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Adapting Hokkaido Hatchery Strategies to Regional Ocean Conditions Can Improve Chum Salmon Survival and Reduce Variability

Mitsuhiro Nagata[1], Yasuyuki Miyakoshi[1], Makoto Fujiwara[1], Kiyoshi Kasugai[1], Daisei Ando[1], Mitsuru Torao[2], Hayato Saneyoshi[2], and James R. Irvine[3]

[1]*Salmon and Freshwater Fisheries Research Institute, Hokkaido Research Organization, 3-373 Kitakashiwagi, Eniwa, Hokkaido 061-1433, Japan*
[2]*Doto Research Branch, Salmon and Freshwater Fisheries Research Institute, Hokkaido Research Organization, 3-1-10 Maruyama, Nakashibetsu, Hokkaido 086-1164, Japan*
[3]*Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada*

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Abstract: Returns of chum salmon in Hokkaido, Japan, have increased remarkably since the 1970s, but there have been significant regional variations in survival. We surveyed chum salmon dynamics in several regions to test the hypothesis that variations in survival were related to the nearshore ocean environment, especially sea surface temperatures (SSTs). Time series analyses of return rate data for chum salmon from 14 regions around Hokkaido revealed 4 geographical groups (Japan Sea, Okhotsk Sea, Nemuro Strait, and Pacific Ocean) that had distinct survival patterns. In the Okhotsk Sea, Nemuro Strait, and Eastern Pacific Ocean, survival patterns were associated with SST patterns in the nearshore environment at the times and places occupied by young chum salmon. In the Okhotsk Sea, SSTs below 8°C appeared to restrict the offshore movement of juvenile chum salmon, while SSTs over 13°C accelerated their offshore movement, apparently resulting in salmon moving prematurely. We recommend that SSTs of 7–11°C are most appropriate for the release of chum salmon. As SSTs are expected to warm but also become increasingly variable as a result of climate change, we encourage an adaptive approach whereby the nearshore environment is monitored in order to align juvenile chum salmon releases with optimal conditions.

Keywords: chum salmon, return rate, SST, regional variation, hatchery strategy, monitoring

INTRODUCTION

Hokkaido chum salmon (*Oncorhynchus keta*) hatchery programs began in the late 19th century with the introduction of hatchery techniques from the United States of America, although there were many failures until the 1960s (Kobayashi 1980). A remarkable recovery of Hokkaido chum salmon populations occurred in the 1970s with improvements in hatchery techniques, including the release of larger fry (Kobayashi 1980; Kaeriyama 1989). In addition, marine survival increased as a result of shifts in ocean conditions in the North Pacific Ocean (Beamish and Bouillon 1993; Kaeriyama 1999; Irvine and Fukuwaka 2011). However, since the late 1990s, chum salmon returns have varied greatly among regions in Hokkaido despite relatively consistent releases of hatchery fry (Nagata et al. 2012; Miyakoshi et al. 2013). More recently, returns have declined in the southern Japan Sea, Nemuro Strait and the Eastern Pacific Ocean regions of Hokkaido (Fig. 1).

The production and survival of Pacific salmon (*Oncorhynchus* spp.) are affected not only by long-term climate and oceanographic conditions indexed by the PDO (Pacific Decadal Oscillation) and the ALPI (Aleutian Low Pressure Index) (Beamish and Bouillon 1993; Hare et al. 1999), but also by regional physical and biological ocean conditions (Willette et al. 2001; Mueter et al. 2002; Pyper et al. 2005; Saito and Nagasawa 2009; Zimmerman et al. 2015). High mortalities of chum and pink salmon that migrate seaward soon after fry emergence occur during early life, including their time in fresh water (Bax 1983; Willette et al. 2001; Fukuwaka and Suzuki 2002; Mueter et al. 2002; Morita et al. 2015). Japanese juvenile chum salmon move from coastal waters to the Okhotsk Sea where they reside until fall (Ueno et al. 1998; Urawa et al. 2001, 2004).

All correspondence should be addressed to M. Nagata.
e-mail: nagata-mitsuhiro@hro.or.jp

