Trends in Abundance and Biological Characteristics of Pink Salmon (*Oncorhynchus gorbuscha*) in the North Pacific Ocean

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Abstract: Pink salmon are the most widely distributed species of the genus *Oncorhynchus*. Biennial cycles in the timing of the spawning migration and catch values are characteristic of pink salmon stock dynamics. Over the long term, two periods of high levels of abundance have been observed on both the Asian and North American coasts of the Pacific Ocean. Large-scale trends in abundance vary less than regional abundances. Coincidences in trends in catch dynamics among odd-year and even-year broodlines were found for several fishery regions. The observed relationships suggest a response of both broodlines to global factors that influence pink salmon reproduction and survival. Trends in abundance are influenced by global factors that are not necessarily cyclical. The dynamics of solar activity and an increase in ocean heat content play a significant role in their cumulative effect. Current pink salmon stock abundance may be close to a historic maximum. There is reason to expect that this level will continue in the near future under the influence of increasing ocean heat content. Pink salmon biological characteristics are related to levels of stock abundance. Average size in specific regions can also be related to the structure of regional salmon stocks which consist of a variety of seasonal races and ecological groupings.

Keywords: pink salmon, abundance dynamics, solar activity, ocean heat content

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) are the most widely distributed Pacific salmon species of the genus *Oncorhynchus*. They occupy an area from 38° N in the Sea of Japan to the Aleutian Island and from the southeastern Sea of Okhotsk to the Gulf of Alaska where they overwinter (Heard 1991; Shuntov 1994). In contrast to other Pacific salmon, the distribution of pink salmon extends into the Arctic. At their southernmost distribution, spawning pink salmon populations enter rivers from Hokkaido and the northern Korean Peninsula to the Lena River in Asia, and from the Sacramento River in California to the Mackenzie River in Arctic Canada. Most spawning populations are situated between 45° and 65°N (Mathisen 1994; Temnykh 2005). The most abundant pink salmon populations spawn in rivers of Sakhalin and the southern Kuril Islands, the western and eastern coasts of the Kamchatka Peninsula, and central and southeastern Alaska.

Human introductions have created several pink salmon stocks beyond the Pacific Ocean. One of the largest acclimatized stocks is well established in the Great Lakes in the United States and Canada (Kocik et al. 1991). In 1956, pink salmon were accidentally introduced into Lake Superior in very small numbers (about 100 fish). Since that time, they have become permanent members of the pelagic ecosystem in Lake Superior, Lake Huron and Lake Michigan (Kelso and Noltie 1990). Despite significant changes in life span (some fish mature at 3 and even 4 years of age) two-year cycles in the abundance of pink salmon were observed in the St. Marys River that connects Lake Superior and Lake Huron. There, catch-per-unit-effort was greater in even years (57 fish/night) than in odd years (30 fish/night) (Kennedy et al. 2005) indicating the dominance of the even-year cycle.

In Russia, pink salmon have been introduced into the Barents and White seas. Pink salmon spawning migrations in these areas reached 155,400 fish in 2001. Fish from this stock have strayed to Iceland, Scotland and as far as the southern coast of Norway. However, it was only the odd-year broodline that reproduced successfully. All efforts to produce an even-year broodline have been unsuccessful despite the fact that the same technology was used for both lines. The odd-year and even-year broodlines have significantly different gene pools. The levels of divergence along their respective genetic markers are higher than between the different local groups within each of these broodlines (Glubokovsky 1995).

One of the most characteristic features of pink salmon abundance dynamics is their two- year life cycle. The levels of spawning stock abundance differ markedly between odd- and even-year broodlines: high levels in odd years and low

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levels in even years, and *vice versa*. The dominance of even-year or odd-year populations, may persist for long periods of time while stocks in neighboring regions may show the opposite dynamics; for example, on the western and eastern Kamchatka coasts, respectively. Therefore, we analyzed the trends in abundance and biological characteristics of pink salmon, paying special attention to both similarities and differences between odd-year and even-year broodlines. Additional attention was paid to recently revealed coincidences in trends for some regional groups (Radchenko 2004). The causes and applicability of this phenomenon for forecasting pink salmon abundance dynamics are discussed.

Preliminary analysis reveals two important global climate factors that affect pink salmon stock abundance. The first is the influence of precipitation and air temperature on the spawning grounds, especially in winter and early spring (Goryainov & Shatilina 2003). The second is the influence of atmospheric circulation patterns on surface water along feeding and migration routes. On a global scale, variability in these climate parameters is determined by interrelated, but different, global processes with different periodicities. The patterns of atmospheric circulation are determined by the earth's rotation velocity (Klyashtorin and Sidorenkov 1996). Variability in air temperature is related to solar activity although it does not depend on the intensity of long-wave radiation directly. Below, we also analyze the long-term dynamics in the average annual values of the Wolf numbers, which characterize solar activity.

MATERIALS AND METHODS

Catch dynamics is the basic index of Pacific salmon stock abundance. This index remains as almost the only measure of abundance for large geographical regions, that is obtained by direct observation. Most other indices are determined using extrapolation to some degree. In this connection, we pay significant attention to the analysis of Pacific salmon catch statistics (Chigirinsky 1993; Henderson and Graham, 1998; Hiroi 1998; Kope and Wainwright 1998; Radchenko 1998; Karpenko and Rassadnikov 2004; Eggers et al. 2004).

Data analysis of the absolute abundance of pink salmon seems to be preferable to reveal trends and regularities in abundance dynamics. However, such data series are still rare and relatively short in the majority of regions. Observations of pink salmon absolute abundance have been actively conducted in the major fishery regions on the Russian coast since the beginning of the 1960s. Varnavskaya et al. (1995) compared dynamics of pink salmon catch and absolute abundance (i.e. catch + escapement) in 1960–1993. They noted that distinctions are negligible in most cases, although sometimes, such as for the odd-year broodline in western Kamchatka, the northern Okhotsk Sea coast, the Amur River and the Primorie region, discrepancies between catch data and spawner abundance are clearly recognizable. However, the portion of pink salmon catch in those regions averaged only 16.1% of the total pink salmon harvest on the Russian coast in odd years between 1960 and 1993. Catch and absolute abundance data summarized by Antonov (2005) for Aniva Bay have a close correlation (R^2 = 0.97) for 1971–2004. This indicates that it is appropriate to use pink salmon catch data for analysis of abundance dynamics, at least for the period after stabilization of fishery.

Data on the total pink salmon catches on the Asian and North American coasts for 1925–2001 were taken from the review prepared by the Working Group on Stock Assessment (CSRS) of the North Pacific Anadromous Fish Commission (Eggers et al. 2004). The catch series for the Russian coast for 1900–1986 are based on the statistical summary (Yanovskaya et al. 1989) prepared by the All-Russian Scientific Research Institute of Fisheries and Oceanography (VNIRO, Moscow). Data for 1900–1906 are incomplete and include information from the Sakhalin – Kuril Island region only. Data for 1940–1947 were taken from Tables 5 and 10 from Yanovskaya et al. (1989). Information on the Japanese catch on southern Sakhalin and Kuril Islands and areas of the concession fishery were taken from the INPFC Bulletin No. 39, Table 43, 1979. Total weight was estimated from catch in numbers multiplied by the average pink salmon body weight (1,300 g for 1936–1942) in several Sea of Okhotsk coastal fishery regions. Since Japanese data on this pink salmon fishery became available (Eggers et al. 2004), they were included in the total Japanese catch calculation of the present-day Russian coast for 1925–1945. A comparison of two data series revealed that the previous pink salmon harvest was underestimated in those years. The average catch from the CSRS report (109,110 t for the 21 years) exceeds the estimate (101,980 t) from the VNIRO report by 6.5%. Therefore, the catch data series for 1906–1924 from the VNIRO report were corrected by a multiplication factor of 1.07. Catch data for the Russian fishery on the eastern and western Kamchatka coasts were not available for 1931 and 1933. Only data from the Japanese concession fishery were used in the analysis for those years: 6,817 (1931) and 17,330 t (1933) (eastern coast); 10,250 and 10,350, respectively, (western coast). Therefore, total catch can be underestimated to be 5,000–6,000 t for eastern Kamchatka and 7,000–10,000 for western Kamchatka for 1931 and 1933. After 1986, data on the Russian catch were taken from the TINRO-Centre (Vladivostok) archive, and verified with data in the NPAFC annual reports and statistical yearbooks. All salmon catch values in this report are given in metric tons (t).

To compare trends in pink salmon catch dynamics for odd- and even-year pink salmon broodlines, the abundances were analyzed separately, which makes it possible to standardize the differences in absolute values of stock abundance. In our study, trends in catch dynamics for pink salmon were calculated as the arithmetic difference of the "expected" catch calculated as the mean value of the four previous years in the odd years or even years and the actual catch. These methods of calculation were applied to reduce noise and provide a clearer picture of trend dynamics.

$$C_{exp\ 2004} = (C_{act\ 1996}+C_{act\ 1998}+C_{act\ 2000}+C_{act\ 2002})/4$$

$$D_{2004} = C_{act\ 2004} - C_{exp\ 2004},$$

where $C_{exp\ i}$ is "expected" catch for the corresponding year; $C_{act\ i}$ is actual catch for the corresponding year; and D_i is the deviation of actual catch from the "expected" catch in the corresponding year.

