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Variability in Freshwater, Estuarine, and Marine Residence of Sockeye Salmon *Oncorhynchus nerka* within the Copper and Bering River Deltas, Alaska

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ABSTRACT Variability in the duration of freshwater and marine residence of sockeye salmon *Oncorhynchus nerka* has been recognized for some time and is the basis for separating the species into different life history strategies. We analyzed the results of annual age-composition surveys of spawning sockeye salmon conducted by Alaska Department of Fish and Game in the Copper River Delta and Bering River regions of southcentral Alaska from 1990 to 2004 to quantify the variability in freshwater and marine residence time. Significant variation among years and among locations was detected by multivariate analysis of similarity. The two most common life history forms were sockeye salmon that spent one winter in freshwater after emergence followed by either 2 or 3 years in marine waters before returning to spawn (1.2 or 1.3 European age notation). Sockeye salmon exhibiting these two strategies accounted for 36% and 46%, respectively, of all sockeye salmon aged over the 14 year surveys (n = 93,936). Sockeye salmon spending less than 1 year in freshwater following emergence (0.1, 0.2, 0.3 and 0.4) accounted for 14% of all adult sockeye salmon surveyed compared to 82% that spent 1 year in freshwater (1.1, 1.2, 1.3, 1.4) and 4% that spent 2 years (2.1, 2.2, 2.3). Only one fish was aged that spent 3 years in freshwater. Large interannual and among site variability in the proportion of fishes that spend 0 years in freshwater was apparent. The magnitude of 0-type sockeye salmon was best correlated with site locations (sloughs had a higher proportion than lake sites). Despite the low average contribution of 0-type sockeye salmon to the adult spawning population, large numbers of sockeye salmon leave freshwater as age-0 fry and parr. These sockeye salmon can be found in the estuarine waters near the outflow of major sloughs and rivers for a 45-d period coinciding with peak out-migration from freshwater areas. All juvenile stages of sockeye salmon seem to have similar residence time in the estuary, suggesting that for sockeye salmon out-migration at an early age does not lead to longer nearshore residence time for sockeye salmon.

Sockeye salmon *Oncorhynchus nerka* are an integral component of the socioeconomic and ecological landscape of the North Pacific. As with many anadromous salmonid species, sockeye salmon demonstrate a significant diversity in life history strategies or "ecotypes" (Hendry et al. 2001) associated with the degree and timing of anadromy. This range includes sockeye salmon populations that are resident in freshwater lakes for their entire life ("kokanee"), and populations that migrate to marine waters after residing in coastal rivers less than 1 year ("ocean" or "sea type"), freshwater off-channel river habitats for 1–2 years ("river" or "stream"

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type), or in lacustrine systems ("lake type"; Groot and Margolis 1991; Gustafson and Winans 1999; Quinn 2005). Rather than discrete types, anadromous sockeye salmon represent a continuum of variability in freshwater residence time (Quinn 2005). Genetic analysis has found little differentiation between river- and sea-type sockeye salmon compared to the highly divergent lake-type sockeye salmon (Gustafson and Winans 1999). This lack of genetic differentiation suggests that a high level of gene flow exists between river and sea-type forms and that residence time in freshwater is not fixed.

Residence time of juvenile salmon in nearshore and estuarine habitats has been suggested to be correlated to some degree with age of out-migration from freshwater habitats (Itwata and Komatsu 1984; Heifetz et al. 1989). Juvenile sockeye salmon have been found in estuaries as age 0 fry, 0, 1, and 2 year-old parr or smolt. For sea-type sockeye salmon, estuarine rearing may be critical for survival and is generally thought to be much longer for sea-type than other sockeye salmon with longer freshwater rearing. Heifetz et al. (1989) reported an estuarine rearing time of 3–4 months in the Situk River estuary, Southeast Alaska. Similar estuarine rearing times have been reported for sea-type sockeye salmon in the Fraser River Delta, British Columbia (Birtwell et al. 1987). Once in estuarine waters, juvenile salmon must physiologically adapt to oceanic conditions, assimilate information needed to return as adults, and avoid a new suite of predators. The long spatial gradient in salinity common in many estuaries aids physiological adaptation to marine waters (Itwata and Komatsu 1984; Heifetz et al. 1989). Size of an individual also greatly influences the speed of this physiological adaptation and may be partly responsible for the pattern of longer residence time for smaller juveniles (Heifetz et al. 1989).

In addition to variability in freshwater and estuarine residence, anadromous sockeye salmon populations show variability in marine residence, ranging from 1 to 4 years, with the majority spending 2–3 years in marine waters (Groot and Margolis 1991; Quinn 2005). Here, we examine 14 years (1990–2004) of annual surveys by the Alaska Department of Fish and Game (ADFG) of sockeye salmon that have returned to spawning areas in the Copper River Delta and Bering River region of southcentral Alaska. We utilize this database to quantify the spatial and temporal variability in the age of out-migration and the relative contribution of differing freshwater and marine residence strategies to the surviving spawners of a typical north Pacific Coast watershed. Further, we report the findings of recent field work designed to examine estuarine habitat utilization of juvenile sockeye salmon in the western portion of the Copper River Delta. Eventually, merging of both data sets will allow evaluation of the degree to which climatological and biological factors influence residency time in freshwater, estuarine, and marine waters.

