

Effect of global warming on the life history and population dynamics of Japanese chum salmon

Masahide Kaeriyama · Hyunju Seo ·
Yu-xue Qin

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Abstract We have reviewed the effects of long-term climatic/oceanic conditions on the growth, survival, production dynamics, and distribution of Hokkaido chum salmon *Oncorhynchus keta* in Japan during the period 1945–2005 using path analysis, back-calculation, and scale analyses, and applied a prediction method based on the SRES-A1B scenario of the intergovernmental panel on climate change. The populations of Hokkaido chum salmon were found to have had high growth rates at age 1 year since the late 1980s. Path analysis indicated that the growth at age 1 year in the Okhotsk Sea was directly affected by warm sea surface temperature associated with global warming, with the increased growth at age 1 year resulting in higher rates of survival and large population sizes. Predictions on the global warming effects on the chum salmon were (1) decreased carrying capacity and distribution area, (2) occurrence of a strong density-dependent effect, and (3) loss of migration route to the Sea of Okhotsk, especially for Hokkaido chum salmon. We have also outlined the future challenges of establishing a sustainable conservation management scheme for salmon that include adaptive management and precautionary principles, as well as conservation of natural spawning populations and recovery of natural river ecosystems in Japan despite the warming climate.

Keywords Climate change · Global warming · Chum salmon · Life history · Population dynamics · Risk management

Introduction

The Pacific salmon (*Oncorhynchus* spp.) is a diadromous fish that begins its life in freshwater but subsequently migrates between seawater and freshwater during its life cycle. Salmon that migrate to the sea at an early stage of development have a large area of ocean distribution and high biomass, suggesting that such fish evolved the ability to migrate seaward during the Ice Age as a means to utilize the high biological productivity of the ocean and retained the ability to return to freshwater for reproduction [1–3]. Of all the salmon species, the chum salmon *O. keta* and the pink salmon *O. gorbuscha* show the highest degree of evolution, spending a large part of their life histories in the sea [4–6]. In the study reported here, we focused mainly on the chum salmon, discussing its life history and dynamics of biomass with respect to global warming and climate change.

The number of chum salmon returning to Japanese waters significantly increased up to the late 1970s but thereafter decreased and stabilized at around 40–50 million, after peaking at over 80 million in the late 1990s (Fig. 1). Since 2000 there has been a significant decrease in their number, primarily due to the collapse of the diatom–euphausiid food web by coccolith blooms in the eastern Bering Sea ecosystem caused by the 1997/1998 Super El Niño [7, 8]. The disappearance of euphausiids caused a significant population decrease in marine biomass, including that of the Japanese salmon, the Bristol Bay sockeye salmon *O. nerka*, and seabirds, such as the short-tailed shearwater *Puffinus tenuirostris* [7, 9].

Long-term climate change and biomass dynamics of salmon

Salmon biomass is often associated with long-term climate change. The North Pacific Ocean has undergone a climate

M. Kaeriyama (✉) · H. Seo · Y. Qin
Hokkaido University, N15W8, Kita-ku, Sapporo,
Hokkaido 060-0815, Japan
e-mail: salmon@oia.hokudai.ac.jp

Fig. 1 Annual changes in the numbers of returning adult and released juvenile chum salmon in Japan

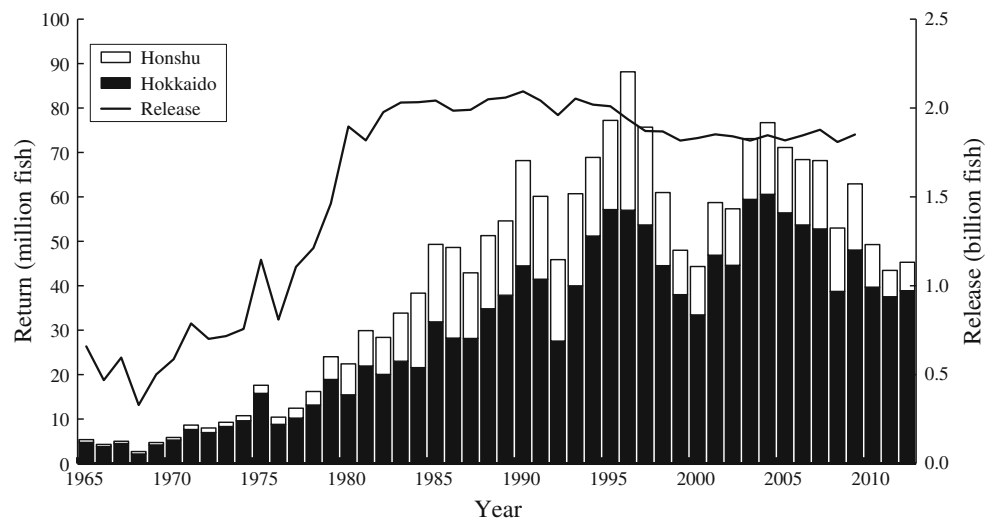
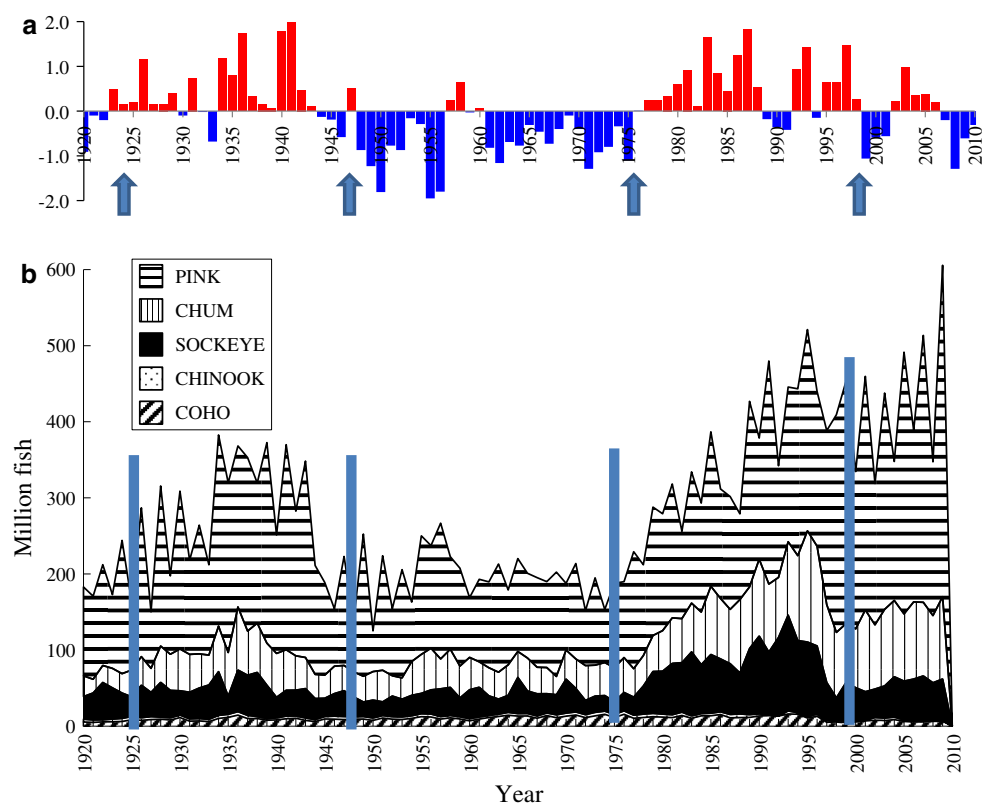


