American Fisheries Society Symposium 70:183–199, 2009
© 2009 by the American Fisheries Society

Estuarine Ecology of Juvenile Salmon in Western Alaska: a Review

Nicola Hillgruber*
University of Alaska Fairbanks, School of Fisheries and Ocean Sciences
17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

Christian E. Zimmerman
U.S. Geological Survey, Alaska Science Center
4210 University Drive, Anchorage, Alaska 99508, USA

Abstract.—In the late 1990s and early 2000s, large declines in numbers of chum salmon *Oncorhynchus keta* and Chinook salmon *O. tshawytscha* returning to the Arctic-Yukon-Kuskokwim (AYK) region (Alaska, USA) illuminated the need for an improved understanding of the variables controlling salmon abundance at all life stages. In addressing questions about salmon abundance, large gaps in our knowledge of basic salmon life history and the critical early marine life stage were revealed. In this paper, results from studies conducted on the estuarine ecology of juvenile salmon in western Alaska are summarized and compared, emphasizing timing and distribution during outmigration, environmental conditions, age and growth, feeding, and energy content of salmon smolts. In western Alaska, water temperature dramatically changes with season, ranging from 0°C after ice melt in late spring/early summer to 19°C in July. Juvenile salmon were found in AYK estuaries from early May until August or September, but to date no information is available on their residence duration or survival probability. Chum salmon were the most abundant juvenile salmon reported, ranging in percent catch from <0.1% to 4.7% and most research effort has focused on this species. Abundances of Chinook salmon, sockeye salmon *O. nerka*, and pink salmon *O. gorbuscha* varied among estuaries, while coho salmon *O. kisutch* juveniles were consistently rare, never amounting to more than 0.8% of the catch. Dietary composition of juvenile salmon was highly variable and a shift was commonly reported from epibenthic and neustonic prey in lower salinity water to pelagic prey in higher salinity water. Gaps in the knowledge of AYK salmon estuarine ecology are still evident. For example, data on outmigration patterns and residence timing and duration, rearing conditions and their effect on diet, growth, and survival are often completely lacking or available only for few selected years and sites. Filling gaps in knowledge concerning salmon use and survival in estuarine and near-shore habitats within the AYK region will aid in assessing the relative roles of all habitats (freshwater to marine) in controlling salmon abundance.

*Corresponding author: nhillgruber@alaska.edu

Introduction

In the watersheds of the Arctic-Yukon-Kuskokwim (AYK) region in Alaska (Figure 1), the estuarine residence of Pacific salmon *Oncorhynchus* is a poorly studied life stage. Salmonids typically experience high and variable size-selective mortality during this stage. For example, mortality rates of chum salmon *O. keta*, after ocean entry, may initially range as high as 31–46% per day in Puget Sound (Bax 1983), or 3–25% per day in coastal waters off the coast of Japan (Fukuwaka and Suzuki 2002). In a recent study on hatchery chum salmon in Southeast Alaska, average daily mortality was estimated to be 8.1% for the first 21 d post release (Wertheimer and Thrower 2007). Reasons for these high and variable mortality rates are assumed to be food limitation (Salo 1991) and size-selective predation (Beamish and Mahnken 2001). Only with a better understanding of the role of rearing conditions, such as food resource availability, predator abundance, and physical environmental variability in controlling survival of juvenile salmon will it be possible to evaluate hypotheses of salmon population regulation in western Alaska.

Estuarine and near-shore dependence differ among salmonid species (Healy 1982a; Thorpe 1994). In comparison to most other anadromous salmonids, chum and pink salmon *O. gorbuscha* enter estuaries at a comparatively smaller size and remain longer in brackish water habitats of estuaries or river plumes than other salmon species, such as coho *O. kisutch* and Chinook salmon *O. tshawytscha* (Healey 1982b; Simenstad et al. 1982; Fukuwaka and Suzuki 2002). Consequently, the period of estuarine residency might be of particular importance for these species (chum and pink salmon) because of the intense size-selective predation pressure they may experience in the marine environment (Parker 1971; Simenstad and Salo 1980; Healy 1982b; Simenstad and Wissmar 1984; Moss et al. 2005). In contrast, Healy (1982a) concluded that the degree of estuary dependence of juvenile Pacific salmon may be a function of the existence and use of alternate nursery habitats and the length of estuarine residence. Following this classification system, he considered Chinook and chum salmon as most dependent, followed by coho salmon, while pink and sockeye salmon *O. nerka* were least dependent on estuarine habitat (Healy 1982a).

Early marine survival is affected by both biotic and abiotic conditions either directly through starvation or indirectly through decreased growth rates, which may result in longer periods of vulnerability to predation. Water temperature is a ubiquitous environmental variable that affects ectothermic animals, such as fish, directly through its effects on metabolic processes. Water temperature affects smolting in salmonids, resulting in such diverse responses as shifts in emigration timing, reversal of smolting, premature smolting, or even death (Richter and Kolmes 2005). In addition, temperature, in conjunction with prey availability and abundance, will determine the growth potential and mortality rates of juvenile chum salmon at this stage (Mason 1974; Healey 1982a; Salo 1991). The metabolic costs of migration, smolting, and maintenance are key energetic constraints on the production and survival of juvenile salmon migrating through estuaries and the near-shore environment (Wissmar and Simenstad 1988).

In the last decade, the abundance of chum and Chinook salmon in the AYK region has fluctuated greatly (Adkison and Finney 2003; Linderman and Bergstrom 2009, this volume; Menard et al. 2009, this volume). Declines in numbers of returning chum and Chinook salmon in the late 1990s and early 2000s caused severe social and economic hardship for the people of the AYK region because of lower catches and the associated