Variability in the catch data deviations (difference from the mean value, 86,568 t in 1956–2004) was also analyzed for the Russian coast to estimate its relationship to the world ocean heat content data (Levitus et al. 2005). The deviation graph has the same form as a graph of the values themselves and is conveniently used for the comparison with the data series, which include both negative and positive values. Increments (in conventional units) of pink salmon catch deviation were calculated to identify any hidden periodicity in salmon abundance under the influence of factors unrelated to the ocean heat content. The numerical significance of the catch data deviation was divided into the arbitrarily-selected number 14.5; the numerical significance of the ocean heat content (in 10^{22} J) was subtracted for each year from 1964–2004. We are aware of the approximateness of these values based on these rapid calculations.

Analysis of moving averages is traditionally used to examine long-term trends that may be masked by short-term factors, in particular, annual variability (Pyper and Peterman 1998; Wertheimer et al. 2001). However, the main objective of this study is variability in pink salmon abundance rather than a general examination of a long-term trend. This objective determined that we study the trends in variability on a medium and long-term scale.

Data on the average annual values of the Wolf numbers, which characterize solar activity, were acquired from the website of the National Geophysical Data Center of the US (ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/SUNSPOT_NUMBERS). Spectral (Fourier) analysis for the recognition of dominant periods of variability in the data series was conducted using STATISTICA software. The Tukey window was used for evaluating spectral density.

RESULTS

The smoothed curve of the pink salmon catch series in the North Pacific is sinusoid with two highs and one low (Fig. 1). Two periods with relatively high levels are separated by years of low abundance (approximately, from the mid 1940s to the mid 1970s). This distribution has been associated with a periodicity in salmon productivity with a return period of 50–60 years (Beamish and Bouillon 1993; Chigirinsky 1993). However, the increase in salmon catch since they were first exploited was undoubtedly dependent on growing market demands, technical progress in harvesting technologies and storage methods. Thus, the average annual catch of Pacific salmon in Aniva Bay was only 160 t in 1876–1902 and increased up to 13,670 t in 1907, following a drop in catches on Hokkaido Island, to satisfy the need for Japanese exports (Antonov 2005). In such periods of gradual increases in catch value, the 2-year cycle of catches in even and odd years was not usually observed. Therefore, it is difficult to judge whether these catch values reflect the level of the stock abundance, and, further, the length of time these periods of the high and low stock abundance last, and the amplitude of their fluctuations. Comparatively high catch values of Pacific salmon in Aniva Bay were observed until 1912, decreasing thereafter. In some other regions, exploitation rates during initial periods are known to be extremely high, where pristine fish stocks are newly fished by an already developed fishery. Such initial dynamics occur in other fisheries including 'fishing up' to some critical level, which is followed by a decline related to deterioration of fish stocks.

It must be emphasized that overharvesting could be not only a result of growing fishery pressure but also of stable fishery efforts toward a deteriorating salmon stock caused by the effect(s) of natural factors. When environmental conditions are unfavorable for fish reproduction, overfishing can be especially harmful. In the same way, pink salmon catch growth since the early 1970s could be related to stock conservation and artificial propagation (i.e. hatcheries) under favorable environmental conditions. All these circumstances could blur the natural duration of periods of high and low stock abundance.

Catch dynamics differed slightly on the North American and Asian sides of the Pacific (Fig. 1). Comparison of cumulative curves, which express the increasing sum of the deviations of the annual catch values from the long-standing average, revealed a close coincidence of pink salmon catch dynamics on both the Asian and North American sides of the Pacific (Beamish and Bouillon 1993; Chigirinsky 1993). Further, for the second half of the 20th century, catch variability on the Asian coast matched that on the North American side, but with some shift in extreme points. The best correlation with the North American catch histogram occurred on a twelve-year cycle, when segments of 1957–2001 for the Asian side and 1945–1989 for the North American side are compared ($r = 0.60$, $p < 0.001$, $n = 45$). It is possible that this was related to a gradual change in the environment and pink salmon stock conditions associated with water circulation in the North Pacific, i.e. from the North American coast to the western Bering Sea coast of Kamchatka, and then, to the western Kamchatka coast and Sakhalin and the Kuril islands. Many hypotheses concerning pink salmon dynamics emphasize how natural and anthropogenic factors affect salmon stock conditions and how it is difficult to determine their significance.

Despite distinctions in absolute abundance of spawning

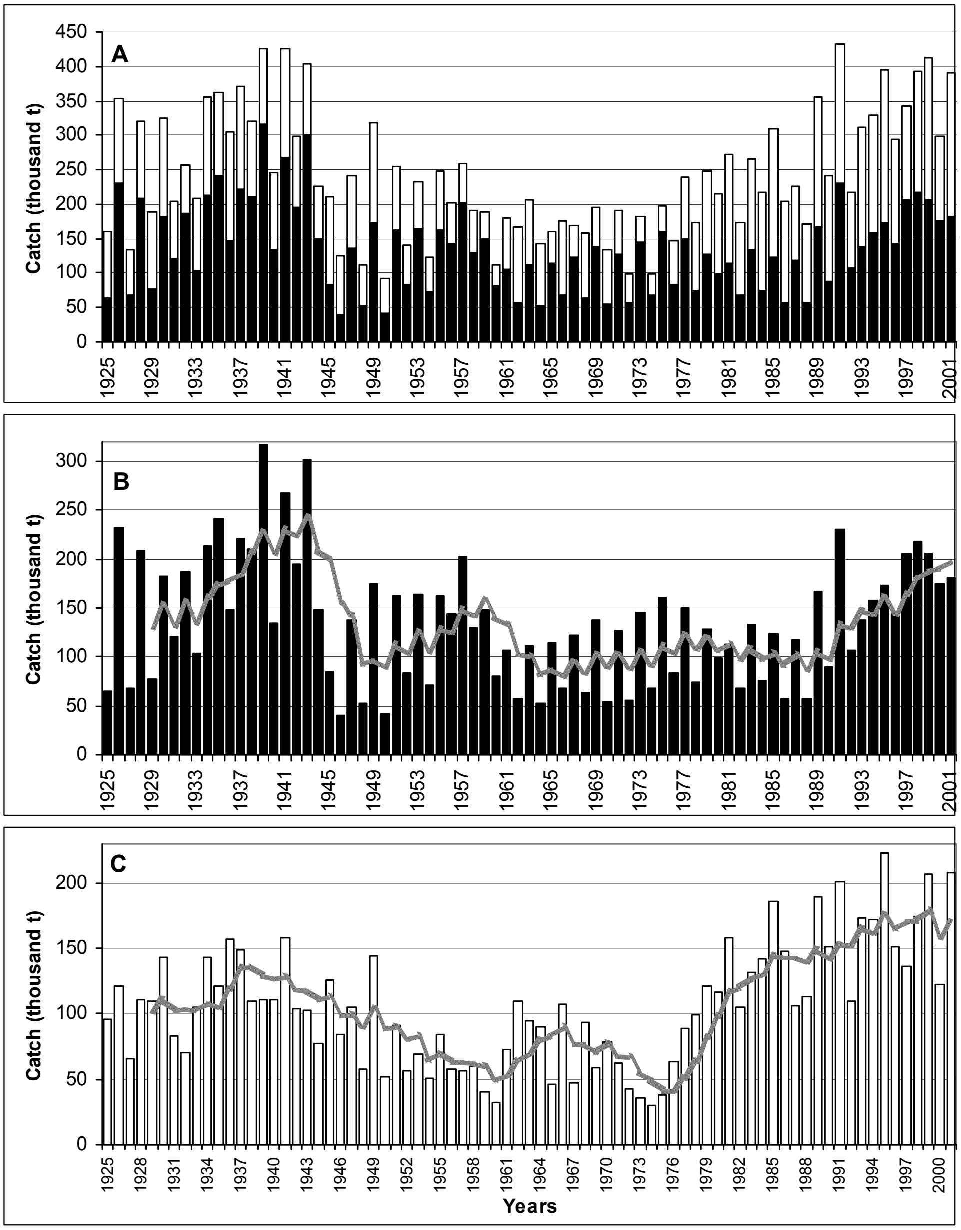

Fig. 1. Pink salmon catch (thousand tonnes) in the North Pacific. A: total; B: Asian coast; C: North American coast.

stock for the majority of stocks, the catch dynamics for the odd-year and even-year broodlines for the entire North Pacific have a moderate relationship (r = 0.49, p < 0.005, n = 38), especially for the last quarter of the 20th century after 1972 (r = 0.82, p < 0.001, n = 15). Summarized regional catch data equalized the difference between broodlines as in the average catch (272,721 t for odd years and 214,503 t for even years) and in extreme values (134,200–431,600 t for odd years and 92,900–392,800 t for even years). The standard deviations of the two data sets are equal (F = 0.80).

