

## Stock-Specific Abundance of Chum Salmon in the Central Gulf of Alaska during Winter

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Urawa, S., T.D. Beacham, S. Sato, T. Kaga, B.A. Agler, R. Josephson, and M. Fukuwaka. 2016. Stock-specific abundance of chum salmon in the central Gulf of Alaska during winter. *N. Pac. Anadr. Fish Comm. Bull.* 6: 153–160. doi:10.23849/npafcb6/153.160.

**Abstract:** Winter is believed to be a critical period for marine salmon survival. In February 2006, a winter research cruise was conducted to examine the stock-specific distribution and biological status of salmon in the central Gulf of Alaska (GOA). By surface trawl, 519 chum salmon (*Oncorhynchus keta*) were caught at seven stations (48–54°N, 145°W) where the surface seawater temperature ranged from 5.2°C (54°N) to 7.0°C (48°N). Ocean age-2 and -3 fish were dominant at all sampling stations, and young fish (ocean age-1) were distributed in the southern stations. The stock composition of chum salmon abundance (CPUE) estimated by microsatellite DNA analysis was 11% western Alaska/Alaska Peninsula, 11% Prince William Sound (PWS), 16% Southeast Alaska (SEAK), 6% northern British Columbia (BC), 17% southern BC, 2% Washington, 17.5% Russian, and 20% Japanese stocks. There was a latitudinal shift in the stock-specific distribution: North American stocks were dominant in northern waters, and Asian stocks were dominant in southern waters. All young fish (ocean age-1) were North American origin (mostly PWS, SEAK and southern BC), while the proportion of Asian (Japan and Russia) stocks increased with ocean age. The samples included 48 otolith-marked fish released from hatcheries in PWS (n = 7), SEAK (n = 37), BC (n = 1), and Japan (n = 1). A comparison of CPUEs estimated by genetic stock identification and otolith mark recoveries suggested that the contribution of hatchery fish was variable among brood years (0–51%, PWS stock; 19–87%, SEAK stock). Microsatellite and otolith mark analyses confirmed that various stocks of North American and Asian chum salmon inhabit the central GOA during winter. Their winter distribution pattern is different among regional stocks or age groups, maybe reflecting stock- or age-specific preferences for habitat water temperatures to maximize survival.

**Keywords:** chum salmon, stock-specific abundance, hatchery contribution, winter, Gulf of Alaska

### INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are widely distributed on the high seas of the North Pacific Ocean (NPO) and adjacent waters. In general their seasonal migration occurs to the north and west during summer/fall and to the south and east during winter/spring (see review by Myers et al. 2007), and they experience various ecosystems throughout their life cycle. Climate and associated ocean ecosystem changes affect trends in the abundance of Pacific salmon (Beamish et al. 1999). Marine mortality of salmon may occur primarily during two specific stages (Farley et al. 2007).

The first stage occurs just after juvenile salmon enter the marine environment; whereas, the second stage occurs following the first summer at sea, when individuals die in late fall and winter as a result of insufficient energy reserves (Beamish and Mahnken 2001). Nomura et al. (2000) reported low lipid levels in chum (*O. keta*) and pink salmon (*O. gorbuscha*) during winter. In particular, ocean age-1 salmon had lower lipid content than older fish, suggesting that young fish may be depleting their energy reserves during the first winter (Nomura et al. 2000; Kaga et al. 2006).

The Gulf of Alaska (GOA) is an important habitat for Pacific salmon. Various stocks of Asian and North American

chum salmon intermingle in this area during the winter (Urawa et al. 1997), while North American stocks are dominant during the summer (Urawa et al. 2000, 2009). In February 2006, a winter research cruise was conducted to examine the spatial distribution and biological status of chum salmon in the NPO including the central GOA (Fukuwaka et al. 2006). Beacham et al. (2009) briefly reported the stock composition of chum salmon mixture samples caught in the GOA during this cruise by microsatellite DNA analysis. In this paper, we examined the stock-specific distribution and abundance of chum salmon and their habitat environment in the winter GOA using their stock estimates and additional catch and water temperature data. In addition, we reported the recovery of otolith-marked chum salmon from the samples and estimated the contribution of hatchery fish to the chum salmon population in the GOA by combining genetic and otolith mark analyses.