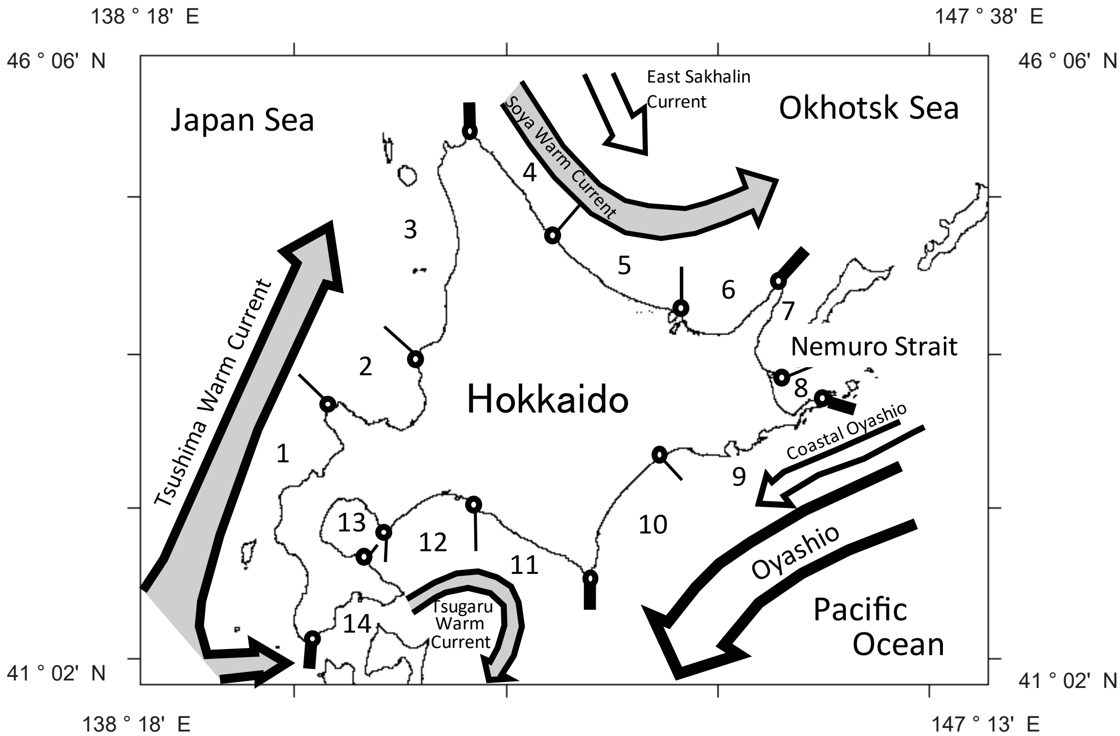

Fig.1. Maps showing the water currents around Hokkaido (modified from Isoda and Kishi 2003) and the 14 regions (1–14) where the Hokkaido Government manages chum salmon fisheries and hatchery programs. The Japan Sea: southern (1 SJS), mid- (2 MSJ), northern (3 NSJ) regions; the Okhotsk Sea: western (4 WOS), mid- (5 MOS), eastern (6 EOS) regions; the Nemuro Strait: northern (7 NNS), southern (8 SNS) regions; the Eastern Pacific Ocean: eastern (9 EEPO), western (10 WEPO) regions; and the Western Pacific Ocean: Hidaka (11 HWPO), Iburi (12 IWPO), Funka Bay (13 FWPO), and Donan (14 DWPO). Arrows show cold (white) and warm water (gray), respectively.

How important is the early marine environment in determining brood stock strength? In Japan, numerous studies on the early life of chum salmon in relation to the coastal environment have examined the optimal timing and size of fish at release (see review by Mayama and Ishida 2003). On the basis of scientific findings and empirical information, it is recommended that chum salmon be reared to at least 1 g in body weight and released when coastal sea surface temperatures (SSTs) are from 5°C to 13°C (Seki 2005; Saito et al. 2009). While earlier studies on Japanese chum salmon supported the release of larger sizes at release to increase survival (Kaeriyama 1999; Nagata and Kaeriyama 2004), more recent studies (Saito and Nagasawa 2009; Saito et al. 2011) have indicated that regional differences in adult returns of chum salmon in Japan are determined primarily by survival during early ocean life, and the influence of size at release on survival varies among regions. Regional-scale environmental effects on survival have also been reported for northeastern Pacific salmon (Pyper et al. 2002, 2005; Zimmerman et al. 2015).

Seki and Shimizu (1996) discovered that return rates for marked juvenile chum salmon released when coastal water temperatures were > 5°C were much higher than for releases when the coastal water temperatures were < 5°C. In addition, when SSTs in the coastal waters of Abashiri Bay in eastern Hokkaido was < 8°C, even though the juvenile chum salmon released were large, they did not move offshore but remained in shallow waters until temperatures exceeded 8°C, apparently resulting in depressed growth due to a lack of prey (Nagata et al. 2007). These results from coastal regions suggested that the coastal ecosystem, including water temperature and food availability, is more important for growth and survival of juvenile chum salmon than fish size at release.

In this paper, we propose a general hypothesis that recent variations in survival in Hokkaido chum salmon populations are closely related to their early marine life history in nearshore environments, especially to variable SSTs. To test our hypothesis, we analyzed survival and SST time-series data for 14 regions around Hokkaido, and reviewed past and on-going surveys of chum salmon population dynamics in relation to coastal ocean condition in these areas. Finally, we propose adaptive hatchery strategies for Hokkaido chum salmon, linking our results to findings in the literature.

MATERIAL AND METHODS

Salmon Data

Chum salmon return rates (survival proxies) were compared among the 14 geographic regions where the Hokkaido Prefectural Government manages fisheries and hatchery programs (Fig. 1; Miyakoshi et al. 2013). While the number of hatchery juvenile chum salmon released increased significantly in the 1970s, release numbers have been relatively stable in each region since the 1980s (Saito and Nagasawa 2009; Nagata et al. 2012). We examined return rates for the 25 brood years from 1983 to 2007. Return rates for each region were calculated using three data sets: the number of juvenile chum salmon released for each brood-year, coastal and river catches during 1985–2014, and age composition data for river catches over the same period. These data were based on values in annual reports (HSH 1983–1998; NASREC 1999–2009; HFH 2002–2009; SFFRI 2010–2013; unpublished data 2014), the Salmon Database 7(1)–14(1) and 7(2)–8(2) published by NASREC (1999–2000), and ten-day reports of commercial catches (HFZCC 2009–2014) and in-river catches (HSEPA 2009–2014). The return rate (*RR*) for each brood year (from 2 to 7 years old) in each region was calculated according to previous papers (see Miyakoshi et al. 2007a; Saito and Nagasawa 2009) as follows:

$$RR = (CC + RC) \times 100 \,/\, FR,$$

where *CC* is the total number of each brood-year adults caught by commercial fisheries in the coastal waters of the region, and *RC* is the total number of each brood-year adults caught in weirs for brood stock in rivers with hatchery operations in the region. *FR* is the total number of each brood-year chum salmon juveniles released from hatcheries in rivers in the region.

We calculated return rate under two assumptions. First, all of the chum salmon are of hatchery origin. Although natural spawning has been reported in many rivers, including rivers with hatchery operations in Hokkaido (Miyakoshi et al. 2012), the number of natural spawners is unknown, but thought to be relatively small. Second, coastal commercial salmon catches are made up primarily of fish returning to rivers in the region where they were caught. In reality, coastal catches are probably mixtures of stocks, comprising different regional populations. Stock identification techniques such as genetics (e.g., Beacham et al. 2008) and otolith mass-marking (e.g., Brenner et al. 2012) can help to evaluate how seriously this assumption has been violated, but have not been used here.