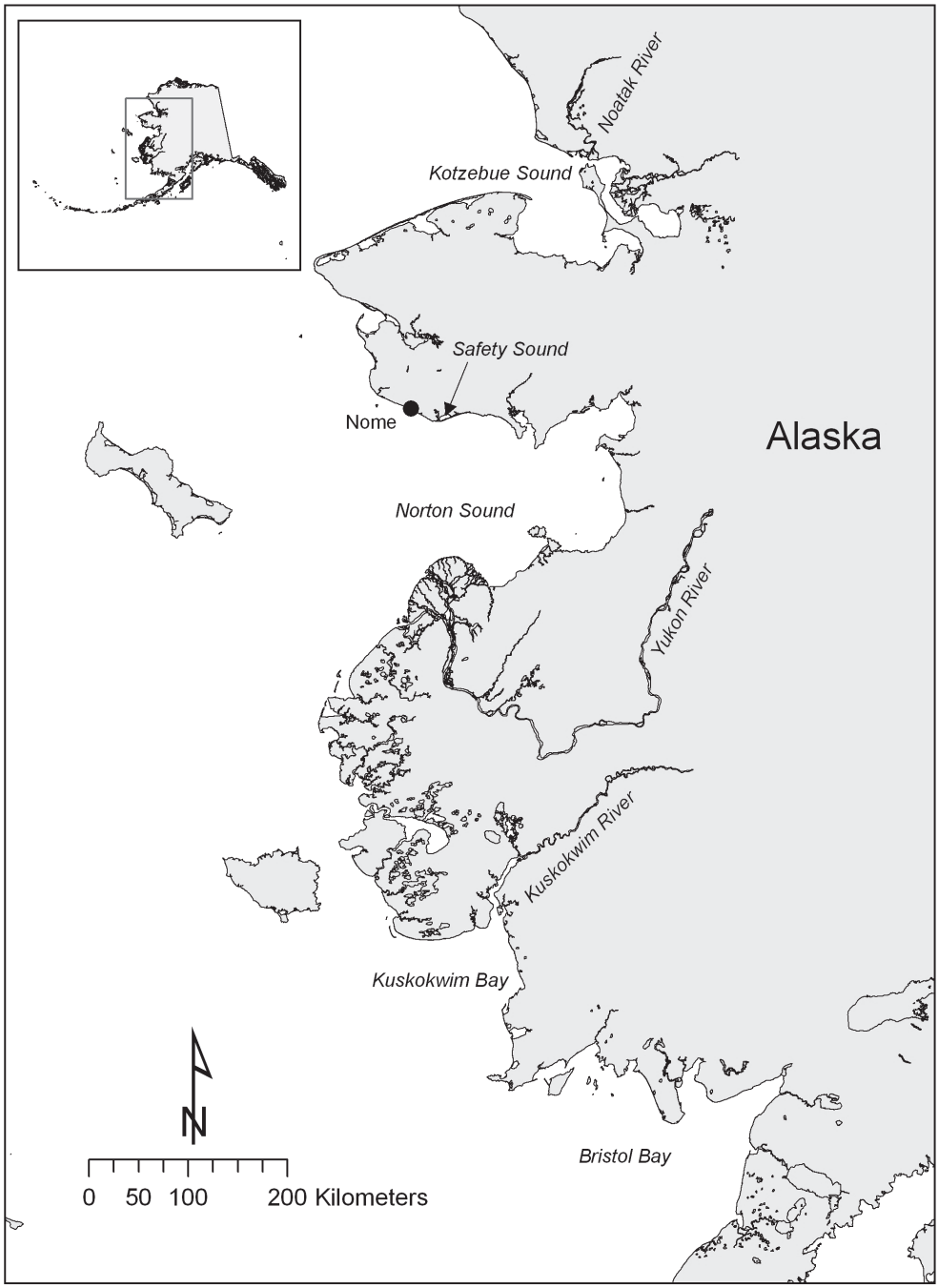

FIGURE 1. Arctic-Yukon-Kuskokwim (AYK) region and estuarine areas that were study sites for juvenile salmon outmigration and rearing habitat use.

regulatory measures directed at reducing fishing pressure (Linderman and Bergstrom 2009, this volume; Bue et al. 2009, this volume; Evenson et al. 2009, this volume). The reasons for these declines are not well understood. In response to the low returns of chum and Chinook salmon to AYK watersheds, a research and restoration plan was designed for the AYK region (AYK SSI 2006); this plan concluded that large gaps in the knowledge of basic salmon life history make it impossible to understand or predict the effect of environmental changes on western Alaska salmon populations. The effects of environmental changes may be particularly dramatic on juvenile salmon during their early marine life, a phase that is poorly studied in the AYK region (NRC 2005).

The overall goal of this review paper is to summarize and compare results from the few studies conducted on the estuarine ecology of juvenile salmon in western Alaska. The emphasis of this review is on chum salmon because the majority of studies examining estuarine ecology of salmon in western Alaska have focused on this species. AYK estuaries are, however, migratory corridors and potential nursery sites for five species of Pacific salmon including Chinook, chum, pink, coho, and sockeye salmon. This review specifically summarizes results on timing and distribution during out-migration, environmental conditions experienced, feeding, growth, and energy content of salmon smolts. In addition, gaps in the knowledge of AYK salmon estuarine ecology are identified with the intention to provide direction for future research.

To encompass the relevant literature for this review, literature searches were conducted with the following electronic search engines: Aquatic Science and Fisheries Abstract ASFA (1971–present) and ISI Web of Science (1980–present). Because most research on estuarine ecology in western Alaska, has not been published in peer-reviewed and indexed journals, the search was extended to include interim and final reports of studies conducted in the nearshore area of western Alaska. Only a few studies were found, conducted between 1982 and 2004, including studies by the Alaska Department of Fish & Game, Division of Fisheries Rehabilitation, Enhancement, and Development (Merritt and Raymond 1983; Raymond et al. 1984), the Outer Continental Shelf Environmental Assessment Program (OCSEAP; Martin et al. 1986; Martin et al. 1987), the Norton Sound Disaster Relief Fund (Nemeth et al. 2003; Nemeth et al. 2006), and the North Pacific Research Board (NPRB, Hillgruber et al. 2007).

General Background of Surveys and Study Areas

Studies focusing on the ecology of salmon at this life stage in western Alaska generally represented short-term (1–3 years) efforts disjunctive in time and space (Table 1). Most research on juvenile salmon (including the near-shore ecology of salmon smolts) in the AYK region has focused on chum salmon in the Norton Sound area (Figure 1) because of the continued financial support provided by the Norton Sound Disaster Relief Fund (Nemeth et al. 2003, 2006).

In the Norton Sound area, estuarine research efforts were conducted from 2002 until 2004 in Safety Sound (Figure 1), an oval-shaped bay fed by the Eldorado/Flambeau River. In Safety Sound, salmon juveniles were collected with fyke nets and beach seines (Table 1). On one date in 2003 and two dates in 2004, surface trawls were used to collect juvenile salmon on a station grid in the near-shore habitat of Norton Sound (Nemeth et al. 2006).

In Kotzebue Sound, a one-year study was conducted on chum salmon smolts (Merritt and Raymond 1983). Incidental data on the

Table 1. Summary of survey areas, dates, sample gears (GN: gill net, BS: beach seine, PS: purse seine, FN: fyke net, ST: surface tow net), and size and peak emigration period for juvenile chum salmon *O. keta*. Study areas are sorted from north to south.

