

Trends in Abundance and Biological Characteristics of Chum Salmon

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Abstract: Chum salmon are the second most abundant salmon in the North Pacific Ocean. In the 1930s, chum salmon were abundant along the Russian coast and in British Columbia. The total catch of chum salmon was small from the late 1940s into the 1970s but increased in the 1980s, reaching historically high levels from the 1990s to the present. Ocean distribution of chum salmon is affected by sea surface temperature. Ocean growth and fish size at maturity decreased in the 1970s and 1980s but recovered in the 1990s and 2000s. These trends in abundance and biological characteristics correlated with ocean conditions. An international cooperative salmon survey by the North Pacific Anadromous Fish Commission may elucidate the mechanisms underlying the relationships among these trends. For conservation and sustainable use of chum salmon stocks, we should monitor the abundance and biological characteristics of chum salmon both in the ocean and in rivers.

Keywords: catch statistics, age at maturity, size at maturity, ocean growth, ocean distribution, chum salmon

INTRODUCTION

The total salmon catches around the North Pacific Ocean were large in the 1930s–early 1940s and the 1980s–2000s (Eggers et al. 2005). These large catches can be attributed in part to the increases in catches of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. Chum salmon are the second most abundant salmon (after pink salmon) in the North Pacific Ocean. The geographical range of natal rivers of chum salmon extends from Kyushu Island, Japan, and California in the south, to Siberia and the Arctic coast of North America in the north (Salo 1991). Chum salmon fry migrate to the sea soon after emerging from their freshwater spawning beds in spring. Juveniles migrate offshore in the first summer. Chum salmon grow rapidly in offshore waters in the North Pacific. They can spend 2–7 years in the ocean before returning to their natal rivers for reproduction.

Pacific salmon are one of the dominant zooplankton feeders in the pelagic ecosystem of the subarctic North Pacific and adjacent seas (Shuntov et al. 1999). Long-term changes in some fish populations and in ocean productivity have coincided with the long-term changes in climate (e.g. Beamish 1995). From the 1970s to the 1990s, a decline in

the size of mature salmon was observed in populations of many rivers around the North Pacific Rim (see review by Bigler et al. 1996; Helle and Hoffman 1998). Simultaneously, total salmon abundance reached a high level. Some researchers think that the ocean growth of salmon is density-dependent (e.g. Ishida et al. 1993). The abundance of salmon and their prey (i.e. zooplankton and micronekton), and biological characteristics (e.g. body size) should also be affected by climate and ocean conditions.

To examine relationships among trends in chum salmon abundance, biological characteristics, and ocean conditions, we examined time series data from commercial catches, offshore research cruises, and monitoring programs in hatcheries.

MATERIALS AND METHODS

Trends in Abundance

We used catch numbers as an index of abundance based on the assumption that the exploitation rate of chum salmon did not change significantly between years and/or was high enough because long time series of reliable statistics for es-

capement around the North Pacific were not available. The levels of commercial catches were used as an index reflecting the trend in abundance of salmon stocks because the proportion of commercial catch was large in relation to total run size across the entire North Pacific (e.g. Beamish and Bouillon 1993; Klyashtorin and Rukhlov 1998). For specific stocks of Pacific salmon, escapement (or the number of hatchery brood stock in the case of Japanese chum salmon) showed trends similar to those in the commercial catch (e.g. Henderson and Graham 1998; Hiroi 1998). Thus we reasoned that trends in catch may reflect trends in the abundance of chum salmon. Catch statistics for chum salmon were obtained from Eggers et al. (2005).

As another index of chum salmon abundance, we used catch per unit effort (CPUE) calculated from Japanese monitoring surveys in the high-seas areas of the central North Pacific (CNP) and Bering Sea (BS) between 170°E and 170°W in June and July. Japanese fisheries research institutes have monitored salmon abundance and distribution beginning in 1952 using drift gillnets. After 1972, they changed to standard research gillnets consisting of ten different mesh sizes each (Takagi 1975). CPUE was calculated as the number of fish caught per 30 tans of research gillnet (i.e. three tans of each mesh size (one tan is 50 m in length)). Because the maximum number of fish examined was 60 per mesh size per operation, we weighted the age composition by the number of fish in three tans of gillnet by each mesh size in the calculation of CPUE by age group. CPUE was averaged for each research station in waters ranging 5–10°C in sea surface temperature (SST) because chum salmon are most commonly found at temperatures between 5 and 10°C (Nagasawa et al. 2005).

Trends in Ocean Distribution

To evaluate the correlation between chum salmon distribution and sea surface temperature, we examined latitudinal (i.e. south-to-north) distribution of chum salmon in July in the CNP and BS. To estimate latitudinal distribution, we used the ratio of average CPUE of the BS to the sum of averaged CPUEs in the BS and CNP. We averaged CPUE in the high-seas area of the BS and CNP. For CPUE in the CNP, we used data collected north of 45°N.

Trends in Fish Size and Age

For fish size and growth during ocean life, we used measurements of fork length in June and July in Japanese gillnet surveys in the CNP and the BS. We averaged fork length of chum salmon caught using a research gillnet by age group. Although a single-mesh gillnet usually has a strong size-selectivity, research gillnets consisting of ten different mesh sizes are less size-selective (Takagi 1975). Ocean growth was calculated as the difference between average fork length of an age group in a year and the average fork length of the

same year-class one year before:

$$G_{a,y} = FL_{a,y} - FL_{a-1,y-1}$$

where $G_{a,y}$ is ocean growth of age group a at year y , and $FL_{a,y}$ is average fork length of age group a at year y .

