Stock Distribution Patterns of Chum Salmon in the Bering Sea and North Pacific Ocean during the Summer and Fall of 2002–2004

Shunpei Sato[1], Shogo Moriya[2], Tomonori Azumaya[3], Hiroyuki Nagoya[1], Syuiti Abe[4], and Shigehiko Urawa[1]

*[1]Gene Conservation Section, National Salmon Resources Center, Fisheries Research Agency,
2-2 Nakanoshima, Toyohira-ku, Sapporo 062-0922, Japan
[2]Business Development Division, Nisshinbo Industries, Inc.,
1-2-3 Onodai, Midori-ku, Chiba 267-0056, Japan
[3]Hokkaido National Fisheries Research Institute, Fisheries Research Agency,
116 Katsurakoi, Kushiro 085-0802, Japan
[4]Graduate School of Fisheries Science, Hokkaido University,
3-1-1 Minato-cho, Hakodate 041-8611, Japan*

Sato, S., S. Moriya, T. Azumaya, H. Nagoya, S. Abe, and S. Urawa. 2009. Stock distribution patterns of chum salmon in the Bering Sea and North Pacific Ocean during the summer and fall of 2002–2004. N. Pac. Anadr. Fish Comm. Bull. 5: 29–37.

Abstract: Stock origin and ocean distribution of chum salmon in the Bering Sea and its adjacent North Pacific waters during the summer and fall of 2002–2004 were estimated using a mitochondrial DNA control region. The percentage of immature chum salmon samples was more than 97% in the fall of 2002 and 2003, and 80–88% in summer 2003 and 2004. The genetic stock identification (GSI) and GSI-estimated CPUE (catch per unit effort) suggested that immature chum salmon were mostly from Japanese and Russian stocks, and they were widely distributed in the Bering Sea. The abundance of North American stocks was much lower than that of Asian stocks in the Bering Sea, while it increased in the North Pacific Ocean in the fall of 2003. In the central Bering Sea, Japanese chum salmon stocks were most predominant among regional stocks. All regional stocks were distributed in proportion to sea surface temperatures (6.6–11.9°C) available during each survey period. The distribution pattern and abundance of chum salmon CPUE in the Bering Sea was different among years and seasons, while those changes were not significantly related to the favorable sea surface temperature range in the Bering Sea.

Keywords: chum salmon, genetic stock identification, mitochondrial DNA, distribution, Bering Sea

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) are the most widely distributed salmon species around the Pacific Rim and are considered an important commercial fisheries resource. Estimation of stock origins of chum salmon is important to clarify the stock assessment and the patterns of ocean migration.

Stock identification of chum salmon on the high seas has been attempted with tagging methods, thermal otolith marking, and genetic characters (e.g. Ishida et al. 1989; Wilmot et al. 1998; Seeb and Crane 1999; Urawa et al. 2000b). Offshore tagging experiments indicated that maturing Japanese chum salmon were widely distributed in the Bering Sea and North Pacific Ocean in summer (Ogura and Ito 1994). Otolith-marked chum salmon were collected in the Bering Sea and North Pacific Ocean, and of those, approximately 90% were found to have been released from Japanese hatcheries (Sato et al. 2009). Genetic stock identification (GSI) analysis were performed using allozyme and mitochondrial DNA (mtDNA) markers, and the results showed that Japanese and Russian chum salmon stocks are predominant in the central Bering Sea during summer and fall (Urawa et al. 2004, 2005, 2009; Moriya et al. 2007, 2009). Those results support the ocean migration model of Japanese chum salmon that shows that immature fish inhabit mainly the Bering Sea after overwintering in the North Pacific Ocean (Urawa 2000; Urawa et al. 2001). However, it is still unclear whether or not the marine distribution of particular stock shows inter-annual changes.

Marine habitat conditions affect salmonid ocean distribution. Ocean temperatures should be an important factor affecting the ocean distribution of chum salmon (Urawa et al. 2000a). Welch et al. (1995) also postulated thermal limits and sea surface temperature (SST) as determinants of salmonid distribution in the open ocean. However, the relationships between distribution pattern of specific stocks and SST are unclear.

Japanese scientists have participated in the Bering/Aleutian Salmon International Survey (BASIS) program to clar-

All correspondence should be addressed to S. Sato.
e-mail: sato.shunpei@fra.affrc.go.jp

ify the effect of environmental factors on the distribution of Pacific salmon in the Bering Sea. In the 2002 and 2003 summer and fall seasons, biological data on Pacific salmon and oceanographic data were collected in the Bering Sea and its adjacent North Pacific waters (Azumaya et al. 2003; NPAFC 2004). In summer 2004, biological and oceanographic surveys for Pacific salmon were also conducted in the Bering Sea and North Pacific Ocean (Azumaya et al. 2005). The objective of the present study was to clarify the inter-annual changes in ocean distribution patterns of chum salmon stocks and to examine the relationships between stock distribution patterns and marine habitat conditions, particularly SST. We estimated the stock origin and ocean distribution of chum salmon in the Bering Sea and North Pacific Ocean during the summer of 2004 using a mtDNA marker. The 2004 estimates were compared with the previous 2002–2003 data and the relationships between stock-specific distribution and SST were examined using randomization tests.

