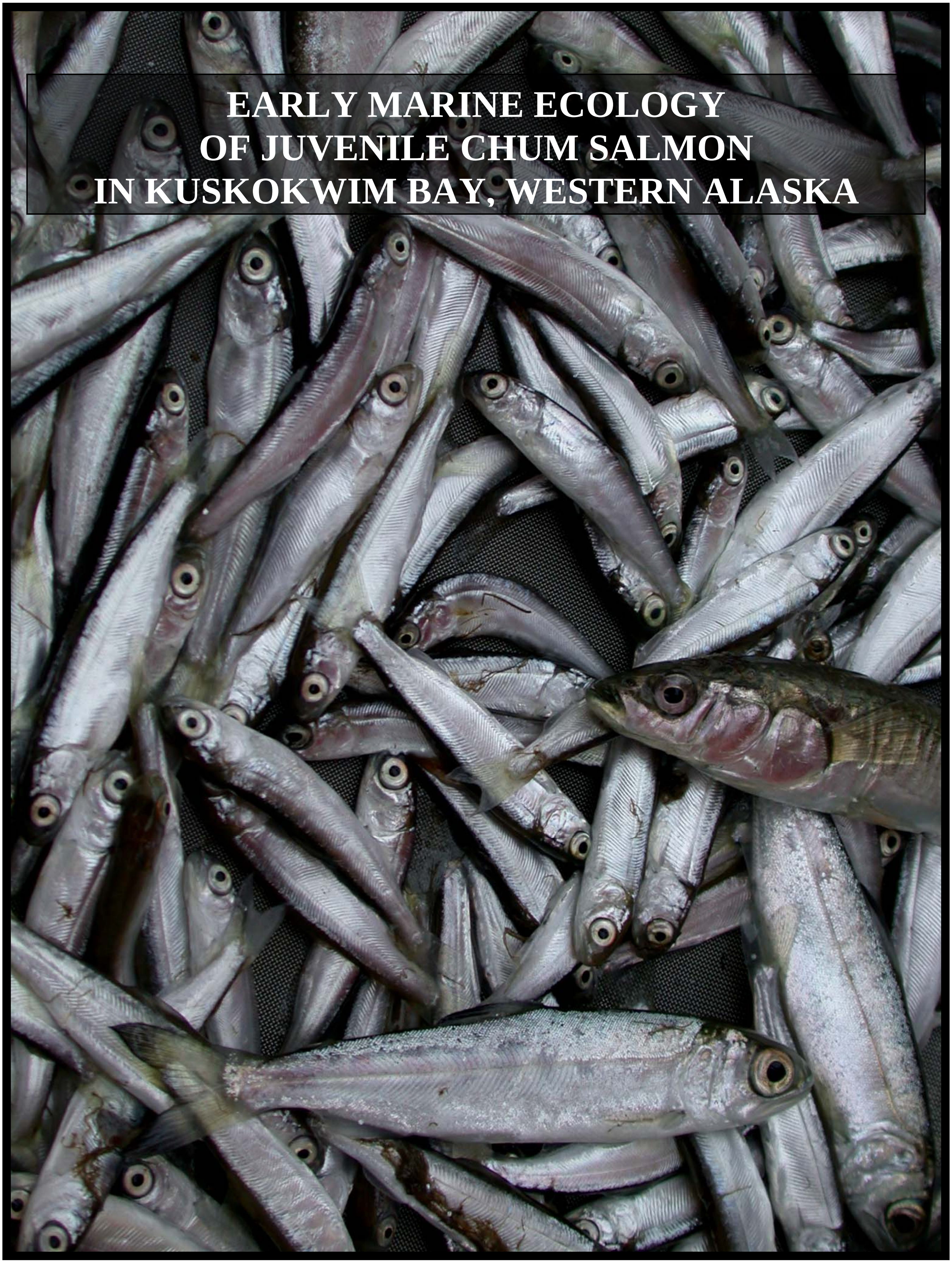
EARLY MARINE ECOLOGY
OF JUVENILE CHUM SALMON
IN KUSKOKWIM BAY, WESTERN ALASKA



NORTH PACIFIC RESEARCH BOARD PROJECT FINAL REPORT

EARLY MARINE ECOLOGY OF JUVENILE CHUM SALMON (*ONCORHYNCHUS KETA*) IN KUSKOKWIM BAY, ALASKA

PROJECT R0327 FINAL REPORT

to

NORTH PACIFIC RESEARCH BOARD
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Abstract