Study Area

The two state fisheries management districts, referred to as the Copper River and Bering River Districts normally encompass the fluvial deltas and the nearshore/estuarine areas formed or influenced by the Copper and Bering Rivers. Included in this region are several smaller glacier fed, coastal rivers to the west (Sheridan River, Scott River) and east (Martin River and Bering River), lakes connected to the Deltas by small rivers or sloughs (Eyak Lake, McKinley Lake to the west of the Copper River and Martin Lake, Little Martin Lake, Tokun Lake, Bering Lake, and Kushtaka Lake to the east of the Copper River). Several sloughs bisect the extensive network of mudflats (~500 km^2), which stretch almost continuously for 115 km from Orca Inlet in south-

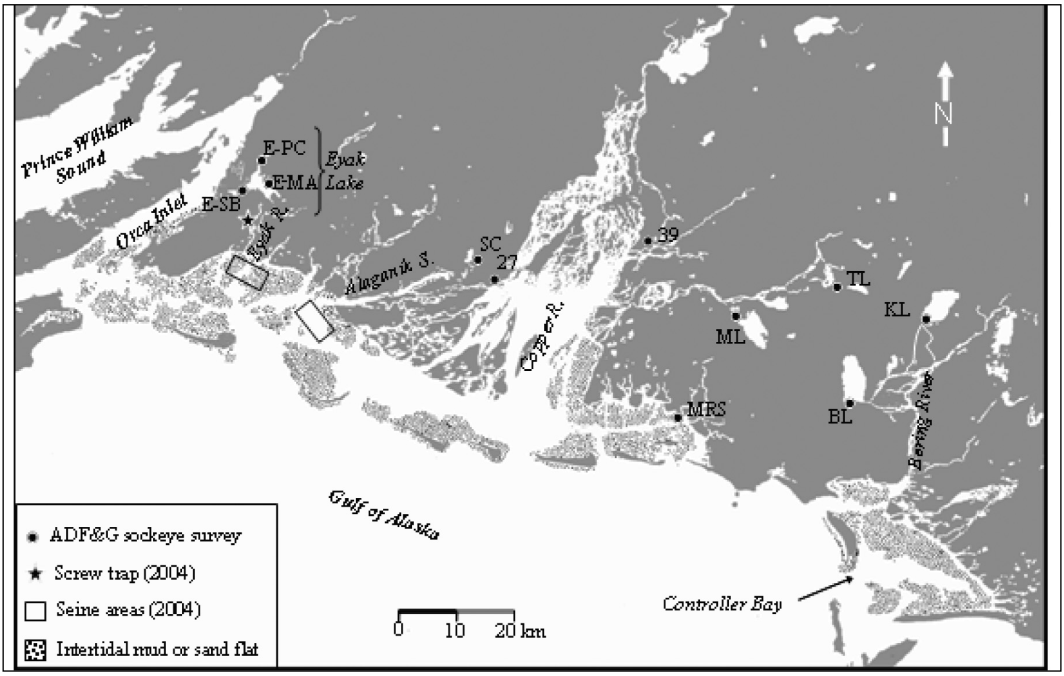

Figure 1. Map of the Copper and Bering River Deltas, Alaska showing the locations of the Alaska Department of Fish and Game sampling sites where returning adult sockeye were collected for age determination, as well as screw trap placement for 2004, and estuarine areas where seine collections were conducted during 2004. Location codes: ESB = Eyak Lake–South Beach, EMA = Eyak Lake–Middle Arm, EPC = Eyak Lake–Power Creek, SC = Salmon Creek, 27 = 27 mi Slough, 39 = 39 mi Slough, MRS = Martin River Slough, ML = Martin Lake, TL = Tokun Lake, BL = Bering Lake, KL = Kushtaka Lake.

eastern Prince William Sound to Controller Bay (Bering River Delta; Figure 1). The Copper and Bering River Deltas' intertidal mudflats and network of sloughs serve as a critical connection between the Gulf of Alaska and a vast expanse of wetlands, rivers, lakes, and glaciers. Some 549 drift gillnet fishers commercially harvest three species of salmon in the two districts: sockeye, coho *O. kisutch*, and Chinook salmon *O. tshawytscha*. Recreational anglers and subsistence fishers also harvest salmon throughout the freshwater wetlands and river systems of the Copper River watershed. The tidal flats serve as both an entry and exit corridor for these salmon (Powers et al. 2002). Since 1978 the State of Alaska has designated the Copper River Delta, including the intertidal habitats, a State Critical Habitat Area. The Alaska National Interest Lands Conservation Act of 1980 (ANILCA) further mandated that the conservation of fish and wildlife and their habitats shall be the primary purpose for the management of the Copper River Delta. This mandate applies to federal lands, with the USDA Forest Service managing all lands above mean high tide.