Fig. 2 Annual changes in the Pacific decadal oscillation (PDO) (a) and catch of Pacific salmon (b) in the North Pacific Ocean. Arrows, bars Years of climate regime shifts (Kaeriyama et al. [11])



change within a cycle of >10 years, as measured by atmosphere and ocean coordinates, and these parameters have been indexed using the Pacific decadal oscillation (PDO). The PDO index is defined as the leading principal component of the North Pacific monthly sea surface temperature (SST) variability (poleward of 20°N for the period extending from 1900 up to the present); a positive value indicates that the SST is lower than the average at the central area of the North Pacific and the SST is higher at the eastern area of the North Pacific and near the equator

[10]. According to the PDO, the amount of harvested salmon from the northern Pacific increases over time when the PDO is positive and decreases when the PDO is negative (Fig. 2) [11].

The PDO is closely related to the strength of the Aleutian Low in the winter, with its value being positive when the pressure is strong and negative when the pressure is weak. On the eastern side of the northern Pacific, including the Bering Sea, westerlies intensify when the strength of the Aleutian Low increases, thereby resulting in

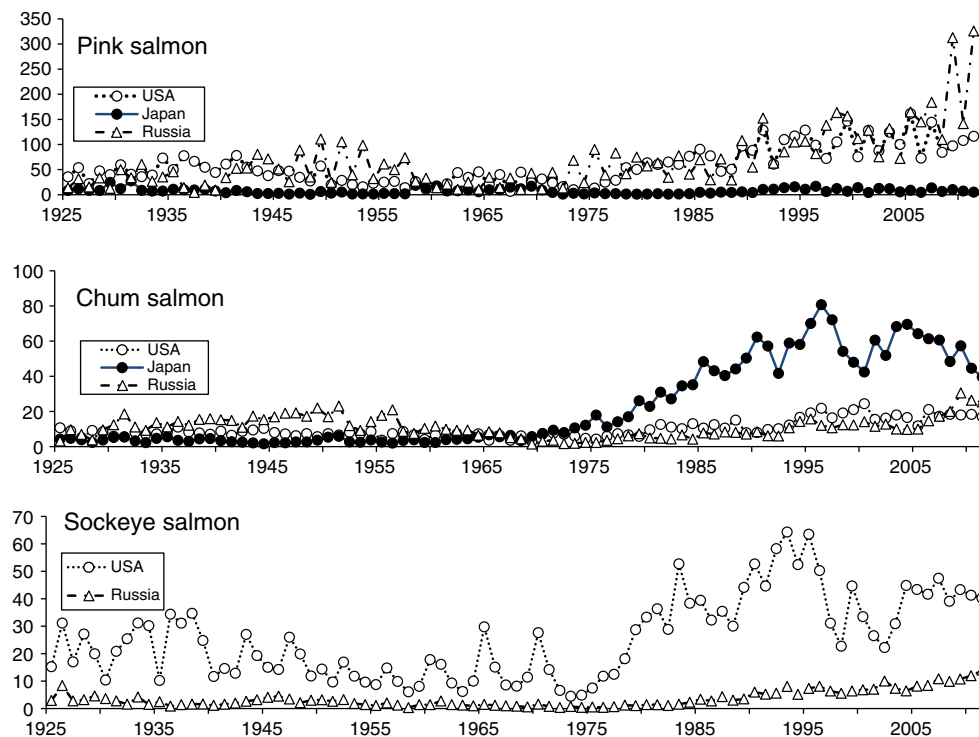


Fig. 3 Annual changes in abundance of pink, chum, and sockeye salmon by country. Units: million individuals. Data were collected by the North Pacific Anadromous Fish Commission (NPAFC) (available at <http://www.npafc.org/new/index.html>)

strengthening of the Subarctic Current and subsequently of the Alaska Current and Alaska Coast Current. Strengthening of the coastal current causes increases in eddy currents, churns the coastal water through synergic interactions with the tide, and carries a large amount of nutrients (e.g., nitrogen and phosphorus) up from the sea bottom to the surface layer. These nutrients are then distributed to the Gulf of Alaska through the Alaska Current and the Alaskan Gyre. At the same time, winter storms become active, vertical mixing of seawater becomes greater, and nutrients at the bottom layer diffuse to the surface layer through a strengthened Aleutian Low in the eastern Bering Sea. Furthermore, a counter-clockwise eddy of low pressure brings in the wet and warm air and warm water from the south, increasing the water temperature at the surface layer of the Gulf of Alaska and the eastern Bering Sea. The Aleutian Low has a significant impact on biological productivity in the Gulf of Alaska and the Bering Sea. Storms in the winter thus improve the carrying capacity of salmon [12–14].

