

Regional and Seasonal Differences in Temperature and Salinity Limitations of Pacific Salmon (*Oncorhynchus* spp.)

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Abstract: The thermal limitations of the distribution of Pacific salmon (*Oncorhynchus* spp.) in relation to sea surface temperatures are well known. We reanalyzed data on salmon distribution and hydrographic measurements, and estimated the limitations of salmon distribution using T-S diagrams. There was a clear relationship between salmon distribution and salinity in the offshore waters of the North Pacific. The upper thermal limit was 13.3°C for sockeye (*O. nerka*), 15.6°C for chum (*O. keta*), 16.6°C for pink (*O. gorbuscha*), 15.7°C for coho (*O. kisutch*) and 13.4°C for chinook (*O. tshawytscha*). The lower thermal limit was 3.3°C for sockeye, 2.7°C for chum, 2.8°C for pink and 3.7°C for coho salmon, respectively. The upper halo-limit was 33.46 psu for sockeye, 34.45 psu for chum, 34.37 psu for pink, 34.26 psu for coho and 33.95 psu for chinook salmon, respectively. The range of thermal and halo-limits for the pink salmon distribution was wider than those of the other species. The range of these parameters for sockeye salmon was narrower than those of the other species. In winter and spring, the southern limit of salmon distribution in the western North Pacific was dependent on the halo-limit. In the eastern North Pacific, the southern limit was dependent on the thermal limit. In summer and autumn, the thermal limit for sockeye salmon was similar to the southern limit for sockeye in the North Pacific. The occurrence of the halo-limit results in seasonal and regional differences in sea temperature at the southern limit of salmon distribution.

Keywords: Pacific salmon, thermal limit, halo-limit, distribution

INTRODUCTION

It is known that Pacific salmon (*Oncorhynchus* spp.), sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*) and chinook (*O. tshawytscha*) are widely distributed in the North Pacific Ocean and adjacent waters. The distributions of these Pacific salmon in offshore waters are affected by both physical factors (temperature and salinity, e.g.) and biological factors. Of the five principal salmon species, sockeye prefer the lowest temperatures although there is considerable overlap with the other species (Manzer et al. 1965; Burgner and Meyers 1983). Manzer et al. (1965) showed that the temperature range in northwestern Pacific waters in winter was 1.5–6°C for sockeye. The southern and eastern limit of sockeye distribution in the North Pacific Ocean in winter was between the 6 and 7°C isotherms. In summer, the southern distribution of salmon in the northwestern North Pacific is approximately along the 13.5°C isotherm. Welch et al. (1995) showed that there were thermal boundaries in the distribution of salmon in the eastern North Pacific in spring. On the other hand, there was an obvious relationship between salmon distributions and salinity in offshore waters in the North Pacific (Favorite and

Hanavan 1963; French et al. 1976; Welch et al. 1995; Welch et al. 1999). Thus, we reanalyzed data on salmon distribution and hydrographic measurements simultaneously.

MATERIALS AND METHODS

To assess the salmon distribution, we considered only data sets where fishing and hydrographic measurements were carried out simultaneously. These data were obtained by the Japanese salmon research vessels, *Kaiyo maru*, *Hokko maru*, *Wakatake maru* from 1991 to 2003, the Hokkaido University training ships *Oshoro maru* and *Hokusei maru* from 1978 to 2002, and the Russian research vessel, R/V *TINRO* in 2003. Fishing gear consisted of non-size-selective research gillnets with 10 different mesh sizes, except for the *Kaiyo maru* and the R/V *TINRO* which used surface trawls. The research objectives of the *Kaiyo maru* and the R/V *TINRO* programs were to determine the ocean distribution of salmon as part of the Bering-Aleutian Salmon International Survey (BASIS) program, which was to understand the effect of environmental factors on distributions of Pacific salmon in the Bering Sea. The research objectives of the programs of the *Hokko maru*, *Wakatake maru*, *Oshoro maru* and *Hokusei maru*

were to monitor Japanese salmon. Observations were made mainly from June to September but data from December to February were also included. Although the locations of the observations were different in each season, they covered the entire North Pacific (Fig. 1). Historical data collected from Japanese salmon research vessels in the offshore waters of the North Pacific Ocean from 1972 to 2001 were used to examine the factors limiting salmon distribution.

Water column properties were defined by the vertical profiles of temperature and salinity for each observation. There are major fronts, the Subarctic Front (4°C isotherm at 100-m depth) and the Subarctic Boundary (34.0 psu at 0 m) in the North Pacific (Favorite et al. 1976). These fronts have the axis of the broad eastward flows. The four areas were divided by water properties as follows: the Subarctic Current System which occurs on the north side of the Subarctic Front, the Transition Domain which is the zone between the Subarctic Front and the Subarctic Boundary, the Subtropical Current System which occurs on the south side of the Subarctic Boundary, and the Alaska Current System in the Gulf of Alaska (Fig. 1). The relationship between water properties and salmon distribution was examined using data at 10 m depth in T-S diagrams. The 10-m depth was chosen because daily mixing and precipitation were evident in the upper 10 m of the water column and salmon were distributed in the upper 40 m of the water column (Ogura and Ishida 1995; Walker et al. 2000; Azumaya and Ishida 2005). Monthly mean values for temperature and salinity with a resolution of 1° latitude by 1° longitude, were supplied by the National Oceanographic Data Center (NODC 1994).

The upper and lower limits of temperature and salinity

from locations where salmon were not caught were examined using T-S diagrams. In this study, we define them as the upper thermal limit and the lower thermal limit, and as the upper halo-limit and the lower halo-limit, respectively.

