percentage of the Bristol Bay run. From 1960 to 1965 the estimated number of age .4 fish in the spawning run ranged from 2,300 fish to 25,600 fish or from 0.01% to 0.22% of the total run.

Immatures Age .2 (July-December)

The immature age .2 sockeye were shown to move south and separate from the concentrations of maturing fish of age .2 in the winter. In the winter and spring, they become intermixed with the newly arrived age .1 immatures. In the summer, they probably repeat the migration they made the previous summer as age .1 fish since age .2 immatures are intermixed with age .1 fish in all areas sampled. Machidori (see footnote 7) shows the immature age .2 sockeye in the Bering Sea in the same general areas as the age .1 sockeye.

Maturing Age .3 (January-June)

The maturing age .3 sockeye, in the winter, are generally distributed in northern areas of the North Pacific Ocean, and in January and February they were also found in the Bering Sea (Figure 23). In these areas, the distribution of age .3 fish overlaps considerably with that of



FIGURE 22.—Tagging location for maturing sockeye salmon tagged in the North Pacific Ocean in April, May, and June 1956–67 and recaptured in Bristol Bay or the Japanese mothership fishery. Percentage recovery for each 5° of longitude is shown below.

⁸Paulus, R. D. 1968. Bristol Bay intermediate high seas inshore test fishing program, Project AFC-6-2, 1968 field season. Alaska Dep. Fish Game, Annu. Tech. Rep. Anadromous Fish Proj., 61 p.



FIGURE 23.—Distribution of age .3 sockeye salmon in winter (data from 1962-70 with the exception of 1964, 1966, and 1968).

maturing age .2 fish but is somewhat north of the latter group. We do not know if these fish remain in the Bering Sea throughout winter and early spring.

By spring, the age .3 sockeye are distributed across the North Pacific Ocean primarily in the Ridge Area and the northern part of the Western Subarctic Intrusion Area waters. Their movements toward Bristol Bay in late spring are assumed to be similar to those described for age .2 sockeye.

INFLUENCE OF WATER AREAS AND CURRENTS ON SALMON MIGRATIONS

In the previous sections we have inferred from various research results the migrations of Bristol Bay sockeye salmon from the time they leave the estuary until they return as maturing fish. We have also shown their distribution in relation to water masses which can be summarized as follows: After leaving the Bering Sea, possibly in Alaskan Stream Area water extruding through Aleutian Islands passes, (Favorite and Ingraham, 1972), the young salmon move southward in winter through the Alaskan Stream and Ridge Areas into the Western Subarctic Intrusion Area waters. In spring they usually are in Transition waters. In early summer they move northward

(a reversal of the winter movement) through the Western Subarctic Intrusion Area to Ridge and Alaskan Stream Area waters. Some components of the population move into central and northern parts of the Bering Sea. The salmon that will mature the following spring remain in northern waters, the Ridge Area primarily, over the winter and spring until they commence the spawning migration. Immature age .2 fish repeat the southward movement they made a year earlier and join the new group of age .1 fish. The matures, in late spring, migrate from the Ridge Area and the northern part of the Western Subarctic Intrusion Area waters through the Alaskan Stream and into the Bering Sea through various passes of the Aleutian Islands.

The influence of these water masses on distribution and migrations of sockeye salmon is not evident from our observations. As demonstrated, sockeye salmon in all life history stages appear to move readily in and out of the various water masses. Although salmon at certain life history stages appeared to associate with certain water masses in some years, a shift in location of water masses in other years was not accompanied by a corresponding shift in salmon distribution. Examples of this were shown in Figure 6; in 1962 and 1967, immatures were mainly found near or south of lat. 50°N and in the Western Subarctic Intrusion Area: but in 1970 when this oceanographic feature was located north of 50°N. most immatures were in the same general location

(near or south of lat. 50°N) but were now mainly in the Transition Area. Bakkala (1971) noted a similar situation in the summer; immatures were usually found in the Ridge Area south of the eastern Aleutian Islands and Alaska Peninsula, but when the Alaskan Stream extended farther offshore, the geographical distribution of salmon was unchanged and the immature salmon were in both the Alaskan Stream and Ridge Areas. His data also demonstrated that whereas immatures south of the eastern Aleutian Islands and Alaska Peninsula were found mainly in the Ridge Area, those south of the central Aleutian Islands were most abundant in the Alaskan Stream. The Alaskan Stream was previously thought to be the major route of westward migration for salmon, but westward migration occurred in the Ridge Area as well. The Subarctic Current, a term used to describe the faster moving waters near the boundary of the Western Subarctic Intrusion and Transition Areas, was also hypothesized to be a route of eastward movement by maturing sockeye salmon in fall and winter, but most maturing fish are far north of this current and probably move east in Ridge Area waters.