The mid- to long-term shift in the PDO from positive to negative or vice versa is called a ‘climate regime shift’ [15]. The PDO showed a strong tendency to be positive between 1975/1976 and the late 1990s, and the salmon population increased during this time. However, it has tended to be negative since 1997/1998, the year when the ‘Super El Niño’, the greatest El Niño of the 20th century,

developed and initiated the next regime shift [7, 9, 16]. The overall amount of harvested salmon in the entire North Pacific has remained at a high level due to the significant increase in pink salmon and chum salmon in Russia (Fig. 3), but the carrying capacity has definitely passed its peak. The number of sockeye salmon has decreased since this peak, and a similar trend has been observed in the Japanese chum salmon [11]. The same trends were also observed in salmon in the U.S. states of Washington and Oregon [17]. Overall, the population of southern chum salmon has decreased since 1997/1998, shifting away from the ‘good-old-days’ that extended from the late 1970s until the shift in climate regime in the late 1990s.

Global warming and biomass dynamics of salmon

Explanations for the mechanism and causes of the recent trend in global warming are largely divided into the rebound theory from the Little Ice Age [18] and the theory of greenhouse gas effects stemming from anthropologic activities [Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC); available at: http://www.ipcc.ch/publications_and_data/ar4/syr/en/contents.html]. A discussion of these proposed mechanisms are beyond the scope of our study, but global warming as currently observed is a fact. The SST of the ocean

Fig. 4 Temporal changes in seasonal sea surface temperature (SST) in the Sea of Japan since 1900 and Pacific Ocean since 1950. Data are from the Japan Meteorological Agency (available at: http://www.data.kishou.go.jp/kaiyou/shindan/a_1/japan_warm/japan_warm.html)

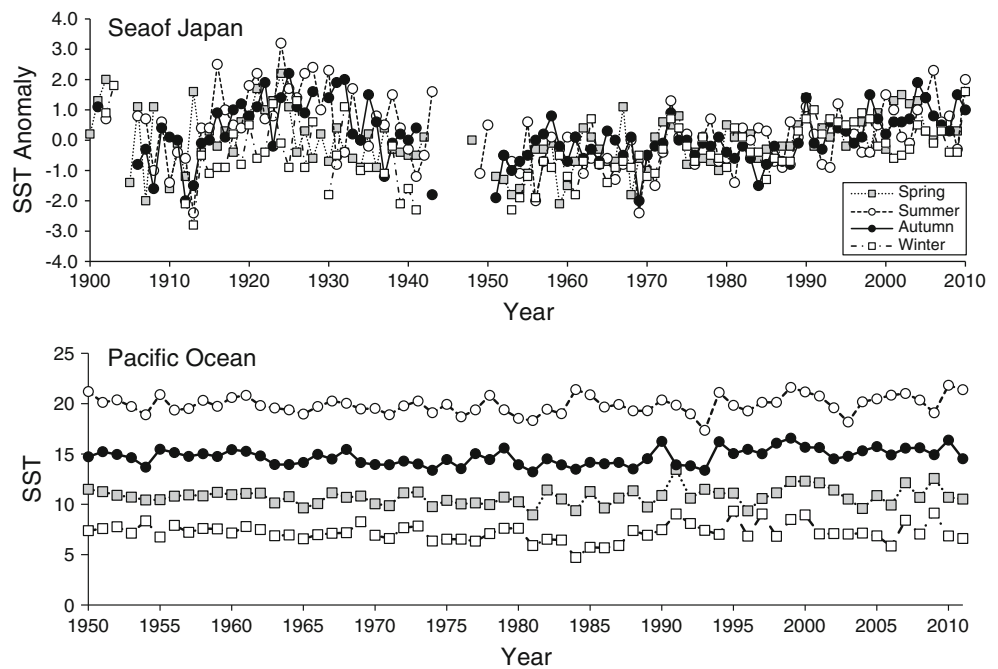


Table 1 Relationship between year and sea surface temperature anomaly in the Sea of Japan and the Pacific Ocean around Japan since 1980^a

Parameters describing relationship between year and SST anomaly	Winter	Spring	Summer	Autumn
Sea of Japan				
R^2	0.079	0.181	0.282	0.551
F	2.473	6.402	11.400	35.566
P	NS	0.017	0.002	<0.001
a	0.020	0.029	0.051	0.066
b	-40	-59	-102	-130
$(T = aY + b)$				
Pacific Ocean around Japan				
R^2	0.098	0.066	0.166	0.361
F	3.273	2.113	5.968	16.946
P	NS	NS	0.021	<0.001
a	0.038	0.028	0.047	0.062
b	-69	-45	-74	-108
$(T = aY + b)$				

SST, Sea surface temperature; NS, not significant

^a Data were obtained from the Japan Meteorological Agency at: http://www.data.kishou.go.jp/kaiyou/shindan/a_1/japan_warm/japan_warm.html

increased from 1.2 to 1.7 °C/100 years in the Sea of Japan, and from 0.6 to 1.3 °C/100 years in the Pacific Ocean around Japan between 1900 and 2011 (Japan Meteorological Agency; available at: http://www.data.kishou.go.jp/kaiyou/shindan/a_1/japan_warm/japan_warm.html). Observations of temporal changes in the SST in the Sea of Japan per season since 1980

have revealed that the greatest impact of global warming occurs in the autumn (rate of increase in temperature: 0.066 °C/year, $R^2 = 0.551$) and the least in the spring (0.029 °C/year, $R^2 = 0.181$; Fig. 4; Table 1).

