

Stock Origins of Chum Salmon (*Oncorhynchus keta*) in the Gulf of Alaska during Winter as Estimated with Microsatellites

Terry D. Beacham¹, John R. Candy¹, Shunpei Sato², Shigehiko Urawa²,
Khai D. Le¹, and Michael Wetklo¹

¹Fisheries and Oceans Canada, Pacific Biological Station,
3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada
²National Salmon Resources Center, Fisheries Research Agency,
2-2 Nakanoshima, Toyohira-ku, Sapporo 062-0922, Japan

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.

Abstract: A microsatellite baseline incorporating over 53,000 chum salmon (*Oncorhynchus keta*) sampled from over 380 locations in Asia and North America was applied to estimate stock composition in mixed-stock fishery samples from the Gulf of Alaska. High resolution of these mixed-stock samples was possible, with 1 reporting group developed for Korean populations, 7 groups for Japanese populations, 8 groups for Russian populations, 15 groups for Alaskan populations, 5 groups for Canadian Yukon River populations, 16 groups for British Columbia populations, and 5 groups for Washington populations. In February 2006 samples from the Gulf of Alaska (145°W), chum salmon in more northern areas (54°N) were primarily of North American origin (55% British Columbia, 30% Alaska), but in more southern areas (48°N), nearly 40% of chum salmon sampled were of Japanese origin (Sea of Okhotsk and Pacific coasts of Hokkaido), and 30% were of Russian origin (Kamchatka and northeast Russia). Ocean age-1 chum salmon spending their first winter in the Gulf of Alaska were almost entirely from southeast Alaska (39%), Prince William Sound (31%), or southern British Columbia (26%). However, by the second winter, 30% of ocean age-2 chum salmon were identified as of Asian origin (18% Japanese, 12% Russian).

Keywords: chum salmon, winter, Gulf of Alaska, stock identification, microsatellites

INTRODUCTION

Stock composition information is important in determining areas of ocean rearing of stocks of immature chum salmon (*Oncorhynchus keta*), and the migration routes used by immature salmon to reach seasonal rearing areas, as well as the routes used by maturing chum salmon to return to natal rivers. Although scale pattern analysis has been used in chum salmon stock identification (Tanaka et al. 1969; Ishida et al. 1989), stock identification based upon analysis of genetic variation has been the main method used in stock identification applications. Initial applications centered on allozymes, whereby the genetic structure of populations potentially contributing to a mixed-stock fishery was determined (Okazaki 1982a,b; Wilmot et al. 1994; Winans et al. 1994; Seeb and Crane 1999a; Efremov 2001) and then this structure was used to estimate the stock composition of samples from mixed-stock fisheries (Beacham et al. 1987; Urawa et al. 1997, 2000, 2009; Wilmot et al. 1998; Winans et al. 1998; Seeb and Crane 1999b). Additionally, sequence variation in mitochondrial (mt) DNA has been used to evaluate population structure (Ginatulina 1992; Sato et al. 2001, 2004) and to estimate stock compositions of chum salmon in the Bering

Sea and North Pacific Ocean (Moriya et al. 2007; Sato et al. 2009). Microsatellites have also been demonstrated to be effective in determining population structure of chum salmon and estimating stock composition in fisheries in local areas in both Asia (Beacham et al. 2008b,c) and North America (Beacham et al. 2008a), as well as providing high resolution stock composition estimates for complex mixed-stock samples in North Pacific and Bering Sea sampling (Beacham et al. unpub. data).

Accurate, cost-effective identification of chum salmon to region of origin is important to our understanding of stock-specific responses to recent climatic regime shifts in the north Pacific Ocean (Welch et al. 2000; Mueter et al. 2002). Identification of marine factors responsible for survival variation observed in salmon stocks requires identification of fish sampled in marine environments to stock of origin as an initial step. The potential mixing of many chum salmon stocks throughout their marine existence necessitates identification of fish from mixed-stock samples for delineation of stock-specific migration pathways and marine feeding areas (Brodeur et al. 2003), and for evaluation of physiological status during spawning migrations (Cooke et al. 2004).

In the present study, mixed-stock samples from the Gulf

of Alaska were analyzed for stock composition through analysis of 14 microsatellites by incorporating a 381-population baseline including populations from Korea, Japan, Russia, Alaska, the Yukon Territory, British Columbia, and Washington. Comparisons of presence and absence of specific stocks of salmon in the areas surveyed are outlined.

MATERIALS AND METHODS

Baseline Populations

The baseline survey consisted of the analysis of over 53,000 chum salmon from 381 populations from Korea, Japan, Russia, Alaska, Canada, and Washington, with the sampling sites or populations surveyed in each geographic region outlined by Beacham et al. (unpub. data). Information on regional population structure has been outlined previously for Japanese populations (Beacham et al. 2008b), Russian populations (Beacham et al. 2008c), western Alaska populations (Beacham et al. 2009b) and British Columbia populations (Beacham et al. 2008a). Pacific Rim population structure of chum salmon was reported by Beacham et al. (2009a).

Marine Samples and Laboratory Analysis

A series of six samples was collected during a research cruise in the Gulf of Alaska during February 2006 between approximately latitude 48°N–53°N along longitude 145°W (Fig. 1). The age of virtually all individuals in these six samples was determined by analysis of scales, and variation in stock composition attributable to both location and age was conducted subsequently.

Laboratory Analysis

Tissue samples from the marine samples were collected, preserved in 95% ethanol, and DNA subsequently extracted. Extracted DNA from 2006 Gulf of Alaska samples was sent to the Molecular Genetics Laboratory (MGL) at the Pacific Biological Station for subsequent analysis. Once extracted DNA was available, surveys of variation at 14 microsatellite loci were conducted: Ots3 (Banks et al. 1999), Oke3 (Buchholz et al. 2001), Oki2 (Smith et al. 1998), Oki100 (Beacham et al. 2008b), Omm1070 (Rexroad et al. 2001), Omy1011 (Spies et al. 2005), One101, One102, One104, One111, and One114 (Olsen et al. 2000), Ots103 (Nelson and Beacham 1999), Ssa419 (Cairney et al. 2000), and OtsG68 (Williamson et al. 2002).

