Density Interactions between Pink Salmon (*Oncorhynchus gorbuscha*) and Chum Salmon(*O. keta*) and their Possible Effects on Distribution and Growth in the North Pacific Ocean and Bering Sea

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Key words: Pink salmon, chum salmon, interaction, density, distribution, growth, Pacific Ocean

Abstract: The long-term mean spatial and temporal distributions of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in the North Pacific Ocean were investigated using data collected on board Japanese salmon research vessels from 1972 to 1998. The distribution patterns of chum salmon differed between odd- and even-number years, and were more concentrated to the west in even-number years of low pink salmon abundance. In the Bering Sea, the density of pink salmon was higher in odd-number years than in even-number years, and density of chum salmon showed an opposite trend (higher in even than in odd-number years). Also chum salmon distribution shifted southeastward in odd-number years. These results suggest that there is a possible interaction between pink and chum salmon. The mean fork length of maturing pink salmon decreased from 1972 to 1998. Decreasing trends in fork length of age 3–5 chum salmon were also found during the same period. Significant negative relationships between density and mean growth of age 2–4 chum salmon were observed in the Bering Sea, although there was no relationship between density of pink salmon and mean growth of chum salmon directly. These results suggest that the growth of age 2–4 chum salmon is affected by intra-species in the Bering Sea and the abundance of pink salmon influenced the growth of chum salmon indirectly.

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant salmon species, followed by chum salmon (*O. keta*) in the North Pacific Ocean. For two decades, the abundance of Pacific salmon especially pink and chum salmon has been high and hatchery production has increased, while the body size of both fish has decreased accordingly. Recent research indicated density-dependent effects on growth for some salmonid stocks in the marine environment (Peterman 1978; Rogers 1980; Beacham and Starr 1982; McGie 1984; Ishida et al. 1993). For chum and pink salmon direct and indirect evidence indicated that density-dependent effects were observed in the early marine environment (Birman 1960). Tadokoro et al. (1996) examined the abundance and stomach contents of salmonids in later life and the biomass of prey organisms, and suggested that there might be a limitation in the available prey resource for production of salmonids. This implied competitive interaction between pink and chum salmon during their marine life stages. Ishida et al. (1993) concluded that density-dependent factors explained 35% of the decrease in average size of chum salmon in the central North Pacific. Walker et al. (1998) also showed that scale-edge growth of chum salmon was negatively correlated with Asian pink and chum salmon abundance, and pink salmon abundance might influence the third-year growth of chum salmon in the North Pacific Ocean. Smoker (1984) examined the effect of interaction between pink and chum on stock dynamics using a model which contrasted genetic and nongenetic mechanisms of determination of maturation age of chum salmon. From his model results, the genetic mechanism (high heritability of maturation age) lead to results similar to observed stock dynamics.

However, it is not clear how chum salmon are affected by the pink salmon abundance, and whether the growth of chum salmon is a result of intra- or inter-species interaction in offshore waters of the North Pacific Ocean. In this study, we examine the monthly long-term mean distribution, interannual changes in abundance of pink and chum salmon, and a possibility of inter-species interaction between pink and chum salmon.

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MATERIAL AND METHODS

The data used were collected on board Japanese salmon research vessels in offshore waters of the North Pacific Ocean from 1972 to 1998. The total number of operations during the 27 year period from 1972 to 1998 in the North Pacific Ocean was 9,562 (Fig. 1). However, the number of operations in the eastern North Pacific Ocean was smaller than that in the western North Pacific Ocean. Salmon research vessels have used research-type gillnets and commercial-type gillnets. We analyzed the data obtained by research-type gillnets because this gear is non-selective (containing 10 different mesh sizes ranging from 48 to 157 mm; Takagi 1975). To describe the distribution of pink and chum salmon, data from the area between 30°N–65°N, 130°E–130°W were stratified by month, by 2 degree latitude by 5 degree longitude areas (2° × 5° grid), and by species. To describe monthly changes in distribution of pink and chum salmon, indexes of the long-term mean density of each species over the 2° × 5° grid were calculated for each month of the year. The number of fish caught and the number of tans of gillnets fished were summed monthly and the density index (catch-per-unit effort, CPUE) in each grid was calculated as follows:

CPUE= total catch in number/total effort (in units of 30 tans of gillnet).

The proportions of maturing and immature fish in each grid were calculated based on Takagi's (1961) maturity definition, which is based on gonad weight.

RESULTS

Horizontal Distribution of Pink and Chum Salmon

Pink salmon were distributed in a wide zonal band along the 42°N line from 142°E to 165°W in April and May, and were the most abundant around 155°E (Fig. 2). However, pink salmon were not distributed in the area north of 50°N. In June and July, pink salmon extended their distribution to the area south of 62°N in the Bering Sea. The density of pink salmon between 150°E and 165°E and between 42°N and 55°N exceeded 100 fish per 30 tans. The area of relatively high density shifted westward from April to July. In August and September, pink salmon were distributed only in the coastal area, and they were not caught in offshore waters in October. The monthly changes in distribution of pink salmon densities appear to indicate their return migration to the spawning area.