For trends in size and age of mature chum salmon, we used fish measurement data from the monitoring of hatchery brood stocks in the Ishikari River, Hokkaido, Japan. We considered the Ishikari River chum salmon as representative of Asian chum salmon stocks because trends in size and age of mature fish were similar to other Asian stocks (Ishida et al. 1993). We averaged the fork length of four-year-old fish because the dominant age of maturation was four years old in the river. Age at maturity by brood year was weighted by the numbers of adults caught in the river and averaged.

Relationships among Trends

For the relationships among ocean conditions, abundance, and biological characteristics of chum salmon, we used the multiple regression analysis with a stepwise selection of independent variables ($P \leq 0.05$ to add, $P \geq 0.10$ to remove). As indices of ocean conditions, we used the average Pacific Decadal Oscillation (PDO) index from June to September and average SST at 47–49°N, 179°E–179°W for July (SST, CNP) obtained from the Japan Meteorological Agency. PDO was the leading principle component from the empirical orthogonal function analysis of monthly sea surface temperature anomalies poleward of 20°N in the Pacific basin, which was consistent with salmon catches in the northeast Pacific (Mantua et al. 1997). As an index of spawner abundance, we used the time series data of chum salmon catches in Russia and Japan (excluding offshore catches) because Asian stocks were dominant in the CNP and the BS (Seeb et al. 2004). Coastal catches should be proportional to the level of escapement under the assumption that the exploitation rate did not change significantly between years and/or was high enough. Catches and CPUEs were log-transformed as usually recommended for abundance statistics.

RESULTS

Trends in Abundance

There are two periods with large catches of chum salmon around the North Pacific Ocean: the 1930s and early 1940s, and the 1980s to 2000s (Fig. 1). In the 1930s and early 1940s, large catches of chum salmon were recorded in Russia, but catches in Japan were relatively small. In the same period, catches in British Columbia and southeast Alaska were large in comparison to other areas in North America. After World War II, Japanese high-seas fisheries grew under the conventions of two treaties: the International Convention for the High Seas Fisheries of the North Pacific

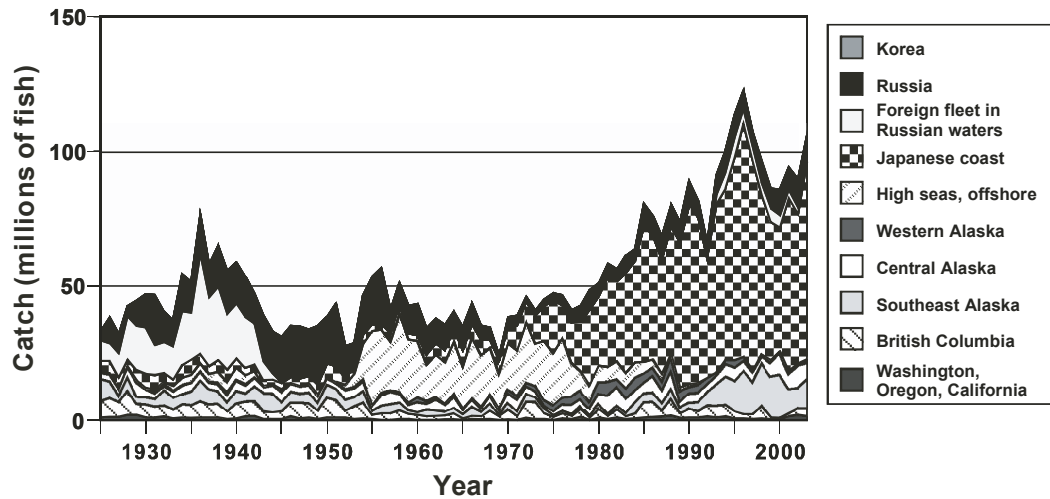


Fig. 1. Catches of chum salmon by area around the North Pacific Ocean, 1925-2003 (modified from Eggers et al. 2005). The Korean catch could not be distinguished from catches in other regions because of the small numbers.

