Density-Dependent Growth of Sockeye Salmon in the North Pacific Ocean

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Mathisen, O. A., L. Fair, R. J. Beamish and V. Bugaev. 2007. Density-dependent growth of sockeye salmon in the north Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. 4: 299–310.

Abstract: Length measurements were obtained for sockeye salmon from several major rivers around the perimeter of the North Pacific Ocean. The salmon from the Kvichak River in Bristol Bay, Alaska exhibit strong cyclic changes in abundance, usually with a period of 5 years. The lengths of salmon show the same cyclic changes but are inversely related to the magnitude of salmon abundance. The same relationship was found for all streams in Bristol Bay. The strength of this association was measured by the correlation coefficients between the same age-classes in other districts. High values were interpreted as occupation of overlapping feeding areas by each age-class during the last year in the ocean before salmon reach full maturity. There was some overlap in feeding areas of salmon from neighboring districts such as the Copper River and the Karluk/Chignik watersheds in Alaska. No association was found between Bristol Bay sockeye salmon and their counterparts in either Russia or the Fraser River, British Columbia, Canada.

Keywords: sockeye salmon, length measurements, feeding migrations

BACKGROUND

Workers in the commercial canning industry in Bristol Bay, Alaska, have been well aware that the average length and weight of sockeye salmon (*Oncorhynchus nerka*) changes periodically. During peak years of the sockeye salmon in the Kvichak River, Bristol Bay, Alaska, one or two additional salmon were always required to produce a 21.8-kg case of processed fish than in off-peak years because the sockeye are consistently smaller during peak years. This is illustrated in Fig. 1, which shows the inverse relationship between abundance of sockeye salmon and the mean length of age 2.2 females. However, no one related the smaller fish size to limits in the carrying capacity of either the open ocean or coastal waters.

With the resumption of high seas fishing for Pacific salmon by Japan after the end of WWII, it became important to identify and understand the migration paths and continent of origin of the salmon being caught. The first large-scale tagging experiments were conducted by the Fisheries Research Institute at University of Washington. The salmon were caught in a large purse seine, the mouth of which was kept open for half an hour facing the direction of the surface currents. Salmon were never caught during the opening set. This observation demonstrated the important fact that juvenile salmon drift along with the surface currents. The fourth dimension, time, must therefore be added to the geometric coordinates at place of tagging. A first model of the ocean drift of sockeye salmon was given by Royce et al. (1968).

Other tagging experiments followed, conducted by the nations bordering the North Pacific Ocean. In an effort to summarize our knowledge French and Bakkala (1974) presented a model of the oceanic migration of Bristol Bay sockeye salmon. However, the number of tags recovered from the commercial fishery and spawning ground surveys remained small. Another important step was to identify the place of origin of all high seas salmon through genetic analysis (Habitcht et al. 2005).

Each salmon carries a bit of its oceanic history in the pattern of its scales. Many retrospective studies of scale collections have been made over the years. When optical scanning methodologies were developed, scale analysis became an important tool to understand the life history of salmon (Isakov et al. 2001). Another step in this developmental process was to consider numbers and widths of individual scale rings (Ruggerone et al. 2005).

Another approach to understanding the ocean life of sockeye salmon is to study parameters such as survival rates of returning fish. Peterman et al. (1999) analyzed the covariance between adjacent sockeye salmon stocks in the Fraser River, BC, and those in Bristol Bay, Alaska. He concluded that there was no connection between sockeye in either river

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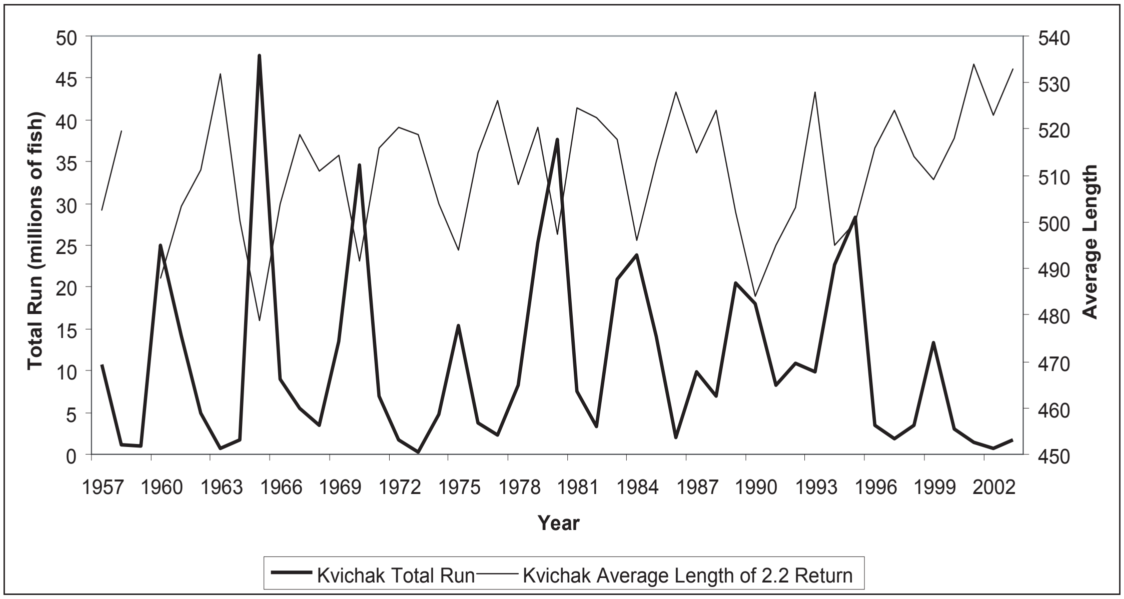

Fig. 1. The inverse relationship between the magnitude of sockeye salmon run to the Kvichak River, Bristol Bay, Alaska, and the mean length of age 2.2 females. Time period covered 1957 to 2003.

system. In the present study we compare the mean lengths of the various stocks of sockeye salmon to determine the relationships between various populations.