Little is known about the estuarine residence of juvenile chum salmon (*Oncorhynchus keta*) in western Alaska. It is at this stage, however, that juveniles might experience high mortality rates that may ultimately determine year class strength. Recent fluctuations in the abundance of chum salmon in the Kuskokwim River have demonstrated a need for more information on chum salmon life history, but particularly on factors impacting the critical estuarine life stage. Here we present results on spatial and temporal patterns of estuarine distribution, diet, and condition of chum salmon juveniles in 2003 and 2004 in Kuskokwim Bay. In addition, we used spatially-explicit foraging/bioenergetic modeling to assess the growth potential of Kuskokwim Bay habitats for outmigrating juvenile chum salmon in 2004, based on an intensive field sampling program in that year. Based on zooplankton abundance, water temperatures and turbidity, we modeled growth potential for small and large juveniles outmigrating early, in the middle and towards the end of the season. Our results provide the first data on timing of outmigration and estuarine distribution of chum salmon in relation to seasonally and spatially changing environmental conditions in Kuskokwim Bay. In addition, we determined seasonal and spatial patterns in diet and energy density of juvenile chum salmon and estimated the post-emergence age and duration of residence for chum salmon juveniles in Kuskokwim Bay. Our results indicate that timing of outmigration may be of high importance for the condition, growth, and subsequent survival probability. Further research is needed to more closely examine the role of changing environmental conditions, on estuarine residence, condition, and growth of juvenile salmonids in Kuskokwim Bay, particularly in light of the observed changing climatic conditions in the Bering Sea.

Keywords

Chum salmon, *Oncorhynchus keta*, western Alaska, smolts, distribution, outmigration, estuarine residence, diet, energy density, Wisconsin model

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STUDY CHRONOLOGY

This study was initiated on May 1, 2003 and ended on November 30, 2006. Field work was conducted in June, July and August of 2003 and May 16 until June 12 of 2004. The third year of this study was devoted to laboratory analysis of prey, diet, energy density and otoliths of juvenile chum salmon, as well as data analysis and report writing. Semiannual reports were submitted June 2003, January 2004, June 2004, January 2005, June 2005, January 2006, and June 2006. The final report was prepared for January 2007.

INTRODUCTION

The transition from freshwater to the marine phase is a critical period of high and variable mortality in the life history of salmonids (Pearcy 1992). In chum salmon (*Oncorhynchus keta*), mortality rates initially following ocean entry may 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 & 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 days post release (Wertheimer & Thrower *in press*). Reasons for these high and variable mortality rates are assumed to be food limitation (Salo 1991) and size-selective predation pressure (Beamish & Mahnken 2001). However, only little is known about the early marine ecology of juvenile chum salmon from western Alaska. A better understanding of environmental conditions, food resource availability, and growth of juvenile chum salmon during their early marine residence is needed to evaluate hypotheses of chum salmon population regulation in western Alaska.

Estuary and nearshore dependence differ among salmonid species (Thorpe 1994). In comparison to most other anadromous salmonids, chum salmon enter estuaries at a comparatively small size and remain longer in brackish water habitats of estuaries or river plumes (Healey 1982, Simenstad et al. 1982, Fukuwaka and Suzuki 1998). Thus, the period of estuarine residency might be particularly important for chum salmon juveniles because rapid growth and subsequent larger size might substantially reduce the risk of intense size-selective predation pressure in the marine environment (Parker 1971, Simenstad and Salo 1980, Healy 1982b, Simenstad and Wissmar 1984).

Estuarine food density and composition may affect early marine survival, either directly through starvation or indirectly through decreased growth rates, ultimately leading to longer duration at stages particularly vulnerable to predation. While no data exist on diet and prey selectivity of juvenile chum salmon from the Kuskokwim Bay area, chum salmon elsewhere apparently rely on a detritus-based food web (Sibert et al. 1977, Salo 1991). Several studies have indicated the predominance of small harpacticoid copepods in the diet of chum juveniles during their residence in estuaries (Healey 1979, Landingham 1982). Observed variations in growth rates of chum salmon juveniles might be due to difference in the composition of their diet, possibly resulting in variations in mortality rates.