RESULTS

Figure 2 shows the characteristics of water masses at 10 m depth for each station, and whether salmon were caught. Chum salmon were not caught at temperatures above the red line (15.6°C) and below the blue line (2.7°C), and they were not caught at salinities to the right of the purple line (34.45 psu) (Fig. 2a). In this study, we define the temperatures indicated by the red and blue lines as the upper thermal limit and the lower thermal limit, respectively. The salinity indicated by the purple line is defined as the upper halo-limit. Areas that are enclosed by the thermal and halo-limits in the T-S diagram indicate acceptable thermal and halo-limits for chum salmon. This result showed that chum salmon were widely distributed from the Subarctic Current System to the Subtropical Current System. Relatively high densities of chum salmon were seen at salinities < 33.25 psu. Relatively high densities of sockeye were seen at < 33.25 psu, similar to chum salmon (Fig. 2b). However, sockeye salmon were not caught at salinities > 33.46 psu. The halo-limit, 33.46 psu for sockeye salmon, was much lower than that for chum salmon. Sockeye salmon were distributed in the Subarctic Current System and the Alaska Current System. In other words, they were not distributed in the southern part of the Transition Domain and the Subtropical Current System.

Using a similar method, thermal and halo-limits for

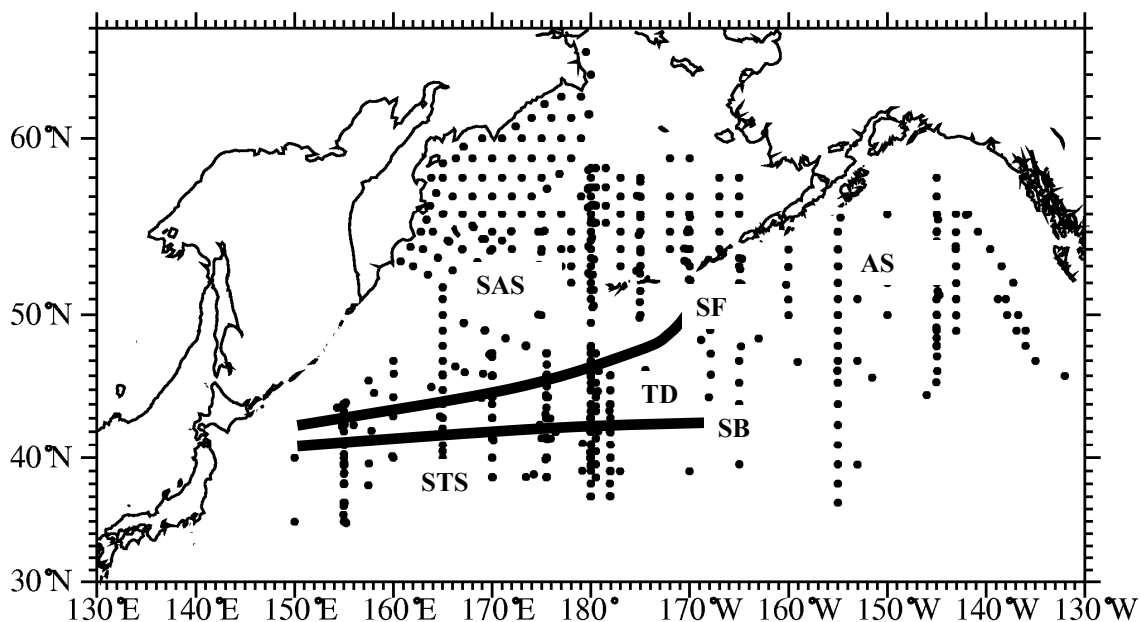


Fig. 1. Map of locations of fishing and hydrographic measurements and schematic view of four current systems: Subarctic Current System (SAS), Transition Domain (TD), Subtropical Current System (STS), and Alaska Current System (AS), and two fronts: Subarctic Front (SF) and Subarctic Boundary (SB).

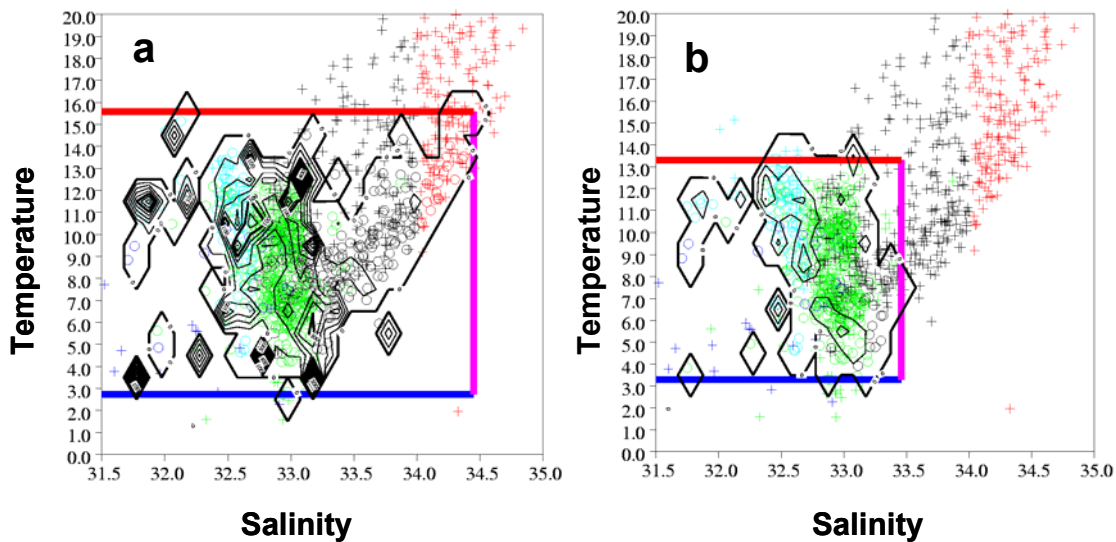


Fig. 2. Results of fishing operations as T-S diagrams with the upper thermal limit (red line), the lower thermal-limit (blue line) and the upper halo-limit (purple line) for chum salmon (a) and sockeye salmon (b). Crosses indicate no catch, and circles indicate catch. Green is the Subarctic Current System, black indicates the Transition Domain, red indicates the Subtropical Current System, and blue indicates the Alaska Current System. Contour indicates CPUE of salmon (number of fish per 30-tan research gillnets or 1-h trawl) at intervals (thin black line) of 20 fish.