MATERIALS AND METHODS

The data for this study were obtained from the archives of many research institutions around the Pacific Rim that are managing and monitoring salmon resources. Sockeye salmon are distributed from the southern tip of the Kamchatka Peninsula through watersheds along the North Pacific coastline, including the Bering Sea, to the southern border of the state of Oregon. Small populations are occasionally found south of these two endpoints on both sides of the North Pacific Ocean (Fig. 2).

From this wide area, we selected stocks from several rivers for this study. The choices were based on importance to the salmon fishery within particular areas but also on the availability of data (Table 1).

The majority of rivers examined in this study are located

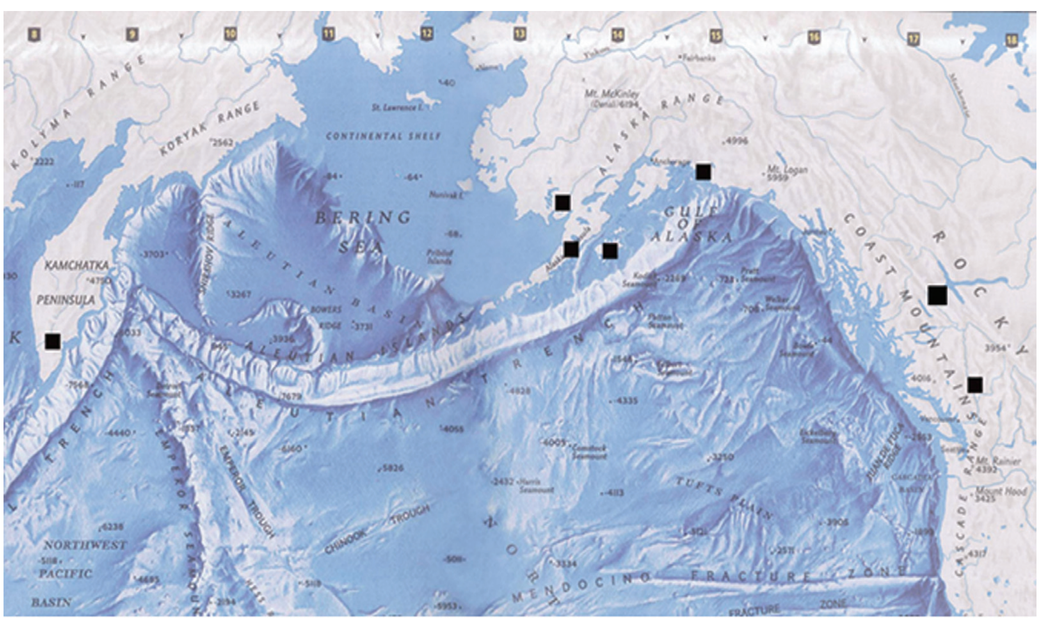

Fig. 2. Map of the North Pacific Basin and the Bering Sea with sites of collection of measurements. Locations—West to East: Kamchatka Peninsula, Bristol Bay, Chignik River, Karluk River, Copper River, Skeena River and Fraser River.

Table 1. Summary of locations and rivers with available measurements.

Area	Rivers and lakes	Measurement
Russia	Ozernaya & Kamchatka rivers	Standard Length
Chignik	Chignik River	ME – FT
Karluk	Karluk River	ME - FT
Bristol Bay	All	ME – FT
Prince William Sound	Copper River & Eshamy Lake	ME – FT
British Columbia	Skeena and Fraser rivers (Cultus Lake, Adams River & Chilko Lake)	Standard Length

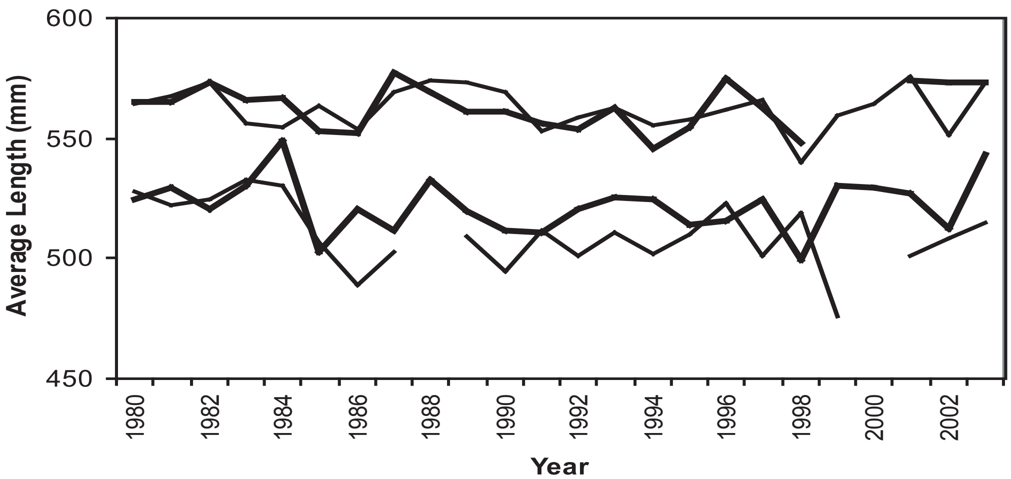

Fig. 3. Mean lengths of age 2.2 (bottom) and 2.3 (top) sockeye salmon in the catch (heavy line) and escapement (light line) in the Togiak River, Bristol Bay. The breaks in lines indicate missing data.

within the state of Alaska. Bristol Bay contains the heaviest concentration of spawning sockeye and the broadest extent of spawning grounds and rearing areas. We also studied sockeye from the Fraser River, BC, an area with many large stocks of spawning sockeye salmon.

Most of the data are based on measurements taken from mid-eye (ME) to the fork of the tail (FT) of the fish. By taking measurements along the skeletal structure it is possible to compare salmon from different spawning grounds, thus avoiding the problems introduced as a result of sexual dimorphism in salmon caught in the commercial fishery. Equations to convert from one type of length measurement to another were developed by Duncan (1956). Originally it was hoped that length measurements could be used to identify different salmon races, but this turned out not to be possible. The other measurements were standard length (from the tip of the snout to the fork of the tail). Wherever possible, comparisons are based on measurements of females.