**MATERIALS AND METHODS**

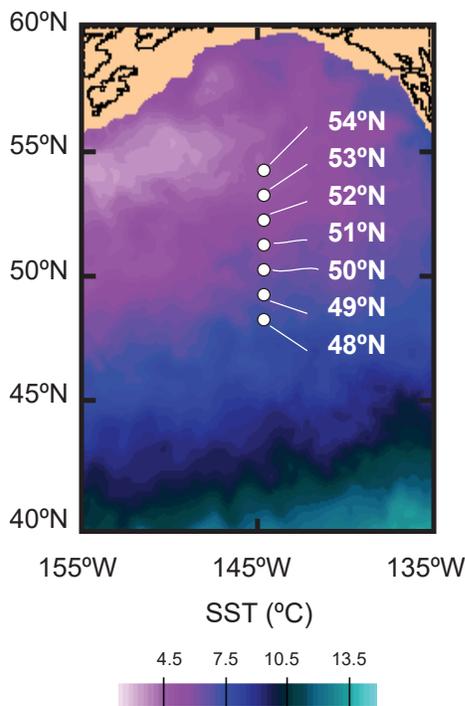
**Fish Samples**

Fish were caught at seven stations (48–54°N along 145°W, Fig. 1) in the central GOA by a surface trawl (net mouth: approximately 50 m x 50 m) from the Japanese R/V *Kaiyo maru* moving at 5 kn for 1 hour on 15–18 February 2006 (Fukuwaka et al. 2006). The fork length, body weight and gonad weight of each fish were recorded, and scales

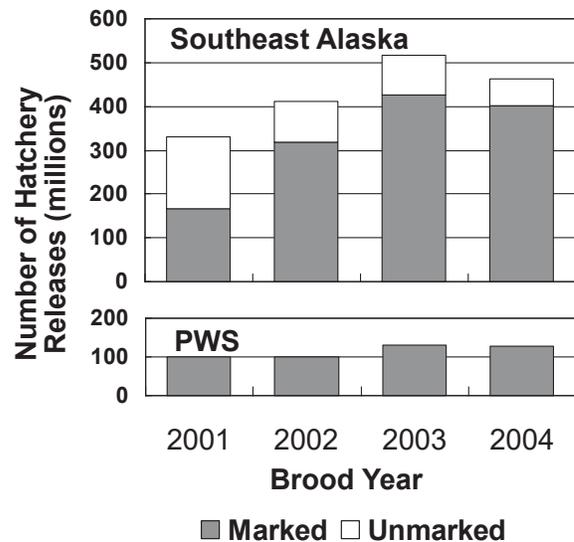
were removed for age determination. In addition, the pectoral fin and two sagittal otoliths were collected from each chum salmon. The sagittal otoliths were cleaned and placed in 96-well microplates for detection of otolith marks at the Mark, Tag, and Age Laboratory, Alaska Department of Fish and Game (ADFG), Juneau, Alaska, USA. The fin samples were preserved in 95% ethanol for genetic stock identification at the Pacific Biological Station, Nanaimo, BC, Canada. The catch per unit effort (CPUE) was calculated as the total number of fish caught per 1-h trawl.

**Genetic Stock Identification (GSI)**

DNA was extracted from the fin samples, variations at 14 microsatellite loci (*Ots3*, *Oke3*, *Oki2*, *Oki100*, *Omm1070*, *Omy1011*, *One101*, *One102*, *One104*, *One111*, *One114*, *Ots103*, *Ssa419*, and *OtsG68*) were surveyed, and genotypes were determined for each locus in each sample (Beacham et al. 2009). The statistical software program (SPAM version 3.7) was used to estimate stock composition of mixture samples. The baseline data set included 354 populations, covering major spawning stocks in North America and Asia. The reporting regions were: Fall Yukon, Western Alaska/Alaska Peninsula (WAK/AKP), Southeast Alaska (SEAK), Kodiak, Prince William Sound (PWS), Northern British Columbia (BC), Southern BC, Washington, Japan, Russia, and Korea. Simulation studies indicated that all reporting regions showed > 90% accuracy when true group contributions were 100%. Stock-specific CPUE was calculated by using the GSI estimates and catch data (CPUE) of chum salmon (Fukuwaka et al. 2006).



**Fig. 1.** Map showing sampling locations in the central Gulf of Alaska with a satellite image of sea surface temperatures (SST) on 15–18 February, 2006. (Data source: [www7320.nrlssc.navy.mil/global\\_nlom/westc.html](http://www7320.nrlssc.navy.mil/global_nlom/westc.html)).



**Fig. 2.** Number of otolith-marked and unmarked chum salmon fry released from hatcheries in Southeast Alaska and Prince William Sound (PWS). Data sources: Agler et al. 2002, 2003, 2004, 2005; NPAFC 2016.

**Thermal Otolith Marks**

The left sagittal otoliths ( $n = 519$ ) were glued to petrographic slides with thermoplastic cement and then ground to a thin section. They were examined under a transmitted light compound microscope to observe the microstructure patterns. These patterns were compared to mark patterns in the database of otolith mark releases (<http://npafc.taglab.org>; Johnson et al. 2006) to determine hatchery origins. All otoliths were read independently by two readers.