MATERIALS AND METHODS

Fish Samples and DNA Extraction

Samples of chum salmon were collected from 18 stations in the Bering Sea and North Pacific Ocean (50°38'N–57°58'N, 175°14'E–170°00'W) aboard the research vessel R/V *Kaiyo maru* between 24 June and 8 July 2004 (Table 1). A net was trawled in the surface layer (down to 50m) for 1 hour at 5 knots. We calculated the catch per unit effort (CPUE) of chum salmon as the number of chum salmon caught per one hour of trawling at a station. Whole blood samples were collected from the caudal vasculature or gills of chum salmon (n = 1,014) and frozen at -40°C. DNA was isolated from the whole blood samples by a Puregene™ DNA purification kit (QIAGEN Inc., Valencia, CA) following the manufacturer's instructions. DNA was extracted at the laboratory of the National Salmon Resources Center, Fisheries Research Agency.

MtDNA Analysis and GSI Estimation

Thirty mtDNA haplotypes of chum salmon that were collected from the Bering Sea and North Pacific Ocean were detected by the DNA microarray method (Moriya et al. 2005) and assigned origins (Japanese, Russian, or North American stocks) using a previously reported mtDNA dataset (Yoon et al. 2008) as baseline data. This baseline data was created from about 4,200 individuals from 96 populations of chum salmon in the Pacific Rim. In previous simulation studies using this baseline data, estimates for the Japanese and North American regions were about 90% accurate (91.6% for Japanese stocks and 94.5% for North American stocks), whereas an estimate for the Russian region was 80.2% accurate (Moriya et al. 2009).

Stock contributions of the mixed samples were estimated via a conditional maximum likelihood (Pella and Milner 1987; Masuda et al. 1991). A conjugate-gradient searching algorithm using a square root transformation was used because it provides good performance with large baselines and small stock differences (Pella et al. 1996). Standard deviations and 90% symmetric confidence intervals were estimated by 1,000 bootstrap resamplings of the baseline and mixture samples. Estimates were made to individual stock and then pooled to regional stock groups: Japan, Russia, and North America. These regional stock groups were categorized based on previous genetic analysis for the baseline data set of 96 populations of chum salmon in the Pacific Rim (Yoon et al. 2008). Computations were performed with the Statistics Programs for Analyzing Mixtures (SPAM version 3.7b), which was originally developed by Debevec et al. (2000).

Estimation of Stock-specific CPUE

GSI-estimated CPUE of chum salmon by stock origin in the Bering Sea and North Pacific Ocean was calculated for five areas: central Bering Sea (55°57'N–58°30'N, 179°42'E–174°42'W), southern Bering Sea (51°41'N–54°40'N, 179°42'E–174°59'W), eastern Bering Sea (53°05'N–56°00'N, 169°57'W–170°34'W), western Bering Sea (52°52'N–56°10'N, 172°30'E–177°29'E), and North Pacific Ocean (49°50'N–53°29'N, 164°46'W–174°49'W) in each survey period (2002 fall, 2003 summer and fall, and 2004 summer). The GSI data during summer and fall of 2002 and 2003 were referenced from Moriya et al. (2009). CPUE data for chum salmon during 2002–2004 are shown in Fig. 1.

Randomization Test

The randomization test of cumulative frequency was used to show the difference in distribution for each regional stock group and SST (Perry and Smith 1994). In this test, the Cramer-von Mises test statistics and 999 permutations of random combinations of 2 variants were used for the significance (Syrjala 1996). Relationships between the distribution of each regional stock and SST were tested by the randomization test for cumulative functions of CPUE and stations over SST in each year. The randomization test was calculated using an EXCEL macro.

RESULTS

Distribution and Maturity

A total of 2,149 chum salmon were collected in summer of 2004. Chum salmon were widely distributed in the survey areas during 2002–2004 (Fig. 1). The abundance of chum salmon in the Bering Sea was higher than the abundance in the North Pacific Ocean during summer/fall 2003 and sum-

Table 1. Survey areas and stations, sampling locations, date of collection, sea surface temperature, number of genetic samples, and stock contribution estimates of immature chum salmon in the Bering Sea and North Pacific Ocean during the summer of 2004. SST, sea surface temperature; N, number of genetic samples; SD, standard deviation; CI, symmetric confidence interval.