The metabolic costs of migration and maintenance are key energetic constraints on the production and survival of juvenile chum salmon migrating through estuaries and the nearshore environment (Wissmar & Simenstad 1988). As a result, sea surface temperature and encountered prey availability and abundance in these habitats may be important factors determining the growth potential and mortality rates of juvenile chum salmon at this stage (Mason 1974, Healey 1982a, Salo 1992).

To our knowledge, this study is the first to examine the early estuarine ecology of juvenile chum salmon in Kuskokwim Bay, Alaska. The goal of this study was to document seasonal and spatial patterns of distribution of chum salmon juveniles during their first summer in the nearshore area of Kuskokwim Bay. In addition, we determined prey selection, condition, and growth in relation to the prey environment and used spatially explicit foraging/bioenergetic modeling to understand observed patterns.

STUDY OBJECTIVES

1. Determine the spatial and seasonal distribution of chum salmon juveniles throughout Kuskokwim Bay
2. Assess the spatial and seasonal patterns of environmental variables
3. Describe the relationship between juvenile distribution patterns and these variables.
4. Describe the food habits of juvenile chum salmon
5. Analyze length, weight, condition of juvenile chum salmon
6. Examine diurnal feeding patterns of juvenile chum salmon
7. Analyze growth of chum salmon.
8. Model the bioenergetics and growth of chum salmon juveniles in Kuskokwim Bay

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CHAPTER 1 – FISH DISTRIBUTION

Spatial and temporal distribution of chum salmon (*Oncorhynchus keta*) juveniles in Kuskokwim Bay, Western Alaska, in relation to environmental variables.

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Abstract

Little is known about the estuarine residence of juvenile chum salmon (*Oncorhynchus keta*) in western Alaska. Here we present first results on the timing of outmigration and spatial and temporal patterns of distribution of juvenile salmonids in Kuskokwim Bay in reference to patterns in physical parameters. Juvenile salmonids were collected in two years, 2003 and 2004, using a modified Kvichak surface trawl. In the two years of the study, all five species of juvenile Pacific salmon were caught. Chum salmon were the most abundant salmonid taxon by nearly one order of magnitude, followed by coho salmon (*O. kisutch*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*), and sockeye salmon (*O. nerka*) in order of their abundance. No sockeye salmon were collected in 2003, while they made up only 0.14% of the total catch in 2004. Combining data from both study years, we determined an estuarine residence period for chum salmon juveniles from the middle of May until late July; no chum salmon were caught in August. Environmental conditions, particularly sea surface temperature (SST) changed remarkably during the juvenile outmigration, with uniformly low temperatures of 7˚C in May, increasing to SST as high as 15.6˚C in June. In May, distribution of juvenile chum salmon was confined primarily to the waters of the river plume, with fish leaving the plume towards the later part of their outmigration, indicating that they were using the river plume as a staging area to adjust to higher salinity water and possibly as a nursery area to protect them from visual predators. During their residence in Kuskokwim Bay, chum salmon juveniles were apparently growing in size; however, concurrent reductions in energy density raise questions about the quality of the bay as a nursery habitat for chum salmon juveniles.

Introduction

Chum salmon (*Oncorhynchus keta*) are an important economic and cultural resource of western Alaska. Declines in numbers of chum salmon returning to the Kuskokwim and the Yukon rivers since 1998 have resulted in closures and restrictions of commercial and subsistence fisheries in western Alaska. To date, the causes of declines and later rebounds of some Pacific salmon populations in western Alaska are unknown. Because so little information exists about the early life history of anadromous salmon populations in western Alaska, it is difficult to develop or test hypotheses concerning mechanisms regulating population size and the role of environmental variation.

Estuaries are dynamic systems with strong gradients in physical and biological variables. These systems have been suggested to be of primary importance, providing migratory pathways and often also nursery habitat for early life stages of Pacific salmon migrating from freshwater to marine environments. Estuarine residence is considered a critical period of relatively high and variable mortality rates (Parker 1971, Healey 1982, Bax 1983, Fukawaka & Suzuki 2002, Wertheimer & Thrower *in press*) and may ultimately determine year-class strength. Among other factors, smolt size at ocean entry may be an important determinant for the survival probability of Pacific salmon populations (Wertheimer & Thrower *in press*).