A large number of otolith-marked chum salmon fry (brood years 2001–2004) was released annually in PWS and SEAK (Agler et al. 2002, 2003, 2004, 2005). In PWS, all hatchery chum salmon fry were produced at the Wally Noerenberg Hatchery, from which approximately one hundred million fry were released annually after being 100% otolith marked (Fig. 2). Three to five hundred million otolith-marked chum salmon fry were annually released from the Macaulay, Hidden Falls and Neets Bay hatcheries in SEAK, where the percentage of otolith-marked fish among hatchery releases was 51–85% for the 2001–2004 brood years (Fig. 2). The contribution of hatchery fish to PWS and SEAK chum salmon (brood years 2001–2004) existing in the GOA was estimated by comparing CPUEs of PWS and SEAK chum salmon determined by GSI (i.e., hatchery + wild fish) and otolith mark (hatchery fish) recoveries. CPUE of PWS or SEAK hatchery fish was determined with the following formula: CPUE of hatchery fish equals the number of PWS or SEAK otolith-marked fish caught per 1-h trawl divided by the ratio of otolith-marked fish among the total fish released from PWS or SEAK.

**RESULTS**

**Ocean Distribution**

A total of 519 chum salmon was caught at seven stations (48–54°N, 145°W) in the central GOA, where the sea surface temperature (SST) ranged from 5.0 to 5.7°C

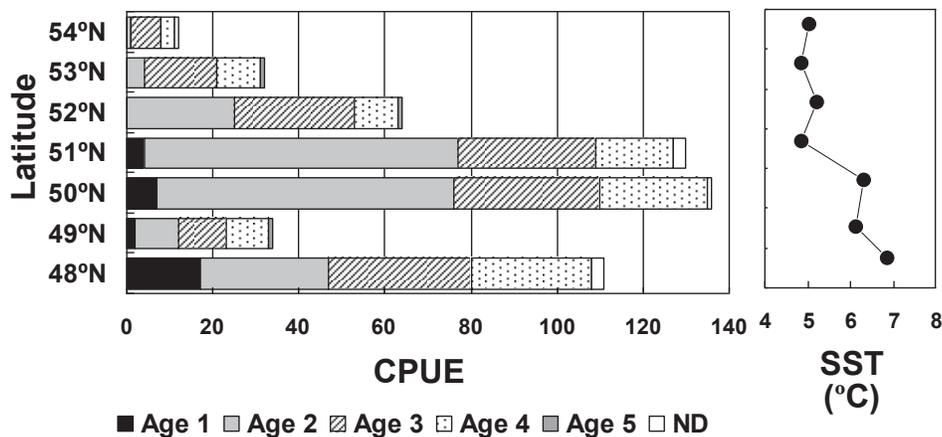
along 51–54°N and from 6.3 to 7.0°C along 48–50°N (Figs. 1 and 3). The CPUE of chum salmon was highest in the transition of SST between 50°N and 51°N (Fig. 3). Ocean age-2 and -3 fish were dominant at all sampling stations, and younger fish (ocean age-1) were distributed in southern waters (Fig. 3).

**Stock-specific Abundance Estimated by GSI**

Young fish (ocean age-1) had a relatively low CPUE, and all were of North American origin (mostly PWS, SEAK and southern BC; Fig. 4). Among ocean age-2 to -4 fish, the CPUE of Asian (Japanese and Russian) stocks was stable, while that of North American stocks decreased with ocean age. The WAK/AKP stock was almost absent in ocean age-1 fish, but comprised 4.5–16.6% of ocean age-2 to -4 fish. Asian and Alaskan stocks were relatively abundant between 48°N and 51°N, while BC stocks were fairly common in northern waters (50–53°N; Fig. 5). The estimated stock composition of chum salmon abundance in the survey area was 20% Japanese, 17.5% Russian, 11% WAK/AKP, 11% PWS, 16% SEAK, 6% northern BC, 17% southern BC, and 2% Washington stocks. Fall Yukon, Kodiak and Korean chum salmon stocks were rarely detected.

**Recoveries of Otolith-marked Fish**

The samples included 48 otolith-marked chum salmon (9.2% of samples examined). The recovered otolith-marked fish were released from the Wally Noerenberg Hatchery ( $n = 10$ ) in PWS; the Macaulay ( $n = 26$ ), Hidden Falls ( $n = 3$ ) and Neets Bay ( $n = 7$ ) hatcheries in SEAK; the Nititat Hatchery ( $n = 1$ ) in southern Vancouver Island, BC; and the Katagishi Hatchery ( $n = 1$ ) on the Pacific coast of Honshu, Japan (Table 1). A comparison of CPUEs estimated by GSI and otolith mark recoveries demonstrated that the contribution of hatchery fish was relatively high (56–87%) in ocean age-1 to -3 SEAK chum salmon, while it was low (0–30%) in PWS chum salmon, except for ocean age-1 fish (Fig. 6).



**Fig. 3.** CPUE (number of fish caught per 1-h trawl) of chum salmon by ocean age and sea surface temperature (SST) at seven sampling stations (48–54°N, 145°W) in the Gulf of Alaska. ND means the ocean age was not determined.