PCR DNA amplifications were conducted using DNA

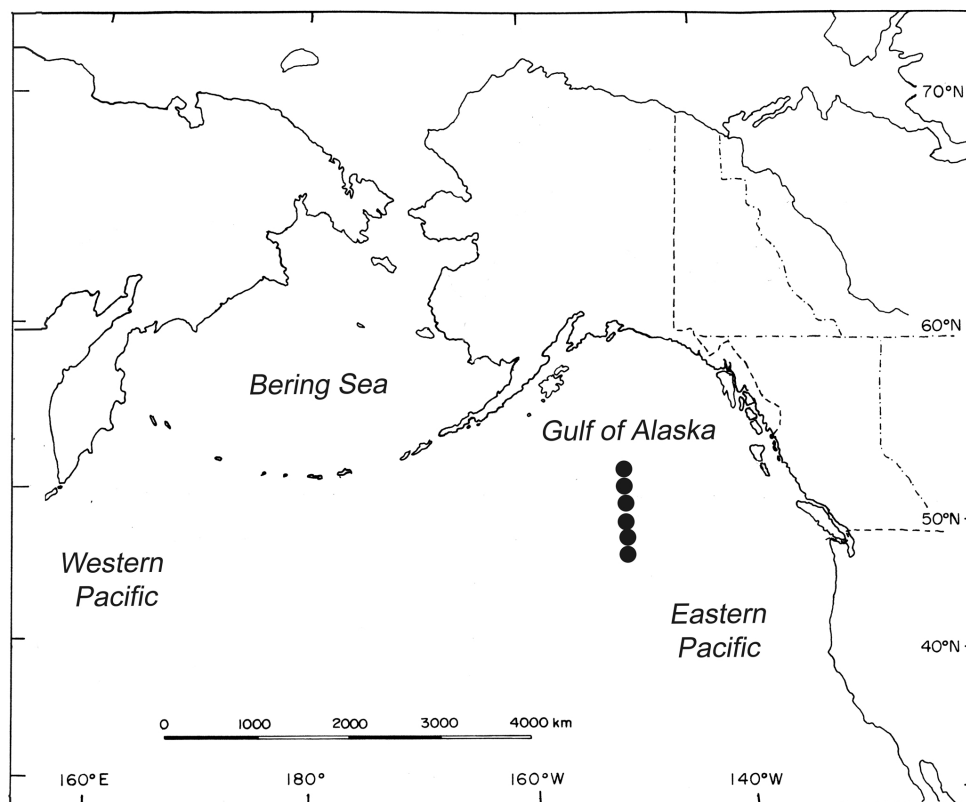


Fig. 1. Map indicating the locations of six samples collected during a February 2006 cruise of the R/V *Kaiyo-maru* in the Gulf of Alaska and eastern Pacific Ocean.

Engine Cycler Tetrad2 (BioRad, Hercules, CA) in 6- μ l volumes consisting of 0.15 units of Taq polymerase, 1 μ l of extracted DNA, 1x PCR buffer (Qiagen, Mississauga, Ontario), 60 μ M each nucleotide, 0.40 μ M of each primer, and deionized H₂O. The thermal cycling profile involved one cycle of 15 min at 95°C, followed by 30–40 cycles of 20 sec at 94°C, 30–60 sec at 47–65°C and 30–60 sec at 68–72°C (depending on the locus). Specific PCR conditions for a particular locus could vary from this general outline and were outlined by Beacham et al. (2009b). PCR fragments were size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, CA) using an internal lane sizing standard.

Estimation of Stock Composition in Mixed-stock Samples

The BAYES routine of Pella and Masuda (2001) was modified by our laboratory to a C++-based program (cBayes), which is available from our laboratory website (Neaves et al. 2005). In the analysis, ten 20,000-iteration Monte Carlo Markov chains of estimated stock compositions were produced, with initial starting values for each chain set at 0.90 for a particular population that was different for each chain. Estimated stock compositions were considered to have converged when the shrink factor was < 1.2 for the 10 chains (Pella and Masuda 2001), and thus the starting values were considered to be irrelevant (uninformative prior). Stock composition estimates converged before 20,000 iterations, and no further improvements in the estimates were observed in excess of 20,000 iterations. Therefore, 20,000 iterations was set as the standard in the analysis. The last 1,000 iterations from each of the 10 chains were then combined, and for each fish the probability of originating from each population in the baseline was determined. These individual probabilities were summed over all fish in the sample, and divided by the number of fish sampled to provide the point estimate of stock composition. Standard deviations of estimated stock compositions were determined from the last 1,000 iterations from each of the 10 chains incorporated in the analysis.

RESULTS

Winter distribution of chum salmon along 145°W longitude in 2006 was evaluated between 48°N and 53°N. In the most northerly location sampled (53°N), sample size was modest (N=32), but chum salmon originating from the central coast of British Columbia (19%), the Fraser River (15%) in southern British Columbia, and southeast Alaska (12%) were identified as the most relatively abundant stocks (Table 1). Contributions were also identified from chum salmon originating from southern coastal British Columbia (8%) and Prince William Sound (7%). Asian chum salmon detected were limited to those from Kamchatka (8%) and northeast

Russia (3%). Sampling at 52°N indicated that chum salmon from southeast Alaska (23%), the Fraser River (23%), Prince William Sound (15%), and the west coast of Vancouver Island (13%) accounted for 74% of the chum salmon sampled. Asian chum salmon accounted for 8% of the fish sampled from this location, with the largest stock from the Sea of Okhotsk coast of Hokkaido (5%). Sampling at 51°N indicated that chum salmon from southeast Alaska were the most relatively abundant stock (22%), followed by chum salmon from Prince William Sound (17%) and the Fraser River (9%) (Table 1). Chum salmon from Norton Sound and the lower Yukon River constituted approximately 11% of the individuals sampled. Asian chum salmon were estimated to constitute 26% of the individuals sampled, with Russian chum salmon identified almost exclusively from Kamchatka (7%) and northeast Russia (8%), and Japanese chum salmon almost exclusively from the Sea of Okhotsk coast and Nemuro Strait region of Hokkaido (10%). Sampling from these three sites indicated an increasing proportion of Asian chum salmon from north to south, a dominant presence of chum salmon from southeast Alaska and Prince William Sound in the samples, little evidence of chum salmon from northern British Columbia, and evidence of chum salmon from southern British Columbia, Washington, and western Alaska.