Although recognized as a critical period, very little work has been done on this life history stage throughout most of western Alaska. Estuarine dependence or use differs among anadromous Pacific salmon species (Thorpe 1994). Chum salmon, for example, enter estuarine habitats shortly after emergence from the gravel during the first year of their lives and at a very small size. After leaving the rivers, chum salmon juveniles remain longer in brackish water habitats of estuaries or river plumes (Healey 1982, Simenstad et al. 1982, Fukuwaka & Suzuki 1998). The period of estuarine residency might be particularly important for chum salmon juveniles because rapid growth and subsequent larger size might substantially reduce the risk of size-selective predation in the marine environment. The metabolic costs of migration and maintenance are key energetic constraints on the production and survival of juvenile chum salmon migrating through estuaries (Wissmar & Simenstad 1988). As a result, temperature and prey abundance experienced by juvenile chum salmon entering these habitats may determine the growth potential and mortality rates of fish at this stage (Mason 1974, Healey 1982, Salo 1992).

Kuskokwim Bay is a wide and shallow estuary that opens into the southeastern Bering Sea. The bay is fed primarily by the glacially turbid Kuskokwim River, the second largest drainage in Alaska (approximately 1,100 km). The river plume follows the eastern shore and extends far into the estuary. Kuskokwim Bay provides a migratory pathway and possible nursery habitat for all five species of Pacific salmon, including pink (*Oncorhynchus gorbuscha*), chum, coho (*O. kisutch*), sockeye (*O. nerka*) and Chinook (*O. tshawytscha*) salmon.

This study represents the first sampling effort on juvenile salmonids in the estuarine habitat of Kuskokwim Bay. To date, no information is available on timing of outmigration, residence duration, and estuarine distribution for juvenile salmonids in Kuskokwim Bay. The main goal for this paper was to identify duration and timing of outmigration for juvenile chum salmon in Kuskokwim Bay and to examine juvenile chum salmon abundance and distributional patterns in comparison to environmental factors. Specifically, our objectives were to (1) determine the timing of chum salmon outmigration, (2) describe distributional patterns of chum salmon, and to (3) describe the seasonal and spatial patterns in environmental variables experienced by juvenile chum salmon during their estuarine residence.

Material and Methods

Sampling was conducted in two years, 2003 and 2004, in Kuskokwim Bay, Western Alaska (Figure 1). In 2003, sampling was carried out off the S/V "Eileen O'Farrel" during three research cruises, June 23-25, July 24-26, and August 26-30 (Table 1); during the second year of this study, sampling was conducted on the F/V "Namorada" from May 17 until June 11, 2004. Due to the deeper draft of the vessel used in 2003, sampling was restricted to fewer stations in the eastern part of the bay. In addition, for logistic reasons, sampling in 2003 started in late June, at a time when the majority of chum salmon smolts had presumably already left the bay. Consequently, for the purpose of this report, data from 2003 will be used only to supplement 2004 data if necessary.

Samples were collected on a station grid of regularly spaced stations, every 15 minutes of latitude and 7.5 minutes of longitude (Figure 1). At each station physical data were recorded with a SeaBird Electronics SBE-19 Seacat CTD (conductivity, temperature, depth) profiler. In 2004, the CTD was equipped with two additional sensors, namely a Wetstar fluorometer and a D&A Instruments transmissometer. Juvenile fish were collected using a modified Kvichak surface trawl with a net opening of 3.1 m x 3.1 m, fished with two shrimp trawl doors. Floats at the headrope and weights at the footrope provided vertical spread and assured that the net fished the upper 3.0 m of the water column. The trawl was fished for 10-30 minutes. After recovery of the trawl, all fish were anesthetized in MS-222 prior to further handling. Fish treatment followed a protocol approved by the UAF Animal Care and Use Committee (IACUC # 03-18). All fish were identified to species, if possible, and counted if the total catch was less than about 500 specimens. All fish or a sub-sample of each taxon were measured to the nearest 1.0 mm fork length (FL). All salmonids were frozen and returned to the lab for subsequent analyses of diet (Chapter 2), energy density (Chapter 3), and age (Chapter 4).

Sample analyses were distributed between the Fisheries Division of the School of Fisheries and Ocean Sciences (SFOS, UAF) and the U.S. Geological Survey, Alaska Science Center (USGS). Prior to further processing, all juvenile salmonid identifications were confirmed in the lab; individual fish were measured in length to the nearest 1.0 mm FL and weighted to the nearest 0.1 g wet weight. Otoliths were extracted for subsequent age estimates and microchemistry analysis at the U.S. Geological Survey (Chapter 4) and stomach contents were removed for subsequent dietary analysis at the University of Alaska Fairbanks (Chapter 2). The whole remaining fish tissue was retained for later analysis of energetic body content (Chapter 3).