In summary, it could not be demonstrated that defined oceanographic features of the North Pacific Ocean had any direct influence on the north-south movements and distribution of sockeye salmon. Their movements and distribution may be governed by other environmental conditions such as water temperature or food abundance.

Research vessel catch data and the variable numbers of Bristol Bay sockeye available to the Japanese mothership fishery indicate that maturing Bristol Bay sockeye make eastward migrations in the North Pacific Ocean in the fall or winter and that the proportion of Bristol Bay fish making this migration or the extent of these migrations vary between some years. This is perhaps influenced by the interaction of the Alaskan and Western Subarctic Gyres and possibly by the recirculation of Alaskan Stream waters. Maturing Bristol Bay sockeye are found mainly in the Alaskan Gyre in spring, and if the westward extent of this gyre is limited by the strength of the Western Subarctic Gyre, the westward distribution of maturing sockeye may also be limited. (See Figure 24 for the location of the two gyres.) We have no direct evidence to support this possibility.

MODEL OF MIGRATION OF BRISTOL BAY SOCKEYE SALMON

From the accumulated knowledge of distribution and migration of Bristol Bay sockeye salmon, we have diagrammed a model of their movements from the time they leave the estuary until they return. The model differs from that given by Royce et al. (1968), but the two models are in agreement in regard to the major areas in which the salmon are found.



FIGURE 24.—Schematic diagram of surface circulation in the Subarctic North Pacific to illustrate the general location of the Alaskan and Western Subarctic Gyres (from Dodimead, Favorite, and Hirano, Figure 109, 1963).



FIGURE 25.-Model of migration of Bristol Bay sockeye salmon.

The new model calls attention to changes in migration or distribution patterns from year to year—which could affect indices of abundance that are based on data from only one area or time period.

A graphical illustration of the model appears in Figure 25, and a brief narrative account follows.

First Year at Sea

Juveniles Age .0 (July-December)

Juveniles, age .0 fish, after leaving the rivers of Bristol Bay, move southwest along the north side of the Alaska Peninsula, and by mid-September many still remain east of long. $165^{\circ}W$ and within 90 miles (167 km) of shore. In late fall or early winter the juveniles move southwestward along the Aleutian Islands and then proceed south through various passes, most likely between long. $179^{\circ}E$ and $169^{\circ}W$. The migration out of the Bering Sea may be motivated by lowered surface water temperatures and reduced food supplies—juveniles generally are not found in surface waters with temperatures less than $3^{\circ}C$. Principal routes of migration may be through Aleutian Islands passes where the Alaskan Stream branches into the Bering Sea.

Immatures Age .1 (January-May)

The immatures (age .1 on 1 January), after reaching the North Pacific Ocean, move southward through the Alaskan Stream and Ridge Area and by midwinter become located primarily south of lat. 50° N in Western Subarctic Instrusion or Transition Area waters. There is no evidence that the young fish follow major currents during the southward movement; they move southward over a broad east-west area. The young immatures are probably in search of food sources and favorable water temperatures (3.5–6.0°C) that prevail in more southern waters.

In early spring the immatures shift somewhat farther south and become more sharply separated from the matures (sockeye salmon from an earlier brood year). By April and May the immature age .1 fish have reached their southern limit of migration over a broad area from about long. 175° E to 145° W and are found from about long. 45° to 50° N in Transition and Western Subarctic Intrusion waters—an area of favorable water temperatures, $4.5-6.0^{\circ}$ C, and food sources.

Second Year at Sea

Immatures Age .1 (June-September)

In June the immatures start a return northward movement over a broad east-west area. This movement may be related to the increase in surface water temperatures and subsequent zooplankton blooms from south to north.

By July, the age .1 fish have moved north from areas occupied in the spring and are mainly located north of lat. 50°N in the Alaskan Stream and Ridge Areas. These waters in summer have more abundant food than other water areas of the Subarctic Pacific Region, which probably accounts for the distribution of sockeye on the north-south plane. On an east-west plane, the immature sockeye are distributed over a wide area, from about long. 170°E to about 160°W. Most of the fish are moving in a westerly direction during the summer, but recirculation of immatures or limited westerly movement maintains the wide east-west distribution through the summer. Some elements of the population move north into the Bering Sea in summer and become distributed in the central Bering Sea to at least lat. 60°N. The majority of the population remains south of the Aleutian Islands.