From late April to August extensive snow and ice melt in the Copper and Bering River drainage basins results in elevated river discharge (up to 5,300 m^3 s^{-1} for the Copper River during this period [Brabets 1997]). The large discharge of freshwater within the semi-enclosed, nearshore area of the Copper River Delta results in system-wide lowering of salinities, particularly near outflows of river and sloughs. Salinity ranges from 2 to 10 practical salinity units (psu) from mid-May to mid-September in many nearshore areas of the western Copper River Delta (Powers et al. 2002, 2006). Few data are available from the nearshore areas of the eastern Copper River Delta and Bering River Delta (Controller Bay); however, it is reasonable to assume that discharge from the Copper, Bering, and Martin rivers also dramatically reduce salinity in the nearshore areas of the eastern Copper and Bering River Deltas. During periods of reduced river discharge (mid-September to early May) salinity ranges from 15 to 24 psu in areas near the outflows of sloughs and rivers on the western Copper River Delta (Powers et al. 2002; Powers and Bishop, unpublished data). Adult sockeye salmon begin up-estuary and up-river migration between May and June as river ice breaks up and discharge of rivers increases. A large commercial fishery occurs in the estuarine and nearshore marine waters of the Copper and Bering River Deltas during this same period. On average (1995–2004), the 500+ permitted commercial fishers annually harvest 1.5 million sockeye salmon. Personal use and subsistence fisheries annually harvest an additional 200,000 sockeye salmon during this period at upriver areas, Glennallen and Chitnia (Ashe et al. 2005).

Methods

Age Composition of Returning Sockeye Salmon

The Alaska Department of Fish and Game performs annual collections of adult sockeye salmon at 11 locations throughout the Copper and Bering River Deltas (Figure 1). The sockeye salmon collections are added to brood tables used for escapement goal analysis and preseason forecasts (e.g., Bue et al. 2002). Three sites are located within Eyak Lake and include one collection site on the southern shoreline of the lake (Eyak South Beach), one in the middle arm portion of the lake (Eyak- Middle Arm), and one in a creek feeding into the lake (Eyak Lake -Power Creek). Three sites are located in the upper reaches of wetland sloughs on the Copper River Delta (Salmon Creek, 27 mi Slough, and 39 mi Slough). Three sites are located in the Martin River watershed, which feeds into the eastern Copper River Delta: Martin River Slough, Martin Lake, and Tokun Lake. The final two sites are located near the Bering River, which empties into Controller Bay: Bering Lake and Kushtaka Lake. Depending on location, collections are made once or twice during the period from mid-June to mid-September.

Age determinations were made by analysis of growth ring patterns on scales removed from below the dorsal fin and above the mid line of adult sockeye salmon by ADFG scientists. Because the outer margins of scales of most fish are reabsorbed a direct reading would underestimate the marine age. To avoid this bias, length frequencies were also examined by sex and location to determine the marine age. European notation for anadromous fish ages is used with the first number referring to years spent in freshwater and the second number denoting years in marine waters. For example, 0.3 would indicate a sockeye salmon that did not overwinter in freshwater after emergence and spent 3 winters in marine water. An age of 2.2 would indicate a sockeye salmon that spent 2 years in freshwater and 2 years in marine water. Summing the two numbers and adding one will produce the total age of the fish and allows calculation of the year deposited. For example, the egg for a 2.2 sockeye salmon collected in 2000 would have been deposited in summer 1995 and emerged in early 1996.

Utilizing the ADFG data set for the 11 locations surveyed from 1990 through 2004 in the Copper and Bering River districts, we used a series of multivariate tests to examine spatial and temporal variability in the relative contribution of different sockeye salmon life histories (i.e., combination of freshwater and marine residence time) to the successful spawning population. To determine whether there was similarity among the 11 sampling locations with respect to the proportion of sockeye salmon of each life history, we performed an Analysis of Similarity (ANOSIM, Primer ver. 6, Clarke and Warwick 2001) using 11 dependent variables that represented the proportion of sockeye salmon in each survey year as classified by years spent in fresh and marine waters (i.e., 0.1, 0.2, 0.3, 0.4, 1.1, 1.2, 1.3, 1.4, 2.1, 2.2 and 2.3). To assess spatial patterns with ANOSIM, we analyzed the multivariate pattern among locations using each of the 14 years of the survey as replicates. To examine interannual patterns, we examined the proportion of sockeye salmon assigned to each of 11 age categories each year using the 11 locations as replicates. For the ANOSIM procedure, a matrix of Bray-Curtis similarities between samples (location * year combinations in our study) is created from untransformed data. Significant differences in rank similarities between groups are tested and a global R statistic (analogous to the F value in an analysis of variance (ANOVA)) is calculated through repeated random permutations of the data. If the R statistic is significant at $P < 0.05$ (i.e., the null hypothesis that no difference between groups exists is rejected), then pairwise comparisons between locations or years is conducted with $P < 0.05$ indicating significant difference (Clarke and Warwick 2001; Smith 2003). We determined which age categories primarily accounted for the difference among locations or years by performing SIMPER analysis (species contribution to similarity, PRIMER ver. 6) on the data matrix. Finally, similarities among location or years were graphically represented by non-metric MDS ordination based on BrayCurtis similarity distances.