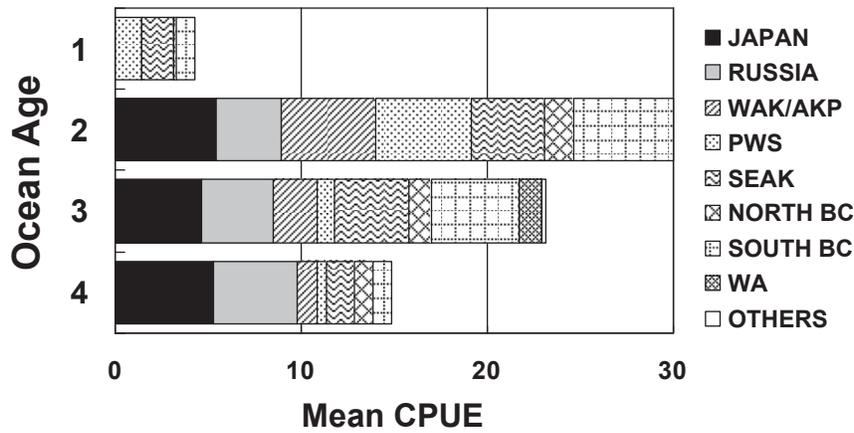


Fig. 4. Stock-specific mean CPUE (number of fish caught per 1-h trawl) of ocean age-1 to -4 chum salmon estimated by microsatellite DNA analysis. WAK/ AKP, West Alaska and Alaska Peninsula; PWS, Prince William Sound; SEAK, Southeast Alaska; WA, Washington.

DISCUSSION

Stock-specific Distribution and Abundance

This study confirmed that Asian and North American chum salmon cohabit in the central GOA during winter. Their abundance was dominated by various regional stocks from Japan (20%), Russia (17.5%), south BC (17%), SEAK (16%), WAK/AKP (11%), and PWS (11%). Allozyme analysis (Urawa et al. 1997) provided a similar estimate that chum salmon caught in the central GOA (48–54°N, 144–

148°W) during January 1996 consisted of 19% Japanese, 10% Russian, 35% Alaskan, 19% BC, and 17% Washington stocks.

Even within the limited survey area of the central GOA, the winter distribution pattern of chum salmon appears different among regional stocks and among age groups. Asian (Japanese and Russian) stocks were mainly distributed in the southern area (48–50°N) where SST exceeded 6°C; whereas, BC stocks were relatively abundant in the cooler northern area (51–54°N). Alaskan stocks were relatively abundant in the SST transition area (50–51°N). Most young chum salm-

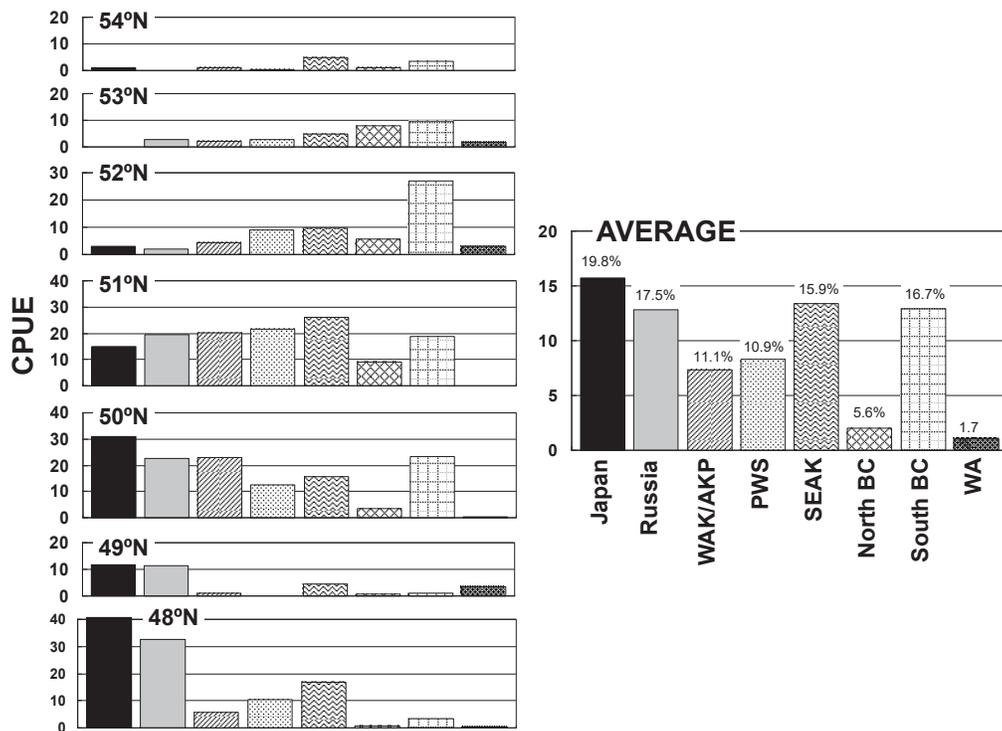


Fig. 5. Stock-specific CPUE (number of fish caught per 1-h trawl) of chum salmon caught at each sampling station. WAK/AKP, West Alaska and Alaska Peninsula; PWS, Prince William Sound; SEAK, Southeast Alaska; WA, Washington.