SST Data

According to Kaeriyama (1989), juvenile chum salmon less than 120 mm fork length reside in coastal regions for lengthy periods before moving offshore. Around Hokkaido, most juvenile chum salmon are initially distributed within 30 km from shore, with some differences among regions (within 18 km in the Okhotsk Sea; 20 km in the Japan Sea; 30 km in the Pacific Ocean; Irie 1990). Thus, the regions for study of the early life of juvenile chum salmon encompass coastal areas within 30 km offshore in the 14 regions around Hokkaido. It is known that there are differences of about one month in the duration of early ocean life for chum salmon among the regions (e.g., Kaeriyama 1989; Irie 1990; Mayama and Ishida 2003). In this paper, in order to compare SST trends among the 14 regions, we assumed that the duration of early ocean life for chum salmon was from 1 April to 31 July because most of juvenile chum salmon are captured mainly for 4 months from April to July in the coastal waters around Hokkaido (Irie 1990; Kawamura et al. 2000b; Mayama and Ishida 2003; Nagata et al. 2007). Annual SST anomalies were calculated as deviations from long-term averages for the 24 years from 1985 to 2008 when chum salmon juveniles from the 1984–2007 brood years were in coastal waters. Earlier (pre-1985) fine-scale SST data were not available. The original SST data during 1985–2008 within 30 km offshore were provided by the Japan Meteorological Agency as 10-day mean sea-surface temperatures analyzed for 0.25-degree by 0.25-degree grid points (NEAR-GOOS regional real time data base; http://ds.data.jma.go.jp/gmd/goos/data/database.html).

Regional Surveys

We have surveyed local distributions and growth of juvenile chum salmon as well as habitat conditions including water temperature and prey abundance in rivers and coastal waters of Hokkaido since the 1990s. Here we summarize results from this earlier work relating the distribution and growth of juvenile chum salmon to SSTs for three regions around Hokkaido (the northern Japan Sea, the eastern Okhotsk Sea, and the southern Nemuro Strait). We compare our findings with those in the literature in order to develop recommendations for changes in hatchery operations that can benefit chum salmon.

Statistical Analysis

Correlations between survival and SST for major regions were calculated by the Spearman rank correlation (Zar 1984) that does not require an assumption of normal distribution. Clustering of correlation coefficients used the unweighted pair group method with arithmetic means (UPGMA, Sneath and Sokal 1973).

RESULTS AND DISCUSSION

Return Rate Anomalies and Regional Covariation

Return rate anomalies as deviations for each brood year from the long-term average (1983 to 2007) were calculated for the 14 regions (Fig. 2). Correlations between various regions of Hokkaido were significant (Fig. 3); the cluster analysis revealed five distinct regional groups (A–E) at the 0.40 coefficient level ($P = 0.05$; Fig. 4). Regions within the A, C, D, and E groups were adjacent to each other. The

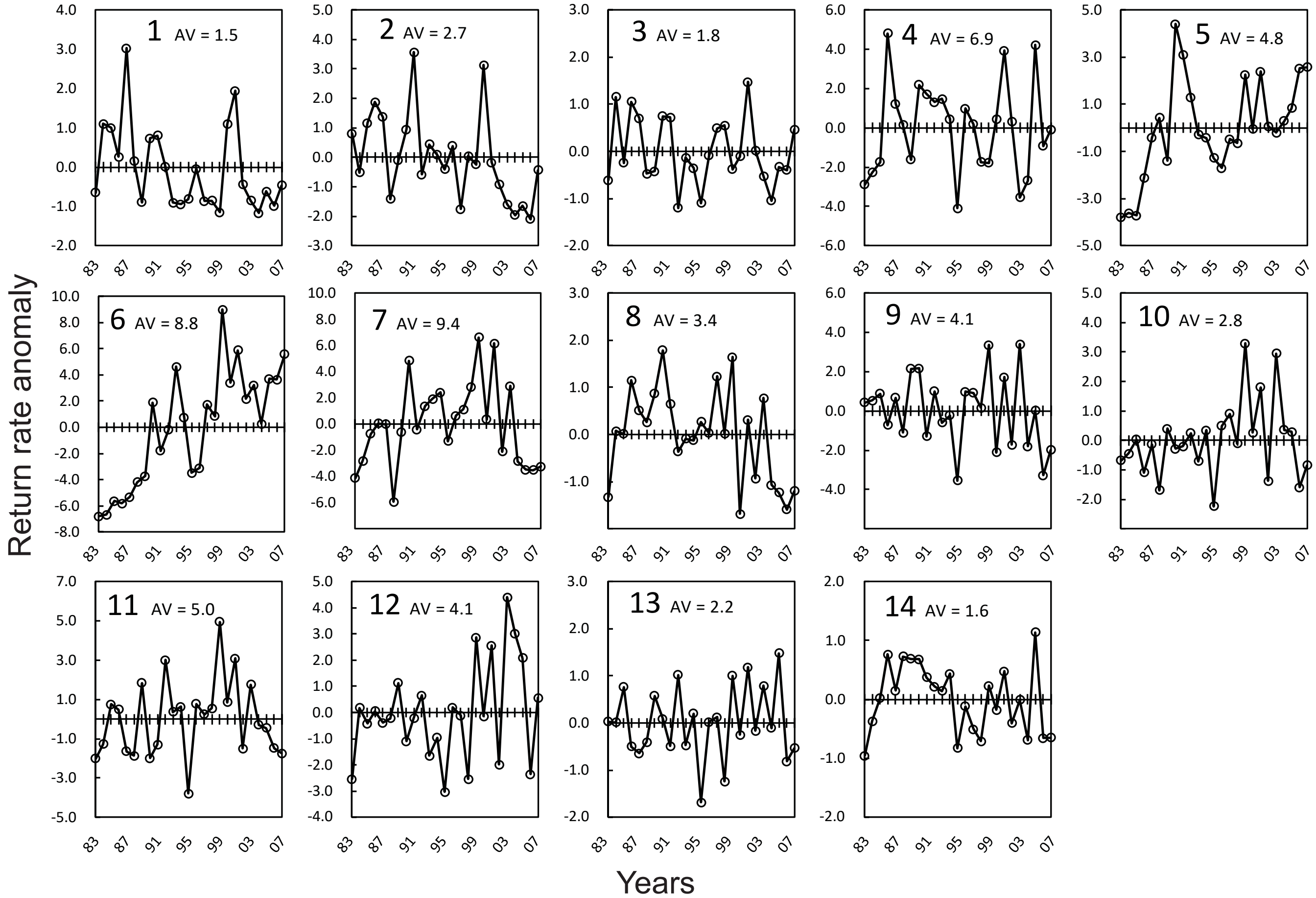

Fig. 2. Return rate anomalies (deviations from a long-term average) for chum salmon in the 14 regions (1983-2007 brood years). Return rate in each region = (total number of catch in coastal waters (commercial) and rivers (brood stock)) x 100 / (total number of hatchery juveniles). Age composition of brood year is from 2 years to 7 years old. AV means the average of return rates for all brood years. Regions described in Fig. 1.