Areas/Stations	Latitude	Longitude	Date	SST	N	Estimate ± SD (90% CI)		
						Japan	Russia	North America
Central Bering Sea								
H07	57°58'N	174°42'W	Jun 29	8.7	72	0.674±0.125 (0.493-0.919)	0.196±0.157 (0.001-0.466)	0.130±0.135 (0.000-0.365)
H09	56°01'N	174°42'W	Jun 30	8.2	76	0.613±0.122 (0.415-0.838)	0.243±0.160 (0.008-0.518)	0.143±0.135 (0.000-0.364)
H20	56°21'N	179°52'W	Jul 6	8.3	80	0.599±0.129 (0.423-0.863)	0.191±0.175 (0.001-0.510)	0.210±0.172 (0.001-0.470)
H21	57°20'N	179°53'W	Jul 6	8.4	53	0.596±0.148 (0.366-0.868)	0.361±0.166 (0.064-0.613)	0.043±0.088 (0.000-0.261)
Total				8.4*	281	0.647±0.087 (0.525-0.798)	0.236±0.113 (0.060-0.427)	0.117±0.098 (0.000-0.295)
Southern Bering Sea								
H11	54°10'N	175°02'W	Jul 1	7.9	84	0.333±0.147 (0.124-0.615)	0.581±0.193 (0.214-0.846)	0.087±0.138 (0.000-0.395)
H18	54°35'N	179°46'E	Jul 5	7.7	93	0.475±0.141 (0.271-0.763)	0.367±0.206 (0.022-0.684)	0.158±0.173 (0.000-0.460)
Total				7.8*	177	0.389±0.126 (0.188-0.610)	0.488±0.161 (0.205-0.723)	0.123±0.120 (0.000-0.355)
Eastern Bering Sea								
H03	53°05'N	170°22'W	Jun 27	7.6	57	0.257±0.144 (0.047-0.523)	0.607±0.203 (0.243-0.908)	0.136±0.168 (0.001-0.472)
H04	53°56'N	170°01'W	Jun 27	7.2	34	0.470±0.174 (0.175-0.750)	0.474±0.203 (0.093-0.804)	0.056±0.109 (0.000-0.332)
H05	55°04'N	170°01'W	Jun 28	8.5	34	0.535±0.148 (0.312-0.804)	0.157±0.208 (0.001-0.595)	0.309±0.208 (0.003-0.590)
H06	55°40'N	170°05'W	Jun 28	9.1	42	0.655±0.163 (0.380-0.945)	0.177±0.184 (0.003-0.530)	0.168±0.154 (0.003-0.430)
Total				8.1*	167	0.462±0.108 (0.292-0.654)	0.430±0.150 (0.157-0.660)	0.108±0.110 (0.000-0.322)
Western Bering Sea								
H22	55°57'N	175°17'E	Jul 7	8.8	75	0.177±0.127 (0.007-0.442)	0.522±0.265 (0.084-0.906)	0.300±0.254 (0.001-0.685)
H23	55°05'N	175°14'E	Jul 7	7.9	77	0.190±0.124 (0.028-0.424)	0.542±0.295 (0.060-0.927)	0.268±0.284 (0.001-0.717)
H24	53°57'N	175°16'E	Jul 8	8.1	21	0.143±0.114 (0.000-0.360)	0.367±0.367 (0.002-0.959)	0.490±0.348 (0.006-0.905)
H25	52°58'N	175°16'E	Jul 8	7.2	13	0.160±0.110 (0.000-0.366)	0.138±0.165 (0.002-0.465)	0.703±0.191 (0.313-0.980)
Total				8.0*	186	0.156±0.090 (0.008-0.330)	0.557±0.187 (0.247-0.855)	0.267±0.179 (0.012-0.576)
North Pacific Ocean								
H01	50°53'N	170°10'W	Jun 26	8.8	65	0.498±0.156 (0.273-0.811)	0.198±0.213 (0.005-0.607)	0.305±0.195 (0.002-0.570)
H02	51°49'N	170°00'W	Jun 26	8.6	71	0.450±0.137 (0.257-0.720)	0.327±0.207 (0.002-0.655)	0.223±0.181 (0.006-0.543)
H13	51°40'N	175°06'W	Jul 2	8.3	56	0.412±0.118 (0.230-0.618)	0.416±0.223 (0.011-0.743)	0.173±0.194 (0.000-0.542)
H14	50°38'N	180°00'	Jul 3	7.4	11	0.282±0.143 (0.091-0.545)	0.018±0.045 (0.001-0.041)	0.700±0.153 (0.421-0.907)
Total				8.6*	203	0.431±0.100 (0.273-0.610)	0.337±0.163 (0.060-0.591)	0.233±0.141 (0.033-0.482)

*Average SST in each survey area.

mer 2004. However, their distribution patterns in the Bering Sea were different among those three years and seasons. In 2002, chum salmon were mainly collected in the southern Bering Sea between 172°30'W–177°30'W (Fig. 1A). In 2003, chum salmon were widely distributed in the survey areas of the Bering Sea, but the CPUE in fall was higher than that in summer (Fig. 1B, C). In 2004, about 30% of chum salmon were caught at a single station (H18, see Fig. 1D). The percentage of immature chum salmon samples was > 97% in the fall of 2002 and 2003. On the other hand, the occurrence of immature fish was < 90% in summer 2003 and 2004 (80.2% in 2003 and 88.1% in 2004).

Genetic Stock Identification

The stock composition of immature chum salmon in the Bering Sea and North Pacific Ocean in the summer of 2004 is shown in Table 1. The stock composition in the central Bering Sea (H07, H09, H20, and H21) was 59.6–67.4% Japanese, 19.1–36.1% Russian, and 4.3–21.0% North American stocks. The estimated stock composition of chum salmon in the southern Bering Sea (H11 and H18) was 33.3–47.5% Japanese, 36.7–58.1% Russian, and 8.7–15.8% North American stocks. Chum salmon in the eastern Bering Sea (H03–06) were estimated to be 25.7–65.5% Japanese, 15.7–60.7% Russian, and 5.6–30.9% North American stocks. The stock composition in the western Bering Sea (H22–H25) was 14.3–19.0% Japanese, 13.8–54.2% Russian, and 26.8–70.3% North American stocks. In the North Pacific Ocean (H01, H02, H13, and H14), the stock composition was estimated to be 28.2–49.8% Japanese, 1.8–41.6% Russian, and 17.3–70.0% North American chum salmon.

CPUE Distribution

GSI-estimated CPUE analysis of immature chum salmon indicated that Asian (Japanese and Russian) stocks were widely distributed in the surveyed areas, and were relatively abundant in the central and southern Bering Sea (Fig. 2, Table 2). Particularly, Japanese stocks were predominant in the central Bering Sea during 2002–2004. Stock abundance in the southern Bering Sea fluctuated highly among years. The CPUE of Russian stocks was higher than that of Japanese and North American stocks in the western Bering Sea during 2002–2004. The abundance of North American stocks was much lower than that of Asian stocks in the Bering Sea (Fig. 2, Table 2). In the North Pacific Ocean, North American stocks showed a high CPUE in fall 2003, while their CPUE was almost the same or lower than other stocks in summer 2003 and 2004 (Fig. 2).