The salmon return in a year at different ages. The most common freshwater ages are 1. and 2. following the notation of Koo (1962). There are a few streams where 0. sockeye are common while in other streams 3. salmon are encountered. However, each of these groups is small in number and not included in this study.

We see a similar pattern for sockeye salmon differing in saltwater age. Two groups, .2 and .3, (two- and three- sea-year, respectively) form the major part of a year's returns. Jacks (or .1 salmon) are not retained by the gill nets in use today. They represent a small fraction of salmon returns and are not included in this study.

RESULTS

Net Selectivity

Most length measurements of sockeye salmon in Alaska were from fish seined at river mouths. These salmon had first to pass through the corresponding fishing district. Linen gill nets were in use from the inception of the fishery in the 1880s to the 1950s. During this time period the mesh size decreased from 6 ¼" stretched mesh to 5 ½". The old nets were highly selective for size and retained larger fish, especially males (Mathisen 1971).

Since the mid fifties monofilament nylon gill nets with a stretched mesh size of 5 3/8" have been used in Alaska. In order to compare the length distributions obtained in the

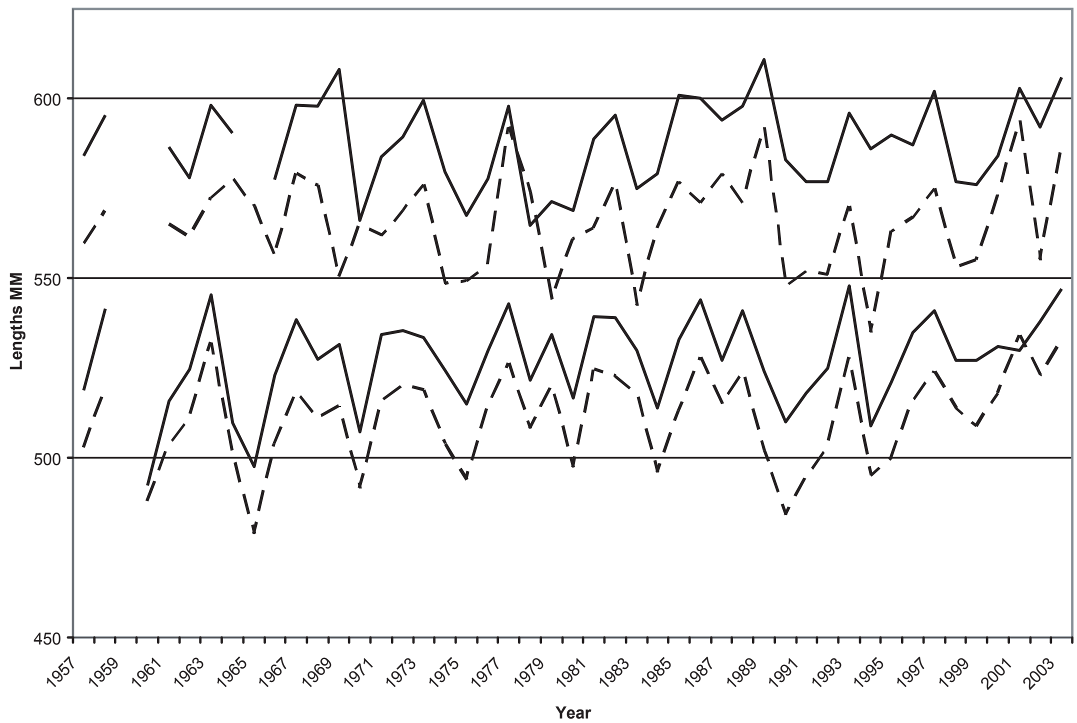

Fig. 4. Mean lengths of male (solid line) and female (broken line) sockeye salmon from the Kvichak River in Bristol Bay. Top: age 2.3; bottom: age 2.2.

commercial fishery with escapement numbers we selected the Togiak River in Bristol Bay. It is the most westerly major river in Bristol Bay with a commercial fishery. There is no possibility that sockeye salmon from the other rivers in this study could be mixed with the Togiak salmon. As seen in Fig. 3, the length distribution observed in the commercial fishery and that obtained in the escapement from the Togiak River do not indicate any size selectivity for 2.3 fish (a pairwise t-test gave a value of $P = 7681$). For the 2.2 sockeye there is a significant value ($P = 0.004$). It should be remembered that we had no means to sort out the sampling error. With this reservation, we decided to treat the mean length distributions from escapement data as interchangeable with mean length distributions for the entire stock. This provided the advantage of using the length distribution from a homogenous stock of salmon, not from a mixed stock, which is the case in the commercial catch. Thus, we conclude that for this study the mean lengths in the escapement data are representative of the total run.

Variation in Length

Comparison of the Kvichak River Age/Sex Groups of Sockeye Salmon

Figure 4 shows a comparison of age groups, 2.2 and 2.3, for males and females. The difference in mean length between males and females of the same age varies from one to two centimeters. Some years show a larger spread between the sexes, which might be the result of sample variability. Likewise, there is a larger spread (5–6 cm) in length between .2 and .3 fish of either sex. There is more variability in age .3 between the two sexes than for the age .2 fish. A comparison of the correlation coefficients for males and females for the principal age-classes are shown in Table 2.

Table 2. Pearson correlation coefficients in length between sockeye salmon sexes by age group in the Kvichak River, Bristol Bay.

Age-class	Correlation	Sample size	Significance
1.2	0.75	40	$P < 0.01$
1.3	0.75	40	$p < 0.01$
2.2	0.93	47	$P < 0.01$
2.3	0.63	47	$P < 0.01$

There is a high correlation between males and females for all age groups, especially age group 2.2. The correlation coefficient is as high as one would expect from visual inspection of the graph. On this basis we conclude that males and females are mixed together during ocean residence, or at least during the final year before they return to spawn.. We use the magnitude of the correlation coefficients as a measure of overlap in feeding areas.