In April and May, chum salmon were widely distributed in the area east of 145°E and north of 40°N in the western North Pacific, but the center of distribution for maturing fish was farther north than that of immature fish (Fig. 3). From June to July, the distribution of maturing chum salmon shifted progressively northwestward to the coast of Kamchatka, and northeastward to the Alaska coast. Immature chum salmon were widely distributed from 40°N to 60°N and they were most abundant in the Bering Sea. In August and September, maturing fish were rarely caught in offshore waters. In October, when fishing

Fig. 1. The distribution of operations (1972 to 1998) used in calculating area averages for this study. The western North Pacific (160°E–170°E, 38°N–52°N, 170°E–180°, 38°N–48°N), the Bering Sea (175°E–175°W, 55°N–59°N) and the eastern North Pacific (140°W–150°W, 48°N–58°N).

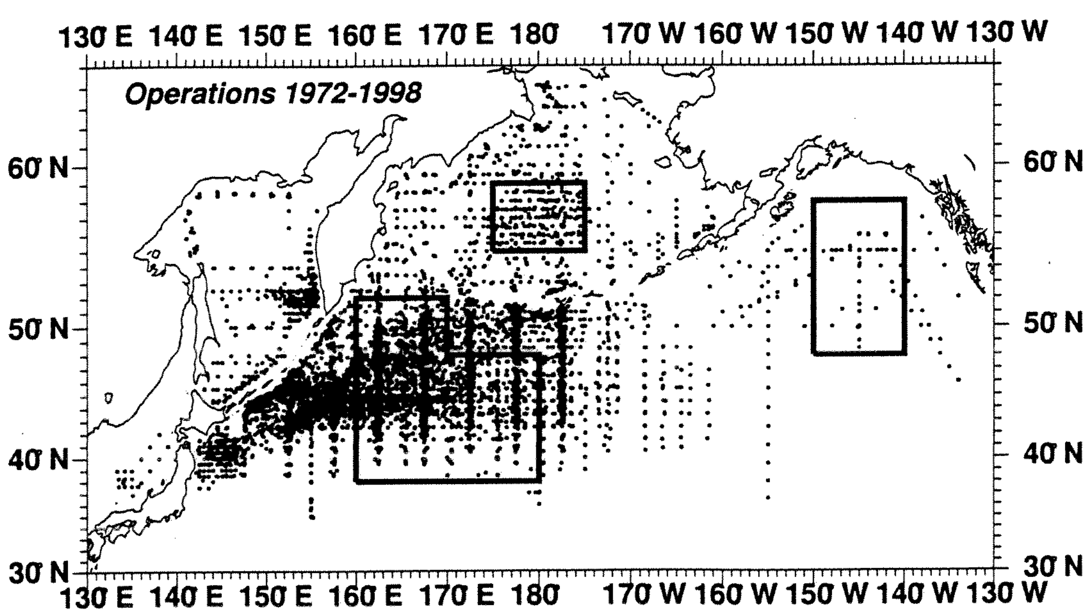


Fig. 2. Densities of pink salmon in the North Pacific Ocean in March to October averaged over 27 years, 1972–1998.