Most of regional groupings of pink salmon demonstrate considerably less similarity between catch data series in the even and odd years. The correlations are poor (p > 0.05) for regions such as the western and eastern Kamchatka coasts, British Columbia, and the northern coast of the Sea of Okhotsk. Fishery statistics exist only for the odd-year broodline at the southern limit of pink salmon distribution on the US coast – in Washington, Oregon and California. On the Asian coast, pink salmon groupings from the Sakhalin-Kuril Islands region, eastern Kamchatka, and, to a lesser degree from Iturup Island, show the continued reproduction of the odd-year broodline (Fig. 2). The even-year broodline is maintained by pink salmon reproduction on the western Kamchatka coast and the southern Kuril Islands. On the American side, there are two extreme geographical regions: western Alaska and the states of Washington, Oregon and California that demonstrate the significant dominance of one broodline, while three other regions are characterized by similar values for

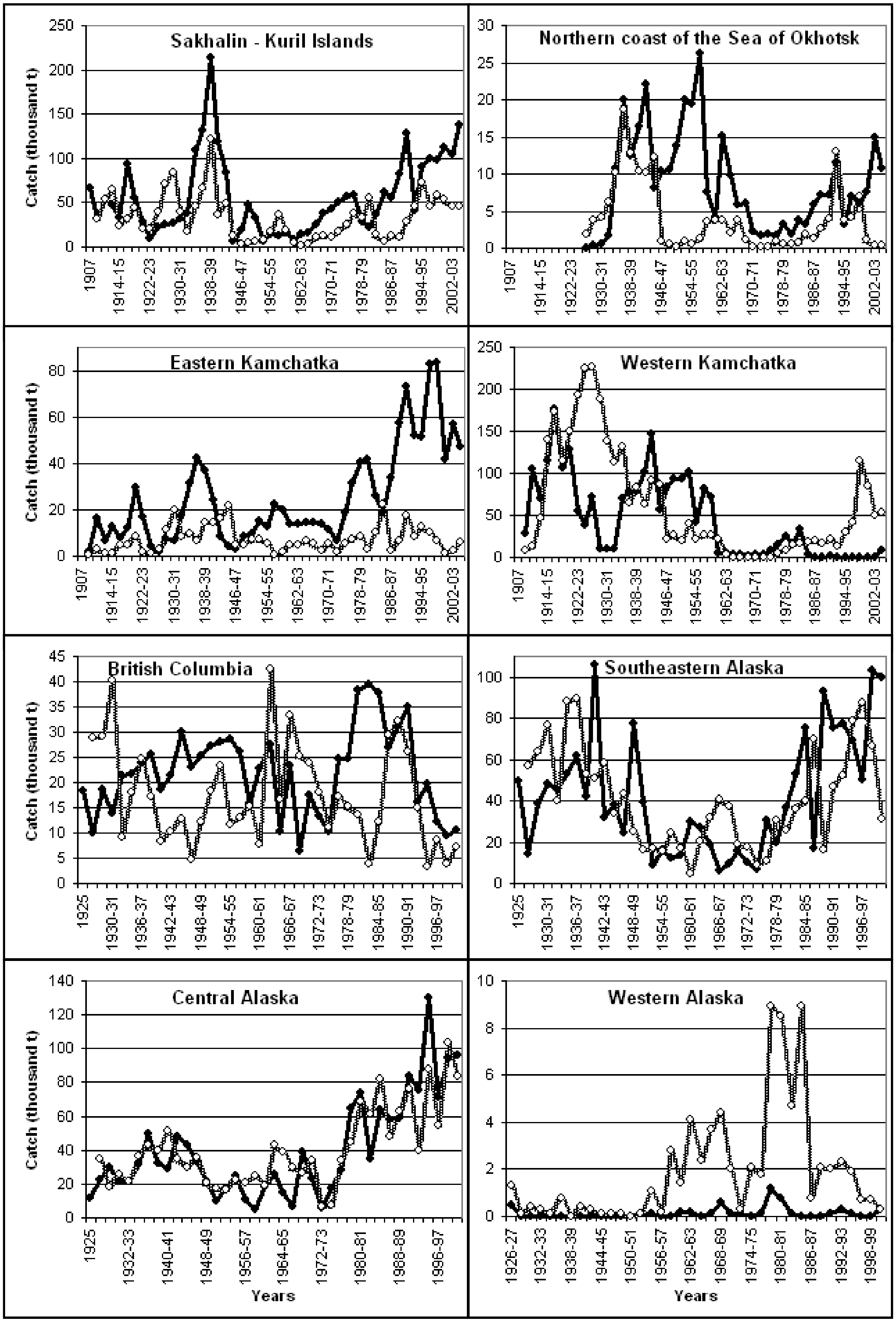

Fig. 2. Pink salmon catch (thousand tonnes) in the major fishery regions in the North Pacific. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline.

annual pink salmon catch variability (Fig. 2). However, for the British Columbia coast, this similarity was evident after the 1990s, with the notable decline in catch values in the odd years as well as in the even years. This decline was unrelated to pink salmon abundance, which may be at historic high levels (Beamish et al. 2004). In southeastern Alaska, the years after 1985 were marked by a lack of similarity.

Catch dynamics of the entire pink salmon stock is more smoothed and similar on the scale of the whole Pacific Ocean or even on the scale of the Asian and American coasts separately than variations in the regional stocks. A dynamic equilibrium of even-year and odd-year broodline biomass on an oceanic scale appears because of the differences in the contribution of large regional pink salmon groupings to the total. Pink salmon stocks of western Kamchatka, western and central Alaska, and western Iturup Island contribute significantly to the total even-year broodline abundance. Eastern Kamchatka, central and southeastern Alaska and eastern Sakhalin Island stocks have contributed to the odd-year broodline abundance in recent years. Alternating the production of broodlines in the different regions demonstrates the unique life strategy of pink salmon, which is directed toward the maintenance of a sustainable level of reproduction for the species as a whole. This sustainable level likely corresponds to optimal exploration for food resources in the open waters of Pacific Ocean along feeding and migration routes and to the prevailing environmental and forage conditions.

Before 1934–35, the annual pink salmon catch level in Asia and in the entire North Pacific in even years exceeded the catch in the odd years. This phenomenon is explained by the larger contribution of stock from the western Kamchatka coast to the total Russian pink salmon catch in those years (56.0–75.2% in 1924–1934), where the even-year broodline still predominates (Radchenko 1998).

The trend in pink salmon catches in the North Pacific reveals a gradual decline of both broodlines until 1945–1946 (Fig. 3). Then, some stabilization occurred as shown by growth of the actual catch relative to the “expected” value, i.e. to the average for the four previous years. Deviations of actual catch from the “expected” catch have tended toward zero in the corresponding years. A relatively stable period lasted until 1973–1974. There was a period of growth up to 1987–1988, followed by one continuing until the present time. At the same time, catches were highly unstable. An alternating pattern of more or less productive generations occurred in both broodlines, at least during the last 10 cycles (or 20 years). The “saw tooth” catch deviations in recent years were not evident in previous years. Taking into consideration this high level of pink salmon abundance, it may be that a density-dependent factor was at play. However, inside the regional groupings, a regular alternating pattern was not observed in the catch values or the deviations from “expected” ones, neither for the even-year nor odd-year broodline (Figs. 2 and 4). If density-dependent factors affect pink salmon populations during the freshwater life stage, a more abundant generation of spawners could result in relatively less abundant progeny and *vice versa*. Variability of such abundance indices should first be evident at a regional level. Further, we suppose that the existence of density-dependent

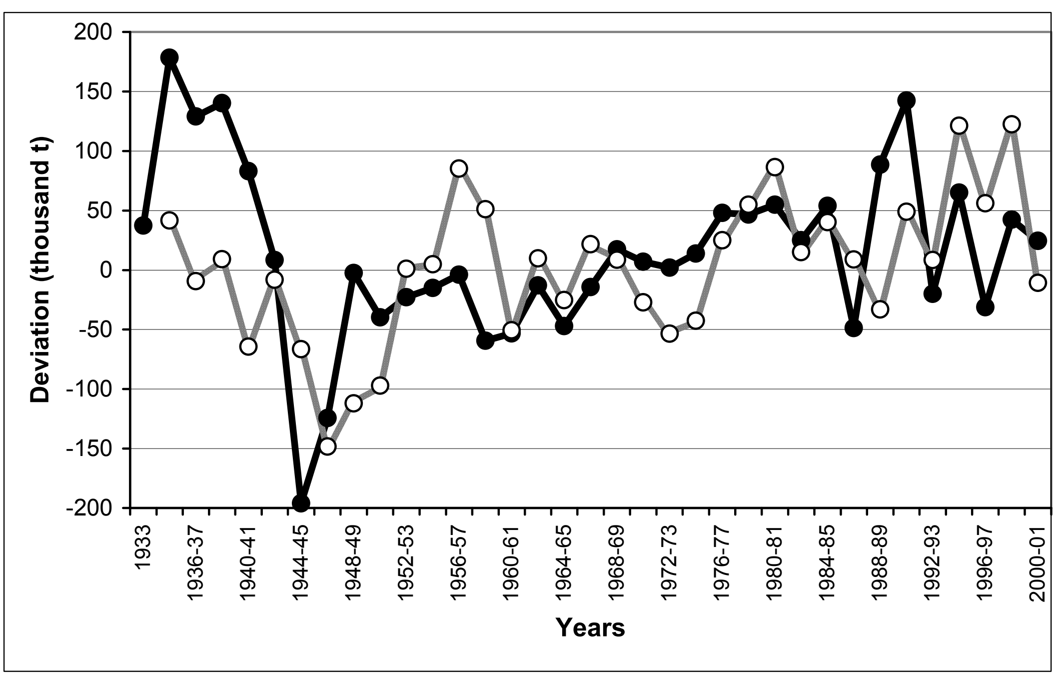

Fig. 3. Trends in pink salmon catch (thousand tonnes) in the North Pacific, 1933–2001. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline. Explanations of trend calculations are given in the text.