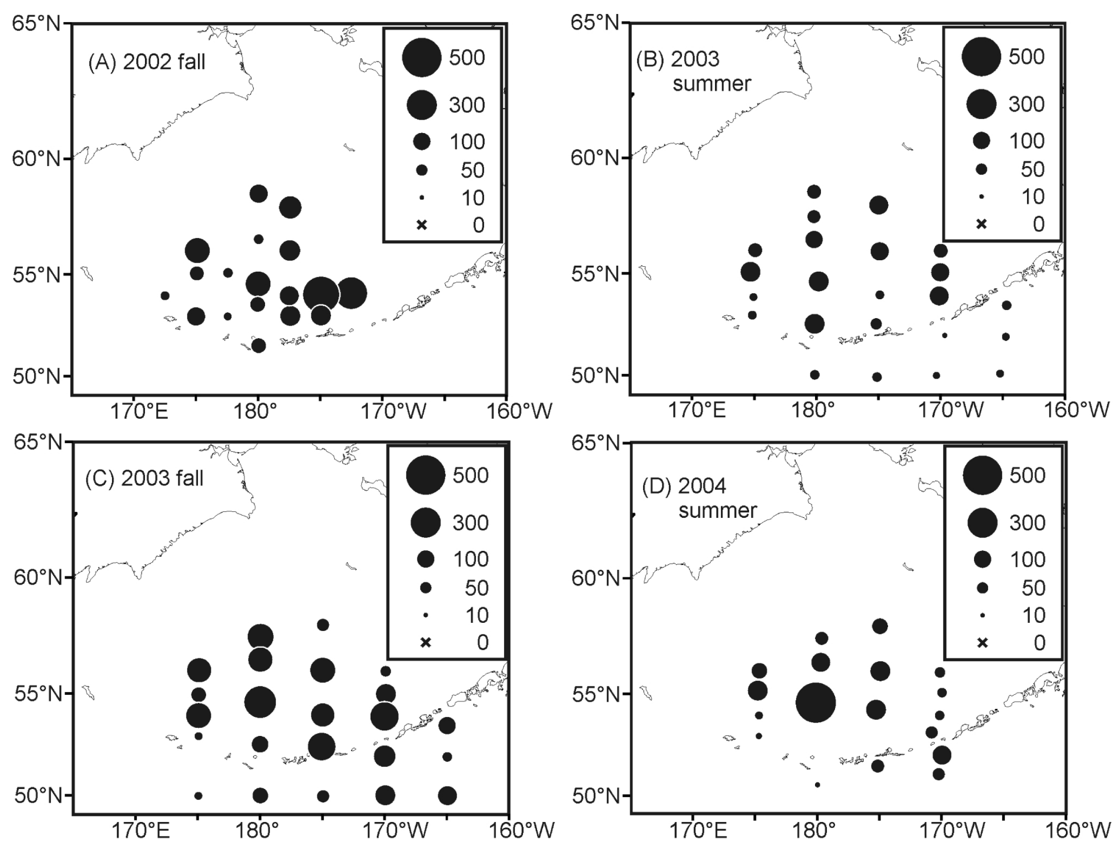

Fig. 1. Catch per unit effort (CPUE) distribution of chum salmon in the Bering Sea and North Pacific Ocean in the fall of 2002 (A), the summer (B) and fall (C) of 2003, and the summer of 2004 (D). CPUE indicates the number of catches per one-hour trawl.

Table 2. Estimation of stock-specific CPUE of immature chum salmon in five surveyed areas of the Bering Sea and North Pacific Ocean during the summer and fall of 2002-2004. CPUE, the number of catches per one hour trawl; St., number of stations in each survey area; CI, symmetric confidence interval. Genetic-estimated CPUE data from 2002-2003 were calculated using GSI data from Moriya et al. (2009).

Seasons (sampling date)/Areas	St.	Mean SST	CPUE (Mean ± SD (90% CI))		
			Japan	Russia	North America
2002 fall (Sep 3-18)					
Central Bering Sea	4	10.2	72.8±10.9 (55.3-90.6)	40.5±14.7 (12.0-61.7)	6.5±10.2 (0.0-29.8)
Southern Bering Sea	7	9.0	55.3±18.6 (33.4-89.5)	87.2±39.0 (11.1-131.2)	25.5±33.1 (0.0-9409)
Western Bering Sea	6	9.9	27.1±9.6 (15.9-46.1)	41.5±19.7 (3.5-63.7)	12.3±12.3 (0.0-47.3)
2003 summer (Jun 28-Jul 18)					
Central Bering Sea	5	8.0	55.7±10.5 (38.4-72.8)	26.3±13.0 (3.9-47.0)	10.6±8.6 (0.0-27.6)
Southern Bering Sea	4	7.7	46.6±10.2 (30.2-64.6)	29.8±14.2 (3.9-51.4)	10.7±11.0 (0.0-32.7)
Western Bering Sea	4	7.3	38.4±6.5 (15.3-37.0)	22.4±8.8 (8.5-43.7)	6.2±6.4 (0.2-27.5)
Eastern Bering Sea	3	9.1	58.7±9.9 (39.4-72.4)	34.3±13.5 (11.7-55.0)	9.4±9.7 (0.0-29.0)
North Pacific Ocean	7	9.5	7.0±2.4 (3.9-11.3)	13.6±5.8 (3.9-23.1)	9.3±5.6 (0.4-18.9)
2003 fall (Aug 30-Sep 19)					
Central Bering Sea	4	10.8	89.8±17.0 (63.6-119.1)	58.4±24.0 (17.1-96.3)	23.1±18.2 (0.3-58.1)
Southern Bering Sea	4	9.3	104.8±19.9 (74.6-139.8)	63.7±27.6 (19.7-110.3)	45.5±23.5 (10.7-86.8)
Western Bering Sea	4	10.1	36.3±10.7 (20.5-55.6)	64.8±20.5 (28.3-95.0)	24.1±17.8 (0.4-56.4)
Eastern Bering Sea	3	10.7	34.9±13.1 (15.3-56.1)	67.2±25.4 (22.8-106.0)	44.0±22.9 (10.7-84.2)
North Pacific Ocean	7	11.7	20.7±6.0 (11.7-28.7)	23.4±14.7 (3.1-46.4)	56.3±14.2 (26.9-69.8)
2004 summer (Jun 26-Jul 8)					
Central Bering Sea	4	8.4	79.6±10.7 (64.6-98.2)	29.0±13.9 (7.4-52.5)	14.4±12.1 (0.0-36.3)
Southern Bering Sea	2	7.8	154.2±50.0 (74.5-241.9)	193.5±63.8 (81.3-286.7)	48.8±47.6 (0.0-140.8)
Western Bering Sea	4	8.0	13.0±7.5 (0.7-27.5)	46.4±15.6 (20.6-71.2)	22.2±14.9 (1.0-48.0)
Eastern Bering Sea	4	8.1	25.6±6.0 (16.2-36.3)	23.9±8.3 (8.7-36.6)	6.0±6.1 (0.0-17.9)
North Pacific Ocean	4	8.3	33.3±7.7 (21.1-47.2)	26.1±12.6 (4.6-45.7)	18.0±10.9 (2.5-37.3)