Catch per unit effort (CPUE) was calculated for trawl-caught fishes. CPUE was expressed as the number of individuals per species collected in 1 hour of fishing effort. CPUE values were ln(x+1) transformed to normalize the data. Environmental data were averaged by cruise and week (2004) and compared between weeks (2004) and cruises (2003) within sampling year using ANOVA.

Results

General

In 2003, due to a later than anticipated allocation of funds, a first exploratory cruise could not be conducted until the end of June. Sampling occurred June 23-26, 2003, with Bethel being used as the port of departure and arrival. During the first cruise, all equipment was successfully deployed and a total 11 stations were completed (Table 1). Further research cruises in 2003 were conducted at the end of July and the end of August (Table 1).

In 2004, a different sampling design was developed to better deal with the logistic problems of conducting field research in this remote location. Instead of Bethel as our home port, we used Quinhagak, located at the eastern shore of Kuskokwim Bay. Sampling began earlier in the season, in response to data obtained from 2003. In 2004, sampling was conducted May 15-June 15, 2004 (Table 1).

Environmental Conditions

Only a limited number of stations were sampled in 2003. Environmental conditions in 2003 were similar to those observed in 2004, with, sea surface temperature (SST) averaging to 14.5˚C (SD=1.2) in late June, 14.9˚C (SD=0.3) in late July, decreasing to 13.5˚C (SD=0.8) in late August. There was a significant difference in SST with month in 2003 (ANOVA, $F_{2,25}$=8.18, p<0.01).

In 2004, a larger number of sampled stations allowed for a better spatial and seasonal comparison of environmental data. In the first week of sampling in 2004 SST throughout the bay was homogenously at 7 °C, but increased towards the last week of sampling to temperatures of 14°C at the head of the estuary and 10-12°C in the bay (Figure 2). SST significantly increased with sampling week from 6˚ - 8˚C in the first week of sampling to maximum temperatures of 15.6˚C during the last sampling week (ANOVA, $F_{3,68}$=31.18, p<0.001). SST was notably warmer in the mouth of Kuskokwim River and declined towards the outer Kuskokwim Bay. No significant differences in sea surface salinity (SSS) with sampling week were detected. However, SSS differed significantly with sampling station (ANOVA, $F_{21,50}$=77.01, p<0.001), ranging 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 shore of Kuskokwim Bay (Figure 3).

In 2004, optical backscatter (OBS) was recorded as a measure of turbidity. OBS values ranged from 2-116 at 2-m water depth (Figure 4). Peak turbidity was observed in week 1 at the head of the estuary, with turbidity levels declining towards the end of the 2004 sampling effort. In addition, fluorescence was recorded as an indicator of chlorophyll-a concentration and fluorescence values at 2-m water depth were plotted (Figure 5). Highest values were observed to the west of the Kuskokwim River plume in the area of the Ishkowik River outflow.

Fish Catch Composition

Total number of fish captured increased substantially from 2003 to 2004, with a total of 17,877 fish caught in 2003 and a total of 26,625 fish in 2004 (Table 2, 3). In both year, the majority of the collected specimens were represented by four species, including two species of smelt (Osmeridae), pond smelt (*Hypomesus olidus*) and rainbow smelt (*Osmerus mordax*), as well as two species of stickleback (Gasterosteidae), threespine stickleback (*Gasterosteus aculeatus*) and ninespine stickleback (*Pungitius pungitius*). However, 2003 was also characterized by high catches of Pacific herring (*Clupea pallasii*) juveniles. In comparison, only one herring was caught in 2004; instead, large numbers of juvenile Pacific sandlance (*Ammodytes hexapterus*) were collected on few stations, demonstrating their patchy distribution.

During the two years of our study, all five species of Pacific salmon were collected; however, catches of salmon juveniles increased dramatically from 2003 to 2004 as a result of the larger number of stations sampled and the earlier sampling time. In both years, chum salmon juveniles were the most abundant salmonid species, making up 0.38% and 4.68% of the total catch in 2003 and 2004, respectively (Table 2, 3). All other juvenile salmonid species were substantially less abundant, namely coho, pink, Chinook, and sockeye salmon in order of their abundance. No sockeye salmon were collected in 2003, while they made up only 0.14% of the total catch in 2004.