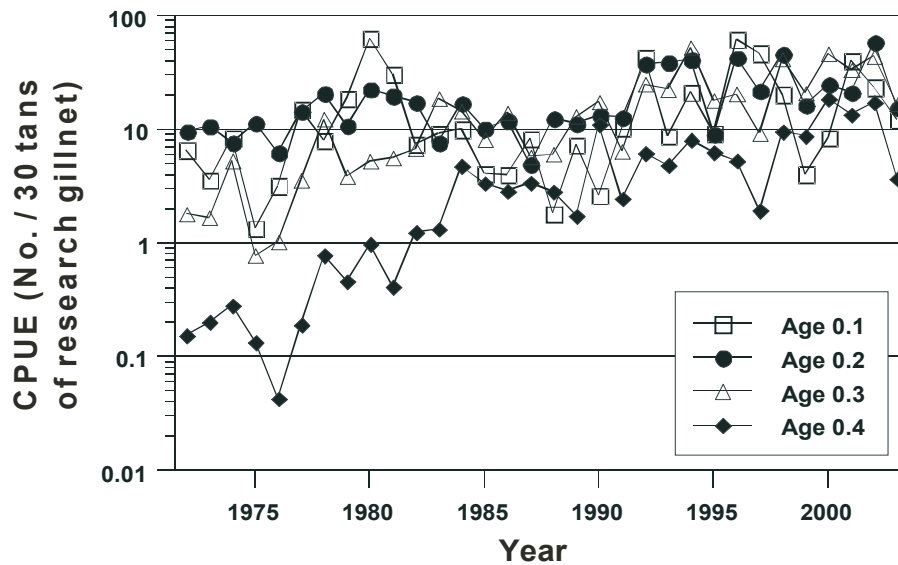


Fig. 2. Catch per unit effort (CPUE, number of fish per 30 tans of research gillnet) of chum salmon by age in waters 5–10°C in sea surface temperature in the central North Pacific Ocean and the Bering Sea, 1972-2003.

Ocean involving Japan, Canada and the United States, and the USSR – Japan Fisheries Agreement. During the same period, catches in coastal and river fisheries were small both in Asia and North America. During the latter half of the 1970s and 1980s, catches in the high-seas areas gradually decreased due to reduced quotas, and limits in fishing areas and fishing durations for high-seas fisheries. Simultaneously, the total catch of chum salmon increased significantly, largely due to the contribution from Japanese coastal fisheries. In 1993, high-seas salmon fisheries were closed due to the Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean and the United Nation's General Assembly resolution 46/215, which ensured a moratorium on large-scale pelagic high-seas driftnet fishing. Since the

1980s, chum salmon catches along the Japanese coast have increased significantly, but catches in Russian waters have remained small. In North America, catches in southeast Alaska have increased, but catches in other areas have remained small. At the present time, chum salmon catches and abundance are at historic high levels.

Chum salmon CPUEs in the high-seas areas of the CNP and BS have increased since the 1970s (Fig. 2). Although the CPUE of age 0.1 fish fluctuated around 10 ($r = 0.281$, $P = 0.119$), CPUEs of age 0.2, 0.3, and 0.4 fish increased ($r = 0.556$, $P < 0.001$ for age 0.2; $r = 0.741$, $P < 0.001$ for age 0.3; $r = 0.762$, $P < 0.001$ for age 0.4). This increase in CPUE coincided with the increase of overall coastal catches around the North Pacific ($r = 0.474$, $P = 0.006$ for age 0.2 CPUE; $r =$

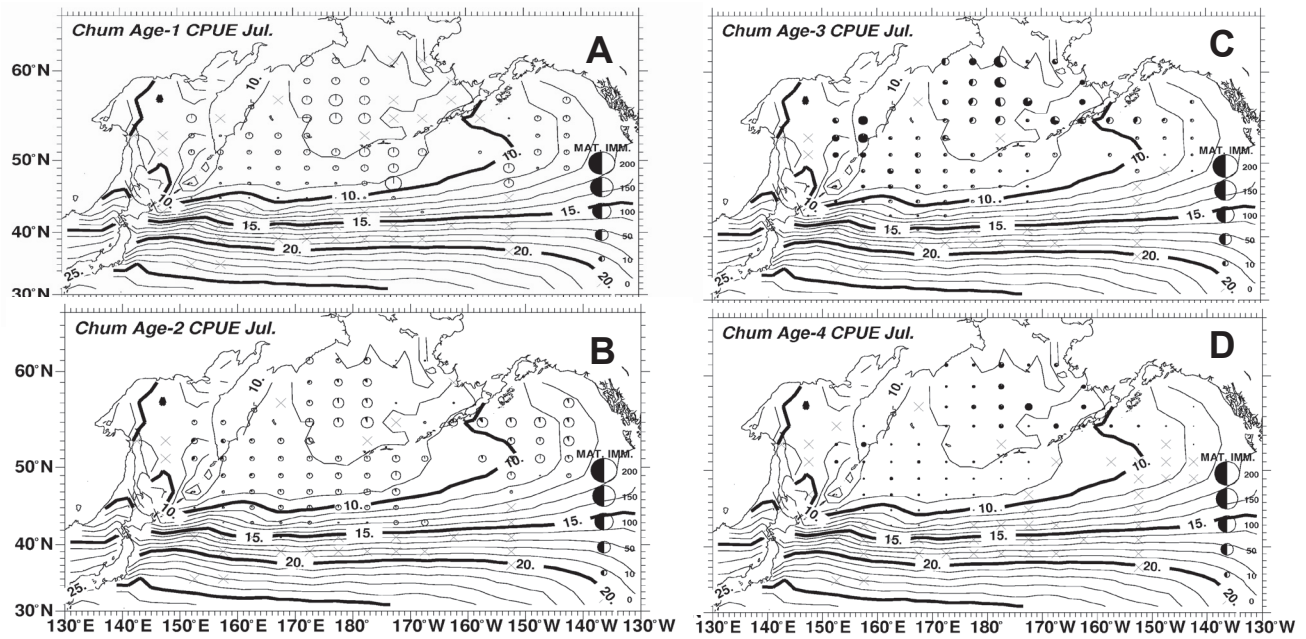


Fig. 3. Ocean distribution of chum salmon in the North Pacific Ocean for age 0.1 fish (A), age 0.2 fish (B), age 0.3 fish (C), and age 0.4 fish (D) in July in 1972–2002. Size of circle indicates catch per unit effort (CPUE, number of fish per 30 tans of research gillnet). Solid areas in circles indicate the proportion of maturing fish; MAT maturing, IMM, immature. “X” indicates zero CPUE. Lines indicate sea surface temperature (°C).