In the southern section of the survey, starting at 50°N, the single most abundant stock was the Sea of Okhotsk coast of Hokkaido (13%), followed by the southeast Alaska (12%) and Prince William Sound stocks (10%) (Table 1). Asian chum salmon accounted for 39% of the sample (23% Japanese, 16% Russian), with the Russian contribution largely accounted for by Kamchatka and northeast Russia stocks. Chum salmon from northern North America in Kotzebue Sound (3%), Norton Sound (7%), and the Yukon River (3%) were also identified as present in the sample. Asian chum salmon increased substantially in relative abundance in the sample from 49°N, with Japanese (34%) and Russian (35%) chum salmon substantial contributors to the catch. Japanese chum salmon were largely from the Pacific coast (21%) and Nemuro Strait (12%) regions of Hokkaido. Russian chum salmon were largely from northeast Russia (24%), Magadan (6%), and Kamchatka (4%). North American chum salmon were largely from southeast Alaska (12%) and Washington (12%). Asian chum salmon again dominated at the most southern sampling site (48°N), with 66% of the fish sampled of Asian origin. Japanese chum salmon, at 37% of the fish sampled, were largely from the Sea of Okhotsk coast (28%) and Pacific coast (9%) regions of Hokkaido. Russian chum salmon, constituting 28% of the fish sampled, were largely from Kamchatka (12%), northeast Russia (7%), and Sakhalin Island (6%). Chum salmon from North America were identified as originating mainly from southeast Alaska (15%) and Prince William Sound (9%). Asian chum salmon dominated at the southern sampling sites, with Japanese chum salmon estimated to be largely derived from the Sea of Okhotsk, Nemuro Strait, and Pacific coastal regions of Hok-

Table 1. Estimated stock compositions (percentage, SD in parentheses) of six mixed-stock samples of chum salmon sampled in the Gulf of Alaska during February 2006. Region codes are: QCI (Queen Charlotte Islands), BC (British Columbia), ECVI (east coast Vancouver Island), WCVI (west coast Vancouver Island).