Study area	Survey year	Survey date	Sample gears	FL [mm]	Peak emigration
Kotzebue Sound[1]	1979–1982	06/01–08/15	BS	n/a	late June
Kotzebue Sound[2]	1980	06/06–08/04	BS	35–50	n/a
Safety Sound[3]	2002	07/02–07/20	FN	55–75	mid July
Safety Sound[4]	2003	06/07–07/21	FN, BS, ST	35–80	mid June and mid July
	2004	06/03–07/31	FN, BS, ST	39–65	mid June
Yukon River delta[5]	1984	12/03–12/13	GN	n/a	n/a
	1985	06/14–09/18	PS, FN, BS, GN	30–109	late June
Yukon River delta[6]	1986	06/06–08/08	BS, ST	29–107	mid/late June
Kuskokwim Bay[7]	2003	06/20–08/26	ST	42–65	mid June
	2004	05/15–06/16	ST	31–66	mid June

[1]Raymond et al. 1984, [2]Merritt and Raymond 1983, [3]Nemeth et al. 2003, [4]Nemeth et al. 2006, [5]Martin et al. 1986, [6]Martin et al. 1987, [7]Hillgruber et al. 2007

timing of occurrence of juvenile chum salmon in Kotzebue Sound were also presented by Raymond et al. (1984). Two studies were carried out in the Yukon River delta as part of an effort directed at examining the effects of a potential oil spill on the estuarine fish community (Martin et al. 1986, 1987); fish were collected with beach seines and surface townets (Table 1). The Yukon River delta studies focused primarily on chum, Chinook, and pink salmon smolts, and yielded only limited data on coho salmon ($N = 4$).

Finally, a two-year pilot study was conducted in Kuskokwim Bay (Hillgruber et al. 2007), a large, shallow, and open estuary fed by the Kuskokwim River in the northeast corner and opening in the west and southwest to the Bering Sea. Sampling of juvenile salmon was conducted using a surface trawl (Table 1). While all species of juvenile salmon were collected, the research was focused on chum salmon feeding success and condition (Burril 2007), and on age and estuarine residence (Hillgruber et al. 2007).

Environmental Conditions

Estuaries are dynamic systems with strong spatial gradients in physical and biological variables, and large seasonal variations in environmental conditions. In AYK estuaries, water temperature is the physical variable expected to most dramatically change with season, because rivers and bays are generally frozen until late spring. Timing of ice break-up is related to Bering Sea climatic and, thus, oceanographic conditions (Stabeno et al. 2007). Based on mean bottom temperature in the eastern Bering Sea, the six warmest years since 1982 were 1996, 1998, and 2002–2005, while 1986, 1992, 1994–1995, 1999, and 2006 were the coldest in the same time frame (Spencer 2008). This environmental variability likely affects timing of ontogenetic events in ectothermic animals, such as juvenile salmonids (Houde 1989).

Following ice break-up, sea surface temperature (SST) in Kuskokwim Bay, the most southerly bay of the AYK region, was

homogenously cool (6–8°C) in the middle of May at the onset of juvenile salmon outmigration; it increased to 14°C at the head of the estuary and 10–12°C in the bay towards the middle of June 2004, and the maximum measured SST was 15.6°C (Hillgruber et al. 2007). In 2003, environmental sampling was limited to only few stations later in the season; SST was >14.0°C in late June and late July, slightly decreasing to 13.5°C in late August. Notably higher temperatures were measured in Safety Sound (northern AYK region), where SST increased from 9.6°C on July 2 to 16.2°C on July 20 at the outlet of Safety Sound into Norton Sound and from 16.6°C to 19.6°C at the head of the bay as measured in 2002 (Nemeth et al. 2003). In addition, interannual differences in the water temperature were apparent, with higher temperatures and an earlier ice break-up in 2004 than in 2003 (Nemeth et al. 2006). Similar seasonal variations in SST were also observed from the Yukon River delta, with temperatures in the delta front areas increasing from 3.9°C in early June to 17.2°C in mid-June (Martin et al. 1987). SST was quite variable, probably a result of tidal and wind (speed, direction) influence on water conditions.

Sea surface salinity (SSS) in estuaries tends to vary horizontally and vertically, but less so seasonally (e.g., Hillgruber et al. 2007). In Kuskokwim Bay, SSS ranged from 0 in the river mouth to values exceeding 30 in the western and northern part of the bay. SSS plots revealed a freshwater plume from the Kuskokwim River extending along the eastern shoreline. In addition, a strong vertical stratification was apparent in estuarine waters of the Yukon River delta, with fresher water at the surface and water of higher salinity at the bottom (Martin et al. 1987); this stratification was most strongly developed in early June, but weakened in August, probably as the result of increased mixing.

The large watersheds in the AYK region vary dramatically in water clarity as a result of differential loads of glacial silt and suspended sediment. While Kuskokwim Bay and the Yukon River delta receive highly turbid freshwater, Norton Sound is fed by relatively clear rivers. In Kuskokwim Bay, optical backscatter (OBS) was recorded in 2004 as a measure of turbidity. OBS values ranged from 2 to 116 NTU (Nephelometric Turbidity Units) in the surface waters, and turbidity corresponded to the freshwater plume of the Kuskokwim River. Peak turbidity was observed early in the season and at the head of the estuary, with turbidity levels declining towards the end of the 2004 sampling effort. In the Yukon River delta, water clarity was determined with Secchi disk readings. Water clarity was low throughout the summer sampling. Clarity increased with distance from shore, increasing from ≤0.3 m to 1.2 m in offshore waters (Martin et al. 1987).

The interplay of environmental variables needs to be considered to evaluate rearing conditions for juvenile salmon. High temperatures in the surface waters of the river outflows might increase metabolic demands to a level not easily balanced by food availability and intake. While juveniles may vertically migrate to avoid the highest temperatures in the surface waters, the equally high turbidity levels could severely limit visual prey detection at depth and reduce feeding success. Consequently, juvenile fish staging in low salinity surface waters of Kuskokwim Bay and the Yukon River Delta likely face a compromise between increased metabolic demands and simultaneous decreased feeding success.

Estuarine Fish Communities in Western Alaska

The estuarine fish community in western Alaska was dominated by smelts (Osmeridae), whitefishes (Coregoninae), and sticklebacks (Gasterosteidae) (Table 2). In addition, small schooling fishes such as juvenile stages

TABLE 2. Total catch composition of main fish taxa in western Alaska estuarine systems. Blank cells indicate zero catches and j = Juveniles.