Sockeye Salmon in Estuarine Areas

While analysis of the ADFG data set allows for assessment of spatial and temporal variability in the duration of fresh and marine water use, assessment of estuarine habitat use is not possible with existing data sets. Because residence time in estuarine areas is normally less than 1 year and growth of scales is probably similar between estuarine and marine waters, analysis of scale growth reveals little information that would separate marine and estuarine phases. As part of a 3-year project to assess estuarine habitat use of sockeye and coho salmon, we conducted seine sampling in the upper estuarine waters of the western Copper River Delta in 2004. In the estuarine waters near the outflows of the Eyak River and Alaganik Slough, a tidally-influenced slough that extends from the estuary into the freshwater wetlands of the delta, we established a sampling program that was designed to capture exiting smolt, parr, and fry in the shallow, subtidal sloughs of the upper mudflat areas. Two areas, one near the higher tidal elevations, 900 and 1600 m from the boundary between wetlands vegetation and mudflats (high), and a second at a lower tidal elevation (greater tidal inundation) and 3,000 and 3,400 m from the wetland boundary (low), were established in small tidal sloughs off the main channel outflow of the Eyak River and Alaganik Slough, respectively. Three to six replicate seines pulls (20 m each) were performed in each area; the locations of each seine pull within the four areas (Eyak high, Eyak low, Alaganik high, Alaganik low) were chosen haphazardly from the general area during each collection period. The seine used for collection was made of 4 mm delta mesh and was 8 m wide and 1.2 m high with a 1.2 m × 1.2 m bag attached to the mid region. Seine collections were performed on a weekly basis from the end of May through mid-October 2004, although inclement weather forced bimonthly sampling during some periods. All salmonids were identified to species, measured (total length [TL] in mm), and classified as fry, parr, or smolt. A random subsample of parr and smolt were frozen and scales removed for age determination.

In order to evaluate the timing of juvenile salmonid entry to the estuary, we installed and maintained a screw trap (aluminum with 1.5 m diameter drum turned by river water) near the outflow of the Eyak River (located below Lake Eyak immediately downstream of a small dam). The screw trap was established 50 m downstream of the dam, in the center of the river channel. The center location was chosen to ensure adequate flow to turn the screw trap. Water flow near either side of the rock lined shoreline was too low to effectively turn the screw trap. The large width of the river (~ 10 m) and the need to not restrict public access to recreational fishermen prevented enclosing this portion of river with weirs or nets. Consequently, capture of juvenile sockeye by the Eyak screw trap is used as an indication of timing of out-migration and relative abundance of different juvenile stages (fry, parr, and smolt) not as an absolute value. River flow rates at the screw trap were monitored using a General Oceanics plankton net flowmeter placed near the mouth of the screw trap. The Eyak screw trap was installed on May 22, 2004 and monitored on a daily or 2-d interval depending on weather until November 4, 2004. The trap ran continuously during the period with no repair needed and only minimal periods of low river flow.

Seine and screw trap data were converted to catch per unit effort (CPUE) (#/20 m seine pull or #/h for screw trap) and graphed to examine temporal trends. Seine data were also analyzed by paired *t*-tests to determine whether differences in the abundance of sockeye fry, parr, and smolt existed between high and low tidal elevations. An average catch of the seine pulls was calculated for each collection period and high and low elevations were compared separately for Alaganik and Eyak areas using each sampling data as a replicate for the test.

Results

Age Composition of Returning Sockeye Salmon

A total of 93,936 sockeye salmon was aged by ADFG scientists from 11 locations in the Copper and Bering River Deltas. Overall, the two most common life history forms were sockeye salmon that spent one winter in freshwater after emergence followed by 2 or 3 years in

Table 1.
Age of sockeye expressed as freshwater/marine years for sockeye collected at 11 different spawning locations throughout the Copper River and Bering River Deltas. Table presents percentage of total sockeye (n = 93,936) surveyed annually from 1990 - 2004 by the Alaska Department of Fish and Game.

	Age Group										
	Age 2	*Age 3*		*Age 4*			*Age 5*			*Age 6*	
Location	*0.1*	*0.2*	*1.1*	*0.3*	*1.2*	*2.1*	*0.4*	*1.3*	*2.2*	*1.4*	*2.3*
Eyak South Beach	0.00	2.70	0.19	5.68	36.93	0.00	0.03	53.73	0.19	0.09	0.49
Eyak Middle Arm	0.00	1.94	1.08	6.31	29.74	0.01	0.04	59.49	0.46	0.19	0.67
Eyak Power Creek	0.00	2.81	2.80	4.39	41.94	0.00	0.00	45.41	0.95	0.05	1.52
Salmon Creek	0.00	5.15	2.07	7.12	41.80	0.00	0.01	42.95	0.44	0.07	0.33
27 mile Slough	0.00	14.99	1.35	14.61	34.95	0.00	0.03	33.21	0.33	0.09	0.27
39 mile Slough	0.12	3.25	5.10	6.41	31.54	0.00	0.00	52.51	0.27	0.09	0.48
Martin Lake	0.07	3.24	8.58	2.46	59.57	0.00	0.00	25.19	0.64	0.00	0.19
Tokun Lake	0.00	0.23	0.53	1.27	32.29	0.00	0.01	64.77	0.29	0.11	0.49
Martin River Slough	0.05	34.94	1.12	24.05	21.76	0.05	0.00	17.22	0.18	0.08	0.18
Bering Lake	0.01	2.01	2.59	8.25	25.51	0.00	0.00	61.20	0.03	0.14	0.15
Kushtaka Lake	0.00	0.54	1.81	0.90	40.71	0.02	0.02	47.04	4.04	0.11	3.81

marine waters before returning to spawn (1.2 or 1.3, Table 1). Sockeye salmon exhibiting these two strategies accounted for 36% and 46%, respectively, of all fish aged over the 14 years of surveys. Sockeye salmon spending less than 1 year in freshwater following emergence (0.1, 0.2, 0.3 and 0.4) accounted for 14% of all sockeye salmon surveyed compared to 82% that spent 1 year in freshwater (1.1, 1.2, 1.3, 1.4) and 4% that spent 2 years (2.1, 2.2, 2.3). Only 1 out of the 93,936 sockeye salmon aged spent 3 years in freshwater (Kushtaka Lake, age 3.3) before migrating to marine waters. The majority (54%) of sockeye salmon spent 3 years in marine waters followed by 2 years (44%), 1 year (2%), and 4 years (0.1%).