**Table 1.** Number of otolith-marked chum salmon caught in the central Gulf of Alaska on 15-18 February 2006. BC, British Columbia, Canada; PWS, Prince William Sound, Alaska; SEAK, Southeast Alaska. Number of samples refers to the number of chum salmon examined for otolith marks at each location.

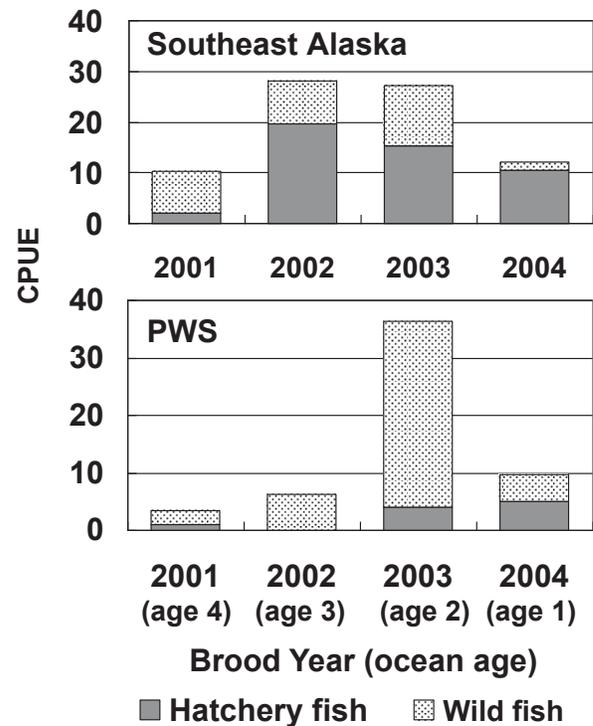
Sampling location	47°54'N 144°49'W	48°53'N 144°49'W	49°52'N 144°52'W	50°52'N 144°52'W	52°09'N 144°58'W	53°01'N 145°00'W	53°56'N 144°46'W	Total
Sampling date	18-Feb	18-Feb	17-Feb	17-Feb	16-Feb	16-Feb	15-Feb	
Number of samples	111	34	136	130	64	32	12	519
<b>Otolith-marked chum release locations</b>								
Wally Noerenberg Hatchery (PWS)	5	0	0	3	1	1	0	10
Macaulay Hatchery (SEAK)	3	2	4	6	8	3	0	26
Hidden Falls Hatchery (SEAK)	2			1			0	3
Neets Bay Hatchery (SEAK)	1	1		3	2		0	7
Nitinat Hatchery (BC)	1							1
Katagishi Hatchery (Japan)				1				1
<b>Total</b>	12	3	4	14	11	4	0	48
<b>% of otolith-marked fish in the sample</b>	10.8	8.8	2.9	10.8	17.2	12.5	0.0	9.2

on (ocean age-1) were distributed in the warmer southern areas (48–51°N), although these fish did not include Asian or WAK/AKP stocks. Young Asian chum salmon were found in the western NPO during the first winter (Urawa et al. 1997, 2001). The ocean distribution of WAK/AKP and Fall Yukon stocks during the first winter is unknown, although they appeared in the GOA after the first winter as shown by Urawa et al. (2009) and this paper. In addition, a low abundance of young chum salmon from other North American stocks in the survey area suggested that most were distributed in other areas during winter. McCraney et al. (2012) estimated ocean age-1 chum salmon originating from the eastern GOA/Pacific Northwest coast were distributed with Asian stocks in the eastern waters of the central NPO during February and March.

**Winter Habitat**

The winter distribution pattern may reflect stock- or age-specific preferences for water temperatures that maximize survival. Winter water temperatures in chum salmon habitat is usually lower than summer SST. The mean SST of pink and chum salmon habitats was geographically different in the western NPO and the GOA in the winter of 1996, 1998 and 2006 (Fig. 7). In the western NPO, the mean SST of pink salmon habitat was 4.3–4.7°C; whereas the mean SST of ocean age-1 chum salmon was 3.9–4.5°C, and that of older chum salmon habitat was 3.3–3.7°C. In the GOA, the mean SST of pink salmon habitat was 6.2–7.2°C, while that observed for ocean age-1 chum salmon was 6.5°C, and the mean SST of the older chum salmon habitat was 6.0–6.2°C. Thus, the SST of their winter habitats was almost 2°C higher in the GOA than the western NPO. It was also notable that the mean SST of the winter

habitat in each area was almost stable across the three years (1996, 1998, and 2006), and the range of SST was relatively narrow except for pink salmon habitat in 2006. These observations suggest that salmon select similar temperature