pink, coho and chinook salmon are shown in Fig. 3. Vertical profiles for temperature and salinity from depths of 10 to 1000 m at each station are also shown in the T-S diagram. For all species, a lower halo-limit was not detected, and the lower thermal limit for chinook salmon was < 1.6°C. The thermal and halo-limits by species are listed in Table 1. The range of the thermal and halo-limits for pink salmon was wider than that for other species. The range for sockeye salmon was narrower than that of other species. Pink salmon were widely distributed from the Subarctic Current System to the Subtropical Current System, similar to chum salmon. Lower thermal limits for coho salmon were higher than those for other species. The upper thermal limit for coho salmon was similar to those for chum and pink salmon. The upper halo-limit for coho salmon was lower than those for chum and pink salmon. Chinook salmon were distributed from the Subarctic Current System to the Transition Domain. The upper thermal limit for chinook salmon was similar to that for sockeye salmon.

We compared the thermal and halo-limits for sockeye salmon using historical catch data for spring and summer (Fig. 4). We found that in spring, sockeye salmon were not distributed south of the halo-limit (thick line), and that in summer they were not distributed south of the thermal limit (thin line). These results indicate that the thermal and halo-limits estimated in this study are appropriate as the distributional limits for the seasonal and latitudinal distribution of salmon.

Figure 5 shows the horizontal distribution of the acceptable thermal and halo-habitat and the Subarctic Front and the Subarctic Boundary in the North Pacific in winter and summer for sockeye and chum salmon, respectively. The relationship between Pacific salmon distribution and three

water column properties are listed in Table 2. In winter, the habitat with acceptable sea conditions for sockeye salmon in the western North Pacific was much narrower than that in the eastern North Pacific (Fig. 5a). The southern limit of sockeye salmon distribution in the western North Pacific corre-

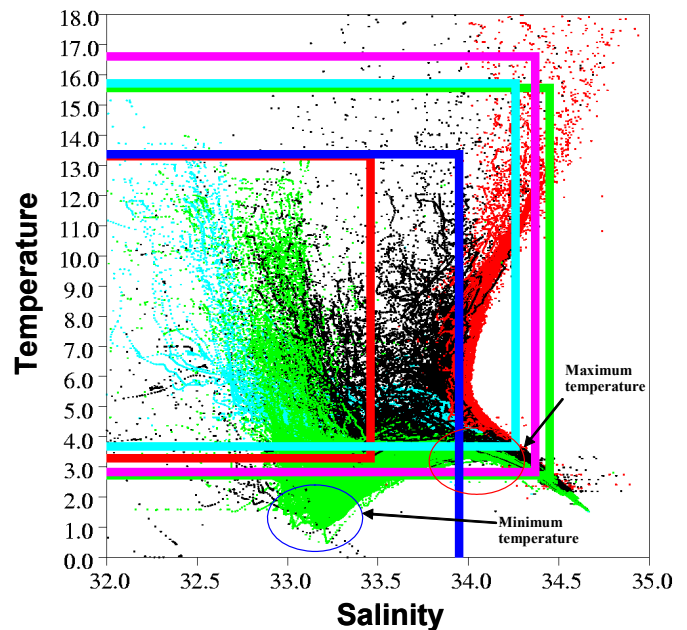


Fig. 3. The thermal and halo-limits for sockeye (red line), chum (green line), pink (purple line), coho (pale blue line), and chinook salmon (darker blue line) and the vertical profiles from 10 m to 1000 m at the observation points. Green dots indicate the Subarctic Current System, black dots indicate the Transition Domain, red dots indicate the Subtropical Current System, and pale blue dots indicate the Alaska Current System. Blue and red circles indicate the minimum and the maximum temperature, respectively.

Table 1. Thermal and halo-limits of salmon distribution.

Species	Upper thermal limit (°C)	Lower thermal limit (°C)	Upper halo-limit (PSU)
Sockeye	13.3	3.3	33.46
Chum	15.6	2.7	34.45
Pink	16.6	2.8	34.37
Coho	15.7	3.7	34.26
Chinook	13.4	-	33.95

Table 2. Relationship between the fronts in the North Pacific and salmon distribution. + is distribution, - is no distribution, and = is the boundary of the southern or northern distribution.