Common name	Scientific name	Kuskokwim Bay		Yukon River Delta			Safety Sound		
		2003	2004	1984	1985	1986	2002	2003*	2004*
Chum salmon (j)	*Oncorhynchus keta*	0.4	4.7		2.0	4.7	2.5	1	<0.1
Chinook salmon (j)	*Oncorhynchus tshawytscha*	<0.1	0.2		0.1	0.2	<0.1	<0.1	<0.1
Coho salmon (j)	*Oncorhynchus kisutch*	<0.1	0.8		<0.1		0.1	<0.1	<0.1
Pink salmon (j)	*Oncorhynchus gorbuscha*	<0.1	0.3		0.2		3.5	3	<0.1
Sockeye salmon (j)	*Oncorhynchus nerka*		0.1				0.1		<0.1
Inconnu	*Stenodus leucichthys*			31.8	7.1	0.1		<0.1	
Humpback whitefish	*Coregonus pidschian*			7.1	1.9	<0.1	0.0	4	<0.1
Round whitefish	*Prosopium cylindraceum*							4	<0.1
Least cisco	*Coregonus sardinella*			5.9	1.5	0.4	7.3	23	6
Arctic cisco	*Coregonus autumnalis*				<0.1				
Bering cisco	*Coregonus laurettae*			9.4	0.5	<0.1	11.8	2	<0.1
Broad whitefish	*Coregonus nasus*			2.4	0.2	<0.1		<0.1	
Unidentified whitefishes	Coregoninae		<0.1		53.2	4.9			
Northern pike	*Esox lucius*			2.4	0.2				
Rainbow smelt	*Osmerus mordax*	2.8	41.3	29.4[1]	8.2[1]	9.8[1]	6.2	12	1
Pond smelt	*Hypomesus olidus*	61.6	44.3		1.2				
Unidentified smelt	Osmeridae				4.2	28.6			
Ninespine stickleback	*Pungitius pungitius*	15.6	5.1		6.6	46.5	4	1	
Threespine stickleback	*Gasterosteus aculeatus*	5.8	0.3		<0.1		5.0	10	68
Pacific herring	*Clupea pallasii*	13.8	<0.1		0.6	2.0	0.2	<0.1	<0.1
Pacific sandlance	*Ammodytes hexapterus*		2.8			<0.1			
Saffron cod	*Eleginus gracilis*	<0.1			3.2	0.6	18.5	13	16
Burbot	*Lota lota*	<0.1		10.6	2.9	0.6		<0.1	<0.1
Arctic flounder	*Pleuronectes glacialis*	<0.1	<0.1		3.4	0.2	36.0	15	5
Starry flounder	*Platichthys stellatus*				1.1	<0.1	1.0	3	1
Arctic lamprey	*Lampetra camtschatica*	<0.1	0.1		0.1	1.2			
Fourhorn sculpin	*Myoxocephalus quadricornis*			1.2	0.3	<0.1	3.4	4	1

*rounded to full number.

[1]identified by Martin et al. (1986, 1987) as Boreal smelt *Osmerus eperlanus*

of Pacific herring *Clupea pallasii* and Pacific sand lance *Ammodytes hexapterus* occurred sporadically in large abundances. Juvenile salmonids were significantly less abundant (Table 2), never making up more than 5% of the total catch. In all AYK estuaries, chum salmon were the most abundant species of Pacific salmon, while sockeye salmon were the least abundant (Table 2).

Timing and Relative Abundance of Juvenile Salmon Out-Migration

Chum salmon.—In AYK estuaries, chum salmon catch ranged from <0.1% to 4.7% (Table 2). Patterns of peak out-migration of chum salmon in western Alaska also appear to be similar among different watersheds. Peak numbers of chum salmon in Kuskokwim Bay were caught in the middle of June in 2004 and in late June in 2003 (Table 1), the latter probably due to the late start of field work that year. Numbers of chum salmon smolts were substantially lower in late July ($N = 3$), and no chum salmon juveniles were caught in late August (Hillgruber et al. 2007). In the Yukon River delta, sampling in 1986 began in early June (Table 1) and chum salmon peak out-migration occurred on June 18, with numbers declining in July and August (Martin et al. 1987). In Safety Sound, peak out-migration differed with the sampling site: juvenile chum salmon catches peaked in mid-June at the head of Safety Sound, while at the outlet site between Safety Sound and Norton Sound, chum salmon out-migration was bimodal, with one group emigrating in June and a second one in mid to late July (Table 1; Nemeth et al. 2003, 2006).

Few data exist on the timing of estuarine residence of chum salmon in western Alaska, but based on results from other estuarine studies, a protracted duration of residence seems likely. For example, in southeastern Alaska, juvenile chum salmon were caught in the littoral habitat of Taku Inlet from the middle of April until late June in 2004 and 2005 (Reese et al. in press). Similarly, in northern Cook Inlet in southcentral Alaska, juvenile chum salmon were caught in June and July (Moulton 1997). In the Yukon and Kuskokwim rivers, juvenile chum salmon probably begin their out-migration in early May prior to ice break-up. This predicted migration timing is supported by Martin et al. (1987), who used emergence timing of chum salmon fry in the upper tributaries to estimate timing of out-migration into the delta. In Kuskokwim Bay, first catches of chum salmon fry in 2004 were recorded on May 15 (Hillgruber et al. 2007); because this date was the first day of field sampling, juvenile chum salmon had likely entered the bay prior to this date. This observation was supported by results from the upper Yukon River, in 2002 to 2004, where chum salmon downstream migration was well underway at the onset of sampling in middle to late May, suggesting an even earlier peak (Bradford et al. 2008). The total duration of the chum salmon out-migration in AYK estuaries may be substantially drawn out over the summer period. Chum salmon juveniles residing in the Yukon River delta have been reported to be present as late as September 13 (Martin et al. 1986). In addition, chum salmon fry in the upper Yukon River tributaries were observed into late July (Bradford et al. 2008) and even August (Gissberg and Benning 1965), suggesting an estuarine arrival well into September. Because environmental conditions such as water temperature and prey availability change dramatically from May through September, it is likely that different cohorts (i.e., temporal groups of juvenile salmon) will experience large differences in estuarine rearing conditions. No information is available on origin, feeding success, growth rates, and survival probability of those juvenile chum salmon that emerge late in the season or rear longer in the upper tributaries and arrive in the estuaries in August and September.

Chinook, coho, pink, and sockeye salmon.—Chinook salmon migration into AYK estuaries appears to occur later in the season than that of chum salmon juveniles. In the Yukon River delta, Chinook salmon juveniles were the second most abundant salmon (Table 2) and were collected from early June until early August, with a peak catch per unit effort (CPUE) occurring in late June (Martin et al. 1987). In the upper Yukon River, downstream migration of Chinook salmon was also later than for chum salmon and differed between age-0 and age-1 juveniles (Bradford et al. 2008); age-0 catches peaked in late June, while age-1 fry downstream migration was in progress at the beginning of sampling in May. Similar observations were made in Kuskokwim Bay, where Chinook salmon represented the fourth most abundant salmon taxon after chum, coho, and pink salmon (Hillgruber et al. 2007). No juvenile Chinook salmon were caught before June, and peak catches were observed in the middle of June.

Coho salmon juveniles were rare in AYK estuaries, and never amounted to more than 0.8% of the catch (Table 2). In the Yukon River delta, only one specimen was collected on July 25, 1985 (Martin et al. 1986), and no coho salmon were caught in the summer of 1986 (Martin et al. 1987). In comparison, coho salmon were abundant in Kuskokwim Bay, where catches peaked in late May in 2004 and CPUE was substantially lower in June. Abundances of coho salmon juveniles were highest at the head of the bay, but estuarine distribution of coho salmon juveniles was widespread, with catches occurring even from the station furthest offshore (Hillgruber et al. 2007).