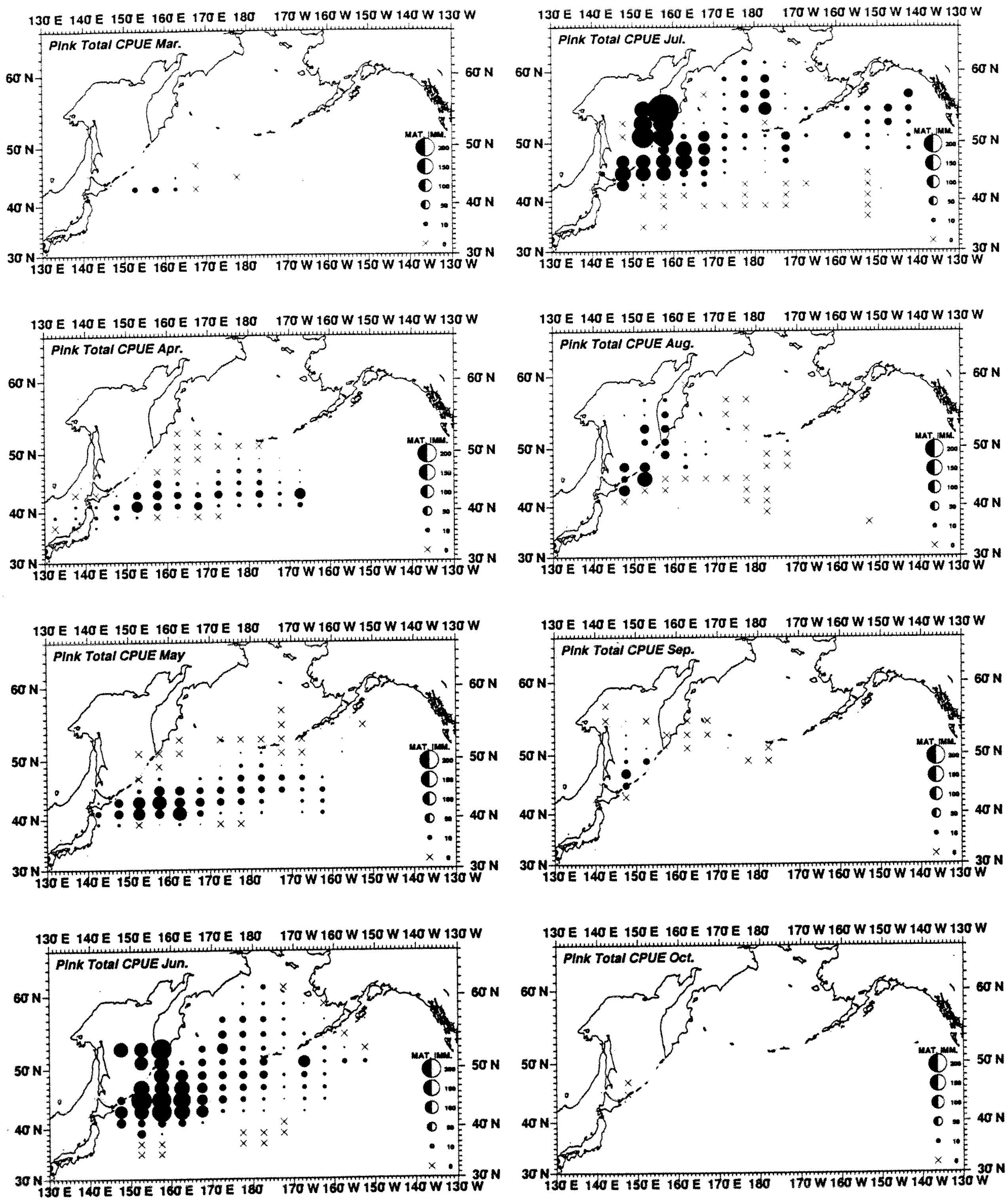
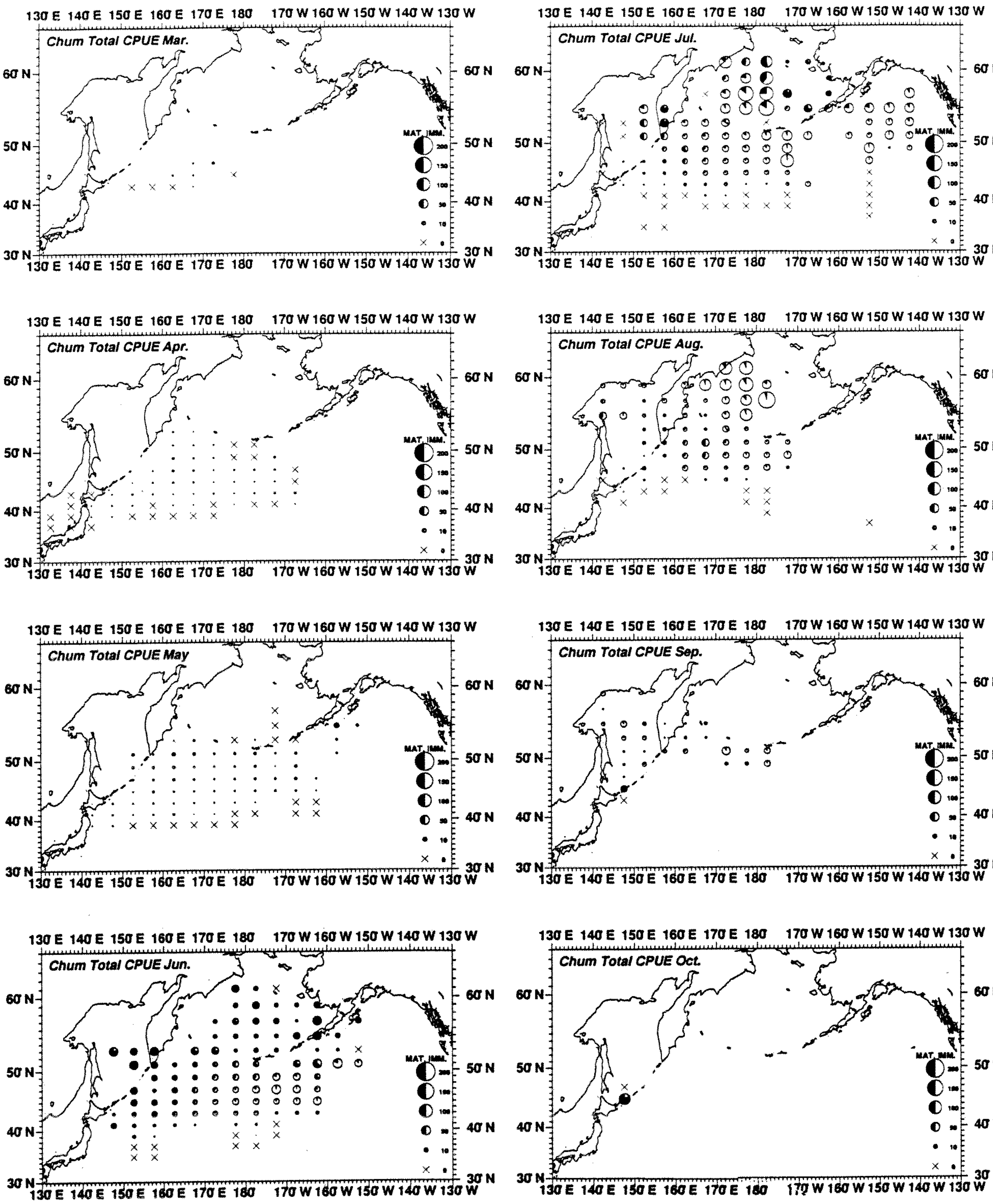


Fig. 3. Densities of chum salmon in the North Pacific Ocean in March to October averaged over 27 years, 1972–1998.



operations were limited to near the coast, the proportion of maturing fish was high. The proportion of immature fish in offshore waters increased as the season progressed and immature chum migrated from south to north in offshore waters. These results show that the distributions of pink salmon and chum salmon have overlapped in offshore waters, especially in the western North Pacific and in the Bering Sea from April to July.