The continuity of the Alaskan Stream and Alaskan Gyre or the eastward intrusion of the Western Subarctic Gyre are oceanic features that may influence the western limits of distribution of Bristol Bay immature sockeye.

Separation of Immature and Maturing Sockeye (October-May)

In January and February of this period (the sockeye now become age .2 fish), they separate into immature and maturing components. The immature group will remain at sea a third year before maturing and will follow a somewhat different migration pattern (as shown in Figure 25 C) than the maturing group (Figure 25 E). The remaining period at sea for the immature group will be discussed following the description of movements of the maturing fish.

Maturing Age .1 to Age .2 (October-May)

The age .1 sockeye which will mature the following spring remain in the more northerly waters of the North Pacific Ocean (primarily north of lat. 50°N in the Alaskan Stream and Ridge Areas) throughout fall, winter, and spring until they begin their inshore migration. The extensive east-west distribution of sockeye (which was noted previously) is maintained. Evidence of varying catch rates of Bristol Bay sockeye by the Japanese mothership fishery west of long. 175°W (rates have varied between years from 2.2 to 35.2% of the total run) suggests that the distribution of maturing sockeye shifts to the east in fall and winter and that the magnitude and extent of this movement governs the availability of sockeye to the Japanese fishing fleet.

During this period, the maturing sockeye salmon are associated with the Alaskan Gyre primarily the Ridge Area, but they are also found in the Western Subarctic Intrusion and Transition Areas, depending upon the location of these oceanic features.

The areas from which the maturing Bristol Bay fish initiate their inshore migration essentially have been established by April as a result of previous migrations. At that time their routes of inshore migration (and the proportion of the population available to the Japanese mothership fishery) have been determined, and variations in oceanographic features are assumed to have little effect on these inshore routes of migration.

Maturing Age .2 (June-July)

In June the spawning migration toward Bristol Bay is northward through Alaskan Stream waters and through various Aleutian Islands passes into the Bering Sea. Maturing age .2 fish move eastward over a broad south-north area extending from the Aleutian Islands to about lat. 58°N. As they approach Bristol Bay the schools of fish become more concentrated, and their main route of migration is about 40–60 miles (74–111 km) from the north side of the Alaska Peninsula.

Third Year at Sea

The fish that remain immature through their second year at sea separate from the maturing component in midwinter and move into more southern waters of the North Pacific (Figure 25 C). Here they are joined by the new group of age .1 fish; the two age groups repeat the migrations already described and shown in Figures 25 D, E, and F.

ACKNOWLEDGMENTS

We are indebted to the Oceanographic Unit (F. Favorite, Program Leader) of the Northwest Fisheries Center (NWFC), National Marine Fisheries Service, NOAA, for definition of oceanographic features and stimulating discussions on the oceanography of the Subarctic Pacific Region. The Stock Identification and Aging Unit of the NWFC (R. Major, Program Leader) provided all salmon age readings from scale samples obtained during the various research cruises. W. Royce, L. Smith, and A. Hartt of the Fisheries Research Institute, University of Washington, authors of a paper on the ocean migrations of Bristol Bay sockeye (Royce et al., 1968), kindly read the manuscript and, although they view the migrations somewhat differently than the present authors, offered many useful suggestions that were incorporated into the paper.

LITERATURE CITED

BAKKALA, R. G.

1971. Distribution and migration of immature sockeye salmon taken by U.S. research vessels with gillnets in offshore waters, 1956-67. Int. North Pac. Fish. Comm., Bull. 27:1-70.

- BAKKALA, R., AND R. FRENCH.
 - 1971. U.S. & Japan continue cooperative research in North Pacific (1970-71). Commer. Fish. Rev. 33(9): 41-52.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO.

1963. Salmon of the North Pacific Ocean—Part II. Review of oceanography of the Subarctic Pacific Region. Int. North Pac. Fish. Comm., Bull. 13, 195 p.

Dunn, J. R.

1969. Direction of movement of salmon in the North Pacific Ocean, Bering Sea, and Gulf of Alaska as indicated by surface gillnet catches, 1962-65. Int. North Pac. Fish. Comm., Bull. 26:27-55.

FAVORITE, F., AND W. J. INGRAHAM, JR.