Latitude	53°01' N	52°09' N	50°52' N	49°52' N	48°53' N	47°54' N
Longitude	145°00' W	144°58' W	144°52' W	144°53' W	144°49' W	144°49' W
Date	16 February	16 February	17 February	17 February	18 February	18 February
Number of samples	32	64	130	136	34	111
Honshu Sea of Japan	0.0 (0.4)	0.0 (0.2)	0.1 (0.3)	1.3 (2.6)	0.3 (1.7)	0.0 (0.2)
Honshu Pacific	0.0 (0.3)	0.0 (0.2)	0.3 (0.7)	0.2 (0.6)	0.3 (1.4)	0.1 (0.5)
Hokkaido Sea of Japan	0.0 (0.3)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.3 (1.3)	0.0 (0.1)
Hokkaido Sea of Okhotsk	0.4 (1.5)	4.9 (2.8)	3.3 (2.0)	13.1 (4.7)	0.6 (2.2)	27.8 (5.2)
Nemuro Strait	0.0 (0.2)	0.0 (0.1)	6.2 (2.5)	2.3 (3.3)	11.8 (6.7)	0.1 (0.4)
Hokkaido eastern Pacific	0.0 (0.2)	0.0 (0.1)	0.7 (1.5)	0.0 (0.2)	11.6 (6.0)	3.4 (3.5)
Hokkaido western Pacific	0.0 (0.3)	0.0 (0.2)	0.8 (1.4)	6.0 (3.6)	9.1 (6.4)	5.7 (3.3)
Sakhalin	0.0 (0.4)	0.0 (0.2)	0.0 (0.1)	0.0 (0.1)	0.0 (0.3)	5.7 (2.5)
Magadan	0.1 (1.0)	2.6 (2.6)	0.2 (0.7)	2.4 (1.8)	6.1 (5.5)	3.0 (2.4)
Northern Sea of Okhotsk	0.0 (0.2)	0.0 (0.2)	0.4 (1.1)	0.0 (0.1)	0.1 (1.2)	0.0 (0.3)
West Kamchatka	5.9 (6.5)	0.3 (1.1)	4.3 (3.3)	9.3 (3.2)	3.3 (4.8)	12.3 (4.4)
East Kamchatka	1.9 (3.9)	0.0 (0.5)	2.4 (2.6)	0.1 (0.6)	0.9 (2.4)	0.0 (0.3)
Northeast Russia	3.3 (4.7)	0.0 (0.3)	7.7 (2.6)	4.5 (2.1)	24.1 (8.9)	7.4 (4.0)
Kotzebue Sound	0.0 (0.5)	0.2 (0.8)	0.9 (1.8)	2.5 (1.7)	0.2 (1.3)	0.0 (0.2)
Norton Sound	1.2 (3.1)	2.9 (3.4)	6.1 (4.4)	7.1 (4.5)	1.7 (3.2)	4.2 (2.9)
Yukon lower summer	1.8 (3.6)	0.2 (1.0)	4.4 (3.4)	1.1 (2.3)	0.1 (0.9)	0.3 (1.2)
Yukon upper Alaska fall	0.0 (0.4)	0.0 (0.2)	0.2 (0.8)	1.7 (1.5)	0.1 (0.8)	0.7 (1.1)
Yukon mainstem Canada	0.0 (0.4)	0.0 (0.2)	0.0 (0.3)	0.4 (0.8)	0.0 (0.3)	0.0 (0.3)
Yukon Porcupine Canada	0.0 (0.4)	0.0 (0.1)	0.0 (0.2)	0.1 (0.4)	0.0 (0.2)	0.0 (0.3)
Nushagak summer	0.0 (0.5)	0.0 (0.4)	0.4 (1.2)	0.1 (0.6)	0.0 (0.5)	0.0 (0.4)
Kuskokwim Bay/ River	0.5 (2.2)	0.1 (0.5)	0.1 (0.7)	1.7 (2.8)	0.4 (1.7)	0.4 (1.2)
Northeast Bristol Bay	0.0 (0.5)	3.6 (4.0)	0.0 (0.3)	1.8 (2.4)	0.1 (0.6)	0.1 (0.4)
Southwest Bristol Bay	0.0 (0.4)	0.0 (0.3)	0.1 (0.6)	0.0 (0.2)	0.0 (0.4)	0.0 (0.1)
North Peninsula	0.0 (0.2)	0.0 (0.4)	2.7 (1.7)	1.2 (1.4)	0.0 (0.3)	0.0 (0.2)
Southwest Peninsula	0.6 (2.2)	0.0 (0.2)	0.0 (0.3)	0.1 (0.6)	0.2 (1.0)	0.0 (0.1)
Southeast Peninsula	0.3 (1.2)	0.1 (0.5)	0.1 (0.4)	0.0 (0.2)	0.0 (0.4)	0.1 (0.3)
Kodiak Island	0.0 (0.3)	0.0 (0.2)	0.0 (0.2)	1.6 (1.1)	0.0 (0.2)	0.0 (0.1)
Prince William Sound	7.2 (6.5)	15.3 (5.8)	16.8 (3.7)	9.6 (3.0)	0.4 (1.5)	9.3 (3.0)
SE Alaska	12.2 (10.4)	23.2 (8.0)	21.8 (4.8)	11.8 (4.0)	12.2 (6.2)	15.0 (3.9)
Taku	0.1 (0.8)	0.7 (2.0)	0.1 (0.5)	0.1 (0.6)	0.0 (0.4)	0.0 (0.3)
QCI west	1.9 (4.0)	0.0 (0.4)	0.1 (0.4)	0.3 (0.8)	0.0 (0.5)	0.0 (0.3)
QCI east	0.1 (0.9)	0.4 (1.5)	0.1 (0.4)	0.1 (0.5)	0.4 (1.7)	0.1 (0.4)
QCI Skidegate	0.1 (0.8)	0.2 (1.1)	0.0 (0.2)	0.6 (1.2)	0.0 (0.4)	0.1 (0.4)
BC north	2.4 (6.9)	0.6 (1.9)	1.2 (2.2)	0.3 (1.0)	0.9 (2.7)	0.1 (0.5)
Skeena	0.0 (0.7)	0.5 (1.6)	0.1 (0.6)	0.0 (0.2)	0.0 (0.6)	0.3 (0.9)
BC Grenville	6.0 (10.5)	0.1 (0.8)	0.0 (0.4)	0.1 (0.4)	0.2 (1.3)	0.1 (0.6)
BC central	19.4 (10.4)	0.5 (1.7)	4.4 (2.9)	0.5 (1.2)	0.7 (2.5)	0.3 (1.0)
BC Rivers Inlet	0.2 (1.3)	0.0 (0.5)	0.1 (0.4)	0.1 (0.4)	0.0 (0.4)	0.0 (0.3)
Johnstone Strait	0.2 (1.6)	0.3 (1.4)	0.0 (0.2)	0.0 (0.3)	0.0 (0.4)	0.3 (0.7)
BC south	8.4 (8.4)	2.8 (4.7)	0.4 (1.1)	2.9 (3.1)	0.6 (2.4)	0.7 (1.3)
ECVI	4.0 (6.9)	0.5 (1.6)	0.3 (1.0)	2.1 (2.7)	0.2 (1.4)	0.0 (0.3)
WCVI	0.5 (2.6)	13.1 (4.6)	3.7 (2.0)	7.1 (2.7)	0.3 (1.5)	0.0 (0.2)
Fraser	15.2 (9.1)	22.6 (7.1)	9.2 (3.1)	4.5 (2.7)	0.9 (2.9)	2.3 (1.9)
North Puget Sound	0.1 (1.1)	1.4 (3.5)	0.0 (0.3)	0.4 (1.5)	1.0 (3.1)	0.2 (0.7)

Table 1 (continued).

Latitude	53°01' N	52°09' N	50°52' N	49°52' N	48°53' N	47°54' N
Longitude	145°00' W	144°58' W	144°52' W	144°53' W	144°49' W	144°49' W
Date	16 February	16 February	17 February	17 February	18 February	18 February
South Puget Sound	2.2 (4.3)	0.1 (0.5)	0.0 (0.2)	0.0 (0.1)	0.6 (2.3)	0.0 (0.1)
Hood Canal	0.0 (0.3)	1.5 (2.9)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)
Juan de Fuca Strait	3.2 (5.9)	1.0 (2.4)	0.0 (0.1)	0.0 (0.2)	10.0 (7.0)	0.0 (0.1)
Coastal Washington	0.2 (1.2)	0.0 (0.2)	0.0 (0.1)	0.7 (1.3)	0.0 (0.3)	0.0 (0.1)
Values by region						
Japan	0.4 (1.7)	4.9 (2.8)	11.3 (92.9)	23.0 (3.7)	34.1 (8.1)	37.1 (4.8)
Russia	11.3 (7.5)	3.0 (2.6)	15.1 (3.8)	16.3 (3.8)	34.5 (8.7)	28.4 (5.2)
Western Alaska	3.6 (4.6)	6.9 (3.5)	12.2 (3.3)	16.0 (3.6)	2.6 (3.8)	5.6 (2.9)
Central/Southeast Alaska	20.3 (10.7)	38.7 (8.3)	41.6 (5.5)	24.4 (4.4)	12.9 (6.3)	24.4 (4.4)
Canada Yukon	0.0 (0.7)	0.0 (0.3)	0.1 (0.4)	0.4 (0.9)	0.0 (0.5)	0.1 (0.5)
Northern British Columbia	30.2 (12.7)	3.2 (4.4)	6.1 (3.7)	2.1 (2.2)	2.4 (4.0)	1.0 (1.7)
Southern British Columbia	28.3 (11.7)	39.3 (7.5)	13.6 (3.5)	16.6 (3.7)	2.0 (4.2)	3.2 (2.2)
Washington	5.8 (5.2)	4.0 (4.6)	0.1 (0.4)	1.2 (1.9)	11.6 (6.9)	0.2 (0.7)

kaido. Russian chum salmon were identified as primarily from Kamchatka and northeast Russia.