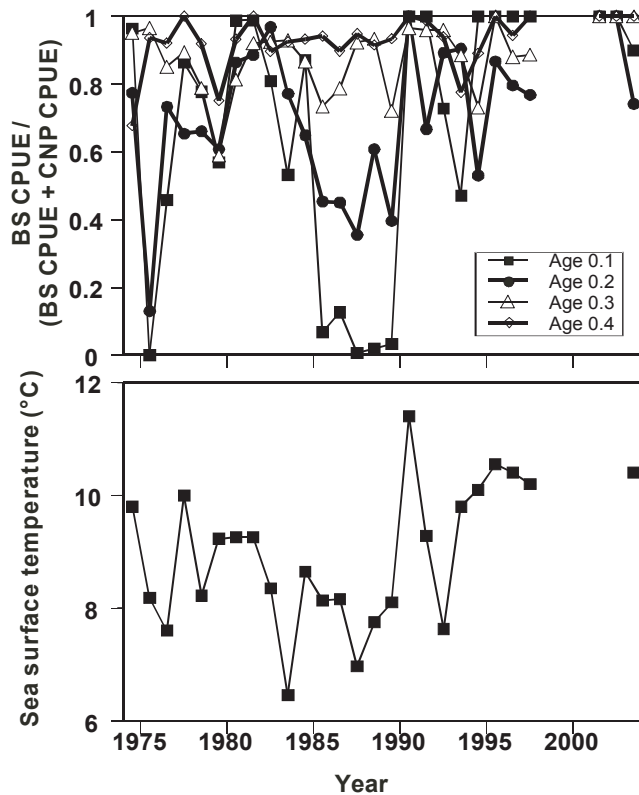


Fig. 4. Ratio of catch per unit effort (CPUE, number of fish per 30 tans of research gillnet) of chum salmon in the Bering Sea (BS) to the sum of CPUEs in the central North Pacific (CNP) and BS by age group with mean sea surface temperature (SST) at 47–49°N, 179°E–179°W July, 1974–1997, 2001–2003.

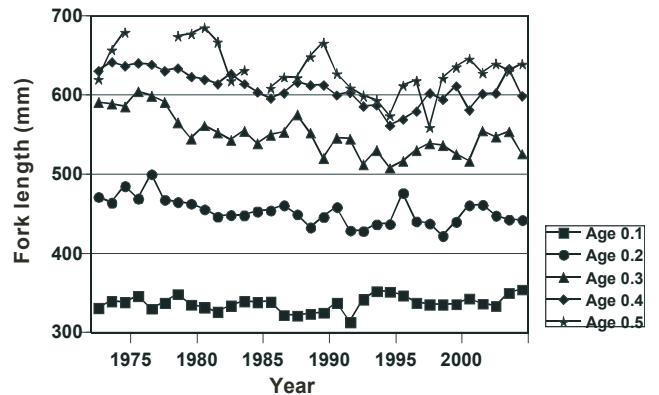


Fig. 5. Mean fork length of chum salmon caught in research gillnets in the central North Pacific and the Bering Sea by age group, 1972–2004.

0.607, $P < 0.001$ for age 0.3 CPUE; $r = 0.592$, $P < 0.001$ for age 0.4 CPUE).

Ocean Distribution

In July, chum salmon were distributed mainly in the BS and the Gulf of Alaska (Fig. 3). Age 0.1 fish were distributed in waters with SST $< 10^{\circ}\text{C}$ in the CNP as well as the BS (Fig. 3A). The distribution of age 0.2 fish was similar to the distribution of age 0.1 fish (Fig. 3B). On the other hand, 0.3 and 0.4 fish were distributed mainly in the BS (Fig. 3C, D).

Age 0.1 and 0.2 fish were distributed in the BS when SST were high in the CNP (Fig. 4). At low SST, these fish