- 1972. Influence of Bowers Ridge on circulation in Bering Sea and influence of Amchitka Branch, Alaskan Stream, on migration paths of sockeye salmon. In A. Y. Takenouti (chief editor), Biological oceanography of the northern North Pacific Ocean, dedicated to Sigeru Motoda, p. 13-29. Idemitsu Shoten, Tokyo, Japan.
- FAVORITE, F., W. J. INGRAHAM, JR., AND D. M. FISK.
- 1972. Oceanography. Int. North Pac. Fish. Comm., Annu. Rep. 1970:90-98.
- FISHERIES AGENCY OF JAPAN.
 - 1966. Report on research by Japan for the International North Pacific Fisheries Commission during the year 1964. Int. North Pac. Fish. Comm., Annu. Rep. 1964: 48-79.
- FISHERIES RESEARCH INSTITUTE.
 - 1964. Tag returns-1964-United States high seas tagging. Univ. Wash., Coll. Fish., Fis. Res. Inst. Circ. 263, 20 p.
- FRENCH, R.
 - 1964. Salmon distribution and abundance on the high seas—summer season—1963. Int. North Pac. Fish. Comm., Annu. Rep. 1963:121-131.
- FRENCH, R., R. BAKKALA, J. DUNN, AND D. SUTHERLAND. 1971. Ocean distribution, abundance, and migration of salmon. Int. North Pac. Fish. Comm., Annu. Rep. 1969:89-102.

FRENCH, R. R., R. G. BAKKALA, M. OSAKO, AND J. ITO.

- 1971. Distribution of salmon and related oceanographic features in the North Pacific Ocean, spring 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-625, 22 p.
- FRENCH, R., D. CRADDOCK, R. BAKKALA, J. DUNN, AND K. THORSON.
 - 1967. Ocean distribution, abundance, and migrations of salmon. Int. North Pac. Fish. Comm., Annu. Rep. 1966:78-89.

FRENCH, R. R., D. R. CRADDOCK, AND J. R. DUNN.

- 1967. Distribution and abundance of salmon. Int. North Pac. Fish. Comm., Annu. Rep. 1965:82-94.
- HARTT, A. C.
 - 1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956-1958. Int. North Pac. Fish. Comm., Bull. 6, 157 p.
 - 1966. Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, 1959-1960. Int. North Pac. Fish. Comm., Bull. 19, 141 p.

HARTT, A. C., M. B. DELL, AND L. S. SMITH.

1969. Tagging and sampling. Int. North Pac. Fish. Comm., Annu. Rep. 1967:78-85. HARTT, A. C., L. S. SMITH, M. B. DELL, AND R. V. KILAMBI. 1967. Tagging and sampling. Int. North Pac. Fish. Comm., Annu. Rep. 1966:73-78.

KONDO, H., Y. HIRANO, N. NAKAYAMA, AND M. MIYAKE.

1965. Offshore distribution and migration of Pacific salmon (genus Oncorhynchus) based on tagging studies (1958-1961). Int. North Pac. Fish. Comm., Bull. 17, 213 p.

- 1962. Age designation in salmon. In T. S. Y. Koo (editor), Studies of Alaska red salmon, p. 37-48. Univ. Wash. Publ. Fish., New Ser. 1.
- LARKINS, H. A.
 - 1964. Direction of movement of salmon in the North Pacific Ocean, Bering Sea and Gulf of Alaska as indicated by surface gillnet catches, 1961. Int. North Pac. Fish. Comm., Bull. 14:49-58.

MCALISTER, W. B., W. J. INGRAHAM, JR., D. DAY, AND

J. LARRANCE.

- 1969. Oceanography. Int. North Pac. Fish. Comm., Annu. Rep. 1967:97-107.
- 1970. Oceanography. Int. North Pac. Fish. Comm., Annu. Rep. 1968:90-101.

MARGOLIS, L., F. C. CLEAVER, Y. FUKUDA, AND H. GODFREY. 1966. Salmon of the North Pacific Ocean—Part VI. Sockeye salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 20, 70 p.

- OSSIANDER, F. J. (EDITOR).
 - 1965. Bristol Bay red salmon forecast of run for 1965. Alaska Dep. Fish Game, Inf. Leafl. 59, 22 p.

PETERSON, A. E.

1971. Statistics of Japanese mothership salmon fishery. Int. North Pac. Fish. Comm., Annu. Rep. 1969:119-125.

ROGERS, D. E.

- 1970. Forecast of the sockeye salmon run to Bristol Bay in 1970, based on purse seine catches of immature sockeye salmon south of Adak. Univ. Wash. Coll. Fish., Fish. Res. Inst. Circ. 70-3, 21 p.
- ROTHSCHILD, B. J., A. C. HARTT, D. E. ROGERS, AND M. B. DELL. 1971. Tagging and sampling. Int. North Pac. Fish. Comm., Annu. Rep. 1969:67–89.

ROYCE, W. F., L. S. SMITH, AND A. C. HARTT.

1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. U.S. Fish Wildl. Serv., Fish. Bull. 66:441-462.

Koo, T. S. Y.