Sockeye salmon juveniles were only infrequently caught in Kuskokwim Bay, representing no more than 0.1% of the catch (Hillgruber et al. 2007). At the head of Kuskokwim Bay, sockeye salmon juveniles were only collected in May of 2004, with catches peaking at the end of May. Overall catches of sockeye salmon juveniles were very low in 2004 and no sockeye salmon were captured in 2003. The pattern of sockeye salmon distribution and migration appears to indicate only one migration cohort.

Pink salmon amounted to 3% of the total CPUE in 2003 in Safety Sound, but declined to 0% in 2004 (Nemeth et al. 2006). This pattern was consistent with the strong even-year run and weak odd-year pink salmon populations present in Norton Sound area streams. No data on seasonal patterns of out-migration of pink salmon juveniles were presented. Similarly, pink salmon were of low abundance in the Yukon River delta, amounting to only 0.2% of the catch in 1985 (Martin et al. 1986); no pink salmon were caught in 1986 (Martin et al. 1987). In Kuskokwim Bay, pink salmon juveniles represented the third most abundant juvenile salmon taxon in 2004 (Hillgruber et al. 2007). Pink salmon were collected from the middle of May until the middle of June, with peak catches at the end of May. Positive pink salmon catches were also documented for June and July in 2003; no pink salmon were collected in August (Hillgruber et al. 2007). Similar results were obtained from the Yukon River delta, where pink salmon catches peaked in the middle/end of June and declined rapidly thereafter (Martin et al. 1986); few fish were observed in July and no pink salmon were caught in August.

Size, Age, and Duration of Estuarine Residence of Juvenile Salmon

Chum salmon.—Chum salmon length frequency distributions during estuarine residence were similar in Safety Sound, Kuskokwim Bay, and the Yukon River delta (Table 1). Differences between the studies were likely the result of different sampling dates and study durations; for example, the broadest size frequency distribution for chum

Table 3. Study area, number of fish examined, capture date, post-emergence otolith increments, and back-calculated date of emergence for juvenile chum salmon collected in the Yukon River delta in June 19–30, 1985, and in Kuskokwim Bay in May 15–June 16, 2004.

Study area	*N*	Capture dates	Post-emergence age	Emergence dates
Yukon River Delta[1]	30	June 19–June 30	13–29	May 27–June 12
Kuskokwim Bay[2]	192	May 17–June 11	12–44	April 19–May 24

[1]Martin et al. 1986; [2]Hillgruber et al. 2007

salmon juveniles was observed in the Yukon River delta, where sampling began in early June and lasted until September.

Fork length distributions of chum salmon were consistent with a continuing influx of small fry into the estuaries. For example, chum salmon in the 45 mm length class were caught as late as July 16 in Safety Sound (Nemeth et al. 2006). Based on size and catch date, the authors identified four distinct groupings of chum salmon migrating into Safety Sound in 2003 and 2004. In the upper Yukon River, chum salmon juveniles also displayed differences in fork length during the period of downstream migration, i.e., a decrease in mean size of 3 mm FL from May to July (Bradford et al. 2008).

To determine age in days of juvenile chum salmon, Martin et al. (1986) counted the number of otolith increments from the assumed point of emergence to the edge. The emergence check was defined at the point of transition from dark and irregularly spaced to more weakly expressed and regularly spaced increments. Martin et al. (1986) identified this transition point as the hatch check. The small number of increments, however, makes it more likely that this structure corresponds to the emergence from the gravel rather than the hatching of chum salmon eggs, which occurs in fall or winter (J. Finn, U.S. Geological Survey, personal communication). For the purpose of this review, the results will be interpreted from the microstructure analysis as post-emergence increments. The post-emergence age of Yukon River delta chum salmon ranged from 11 to 59 d for fish in the size range of 33–68 mm FL; in Kuskokwim Bay, the age ranged from 12 to 44 d post-emergence for fish in the size range from 45 to 51 mm FL (Table 3). In the Yukon River delta, the number of post-emergence increments was correlated with the fork length of chum salmon (r^2 = 0.65, n = 197, P < 0.001; Martin et al. 1986). The relationship between otolith increments and fork lengths was weaker for fish from Kuskokwim Bay, but was still statistically significant (r^2 = 0.31, n = 192, P < 0.001; Hillgruber et al. 2007).

Only limited information was available on estuarine residence of chum salmon juveniles in western Alaska. In the Yukon River delta, otoliths of 339 chum salmon juveniles in the 33.0–68.4 mm FL size range were examined to determine age and duration of estuarine residence (Martin et al. 1987). Estuarine residence was expected to be recognizable by increased otolith increment width as a result of increased growth rates typically experienced by juvenile salmonids in near-shore waters, but no transition zone in increment width could be identified for Yukon River chum salmon. As a result, duration of estuarine residence could not be estimated (Martin et al. 1987). In Kuskokwim Bay, otolith strontium-to-calcium ratios (Sr/Ca), which are correlated with salinity (Zimmerman 2005), were used as a means of identifying the point of saltwater entry (Hillgruber et

al. 2007); preliminary results based on eight otoliths indicate an estuarine residence duration ranging from 8 to 18 d for juvenile chum salmon. Because these fish were captured in the bay, these estimates were minimums and do not represent the total time spent in Kuskokwim Bay.

Chinook, coho, pink, and sockeye salmon.—In the estuarine waters of the Yukon River delta, juvenile Chinook salmon ranged in size from 69 to 128 mm FL with a mean of 96.4 mm FL in 1986 (Martin et al. 1987). Outmigrating Chinook salmon had a bimodal size distribution with the minimum value between the modes located at 102 mm FL. Geographic differences in the size distribution of Chinook salmon size classes were apparent, with fish <102 mm FL more predominant on southerly stations and fish >102 mm FL predominating on northerly stations (Martin et al. 1987). In Kuskokwim Bay, Chinook salmon size distribution ranged from 73 to 113 mm FL with a mean length of 87.1 mm FL. The majority of the fish had a size <100 mm FL, with only 9 fish >100 mm FL. For the Kuskokwim River, based on ages of returning adult Chinook salmon, age-1 (i.e., one winter in freshwater) smolts were dominant but some freshwater age-2 fish were encountered (Molyneaux et al. 2006). Juvenile Chinook salmon from the Yukon River delta or Kuskokwim Bay reached a fork length that in other studies was attributed to a freshwater age-2 (Moulton 1997). These results were in agreement with the observation that these stream-type Chinook salmon were predicted to predominate in populations north of 56°N latitude, with smolt age-2 and age-3 becoming more abundant with increasing latitude and distance from the sea (Taylor 1990). No data concerning age or growth and duration of nearshore residence of coho, pink, or sockeye salmon juveniles in western Alaska were available.