Relationships between Stock-specific Distribution and SST

Associations between cumulative frequencies of genetic-estimated CPUE for three regional stocks and cumulative frequency of SST in each survey period were estimated based on stock CPUE and SST data at each survey station. All regional stocks were distributed in proportion to the available SST (6.6–11.9°C) in each survey period (Fig. 3). The test values for statistical significance in 2002 fall indicated negative values (Japanese stock, $P = 0.085$; Russian stock, $P = 0.401$; North American stock, $P = 0.534$) (Fig. 3A). In the 2003 summer and fall, the randomization test showed non-significant correlations between the distribution of each regional stock and observed SST (summer: Japanese stock, $P = 0.187$; Russian stock, $P = 0.972$; North American stock, $P = 0.699$) (Fig. 3B); (fall: Japanese stock, $P = 0.052$; Russian stock, $P = 0.981$; North American stock, $P = 0.508$) (Fig. 3C). In the summer of 2004, the test values for statistical significance also indicated negative values (Japanese stock, $P = 0.876$; Russian stock, $P = 0.749$; North American stock, $P = 0.1$) (Fig. 3D).

DISCUSSION

Our genetic stock estimates and GSI-estimated CPUE indicated that immature chum salmon were mostly of Asian (Japanese and Russian) origin, and were widely distributed in the surveyed areas of the Bering Sea during summer and fall. The abundance of immature North American stocks was lowest in the Bering Sea during 2002–2004. Previous allozyme analysis indicated that the relative abundance of immature North American stocks was low in the Bering Sea and high in the eastern North Pacific Ocean (Urawa et al. 2005, 2009). Many otolith-marked chum salmon released from North American hatcheries were found in the southern Bering Sea and eastern North Pacific Ocean (Urawa et al. 2005, 2009). These results suggest that the North American stocks are mainly distributed in the North Pacific Ocean.

Japanese stocks were predominant in the central Bering Sea during summer and fall of 2002–2004 compared to chum salmon stocks from all other countries. Allozyme analyses also indicated that Japanese immature chum salmon were most abundant in the central Bering Sea during summer and fall 2002 and 2003 (Urawa et al. 2004, 2005). Why do

Japanese chum salmon migrate and distribute themselves in the central Bering Sea? Urawa et al. (2005, 2009) suggested that one reason may be related with their overwintering habitats. Japanese chum salmon stay in a narrow region of the western North Pacific Ocean in the first winter and in the Gulf of Alaska during the following winters (Urawa 2000). During the overwintering period, chum salmon prefer water with low temperatures between 4°C and 8°C (Nagasawa 2000). The habitat in this temperature range was more widely available in the eastern North Pacific than the western North Pacific Ocean (Urawa et al. 2005). For Japanese chum salmon in the eastern North Pacific, the shortest homing migration route is through the Bering Sea (Urawa 2000; Urawa et al. 2005). MtDNA analysis of chum salmon in the North Pacific Ocean in spring 2006 indicated that the abundance of Japanese stocks was higher in the central (180°) than in the western (165°E–175°E) North Pacific Ocean (Sato et al. 2007). Perhaps Japanese chum salmon start to move into the Bering Sea in late June or early July as estimated by Urawa et al. (2001, 2005, 2009), and then rapidly move into the central Bering Sea.

The CPUE distribution of chum salmon in the Bering Sea was different among years and seasons. The chum salmon CPUE in fall 2002 was higher than in fall 2003, while the CPUE in summer 2003 was lower than in summer 2004. The CPUE of chum salmon in fall 2003 was also higher than in summer 2003. Previous studies indicated that the density and distribution of chum salmon in the Bering Sea fluctuates