Although the average percentage of sockeye salmon spending less than 1 year in freshwater is relatively low (14%), interannual and spatial variability of the contribution of these 0 type fish is quite high (0–66%, Table 2). Using age estimates from scales, it is possible to back-calculate the percentage of fish that left freshwater habitat before their first winter after emergence (i.e., 0.1, 0.2, 0.3, and 0.4) and successfully returned to spawn. The original data set from 1990 through 2004, allowed reconstruction of 10 years (1988–1997) for most locations. Incomplete sampling (i.e., 1 or 2 missed sampling years) allowed only partial reconstruction of the data matrix for three sites: Kushtaka Lake, 39 mi Slough, and Martin River Slough. Of the 11 locations, slough type habitats had the highest percentage of fish that migrated to marine waters before their first winter. On average, 28% of sockeye salmon aged in the 4 slough locations left freshwater habitats before their first winter (Martin River Slough = 55%, 27 mi Slough = 33%, Salmon Creek = 13%, and 39 mi Slough = 11%). In contrast, an average of 7% of sockeye salmon aged from the 7 lake locations left freshwater before the first winter. Highest values for the lake locations were collected from Bering Lake (12%) and lowest from Tokun Lake (1%).

Significant differences among locations (ANOSIM global test, $R = 0.28$, $P < 0.01$) and among years (ANOSIM global test, $R = 0.03$, $P = 0.04$) were seen in the proportional contribution of the 11 different freshwater/marine age groups of sockeye salmon. Although significant, the low global R value (0 value indicates samples are indistinguishable) for the ANOSIM examining the effect of year, as well as the nMDS plot, indicates a high degree of similarity among most years (Figure 2). Pairwise comparisons of years found significant differences ($P < 0.05$) between two groups of years: 1990,

Table 2.
Percentage of sockeye that migrated from freshwater habitat to marine waters prior to their first winter after emergence. Year class refers to the period that eggs were deposited. Entry into freshwater would have occurred in the following year. Data is based on reconstruction of Alaska Department of Fish and Game annual survey of adult sockeye spawners.

	Year Class											
Location	*1987*	*1988*	*1989*	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*	*1996*	*1997*	*Average*
Tokun Lake	1.21	0.95	1.55	0.22	0.64	0.57	2.54	0.47	0.39	0.00	1.53	0.92
Kushtaka Lake	7.15	1.66	0.21	1.73	1.48	2.41	2.54	3.04	--	--	--	2.53
Eyak Power Creek	1.71	27.00	0.57	3.93	7.02	4.18	3.12	4.48	2.00	12.45	5.81	6.57
Martin Lake	7.57	5.06	18.29	6.47	0.97	2.86	31.68	4.03	1.18	1.63	10.54	8.21
Eyak South Beach	10.96	2.24	14.37	4.18	6.31	2.32	19.45	7.78	2.19	4.72	17.31	8.35
Eyak Middle Arm	13.46	2.92	4.21	18.34	10.55	8.09	9.53	4.09	4.45	21.06	10.63	9.76
39 mile Slough	20.12	1.03	14.61	4.43	3.10	1.09	33.09	--	--	--	--	11.07
Bering Lake	11.32	1.05	12.53	1.56	2.38	2.13	27.11	3.30	24.92	1.76	41.44	11.77
Salmon Creek	14.11	2.62	7.57	9.90	11.90	7.76	17.19	5.94	15.74	28.97	22.10	13.07
27 mile Slough	38.82	29.67	36.61	15.60	18.84	20.63	47.46	19.90	23.82	41.41	66.84	32.69
Martin River Slough	53.03	43.09	55.87	42.80	51.66	49.87	77.14	69.22	--	--	--	55.33

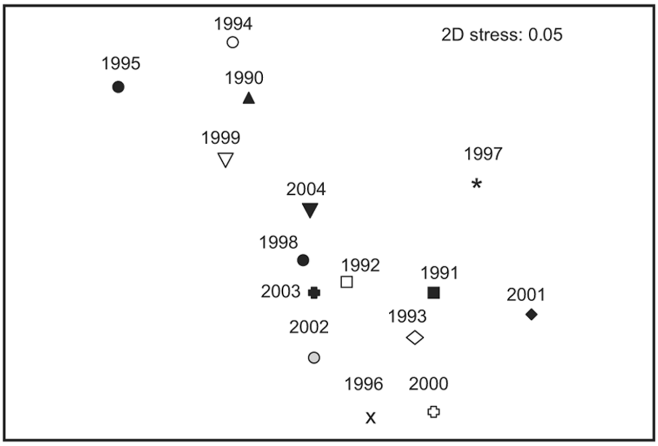

Figure 2. nMDS plot of survey years 1990–2004 based on the proportion of sockeye aged by Alaska Department of Fish and Game that were classified into 11 different freshwater/marine age categories. Little separation of survey years was detected by the analysis of similarity performed on the data set (ANOSIM R = 0.03). Points represent averages of untransformed data across 11 sampling locations for each year and stress indicates the degree to which the plot represents the data (stresses of >0.15 are considered good representations where there is minimal risk of misinterpretation).