A-group comprised three regions (1, 2, 3; Fig. 1) within the Japan Sea, characterized by variable but decreasing return rates. In contrast, the C-group contained mid- and eastern regions (5, 6) in the Okhotsk Sea that exhibited gradual survival increases. The D-group contained two regions (7, 8) of the Nemuro Strait, which were characterized by high return rates in the early brood years but large decreases in recent brood years. The E-group contained most regions of the Pacific Ocean, excluding 14, which were characterized by expanding variation in recent years. The B-group comprised the west region (4) of the Okhotsk Sea and the Donan region (14) in the Pacific Ocean, although the two regions were geographically isolated. This group clustered close to the A-group in the Japan Sea.

When Saito and Nagasawa (2009) compared return rate correlations among five large regions (Japan Sea, Okhotsk Sea, Nemuro Strait, Eastern Pacific Ocean and Western Pacific Ocean) of Hokkaido for the 1976–1998 brood years (23 years), they concluded that return rates were similar within the Okhotsk Sea-Nemuro Strait. This difference between their study and ours appears to be caused by recent reductions in return rates in Nemuro Strait (Fig. 2).

Sea Surface Temperature Anomalies and Regional Variation

We analyzed annual SST variations among the 14 regions as an indicator of coastal ocean environments where chum salmon (1984–2007 brood years) spent their early marine lives. SST anomalies (April to July, 1985–2008) among the 14 regions showed different patterns, often significant (Figs. 5, 6). Five adjacent groups (A–E) were found at the 0.85 coefficient level ($P < 0.001$) using UPGMA cluster analysis (Fig. 7). The E-group comprised the mid and south regions (1, 2) of the Japan Sea, and the Donan and Funka Bay regions (13, 14) in southwestern areas of the Pacific Ocean, characterized by relatively high average SSTs (11.8–13.4°C) that had been gradually increasing (Fig. 5). Young salmon from this area would be strongly affected by the Tsushima Warm and Tsugaru Warm currents (Fig. 1, Isoda and Kishi 2003). Farther north, the A-group comprising the northern region (3) of the Japan Sea and the western region (4) of the Okhotsk Sea had lower average SSTs (8.3–11.1°C) than the previous group, but it gradually increased (Fig. 5). Fish in this area would be less strongly affected by

1														
2	0.49													
3	0.57	0.41												
4	0.41	0.34	0.53											
5	−0.02	−0.23	0.06	0.36										
6	−0.32	−0.31	0.06	0.21	0.68									
7	−0.02	0.29	0.28	0.26	0.13	0.38								
8	0.12	0.19	0.33	0.10	−0.02	−0.13	0.53							
9	0.09	0.06	0.10	0.05	−0.09	0.00	0.61	0.59						
10	−0.17	−0.07	−0.02	0.00	0.01	0.29	0.58	0.27	0.67					
11	−0.10	0.05	−0.03	0.11	−0.06	0.28	0.63	0.16	0.53	0.77				
12	−0.29	−0.29	−0.03	0.08	0.24	0.26	0.21	0.22	0.44	0.69	0.60			
13	−0.01	−0.19	−0.16	0.11	0.06	0.19	0.33	0.14	0.71	0.71	0.58	0.59		
14	0.28	0.23	0.22	0.67	0.25	0.04	0.25	0.42	0.37	0.20	0.30	0.38	0.44	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14

Fig. 3. Spearman rank correlation coefficients (r_s) among chum salmon return rates of the 14 regions in Hokkaido. Correlations in dark gray boxes are significant (P < 0.01); light gray boxes indicate correlations for which 0.05 ≤ P < 0.01. Regions described in Fig. 1.

the Tsushima Warm Current than fish in the E-group. The mid- and eastern regions (5, 6) of the Okhotsk Sea and the northern region (7) of the Nemuro Strait were included in the B-group that had the lowest average SSTs (6.6–7.3°C) and relatively little variation in SST anomalies (Fig. 5). Because the Okhotsk Sea is frozen during winter, cold seawater conditions dominate in early spring, followed by warm coastal waters from the Soya Warm Current (Asami et al. 2007; Sawada et al. 2007). The C-group included the southern region (8) of the Nemuro Strait and the eastern region (9) of the Eastern Pacific Ocean, with the lowest average SST (6.8–7.3°C) similar to the B-group, and highly variable SST (Fig. 5). The Eastern Pacific Ocean is influenced by the cold Coastal Oyashio Current (Fig. 1). The western region (10) of the Eastern Pacific Ocean, the Hidaka (11) and Iburi (12) regions of the Western Pacific Ocean were included in the D-group. Average SSTs were 8.9–10.9°C, intermediate between the east and west regions (Fig. 5). Although SST fluctuations were large, similar to the C-group, SSTs have recently decreased.

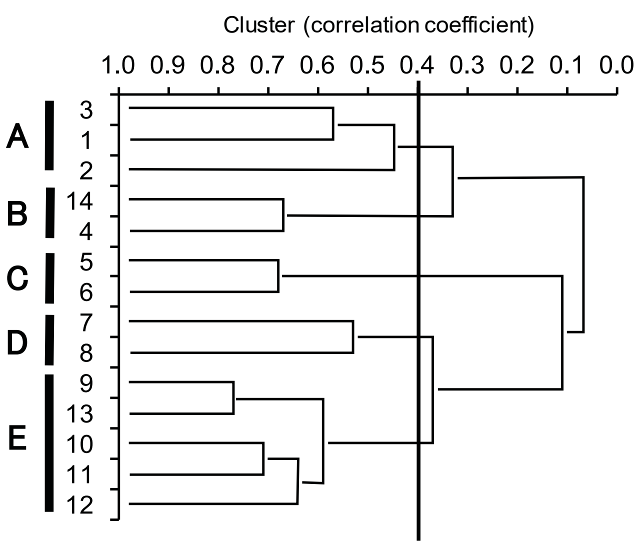

Fig. 4. Dendrogram showing UPGMA clustering of 14 regions into five regional groups with significant correlation (0.40) cut off at P = 0.05. Regions described in Fig. 1.