Comparison of Streams in Bristol Bay

We compared length distributions of sockeye salmon from the Kvichak River and the nearby Naknek River in

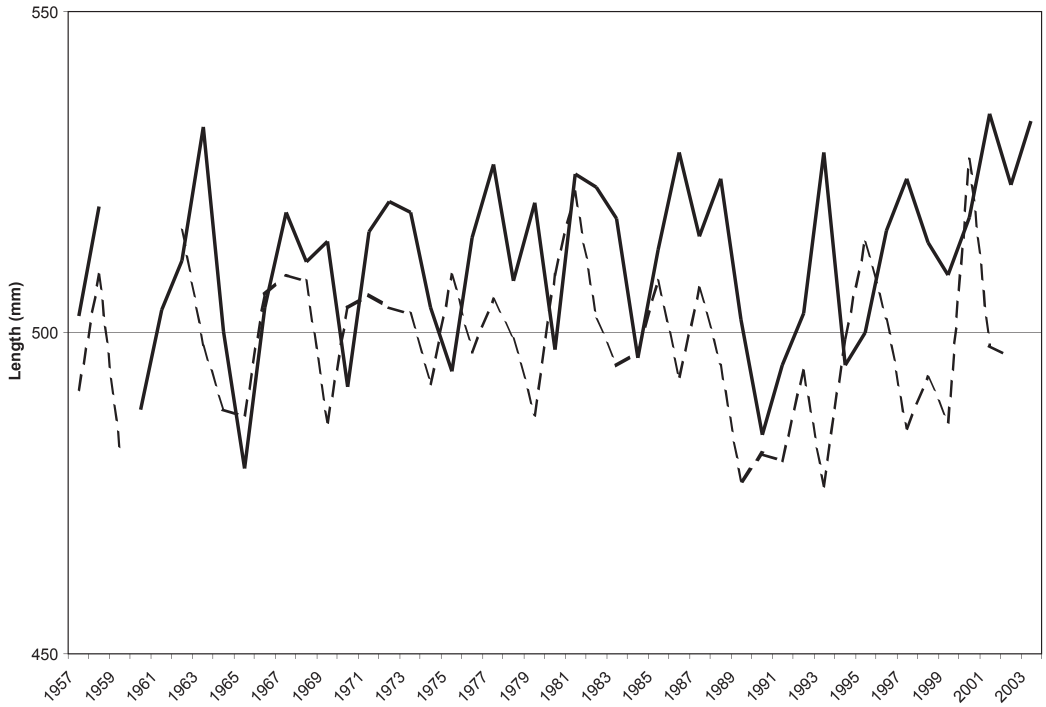

Fig. 5. Mean lengths of female sockeye salmon (age 2.2) from the Kvichak (solid line) and Naknek (broken line) rivers in Bristol Bay.

Table 3. Pearson correlation coefficients between the mean length of sockeye salmon in the Kvichak River and other rivers in Bristol Bay. Significant (α = 0.05) relationships are noted in bold and italics. Sample size is 42 in each case.

River	Age-class	
	2.2	2.3
Naknek	***0.66***	***0.58***
Egegik	***0.54***	***0.32***
Ugashik	***0.59***	0.28
Igushik	0.12	***0.49***
Wood	0.27	***0.44***
Togiak	-0.03	***0.30***

Bristol Bay. We saw similar fluctuations in mean length in both rivers (Fig. 5 and Table 3). The cyclic fluctuations are less pronounced in the Naknek River. Historically, the production of sockeye salmon in the Naknek River, measured in numbers, has been much more stable than in the larger Kvichak River. The regression coefficients for Kvichak Bay and the Egegik and Ugashik rivers are high for age 2.2, and also for age 2.3, although less so. In the Igushik, Wood and Togiak rivers there is no significant correlation for age 2.2 but a significant correlation for age 2.3 salmon. This could be interpreted that .3 fish have an extra year to travel out of or into feeding areas for salmon from different rivers.

There are variations within such a large number of salmon stocks. A comparison with a large river system such as the Wood River demonstrates this variability. In Fig. 6, the mean length of females age 2.2 for the Wood River is more out of phase than in phase with the corresponding curve for the Kvichak River females of the same age. But when the mean length for females age 2.3 is plotted, the two graphs are more synchronized (Table 3).

We conclude that despite noted discrepancies, the sockeye salmon from the various rivers in Bristol Bay have many growth features in common such that they can be dealt with as a single unit.

Comparison of Districts

We compared mean lengths for Kvichak River age 2.2 females and Copper River (Prince Williams Sound) age 1.2 females. This choice was necessitated because the 2.2 age-class of Copper River sockeye is not abundant (Fig. 7). There are fluctuations in mean length over time for the Copper River fish, but they are small compared to the Kvichak River fluctuations. Further, they are not well synchronized with the Kvichak salmon run. It should be noted that there is a significant correlation coefficient between age 1.2 fish from the Copper River and age 2.2 fish from the Kvichak River, which suggests overlapping feeding grounds between the numerically strong Kvichak run and the much smaller Copper River run. We suggest that this took place closer to the Copper River sockeye salmon feeding grounds and therefore represents a tentative eastern boundary for the Bristol Bay salmon.