1994, 1995, and 2004 each differed from 1996, 2000, 2001, and 2002. SIMPER analysis indicated that the proportions of 1.2 and 1.3 sockeye salmon contributed to the majority of this pattern (> 75%). Higher than average proportions of 1.3 and lower than average percentage of 1.2 characterized 1996, 2000, 2001, and 2002 sockeye returns (Table 3). The opposite pattern characterized 1990, 1994, 1995, and 2004 returns with higher than average 1.2 sockeye returning. Thus, the proportional contribution of the various freshwater and marine age categories was relatively similar between years across all locations; however, some differences in the relative contribution of 1.2 and 1.3 sockeye were evident.

Table 3.

Percentage of sockeye by age group, expressed as freshwater/marine years, for total sockeye (n = 93,936) surveyed annually from 1990 - 2004 by the Alaska Division of Fish and Game. Values reported are averaged over 11 different spawning locations throughout the Copper River and Bering River Deltas. Total estimated escapement is also reported based on surveys conducted by the Alaska Division of Fish and Game .

	Age Group											
	Age 2	*Age 3*		*Age 4*			*Age 5*			*Age 6*		
Year of collection	*0.1*	*0.2*	*1.1*	*0.3*	*1.2*	*2.1*	*0.4*	*1.3*	*2.2*	*1.4*	*2.3*	*Escapement*
1990	0.30	8.70	2.60	7.90	41.00	0.10	0.05	34.00	3.20	0.20	1.90	146,690
1991	0.00	1.90	1.60	10.90	37.30	0.00	0.00	47.80	0.10	0.00	0.40	181,000
1992	0.11	6.59	1.45	3.83	42.36	0.03	0.01	44.14	0.72	0.01	0.76	153,654
1993	0.10	7.21	3.21	5.00	27.85	0.05	0.00	54.96	0.39	0.14	1.08	115,440
1994	0.13	7.26	7.90	7.18	42.04	0.03	0.08	34.44	0.49	0.11	0.34	156,740
1995	0.10	3.09	5.16	4.25	56.66	0.14	0.00	30.27	0.08	0.03	0.20	152,740
1996	0.16	12.39	1.61	2.69	41.01	0.00	0.04	41.57	0.12	0.14	0.28	130,940
1997	0.08	6.46	2.10	18.51	29.65	0.01	0.00	42.87	0.11	0.07	0.12	145,125
1998	0.14	4.96	5.18	4.46	34.88	0.00	0.01	50.19	0.09	0.02	0.06	175,000
1999	0.04	7.84	0.57	8.01	49.98	0.00	0.01	33.22	0.09	0.07	0.18	201,850
2000	0.13	10.69	1.36	9.23	32.84	0.00	0.05	45.45	0.00	0.15	0.09	196,090
2001	0.04	1.73	1.64	12.97	32.42	0.00	0.03	51.00	0.00	0.01	0.17	142,130
2002	0.00	6.19	0.32	3.49	35.06	0.00	0.00	54.76	0.10	0.06	0.03	151,470
2003	0.06	5.74	3.16	3.44	38.49	0.03	0.00	48.51	0.30	0.02	0.26	146,300
2004	0.03	2.55	0.91	4.23	55.45	0.00	0.01	36.58	0.09	0.07	0.08	138,770
Average	0.09	6.22	2.59	7.07	39.80	0.03	0.02	43.32	0.39	0.07	0.40	155,596

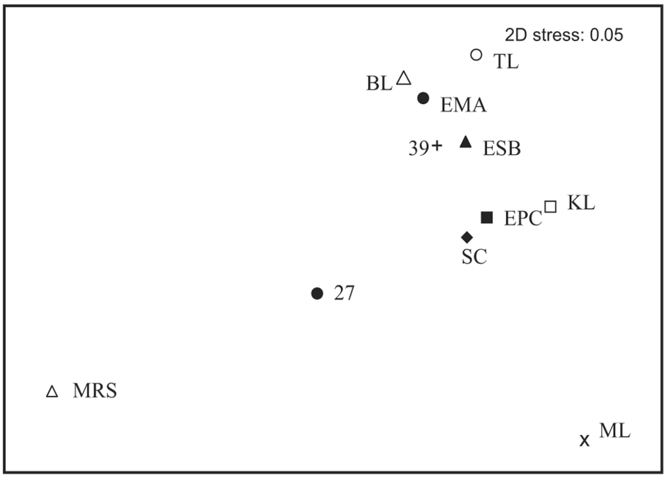

Figure 3. nMDS plot of survey locations based on the proportion of sockeye aged by Alaska Department of Fish and Game that were classified into 11 different freshwater/marine age categories. Separation between several locations was detected by the analysis of similarity performed on the data set (ANOSIM R = 0.28). Points represent averages of untransformed data over all survey years for each sampling location.