Management Implications of Regional Variability in Survival

It is perhaps surprising that in the relatively small island of Hokkaido, 5 regional groups with distinct return rate patterns were identified by clustering correlation coefficients. However, the coastal oceanography of the island of Hokkaido is complex (Fig.1). There is much published literature that suggests that high mortality of chum salmon may be caused by physical and biological factors in their early life stages, including the period in fresh water (e.g., Bax 1983; Pearcy 1989; Fukuwaka and Suzuki 2002; Saito and Nagasawa 2009; Morita et al. 2015). In this paper we found that regional groupings of SST variation were similar to regional groupings of return rates (Figs. 4, 7), implying that variations in return rates were linked to early marine conditions such as SST. Hokkaido chum salmon are produced primarily by hatcheries, although some natural spawning takes place (Miyakoshi et al. 2012; Morita et al. 2013). In hatcheries, there is limited flexibility in release timing due to finite water supplies and rearing space. Surveys of the distribution and growth of juvenile chum salmon in Hokkaido suggested that variations in chum salmon survival might be caused by matches or mis-matches between the timing of release of juvenile salmon and coastal water conditions that affect food production and predation during their early life (Nagata et al. 2007). If our general hypothesis that recent sur-

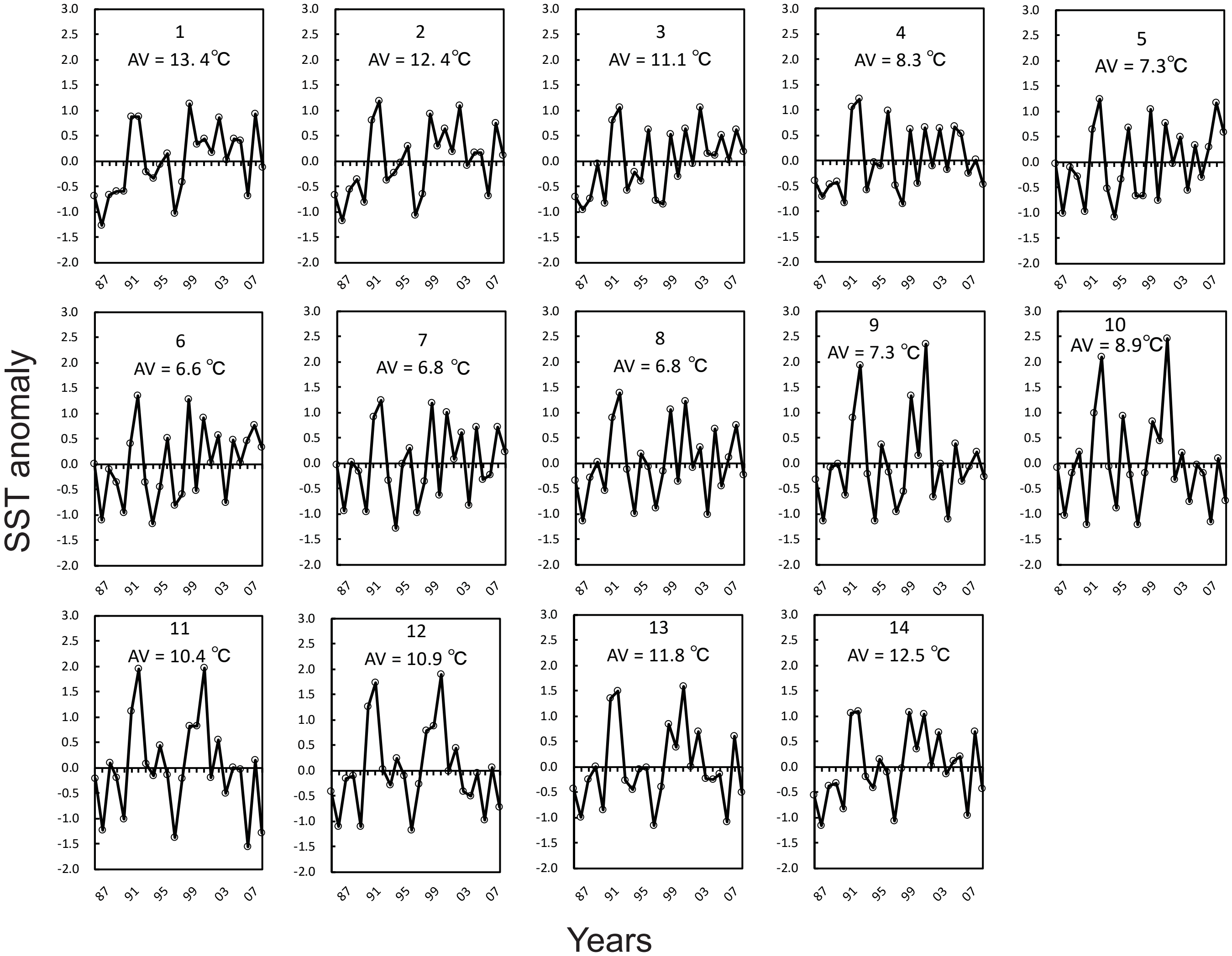

Fig. 5. April–July SST anomalies (deviations from a long-term average) within 30 km offshore of the 14 regions around Hokkaido during 1985–2008. AV is the average SST during the 4 months in 24 years. Regions described in Fig. 1.

vival variations in Hokkaido chum salmon populations are closely related to their early marine life history in nearshore environments is true, it may be appropriate to alter stocking strategies to reduce variation in the numbers of returning chum salmon (Nagata et al. 2007). An alternative approach is to stagger hatchery releases over an extended period to increase the likelihood that some release groups will migrate when conditions are optimal, regardless of when that might be (Irvine et al. 2013; Morita and Nakashima 2015). We tested our hypothesis using findings in the literature augmented by results from our own coastal surveys to provide region-specific hatchery recommendations intended to enhance chum salmon survival.