Species	Subarctic Front		Transition Domain		Subarctic Boundary	
	Winter	Summer	Winter	Summer	Winter	Summer
Sockeye	=	=	-	-	-	-
Chum	+	+	+	=	+	-
Pink	+	+	+	=	+	-
Coho	=	+	+	=	=	-
Chinook	+	=	+	-	=	-

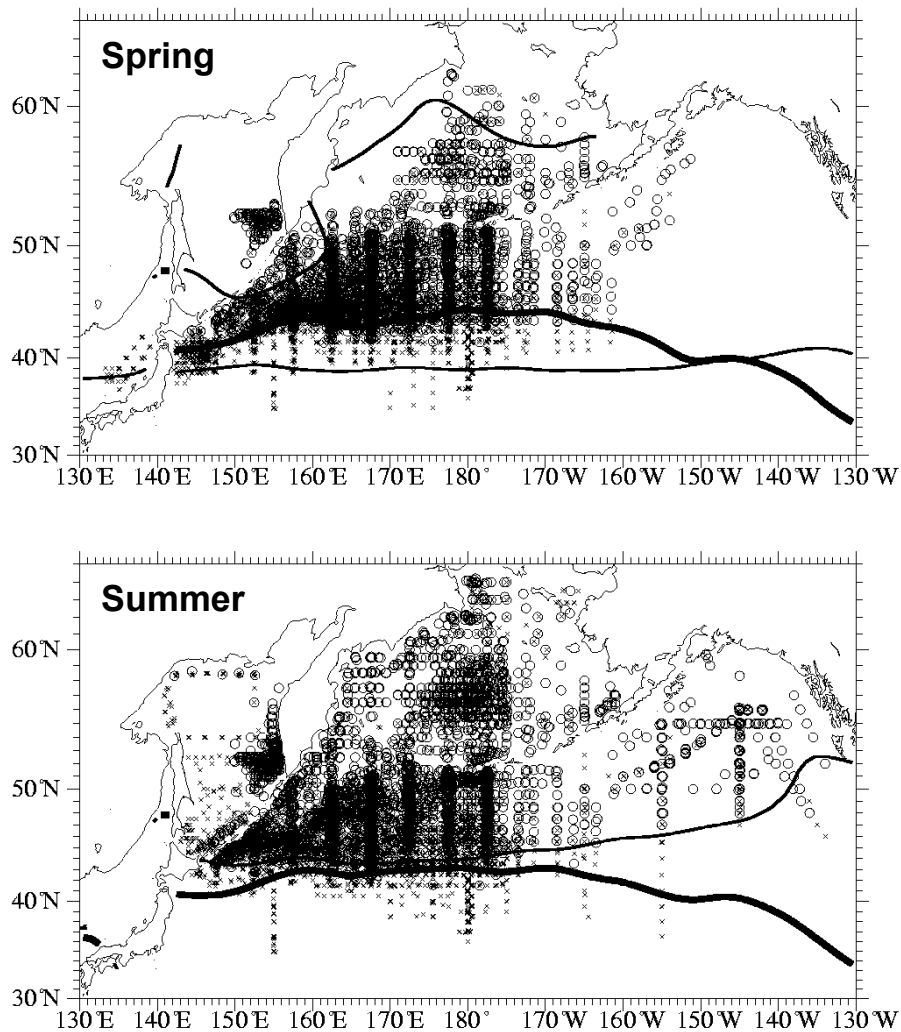


Fig. 4. Comparison between the thermal (thin line) and halo-limit (thick line) and the historical observations for sockeye salmon in spring and summer. X's indicate no catch and circles indicate catch.