Stock composition showed considerable differences among the age-classes of chum salmon evaluated. Chum salmon typically spend 1–4 winters rearing in the ocean. Ocean age-1 chum salmon spending their first winter in the ocean were almost entirely from southeast Alaska (39%), Prince William Sound (31%), or southern British Columbia (26%) (Table 2). No ocean age-1 individuals were identified as Asian in origin. However, by the second winter, 30% of chum salmon of ocean age-2 were identified as of Asian origin (18% Japanese, 12% Russian). Ocean age-2 North American fish were estimated to be from British Columbia (27%), Prince William Sound (18%), western Alaska (13%), and southeast Alaska (8%). Asian chum salmon accounted for 36% of ocean age-3 chum salmon (20% Japanese, 16% Russian), with ocean age-3 North American chum salmon ranging from western Alaska to Washington (Table 2). Ocean age-4 chum salmon were predominately (66%) Asian in origin (36% Japanese, 30% Russian). Higher proportions of ocean age-4 chum salmon from North America were generally observed in more northerly stocks (central and southeast Alaska 14%, southern British Columbia 4%, and Washington 4%).

DISCUSSION

The present microsatellite stock identification study indicated that various stocks of Asian and North American chum salmon stocks intermingled in the central Gulf of Alaska during winter. A similar result was obtained by allozyme analysis for chum salmon collected in the same region during the winter of 1996 (Urawa et al. 1997).

Ocean age-1 chum salmon spending their first winter in the ocean in the Gulf of Alaska along 145°W were all of

North American origin, primarily from regions directly adjacent (Prince William Sound, southeast Alaska) to the sampling locations. No migration of ocean age-1 (2004 brood year) Asian chum salmon into the region was observed. Allozyme stock identification has indicated that Japanese chum salmon inhabit in the western North Pacific Ocean during their first winter, move into the Bering Sea in the summer, and migrate into the Gulf of Alaska for their second winter (Urawa 2000, 2004; Urawa et al. 2001, 2009). The present study supported this migration model, and indicated that ocean age-2 Asian chum salmon had moved into the Gulf of Alaska after the second summer of marine rearing (2003 brood year), as did chum salmon from western Alaska. However, Russian chum salmon of this age were primarily of northeast Russia origin, with virtually no 2003 broodyear chum salmon from Kamchatka observed. Substantial differences in survival rates, broodyear spawning abundances, or sampling variation could account for the observed differences in age composition between northeast Russia and Kamchatka, but perhaps the results may reflect a differential migration pattern between chum salmon of northeast Russia and Kamchatka origin chum salmon of this age. Older Russian chum salmon were primarily of Kamchatka origin, so it is possible that the lack of 2003 brood year salmon from Kamchatka may reflect a slower rate of migration into the Gulf of Alaska of this stock. In the Gulf of Alaska, Russian chum salmon originated primarily from northeast Russia and Kamchatka, so these differences reflect either differences in survival and spawning abundance, or a more eastward migration pattern of these stocks compared with other stocks in Russia.

Japanese chum salmon in the Gulf of Alaska originated entirely from the Sea of Okhotsk coast, Nemuro Strait, and Pacific coast regions of Hokkaido. Production from these areas accounts for about 75% of total production of Japanese

Table 2. Estimated stock compositions (percentage, SD in parentheses) by age of 519 chum salmon sampled in the Gulf of Alaska during February 2006. Region codes are as outlined in Table 1.