Eastern Region of the Okhotsk Sea

Mean return rate of chum salmon and SSTs in this region were 8.8% and 6.6°C, respectively, the highest and coolest in the 14 regions; both return rates and SSTs tended to increase gradually (6 in Figs. 1, 2, and 5). Juvenile chum salmon have been released from late April to early June in this region (Table 1). We surveyed the spatial and temporal distribution of marked juvenile chum salmon and ocean conditions in the littoral and coastal waters of Abashiri Bay from 2002 to 2005 when juvenile salmon from the 2001 to 2004 brood years migrated to the sea. Juvenile salmon were densely distributed in coastal waters ranging from 8–13°C. Marked juveniles reached 60–80 mm in fork length before moving offshore. During cool years (2003 and 2005), when SST did not reach 8°C in May, juvenile salmon did not move offshore from the littoral zone water until June, and growth was slow. In contrast, in warm years (2002 and 2004), salmon dispersed quickly from coastal littoral waters to the offshore (1–7 km) where they had an extended residency and grew rapidly (Table 1; Nagata et al. 2007; Miyakoshi et al. 2007c). Return rates were much lower for fish leaving in cool years (2003 and 2005, corresponding to brood years 2002 and 2004) than for fish leaving in warm years (2002 and 2004,

1														
2	0.95													
3	0.83	0.89												
4	0.77	0.83	0.87											
5	0.68	0.73	0.81	0.72										
6	0.72	0.76	0.82	0.74	0.97									
7	0.73	0.78	0.76	0.74	0.95	0.93								
8	0.69	0.71	0.69	0.67	0.85	0.86	0.90							
9	0.66	0.67	0.60	0.59	0.73	0.76	0.82	0.90						
10	0.67	0.71	0.52	0.55	0.56	0.58	0.72	0.77	0.87					
11	0.78	0.79	0.57	0.63	0.50	0.55	0.66	0.68	0.78	0.90				
12	0.82	0.82	0.61	0.59	0.52	0.57	0.63	0.68	0.72	0.89	0.93			
13	0.85	0.90	0.74	0.72	0.65	0.67	0.74	0.72	0.73	0.85	0.88	0.92		
14	0.94	0.91	0.73	0.72	0.62	0.67	0.73	0.73	0.74	0.83	0.89	0.89	0.93	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14

Fig. 6. Spearman rank correlation coefficients (r_s) among SST of the 14 regions in Hokkaido. Correlations in dark gray boxes are significant ($P \leq 0.001$); light gray boxes indicate correlations for which $0.01 \leq P < 0.001$. Although there are similar trend in correlation coefficient compared to return rate, assuming that cut off of correlation coefficient was at 0.85, the 5 regional groups were produced. Regions described in Fig. 1.

corresponding to brood years 2001 and 2003; Figs. 2, 5). These results support our hypothesis.

To reduce variability in annual survival, we recommend that chum salmon fry be released when coastal waters are between 7 to 11°C (Nagata et al. 2007). We further suggest using the sea level difference between Wakkanai in northernmost Hokkaido and Abashiri as an index of the strength of the Soya Warm Current driving warmer conditions (Aota 1984; Asami et al. 2007; Sawada et al. 2007).

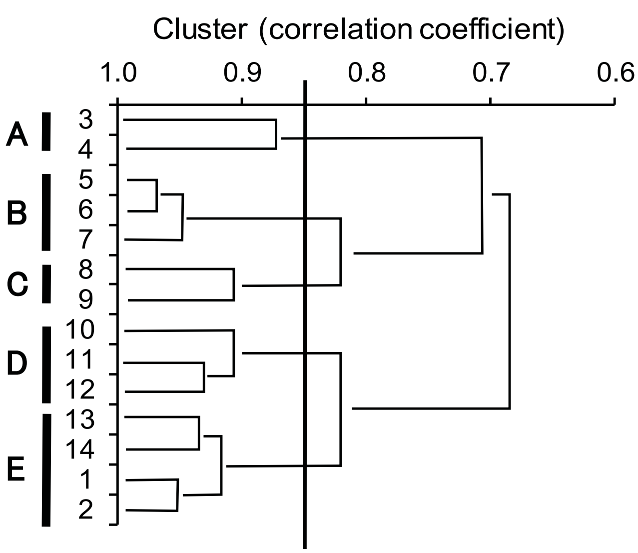

Fig. 7. Dendrogram showing UPGMA clustering of 14 regions into five regional groups with significant correlation (0.850) cut off at $P < 0.001$. Regions described in Fig. 1.

Southern Region of Nemuro Strait

The overall mean return rate was 3.4% although rates have decreased recently (8 in Figs. 1, 2). Mean SST was 6.8°C and SSTs showed no trend (Fig. 5). Juvenile chum salmon have been released from mid-March to late-May (Table 1). We surveyed the spatial and temporal distribution of marked juvenile chum salmon in coastal waters of Nemuro Bay and the Nishibetsu River from 2007 to 2010 when juvenile chum salmon from the 2006 to 2009 brood years migrated to the sea. Juvenile chum salmon had been released into the Nishibetsu River from hatcheries 100 km upstream from the river mouth (Kasugai et al. 2012, 2013). Earlier releases took longer to migrate downstream to the sea than later releases (Kasugai et al. 2013). In addition, ATP (adenosine triphosphate) levels, an index of fish quality, declined during downstream migration (Mizuno et al. 2007; Mizuno and Misaka 2012; Mizuno 2013). Optimal SSTs for juvenile chum salmon in coastal waters ranged from 8˚C to 13˚C and marked juveniles reached 70–80 mm in fork length before moving offshore (Table 1). Juvenile salmon were restricted to littoral waters when nearshore SSTs were below 8˚C (Kasugai et al. 2012), which is consistent with the Abashiri Bay. Return rates were lower for early released groups than for later groups (K. Kasugai, unpublished data), probably because of high mortality in the river and/or estuary and the marine littoral zone before the fish migrated offshore (Kasugai et al. 2012, 2013). These results support our hypothesis excluding the reduction of fish quality in the river. We recommend hatchery releases be dispersed along lengthy rivers rather than at one or a few mass-release locations, and that releases be controlled to utilize optimal coastal temperatures > 8˚C.

Table 1. Summary of ocean conditions, release timing, distribution, and growth of juvenile chum during their early life for three regions (3, northern region of the Japan Sea; 6, eastern region of the Okhotsk Sea; 8, southern region of the Nemuro Strait) and recommendations for hatchery programs. FL is fork length (mm).