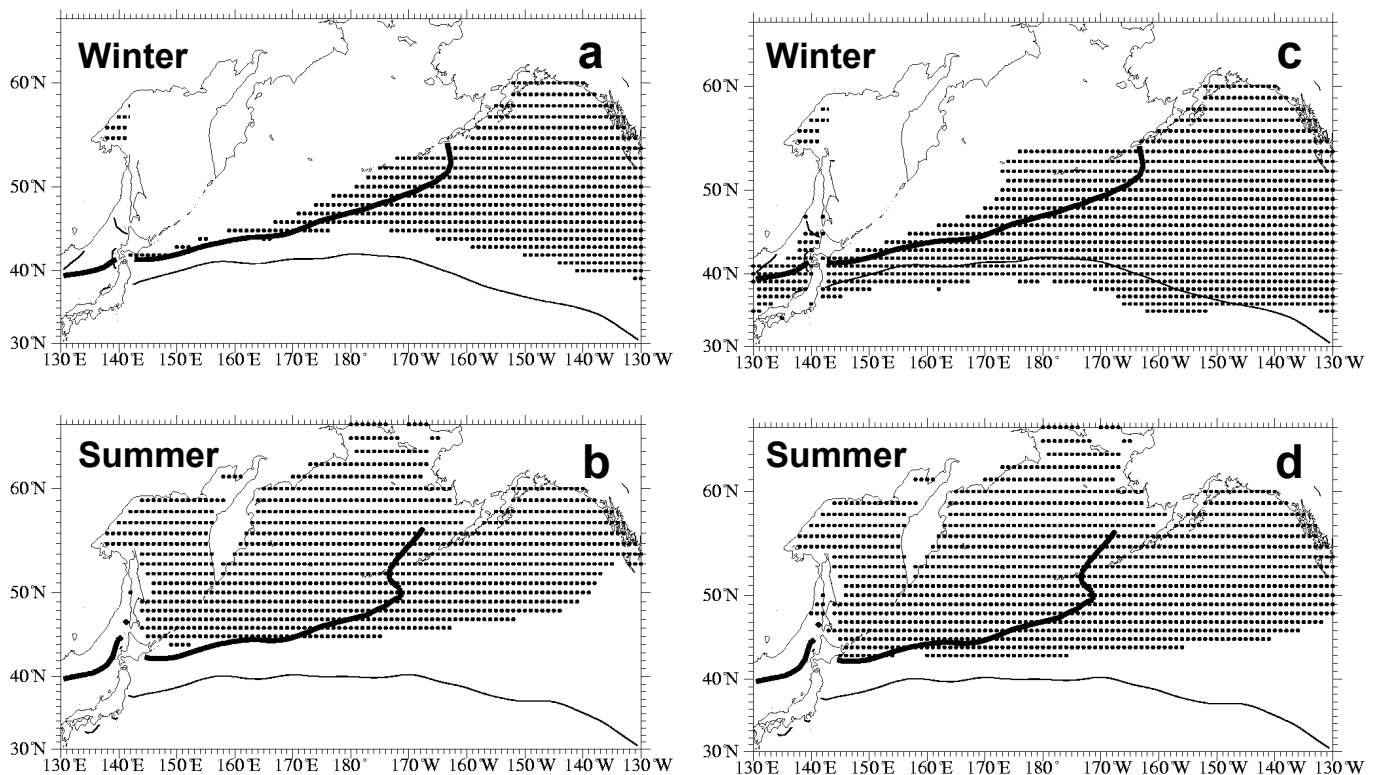


Fig. 5. Horizontal distributions of the thermal and halo-habitat (dots), the Subarctic Front (thick line) and the Subarctic Boundary (thin line). (a) winter, (b) summer for sockeye salmon; and (c) winter, (d) summer for chum salmon.

sponded to the Subarctic Front in both winter and summer (Fig. 5a,b). In summer, the southern limit of sockeye salmon distribution was located between 45°N to 50°N in the North Pacific and at 54°N near the coast of Alaska (Fig. 5b). In winter, the southern limit of chum and pink salmon distribution extended over the Subarctic Boundary in the North Pacific (Fig. 5c, Fig. 6a). The northern limit was located north of the Aleutian Islands. The southern limit of their distributions was located in the Transition Domain in summer (Fig. 5d, Fig. 6b). The southern limit of coho salmon distribution was located at the Subarctic Boundary, and the northern limit was located at the Subarctic Front in winter (Fig. 6c). Thus, the acceptable thermal and halo-habitats for coho salmon correspond to the Transition Domain. The southern limit of coho salmon distribution was located in the Transition Domain in summer, similar to that of chum and pink salmon (Fig. 6d). The southern limit of chinook salmon distribution in winter was located at the Subarctic Boundary. It was located at the Subarctic Front in summer.

Figure 7 shows the seasonal changes in the habitat of sockeye salmon. In winter and spring in the western North Pacific, the southern limit of distribution was dependent on the halo-limit. In the eastern North Pacific, the southern limit was dependent on the thermal limit during all seasons. By contrast, in summer, the thermal limit is similar to the southern limit of distribution in the North Pacific. The results for

sockeye salmon were similar to those for chum, pink, and coho salmon. Thus, the halo-limit during winter and spring was more important in determining the southern limit of Pacific salmon distribution rather than the thermal limit in the western North Pacific. If we examine the thermal limit of salmon distribution in the western North Pacific using only water temperature and fishing data collected in winter and spring, the calculated thermal limit will be the apparent limitation for salmon.

Areas of acceptable thermal and halo-habitat of salmon in winter and summer are listed in Table 3. The range of areas of thermal and halo-habitat for chum salmon in winter was wider than those for the other species. The range of areas of thermal and halo-habitat for sockeye salmon was the narrowest compared to other species in both winter and summer. In summer, areas of thermal and halo-habitat for pink salmon were wider than those for other species. The areas of thermal and halo-habitat for sockeye and coho salmon increase in summer. On the other hand, the areas of thermal and halo-habitat for chum and pink salmon decrease in summer because the southern limit of chum and pink salmon distribution shifts northward by about 10°N in the eastern North Pacific.

We examined the seasonal and regional changes in temperature at the southern limit of sockeye salmon distribution at 160°E (squares), 180° (triangles) and 150°W (circles)