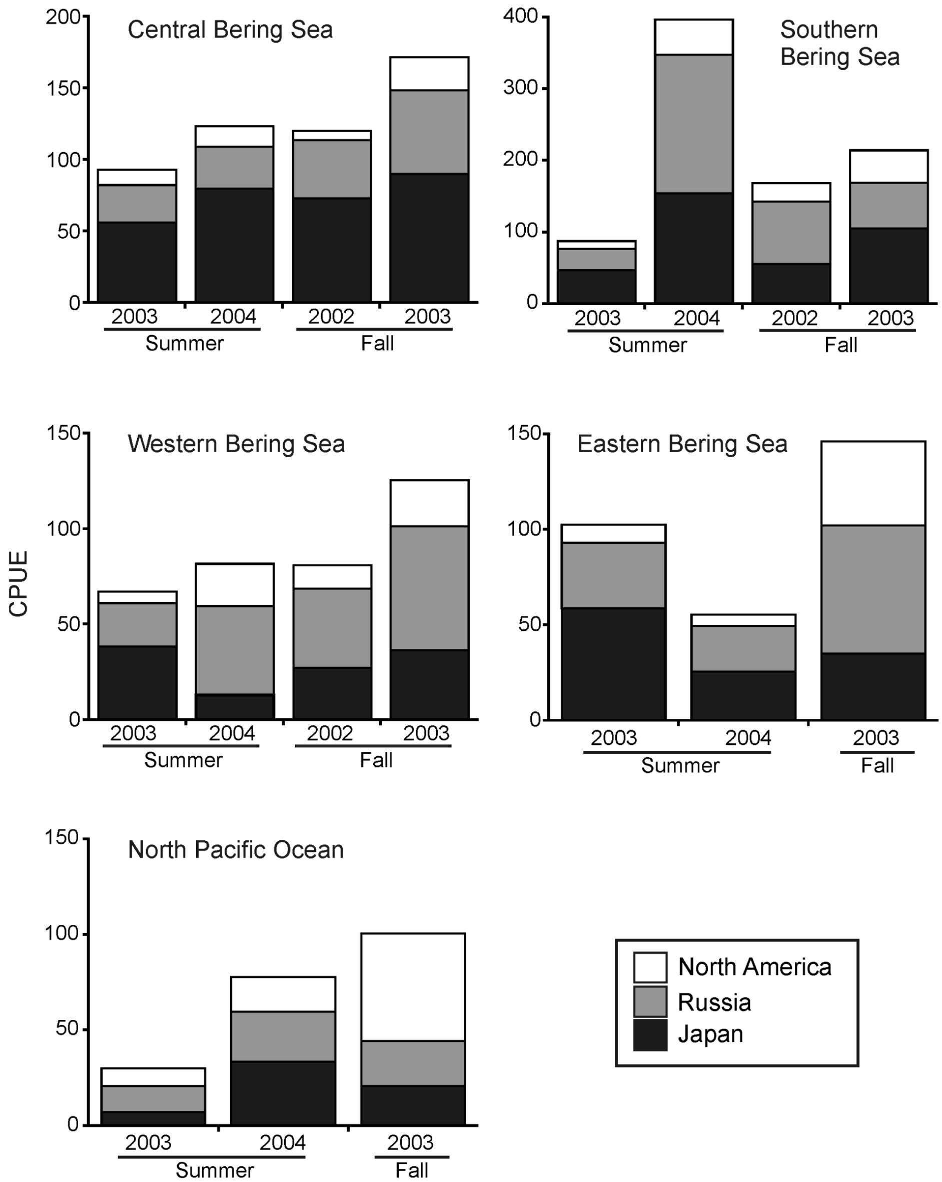

Fig. 2. Estimation of stock-specific CPUE of immature chum salmon in the five surveyed areas of the Bering Sea and North Pacific Ocean during 2002-2004. CPUE as in Fig. 1.

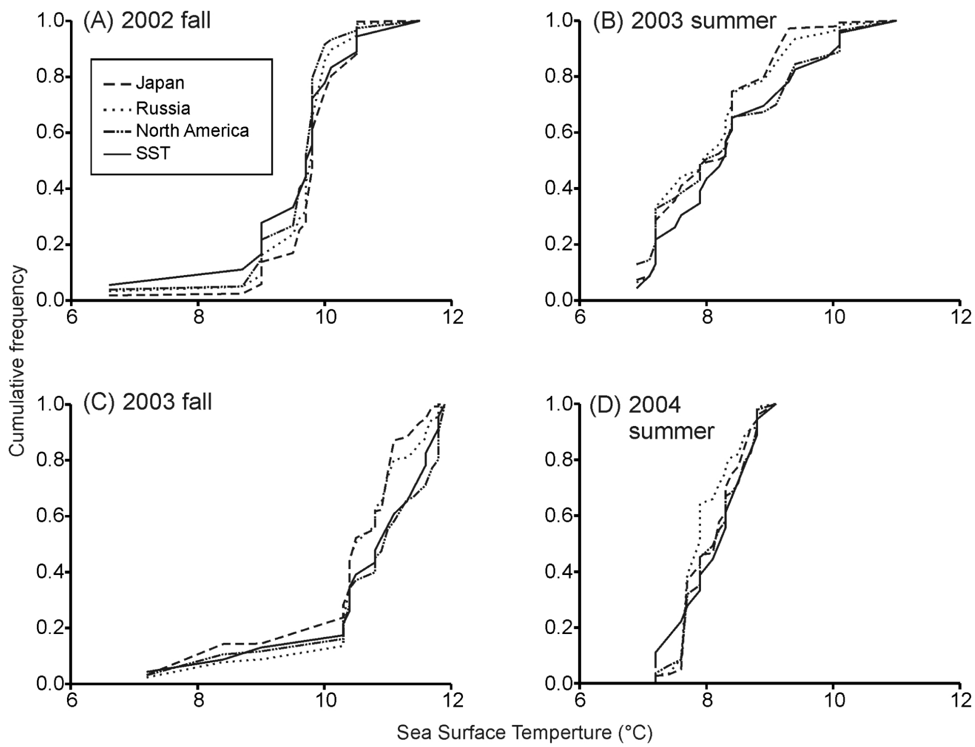

Fig. 3. Relationships between cumulative frequencies of GSI-estimated CPUE of immature chum salmon for three regional stocks (Japan, Russia, and North America) and sea surface temperature (SST) in the fall of 2002 (A), the summer (B) and fall (C) of 2003, and the summer of 2004 (D).

between odd and even years, because the interaction between pink (*O. gorbuscha*) and chum salmon changes their density and distribution (Azumaya and Ishida 2000). On the other hand, most pink salmon leave from the offshore of the Bering Sea by August for their spawning migration. Thus, pink salmon may influence the spatial and temporal distribution and abundance of chum salmon during early and mid summer, while pink salmon may have no impact on the distribution of immature chum salmon in the late summer and fall.