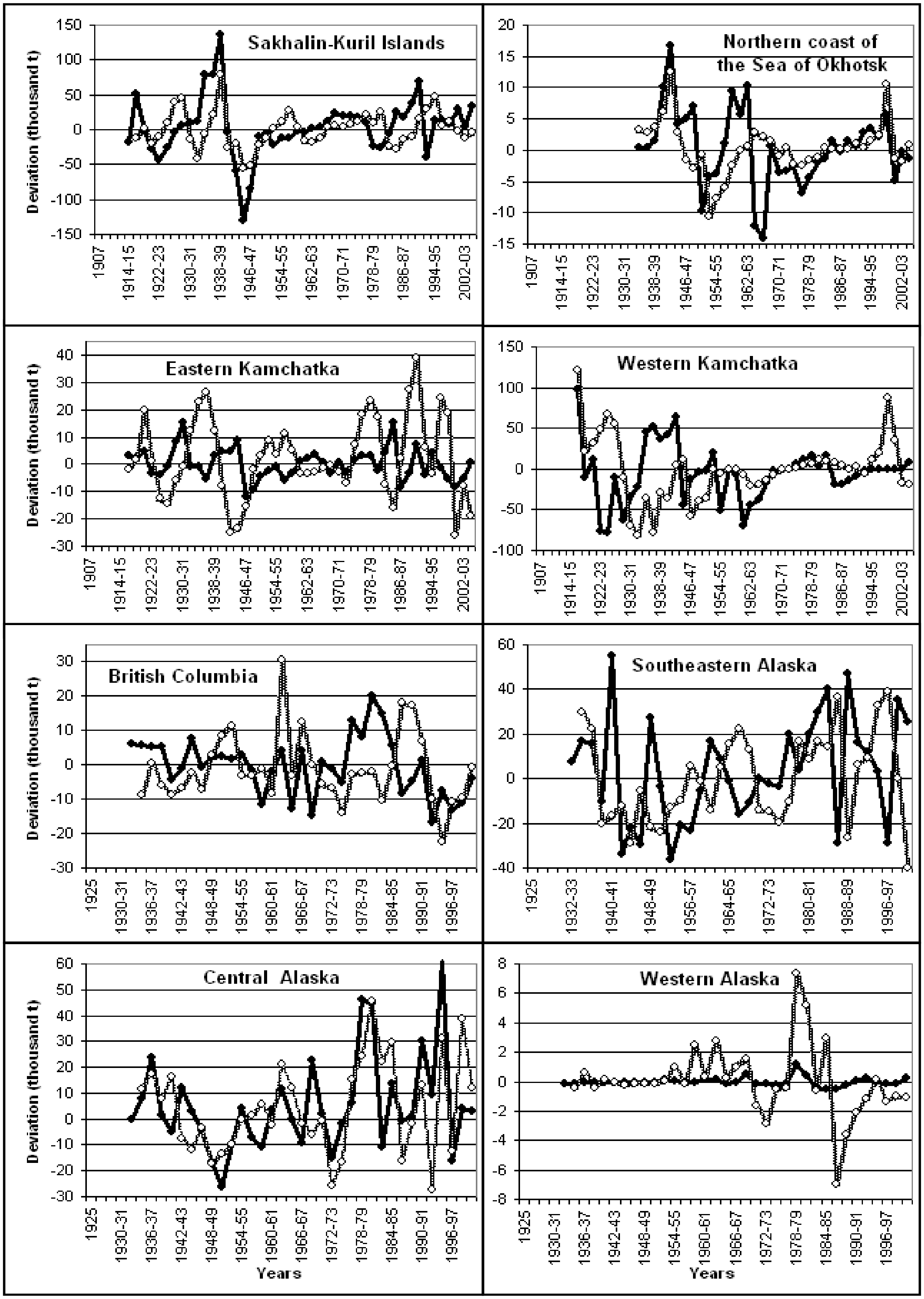

Fig. 4. Deviation of pink salmon catch (thousand tonnes) in the major fishery regions in the North Pacific. Black line and solid circles: odd-year broodline; gray line and open circles: even-year broodline.

factors that have an effect on the entire pink salmon population in the North Pacific Ocean affects salmon during feeding migrations, i.e. we assume that there is interference of stocks in the Pacific Ocean. These factors contribute to the overall marine survival of pink salmon.

For all the Russian coasts, total catch dynamics was closely matched in odd and even years (Fig. 5). One large distinction is the sharp decline that occurred during the odd years in 1923. It could be explained by a decrease in the pink salmon run to the Kamchatka Peninsula, the main location of the salmon fishery in Russia at the time. During the odd years of 1923–1933, the total Russian catch of pink salmon fell to 33,000–42,000 t, with the foreign catch falling below to 58,033-86,527 t. Development of the pink salmon fishery on Sakhalin Island, where odd-year populations predominate, contributed to the increase in odd-year catches. The pink salmon catch increased sharply, reaching an absolute maximum value for the region (213,400 t in 1939), with the development of the Japanese fishery. Odd-year dominance of the interannual catch structure, which was formed during the 1930s, has been maintained for all the Russian coasts up to the present time. Despite this predominance in absolute values, catch data series for the odd-year and even-year broodlines demonstrate a strong correlation ($r = 0.79$, $p < 0.001$) since 1939.