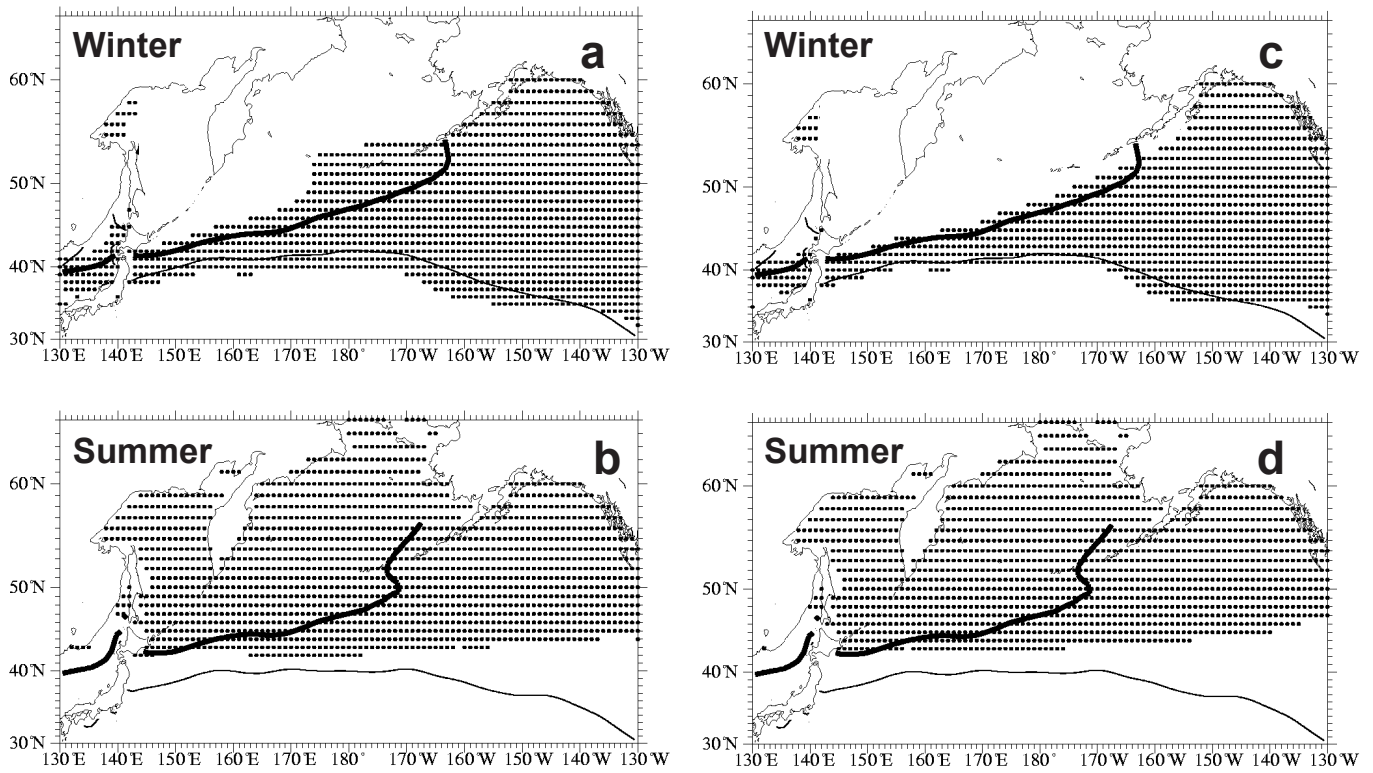


Fig. 6. Same plot as in Fig. 5 but in (a) winter, (b) summer for pink salmon; and (c) winter, (d) summer for coho salmon.

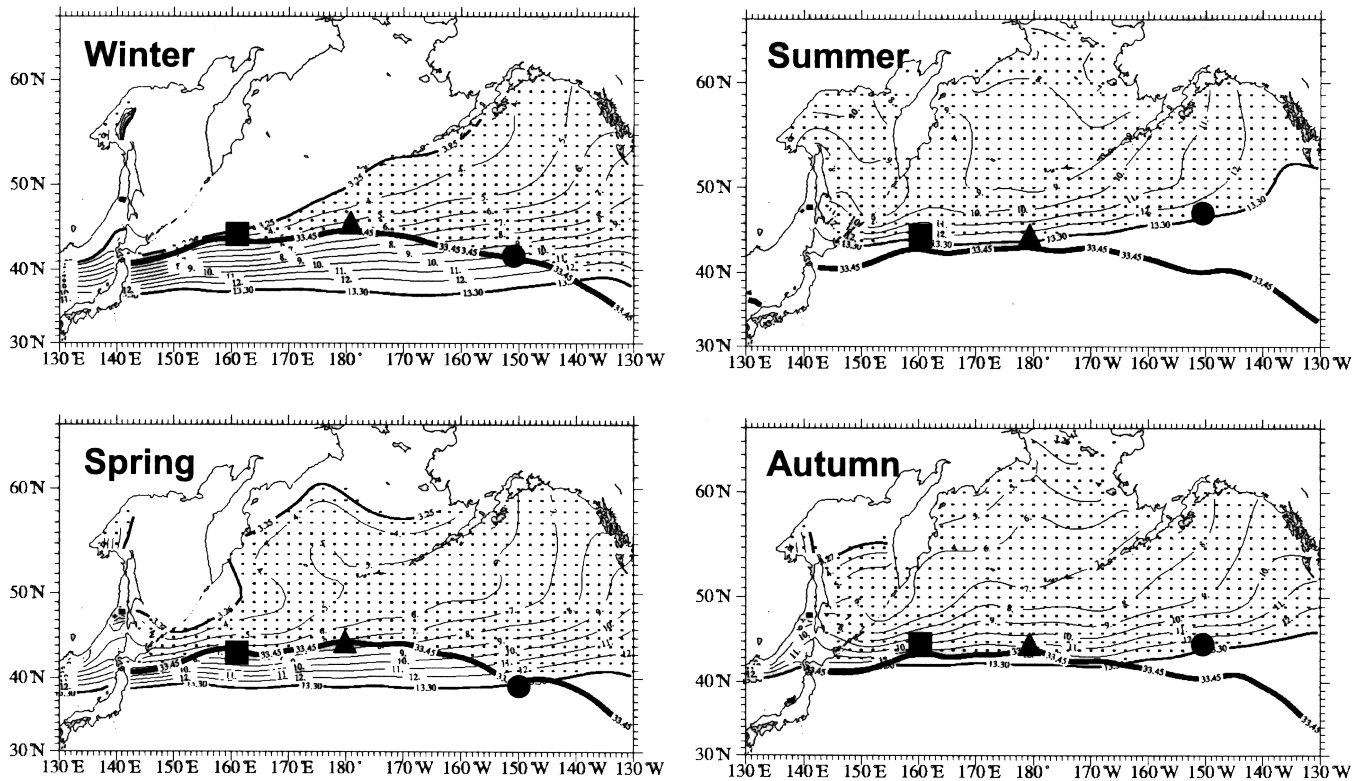


Fig. 7. Seasonal changes in the thermal (thin line) and halo-limits (thick line) for sockeye salmon. Dots indicate the thermal and halo-habitat. Solid squares (160°E), triangles (180°) and circles (150°W) indicate the locations where the seasonal changes in temperature at the southern limit were investigated. Contour lines indicate sea surface temperature.

Table 3. Areas of acceptable thermal and halo-habitat of salmon in winter and summer ($\times 10^7$ km²). * In the case of climate warming.