Pink salmon were more widely distributed in odd-number years than in even-number years (Fig. 4). Moreover, the density of pink salmon was also higher in odd-number years than in even-number years except in the Gulf of Alaska. Particularly in the Bering Sea, odd-number year density exceeded 50 fish per 30 tans, while they were less than 10 fish per 30 tans in even-number years. Thus, a difference in the distribution and density of pink salmon between odd and even-number years is evident in offshore waters of the North Pacific Ocean.

No difference in chum salmon density between odd and even-number years was observed in the western North Pacific (Fig. 5). However, the density of chum salmon in the Bering Sea was lower in odd-number years and higher in even-number years, and was especially clear. On the contrary, in the eastern North Pacific, the density was higher in odd-number years, and lower in even-number years, though the difference was less distinct.

Pink salmon densities in odd-number years relative to even-number years were highest in areas north of 45°N in the western North Pacific and in the Bering Sea (Fig. 6a). These areas correspond to regions where chum salmon densities were the lowest in odd-number years relative to even-number years (Fig. 6b). Chum salmon densities were also higher in odd-number relative to even-number years between 180° to 170°W around 46°N, and in the Gulf of Alaska. From these results, it appears that the change in distributions of chum salmon was associated with the odd/even year fluctuations of pink salmon density.

Interannual Changes in Relative Abundance of Pink and Chum Salmon

To examine interannual variations in relative abundance (density index) of pink and chum salmon, three major survey areas were defined as follows: the western North Pacific (160°E–170°E, 38°N–52°N, 170°E–180°, 38°N–48°N), the Bering Sea (175°E–175°W, 55°N–59°N) and the eastern North Pacific (140°W–150°W, 48°N–58°N), where Japanese salmon research vessels conducted gillnet fishing operations (Fig. 1). The densities of salmon in each area in July were averaged for each year, and a time series of densities of salmon in each area was estimated.

In the western North Pacific, the density of pink salmon in odd-year lines prior to 1985 was higher than that in even-year lines (Fig. 7a). After 1985, the interannual changes in density of pink salmon did not show the odd/even year fluctuation and ranged from

Fig. 4. The distribution of pink salmon in odd- (a) and even- (b) numbered years in July.

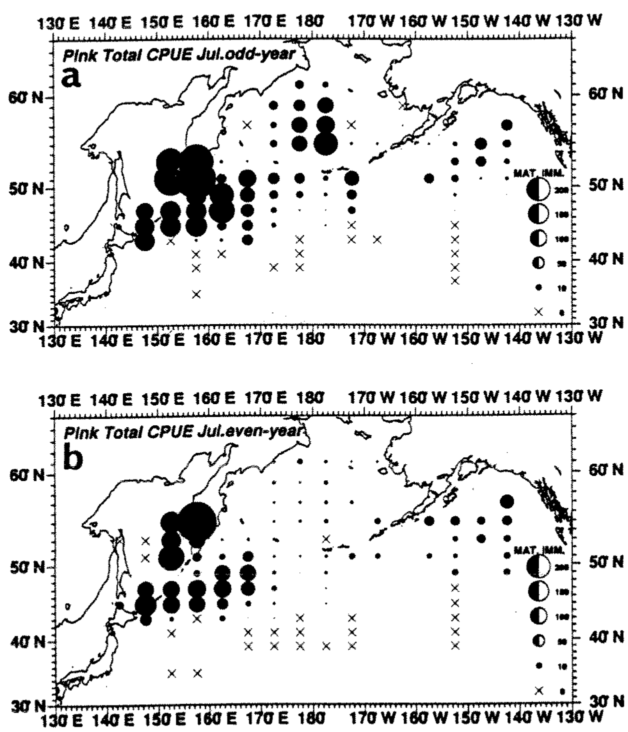


Fig. 5. The distribution of chum salmon in odd- (a) and even- (b) numbered years in July.