Among the fishery regions on the Russian coast, a sig-

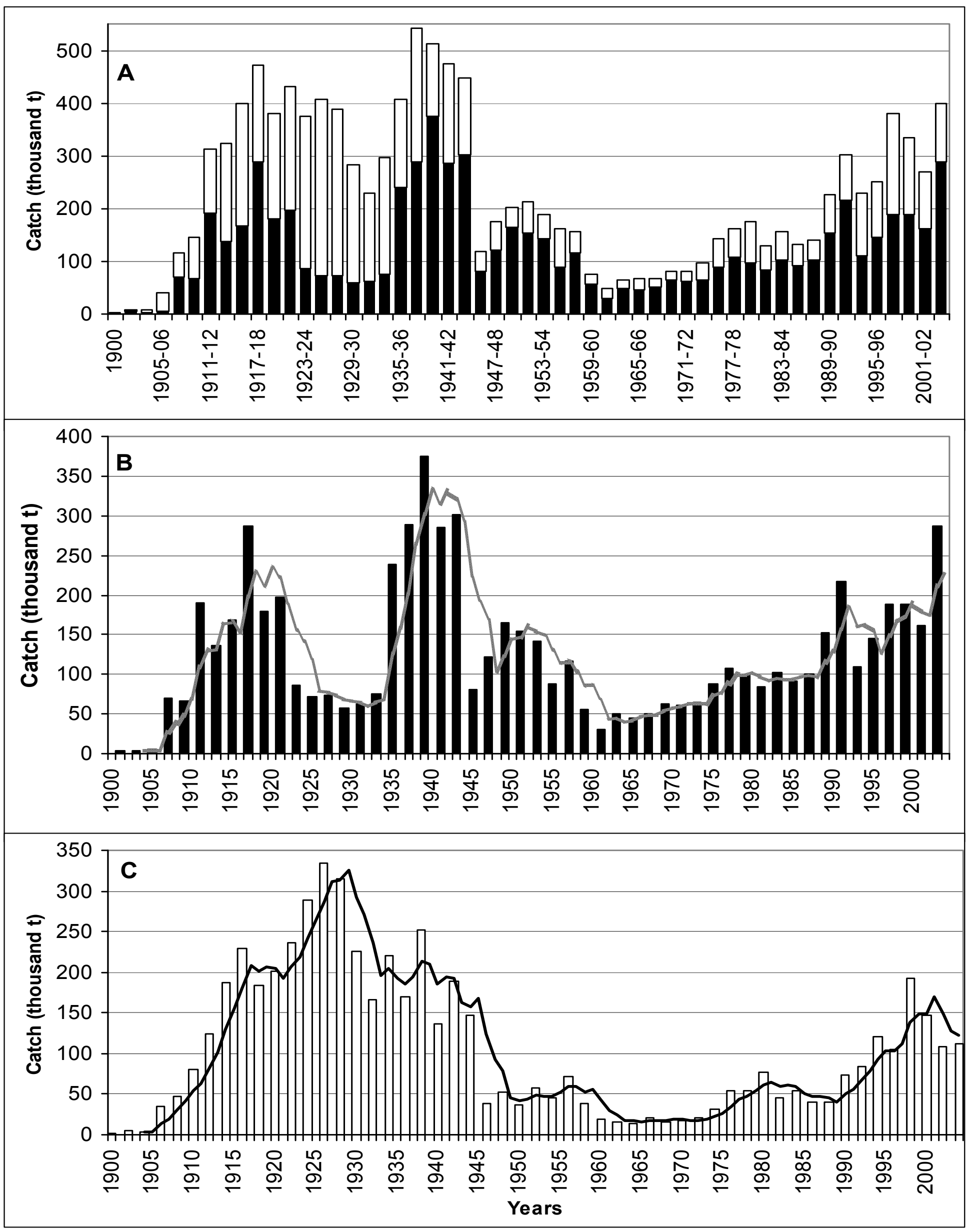

Fig. 5. Pink salmon catch (thousand tonnes) on the Russian coast, 1900–2004. A: total; B: odd years; C: even years. Three-year moving averages are presented on panels B and C by gray and black lines, respectively.

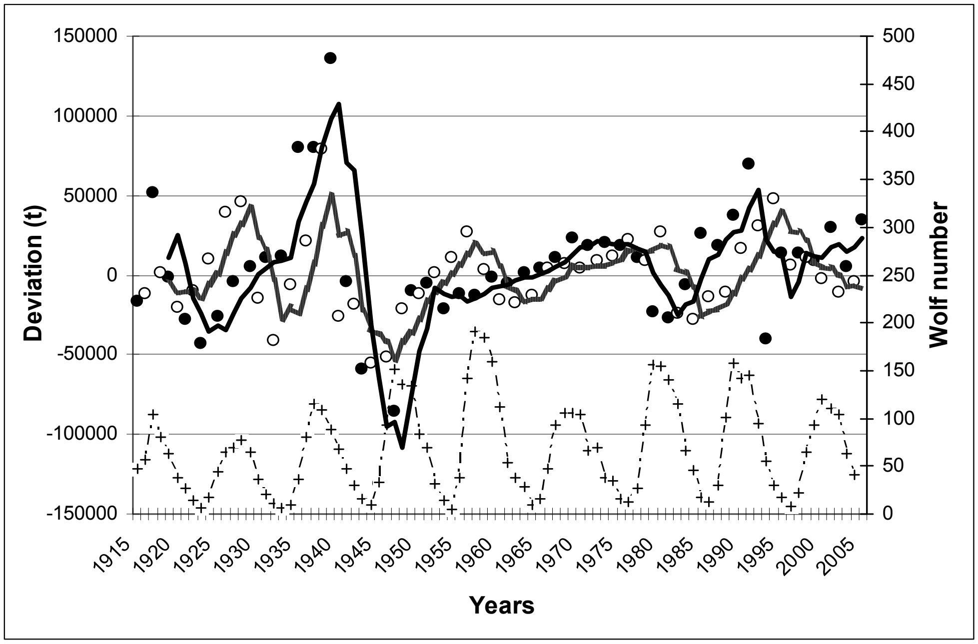

Fig. 6. Trends in pink salmon catch (tonnes) in the Sakhalin-Kuril Islands region, 1915–2005. Black circles: odd-year broodline; open circles: even-year broodline. Three-year moving averages are indicated by the black line for odd years and the gray line for even years. Solar activity is indicated by Wolf number (dotted line and crosses on the right-hand axis).

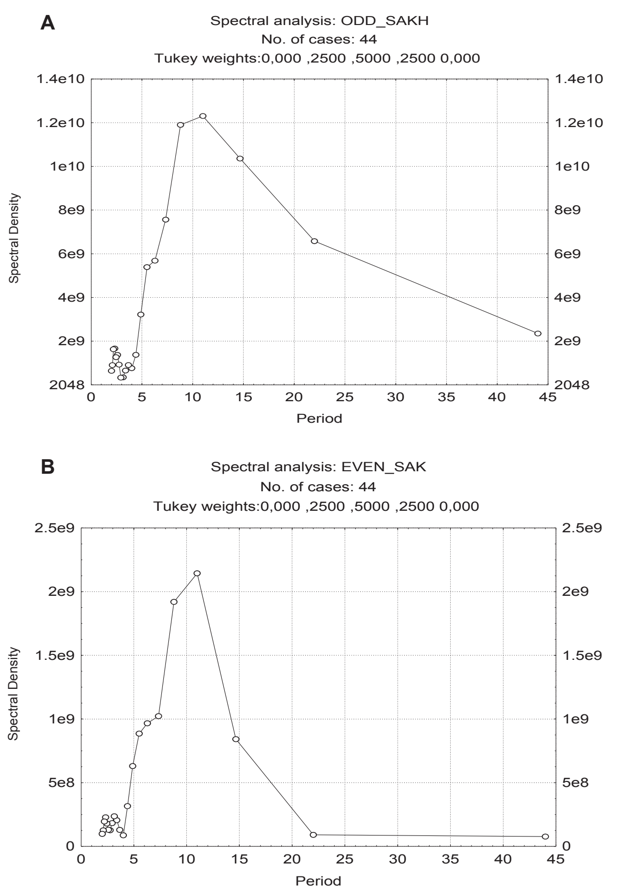

Fig. 7. Periodicity of deviations of expected catch for odd (A) and even (B) years in the Sakhalin-Kuril Islands region, 1915–2005.

nificant relationship between the annual catch data series (1908–2005) among the odd-year and even-year broodlines was found only for Sakhalin and the Kuril islands ($r = 0.59$, $p < 0.001$). On the North American coast, all three fishery regions of Alaska display significant relationships between catch data series (1926–2001) for both broodlines: r = 0.34, $p < 0.05$ for the southeastern coast; $r = 0.85$, $p < 0.001$ for the central coast; and $r = 0.66$, $p < 0.001$ even for western Alaska, where the pink salmon harvest value did not exceed 9,000 t in even years and 1,500 t in the odd years. However, it can be related, to some degree, to a longer data series for the Russian coast (n = 49 instead of 38 pairs of compared years).

When we compared trends in catch dynamics, a significant relationship was found for Sakhalin and the Kuril islands ($r = 0.48$, $p < 0.001$) and for the northern Sea of Okhotsk coast ($r = 0.40$, $p < 0.05$). On the North American coast, two fishery regions show significant relationships between data series of deviations of actual catch from the "expected" catch (1934–2001) for both broodlines: r = 0.59, $p < 0.001$ for central Alaska; and $r = 0.65$, $p < 0.001$ for western Alaska. The relationship was not significant for the southeastern Alaska and British Columbia coasts. Meanwhile, the trend curves are close to each other for southeastern Alaska (Fig. 4). More similarity can be found if we compare different time intervals separately. Thus, until the mid 1960s, the line which characterizes the change in the trend for the even-year broodline, preceded the line for the odd years by approximately one cycle. From the mid 1960s, the extreme points in the curve for the odd years were one cycle ear-

Table 1. Pearson's correlation coefficients (*r*) between normalized pink salmon catch data series and world ocean heat content, 1956–2004 (*n* = 49 for Russian coast; *n* = 46 for other areas). All relationships are statistically significant (*p* < 0.001).

	World ocean, 0-700 m	Northern Hemisphere, 0-700 m	World ocean, 0–300 m
Russian coast	0.59	0.58	0.63
American coast	0.48	0.53	0.57
Whole North Pacific	0.47	0.51	0.54

lier. From the late 1980s, the trend in the curves for both broodlines shows opposite changes, revealing the significant negative relationship for 1976–2001. We can suggest the occurrence of some prominent events, which affected the trend in pink salmon catch dynamics in the mid 1960s and 1980s. Local management changes likely strongly influenced the relationship. Pre-statehood federal mismanagement in Alaska led to pink salmon stocks being over-fished, resulting in a sharp reduction in catches at the beginning of 1960s (Heard 2001); an increase in the proportion of hatchery salmon in the general returns in 1980s (Hilborn and Eggers 2001) and management efforts for salmon stocks being undertaken in recent years, in particular, the establishment of a cumulative escapement goal for Prince William Sound by the Alaska Department of Fish and Game since 1934 (Wertheimer et al. 2001). All these factors may have blurred the trend dynamics compared to trends in other regions.

On the Russian coast, the deviations of actual pink salmon catches from "expected" catches for the odd-year and even-year broodlines were especially close for the Sakhalin – Kuril Islands region (Fig. 6). Coincidence of the trend curves for the odd-year and even-year broodlines was more apparent in the second half of the 20th century. Some sections of the curves, in particular those for the second half of the 20th century, completely coincided with the shift of curves relative to each other for four years (Fig. 6).