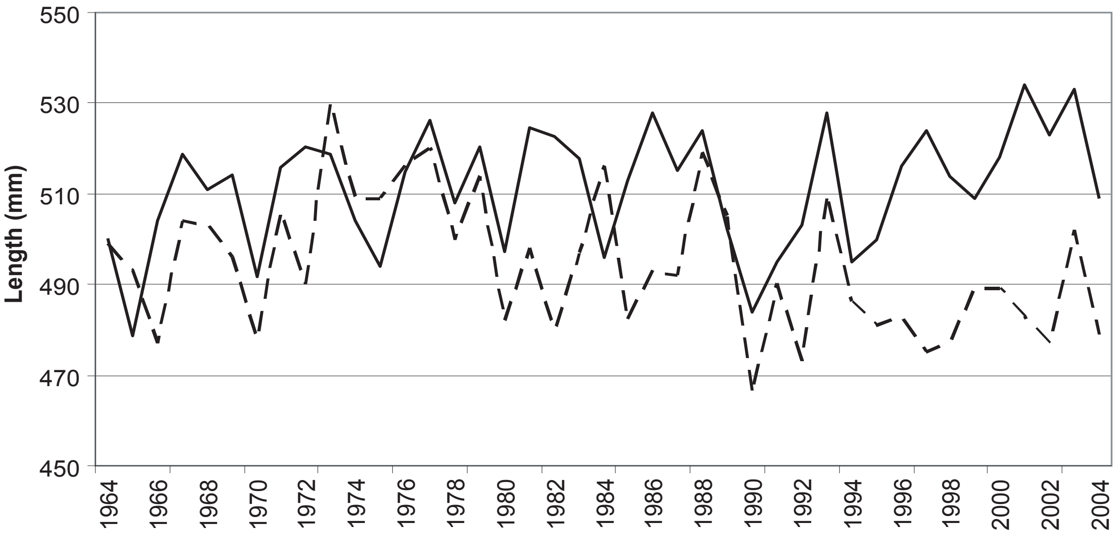

Fig. 6. Mean lengths of female sockeye salmon (age 2.2) from the Kvichak (solid line) and Wood (broken line) rivers in Bristol Bay.

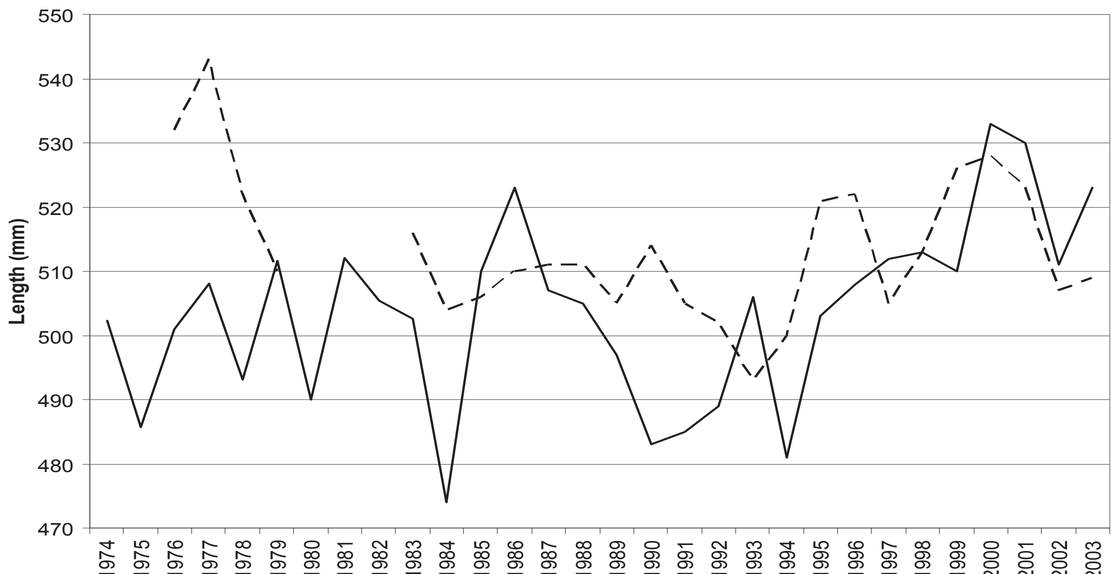

Fig. 7. Mean lengths of female sockeye salmon (age 1.2) from the Copper River (broken line) in Prince William Sound and the Kvichak River (solid line) in Bristol Bay.

We then compared the sockeye salmon runs to the Chignik River in Alaska Peninsula and the Karluk River on Kodiak Island (Fig. 8). The amplitudes of the oscillations are smaller than seen elsewhere with the two graphs in phase during 1986–2004. Still, it is important to note that the age-class 2.2 in both rivers failed to produce significant correlation coefficients with the Kvichak 2.2 females, while the 2.3 salmon in both rivers had significant correlation values.

We have length measurements from two major rivers on the Kamchatka Peninsula, the Kamchatka and Ozernaya rivers. The measurements have been combined in Fig. 9. These graphs show that a 1. or a 2. freshwater life history does not affect the final length at maturity. There are pronounced cyclic changes in the length measurements, with lengths of the females increasing by up to 5 cm from peak to off-peak years. The data show no indication of overlapping feeding grounds such as those shown for Bristol Bay sockeye (see Table 3). This is in line with the annual north–south migrations of the sockeye salmon in the Far East (Radchenko and Mathisen 2004).

The Adams River and Chilko Lake, British Columbia, represent two spawning locations that are geographically distant from each other. Nevertheless, a plot of the mean lengths of these two populations shows that they vary synchronously. Because we assume that synchronous changes in mean length indicate overlapping feeding areas (Fig. 10), we

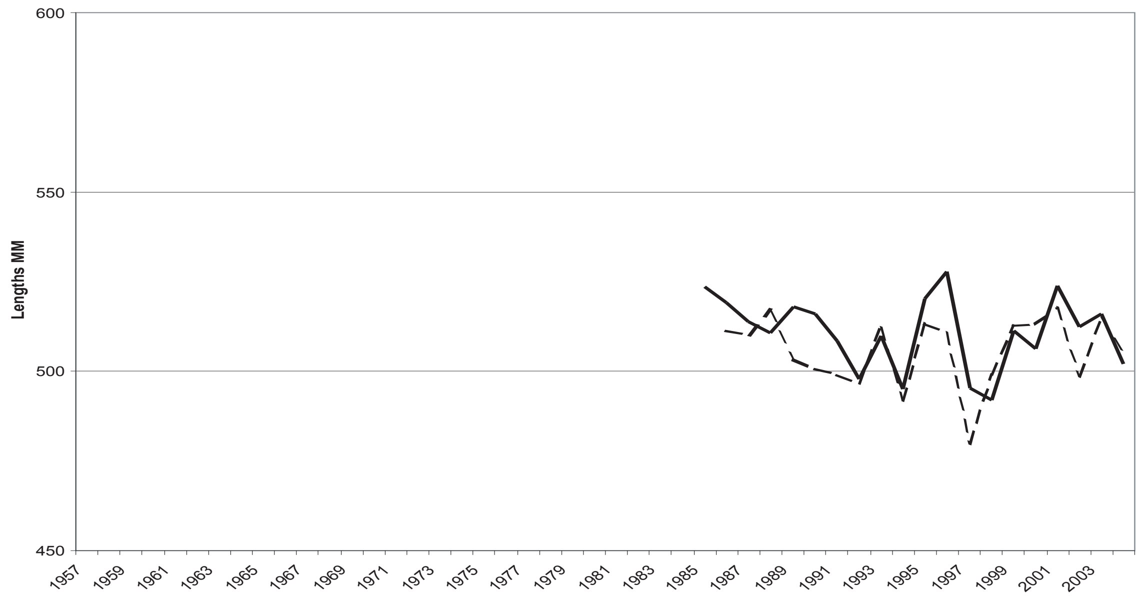

Fig. 8. Mean lengths of female sockeye salmon (age 2.2) from the Karluk River (broken line) on Kodiak Island and the Chignik River (solid line) in Alaska Peninsula.