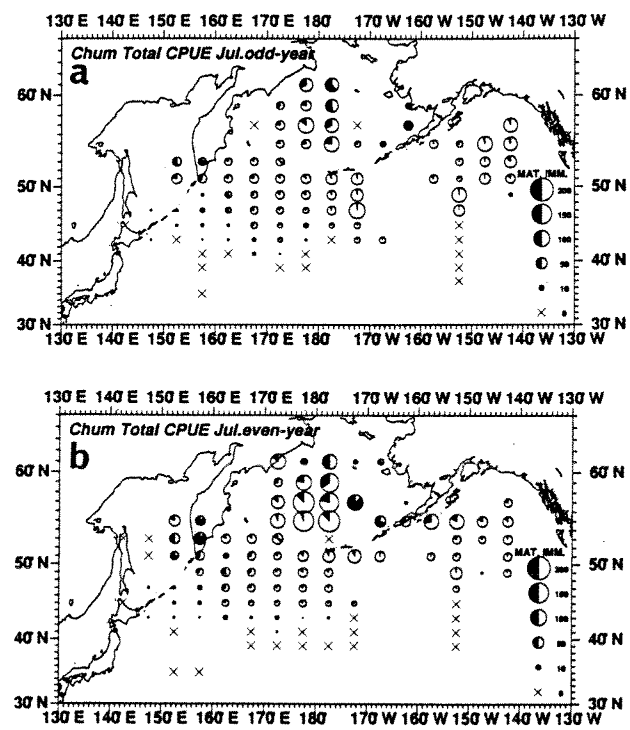
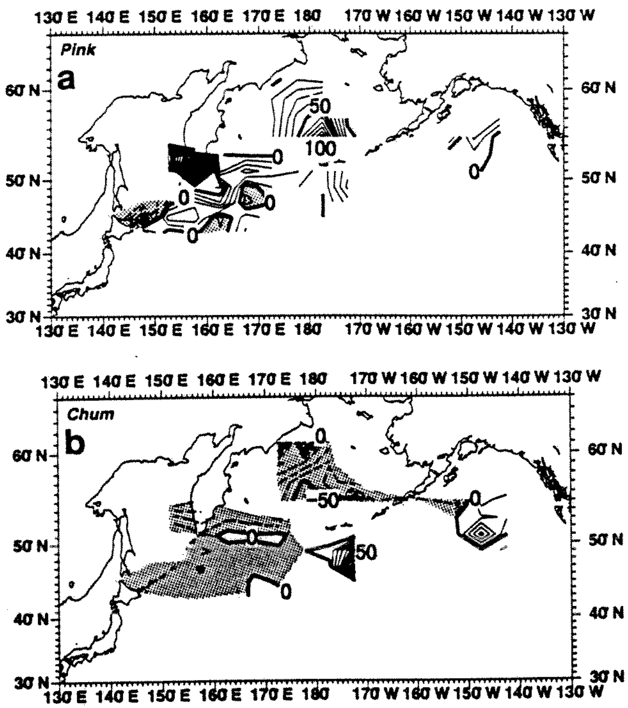


Fig. 6. Density of pink salmon (a) and chum salmon (b) in odd-numbered years relative to density in even-numbered years in the North Pacific Ocean and Bering Sea. (a) Pink salmon, (b) Chum salmon. The contour interval is 10 fish per 30 tans and negative contours (= density in odd-number years lower than that in even-number years) are dashed, and the area between is shaded.