The comparison of the curves with the dynamics of the solar activity, expressed in Wolf numbers, showed that each of four 22-year cycles of solar activity includes the complete cycle of fluctuations in the catch dynamics trend. Spectral analysis revealed a clear 22-year cycle for trends for the even-year broodline (Fig. 7). Cycles appear unequal on the curve for the odd-year broodline. The longer cycles are separated by shorter ones and that is reflected in the results of the spectral analysis. The periodogram (by period) for the odd-year broodline is characterized by two contiguous maximums which correspond to cycles of 18 and 22 years. This may be related to the sharp decline in pink salmon catches on the Kamchatka coast in the 1920s and subsequent changes in the inter-regional ratios of catches.

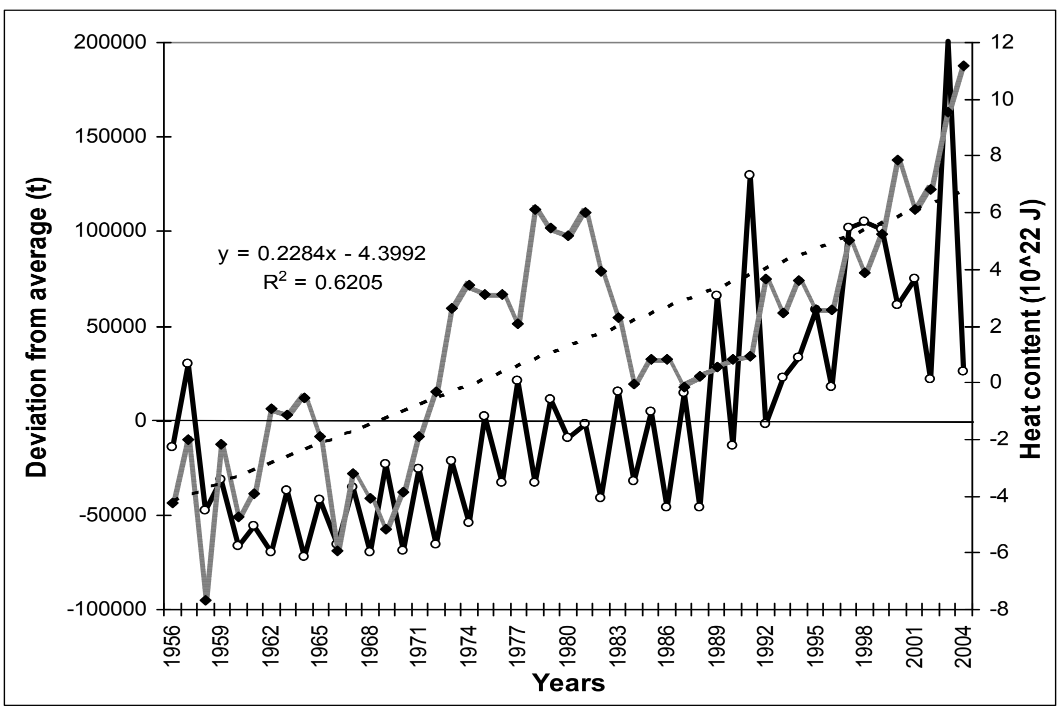

Fig. 8. Ocean heat content for the 0-700 m layer (gray line, solid diamonds, after Levitus 2005) and deviation from average of pink salmon catch (black line, open circles) on the Russian coast, 1956–2004. Trend in ocean heat content is indicated by the dashed line.

Another recognizable dependence of pink salmon catch dynamics on global physical factors was recently found. Pink salmon catch dynamics on the Russian coast correlate (r = 0.59, $p < 0.001$) with the increase in yearly world ocean heat content for the 0–700-m layer (Levitus et al. 2005). Assessing the statistical significance of other relationships shows that correlation coefficients do not change notably when data are replaced with ocean heat content data for the Northern Hemisphere only (r = 0.58) and for the upper 300-m layer (r = 0.63). Relationships are also significant for the total pink salmon catch in the North Pacific and on the North American coast (Table 1). It can be expected that the dependence is rather general and reflective of the integrated impacts. It is impossible to compare catch data for specific salmon populations and heat content at the location of its feeding and migration route. The limitation of ocean heat content data by a sample of observations for the Pacific Ocean and Northern Pacific weakens relationships for all three regions (Table 1). However, correlations improved with the restriction of ocean heat content data to the thinner, upper ocean layer, closer to the habitat of Pacific salmon.

The graph of the pink salmon catch deviations on the Russian coast (1956–2004) varied similarly to the graph of yearly world ocean heat content for the 0–700-m layer (Levitus et al. 2005). The trajectories approximating pink salmon catch and ocean heat content data are rather flat (Fig. 8). Relationships between catch dynamics and general ocean heat content are stable. Correlation coefficients change insignificantly with shifts of the data series each relative to the other for one year. Furthermore, the highest correlation coefficients (0.65 instead of 0.63 for the Russian coast, 300-m layer) are seen with ocean heat content data series advanced by one year. This emphasizes that ocean heat content is determined by climate and synoptic conditions in previous years. For this reason, ocean heat content has shown a steady increase since 1956 in spite of some periodic variability (Levitus et al. 2005). The corresponding curve from Fig. 8 can be approximated by a straight line (y = 0.2284x – 4.3992) with R^2 = 0.62.

Pink salmon biological characteristics depend on stock abundance. In general, body weight and, to a lesser degree, length, of maturing pink salmon in the southern Okhotsk Sea and Pacific waters off the Kuril Islands in the summer of 1991–2003 changed in relation to different levels of their total biomass for the Sea of Okhotsk region (Radchenko 2001; Temnykh 2005). However, for particular cases, correlations between pink salmon body size and abundance level were both positive and negative in different regions, broodlines and time series (Temnykh 2005). As for juvenile pink salmon body weight, the smallest juveniles were sampled in the Sea of Okhotsk region after the largest downstream migration of 1993 (5.08 billion fish), whereas the largest ones were collected after the smallest downstream migration in 1994 (2.63 million fish). Before 1991–1992, the weight of spawners was, to a large degree, dependent on the size of migrating stock. According to coastal fishery data, it equaled 1.25 kg in the productive year 1991, and 1.50 kg in the unproductive year 1992. However, pink salmon broodlines that returned

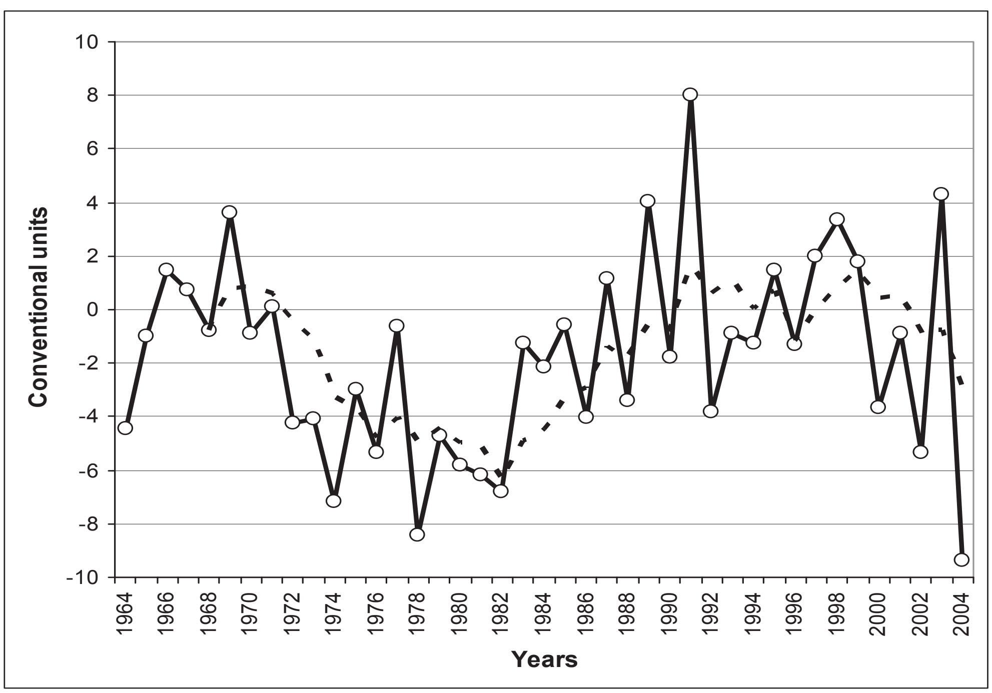

Fig. 9. Variability in increments (in conventional units) of pink salmon catch deviations after subtraction of ocean heat content for the 0-700 m layer, 1964–2004. Five-year moving averages are indicated by the dashed line.

to spawn in 1994–1997 support the correlation between the initial weight of juveniles entering the ocean and the final weight of spawners. Smaller spawners returned from the smallest outmigrants, and larger spawners from the larger ones independent of the total abundance of spawning stocks (Radchenko 2001).