	All	Ocean age 1	Ocean age 2	Ocean age 3	Ocean age 4	Undetermined
Number of samples	519	30	212	162	104	12
Honshu Sea of Japan	0.0 (0.1)	0.0 (0.4)	0.0 (0.2)	0.0 (0.3)	0.0 (0.3)	0.0 (1.0)
Honshu Pacific	0.0 (0.1)	0.0 (0.4)	0.0 (0.1)	0.1 (0.4)	0.3 (0.9)	0.0 (0.9)
Hokkaido Sea of Japan	0.0 (0.0)	0.0 (0.3)	0.0 (0.3)	0.0 (0.1)	0.0 (0.1)	2.7 (5.8)
Hokkaido Sea of Okhotsk	11.7 (1.8)	0.0 (0.3)	8.1 (2.7)	12.1 (3.3)	24.9 (5.3)	1.0 (3.8)
Nemuro Strait	1.4 (1.1)	0.0 (0.2)	0.0 (0.1)	4.7 (3.1)	0.6 (1.8)	2.0 (5.0)
Hokkaido eastern Pacific	2.6 (1.0)	0.0 (0.3)	1.7 (1.9)	3.0 (2.0)	3.7 (2.5)	1.4 (4.3)
Hokkaido western Pacific	5.6 (1.3)	0.0 (0.3)	8.2 (2.3)	0.3 (0.9)	6.6 (3.2)	1.6 (4.3)
Sakhalin	1.0 (0.5)	0.0 (0.3)	1.6 (1.0)	0.1 (0.3)	1.8 (1.7)	0.0 (0.6)
Magadan	1.5 (0.8)	0.0 (0.6)	0.4 (0.8)	0.0 (0.3)	6.7 (3.1)	0.0 (1.0)
West Kamchatka	6.9 (1.6)	0.1 (0.9)	0.6 (1.1)	15.1 (3.5)	9.4 (4.2)	0.0 (0.9)
East Kamchatka	0.9 (1.5)	0.0 (0.6)	0.3 (0.7)	0.3 (1.1)	2.2 (4.2)	0.0 (1.0)
Northeast Russia	7.2 (1.4)	0.0 (0.2)	9.2 (2.2)	0.4 (1.0)	9.3 (3.2)	0.0 (0.5)
Kotzebue Sound	1.9 (0.8)	0.0 (0.4)	2.1 (1.2)	0.1 (0.4)	0.0 (0.3)	0.0 (0.9)
Norton Sound	4.8 (1.5)	0.0 (0.5)	8.5 (2.5)	7.4 (3.0)	0.3 (1.0)	7.0 (7.3)
Yukon lower summer	0.2 (0.6)	0.0 (0.6)	0.1 (0.5)	0.6 (1.4)	4.5 (2.9)	0.4 (2.6)
Yukon Upper Alaska fall	0.9 (0.6)	0.0 (0.3)	1.5 (1.3)	0.6 (0.9)	0.0 (0.1)	0.0 (0.7)
Yukon mainstem Canada	0.1 (0.3)	0.0 (0.3)	0.4 (0.9)	0.0 (0.3)	0.0 (0.1)	0.0 (0.9)
Yukon White	0.0 (0.0)	0.0 (0.3)	0.0 (0.0)	0.1 (0.3)	0.0 (0.1)	0.0 (0.6)
Yukon Porcupine Canada	0.0 (0.1)	0.0 (0.3)	0.1 (0.5)	0.1 (0.3)	0.0 (0.1)	0.0 (0.7)
Nushagak summer	0.1 (0.4)	0.0 (0.2)	0.0 (0.1)	1.5 (1.9)	0.0 (0.2)	0.3 (2.4)
Kuskokwim Bay/ River	0.3 (0.7)	0.0 (0.4)	0.3 (0.8)	0.2 (0.9)	0.2 (0.8)	0.7 (2.7)
Northeast Bristol Bay	0.9 (1.2)	0.0 (0.3)	0.8 (1.3)	0.3 (1.0)	0.1 (0.6)	0.0 (0.6)
North Peninsula	0.9 (0.5)	0.0 (0.3)	1.7 (1.0)	0.0 (0.1)	2.3 (1.9)	0.0 (0.8)
Southwest Peninsula	0.0 (0.1)	0.3 (1.3)	0.1 (0.3)	0.0 (0.3)	0.1 (0.4)	0.0 (0.5)
Southeast Peninsula	0.1 (0.2)	0.0 (0.4)	0.6 (1.0)	0.0 (0.1)	0.0 (0.3)	0.0 (0.9)
Kodiak Island	0.4 (0.3)	0.0 (0.2)	0.6 (0.6)	0.6 (0.6)	0.0 (0.1)	0.0 (0.6)
Prince William Sound	11.3 (1.6)	30.5 (10.6)	17.9 (2.9)	4.1 (1.8)	2.8 (2.7)	1.0 (4.4)
SE Alaska	18.0 (2.2)	38.7 (12.0)	7.5 (3.6)	18.2 (3.8)	9.3 (3.9)	42.5 (15.5)
Taku	0.1 (0.3)	0.6 (2.7)	0.0 (0.2)	0.3 (0.8)	0.0 (0.3)	9.3 (8.9)
QCI west	0.0 (0.1)	0.5 (2.2)	0.1 (0.4)	0.0 (0.2)	0.1 (0.6)	0.0 (1.2)
QCI east	0.1 (0.3)	1.0 (3.3)	0.0 (0.3)	0.0 (0.2)	0.0 (0.3)	0.0 (1.6)
QCI Skidegate	0.1 (0.2)	0.1 (0.7)	0.1 (0.4)	0.0 (0.2)	0.2 (0.7)	0.0 (1.4)
BC north	0.3 (0.8)	0.3 (1.7)	0.5 (1.2)	0.3 (1.1)	0.9 (1.9)	0.3 (2.7)
Skeena	0.0 (0.1)	0.4 (1.8)	0.0 (0.2)	0.0 (0.2)	0.0 (0.2)	0.1 (2.2)
BC Grenville	0.4 (0.7)	0.2 (1.7)	6.5 (3.5)	0.0 (0.3)	1.6 (2.2)	0.0 (1.1)
BC central	1.7 (1.0)	0.6 (2.4)	2.7 (2.0)	3.5 (2.7)	3.4 (3.7)	0.0 (2.5)
BC Rivers Inlet	0.0 (0.1)	0.1 (0.8)	0.0 (0.2)	0.0 (0.1)	0.7 (1.9)	0.0 (1.1)
Johnstone Strait	0.0 (0.2)	0.4 (1.6)	0.0 (0.2)	0.0 (0.2)	0.0 (0.3)	0.0 (1.7)
BC south	3.6 (1.5)	6.4 (7.3)	4.1 (2.6)	0.4 (1.2)	0.1 (0.5)	14.0 (14.7)
ECVI	1.5 (1.7)	10.0 (9.3)	2.3 (2.3)	5.5 (3.3)	0.1 (0.7)	12.6 (15.4)
WCVI	4.6 (1.2)	0.6 (2.4)	4.4 (1.7)	5.2 (2.3)	1.8 (1.5)	0.0 (1.3)
Fraser	7.3 (1.6)	8.9 (8.1)	6.4 (2.4)	7.1 (2.9)	2.2 (2.8)	1.9 (6.1)
North Puget Sound	0.0 (0.2)	0.0 (0.5)	0.5 (1.1)	0.3 (1.1)	3.7 (3.7)	0.7 (3.1)
South Puget Sound	0.2 (0.4)	0.0 (0.6)	0.0 (0.1)	2.6 (1.7)	0.0 (0.1)	0.0 (0.7)
Hood Canal	0.2 (0.4)	0.0 (0.3)	0.0 (0.1)	0.9 (1.5)	0.0 (0.1)	0.1 (1.3)
Juan de Fuca Strait	1.0 (0.8)	0.0 (0.3)	0.1 (0.4)	3.5 (1.8)	0.0 (0.2)	0.0 (0.8)
Coastal Washington	0.0 (0.2)	0.0 (0.3)	0.0 (0.1)	0.2 (0.7)	0.0 (0.1)	0.0 (0.7)

Table 2 (continued).