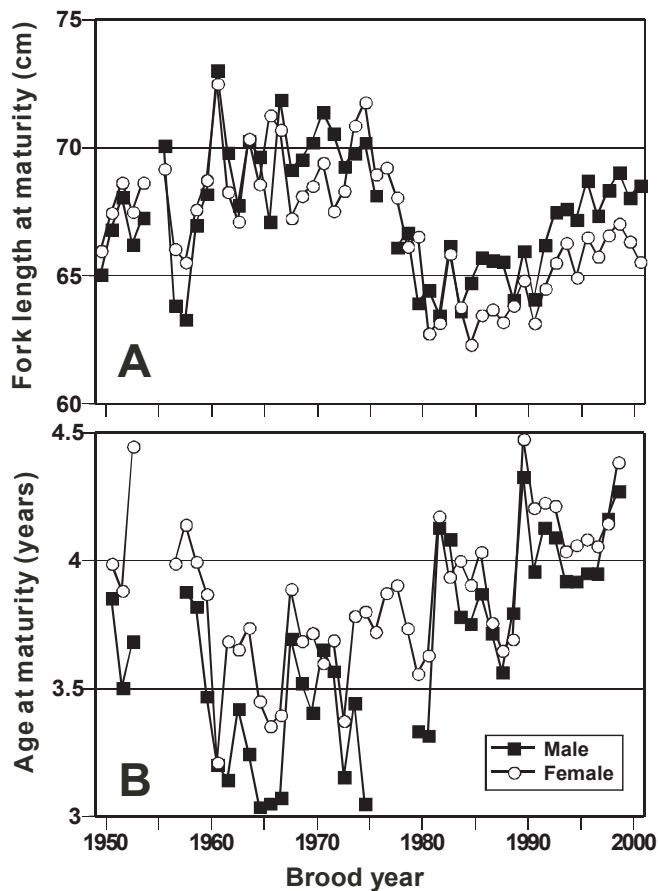


Fig. 6. Mean fork length of mature four-year-old chum salmon (A) and mean age of mature chum salmon by brood year (B) in the Ishikari River, Hokkaido, Japan.

were also distributed in the CNP. The ratios of age 0.1 and 0.2 fish distributed in the BS correlated positively with SST in the CNP ($r = 0.684$, $P < 0.001$ for age 0.1 and $r = 0.421$, $P = 0.036$ for age 0.2). On the other hand, age 0.3 and 0.4 fish were always distributed in the BS. The ratio of 0.3 and 0.4 fish distributed in the BS did not correlate with SST in the CNP ($r = 0.129$, $P = 0.536$ for age 0.3, and $r = 0.083$, $P = 0.695$ for age 0.4).

Trends in Fish Size and Age

Mean fork length by age group of chum salmon decreased from the 1970s to the 1990s, but has increased recently (Fig. 5). While mean fork length of age 0.1 fish did not change appreciably ($r = 0.229$, $P = 0.200$), mean fork lengths of age 0.2, 0.3, 0.4, and 0.5 fish decreased from the 1970s to the mid 1990s ($r = -0.575$, $P < 0.001$ for age 0.2; $r = -0.717$, $P < 0.001$ for age 0.3; $r = -0.672$, $P < 0.001$ for age 0.4; $r = -0.448$, $P = 0.015$ for age 0.5). Since 1994, fork lengths of age 0.3, 0.4, and 0.5 fish have increased. The larger change in fork length of fish older than age 0.1 fish indicate that ocean growth in offshore waters changed tem-

porally. Ocean growth of chum salmon has recovered since the 1990s.

Mean fork length of mature four-year-old chum salmon was large in the 1960s and 1970s year-classes, decreased in the 1970s and 1980s ($r = -0.846$, $P < 0.001$ for males and $r = -0.747$, $P < 0.001$ for females in the 1971–1990 year-classes), and recovered in the 1990s and 2000s ($r = 0.845$, $P < 0.001$ for males and $r = 0.802$, $P < 0.001$ for females in the 1991–2004 year-classes) (Fig. 6A). These changes coincided with changes in fish size during ocean life ($r = 0.543$, $P = 0.001$ for males and $r = 0.595$, $P < 0.001$ for females with ocean fork length of age 0.3 fish).

The mean age of mature fish decreased in the 1950s year-classes but has increased since the 1960s ($r = 0.813$, $P < 0.001$ for males and $r = 0.745$, $P < 0.001$ for females after the 1960 year-class) (Fig. 6B).

Relationships among Trends

The regression analysis showed a synchronization of trends in ocean conditions, abundance, and biological characteristics of chum salmon (Fig. 7). Offshore CPUE of age 0.2 fish correlated with the coastal catches in Asia three years before. Coastal catches should be proportional to spawner abundance, if the exploitation rate did not change significantly and/or was high enough. CPUE correlated also with the summer PDO two years before, which should correlate with ocean conditions during the first summer of ocean life. CPUE of age 0.2 fish correlated with CPUE of age 0.3 fish of the same year-class and with coastal catches one year after, which included mainly age 0.3 (four-year-old) fish.

Ocean growth of age 0.2 fish correlated negatively with CPUE (Fig. 7). Fork length of age 0.2 fish in offshore waters correlated positively with age at maturity for the same year-class and size of mature fish in the same year. These relationships indicate that trends in abundance and biological characteristics are affected by ocean conditions.

Sea surface temperatures in the CNP in July correlated positively with the ratio of the BS CPUE (Figs. 4 and 7). This indicates that ocean distributions of chum salmon are affected by SST.

DISCUSSION

Abundance and Ocean Conditions

Regions in which large catches of chum salmon were recorded were different in the 1930s–early 1940s compared to the 1980s–2000s. While large catches were recorded in Russia, southeast Alaska, and Canada in the 1930s and early 1940s, large catches recorded in the 1980s–2000s were in Japan and southeast Alaska where hatchery programs have been well developed. This supports the hypothesis that the recent increases in chum abundance may be a result of the development of hatchery programs and improved hatchery