**Fig. 6.** Estimated contributions of hatchery fish to abundance (CPUE: number of fish caught per 1-hr trawl) of Southeast Alaska and Prince William Sound (PWS) chum salmon in the central Gulf of Alaska. Age refers to the ocean age of the fish.

regimes each winter, although the winter SST in the western subarctic water is variable partly due to the Kuroshio extension (Sugimoto et al. 2014). Consequently, their winter habitat may shift when the seawater temperature increases with future climate warming, as estimated by Welch et al. (1995), Azumaya et al. (2007), Abdul-Aziz et al. (2011), and Kaeriyama et al. (2014).

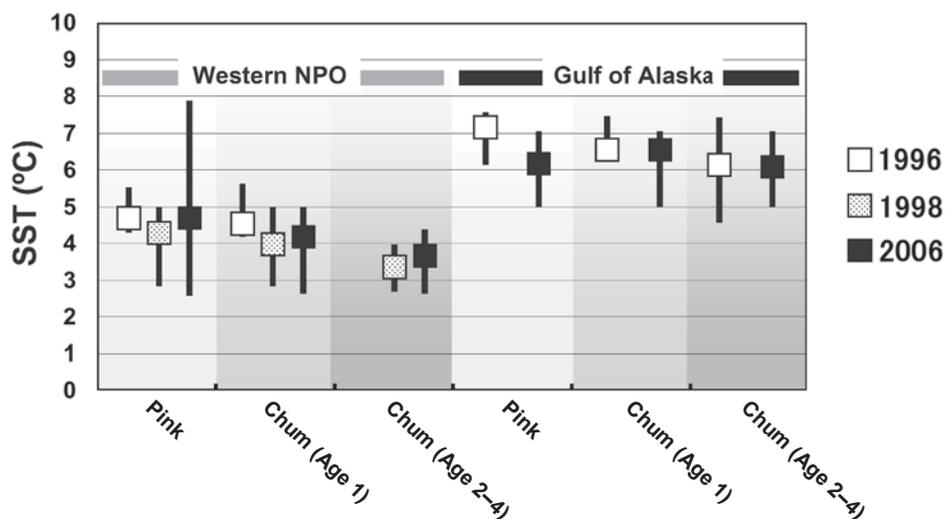
The spatial and temporal partitioning of oceanic habitat by species, regional stocks, and life-history stages, suggests adaptation to limited winter resources at an evolutionary scale (Myers et al. 2016). Why do Asian and North American stocks of chum salmon assemble in the GOA during winter? The winter habitat (4–7°C) favorable for chum salmon is widely available in the GOA (Fig. 1), but it is more limited in the western NPO (Urawa 2000). Young Asian chum salmon (ocean age-1) are distributed mainly within the limited western subarctic winter habitat. This habitat space may be insufficient for immature and maturing fish. They then migrate into the GOA the following winter. However, the winter carrying capacity in the GOA is uncertain. The winter zooplankton biomass was higher in the western North Pacific Ocean than in the Gulf of Alaska (Nagasawa 2000). The total lipid contents of chum and pink salmon in the GOA were significantly lower than those in the western NPO in the winter of 2006, although the fork length of chum salmon was larger in the GOA than in the western NPO (Kaga et al. 2006). The lipid content of pink salmon was also lower in the GOA than in the western NPO during the winter of 1996 (Nomura et al. 2000). Fukuwaka et al. (2007) estimated that salmon might inhabit cooler water in the western NPO to take advantage of greater foraging opportunities. It is also possible that salmon reduce their metabolic consumption in cooler seawater (Nagasawa 2000).

The stock-specific ocean migration route and timing might be genetically fixed to attain the best growth and survival through a long-term evolutionary process. However, it remains a mystery why most chum salmon stocks inhabit the GOA during winter.

### Hatchery Contributions

A large number of otolith-marked chum salmon is released annually from hatcheries in PWS and SEAK along the GOA coast. Thus, otolith thermal marking is an effective tool for determining the hatchery origin of individual salmon in the high seas (Urawa et al. 2000, 2009) as well as in the coastal waters of GOA (Kondzela and Wilmot 2002). Urawa et al. (2000) reported 14.5% of immature chum salmon caught in the central GOA during June and July 1998 were otolith-marked fish, most of which were released from hatcheries in PWS and SEAK. Kondzela and Wilmot (2002) examined juvenile chum salmon caught at eleven GOA coastal transects between Icy Point and Kodiak Island in July and August 2001, and they found the fraction of otolith-marked fish from hatcheries in PWS and SEAK ranged from 0% to 85%, depending on the sampling locations. Ruggerone et al. (2010) estimated hatchery salmon represented more than 70% of total adult chum salmon abundance in PWS and more than 55% of chum salmon in SEAK.