In contrast to the interannual trends, a higher degree of separation was seen among sampling locations (ANOSIM global test, R = 0.28; nMDS plot, Figure 3). Pairwise comparisons revealed that three locations (Martin Lake, Martin River Slough and 27 mi Slough) differed from each other and all other locations. SIMPER analysis demonstrated that for pairwise comparisons involving 27 mi Slough, the percent contribution of four age categories, 1.2, 1.3, 0.2 and 0.3, accounted for 95% of the dissimilarity (average contribution for 1.2 = 38%, 1.3 = 34%, 0.2 = 15% and 0.3 = 12%). For pairwise comparisons involving the Martin River Slough location, the percent contribution of 0.2 and 0.3 age sockeye to the multivariate pattern accounted for > 50%. SIMPER for Martin Lake contrasts demonstrated a higher relative contribution of 1.2 and 1.3 (70%) sockeye salmon, but also had the highest contribution from 1.1 sockeye salmon than at any other locations (15%). Kushtaka Lake sockeye salmon also showed significant differences from most other locations (with the exception of Eyak Lake's Power Creek) in pairwise comparisons. For Kushtaka Lake, which had very few 0 type sockeye salmon (Table 1), SIMPER analysis demonstrated the high percentage of 1.2 and 1.3 sockeye salmon contributed on average to 85% of the difference. The three Eyak Lake sites, as well as Tokun and Bering Lakes, did not differ from each other in pairwise comparisons. Both the Salmon Creek and 39 mi Slough locations differed from both Tokun and Bering Lakes, but not the three Eyak Lake locations. The former pat-tern was due to the higher percentage of 1.2 and 1.3 sockeye salmon in the Bering and Tokun Lake systems than Salmon Creek or 39 mi Slough.

Sockeye Salmon in Estuarine Areas

During 2004, juvenile sockeye salmon were present in the estuarine areas of the western Copper River Delta for a relatively brief period. Highest abundances of juvenile sockeye salmon were collected from June through July at sampling locations near the outflow of the Eyak River (Figure 4). No difference was detected among fry, parr, or smolt abundance in the Eyak high versus Eyak low tidal elevation zones ($P > 0.05$ for all paired t-tests). Few juvenile sockeye salmon (< 10) were collected near the outflow of Alaganik Slough. For the Eyak River locations, smolt and parr were found in similar densities as fry. This pattern contrasts that of the screw trap at Eyak, which captured drastically high numbers of fry compared with smolt or parr (Figure 5). Highest abundances of fry were captured between May 22 and July 14, 2004 at Eyak River. Parr were captured in the screw trap at Eyak River throughout the May–November study period.

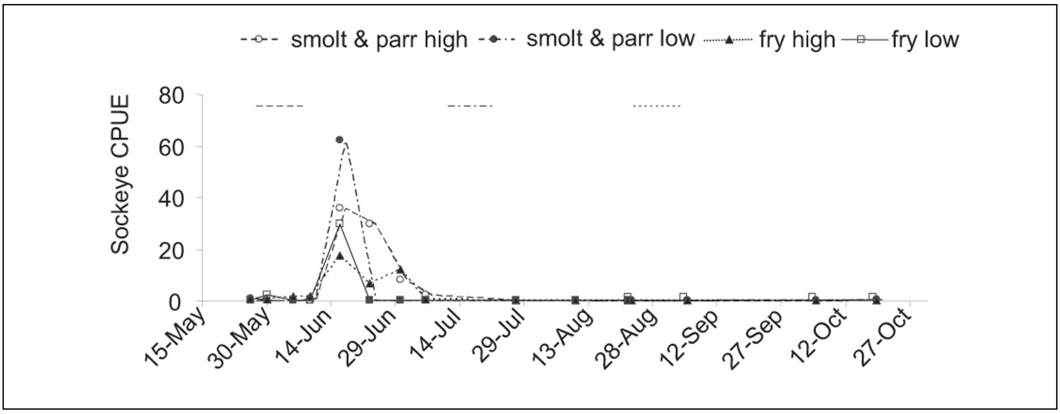

Figure 4. Number of sockeye salmon smolt, parr, and fry collected in seine collections near the outflow of the Eyak River, the western Copper River Delta estuary. Catch per unit effort is the average number of sockeye salmon collected per 20 m seine pull (*n* = 3 or 6 pulls).

Discussion

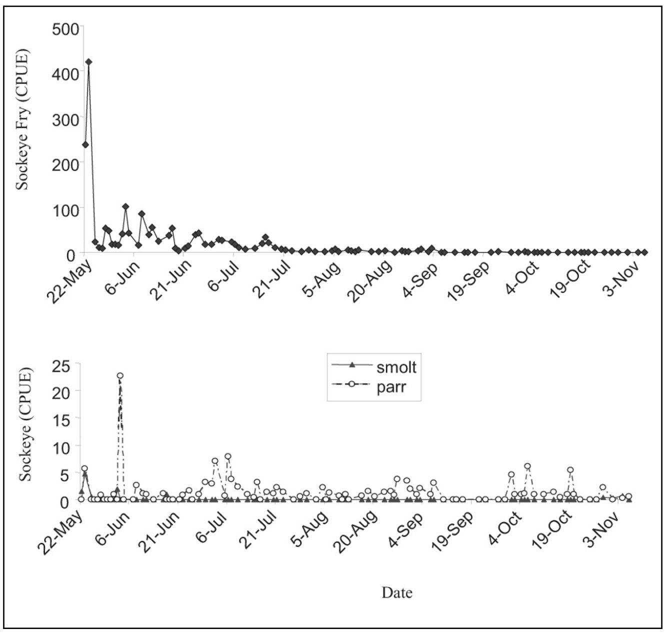

Figure 5. Number of sockeye salmon fry (upper) and smolt and parr (lower) captured in the screw trap placed at Eyak River from May 22 to November 4, 2004. Catch per unit effort is number of sockeye salmon captured 24 h.