Region	Dominant seawater (Fig. 1)	Mean SST and long-term trend April–July (Fig. 5)	Long-term trend of return rate (Fig. 2)	Release timing[1]	Optimal SSTs for residency	FL at offshore movement	Results of coastal survey[2]: Spatial distribution in coastal waters		Survival		Recommendation to improve the hatchery program
							Warm year	Cool year	Warm year	Cool year	
Japan Sea (Region 3)	warm	11.1°C gradually increase	down	mid-March to early-May	6°C < SST < 13°C	70	short residency	long residency	low ?	high ?	recovery of late-run stock
Okhotsk Sea (Region 6)	cold	6.6°C gradually increase from 1990s	up	late-April to early-June	8°C < SST < 13°C	60 < FL < 80	quick dispersal and long residency	restricted dispersal and short residency	high	low	release at 7°C < SST <11°C
Nemuro Strait (Region 8)	cold	6.8°C no trend	up and down	mid-March to late-May	8°C < SST < 13°C	70 < FL < 80	quick dispersal	restricted dispersal	high	low	delayed and dispersed release

[1]Release timing in each region recorded in those years when the coastal survey was conducted.
[2]The coastal surveys in regions 3, 6, and 8 were conducted in 1995–1999, 2002–2005, and 2007–2010, respectively.

Northern Region of Japan Sea

In this region, the mean return rate was 1.8%, one of the lowest, and return rates have either decreased or been low since the 1990s (Figs. 1, 2). Mean SST was 11.1°C, warmer than the Okhotsk and Nemuro Strait regions, and SSTs increased gradually (Fig. 5). The coastal distribution of juvenile chum salmon and predation by seabirds were surveyed off Mashike in 1995–1998 when juvenile chum salmon from 1994–1997 brood years went to sea (Kawamura et al. 1998, 2000a, b). Chum salmon were concentrated in regions with SSTs from 6°C–13°C within 0.5 km of shore. Juvenile chum salmon that reached 3g in body weight and 7cm in fork length tended to move offshore. During warm years (1995 and 1998), the period of time with favorable SSTs (below 13°C) was restricted, resulting in higher competition and predation by seabirds; in cool years (1996 and 1997), the duration of favorable SSTs was greater, which should have benefited juvenile salmon (Kawamura et al. 1998, 2000b). In addition, there was no effect of fish size on return rate (Saneyoshi et al. 2013). These results partly support our hypothesis. However, while SSTs in 1995 and 1998 were warmer than in 1996 and 1997 (Fig. 5), return rates for the 1994 and 1997 brood years that migrated during warm conditions were similar to the 1995 and 1996 brood years with cool conditions (Fig. 2).

Recent low return rates in the Japan Sea may have been caused by ocean conditions not only during the early life stage but also during the homing stage. The numbers of early-run chum salmon (September–October) in the Japan Sea were related to the strength of Tsushima Warm Current in their return year (Kaeriyama et al. 2014). Adult chum salmon may have difficulty migrating when temperatures exceed 20°C, which has been interpreted as a negative effect of global warming (Kaeriyama et al. 2014).

We encourage managers to focus on recovering late-run chum salmon because these fish return later than early-run fish, and are less likely to experience excessively warm water as they migrate along the coast. Traditionally, hatchery programs have focused on early-run chum salmon because they can be caught more conveniently in commercial fisheries. While in the early 1980s both early- and late-run chum were caught in weirs around Hokkaido, in recent years late-run chum have largely disappeared (Miyakoshi et al. 2013). Fortunately late-run chum are reported to spawn naturally in the wild and/or hatchery-operated rivers in recent years (Miyakoshi et al. 2012; Morita et al., 2013).

Long-term Relationships between Return Rates and SST

The close relationship between chum salmon survival and their early marine environments are demonstrated by the results of our regional surveys and other Japanese studies (e.g., Fukuwaka and Suzuki 2002; Saito and Nagasawa 2009). Examining correlations between adult return rates for 24 brood years (1984–2007) and average SST for four months from April to July in 24 years (1985–2008) during