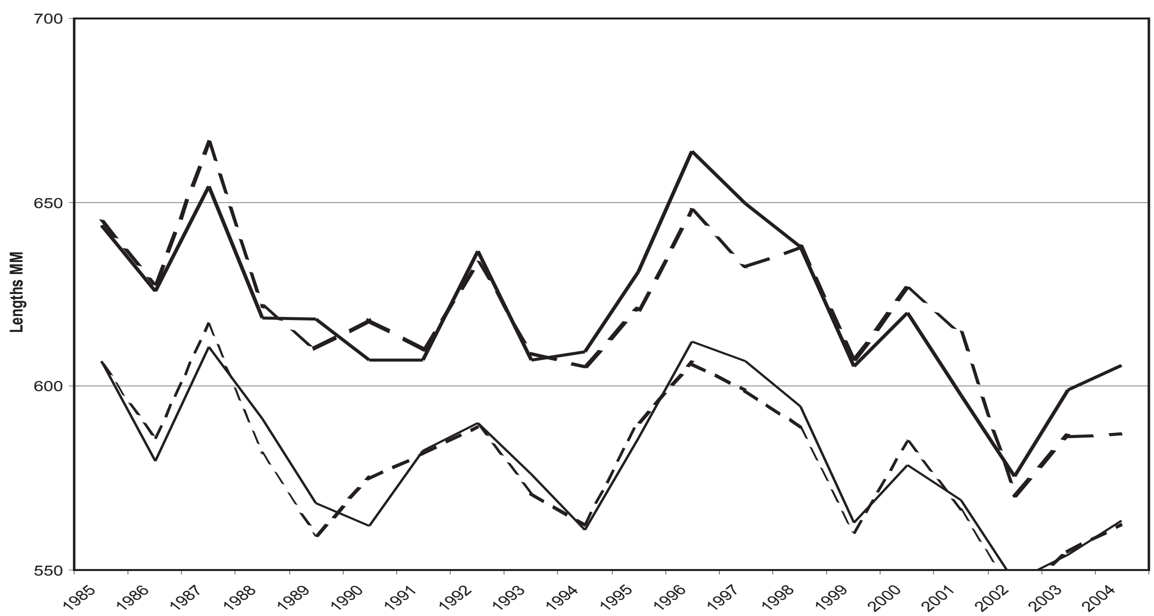

Fig. 9. Mean lengths of male (top) and female (bottom) sockeye salmon from the Kamchatka and Ozernaya rivers in the Kamchatka Peninsula, Russia. Solid lines: age 2.3; broken lines: age 1.3.

then examined the correlation coefficients. The low correlation coefficients (compared to those for the Kvichak salmon, e.g.) suggest that there is no overlap in ocean feeding areas.

There are some indications in Fig. 11 that the mean lengths of Cultus Lake sockeye decline toward the end of the time series. In the Bristol Bay data and elsewhere there is no indication that the mean lengths are declining. If this reduction in mean length was caused by a lowering of ocean productivity, a reduction in mean size would manifest itself at all locations. Hence we suggest that competition for food resources is a major cause.

We have length measurements from the Skeena and Fraser rivers, British Columbia. The Fraser River has the second largest concentration of sockeye salmon in North America, after Bristol Bay. There are a number of different spawning populations. Two of them have been selected and their mean lengths plotted in Fig. 12. This is the longest time series in this study.

The Skeena River lies north of the Fraser River complex (Fig. 2). Salmon in the two rivers differ in age composi-

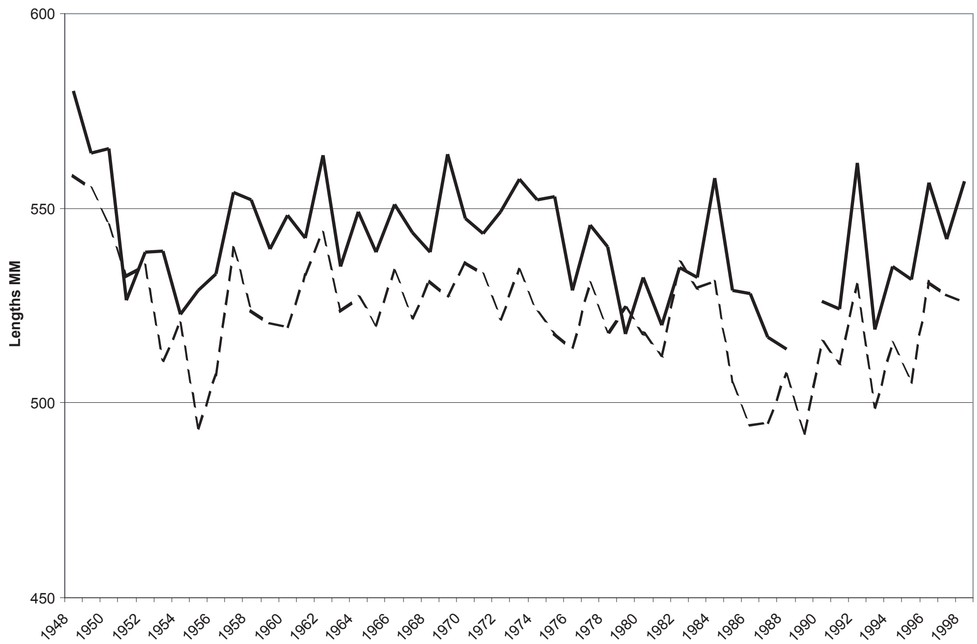

Fig. 10. Mean lengths of female sockeye salmon (age 1.2) from the Adams River (solid line) and Chilko Lake (broken line) in British Columbia.