For better or for worse, global warming is affecting the numbers of salmon. Chum salmon populations in Hokkaido, which migrated en masse in the 1990s, are suspected to have been positively affected by this trend. Salmon populations are considered to suffer from severe mortality immediately after their seaward migration and during the first winter in the ocean. The mortality of Japanese chum salmon released from the hatchery, however, is significantly less during their seaward migration than that of wild fish because they are reared and released from the hatchery and migrate to the sea with a larger body size. After living along the coast for a few months, the Japanese chum salmon spends its time and grows in the Okhotsk Sea during the summer and autumn, then survives the winter in the Western Subarctic Gyre [19]. Consequently, the survival of Japanese chum salmon during their overwintering is significantly affected by its growth up to the autumn in the Okhotsk Sea.

We have analyzed the scales of adult chum salmon returning to the Ishikari River between the 1940s and early 2000 and estimated first-year growth using the back-calculation method (Fig. 5) [20]. The results show that the first-year growth of salmon was significantly favorable from the 1990s to the early 2000s. A significant correlation was also observed between growth and survival rate. Taken together, these results suggest that the survival rate of chum salmon is higher when the growth rate during the period in coastal Japan and in the Okhotsk Sea is greater. On the other hand, first-year growth

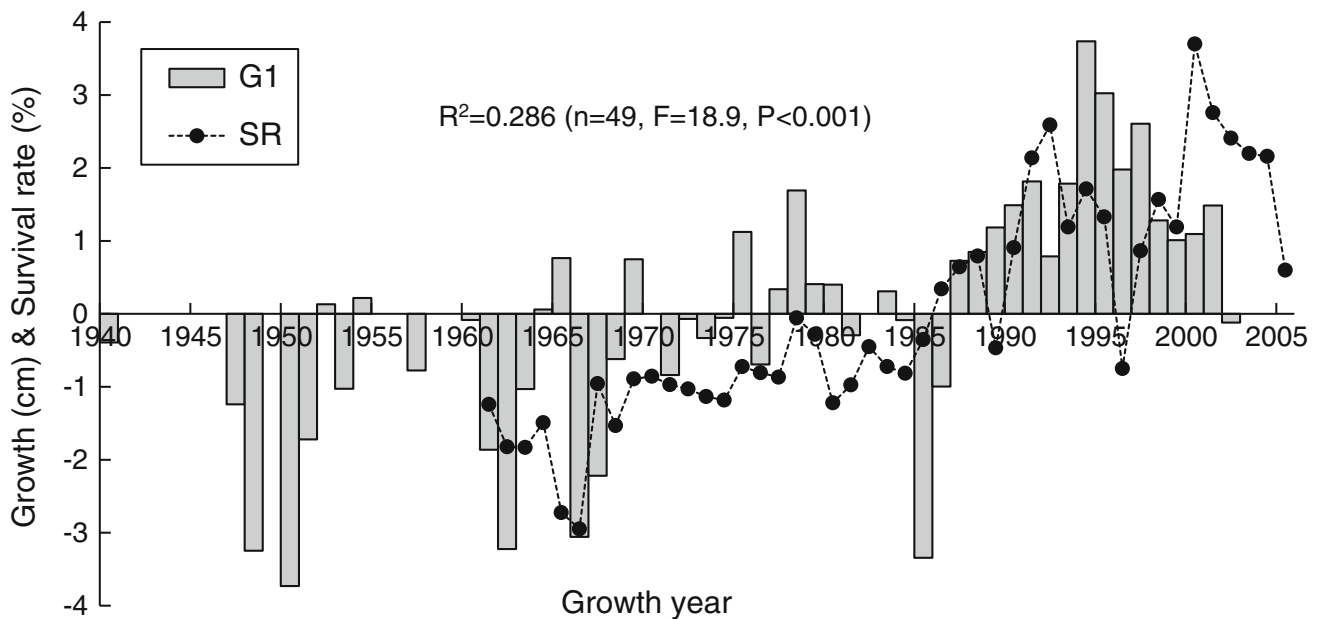


Fig. 5 Temporal changes in anomalies of growth at age 1 year (*G1*) and survival rate (*SR*) of Hokkaido chum salmon. Growth anomaly was calculated for adult chum salmon returning to the Ishikari River using scale analysis and back-calculation. Modified from Seo et al. [20]

showed a positive correlation with the SST during the summer and autumn in the Okhotsk Sea and a negative correlation with the sea ice area in the winter [21]. A path analysis using the various climate change indices was used to analyze the mechanism behind the favorable growth for the Hokkaido chum salmon in the Okhotsk Sea between the 1990s and the early 2000s. A path model analysis is used to describe the directed dependencies among a set of variables, and this analysis includes models equivalent to any form of multiple regression analysis, factor analysis, canonical correlation analysis, and discriminant analysis [Wikipedia: the free encyclopedia; see ‘Path analysis’ (available at: http://en.wikipedia.org/wiki/Main_Page; accessed 9 Sept 2013)]. The results show that temperature anomalies at the earth’s surface [surface air temperature (SAT)] directly affected SSTs during the summer and autumn. Furthermore, the SSTs directly affected the growth of juvenile salmon, increasing the survival rate and population size of Hokkaido chum salmon (Fig. 6). This leads to the conclusion that recent global warming has imparted a positive effect on the Hokkaido chum salmon. The results of the path model revealed that SAT also directly affected the Aleutian Low Pressure Index (ALPI) in the winter season, which in turn affected the PDO.