Juvenile Feeding Success, Prey Composition, and Selection

Chum salmon.—In June–September 1985, a total of 82 stomachs from chum salmon caught in the Yukon River delta were examined for diet composition; of these, 69 (84.1%) contained prey items (Martin et al. 1986). In Safety Sound, chum salmon (n = 178) feeding incidence (% stomachs containing food) was higher than that observed in the Yukon River delta, ranging from 94.5% in 2002 (Nemeth et al. 2003), to 86.8% in 2003 and to 96.2% in 2004 (Nemeth et al. 2006). Feeding incidence in Kuskokwim Bay also varied among sampling years, with 51% in 2003 and 81% in 2004 (Burril 2007). While the low feeding incidence in 2003 is notable, the result could be due to sampling occurring late in the season (Hillgruber et al. 2007). Nonetheless, juvenile chum salmon in estuaries in western Alaska showed feeding incidences lower than those observed at lower latitudes, e.g., from northern Cook Inlet (98.2%; Moulton 1997) and from Hecate Strait, British Columbia (96.8–100%; Healey 1991).

In Kuskokwim Bay, small calanoid copepods (<2.5 mm), harpacticoid copepods, and adult, winged insects were the primary prey items for juvenile chum salmon. Calanoids and insects combined made up >50% of all prey items by number and >80% of the overall prey biomass (Burril 2007). Prey composition changed with size of smolt, with small smolts relying mostly on insects, while large smolts predominantly fed on calanoid copepods. These results are somewhat different from dietary composition of chum salmon from the Yukon River delta (Martin et al. 1986); diet of chum salmon collected from June to September 1985 contained predominantly insects (Chironomidae: Diptera), most of which were winged adults that were probably consumed on the water surface. In

Safety Sound, the diet of chum salmon varied among years, with a dominance of insects and crustaceans (i.e., mysids) in 2002 and 2003, while chironomid larvae and crustaceans were dominant in 2004 (Nemeth et al. 2006). In addition, the dominant marine crustacean was primarily mysids in 2002, and primarily copepods in 2003. These results on early dietary composition of migrating chum salmon smolts are in agreement with other studies on the early diet of these fish; e.g., prey composition of juvenile chum salmon in Prince William Sound in southcentral Alaska was also dominated by harpacticoid copepods and terrestrial insects (Parker and Massa 1993). Similarly, in Cook Inlet insects were also predominant prey items of early juvenile chum salmon (Moulton 1997). With increasing size and transition from near-shore to more offshore and neritic waters, chum salmon also transition from a diet dominated by epibenthic and terrestrial prey to more planktonic feeding patterns (Pearce et al. 1982; Duffy 2003).

In general, the high proportion of drift insects in the diet of chum salmon during estuarine residence makes an estimate of prey selection difficult, because plankton sampling devices likely under-sample these taxa. In Safety Sound, chum salmon were estimated to consume crustaceans at a ratio similar to their occurrence in the water column (Nemeth et al. 2006). These results differed from dietary patterns of chum salmon in Kuskokwim Bay, where chum salmon were apparently selecting small calanoid copepods (Burril 2007).

Chinook, coho, pink, and sockeye salmon.—Data concerning the diet of other juvenile salmon in the AYK region are few or do not exist. Limited data concerning the diet of Chinook salmon in estuaries of the AYK region exist. In Kuskokwim Bay, the diet of juvenile Chinook salmon was dominated by euphausids, mysids, and amphiphods (Hillgruber, unpublished data). Adult insects, predominantly dipterans, were also an important part of their diet. These food items were comparable to the diet of juvenile Chinook salmon observed in Cook Inlet, Alaska, which contained notable numbers of insects, particularly later in the season (Moulton 1997). Elsewhere, Chinook salmon juveniles preyed on a wide variety of resources including insects, amphipods, crab larvae, and plankton (Duffy 2003). In Puget Sound, Washington, Chinook salmon shifted to a diet of fishes at a fork length of approximately 150 mm (Duffy 2003). Chinook salmon of that size were not observed in any of the estuarine studies conducted in western Alaska.

In the Yukon River delta, the small sample size (N = 4) allowed for only a cursory description of the coho salmon diet; coho salmon juveniles examined had fed on an isopod *Saduria enotmon*, other juvenile salmon, and inorganic debris (Martin et al. 1986). No other data on coho salmon diet in AYK estuaries were available. However, coho salmon in Cook Inlet, Alaska, demonstrated large seasonal variations in prey composition, with insects, calanoid copepods, and fish making up the diet in June, while in July, the diet of five coho salmon was dominated (%N = 96.9%) by insects alone (Moulton 1997).

In the Yukon River delta, pink salmon diet was dominated by chironomid adults and benthic larvae (Martin et al. 1986). In addition, planktonic calanoid and cyclopoid copepods were a frequent but less important component of their diet. No data on the diet of pink salmon were available for any of the other watersheds of western Alaska. Observations from the Yukon River delta were not in agreement with pink salmon diets reported from other areas; for example, pink salmon in the estuary of Porcupine Creek in southeast Alaska fed predominantly on pelagic prey, namely on mollusk larvae, calanoid copepods, and fish larvae (Murphy et al. 1988).

No information on the diet of sockeye salmon smolts was available from the AYK

region estuaries; however, juvenile sockeye salmon diet in Bristol Bay was examined by Carlson (1976). Insects were common in the stomachs of sockeye salmon smolts early in the migration (June) and near to freshwater sources. Carlson (1976) presumed that insects were consumed in freshwater and these fish were recent migrants to saltwater. As the season progressed and samples were collected further from freshwater sources, copepods dominated in the diet.

Juvenile Energy Density and Condition

Chum salmon.—Juvenile salmon condition can be estimated by measuring the fish's energy density. Energy density is defined as calories per gram and typically measured using bomb calorimetry. An increase in energy density indicates an increase in lipid storage. In juvenile salmon, the energy density tends to increase with increasing fish size (Trudel et al. 2005), and may vary seasonally or as the result of physiological changes such as smoltification or reproduction (Anthony et al. 2000). In the AYK region, the only data available on the energy density of salmon smolts in estuarine waters were measurements from Kuskokwim Bay (Burril 2007). Chum salmon energy density per gram dry weight significantly decreased with increasing size suggesting that juvenile chum salmon were allocating the majority of their energy to protein synthesis, i.e., growth, and smolting rather than to lipid storage. In addition, energy density decreased with season for fish of any given size-class (Burril 2007), probably as a result of increasing water temperatures and energy demands that were apparently not balanced by an increasing food supply.

Chinook, coho, pink, and sockeye salmon.—No data on energy density and condition of juvenile Chinook, coho, pink, or sockeye salmon for their estuarine residence in western Alaska were available for this review.