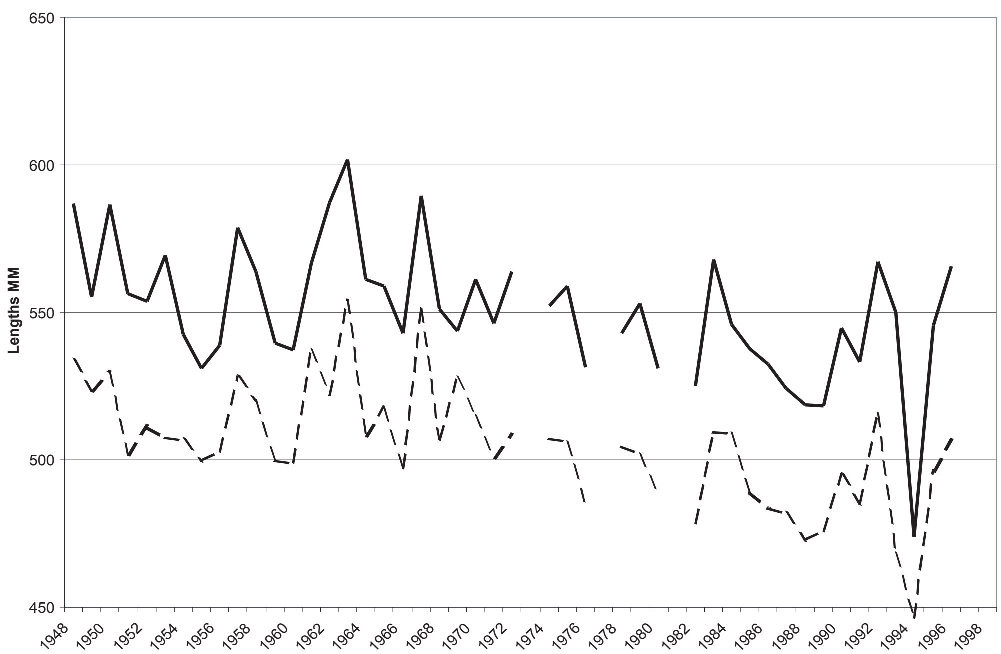

Fig. 11. Mean lengths of male (solid line) and female (broken line) sockeye salmon (age 1.2) from Cultus Lake in British Columbia.

tion and fish having two freshwater annuli are very common in the Skeena River. The mean lengths of .2 and .3 ocean salmon have been plotted in Fig.12. There is no indication of cyclic changes in mean length. The complete geographical segregation of the Fraser and Skeena river systems is shown in Tables 5a and 5b where the correlations coefficients have been calculated. There are no significant relationships between the mean lengths of sockeye in the two river systems.

DISCUSSION

The Structure of Sockeye Salmon Foraging in the Ocean

This study reports on measurements of sockeye salmon from a variety of spawning locations over many years. These time series have been used to make some inferences about the structure of sockeye salmon feeding in the North Pacific Ocean. The underlying assumption is that salmon

Fig. 12. Mean lengths of age 2.2 (heavy line) and 2.3 (light line) sockeye salmon from the Skeena River in British Columbia.

Table 4. Pearson correlation coefficients between the mean length of female sockeye salmon from the Kvichak River and other rivers. Significant (α = 0.05) relationships are noted in bold and italics. Sample sizes are indicated in parentheses.

River	Age-class		
	1.2	2.2	2.3
Karluk		0.18 (20)	***0.67*** (20)
Chignik		0.37 (19)	***0.52*** (19)
Chilko	-0.23 (26)		
Adams	-0.22 (26)		
Cultus	0.11 (26)		
Eshamy	-0.15 (21)		
Copper	***0.50*** (21)		
Ozernaya (Kamchatka Pen.)		0.02 (15)	0.26 (15)
Kamchatka early run			0.10 (20)
Kamchatka late run			0.10 (20)

Table 5a. Relationship to Skeena River and selected stock in the Fraser River (Female 1.2).

	Skeena	Cultus	Adams	Chilko
multiple r		14.8%	-2%	10%
p-value		0.53	0.93	0.66
significance		no	no	no
stationary mean	yes	yes	yes	yes

Table 5b. Relationship to Skeena River and selected stock in the Fraser River (Male 1.2).

	Skeena	Cultus	Adams	Chilko
multiple r		23%	36%	22%
p-value		0.31	0.09	0.3
significance		no	no	no
stationary mean	yes	yes	yes	yes

showing the same growth pattern in the final year of ocean residence must have been feeding together in the ocean during this time.

The length measurements demonstrate two growth patterns. In some cases there is a slow but steady decline with time in average length. The more common mode involves cyclic changes in final length at maturity corresponding to the underlying cycle. The sockeye salmon in Bristol Bay serve as an example.

The seaward migration of smolts takes place toward the end of May and the first part of June. During a time span of 2–3 weeks in excess of half a billion smolts pour into Bristol Bay. Here their migration slows down as they move westward along the Aleutian Chain or over the lower shelf in the Bering Sea (Straty 1975; Jewett et al. 2004; Farley et al. 2005). As fall arrives the juvenile sockeye salmon apparently move south of the Aleutian chain in a manner similar to the Russian sockeye salmon along the eastern coast of Kamchatka (Radchenko and Mathisen 2004). Immature salmon in the age groups .1 or .2 are seldom captured during annual surveys intended for .0 juveniles (E. Farley, Auke Bay Laboratory, Alaska Fisheries Science Center, 11305 Glacier Highway, Juneau, AK 99801-8626, pers. comm.)