In contrast, in the Sea of Japan, the Tsushima Warm Current flows northward. Since the early 1990s, the current has been influenced by the warming climate (Fig. 7a) and, consequently, the abundance of early-run chum salmon returning to the coast of the Sea of Japan decreased during the years when the current was strong (Fig. 7b). The early-run abundance of chum returning by the end of September was found to differ between years when the Tsushima

Warm Current was weak ($2,407 \pm 1,028$ thousand individuals, $n = 14$) and when it was strong ($1,446 \pm 745$ thousand individuals, $n = 11$) [analysis of variance (ANOVA) $F = 6.795$, $P = 0.016$], although analysis of the middle-run abundance returning in October and November indicated no difference between weak years ($1,525 \pm 802$ thousand individuals, $n = 14$) and strong years ($1,490 \pm 754$ thousand individuals, $n = 11$) (ANOVA $F = 0.012$, $P > 0.05$). One explanation may be that it is difficult for adult chum salmon to migrate for spawning in the sea area at high temperatures or those above $20\text{ }^{\circ}\text{C}$ [22]. This trend can be interpreted as a negative effect of global warming.

By examining projected temperature isotherms and applying an optimum ($8\text{--}12\text{ }^{\circ}\text{C}$; optimum growth rate and feeding habit), adaptable ($5\text{--}13\text{ }^{\circ}\text{C}$; available habitat for swimming and feeding), and wintering temperature range ($4\text{--}6\text{ }^{\circ}\text{C}$) of chum salmon based on the SRES-A1B scenario in the Fourth Assessment Report of the IPCC [11], we are capable of predicting the potential marine distribution of chum salmon populations in the North Pacific during the next years and possibly decades (Fig. 8). Based on the simulation, the following predictions can be made:

1. The distribution area of chum salmon has decreased in the Okhotsk Sea, the Gulf of Alaska, and even in the Bering Sea, thereby indicating a decrease in carrying capacity which may possibly have a density-dependent effect.
2. On the other hand, the distribution area is likely to expand to the Arctic Sea such as the Chukchi Sea.

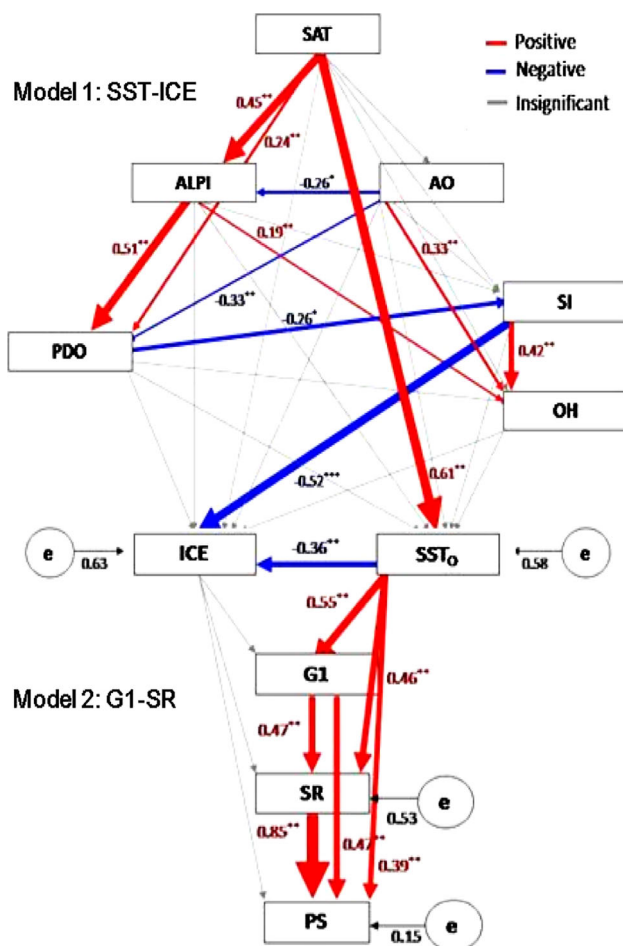


Fig. 6 Path model analyses relationships among global surface air temperature (*SAT*), Aleutian Low Pressure Index (*ALPI*), PDO, Arctic oscillation (*AO*), Siberian high (*SI*), Okhotsk high (*OH*), ice cover area (*ICE*), and summer SST (*SST_O*) in the Sea of Okhotsk (*Model 1*), and relationships among *ICE*, *SST_O*, growth during the first year of life history (*G1*), survival rate (*SR*), and population size (*PS*) of Hokkaido chum salmon (*Model 2*) between 1961 and 2002. The tested path model is indicated by arrows; significantly positive and negative direct paths are shown by unbroken red and blue arrows, respectively. Significantly positive and negative indirect paths are shown by broken red and blue arrows, respectively. Non-significant paths are shown by gray arrows. To aid in the interpretation, the width of lines is approximately proportional to the strength of the relationships. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Numeral values and asterisks show correlation coefficients and probabilities, respectively. The residual variables are shown for *ICE*, *SST_O*, *SR*, and *PS* (thin black arrows). Modified from Seo et al. [20]

3. The migration area in the winter may also shift from the Gulf of Alaska to the Western Subarctic Gyre.
4. In southern distribution areas, such as Japan, there is a risk that the early run of chum salmon lose their route of spawning migration into the coastal sea.
5. Juveniles will be not able to spend adequate time in the coastal sea and be forced to migrate offshore at an earlier developmental stage without attaining sufficient growth.