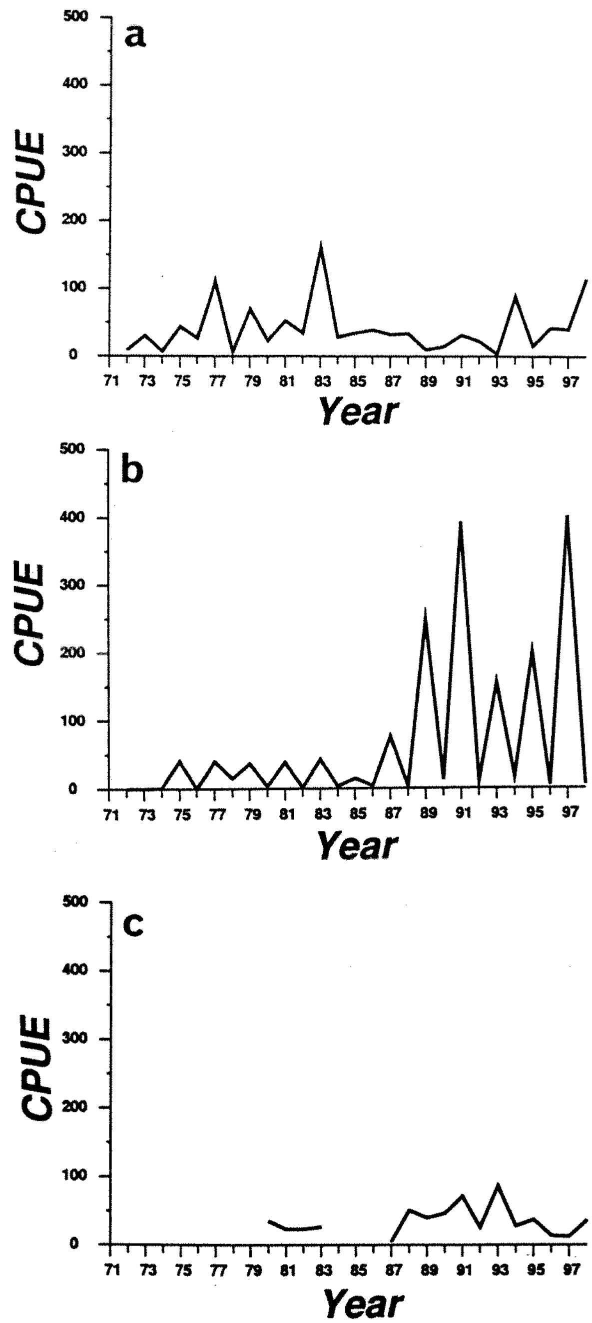


3 to 15 fish per 30 tans. In the Bering Sea, the interannual changes in the density of pink salmon were more variable than those in the western North Pacific. Densities of the odd-year lines remained at about 40 fish per 30 tans until 1989 (Fig. 7b). From 1985 to 1998, the odd-year lines increased sharply to about 200 fish per 30 tans. Conversely, densities in even-year lines remained stable at roughly 5 fish per 30 tans from 1972 to 1998. The densities of pink salmon in odd-year lines was higher than those in even-year lines. There was a significant difference in densities between odd and even-year lines (t test, $p <$ 0.05). In the eastern North Pacific, the variation in the density of pink salmon did not show an odd/even year fluctuation such as in the Bering Sea (Fig. 7 c). The density of pink salmon ranged from 20 to 80 fish per 30 tans.

Immature chum salmon were predominant in the western North Pacific, the Bering Sea and the eastern North Pacific in July (Fig.8a). In the western North Pacific, the density of maturing and immature chum salmon slightly increased from the 1970s to 1990s. The total density of chum salmon was about half or less than that of pink salmon in the western North Pacific.

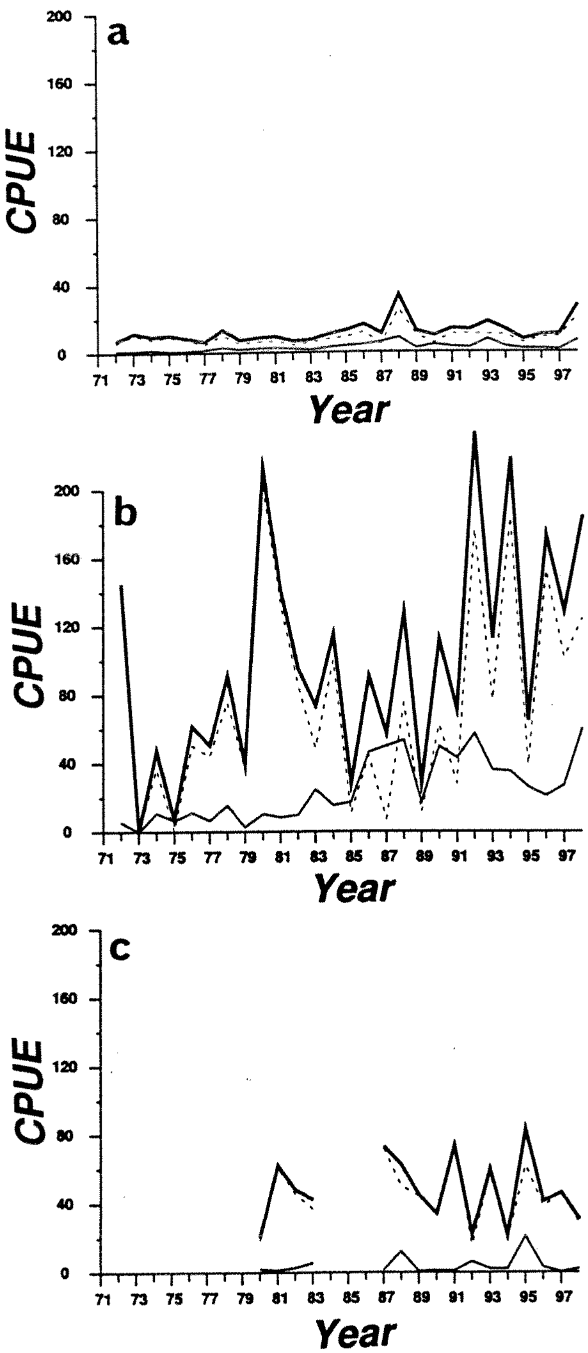
In the Bering Sea, the interannual changes in density of maturing and immature chum salmon showed clearly increasing trends from the 1970s to

Fig. 7. Time series of the density of pink salmon in July in (a) the western North Pacific, (b) the Bering Sea and (c) the eastern North Pacific, respectively.



1990s (Fig. 8b). Moreover, CPUE of immature chum salmon in even-number years was distinctly higher than that in odd-number years. However, the densities of the immature chum salmon and pink salmon in odd and even years were out of phase, although the correlation between pink and chum salmon was not significant statistically. As pink salmon were abundant in odd-number years, immature chum salmon abundance was low. The density of maturing chum salmon did not show the same odd/even year fluctuation as immature chum salmon but did increase from the 1970s to 1990s. Odd/even year fluctuations in density of immature chum salmon in the eastern North Pacific was out of phase with that in the Bering Sea (Fig. 8c). When chum salmon abundance in the Bering Sea was high, the abundance in the eastern North Pacific was low.

Fig. 8. Time series of the density of chum salmon in July in (a) the western North Pacific, (b) the Bering Sea and (c) the eastern North Pacific, respectively. Thin solid line, density of maturing chum salmon. Broken line, density immature maturing chum salmon. Thick solid line, total density of chum salmon.