Our survey found 48 otolith-marked chum salmon at stations in the central GOA during the winter of 2006 (Fig. 1). Most of these marked fish came from hatcheries in PWS and SEAK, and their portion averaged 8.9% (ranging from 0% to 17.2%), which was lower than in summer/fall (Urawa et al. 2000; Kondzela and Wilmot 2002). This might be caused by winter assembly of many stocks from around



**Fig. 7.** Mean sea surface temperature (SST) of pink and chum salmon habitats in the western North Pacific Ocean (NPO) and Gulf of Alaska in the winter of 1996 (Ueno et al. 1996), 1998 (Ishida et al. 1998) and 2006 (Fukuwaka et al. 2006). Bars indicate range of SST. Chum salmon age refers to ocean age of the fish.

the North Pacific Rim. On the other hand, for brood years 2001–2004, we estimated the hatchery contribution of chum salmon in the survey area was 0–52% for the PWS stock and 19–87% for the SEAK stock. It is uncertain whether the high diversity of estimates of hatchery contributions among brood years (ocean ages) indicates annual variation in abundance in hatchery and wild populations or merely probabilistic variation due to small sample sizes.

## CONCLUSIONS

The present microsatellite and otolith mark analyses confirmed that various chum salmon stocks of Asian and North American origins concentrated in the central GOA during winter. Their winter distribution pattern seems slightly different among regional stocks and also among age groups, even within the relatively small area surveyed in the central GOA. We could not determine the southern limit and annual variation in winter salmon distribution in the Gulf of Alaska because our survey was conducted in a single year. In addition, the winter distribution of North American young chum salmon has not been elucidated yet. Additional monitoring research is needed to determine the entire range of winter salmon distribution.

Future climate warming may affect the distribution, trophic condition, and survival of salmon overwintering in the ocean (Myers et al. 2016). The response of salmon to climate-driven changes may be different among regional stocks, depending on their habitat locations. Further winter surveys are required to evaluate the stock-specific salmon response(s) to environmental changes in the western and eastern NPO, as well as to develop models that predict the future distribution and abundance of salmon.

## ACKNOWLEDGMENTS

We thank the crew and researchers on board the R/V *Kaiyo maru* for their devotion to the fish sampling program under serious winter conditions. This study was supported by the Fisheries Agency of Japan.

## REFERENCES

- Abdul-Aziz, O.I., N.J. Mantua, and K.W. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. *Can. J. Fish. Aquat. Sci.* 68: 1660–1680.
- Agler, B.A., D.S. Oxman, P.T. Hagen, E.C. Volk, and J.J. Grimm. 2002. Thermal mark patterns applied to salmon from Alaska, treaty tribes and other Northwest States for brood year 2001. *N. Pac. Anadr. Fish Comm. Doc.* 637. 12 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Agler, B.A., D.S. Oxman, K. Van Kirk, E.C. Volk, and J.J. Grimm. 2003. Thermal mark patterns applied to salmon from Alaska, treaty tribes and other Northwest States for brood year 2002. *N. Pac. Anadr. Fish Comm. Doc.* 704. 13 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Agler, B.A., D.S. Oxman, K. Van Kirk, E.C. Volk, and J.J. Grimm. 2004. Thermal mark patterns applied to salmon from Alaska, treaty tribes and other Northwest States for brood year 2003. *N. Pac. Anadr. Fish Comm. Doc.* 777. 12 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Agler, B.A., R. Josephson, D.S. Oxman, K. Van Kirk, E.C. Volk, and J.J. Grimm. 2005. Thermal mark patterns applied to salmon from Alaska, treaty tribes and other Northwest States for brood year 2004. *N. Pac. Anadr. Fish Comm. Doc.* 870. 12 pp. (Available at [www.npafc.org](http://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](http://www.npafc.org)).
- Beacham, T.D., J.R. Candy, S. Sato, S. Urawa, K.D. Le, and M. Wetklo. 2009. Stock origins of chum salmon (*Oncorhynchus keta*) in the Gulf of Alaska during winter as estimated with microsatellites. *N. Pac. Anadr. Fish Comm. Bull.* 5: 15–23. (Available at [www.npafc.org](http://www.npafc.org)).
- Beamish, R.J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog. Oceanogr.* 49: 423–437.
- Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashatorin, V.V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56: 516–526.
- Farley, E.V., Jr., J.H. Moss, and R.J. Beamish. 2007. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. *N. Pac. Anadr. Fish Comm. Bull.* 4: 311–317.
- Fukuwaka, M., S. Sato, S. Takahashi, T. Onuma, N. Davis, J. Moss, A. Volkov, K.B. Seong, O. Sakai, N. Tanimata, and K. Makino. 2006. International salmon research aboard the R/V *Kaiyo maru* in the North Pacific Ocean during the winter of 2006. *N. Pac. Anadr. Fish Comm. Doc.* 957. 12 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Fukuwaka, M., S. Sato, S. Takahashi, T. Onuma, O. Sakai, N. Tanimata, K. Makino, N.D. Davis, A.F. Volkov, K.B. Seong, and J.H. Moss. 2007. Winter distribution of chum salmon related to environmental variables in the North Pacific. *N. Pac. Anadr. Fish Comm. Tech. Rep.* 7: 29–30. (Available at [www.npafc.org](http://www.npafc.org)).
- Ishida, Y., Y. Ueno, A. Shiimoto, T. Watanabe, T. Azumaya, M.V. Koval, and N.D. Davis. 1998. Japan-Russia-US cooperative survey on overwintering salmonids in the western and central North Pacific Ocean and Bering Sea aboard the *Kaiyo maru*, 3 February–2 March, 1998. *N. Pac. Anadr. Fish Comm. Doc.* 329. 18 pp. (Available at [www.npafc.org](http://www.npafc.org)).