Sockeye salmon that return to the coastal sloughs and lakes of the Copper and Bering River Deltas show significant temporal and spatial variability in the years spent in freshwater and marine environments, but appear to spend a relatively short period in estuarine waters. Although relatively minor, interannual differences between 1990 and 2004 appear to be driven mainly by the relative proportions of 1.2 and 1.3 age sockeye salmon. For 1990, 1994, and 1995, higher than average percentages of sockeye salmon returned after only 2 years in marine waters. These differences may reflect changes in the marine environment. For example the time period prior to the return of fish in 1990, 1994, and 1995 may be associated with years of high ocean productivity in the Gulf of Alaska, whereas return years with a higher than average proportion of 1.3 age sockeye salmon, (2000, 2001, and 2002) may be associated with low productivity in the Gulf of Alaska. Some support for this hypothesis can be found in the fact that the Pacific Decadal Oscillation (PDO) was negative from July 1998 to July 2002 based on the sea surface temperature monthly PDO index (http://tao.atmos.washington.edu/pdo/), a condition usually associated with reduced biological productivity in the

Gulf of Alaska and poor growth conditions for salmon (Mantua et al. 1997; Hare et al. 1999; Mantua and Hare 2002). In contrast, the PDO index was positive during the time period prior to the return of sockeye salmon in 1994 and 1995.

Although interannual variability was relatively minor and may reflect marine conditions, substantial spatial variability existed in the age composition of returning sockeye. The highest proportion of sockeye salmon leaving freshwater habitats prior to their first winter was associated with coastal slough habitats. On average, 28% of sockeye salmon aged in the 4 slough locations left freshwater habitats as age 0 fish. The highest percentage of these 0 age sockeye salmon was reported from the Martin River Slough (average 55%) followed by 27 mi Slough (33%), Salmon Creek (13%) and 39 mi Slough (11%). In contrast, an average of only 7% of sockeye salmon aged from the 7 lake-associated locations left freshwater before the first winter. The exception to the lake pattern was Bering Lake, which had an average of 12% of sockeye salmon migrate before the first winter. Bering Lake is remote and hydrographic conditions are not easily monitored; however, the lake is a shallow system that experiences substantial freezing in many years as well as a high degree of flushing in the summer when the ice dam at Berg Lake breaks. Consequently the system may not provide optimal conditions for extended freshwater residence. With the exception of Bering Lake, the general pattern that slough/river type sockeye salmon are more likely to go to sea in their first year holds true. However, the strategy is not restricted solely to slough/river populations as evidenced by the high percentages of age-0 sockeye salmon migrating to sea from some lake systems during the 14 years of survey (Table 2). Although the average percentage of sockeye salmon leaving freshwater as underyearlings was modest (14%), spatial and interannual variability of this percentage is quite large and may have significant impacts to the sockeye salmon fishery. For example, age-0 sockeye salmon in the Situk River estuary normally make up 20% of the commercial catch and higher percentages have been recorded in some other Alaska fisheries (Heifetz et al. 1989).

Finally, our limited sampling of the estuarine environment near the outflows of the Eyak River and Alaganik Slough provide little support for the theory that sockeye salmon fry spend longer periods of time than parr and smolt in the estuarine waters. Heifetz et al. (1989) reported residence time for sockeye salmon fry of 3–4 months in the low salinity portions of the Situk estuary. It seems improbable based on the limited osmoregulatory ability of fry < 50 mm (Rice et al. 1994) that sockeye salmon fry in our study area would migrate directly to high salinity areas. The low abundance of sockeye salmon fry in the estuarine portion of our study area may be the result of habitat selection or high mortality occurring between the headwater of the river and the upper estuary region. Although large numbers of fry left the Eyak Lake system (Figure 5), 6.5 mi of down river structured habitat is present that would provide rearing area for exiting fry. Murphy et al. (1997), in their study of Taku River sockeye salmon, reported similar findings as our study. They observed large numbers of age-0 sockeye salmon moving downriver, but few captured in the estuary. They determined that sockeye salmon delayed entry into the Taku River estuary by residing in down river habitat. On the western Copper River Delta, our seine sampling covered the entire summer and most of the fall. Few fry, however, were found after mid-July. This suggests that if fry were resident in downriver habitat, they entered the estuary after October 27 or moved back upriver, a migration that has been observed for coho salmon (Miller and Sadro 2003). The lack of structured habitat in the mud and sand flat-dominated Copper River estuary may offer little protection from predators for exiting salmon fry (see Bottom et al. 2005) and result in fry remaining in the lower river habitat or suffering heavy mortality from predators in the unstructured mud bottom of the estuary. High densities of sculpins and flatfish have been recorded in these same areas (Powers and Bishop, unpublished data) and their predation on fry may be a significant source of mortality.

Results of our synthesis of 14 years of survey data on age composition of sockeye salmon and additional estuarine sampling illustrate the variability of freshwater, marine, and estuarine residence in typical coastal area sockeye salmon populations. This diversity of life-histories is a key adaptation for the long-term persistence of salmonid populations in highly variable environments (Healy and Prince 1995). Our study also illustrates the inherent connectivity and interdependency of a variety of coastal habitats (lakes, upper and lower river habitats, wetland sloughs, and estuary) in rearing and maintaining healthy populations of salmon (Ray 2005). The Copper and Bering River Deltas are one of the many systems in coastal Alaska that provide the diverse array of habitats necessary to maintain healthy sockeye salmon populations. Careful stewardship throughout their entire watersheds including lower-river and estuarine areas is necessary to ensure sustainable populations.

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