Timing of Outmigration and Distribution of Juvenile Salmonids

In 2004, chum salmon outmigration commenced in the middle of May (Figure 6). Catches increased in abundance, with peak catches reported in the week of June 6-12, 2004. Catches in 2003 were also highest at the end of June and declined significantly towards July. No chum salmon were collected in August of 2003 (Figure 6). During the first week of sampling in 2004, positive catches for juvenile chum salmon were only reported from station 1-4 at the head of Kuskokwim Bay in salinities of 0-5 (Figure 9). In week 2 and 3, chum salmon juvenile catches increased in abundance with positive catches extending further southward into the bay (Figure 9B, C). Juvenile chum salmon, however, were still primarily caught in waters of the Kuskokwim River plume. Only in week 4 of the 2004 sampling (June 6-12, 2004) did the distribution of chum salmon juveniles extend beyond the river plume, with fish moving into higher salinity water (Figure 9D).

In 2004, pink salmon were collected from the first week until the last week of sampling. Highest CPUEs were observed in week 2 (Figure 7A); however, peak catches of pink salmon were about one order of magnitude lower than peak chum salmon CPUE. In 2003, positive pink salmon catches were documented for June and July; no pink salmon were collected in August. Pink salmon outmigration into Kuskokwim Bay followed no discernable pattern (Figure 11).

Coho salmon juvenile catches peaked in week 2 in 2004. Coho salmon CPUE in June was substantially lower and no coho salmon juveniles were caught in 2003 (Figure 7B). Abundances of coho salmon juveniles were highest at the head of the bay in all weeks of our sampling (Figure 10). Estuarine distribution of coho salmon juveniles was more widespread than that of chum salmon, with coho salmon collected from the southernmost station of our sampling in week 3 (Figure 10C).

At the head of Kuskokwim Bay, sockeye salmon juveniles were only collected in May of 2004 (Figure 8B), with catches peaking in week 2. Overall catches of sockeye juveniles were very low in 2004; in 2003, no sockeye salmon juveniles were caught (Table 2). The estuarine-wide distribution of sockeye salmon appears to indicate one pulse of juveniles migrating out of the river towards the south within the four weeks of sampling (Figure 12).

At the head of the Kuskokwim Bay, a total of only 6 Chinook salmon were caught in week 4 in 2004. No Chinook salmon juveniles were captured before June in 2004 and none were collected after July in 2003 (Figure 8A). Estuarine distribution of Chinook salmon in June was variable, with some fish remaining in the plume of Kuskokwim River, while others appeared more associated with the frontal zone between river and estuarine water (Figure 13).

Chum Salmon Size

Length of juvenile chum salmon capture during our survey ranged from 42-65 mm FL (mean = 49.5, SD = 4.2) in 2003 (Figure 6) and from 31-66 mm (mean = 43.6, SD = 6.0) in 2004 (Figure 7). Mean fork length increased significantly from cruise 1 to cruise 2 in 2003 (ANOVA, $F_{1,57} = 7.53$, $p<0.01$); no chum salmon were caught during cruise 3 in late August. In 2004, mean fork length increased significantly with sampling week (ANOVA, $F_{3,354} = 45.01$, $p< 0.01$), with fish length increasing from a mean length of 36.6 mm FL (SD=3.3) in the first week of sampling to 45.9 mm FL (SD=5.6) in week 4 in 2004. Chum salmon less than 40 mm FL were observed during all weeks of sampling in 2004, indicating that throughout the season new fish were migrating out of Kuskokwim River and entering the bay.

Discussion

The modified Kvichak tow-net used in the present study proved to be a reliable and highly effective sample gear for juvenile stages of estuarine fishes, catching a variety of species and sizes. Juveniles of all species of Pacific salmon were caught in 2004, ranging in size from 31-170 mm FL. The tow-net was equipped with floats in the headrope and weights in the footrope to effectively fish the upper 3 m of the water column. In Cook Inlet, hydroacoustic data suggested that outmigrating juvenile salmonids were oriented near the surface, in the upper 2 m of the water column, particularly in waters of high turbidity (Moulton 1997). Since large areas of Kuskokwim Bay are not much deeper than 3 m, the modified tow-net employed in the present study was an efficient gear for capturing juvenile salmonids in the estuarine waters of Kuskokwim Bay.