During this feeding phase in the life of the sockeye salmon there are ample opportunities for the various stocks to mix. We know that this is true for the Bristol Bay salmon feeding on the high seas. Toward their final year in the sea, the maturing salmon assemble in the coastal waters where in peak years competition for food must be severe as evidenced by a loss of 3 to 5 cm in final length compared to the average length in off-peak years. Ruggerone et al. (2003) have studied the growth of sockeye salmon from the Kvichak and Egegik rivers. Their average scale growth curves show a substantial increase in length (and therefore in weight) during the last year of ocean residence.

In short, the smolts migrate to sea and spread out like a fan, which will close in a counter- clockwise fashion with the onset of winter and bring the juveniles south of the Aleutian Chain. Until maturity the sockeye salmon remain in the current system so time becomes an important factor in addition to the geographic coordinates. The areas serving as nursery grounds presumably will expand or contract according to the total biomass of sockeye salmon. There are distribution maps in the literature, which probably represent maximum expansions.

Although the time series of size for the northern Gulf of Alaska rivers (such as the Copper River) are shorter than for Bristol Bay rivers, only the youngest of the returning fish mix with Bristol Bay salmon, whereas the .3 ocean fish are isolated from the Bristol Bay sockeye judging from the correlation coefficients in Table 3. The Copper River could be considered as the eastern extension of the Bristol Bay sockeye salmon complex.

In regard to the Karluk/Chignik complex, the two curves in Fig. 8 are very similar, as expected from the proximity of the two rivers. Judging from the correlation coefficients the Karluk/Chignik populations do not mix with the Bristol Bay salmon. For the .3 ocean salmon we find that these fish do mix with the Bristol Bay salmon (Table 4). This is the same behavior pattern as observed for the Nushagak River sockeye salmon. One could perhaps use the westward expansion as the limit of the area occupied by the Bristol Bay sockeye salmon complex.

The geographical boundaries of Bristol Bay sockeye salmon should not be considered as solidly fixed. We are dealing with probabilities, and total number of fish becomes one of the governing parameters. The net impression is that the Bristol Bay sockeye salmon travel and feed throughout their life as a homogeneous unit. The sockeye salmon in the Fraser River system do not mix with Bristol Bay salmon as indicated by Peterman et al. (1998) and demonstrated by our length measurements and correlation coefficients. Further, the sockeye salmon from the Kamchatka Peninsula do not mix with their counterparts farther east. Given the rapid advances in genetic identification, we will soon be able to identify the place of origin of juvenile sockeye salmon intercepted on the high seas (Habicht et al. 2005).

Carrying Capacity of the North Pacific Ocean

Recently there have been many reports that claim that the average length of chum salmon is decreasing, and that changes in age composition are occurring (Ishida et al. 1992; Kaeriyama 1998, 2003; Helle and Hoffman 1995, 1998). Some think that these observations are related to changes in climate which, in turn, may have altered the productivity of oceanic nursery grounds. Another more plausible cause is that the carrying capacity of the ocean area in question has been reached or even exceeded. This could be caused, in part, by the rapid expansion of ocean ranching of chum salmon by Japan.

For sockeye salmon it is clear that the ecosystem cannot support runs much larger than those seen today during peak years. High spawning density results in reduced growth of fry. This, in turn, will reduce the survival of the juvenile sockeye salmon feeding in the sea. A self-regulating mechanism of this kind will place an upper limit on the number of spawners that a river can support.

In the Fraser system which has the longest record of measurements to date, we do not find pronounced changes in total length. On the other hand, in streams such as the Stuart and Nadina we see a sharp decline in mean length with the time. In a few cases such as Cultus Lake there are signs of decreasing mean length. There could be a decline in the productivity of the oceanic ecosystem utilized by the sockeye salmon from the Fraser River. However, this would then have a universal character and not be confined to fish from just a few streams. On the other hand, there are man-generated changes to the ecosystems in the eastern part of the Gulf of Alaska. Ocean ranching of pink salmon has been very successful, especially in Prince William Sound. At the same time ocean ranching of the more valuable chum salmon is growing steadily. Helle and Hoffman (1998) report reduced growth and increased age at maturity of wild stocks of chum. There is enough overlap in dietary spectra among salmon to make this a plausible suggestion.

Cyclic Abundance in Sockeye Salmon

The magnitude of salmon runs to many different streams in different locations display cyclic changes in abundance. Figure 9 indicates a strong cycle in abundance for the two streams examined on the Kamchatka Peninsula. The cycle in the Kvichak River has been known since the inception of the fishery. Lately the peak years have been small in the Kvichak system, but at the same time the Egegik runs have been strong such that the total number of salmon returning to the eastern side of Bristol Bay has not changed significantly. There still is discussion about interception of Kvichak salmon in the Egegik District. In the Fraser River there are many streams with cyclic patterns, in addition to that in the well-known Adams River. The year of peak abundance can shift depending upon the life history of the stock under consideration.

The reason for development of sockeye salmon cycles cannot be to increase production or biomass. As pointed out by Mathisen and Sands (2001) the increase in numbers is accompanied by a decrease in weight, leaving the total biomass without significant fluctuations. However, the increase in numbers has a drastic effect on the distribution of the escapement. In 1965, for example, the Kvichak escapement had close to 25 million spawners, with the result that spawners were found in unlikely locations such as over bedrock or rock falls. Clearly one function of a peak year in the salmon cycle is to deliver spawners to all possible sites in the nursery areas.

ACKNOWLEDGEMENTS

As indicated in the text, the data for this study have been drawn from a number of sources. They can only be listed in a summary fashion: Richard A. Merizone, Alaska Department of Fish & Game (ADF&G), Cordova, AK, approved the data from the Copper River. Fred West, ADF&G, Cordova, AK, submitted a file with measurements of sockeye salmon from Eshamy Lake. Matt Foster, ADF&G, Kodiak, AK supplied the data used for the Karluk and Chignik rivers. Al Cass, Department of Fisheries and Ocean, Nanaimo, BC, made available the entire Fraser River length measurements. Vladimir Dubynin, KamchatNIRO, Petropavlovsk, Russia, furnished the data from Ozernaya River, Kamchatka. Dr. Kate Myers shared her knowledge of Pacific salmon in the North Pacific Ocean. Molly O'Neil rearranged the raw data files and prepared the illustrations. To all these people we extend our thanks for their effort in completing this manuscript.

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