DISCUSSION

Similarities in trends in abundance for the odd-year and even-year broodlines cannot be explained by biological effects of fish interaction because fish of both generations spend a brief time in the same waters simultaneously. Direct interrelation and genetic drift between broodlines seems to be negligible. Distinctions between the lines are emphasized by significant differences in abundance levels in most fishery regions and by pink salmon hatchery production in northwestern Russia. It is noteworthy that the hatchery pink salmon population of northern Japan typically shows a biennial cycle in the magnitude of the spawning run and catch value, despite almost equal numbers of fry released in the odd and even years (Radchenko, 2001). The same situation has been observed in the Great Lakes in spite of notable changes in pink salmon life span and the age structure of their populations. Thus, an assumption could be made of the existence of some global factor determining conditions for pink salmon reproduction and survival, which, in turn, causes a response of both broodlines to periodic dynamics independent of differences between them.

Effects of these global factors seem to be interrelated. Goryainov and Shatilina (2003) identified significant relationships between the surface atmospheric pressure field dynamics in the region of the Southern-Asian Low and pink salmon catches a year later. It is known that the Southern-Asian Low determines the intensity of monsoon circulation above the Far East, which, in turn, influences a series of factors, which limit pink salmon abundance during early developmental stages. Nevertheless, the strengthening of the relationships between the salmon catches and the pressure field above the regions along salmon feeding and migration routes was observed in vicinities of the Pacific High and Bering Sea Polar Trough locations in spring (Goryainov & Shatilina 2003). Regions of feeding migrations of separate regional groupings of pink salmon are distinct in the Pacific Ocean (Shuntov 1994). However, environmental factors continue to affect salmon at other stages of their life cycle and the relationships are not strong. Schumacher (1999) emphasized that in spite of the correlations of the dynamics of solar activity with different phenomena on Earth, the reason for hydrometeorological and biological changes does not lie in the dynamics of the solar energy flux, whose variability is insignificant (of about 0.1%, or 2 Vt/m^2 of the ocean surface). Nevertheless, many authors assume that such fluctuations can be sufficient for the initiation of changes in climatic conditions on the Earth's surface as a result of the variability of temperature and the ozone content in the lower and middle atmospheric layers (Schindell et al. 1999; Haigh 2001; Patterson et al. 2004). The same atmospheric processes (variability of temperature and chemical composition) serve as basic components in the chain of signal transfer, initiated by the dynamics of the short-wave component of solar radiation (Häder et al. 2003). Ikeda (1990) assumed that the dynamics of solar activity generates decadal oscillations in the integrated system "atmosphere-ice-ocean" in the Northern Hemisphere. The relation of the solar activity was noted with the air temperature and the atmospheric pressure (Van Loon and Shea, 1999), with the ice cover (Hill and Jones, 1990), with the transfer of water masses and upwelling development (Guisande et al. 2004), and with stock dynamics of many pelagic fish species (Häder et al. 2003; Guisande et al. 2004; Patterson et al. 2004). Solar activity influences fish stocks both directly (through influence of ultraviolet radiation on the roe and fish larvae), and through the state of forage plankton resources, changeability in oceanological conditions, and other climatic parameters.

It can be suggested because of the dependence of pink salmon catch dynamics on the world ocean heat content that the gradual warming of the ocean surface layer as a non-cyclic climate component can influence salmon stock dynamics on a global level with demonstrated periodic variability. In general, pink salmon stocks in the North Pacific are characterized by a relatively high level of abundance driven by significant year-to-year growth since the mid 1970s and especially after the late 1980s. High stock abundance of pink salmon creates an expectation for a decline in the near future, which is generated by decadal scale variability in many global natural factors influencing fish stock conditions. The most frequent question asked about pink salmon dynamics is: When will the stocks begin to decline? Many researchers have tried to answer this question and proposed that pink salmon stocks would decline beginning in the mid 1990s (Chigirinsky 1993), the end of 1990s (Klyashtorin 1997), the first years of the 21st century (Radchenko 2001), and even for 2005 (Kaev 2005).

The effects of periodically varying physical factors were roughly assessed by removing the non-cyclic component. The analyses of pink salmon catch data increments after subtraction of the ocean heat content indices showed that these increments vary on (close to) a decadal scale (Fig. 9). A curve of five-year moving averages displays gradual growth from a minimal level in the early 1980s to the mid 1990s. In the first half of 1990s, the moving averages oscillated slightly near the maximum level followed by a gradual decrease since 1999. It can be concluded that the pink stock decline determined by periodically changing global factors has already happened, approximately in 1999. It could not be detected due to the positive effect of ocean heat content growth since the second half of the 1980s. Spectral analysis, applied to the pink salmon catch increments series, after subtraction of relative heat content units, shows a well-expressed biennial cycle and supposes the existence of a 22-year cycle.

The positive effect of an increasing ocean heat content on pink salmon stock condition likely results in an increase in carrying capacity through stabilization of the food supply. Warmer waters provide favorable conditions for the survival and growth of most sub-Arctic zooplankton species. For example, crustacean growth rates have been found to be above average in warm conditions (Vinogradov and Shushkina 1987). This enhanced growth rate allows for a longer maturation period and spawning season. A meta-analysis of marine copepod species indicates that growth rate is positively correlated with increasing temperature and decreases in generation time allowing more productivity in warmer climates (Huntley and Lopez 1992). Calanoid copepod biomass was much higher in the eastern Bering Sea middle shelf during warm years (Smith and Vidal 1986), likely due to higher growth rates. These findings suggest that ocean water warming enhances ecosystem productivity from the lower trophic levels, particularly for planktonic crustaceans, which play a significant role in the pink salmon diet.

Besides food supply stabilization, one more critical feature of the pink salmon life cycle can be positively influenced by an increasing ocean water heat content. It is well known that the high mortality rate of pink salmon outmigrants occurs in the inshore waters in years of delayed seasonal water heating (Karpenko 1998). Formation of seasonal groupings, or races, is inherent in pink salmon of both broodlines (Kaev 2005). In the Sakhalin-Kuril Islands region, three of them are selected: "spring" Japan Sea grouping, "summer" (or early) and "autumn" (or late) oceanic races (Gritsenko 1981; Kaev 2005). An increase of the "summer" oceanic grouping portion occurred in the last few years. This grouping migrated earlier to the spawning grounds, and its outmigrants migrated to sea earlier.

A significant increase in juvenile pink salmon numbers in the offshore Sea of Okhotsk occurred in 1993 and again in 1999 despite the outmigrants' abundance remaining practically the same (Radchenko 2001). This increase in juvenile pink salmon survival correlates with the increased ocean heat content. Kaev (2005) related the increase of the "summer" oceanic grouping to the lower survival of the "late" race and expected changes in total stock abundance. However, it could be related to the increase in total pink salmon abundance. In 2005, the coastal pink salmon catch in the Sakhalin – Kuril Islands region reached 137,747 t exceeding the previous record of 1991 (128,333 t).

Observations on body weight dynamics lead us to the following conclusion: pink salmon body weight can serve as an index of marine life period success and effects of density-dependent factors but only for generations under the same environmental conditions. For the Sea of Okhotsk region, pink salmon stocks experienced some notable changes in the marine environment after 1991–1992. For the southwestern Bering Sea, it occurred slightly earlier. We can see a clear relationship between outmigrants' body weight and numbers after 1988, but not for all examples (Karpenko 1998). Pink salmon body weight may also depend not only on certain growth conditions, which are determined by the food supply and the hydrological environment. This can be related to the complicated stock structure of the regional pink salmon groups, specific peculiarities of regional stocks as were observed for the Sea of Japan pink salmon (Temnykh 2005). Seasonal races and ecological groupings have preferred development in different years that defines average size dynamics in a specific region, as the "summer" oceanic grouping for the Sakhalin and Kuril Islands area, complicating interpretation of body weights.

CONCLUSIONS

Pink salmon abundance and biological dynamics are complex. Trends in abundance of pink salmon stocks are determined under the influence of global physical factors that can be both periodic and non-cyclical. The solar activity dynamics and increases in ocean heat content play significant roles in this cumulative effect. In this aspect, data for ocean wintering of pink salmon have critical importance for future understanding of Pacific salmon dynamics.

Odd-year and even-year pink salmon broodlines reveal a recognizable relationship in abundance trends in the majority of fishery regions, independent of differences in absolute abundance between them. The existence of a strictly determined response of both broodlines to the periodic dynamics of some global factors, which determine the conditions of pink salmon reproduction and survival, can be regarded as the main cause of the relative permanence of the biennial cycle in the size of spawning runs, catch and escapement.

In general, pink salmon stock abundance in the North Pacific Ocean can be regarded as close to the historic maximum. However, there are grounds to expect that this level will be maintained in the near future in connection with the positive influence of increases in ocean heat content.

REFERENCES

Antonov, A.A. 2005. Biology and dynamics of abundance of pink salmon of the Aniva Bay (Sakhalin Island). Ph.D. thesis, SakhNIRO, Yuzhno-Sakhalinsk. 23 pp. (In Russian).

Beamish, R.J., and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50: 1002–1016.