	All	Ocean age 1	Ocean age 2	Ocean age 3	Ocean age 4	Undetermined
Values by region						
Japan	21.3 (1.9)	0.0 (0.9)	18.0 (2.8)	20.2 (3.3)	36.0 (4.9)	8.7 (7.8)
Russia	17.5 (2.0)	0.2 (1.4)	12.2 (2.6)	16.0 (3.4)	29.5 (5.2)	0.0 (2.0)
Western Alaska	9.3 (1.5)	0.0 (1.2)	13.2 (2.6)	10.8 (2.7)	5.1 (2.7)	8.3 (7.6)
Central/Southeast Alaska	30.6 (2.4)	69.6 (9.9)	28.3 (4.2)	23.0 (3.9)	14.4 (4.9)	43.6 (14.7)
Canada Yukon	0.1 (0.3)	0.0 (0.6)	0.5 (1.0)	0.2 (0.5)	0.0 (0.2)	0.0 (1.6)
Northern British Columbia	2.7 (1.3)	3.7 (5.9)	10.0 (3.9)	4.2 (2.9)	7.0 (4.6)	9.8 (10.3)
Southern British Columbia	17.1 (1.9)	26.4 (9.1)	17.1 (2.9)	18.3 (3.8)	4.3 (3.1)	28.6 (12.9)
Washington	1.4 (0.8)	0.1 (1.0)	0.6 (1.1)	7.4 (2.7)	3.7 (3.7)	0.8 (3.6)

chum salmon, so if Japanese chum salmon are present, substantial contributions from these regions would be expected. However, it is noteworthy that few chum salmon from Honshu or the Sea of Japan coast of Hokkaido were observed in the sampling in the Gulf of Alaska, so chum salmon from these regions either do not migrate as far east as other Japanese chum salmon, or they were south of 48°N during winter residence in the Gulf of Alaska.

Chum salmon from North America were distributed in the more northerly regions sampled in the Gulf of Alaska, and, conversely, Asian chum salmon were more prevalent in the southern regions. Chum salmon from western Alaska were observed in the Gulf of Alaska in winter after two summers of marine residence, but not after one summer. Urawa et al. (2000) indicated that western Alaskan stocks were rarely present among ocean age-1 chum salmon, and increased among ocean age-2 and -3 in the central Gulf of Alaska during the summer of 1998. Therefore, western Alaska chum salmon might not migrate to the Gulf of Alaska after one summer of rearing. Chum salmon from northern British Columbia were only observed in significant proportions in the most northern sample (53°N), perhaps indicative of a more northerly distribution in the Gulf of Alaska for chum salmon from this region. Fraser River chum salmon were also more prevalent at more northern sampling locations in the Gulf of Alaska. Clearly, there was a nonrandom distribution of chum salmon in the Gulf of Alaska during the winter of 2006.

ACKNOWLEDGMENTS

We thank the captain and crew of the R/V *Kaiyo-maru* for sample collection in the Gulf of Alaska.

REFERENCES

- Banks, M.A., M.S. Blouin, B.A. Baldwin, V.K. Rashbrook, H.A. Fitzgerald, S.M. Blankenship, and D. Hedgecock. 1999. Isolation and inheritance of novel microsatellites in chinook salmon (*Oncorhynchus tshawytscha*). *J. Hered.* 90: 281–288.
- Beacham, T.D., A.P. Gould, R.E. Withler, C.B. Murray and L.W. Barner. 1987. Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. *Can. J. Fish. Aquat. Sci.* 44: 1702–1713.
- Beacham, T.D., B. Spilsted, K.D. Le, and M. Wetklo. 2008a. Population structure and stock identification of chum salmon *Oncorhynchus keta* from British Columbia determined with microsatellite DNA variation. *Can. J. Zool.* 89: 1002–1014.
- Beacham, T.D., S. Urawa, K.D. Le, and M. Wetklo. 2008b. Population structure and stock identification of chum salmon from Japan determined with microsatellite DNA variation. *Fish. Sci.* 74: 983–994.
- Beacham, T.D., N.V. Varnavskaya, K.D. Le, and M. Wetklo. 2008c. Determination of population structure and stock identification of chum salmon (*Oncorhynchus keta*) in Russia, determined with microsatellites. *Fish. Bull.* 106: 245–256.
- Beacham, T.D., M. Wetklo, C. Wallace, J.B. Olsen, B.G. Flannery, J.K. Wenburg, W.D. Templin, A. Antonovich, and L.W. Seeb. 2008d. The application of microsatellites for stock identification of Yukon River Chinook salmon. *N. Am. J. Fish. Manage.* 28: 283–295.
- Beacham, T.D., J.R. Candy, K.D. Le, and M. Wetklo. 2009a. Population structure of chum salmon (*Oncorhynchus keta*) across the Pacific Rim, determined from microsatellite analysis. *Fish. Bull.* 107: 244–260.
- Beacham, T.D., K.D. Le, M. Wetklo, B. McIntosh, T. Ming, and K.M. Miller. 2009b. Population structure and stock identification of chum salmon from western Alaska determined with microsatellite and major histocompatibility complex variation. *In* Sustainability of the Arctic-Yukon-Kuskokwim salmon fisheries: what do we know about salmon ecology, management and fisheries? Edited by C.C. Krueger, and C.E. Zimmerman. *Am. Fish. Soc. Symp.* 70. Bethesda, Maryland.
- Brodeur, R.D., K.D. Myers, and J.H. Helle. 2003. Research conducted by the United States on the early ocean life of Pacific salmon. *N. Pac. Anadr. Fish Comm. Bull.* 3: 89–131. (Available at www.npafc.org).
- Buchholz, W.G., S.J. Miller, and W.J. Spearman. 2001. Iso-