Myers et al. (2007) reported that there was a strong negative relation between the relative abundance of Russian chum salmon and SST in the central Bering Sea. They estimated that this correlation might reflect the influence of ocean temperature on run timing: in warm SST years Russian salmon may mature faster and leave the central Bering Sea sooner, resulting in lower CPUEs in July. However, this may not be the case for immature fish. Our randomization test showed non-significant correlations between the distribution of each regional stock of immature chum salmon and observed SST during each survey period. These results suggest that a response to SST may be different for maturing and immature chum salmon.

Azumaya et al. (2007) showed that the upper thermal limit was 15.6°C for chum salmon and that the southern limit of chum salmon distribution was located in the Transition Domain (43°N) in summer. In our study, all regional stocks were distributed in proportion to the available SST (6.6–11.9°C) during summer and fall. This SST range is basically within the “preferred” temperature range of chum salmon. Furthermore, SST anomalies (relative to 1970–2000 mean values) in the Bering Sea for summer and fall of 2002–2004 showed + 0–2°C (Japan Meteorological Agency, data citation: 19 December, 2008). These results suggest that chum salmon can inhabit most areas of the Bering Sea in summer without being affected by thermal limitations. In other words, SST may not be the main factor limiting the distribution of immature chum salmon in summer in the Bering Sea. The ocean distribution and migration patterns of salmon may be affected by the abundance of food organisms, interactions within or between species, ocean conditions, timing and location of spawning, as well as winter habitat (Urawa et al. 2005, 2009). In future studies, we should clarify factors influencing the migration and distribution of chum salmon in the ocean.

ACKNOWLEDGMENTS

We express our thanks to the Captain Jishu Doi, officers, and crews of R/V *Kaiyo maru* for their efforts to collect high-sea samples and oceanographic data. We would like to thank Mr. Masa-aki Fukuwaka, Hokkaido National Fisheries Research Institute, Fisheries Research Agency, Japan, for valuable advice on statistical analysis. The present study was supported by Grants-in-Aid from the Fisheries Agency of Japan.

REFERENCES

Azumaya, T., and Y. Ishida. 2000. 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. N. Pac. Anadr. Fish. Comm. Bull. 2: 165–174. (Available at www.npafc.org).

Azumaya, T., S. Urawa, O. Yamamura, M. Fukuwaka, A. Kusaka, N. Nagasawa, T. Nomura, S. Moriya, and A. Urano. 2003. Results of the survey by *Kaiyo maru* in the Bering Sea, 2002. N. Pac. Anadr. Fish Comm. Doc. 717. 12 pp. (Available at www.npafc.org).

Azumaya, T., T. Nomura, N. Tanimata, O. Sakai, T. Onuma, and S. Sato. 2005. Result of the survey in the Bering Sea in 2004. N. Pac. Anadr. Fish Comm. Doc. 843. 13 pp. (Available at www.npafc.org).

Azumaya, T., T. Nagasawa, O.S. Temnykh, and G.V. Khen. 2007. Regional and seasonal differences in temperature and salinity limitations of Pacific salmon (*Oncorhynchus* spp.). N. Pac. Anadr. Fish Comm. Bull. 4: 179–187. (Available at www.npafc.org).

Debevec, E.M., R.B. Gates, M. Masuda, J. Pella, J. Reynolds, and L.W. Seeb. 2000. SPAM (version 3.2): Statistics Program for Analyzing Mixtures. J. Hered. 91: 509–510.

Ishida, Y., S. Ito, and K. Takagi. 1989. Stock identification of chum salmon *Oncorhynchus keta* from their maturity and scale characters. Nippon Suisan Gakkaishi 55: 651–656.

Japan Meteorological Agency. Archived data of SST in the North Pacific Ocean. Data citation: 19 December, 2008. (Available at www.data.kishou.go.jp/kaiyou/db/kaikyo/jun/sst_pac.html) (In Japanese).

Masuda, M., S. Nelson, and J. Pella. 1991. The computer programs for computing conditional maximum likelihood estimates of stock composition from discrete characters. U.S. Department of Commerce, NOAA/NMFS Auke Bay Laboratories, Juneau, Alaska.

Moriya, S., S. Urawa, O. Suzuki, A. Urano, and S. Abe. 2005. DNA microarray for rapid detection of mitochondrial DNA haplotypes of chum salmon. Mar. Biotechnol. 6: 430–434.

Moriya, S., S. Sato, T. Azumaya, O. Suzuki, S. Urawa, A. Urano, and S. Abe. 2007. Genetic stock identification of chum salmon in the Bering Sea and North Pacific Ocean using mitochondrial DNA microarray. Mar. Biotechnol. 9: 179–191.

Moriya, S., S. Sato, M. Yoon, T. Azumaya, S. Urawa, A. Urano, and S. Abe. 2009. Nonrandom distribution of chum salmon stocks in the Bering Sea and the North Pacific Ocean estimated using mitochondrial DNA microarray. Fish. Sci. 75: 359–367.