Conclusions

The early marine life stage of Pacific salmon represents a critical period that has been little studied in western Alaskan estuarine systems to date. This review identified several gaps in the understanding of the estuarine ecology of juvenile salmon in western Alaska (Table 4). While some data were available for species such as chum or Chinook salmon, other species were nearly completely neglected. In addition, data on out-migration patterns and residence timing and duration, and rearing conditions and their effect on diet, growth, and survival were often completely lacking or available only for selected years and sites. To answer the many questions related to this important life stage, and to evaluate and predict the potential effects of environmental change, long-term data collection is necessary (Moss et al. 2009).

In our experience, the acquisition of these data through field work in remote western Alaska estuaries is logistically very challenging. Estuaries, such as Kuskokwim Bay are shallow and poorly charted. Shallow-draft vessels capable of towing nets are required to sample juvenile salmon and are not typically available. Fuel, water, and other supplies are expensive and difficult to acquire or transport. Consequently, before launching full-scale field work in these remote sites, pilot studies should be conducted to survey sampling sites and address these and other logistical challenges.

Most of the data available to date were on chum salmon, and were mostly lacking for all other species of salmon. Future studies concerning juvenile salmon in western Alaska estuaries should focus on all species to better describe trophic connections. Of the four coho

Table 4. Summary of available data on estuarine rearing conditions and life history parameters of juvenile Pacific salmon in three main watersheds (Kuskokwim Bay, Yukon River delta, Safety Sound) in western Alaska (*indicates that no data are available).

Gaps	Kuskokwim Bay	Yukon River Delta	Safety Sound
Estuarine rearing conditions	5	4	1, 2
Estuarine fish community	5	3, 4	1, 2
Timing of outmigration	A, B, C, D, E[5]	A, B[3,4]	A[1,2]
Estuarine distribution	A, B, C, D, E[5]	A, B[3,4]	*
Estuarine residence	*	*	*
Estuarine prey availability:			
A) Pelagic	5	1, 2	*
B) Epibenthic	*	1	*
C) Neustonic	*	*	*
Estuarine feeding patterns	A[5]	A[3,4]	A[3]
Estuarine diet composition	A[5]	A[3,4]	A[3]
Juvenile condition	A, C[5]	*	*
Estuarine growth	*	A[3,4]	A[1,2]
Juvenile age	A[5]	A[3,4]	*
Estuarine mortality	*	*	*

[1]Nemeth et al. 2003, [2]Nemeth et al. 2006, [3]Martin et al. 1986, [4]Martin et al. 1987, [5]Hillgruber et al. 2007

A: Chum salmon *O. keta*, B: Chinook salmon *O. tshawytscha*, C: Coho salmon *O. kisutch*, D: Pink salmon *O. gorbuscha*, E: Sockeye salmon *O. nerka*

salmon from the Yukon River delta examined for their diet, one was feeding exclusively on unidentified juvenile salmon (Martin et al. 1986). Thus, coho salmon might be an important source of mortality for smaller outmigrating smolts in AYK estuaries. In addition, juvenile salmon other than chum salmon and other estuarine fishes may be important competitors for estuarine habitat and prey. Nemeth et al. (2006) noted a substantial change in the fish catch composition from 2002 and 2003 to 2004, which was demonstrated by a more than 25-fold increase in threespine stickleback *Gasterosteus aculeatus* catches. They suggested that this increase might have resulted in increased competition or even predation pressure for juvenile chum salmon. These findings suggest that future studies focusing on the entire fish community and all prey species are needed to better understand important interconnections that may play an essential role in the population dynamics of juvenile salmon.

No long-term research effort directed at the estuarine residence of juvenile salmonids has occurred in western Alaska. Instead, the only data from the AYK region on this important life stage were derived from a few disjointed studies from different years, different watersheds, and with different sampling regimes. The data currently available were not sufficient to examine interannual differences of the ecology of salmon smolts from western Alaska. Numerous research platforms exist throughout the AYK region to count adult salmon, such as weirs and counting towers, but to date only few studies have attempted to quantify or describe the characteristics of juvenile salmon as they migrate downstream. If we are to better understand the population

dynamics of salmon in western Alaska, more effort is needed to determine survival rates of salmon between emergence and saltwater entry because the mortality at this life stage may be a primary determinant of year-class adult abundance.

The Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative has a goal to "..understand the trends and causes of variation in salmon abundance…"; (AYK SSI 2006). To achieve this goal, significantly more work will be needed to determine the processes that control juvenile Pacific salmon survival in freshwater and estuarine habitats of western Alaska.

Acknowledgments

We thank Sean E. Burril and Carl D. Reese for their contributions to our work on Kuskokwim Bay. We thank the organizers of the AYK SSI symposium for inviting our presentation and this manuscript.

References

Adkison, M. D., and B. P. Finney. 2003. The long-term outlook for salmon returns to Alaska. Alaska Fishery Research Bulletin 10(2):83–94.

Anthony, J. A., D. D. Roby, and K. R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53–78.

AYK SSI (Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative). 2006. Arctic-Yukon-Kuskokwim salmon research and restoration plan. Available from Bering Sea Fishermen's Association, Anchorage, Alaska.

Bax, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Canadian Journal of Fisheries and Aquatic Sciences 40:426–435.

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. Progress in Oceanography 49:423–437.

Bradford, M. J., J. Duncan, and J. W. Jang. 2008. Downstream migration of juvenile salmon and other fishes in the upper Yukon River. Arctic 61:255–264.

Bue, F. J., B. M. Borba, R. Cannon, and C. C. Krueger. 2009. Yukon River fall chum salmon fisheries: management, harvest, and stock abundance. Pages 703–742 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Burril, S. E. 2007. Feeding ecology and energy density of juvenile chum salmon, *Oncorhynchus keta*, from Kuskokwim Bay, western Alaska. Master's thesis. University of Alaska Fairbanks, Fairbanks, Alaska.

Carlson, H. R. 1976. Food of juvenile sockeye salmon, *Oncorhynchus nerka*, in the inshore coastal waters of Bristol Bay, Alaska, 1966–67. Fishery Bulletin 74:458–462.

Duffy, J. 2003. Early marine distribution and trophic interactions of juvenile salmon in Puget Sound. Master's thesis. University of Washington, Seattle.

Evenson, D. F., S. J. Hayes, G. Sandone, and D. J. Bergstrom. 2009. Yukon River Chinook salmon: stock status, harvest, and management. Pages 675–701 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Fukuwaka, M., and T. Suzuki. 2002. Early sea mortality of mark-recaptured juvenile chum salmon in open coastal waters. Journal of Fish Biology 60:3–12.

Gissberg, J. G., and D. S. Benning. 1965. Yukon foundation studies summary report, 1965. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Anchorage, Alaska.