- Johnson, W.F., R.P. Josephson, T.R. Frawley, and D.S. Oxman. 2006. Revised web-based North Pacific salmon otolith mark directory. N. Pac. Anadr. Fish Comm. Doc. 971. 39 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Kaeriyama, M., H. Seo, and Y. Qin. 2014. Effect of global warming on the life history and population dynamics of Japanese chum salmon. *Fish. Sci.* 80: 251–260.
- Kaga, T., S. Sato, M. Fukuwaka, S. Takahashi, T. Nomura, and S. Urawa. 2006. Total lipid contents of winter chum and pink salmon in the western North Pacific Ocean and Gulf of Alaska. N. Pac. Anadr. Fish Comm. Doc. 962. 12 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Kondzela, C., and R. Wilmot. 2002. Origin of juvenile chum salmon from the Gulf of Alaska coastal waters, 2001. ASFS Quarterly Report July-August-September 2002. pp. 1–9.
- McCraney, W.T., E.V. Farley, Jr., C.M. Kondzela, S.V. Naydenko, A.N. Starovoytov, and J. R. Guyon. 2012. Genetic stock identification of overwintering chum salmon in the North Pacific Ocean. *Environ. Biol. Fish.* 94: 663–668.
- 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](http://www.npafc.org)).
- Myers, K.W., J.R. Irvine, E.A. Logerwell, S. Urawa, S.V. Naydenko, A.V. Zavolokin, and N.D. Davis. 2016. Pacific salmon and steelhead: life in a changing winter ocean. N. Pac. Anadr. Fish Comm. Bull. 6: 113–138. doi:10.23849/npafcb6/113.138.
- 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](http://www.npafc.org)).
- Nomura, T., S. Urawa, and Y. Ueno. 2000. Variations in muscle lipid content of high-seas chum and pink salmon in winter. N. Pac. Anadr. Fish Comm. Bull. 2: 43–54. (Available at [www.npafc.org](http://www.npafc.org)).
- North Pacific Anadromous Fish Commission (NPAFC). 2016. NPAFC Pacific salmonid hatchery release statistics (updated 20 July 2016). North Pacific Anadromous Fish Commission, Vancouver. (Available at [www.npafc.org](http://www.npafc.org) accessed July 2016).
- Ruggerone, G.T., R.M. Peterman, B. Dorner, and K.W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Mar. Coast. Fish.* 2: 306–328.
- Sugimoto, S., N. Kobayashi, and K. Hanawa. 2014. Quasi-decadal variation in intensity of the western part of the winter subarctic SST front in the western North Pacific: the influence of Kuroshio extension path state. *J. Phys. Oceanogr.* 44: 2751–2760.
- Ueno, Y., Y. Ishida, A. Shiimoto, S. Urawa, K.W. Myers, J. Morris, and M.V. Koval. 1996. Summary of wintering salmon research aboard the research vessel *Kaiyo-maru* in January 1996. N. Pac. Anadr. Fish Comm. Doc. 213. 20 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Urawa, S. 2000. Ocean migration route of Japanese chum salmon with a reference to future salmon research. *Natl. Salmon Resour. Ctr. Newslett.* 5: 3–9. (In Japanese).
- Urawa, S., Y. Ishida, Y. Ueno, S. Takagi, G. Winans, and N. Davis. 1997. Genetic stock identification of chum salmon in the North Pacific Ocean and Bering Sea during the winter and summer of 1996. N. Pac. Anadr. Fish Comm. Doc. 259. 11 pp. (Available at [www.npafc.org](http://www.npafc.org)).
- Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K. Munk, K.W. Myers, and E.V. Farley, Jr. 2000. Geographical 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](http://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](http://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](http://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.