There was a discrepancy in distributions of immature chum salmon in odd-number years and even-number years (Fig. 6), although the distributions of maturing chum salmon in the Bering Sea did not fluctuate. Densities of immature chum salmon in the Bering Sea and the eastern North Pacific were out of phase. The changes in immature chum salmon density in the Bering Sea reflected the changes in distributions of chum salmon in the eastern North Pacific. These results suggest that the variations in pink salmon abundance in the Bering Sea affect the distribution of immature chum salmon in the Bering Sea and the eastern North Pacific.

Interannual Changes in Age-specific Fork Length and Growth of Pink and Chum Salmon in the Bering Sea

Interannual changes in age-specific fork length and growth of pink and chum salmon in the Bering Sea were investigated. The age-specific fork lengths of salmon in each area were averaged for each year. For chum salmon, the differences in mean fork length from age t to age t+1 were calculated as the age-specific growth at age t+1 for each cohort. Because Ishida et al. (1998) reported that growth rate from spring to summer was greater than that in other seasons, age-specific growth at age t+1 was regarded as growth from age t to age t+1 for that cohort. Thus, the age-specific growth in this study was the change in mean fork length per year.

Mean fork length of maturing pink salmon in the Bering Sea generally decreased over the period of the study (Fig. 9). Mean fork length also showed an odd/even year fluctuation in phase with density, such that fork length in odd-year lines was greater than that in even-year lines. Mean fork length of chum salmon at age 4 and age 5 in the Bering Sea decreased (Fig. 10). The mean fork length at age 2 was around the value of 350 mm and stable. These variations in mean fork length did not show an odd/even year fluctuation similar to density. This result indicated that the size reduction of chum salmon during marine life stage had occurred by age 3.

Growth of chum salmon was negative in the Bering Sea at ages 3 and 4 (Fig. 11). This result indicated that size reduction of chum salmon was due to decreasing growth at ages 3 and 4 in the Bering Sea, and odd/even year fluctuations were found in growth of chum salmon except in 1990 (Fig. 11). The timing of size reduction of chum salmon was consistent with observations of Ishida et al. (1993), Kaeriyama (1998) and Walker et al. (1998) who showed that the growth reduction of Japanese and Russian chum salmon mainly occurred in the third year of ocean life based on analysis of scale patterns. In the present study, the decline of growth in chum salmon at age 4 was also found in the Bering Sea. The fluctuations of

Fig. 9. Time series of the fork length (mm) of pink salmon in July in the Bering Sea. The straight line is the linear regression of fork length on year.

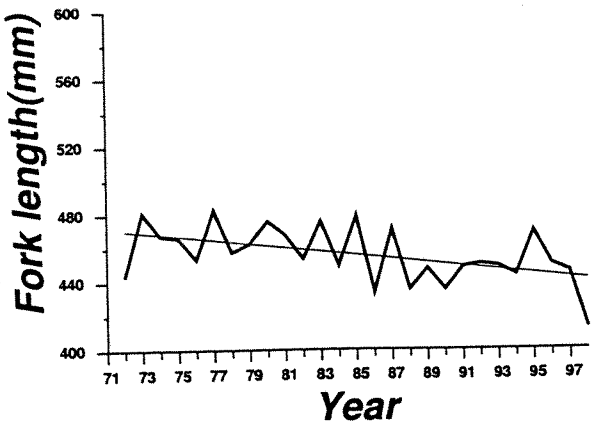


Fig. 10. Time series of the fork length (mm) of chum salmon in July in the Bering Sea. The straight line is the linear regression of fork length on year.

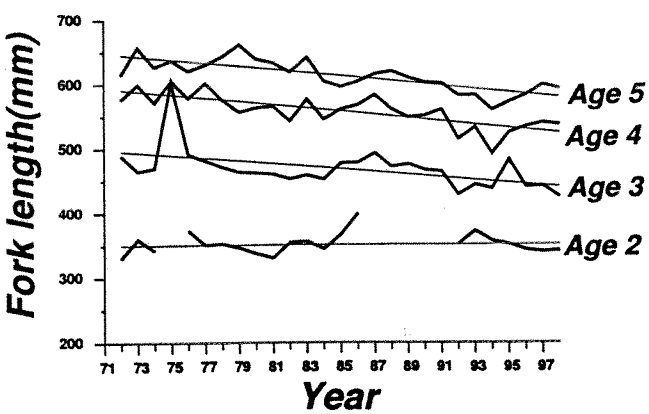
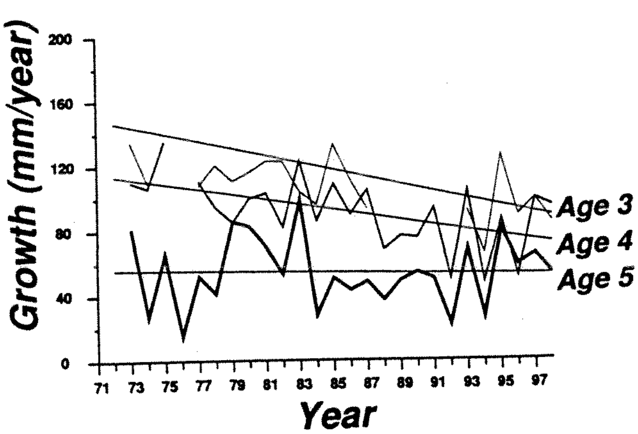


Fig. 11. Time series of the growth (mm/year) of chum salmon in July in the Bering Sea. The straight line is the linear regression of growth on year.