Healey, M. C. 1982a. Juvenile Pacific salmon in estuaries: the life support system. Pages 343–364 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Healey, M. C. 1982b. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Canadian Journal of Fisheries and Aquatic Sciences 39:952–957.

Healey, M. C. 1991. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. Transactions of the American Fisheries Society 120:303–318.

Hillgruber, N., C. E. Zimmerman, S. E. Burril, and L. J. Haldorson. 2007. Early marine ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska. Project R0327, Final Report, North Pacific Research Board, Anchorage, Alaska.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature

and implied latitudinal effects. Fishery Bulletin 87:471–495.

Linderman, J. C., Jr., and D. J. Bergstrom. 2009. Kuskokwim management area: salmon escapement, harvest, and management. Pages 541–599 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Martin D. J., D. R. Glass, C. J. Whitmus, C. A. Simenstad, D. A. Milward, E. C. Volk, M. L. Stevenson, P. Nunes, M. Savoie, and R. A. Grotenfendt. 1986. Distribution, seasonal abundance, and feeding dependencies of juvenile salmon and non-salmonid fishes in the Yukon River Delta. NOAA OCSEAP Final Report 55:381–770.

Martin, D. J., C. J. Whitmus, L. E. Hachmeister, E. C. Volk, and S. L. Schroder. 1987. Distribution and seasonal abundance of juvenile salmon and other fishes in the Yukon Delta. NOAA OCSEAP Final Report 66:123–277.

Mason, J. C. 1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. Journal of the Fisheries Research Board of Canada 31:83–92.

Menard, J., C. C. Krueger, and J. R. Hilsinger. 2009. Norton Sound salmon fisheries: history, stock abundance, and management. Pages 621–673 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Merritt, M. F., and J. A. Raymond. 1983. Early life history of chum salmon in the Noatak River and Kotzebue Sound. Alaska Department of Fish and Game; Division of Fisheries Rehabilitation, Enhancement, and Development Report #1. Juneau, Alaska.

Molyneaux, D. B., D. L. Folletti, and C. A. Shelden. 2006. Salmon age, sex, and length catalog for the Kuskokwim area, 2005. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report N. 3A06–01, Anchorage, Alaska.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. Myers, E. V. Farley, Jr., J. M. Murphy, and J. H. Helle. 2005. Higher marine survival associated with faster growth for pink salmon (*Oncorhynchus gorbuscha*). Transactions of the American Fisheries Society 134:1313–1322.

Moss, J. H., N. Hillgruber, C. Lean, J. Mackenzie-Grieve, K. Mull, K. W. Myers, and T. C. Stark. 2009. Conservation of western Alaska salmon stocks by identifying critical linkages between marine and freshwater life stages and long-term monitoring. Pages 1115–1125 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Moulton, L. L. 1997. Early marine residence, growth, and feeding by juvenile salmon in northern Cook Inlet, Alaska. Alaska Fishery Research Bulletin 4(2):154–177.

Murphy, M. L., J. F. Thedinga, and K. V. Koski. 1988. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska. Fishery Bulletin 86:213–222.

Nemeth, M. J., B. Haley, S. Kinneen, and W. Griffiths. 2003. Ecology of juvenile chum salmon from Norton Sound, Alaska. Annual Report to the Norton Sound Disaster Relief Fund by the Norton Sound Economic Development Corporation and LGL Alaska Research Associates, Inc. Anchorage, Alaska.

Nemeth, M. J., B. Williams, B. Haley, and S. Kinneen. 2006. An ecological comparison of juvenile chum salmon from two watersheds in Norton Sound, Alaska: migration, diet estuarine habitat, and fish community assemblage. Final Report for 2003 and 2004 to the Norton Sound Disaster Relief Fund by the Norton Sound Economic Development Corporation and LGL Alaska Research Associates, Inc. Anchorage, Alaska.

NRC (National Research Council). 2005. Developing a research and restoration plan for Arctic-Yukon-Kuskokwim (western Alaska) salmon. National Academies Press, Washington, D.C.

Parker, R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28:1503–1510.

Parker, D., and J. Massa. 1993. A comparison of diets and apparent growth rates for juvenile pink and chum salmon collected in Prince William Sound, Alaska. Proceedings of the 16th Pink and Chum Salmon Workshop, Juneau, Alaska.

Pearce T. A., J. H. Meyer, and R. S. Boomer. 1982. Distribution and food habits of juvenile salmon in the Nisqually estuary. Washington, 1979–1980. U.S. Fish and Wildlife Service, Olympia, Washington.

Raymond, J. A., M. Merritt, and C. Skaugstad. 1984. Nearshore fishes of Kotzebue Sound in summer. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement, and Development Report 37, Juneau, Alaska.

Reese, C., N. Hillgruber, M. Sturdevant, A. Wertheimer, W. Smoker, and R. Focht. In press. Spatial and temporal distribution and the potential for estuarine interactions between wild and hatchery chum salmon (*Oncorhynchus keta*) in Taku Inlet, Alaska. Fishery Bulletin.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23–49.

Salo, E. O. 1991. Life history of chum salmon. Pages 231–310 *in* C. Groot, and L. Margolis, editors. Pacific salmon: life histories. UBC Press, Vancouver, British Columbia.

Simenstad, C. A., and E. O. Salo. 1980. Foraging success as a determination of estuarine and nearshore carrying capacity of juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal. Pages 21–37 *in* B. R. Melteff, and R. A. Neve, editors. Proceeding of the North Pacific Aquaculture Symposium, Alaska Sea Grant, Anchorage, Alaska.

Simenstad, C. A., and R. C. Wissmar. 1984. Variability in estuarine food webs and production supporting juvenile Pacific salmon (*Oncorhynchus*). Pages 273–286 *in* W. G. Pearcy, editor. Workshop on influence of ocean conditions on the production of salmonids. Marine Science Center, Newport, Oregon.

Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Spencer, P. D. 2008. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfishes. Fisheries Oceanography 17(5):396–410.

Stabeno, P. J., N. A. Bond, and S. A. Salo. 2007. On the recent warming trend of the southeastern Bering Sea. Deep-Sea Research II 54:2599–2618.

Taylor, E. B. 1990. Environmental correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 37:1–17.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17(1A):76–93.

Trudel, M., S. Tucker, J. F. T. Morris, D. A. Higgs, and D. W. Welch. 2005. Indicators of energetic status in juvenile coho salmon and Chinook salmon. North American Journal of Fisheries Management 25:374–390.

Wertheimer, A. C., and F. P. Thrower. 2007. Mortality rates of chum salmon during their early marine residency. Mortality rates of chum salmon during their initial marine residency. Pages 233–247 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Wissmar, R. C., and C. A. Simenstad. 1988. Energetic constraints of juvenile chum salmon (*Oncorhynchus keta*) migrating in estuaries. Canadian Journal of Fisheries and Aquatic Sciences 45:1555–1560.

Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:88–97.