6. The salmon populations are at risk of losing their migration route to the Okhotsk Sea, and their survival greatly depends on whether they are able to find a new migration route along the Chishima Islands [11].

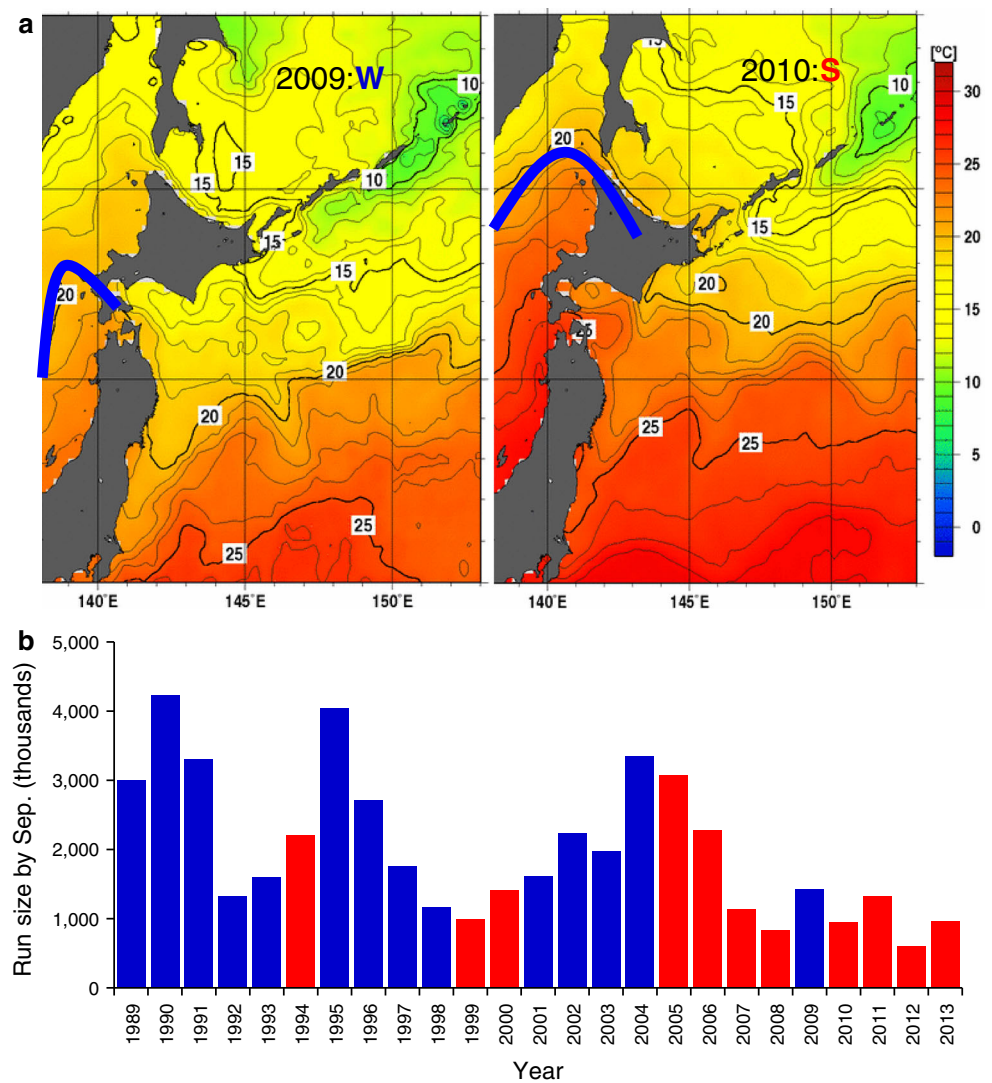
Our predictions also correspond to the results generated by Mantua et al. [23] on the effects of the PDO.

Salmon and ecosystem services

An ecosystem is a system of great uncertainty and reflects the results of an interaction between an inorganic system and an aggregate of organisms that have evolved over a long period. Its function has been maintained by biodiversity in terms of genes, species, and ecosystems. This biodiversity is a product of inter-organismal interactions, including prey–predator relationships, symbiosis and parasitic relationships, and competition over resources, such as food and living space. When any one component of a network disappears, biodiversity declines. Ecosystem services are defined as the benefits that humans have obtained from functions of ecosystems and organisms in the ecosystem. For example, the salmon, which is a keystone species of the North Pacific ecosystem, contributes to ecosystem services by transporting marine-derived nutrients (supporting service), maintaining biodiversity (regulating service), serving as a food source (provisioning service), and acting as an environmental and emotional educational factor, as well as a comfort (cultural service) factor, to the terrestrial ecosystems by returning to the birth river for reproduction.

Hatchery-produced chum salmon (hatchery salmon) exceeds 50 % of the total catch of chum salmon in the North Pacific [8]. The interaction between wild-origin (wild salmon) and hatchery salmon is a serious issue in conservation programs of Pacific salmon in the North Pacific ecosystems. Wild and hatchery chum salmon have been found to exhibit similar reproductive success, with both wild and hatchery males obtaining similar access to nesting females, and females of both types exhibiting similar breeding behaviors and duration of breeding periods [24]. In the Yurappu River, southern Hokkaido, the wild population of chum salmon reproduces naturally during the winter (from December to January) at the lower reach of the river [25], while many hatchery-derived salmon have been observed to reproduce naturally in the fall (from October to middle November) at the upper reach near by the hatchery. The wild population has a higher genetic endemism than the hatchery populations [26]. The genetic differentiation among hatchery populations is very weak despite high genetic diversity in Hokkaido [26, 27] because of excessive egg-transplantation effects [28]. In