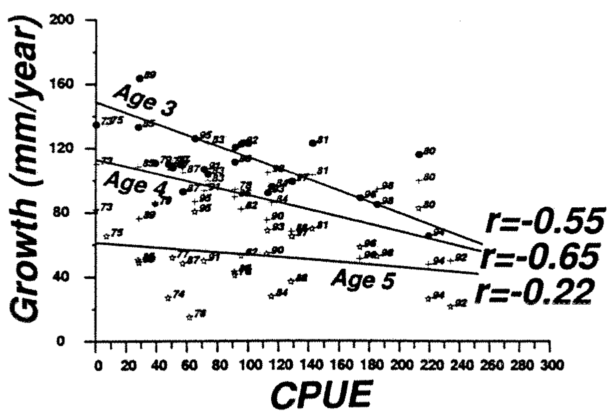
growth of chum salmon may be caused by density-dependent or environmental factors or both. The reason for the decline in growth of chum salmon at age 4 in the Bering Sea is discussed in the next section.

Relationship between Abundance and Growth of Salmon in the Bering Sea

For Pacific salmon, several papers have suggested that density-dependence may limit growth within stocks, among stocks, and among species in the ocean (Kaeriyama 1998, 1996a, b; Ogura et al. 1991; Kaeriyama and Urawa 1992). Helle and Hoffman (1995) have documented age-specific declines in the average size of two North American chum salmon populations. Bigler et al. (1996) also found a decline in average body size in Pacific salmon populations. Ishida et al. (1993) concluded that density-dependent factors explained 35% of the decrease in average size of chum salmon, and the remaining 65% may be explained by ocean conditions and the abundance of other salmon species. If the ocean distribution pattern of pink and chum salmon overlaps as shown in this study and food is limiting, then the significant trophic interaction between species found by Myers (1994) and Bigler et al. (1996) could result in density-dependent limitation of growth. In this study, to examine the possibility of inter- and intra-species density-dependent limitations on growth, we investigated the relationship between age-specific growth and the abundance of salmon. The fork lengths of chum salmon in each year were not compared with the density-dependent factors, because fork lengths of chum salmon are a sum of both physical environmental and density-dependent factors prior to catch. Age-specific growth ($FLt + 1 - FLt$) for each cohort was therefore used instead of mean fork length. The abundance of salmon was the index of total density of both immature and maturing salmon.

For pink salmon, fork length of odd-year lines with high density was larger than that of even-year lines with low density. Although the density-dependent limitations on growth among pink salmon was not seen at first sight, the correlations between fork length of pink salmon and density of odd-year lines in the Bering Sea were significant ($p < 0.05$). This result showed that there was density dependent growth of pink salmon of odd-year lines. Ishida et al. (1996) suggested that the discrepancy in fork length between odd- and even-year lines was due to genetic factors. There were no significant correlations between the density of pink salmon and the growth of chum salmon at each stage in the Bering Sea ($p > 0.05$). This result indicated that the growth of chum salmon was independent of the abundance of pink salmon. However, significant negative correlations with a lag of 0 year were found between the density of chum salmon and the growth of chum salmon at age 3 and 4(r = -0.55, r = -0.65, $p < 0.05$), respectively (Fig.12). When the total density of chum salmon in the Bering Sea was high, the growth of chum at age 3 and 4 decreased. Apparently the growth of chum salmon in this area depends on the abundance of chum salmon itself. The growth of chum at age 5 did not depend on the total density of chum.

Fig. 12. Relationship between density of chum salmon and growth of chum salmon in the Bering Sea.



DISCUSSION AND CONCLUSION

The most important conclusion of this study is that density of chum salmon in the Bering Sea fluctuates between odd and even years, and this variation is out of phase with density of pink salmon in the Bering Sea and with chum salmon in the eastern North Pacific. The difference in the density and distribution of chum salmon between odd and even-number years suggested that chum salmon distributions were affected by pink salmon, and shifted from the Bering Sea to the eastern North Pacific as result of inter-species interaction between pink and chum salmon. A second important finding is that there is no significant relationship between the growth of chum salmon and density of pink salmon, and that growth of pink and chum salmon depend on the abundance of their own species in the Bering Sea. Although pink salmon were the most abundant species in the North Pacific Ocean, the growth of chum salmon was not affected by the abundance of pink salmon. This suggests that the growth of salmon during their marine life is affected by intra-species density. Therefore, for the growth of salmon, there is a possibility of intra-species interaction rather than inter-species interaction in the Bering Sea.

The distribution of chum salmon shifted from the Bering Sea to the eastern North Pacific, altering densities and growth of chum salmon, when abundance of pink salmon increased in the Bering Sea. This suggests that the abundance of pink salmon influenced the growth of chum salmon indirectly. A comparison of pink and chum salmon stomach contents between odd- and even-number years to examine diet overlap would be useful to examine whether pink and chum salmon interact in their feeding. Diet studies are also needed to examine the possibility of intra- or inter-species interaction in the western North Pacific.

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