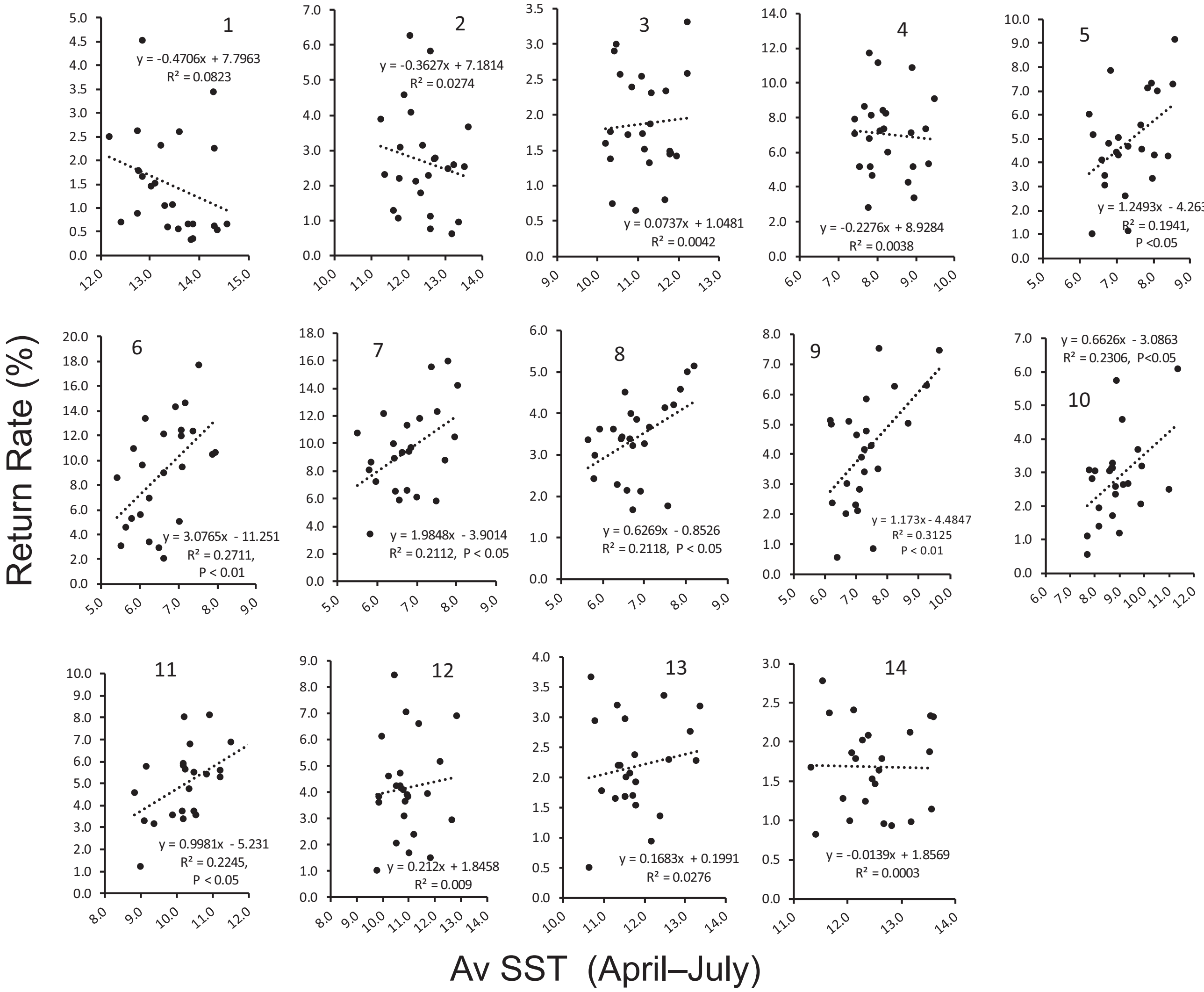

Fig. 8. The relationship between chum salmon return rates for 24 brood years and average SST for April–July during early life for 24 years in 14 regions of Hokkaido. Regions described in Fig. 1.

their early life (Fig. 2 and 5) revealed that in most of eastern Hokkaido, including mid- and eastern regions of the Okhotsk Sea, northern and southern regions of the Nemuro Strait, eastern and western regions of the Eastern Pacific Ocean, and Hidaka region of the Western Pacific Ocean, return rates were significantly positively-correlated with the average SST in the coastal waters where juveniles presumably spent their early marine lives (Fig. 8). The mid- and eastern regions of Okhotsk Sea clustered in the same group (C and B) for return rates and SSTs (Figs. 4, 7), return rates increased along with increases in SSTs from the 1980s to 2000s, especially in the eastern region (Figs. 2, 5), suggesting that the warmer coastal waters resulted in higher survival. Northern and southern regions of Nemuro Strait clustered in the D-group for return rate, but in the B- and C-groups for SSTs, respectively; recent rapid reductions in return rates for both regions were not solely explained by a positive relation between return rate and SSTs (Figs. 2, 8). As shown in the regional survey of the southern region, the recent reductions may be related to the changes in not only ocean environments but also fish quality during the residency in river. Although several regions of Pacific Ocean included in the E-group for return rate and C- or D-group for SSTs showed positive correlation between return rate and SSTs (Fig. 8), there were great annual variations in both indices. Additional regional surveys in the Kushiro coast in the eastern region of the Pacific Ocean also showed that the distribution of juvenile chum salmon was related to coastal seawater temperature affected by the cold Coastal Oyashio Current (Kasugai et al. 2016). In contrast, western regions showed no significant correlations, although negative correlations were found in the mid- and southern regions of the Japan Sea (Fig. 8). Because average SST was colder in eastern than in western regions (Fig. 5), the coolest conditions appeared to negatively affect returns. Therefore, this apparent linkage between adult return rate and SST as an index of the coastal ecosystem during early life supports our hypothesis, especially in the eastern regions occupied predominantly by cold water currents during the early life of chum salmon.

CONCLUSIONS

Hokkaido chum salmon survival patterns were correlated with regional seawater temperatures during their early marine and return migration stages. While the timing of releases of hatchery juvenile chum salmon varies among regions (Miyakoshi et al. 2007b), release timings have not been adjusted to account for the highly variable regional temperatures differences shown in Fig 5. Climate change is expected to result in a decreased carrying capacity for chum salmon in the North Pacific, density-dependent effects, and potentially the loss of migration routes to the Bering Sea (Kaeriyama 2008; Abdul-Aziz et al. 2011). As river and ocean conditions will continue to be affected by anthropogenic activity and climate change, hatchery operations should adapt to environmental changes. We therefore need to continue monitoring physical and biological conditions to detect potential mis-matches between chum salmon and their environments in order to be able to adapt hatchery strategies regionally to take advantage of varying habitat conditions.

In order to enhance the effectiveness of hatchery programs, managers not only need to establish stocking strategies to release juvenile hatchery chum salmon at optimal times to meet suitable environments such as 7–11°C (Nagata et al. 2007), but also to improve the energetic quality of fish to minimize and avoid predation. Tsukamoto (1993) indicated that potential survivability of released chum salmon be evaluated by morphological, physiological and ecological characteristics. For example, juvenile chum salmon with high ATP levels have high quality body condition (Mizuno et al. 2007; Mizuno 2012, 2013). On the other hand, if quality corresponds to fitness in genetics, high quality may influence the ability of juvenile chum salmon to survive and reproduce in natural environments (Taniguchi 1993). Populations are adapted to their regional environments (e.g., Carvalho 1993; Burger 2000; Schindler et al. 2010).

The genetic structure of chum salmon in Hokkaido consists of 5 regional groups (Beacham et al. 2008; Sato and Urawa 2015) that are more or less geographically aligned with the regional clusters found here in adult return rates and SST during their early life (Figs. 4, 7). While genetic diversity of Japanese hatchery chum salmon overall is relatively high (Beacham et al. 2008; Kitada 2014), genetic differentiation within regions may be low, perhaps due to homogenization by previous egg-transplantation projects undertaken by hatchery programs (Yokotani et al. 2009). If this is true, hatchery chum salmon in Hokkaido may be poorly adapted to major changes in river and ocean conditions. Evidence for reduced reproductive success or survival of hatchery fish has accumulated in salmonids such as Atlantic salmon (Milot et al. 2013), steelhead trout (Araki et al. 2007), and coho salmon (Thériault et al. 2011; Zimmerman et al. 2015), species that tend to be reared for lengthy periods before release, although evidence for chum salmon is lacking (Berejikian et al. 2009). Therefore, we need to monitor and conserve regional wild chum salmon (Miyakoshi et al. 2012; Nagata et al. 2012) and to restrict egg transplantation between different genetic populations to avoid genetic disturbance and promote the sustainable use of chum salmon resources in Hokkaido.

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