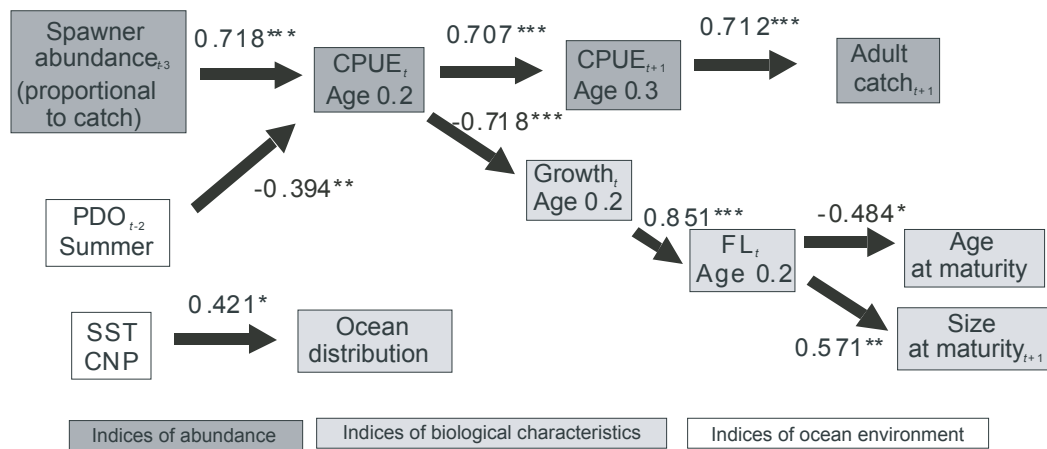


Fig. 7. Relationships among trends in ocean conditions, abundance, and biological characteristics of chum salmon in year *t*. PDO, Pacific Decadal Oscillation; SST, sea surface temperature; CNP, central North Pacific; FL, fork length. Numerical indicates a standard partial regression coefficient or correlation coefficient and asterisks indicate statistical significance (t-test, *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$).

techniques (Mayama 1985; Kaeriyama 1998). However, in a recent review of hatchery programs in Hokkaido, Japan, Morita et al. (2006) indicated that climate change, the closing of high-seas fisheries, and improvements in water quality, as well as hatchery programs, could explain the increase in salmon abundance. To attribute the effectiveness of hatchery programs to the recent increases in chum salmon abundance, we need more information on topics such as differences in ocean mortality of hatchery and wild fish, reliable escape-ment estimates, and freshwater mortality of wild fish.

An alternative hypothesis to explain the different dynamics of chum salmon stocks among regions is the effect of climate change on local populations. Large-scale climate change strongly affects salmon population dynamics (e.g. Beamish and Bouillon 1993; Mantua et al. 1997). Large-scale climate change has resulted in different responses among local ocean micro-climates and ecosystems (Mantua et al. 1997; Nagasawa 2000). Salmon survival responded differently to local SST in northern and southern areas of the Pacific coast of North America (Mueter et al. 2002). Inverse salmon production regimes were observed between Alaska and the west coast of the United States (Hare et al. 1999). Large-scale climate change can result in varying patterns in local population dynamics of chum salmon.

We found correlations between mean summer PDO, adult catches in Asian coastal areas, and offshore CPUEs of chum salmon. The relationship between the ocean climate (e.g. PDO or Aleutian Low Pressure Index) and salmon abundance has been reported by many authors (e.g. Beamish and Bouillon 1993; Mantua et al. 1997). However, the mechanisms underlying the relationship(s) between large-scale climate indices and salmon abundance have not yet been well clarified. Large-scale climate indices often outperform local climatic factors in predicting ecological processes of a local population, when measures of local climate parameters used by ecologists fail to capture complex associations between

climate conditions and ecological factors (Hallet et al. 2004). The strong relationship between local ocean conditions (e.g. coastal sea surface temperature or upwelling) and salmon abundance has also been reported (Fukuwaka and Suzuki 2000; Mueter et al. 2002). Asian chum salmon dominated in the CNP and the BS when we used CPUE as an abundance index in offshore waters (Neave et al. 1976; Seeb et al. 2004). Temporal patterns in population dynamics were not synchronous among chum stocks in Asia (Salo 1991). Different temporal patterns in local population dynamics could be due to differences in terrestrial or ocean environments, or mechanisms controlling population abundance. Although local ocean conditions (or climate) and spawner abundance of chum salmon may determine the abundance of a local population, a large-scale climate index (i.e. PDO) may correlate with offshore CPUE, which includes many local populations.

Distribution and Ocean Conditions

We showed that the offshore distribution of age 0.1 and 0.2 chum salmon was different from that of 0.3 and 0.4 fish and changed with SST in July. It is well known that the offshore distribution of Pacific salmon is affected by SST. Manzer et al. (1965) reviewed the offshore distribution of gillnet catches in the Japanese salmon fishery and the International North Pacific Fisheries Commission salmon research. They indicated that geographical and SST ranges of salmon distribution changed with season. Neave et al. (1976) showed that immature chum salmon were distributed in waters warmer than those occupied by maturing fish from April to June. Sea surface temperature may influence growth and feeding activity because chum salmon are distributed in the surface layer. Pacific salmon might select an SST range to either maximize or ensure somatic growth (Welch et al. 1995; Rand 2002). Maturing chum salmon begin their homing migration

in June (Neave et al. 1976). While younger chum salmon may actively select waters with a preferred range of SST to maximize somatic growth, older and maturing fish might be distributed in cooler waters of the BS and less affected by SST.