Beamish, R.J., A.J. Benson, R.M. Sweeting, and C.M. Neville. 2004. Regimes and the history of the major fisheries off Canada's west coast. Prog. Oceanogr. 60(2-4): 355–385.

Chigirinsky, A.I. 1993. Global nature factors, fisheries and abundance of Pacific salmons. Rybnoye Khoziaystvo (Fisheries) 2: 19–22. (In Russian).

Eggers, D.M., M. Fukuwaka, J. Irvine, and V.I. Karpenko.

2004. Pacific salmon. In Marine ecosystems of the North Pacific. PICES Sp. Pub. 1: 227–261.

Glubokovsky, K.M. 1995. Evolutionary biology of salmonid fishes. Nauka Publ. House, Moscow. 343 pp. (In Russian).

Goryainov, A.A., and T.A. Shatilina. 2003. Dynamics of Asian pink salmon and climatic changes over the Asian – Pacific region in XX century. Biologiya morya 29(6): 429–435. (In Russian).

Gritsenko, O.F. 1981. On population structure of pink salmon *Oncorhynchus gorbuscha* (Walbaum). J. Ichthyol. (Vopr. Ichthyologii) 21(5): 787–799. (In Russian).

Guisande, C., A. Ulla, and P. Thejll. 2004. Solar activity governs abundance of Atlantic Iberian sardine *Sardina pilchardus*. Mar. Ecol. Prog. Ser. 269: 297–301.

Häder, D.-P., H.D. Kumar, R.C. Smith, and R.C Worrest. 2003. Aquatic ecosystems: effects of solar ultraviolet radiation and interactions with other climatic change factors. Photochem. Photobiol. Sci. 2: 39–50.

Haigh, J. 2001. Climate variability and the influence of the sun. Science 294: 2109–2111.

Heard, W.R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver. pp. 119–230.

Heard, W.R. 2001. Alaska salmon enhancement: a successful program for hatchery and wild stocks. Abstract and presentation at 30th U. S./Japan Natural Resources Aquaculture Panel Technical Symposium, Dec. 3–4, 2001, Mote Marine Laboratory, Sarasota, FL. 22 pp. (Available at http://www.lib.noaa.gov/japan/aquaculture/proceedings/report30/heard.htm).

Henderson, M.A., and C.C. Graham. 1998. History and status of Pacific salmon in British Columbia. N. Pac. Anadr. Fish Comm. Bull. 1: 13–22. (Available at http://www.npafc.org).

Hilborn, R., and D. Eggers. 2001. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska: response to comment. Trans. Am. Fish. Soc. 130: 720–724.

Hill, B.T., and S.J. Jones. 1990. The Newfoundland ice extent and the solar cycle from 1860 to 1988. J. Geophys. Res. 95(C4): 5385–5394.

Hiroi, O. 1998. Historical trends of salmon fisheries and stock conditions in Japan. N. Pac. Anadr. Fish Comm. Bull. 1: 23–27. (Available at http://www.npafc.org).

Huntley, M.E., and M.D.G. Lopez. 1992. Temperature-dependent production of marine copepods: a global analysis. Am. Nat. 140: 201–242.

Ikeda, M. 1990. Decadal oscillations of the air–ice–ocean system in the Northern Hemisphere. Atmosphere-Ocean 28: 106–139.

Kaev, A.M. 2005. Expecting and realities of the pink salmon (*Oncorhynchus gorbuscha*) fishery in the Sakhalin region. Izv. TINRO 140: 37–44. (In Russian).

Karpenko, V.I. 1998. Early marine life period of Pacific salmon. Moscow: VNIRO. 166 pp. (In Russian).

Karpenko, V.I., and O.A. Rassadnikov. 2004. Contemporary state (1971–2002) of the Far East Pacific salmon stock abundance. KamchatNIRO Collective papers, Petropavlovsk-Kamchatsky 7: 14–26. (In Russian).

Kelso, J.R.M., and D.B. Noltie. 1990. Abundance of spawning Pacific salmon in two Lake Superior streams, 1981–1987. J. Great Lakes Res. 16(2): 209–215.

Kennedy, A.J., R.W. Greil, R.C. Back, and T.M. Sutton. 2005. Population characteristics and spawning migration dynamics of pink salmon in U.S. waters of the St. Marys River. J. Great Lakes Res. 31(1): 11–21.

Klyashtorin, L.B. 1997. Pacific salmon: climate-linked long-term stock fluctuations. PICES Press 5(2): 2–7, 30–34.

Klyashtorin, L.B., and N.S. Sidorenkov. 1996. The long-term climatic changes and pelagic fish stock fluctuations in the Pacific. Izv. TINRO 119: 33–54. (In Russian).

Kocik, J.F., W.W. Taylor, and W.C. Wagner. 1991. Abundance, size, and recruitment of pink salmon (*Oncorhynchus gorbuscha*) in selected Michigan tributaries of the upper Great Lakes, 1984–1988. J. Great Lakes Res. 17(2): 203–213.

Kope, R., and T. Wainwright. 1998. Trends in the status of Pacific salmon populations in Washington, Oregon, California, and Idaho. N. Pac. Anadr. Fish Comm. Bull. 1: 1–12. (Available at http://www.npafc.org).

Levitus, S., J. Antonov, and T. Boyer. 2005. Warming of the world ocean, 1955–2003. Geophys. Res. Lett., 32, L02604. doi: 10.1029/2004GL021592.

Mathisen, O.A. 1994. Spawning characteristics of the pink salmon (*Oncorhynchus gorbuscha*) in the eastern North Pacific Ocean. Aquacult. Fish. Manage. 25(Suppl. 2): 147–156.

Patterson, R.T., A. Prokoph, C. Wright, A.S. Chang, R.E. Thomson, and D.M. Ware. 2004. Holocene solar variability and pelagic fish productivity in the NE Pacific. Palaeontologia Electronica. 7(1): 17 pp. (Available at http://palaeo-electronica/2004_1/fish2/issue1_04.htm).

Pyper, B.J., and R.M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analysis of fish data. Can. J. Fish. Aquat. Sci. 55: 2127–2140.

Radchenko, V.I. 1998. Historical trends of fisheries and stocks condition of Pacific salmon in Russia. N. Pac. Anadr. Fish Comm. Bull. 1: 28–37. (Available at http://www.npafc.org).

Radchenko, V.I. 2001. Abundance dynamics of pink salmon, *Oncorhynchus gorbuscha*, in the Sea of Okhotsk basin in 1990s. Biologiya morya. 27(2): 91–101. (In Russian).

Radchenko V.I. 2004. Trend coincidence of pink salmon catch dynamics among the odd-years and even-years populations as an evidence of large-scale physical factors effect. The ACIA International Scientific Symposium on Climate Change in the Arctic: Extended Abstracts. Reykjavik, Iceland, 9–12 November, 2004. AMAP Report 2004: 4. Oral session 2: Paper 6. 4 pp.

Schindell, D., D. Rind, N. Balachandran, J. Lean, and P. Lonergan. 1999. Solar cycle variability, ozone, and climate. Science 284: 305–308.

Schumacher, J.D. 1999. Regime shift theory: a review of changing environmental conditions in the Bering Sea and eastern North Pacific Ocean. Proc. Fifth North Pacific Rim Fisheries Conference, December 1–3, Anchorage, Alaska. 19 pp.

Shuntov, V.P. 1994. New data on anadromous migrations of Asian pink salmon. Izv. TINRO 116: 3–41. (In Russian).

Smith, S.L., and J. Vidal. 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. Continental Shelf Res. 5: 215–239.

Temnykh, O.S. 2005. Asiatic pink salmon in sea life period: biology, spatial differentiation, place and role in pelagic communities. Ph.D. thesis, TINRO-Centre, Vladivostok. 47 pp. (In Russian).

van Loon, H., and D.J. Shea. 1999. A probable signal of the 11-year solar cycle in the troposphere of the northern hemisphere. Geophys. Res. Lett. 26: 2893–2896.

Varnavskaya, N.V., M.A. Kudzina, B.B. Vronsky, A.G. Ostroumov, and K.Yu. Nepomnachy. 1995. The comparative characterization of long-term fluctuations in population dynamics of odd-year and even-year broodlines of pink salmon, *Oncorhynchus gorbuscha* (Walbaum), from different region of Asia. KamchatNIRO Collective papers, Petropavlovsk-Kamchatsky 3: 109–119. (In Russian).

Vinogradov, M.E., and E.A. Shushkina. 1987. Functioning of pelagic communities in the oceanic epipelagic layer. Nauka Publ. House. Moscow. 240 pp. (In Russian).

Wertheimer, A.C., W.W. Smoker, T.L. Joyce, and W.R. Heard. 2001. Comment: a review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Trans. Am. Fish. Soc. 130: 712–720.

Yanovskaya, N.V., N.N. Sergeeva, E.A. Bogdan, A.V. Kudryavtseva, I.K. Kalashnikova, and E.A. Romanova. 1989. Catches of Pacific salmon, 1900–1986. Moscow: VNIRO. 213 pp. (In Russian).