Fig. 7 Fluctuation in the strength of Tsushima warm current (TWC) compared to the run size of early-population chum salmon returning to the Sea of Japan coast of Hokkaido. **a** Mean SST isothermal diagrams around Japan in September 2009 (typical of a weak TWC) and 2010 (typical of a strong TWC). **b** Annual change in the run size of early-population chum salmon returning to the Sea of Japan coast of Hokkaido in years of a weak TWC (blue bars) and strong TWC (red bars), respectively. Mean SST isothermal diagrams are from the Japan Meteorological Agency (http://www.data.kishou.go.jp/kaiyou/db/hakodate/Monthly/sst_h.html). Modified from Qin and Kaeriyama [22]



one study [29], carbon ($\delta^{13}\text{C}$) and nitrogen stable isotope ($\delta^{15}\text{N}$) analyses of adult chum salmon returning to the Yurappu River showed that wild salmon had significantly higher values than hatchery fishes. The $\delta^{13}\text{C}$ analysis showed that hatchery salmon varied more widely in $\delta^{13}\text{C}$ levels than wild salmon [29]. Chum salmon mainly feed in coastal habitats and tend to consume prey enriched in $\delta^{13}\text{C}$ relative to those found in offshore regions [11, 30–32]. Wild steelhead trout also foraged on more coastally derived sources, suggesting that they did not travel as far offshore as the hatchery fish [33]. Japanese chum salmon distribute widely throughout the Bering Sea [19]. They have been found to feed on diverse prey in the offshore Bering Sea are low in nutrients and to predominantly consume nekton in the coastal waters of the Aleutian Islands [11]. These observations suggest that wild chum salmon have a higher trophic level than hatchery salmon when at sea. Wild salmon will distribute throughout coastal waters and do not migrate as far offshore as hatchery fish in the Bering Sea,

suggesting that wild chum salmon have a higher ecological niche and adaptability than hatchery salmon in the sea environment despite there being no significant difference in the reproductive success of wild and hatchery salmon in the river environment.

Kawasaki [34] pointed out that the greatest external causes of disturbance of the atmosphere–marine system and fishery resource system are global warming and overfishing, thereby raising the question of how these issues should be managed. This researcher continued the discussion by emphasizing that resource variation is a balance between an increase in the amount of available resources and the intensity of fishery. As such, he stated, mankind needs to escape from the concept of the maximum sustainable yield in which ‘fishing’ is an internal force—rather, mankind should treat the ‘environment’ as a noise and an external force in order to sustainably manage fishery resources. In this sense, there is a limit to business-oriented aquatic resources management schemes

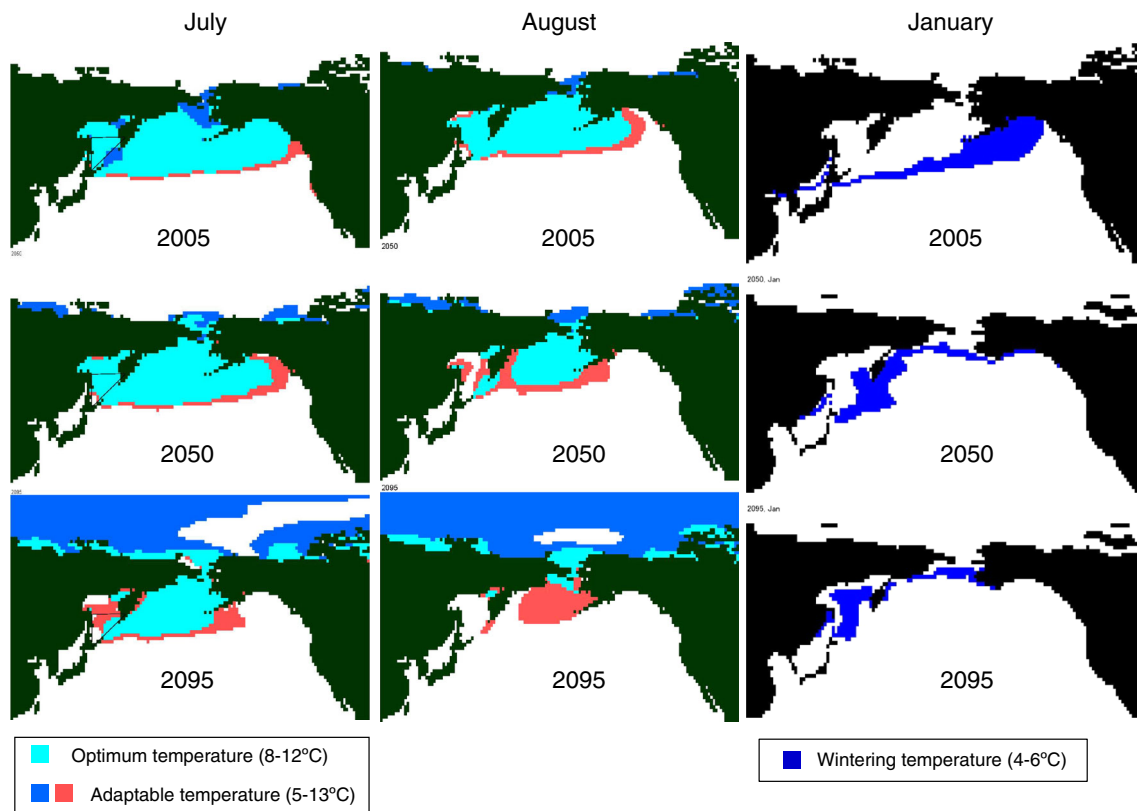


Fig. 8 Prediction of the global warming effect for chum salmon in the North Pacific based on the SRES-A1B scenario. Modified from Kaeriyama et al. [11]

(e.g., the total allowable catch) at a population or species level. At the very least, fisheries resource management should be operated based on the marine ecosystem approach.