Abundance, Ocean Growth, Age, and Size at Maturity

We found a negative correlation between offshore CPUE and ocean growth of chum salmon. Ishida et al. (1993) showed a negative correlation between CPUE and fish size using Japanese research data in offshore CNP, and discussed density-dependent growth of chum salmon. Some authors thought that the density-dependent growth of Pacific salmon could be the result of competition for food (e.g. Ishida et al. 1993; Bigler et al. 1996). Peterman (1987) showed that intraspecific competition for food, such as the negative correlation between fish size of Fraser River pink salmon and the number of fish per zooplankton biomass at ocean station P in the Gulf of Alaska. In addition, interspecific competition for food (i.e. zooplankton) may occur among salmon species or other zooplankton feeders (e.g. Ruggerone et al. 2003). To clarify the mechanisms of density-dependent growth of Pacific salmon, it is necessary to study competition within and among species of salmon and other plankton feeders in the ecosystem of the North Pacific and the BS.

Ocean growth affected age at maturity of the same year-class of chum salmon. Fish size was strongly related to individual fitness because large females can produce large numbers of eggs and large males have some advantages in mating competition (Hendry et al. 2004). Parr of Atlantic salmon males exceeding a threshold size initiated maturation (Myers et al. 1986; Baum et al. 2004). However, physiological studies indicate that somatic growth is linked closely with sexual maturation mediated by the endocrine system, such as the secretion of growth hormone and insulin-like growth factor-I in vertebrates (reviewed by Chandrashekar et al. 2004). Growth history affected maturation stronger than fish size in chum salmon (Morita and Fukuwaka 2006). Although a threshold size for maturation may be necessary to reach sexual maturity, a proximate factor initiating sexual maturity may be the level of ocean growth in chum salmon.

Fork length of age 0.2 fish correlated negatively with age at maturity and positively with size at maturity. Several authors have reported that a decrease in size and an increase in age of mature salmon occurred simultaneously in many populations around the North Pacific from the 1970s to the 1990s (e.g. Ishida et al. 1993; Bigler et al. 1996). In the theory of life-history strategy, an optimal response to a reduced growth rate is an increase in age and decrease in size at maturity (Stearns 1992). Using the scale back-calculation techniques, Morita et al. (2005) indicated that a recent increase in age and decrease in size of Japanese chum salmon could result from a growth reduction during ocean life, supporting the hypothesis that change in age and size at maturity

is an adaptive response.

International Survey for Mechanisms

The North Pacific Anadromous Fish Commission conducted an international survey from 2002 to 2006 called the Bering-Aleutian Salmon International Survey (BASIS) that will form the foundation for long-term, large-scale ecosystem research on salmon in the Bering Sea (NPAFC 2001). The goal of BASIS is to understand the mechanisms underlying the effects of environmental variation and density-dependence on the salmon carrying capacity in the Bering Sea. Key factors determining chum salmon production may occur in the Bering Sea as well as in coastal waters during early ocean life because ocean growth of chum salmon is higher in summer than in other seasons (Ishida et al. 1998). BASIS may elucidate the mechanisms underlying the relationship between trends in abundance and biological characteristics of chum salmon.

CONCLUSIONS

At present, the size and age of chum salmon continues to increase even though chum salmon abundance around the North Pacific is at the highest level ever. In the past, abundance and biological characteristics of chum salmon fluctuated on a decadal scale. Abundance and biological characteristics correlated with each other and were affected by ocean or climate conditions. For conservation and sustainable use of chum salmon stocks, we should monitor the abundance and biological characteristics in rivers and the ocean.

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REFERENCES

- Baum, D., R. Laughton, J.D. Armstrong, and N.B. Metcalfe. 2004. Altitudinal variation in the relationship between growth and maturation rate in salmon parr. *J. Animal Ecol.* 73: 253–260.
- Beamish, R.J. (Editor). 1995. Climate change and northern fish populations. *Can. Sp. Pub. Fish. Aquat. Sci. No.* 121. 739 pp.
- Beamish, R.J. and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* 50: 1002–1016.
- Bigler, B.S., D.W. Welch, and J.H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* 53: 455–465.