Species	Winter		Summer	
Sockeye salmon	0.61	*0.83	0.87	*0.70
Chum salmon	1.24	*1.41	1.06	*0.95
Pink salmon	1.21	*1.47	1.14	*1.03
Coho salmon	0.99	*1.25	1.07	*0.96
Chinook salmon	-	-	-	-

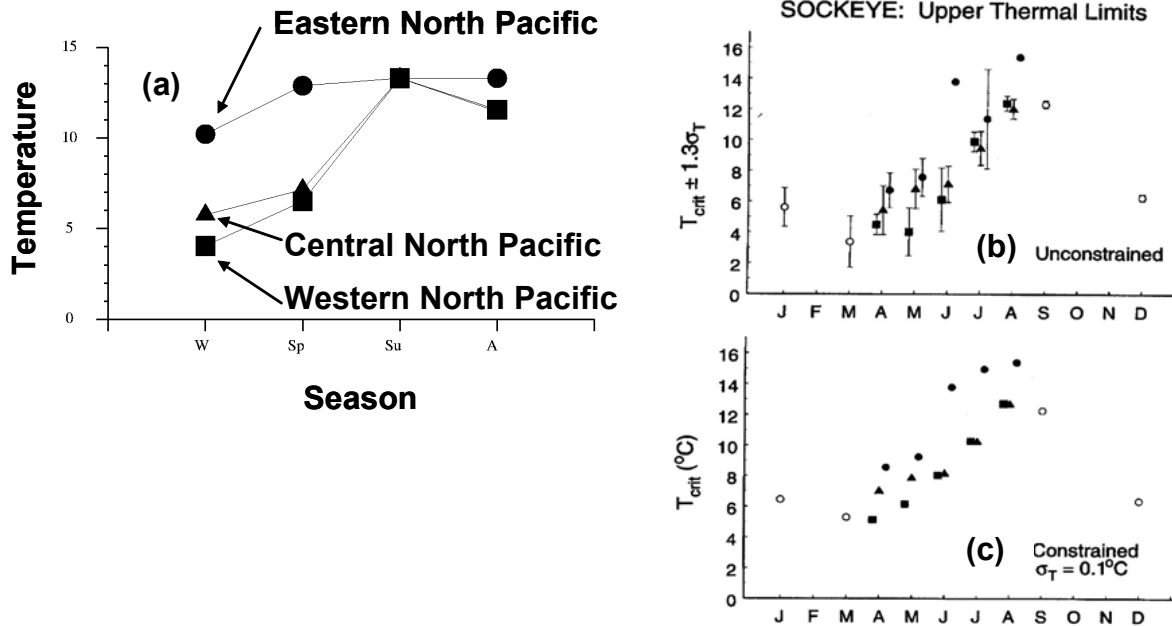


Fig. 8. Seasonal changes in temperature at the southern limit of sockeye salmon in the North Pacific. Estimated critical temperatures defining the southern limit of sockeye distribution, (a) This study and estimated critical temperatures defining the southern limit of sockeye distribution, T_{crit} , in different months; (b) unconstrained, and (c) constrained (from Welch et al. 1999).

(see Fig. 7). The temperatures at the southern limit in the eastern North Pacific were higher than those in the western and the central North Pacific (Fig. 8a). The temperatures at the southern limit in winter were lower than those in summer. It is shown that the temperatures at the southern limit of salmon distribution varies seasonally and regionally.

Because the distribution of salmon is decided by not only horizontal limitations but also vertical limitations in sea conditions, the horizontal distributions of the depth (m) of acceptable thermal and halo-habitat for sockeye salmon in the North Pacific during the summer were examined. The depths of the thermal and halo-habitat for sockeye salmon in the Subarctic Current System were shallower than those in the central and eastern North Pacific (Fig. 9). By contrast, the depths of habitat were < 40 m in the eastern Bering Sea shelf and the Okhotsk Sea. The vertical distribution was limited by the upper halo-limit in the central and eastern North Pacific and by lower thermal limits in the western North Pacific and the Bering Sea.

DISCUSSION

Our study considered catch, while Welch et al. (1995) used CPUE to assess thermal limits. The thermal limits for salmon defined in this study were higher than those found by Welch et al. (1995). However, the trend in the upper thermal limits by species was similar to the temperatures at the southern limit of salmon distribution found by Welch et al. (1995): 10.4°C for chum and pink salmon, 9.4°C for coho salmon, and 8.9°C for sockeye salmon. In this study, we found that not only the thermal barriers but also the halo-barriers form an effective limit to salmon distribution in the North Pacific. If salmon remain in waters within the range of thermal and halo-limits, salmon will be distributed according to their preferred temperature or preferred food habitat. Welch et al. (1995) suggested that when food is limited, salmon move to an environmental temperature that will yield maximum growth. As a result, the temperature at the southern limit of salmon varies seasonally and regionally as shown in Fig. 8b, c (Welch et al. 1999). Our results as shown in Fig. 8a are similar to those of Welch et al. (1999). However, the temperature at the southern limit