The marine ecosystem is a complex and dynamic system with a high degree of uncertainty. It is constantly disturbed by natural factors, such as climate change and the El Niño Southern oscillation, and by anthropogenic factors, such as global warming and overfishing. Artificial control of a marine ecosystem is unrealistic. The structure and functions of the ecosystems depend on biodiversity—specifically, the diversity of species and genes—that has been nurtured by the long history of the Earth and on the process of evolution. The decline in biodiversity observed today means that (some of) the components of a biological interaction are missing, causing a decline in the ecosystem services and simplification of the system. A classic example is the ‘global warming’ phenomenon.

Future challenges

Intrinsically, marine organisms are sustainable resources for human and fishery industries. According to the statistics

generated by the Food and Agriculture Organization of the United Nations [35], approximately 154 million tons of marine organisms are caught globally per year, of which 131 million tons (85 %) are consumed as food by humans. Of these 131 million tons of food, 63.6 million tons (41 %) are produced by aquafarming/aquaculture. The amount of harvested marine organisms that is naturally reproduced has declined since 2000 and is currently estimated to be 90 million tons. Consequently, fishery can no longer be considered as a sustainable resource management, and some marine organisms, such as eels (*Anguilla* spp.) and tuna (*Thunnus* spp.), are now classified as endangered due to overfishing [36, 37]. On the other hand, the amount produced by aquafarming around the world has exponentially increased despite various problems. For example, shrimp farms in Southeast Asia destroy coastal ecosystems, such as mangrove forests, and water pollution caused by large amounts of organic matters and antibiotics used in the farms is becoming a serious problem [38]. Compared to wild fish, high concentration of dioxins and PCBs have been found to accumulate in farmed Atlantic salmon *Salmo salar* [39].

These problems highlight the importance of implementing an ecosystem approach-based risk management

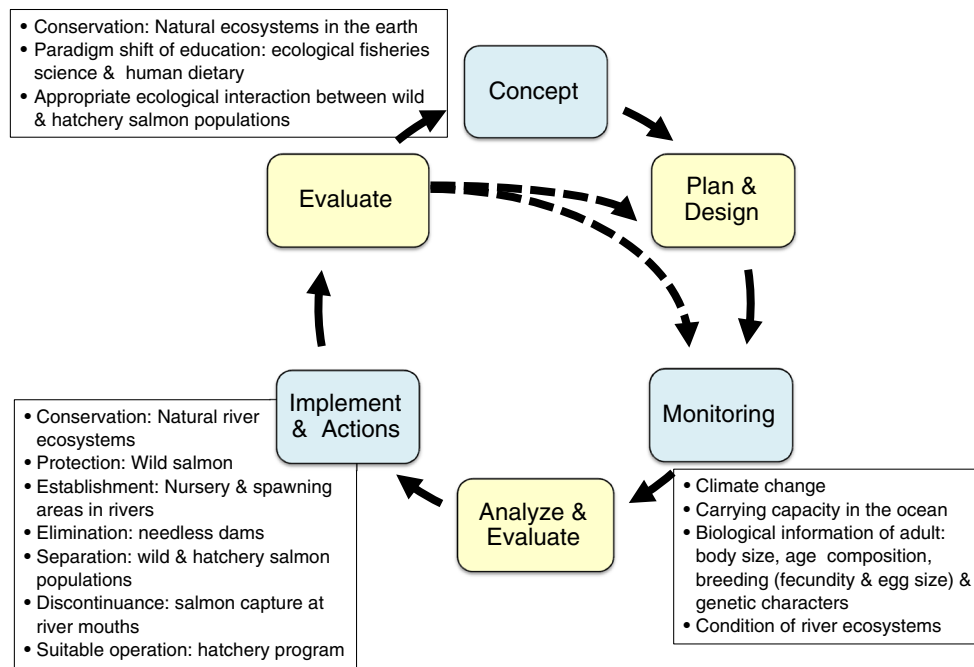


Fig. 9 Conceptual diagram showing the sustainable adaptive management of Pacific salmon. Modified from Kaeriyama et al. [11]

scheme compounded by precautionary principles and adaptive management principles to sustainably conserve the aquatic ecosystems and organisms. Therefore, management should shift to the back-cast method that defines future visions and goals and constantly monitors the current situation. As such, management should reject the forecast method that accepts current conditions without defining a long-term vision and instead merely predicts the future [11].

Ecosystems in Japanese rivers have extensively deviated from their natural state and have become artificial. Conservation of biodiversity in ecosystems is an important and basic task. While the number of artificially hatched and stocked chum salmon has increased, that of wild salmon from natural reproduction has significantly decreased due to the degradation of river ecosystems [40]. Despite the small population size, wild chum salmon are reproducing naturally in about 60 rivers across Hokkaido [41]. As previously noted, these wild salmon have higher trophic levels and genetic-endemism than hatchery fish, as well as an extensive adaptability to environmental change. To address the threat of impending global warming, efforts should focus on rehabilitating and strengthening the resilience of wild fish to generate species that have naturally evolved by natural selection and which are highly adaptable to environmental changes. It is well understood that the restoration of river ecosystems in which fish can live is a basic requirement. Hence, the ecosystem-based approach would be best method for conserving not only the remaining wild salmon populations but also the biodiversity in the

freshwater ecosystem in Japan. This action plan for sustainable conservation of Pacific salmon should be carried on by employing a sustainable adaptive management approach based on feedback control between monitoring (such as climate change, carrying capacity, breeding and genetic characters of salmon, and condition of river ecosystem) and actions (e.g., conservation and rehabilitation of natural riparian ecosystems, protection of wild salmon populations, and zoning between hatchery and wild salmon) under the conditions of a changing climate (Fig. 9) [11].

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