- Chandrashekar, V., D. Zaczek, and A. Bartke. 2004. The consequences of altered somatotrophic system on reproduction. *Biol. Reprod.* 71: 17–27.
- Eggers, D.M., J. Irvine, M. Fukuwaka, and V. Karpenko. 2005. Catch trends and status of North Pacific salmon. NPAFC Doc. 723, Rev. 1. 34 pp. (Available at <http://www.npafc.org>).
- Fukuwaka, M. and T. Suzuki. 2000. Density-dependence of chum salmon in coastal waters of the Japan Sea. *N. Pac. Anadr. Fish Comm. Bull.* 2: 75–81. (Available at <http://www.npafc.org>).
- Hallett, T.B., T. Coulson, J.G. Pilkington, T.H. Clutton-Brock, J.M. Pemberton, and B.T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature (London)* 430: 71–75.
- Hare, S.R., N.J. Mantua, and R.C. Francis. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries* 24: 6–14.
- Helle, J.H. and M.S. Hoffman. 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 1: 81–89. (Available at <http://www.npafc.org>).
- 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>).
- Hendry, A.P., T. Bohlin, B. Jonsson, and O.K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. *In Evolution illuminated: salmon and their relatives. Edited by A. P. Hendry and S. C. Stearns.* Oxford University Press, New York. pp. 92–125.
- 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>).
- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and K. Nagasawa. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. *Can. J. Fish. Aquat. Sci.* 50: 290–295.
- Ishida, Y., S. Ito, Y. Ueno, and J. Sakai. 1998. Seasonal growth patterns of Pacific salmon (*Oncorhynchus* spp.) in offshore waters of the North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 1: 66–80. (Available at <http://www.npafc.org>).
- Kaeriyama, M. 1998. Dynamics of a chum salmon, *Oncorhynchus keta*, population released from Hokkaido in Japan. *N. Pac. Anadr. Fish Comm. Bull.* 1: 90–102. (Available at <http://www.npafc.org>).
- Klyashtorin, L.B. and F.N. Rukhlov. 1998. Long-term climate change and pink salmon stock fluctuations. *N. Pac. Anadr. Fish Comm. Bull.* 1: 464–479. (Available at <http://www.npafc.org>).
- Mantua, J.N., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impact on salmon production. *Bull. Am. Meteorol. Soc.* 78: 1069–1079.
- Manzer, J.I., T. Ishida, A.E. Peterson, and M.G. Hanavan. 1965. Salmon of the North Pacific Ocean – Part V. Offshore distributions of salmon. *Int. North Pac. Fish. Comm. Bull. No. 15.* pp. 1–452.
- Mayama, H. 1985. Technical innovations in chum salmon enhancement with special reference to fry condition and timing of release. *In Proceedings of the eleventh U.S.-Japan meeting on aquaculture, salmon enhancement.* Tokyo, Japan, October 19–20, 1982. *Edited by C.J. Sindermann.* U.S. Dep. Commerce, NOAA Tech. Rep. NMFS 27. pp. 83–86.
- Morita, K. and M. Fukuwaka. 2006. Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. *Evolution* 60: 1516–1521.
- Morita, K., S.H. Morita, M. Fukuwaka, and H. Matsuda. 2005. Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. *Can. J. Fish. Aquat. Sci.* 62: 2752–2759.
- Morita, K., T. Saito, Y. Miyakoshi, M. Fukuwaka, T. Nagasawa, and M. Kaeriyama. 2006. A review of the Pacific salmon hatchery programs on Hokkaido Island, Japan. *ICES J. Mar. Sci.* 63: 1353–1363.
- Mueter, F.J., R.M. Peterman, and B.J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* 59: 456–463.
- Myers, R.A., J.A. Hutchings, and R.J. Gibson. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 43: 1242–1248.
- Nagasawa, K. 2000. Long-term changes in the climate and ocean environment in the Okhotsk Sea and western North Pacific and abundance and body weight of East Sakhalin pink salmon (*Oncorhynchus gorbuscha*). *N. Pac. Anadr. Fish. Comm. Bull.* 2: 203–211. (Available at <http://www.npafc.org>).
- Nagasawa, T., T. Azumaya, and M. Fukuwaka. 2005. Which salmon are using the Bering Sea as their feeding area? (Japanese national overview of BASIS research). *N. Pac. Anadr. Fish Comm. Tech. Rep.* 6: 8–10. (Available at <http://www.npafc.org>).
- Neave, F., T. Yonemori, and R.G. Bakkala. 1976. Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. *Int. North Pac. Fish. Comm. Bull.* 35: 1–79.
- North Pacific Anadromous Fish Commission (NPAFC). 2001. Plan for NPAFC Bering-Aleutian Salmon International Survey (BASIS) 2002–2006. NPAFC Doc. 579,

- Rev. 2. 27 pp. (Available at <http://www.npafc.org>).
- Peterman, R.M. 1987. Review of the components of recruitment of Pacific salmon. *Am. Fish. Soc. Symp.* 1: 417–429.
- Rand, P.S. 2002. Modeling feeding and growth in Gulf of Alaska sockeye salmon: implications for high-seas distribution and migration. *Mar. Ecol. Prog. Ser.* 234: 265–280.
- Ruggerone, G.T., M. Zimmerman, K.W. Myers, J.L. Nielsen, and D.E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific. *Fish. Oceanogr.* 12: 209–219.
- Salo, E.O. 1991. Life history of chum salmon (*Oncorhynchus keta*). In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. University of British Columbia Press, Vancouver. pp. 231–309.
- Seeb, L.W., P.A. Crane, C.M. Kondzela, R.L. Wilmot, S. Urawa, N.V. Varnavskaya, and J.E. Seeb. 2004. Migration of Pacific Rim chum salmon on the high seas: insights from genetic data. *Environ. Biol. Fish.* 69: 21–36.
- Shuntov, V.P., E.P. Dulepova, and V.V. Lapko. 1999. Long-term variations in pelagic communities in the large marine ecosystems of the Northwest Pacific Ocean. In *Large marine ecosystems of the Pacific Rim: assessment, sustainability, and management*. Edited by K. Sherman and Q. Tang. Blackwell Science, Malden, Massachusetts. pp. 48–55.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford. 248 pp.
- Takagi, K. 1975. A non-selective salmon gillnet for research operations. *Int. North Pac. Fish. Comm. Bull.* 32: 13–41.
- Welch, D.W., A.I. Chigirinsky, and Y. Ishida. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. *Can. J. Fish. Aquat. Sci.* 52: 489–503.