Myers, K.W., N.V. Klovach, O.F. Gritsenko, S. Urawa, and T.C. Royer. 2007. Stock-specific distributions of Asian and North American Salmon in the open ocean, interannual changes, and oceanographic conditions. N. Pac. Anadr. Fish. Comm. Bull. 4: 159–177 (Available at www.npafc.org).

Nagasawa, K. 2000. Winter zooplankton biomass in the subarctic North Pacific, with a discussion on the overwintering survival strategy of Pacific salmon (*Oncorhynchus* spp). N. Pac. Anadr. Fish. Comm. Bull. 2: 21–32 (Available at www.npafc.org).

North Pacific Anadromous Fish Commission. 2004. Annual report of the Bering-Aleutian Salmon International Survey (BASIS), 2003. N. Pac. Anadr. Fish Comm. Doc. 769. 78 pp. (Available at www.npafc.org).

Ogura, M., and S. Ito. 1994. Change in the known ocean distribution of Japanese chum salmon, *Oncorhynchus keta*, in relation to the progress of stock enhancement. Can. J. Fish. Aquat. Sci. 51: 501–505.

Pella, J.J., and G.B. Milner. 1987. Use of genetic markers in stock composition analysis. *In* Population Genetics and Fishery Management. *Edited by* N. Ryman and F. Utter. University of Washington Press, Seattle. pp. 247–276.

Pella, J.J., M. Masuda, and S. Nelson. 1996. Search algorithms for computing stock composition of a mixture from traits of individuals by maximum likelihood. NOAA Tech. Memo. NMFS-AFSC No. 61.

Perry, R.I., and S.J. Smith. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 51: 589–602.

Sato, S., T. Kaga, T. Chiba, D. Takasaki, K. Morita, H. Nagoya, and S. Urawa. 2007. Origins and distribution of chum salmon in the western North Pacific Ocean during the spring of 2006. N. Pac. Anadr. Fish Comm. Doc. 1047. 9 pp. (Available at www.npafc.org).

Sato, S., M. Takahashi, N. Watanabe, S. Kitatsuji, D. Takasaki, T. Chiba, S. Imai, Y. Goda, M. Watanabe, M. Fukuwaka, B.A. Agler, and S. Urawa. 2009. Preliminary records of otolith-marked chum salmon found the Bering Sea and North Pacific Ocean in 2006 and 2007. N. Pac. Anadr. Fish Comm. Bull. 5: 99–104. (Available at www.npafc.org).

Seeb, L.W., and P.A. Crane. 1999. Allozymes and mitochondrial DNA discriminate Asian and North American populations of chum salmon in mixed-stock fisheries along the south coast of the Alaska Peninsula. Trans. Am. Fish. Soc. 128: 88–103.

Syrjala, S.E. 1996. A statistical test for a difference between the spatial distributions of two populations. Ecology 77: 75–80.

Urawa, S. 2000. Ocean migration route of Japanese chum salmon with a reference to future salmon research. Nat. Salmon Resources Center Newsletter 5: 3–9. (Available at http://salmon.fra.affrc.go.jp/kankobutu/salmon/salmon05_p03-09.pdf).

Urawa, S., Y. Ishida, and M. Fukuwaka. 2000a. Japanese salmon research in the ocean: a review and future issues. Bull. Nat. Salmon Resources Center 3: 29–38. (Available at http://salmon.fra.affrc.go.jp/kankobutu/bulletin/BNSRC03-05.pdf)

Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K. M. Munk, K.W. Myers, and E.V. Farley, Jr. 2000b. Geographic origin of high-seas chum salmon determined by genetic and thermal otolith markers. N. Pac. Anadr. Fish Comm. Bull. 2: 283–290. (Available at www.npafc.org).

Urawa, S., Y. Ueno, Y. Ishida, L.W. Seeb, P.A. Crane, S. Abe, and N.D. Davis. 2001. A migration model of Japanese chum salmon during early ocean life. N. Pac. Anadr. Fish Comm. Tech. Rep. 2: 1–2. (Available at www.npafc.org).

Urawa, S., T. Azumaya, P.A. Crane, and L.W. Seeb. 2004. Origin and distribution of chum salmon in the Bering Sea during the early fall of 2002: Estimates by allozyme analysis. N. Pac. Anadr. Fish Comm. Doc. 794. 11 pp. (Available at www.npafc.org).

Urawa, S., M. Kawana, T. Azumaya, P.A. Crane, and L.W. Seeb. 2005. Stock-specific ocean distribution of immature chum salmon in the summer and early fall of 2003: estimates by allozyme analysis. N. Pac. Anadr. Fish Comm. Doc. 896. 14 pp. (Available at www.npafc.org).

Urawa, S., S. Sato, P.A. Crane, B. Agler, R. Josephson, and T. Azumaya. 2009. Stock-specific ocean distribution and migration of chum salmon in the Bering Sea and North Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. 5: 131–146. (Available at www.npafc.org).

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.

Wilmot, R.L., C.M. Kondzela, C.M. Guthrie, and M.S. Masuda. 1998. Genetic stock identification of chum salmon harvested incidentally in the 1994 and 1995 Bering Sea trawl fishery. N. Pac. Anadr. Fish Comm. Bull. 1: 285–299. (Available at www.npafc.org).

Yoon, M., S. Sato, J.E. Seeb, V. Brykov, L.W. Seeb, N.V. Varnavskaya, R.L. Wilmot, D.H. Jin, S. Urawa, A. Urano, and S. Abe. 2008. Mitochondrial DNA variation and genetic population structure of chum salmon *Oncorhynchus keta* around the Pacific Rim. J. Fish. Biol. 73: 1256–1266.