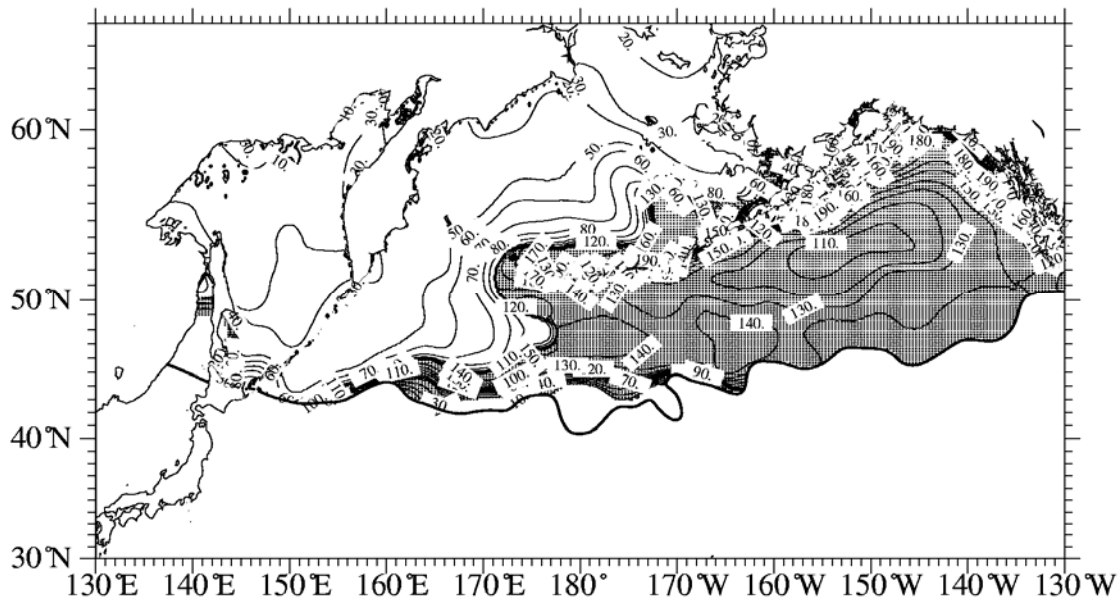


Fig. 9. Horizontal distributions of the depth (m) of the acceptable thermal and halo-habitat for sockeye salmon in the North Pacific during the summer. Thick lines indicate the upper thermal limit; thin contour lines indicate depth. Shaded areas indicate that the vertical distribution of sockeye salmon was limited by the upper halo-limit. The white area indicates that the vertical distribution was limited by the lower thermal limit.

of salmon distribution found by Welch et al. (1999) does not correspond with the detected upper thermal limit in this study. Thus, we note that the halo-limit results in seasonal and regional changes in temperature at the southern limit of salmon distribution. However, it is not clear how salinity affects salmon distribution. It has been suggested that salinity directly influences the metabolism of salmon through their osmotic pressure, and that the limit of food habitat for salmon may be seen as the upper halo-limit. The location of salinity fronts in the North Pacific often corresponds to the upper halo-limit. Studies on the relationships between salinity and metabolism and between salinity and food habitat of salmon will be needed in the future.

The limit of vertical salmon distribution is dependent on the lower thermal limit rather than the upper halo-limit in the Subarctic Current System, the western North Pacific and the Bering Sea (Fig. 9), because vertical changes in salinity are smaller than vertical changes in temperature over the range of thermal and halo-habitats. The characteristic water mass in the Subarctic Current System has minimum temperatures (blue circle in Fig. 3) at a depth of about 150 m and maximum temperatures (red circle in Fig. 3) at a depth of about 250 m. The minimum temperature is the result of cooling of the mixed layer in winter. The maximum temperature is about 1°C higher than the minimum temperature. Because the minimum temperature is < 2°C, and the salinity is about 33.0 to 33.25 psu, the minimum temperature is lower than the lower thermal limit for sockeye, chum, pink and coho salmon (Fig. 3). This suggests that sockeye, pink and coho salmon do not remain in the layer with the minimum temperature for

long periods of time or dive into this layer. Although chum salmon dive into minimum temperature water, they have a high frequency of movement between the sea surface and the minimum temperature layer so that their body temperature does not decrease significantly (Azumaya and Ishida, 2005). The coldest layer limits the vertical distribution of sockeye, chum, pink and coho salmon, such that the depths of habitat in the Subarctic Current System are shallower than those in the central and eastern North Pacific (Fig. 9). By contrast, because the depths of thermal and halo-habitat are < 40 m in the eastern Bering Sea shelf and the Okhotsk Sea, these areas are unsuitable as salmon habitat. The lower thermal limit for chinook salmon was < 1.6°C, which was lower than the minimum temperatures in the Bering Sea and the North Pacific. Thus, there is a possibility that chinook salmon remain in the mixed layer at relatively low temperatures in winter in the Bering Sea and the North Pacific. Ishida et al. (1999) showed that chinook salmon are distributed in the Bering Sea in February.

We speculated about the influence of climate warming on the salmon distribution using thermal and halo-limit. Table 3 shows the area of the acceptable habitat for salmon when the mean water temperature increases by 1.5°C and salinity decreases by 0.2 psu in the North Pacific as a result of homogeneous climate warming. These theoretical climate conditions assume that atmospheric CO₂ concentrations increase by 1% per year over a period of 70 years. In summer, the upper thermal limit shifts northward. Thus, the area of salmon distribution decreases by 13% compared to current values. In particular, the decrease in area in the east-

ern North Pacific is quite remarkable. However, in winter, the lower thermal limit shifts northward, so that the area of salmon distribution increases by 19% compared to today.

In conclusion, we reanalyzed the relationship between salmon distribution and water temperature and salinity in the North Pacific Ocean. The thermal limit and the upper halo-limit of salmon distributions were found. The range of the thermal and halo-limits for pink salmon was wider than that for other species. The range for sockeye salmon was narrower than that for other species. Because the upper halo-limit for sockeye salmon was the lowest of all species, sockeye salmon appeared to be distributed in relatively low temperature water. The occurrence of the halo-limit results in seasonal and regional changes in temperature at the southern limit of salmon distribution.

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