- lation and characterization of chum salmon microsatellite loci and use across species. *Animal Genetics* 32: 160–165.
- Cairney, M., J.B. Taggart, and B. Hoyheim. 2000. Characterization of microsatellite and minisatellite loci in Atlantic salmon (*Salmo salar* L.) and cross-species amplification in other salmonids. *Mol. Ecol.* 9: 2175–2178.
- Cooke, S.J., S.G. Hinch, A.P. Farrell, M. Lapointe, M. Healy, D. Patterson, S. MacDonald, S. Jones, and G. Van Der Draak. 2004. Abnormal migration timing and high en-route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries* 29(2): 22–33.
- Efremov, V.V. 2001. Genetic variation and differentiation of populations of chum salmon *Oncorhynchus keta* (Walbaum) from Southern Russian Far East. *Russ. J. Genetics* 37: 283–289.
- Ginatulina, L.K. 1992. Genetic differentiation among chum salmon, *Oncorhynchus keta* (Walbaum), from Primorye and Sakhalin. *J. Fish Biol.* 40: 33–38.
- Ishida, Y., S. Ito, and K. Takagi. 1989. Stock identification of chum salmon *Oncorhynchus keta* from their maturity and scale characters. *Bull. Japan Soc. Sci. Fish.* 55: 651–656.
- 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.
- Mueter, F.J., R.M. Peterman, and B.J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* 59: 456–463.
- Neaves, P.I., C.G. Wallace, J.R. Candy, and T.D. Beacham. 2005. CBayes: Computer program for mixed stock analysis of allelic data. Version v4.02. (Free program distributed by the authors over the internet from www.pac.dfo-mpo.gc.ca/sci/mgl/Cbayes_e.htm).
- Nelson, R.J., and T.D. Beacham. 1999. Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. *Animal Genetics* 30: 228–229.
- Nikolayeva, Y., and N.I. Semenets. 1983. A contribution to stock differentiation of chum salmon, *Oncorhynchus keta* (Salmonidae), by scale structure in the first year of growth. *J. Ichthyol.* 23: 18–28.
- Okazaki, T. 1982a. Genetic study on population structure in chum salmon (*Oncorhynchus keta*). *Far Seas Fish. Res. Lab. Bull.* 19: 25–116.
- Okazaki, T. 1982b. Geographical distribution of allelic variation of enzymes in chum salmon *Oncorhynchus keta*, river populations of Japan and the effects of transplantation. *Bull. Japan Soc. Sci. Fish.* 48: 1525–1535.
- Olsen, J.B., S.L. Wilson, E.J. Kretschmer, K.C. Jones, and J.E. Seeb. 2000. Characterization of 14 tetranucleotide microsatellite loci derived from sockeye salmon. *Mol. Ecol.* 9: 2185–2187.
- Pella, J., and M. Masuda. 2001. Bayesian methods for analysis of stock mixtures from genetic characters. *Fish. Bull.* 99: 151–167.
- Rexroad, C.E., R.L. Coleman, A.M. Martin, W.K. Hershberger, and J. Killefer. 2001. Thirty-five polymorphic microsatellite markers for rainbow trout (*Oncorhynchus mykiss*). *Animal Genetics* 32: 317–319.
- Sato, S., J. Ando, H. Ando, S. Urawa, A. Urano, and S. Abe. 2001. Genetic variation among Japanese populations of chum salmon inferred from the nucleotide sequences of the mitochondrial DNA control region. *Zool. Sci. (Tokyo)* 18: 99–106.
- Sato, S., H. Kojima, J. Ando, H. Ando, R.L. Wilmot, L.W. Seeb, V. Efremov, L. LeClair, W. Buchholz, D.-H. Jin, S. Urawa, M. Kaeriyama, A. Urano, and S. Abe. 2004. Genetic population structure of chum salmon in the Pacific Rim inferred from mitochondrial DNA sequence variation. *Environ. Biol. Fish.* 69: 37–50.
- 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. (Available at www.npafc.org).
- Seeb, L.W., and P.A. Crane. 1999a. High genetic heterogeneity in chum salmon in Western Alaska, the contact zone between northern and southern lineages. *Trans. Am. Fish. Soc.* 128: 58–87.
- Seeb, L.W., and P.A. Crane. 1999b. 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.
- Smith, C.T., B.F. Koop, and R.J. Nelson. 1998. Isolation and characterization of coho salmon (*Oncorhynchus kisutch*) microsatellites and their use in other salmonids. *Mol. Ecol.* 7: 1613–1621.
- Spies, I.B., D.J. Brasier, P.T.L. O'Reilly, T.R. Seamons, and P. Bentzen. 2005. Development and characterization of novel tetra-, tri-, and dinucleotide microsatellite markers in rainbow trout (*Oncorhynchus mykiss*). *Mol. Ecol. Notes* 5: 278–281.
- Tanaka, S., M.P. Shepard, and H.T. Bilton. 1969. Origin of chum salmon (*Oncorhynchus keta*) in offshore waters of the North Pacific in 1956–1958 as determined from scale studies. *Int. North Pac. Fish. Comm. Bull.* 26: 57–155.
- Urawa, S. 2000. Ocean migration route of Japanese chum salmon with a reference to future salmon research. *National Salmon Resources Center Newsletter* 5: 3–9. (Available at http://salmon.fra.affrc.go.jp/kankobutu/salmon/salmon05_p03-09.pdf).
- Urawa, S. 2004. Stock identification studies of high seas salmon in Japan: a review and future plan. *N. Pac.*

- Anadr. Fish Comm. Tech. Rep. 5: 9–10. (Available at www.npafc.org).
- 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).
- 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).
- 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., 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., B.R. Ward, B.D. Smith, and J.P. Eveson. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fish. Oceanogr. 9: 17–32.
- Williamson, K.S., J.F. Cordes, and B.P. May. 2002. Characterization of microsatellite loci in chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. Mol. Ecol. Notes 2: 17–19.
- Wilmot, R.L., R.J. Everett, W.J. Spearman, R. Baccus, N.V. Varnavskaya, and S.V. Putivkin. 1994. Genetic stock structure of Western Alaska chum salmon and a comparison with Russian Far East stocks. Can. J. Fish. Aquat. Sci. 51 (Suppl. 1): 84–94.
- Wilmot, R.L., C.M. Kondzela, C.M. Guthrie, and M.M. 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).
- Winans, G.A., P.B. Aebersold, S. Urawa, and N.V. Varnavskaya. 1994. Determining continent of origin of chum salmon (*Oncorhynchus keta*) using genetic identification techniques: status of allozyme baseline in Asia. Can. J. Fish. Aquat. Sci. 51 (Suppl. 1): 95–113.
- Winans, G.A., P.B. Aebersold, Y. Ishida, and S. Urawa. 1998. Genetic stock identification of chum salmon in high-seas test fisheries in the western North Pacific Ocean and Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 1: 220–226. (Available at www.npafc.org).