In 2004, chum salmon juveniles began their outmigration into Kuskokwim Bay shortly after ice break-up in the middle of May and continued to be caught until the end of our survey. In 2003, positive catches were recorded as late as July 24-26, albeit with very low numbers. Considering both years of our study, we determine peak outmigration of chum salmon smolts to occur in early June. This is later than observed for chum salmon in lower latitudes (Meehan and Siniff 1962, Duffy et al. 2005, Reese et al. *in prep.*), but is comparable to chum salmon outmigration in western Alaska. In Norton Sound, chum salmon peak outmigration occurred in mid-June, with a second peak occurring in mid-July (Nemeth et al. 2006). In the Yukon River delta, chum salmon juveniles were most abundant in late June, with numbers declining rapidly by early July; no second peak of outmigration was apparent (Martin et al. 1986).

Over the period of chum salmon outmigration, environmental conditions experienced by juvenile fish changed noticeably. Size frequency distribution indicated a continuing influx of small fry (<40 mm FL) throughout the 2004 sampling period, but environmental conditions, especially sea surface temperature, encountered by these early chum salmon juveniles differed markedly with season. SST was uniformly low at the beginning of the outmigration period but increased significantly with sampling week, reaching values as high as 16˚C in the surface water of the Kuskokwim River plume. This increase in SST will increase the metabolic rates of outmigrating, ectothermic juveniles, particularly chum salmon that seem to reside in the freshwater plume longer than other juvenile salmonids before moving out into the cooler and saltier waters of the bay. The observed temperatures are comparable to those observed in other studies targeting river and estuarine waters in western Alaska (Martin et al. 1986, Nemeth et al. 2006) and represent optimal temperatures for juvenile sockeye salmon growth under high food rations (Brett et al. 1969); however, under low food rations, optimal growth for sockeye salmon juveniles occurred at temperatures considerably lower, namely 5˚C (Brett et al. 1969). Energy density of chum salmon juveniles in the present study was decreasing with season (Chapter 3), thus raising the question whether these fish were experiencing optimal food rations for the observed elevated temperatures in June.

Distribution of juvenile chum salmon was confined primarily to the waters of the river plume. Only towards the later part of their outmigration, did they move out of the river plume into waters of higher salinity. These findings are consistent with results from other studies, which demonstrate that juvenile salmonids may use the low-salinity surface waters of river plumes to physiologically adjust to marine conditions (St. John et al. 1992, Fukuwaka & Suzuki 1998). Juvenile salmonids were also more abundant in the waters of the plume and frontal zone of the Columbia River (DeRobertis et al. 2005); however, this pattern was not consistent for all species of juvenile salmonids and results varied interannually. While it has been suggested that these frontal zones may provide increased feeding conditions due to the concentration of prey organisms, no such effect could be determined for the Columbia River plume (DeRobertis et al. 2005). In this study, however, bioenergetic modeling indicated highest growth potential for outmigrating chum salmon in the transition zone between river and estuarine water, thus confirming the idea of improved feeding conditions (Chapter 5). In addition to presenting juvenile salmonids with a staging area before the entry into high-salinity water, the highly turbid waters of the Kuskokwim River plume might also provide these young fish with a refuge from visual predators (Dauvin & Dodson 1990, Thorpe 1994).

Coho salmon were the second most abundant salmonid juveniles collected in 2004. While their outmigration peaked slightly earlier than that of chum salmon, their distributional pattern, particularly early in the season, overlapped that of the smaller chum salmon juveniles, indicating the potential for predation pressure of coho salmon on chum salmon juveniles. Other studies have indicated that coho salmon juveniles are piscivorous, feeding on smaller salmonid fry and smolts (e.g., Parker 1971, Ruggerone & Rogers 1992, Fukuwaka & Suzuki 1998, Landingham et al. 1998). In the present study, coho salmon had a large size advantage (70-170 mm FL) over outmigrating chum salmon. In addition, the abundance of pink salmon fry was low; thus, small chum salmon juveniles were not shielded from predation pressure by the large abundance of outmigrating pink salmon, as reported from other systems (Parker 1971). However, since no dietary analysis on the coho salmon juveniles has been conducted to date, any suggestion of coho salmon predation on chum salmon remains speculative.

The size distribution of juvenile chum salmon in 2004 indicated that very small juvenile chum salmon (i.e., < 40 mm FL) were continuing to enter the bay until early June. In spite of these apparent immigrants as well as the probable loss of larger juveniles leaving the bay, chum salmon were demonstrating apparent growth, significantly increasing in fork length with sampling week. Juvenile salmonids experience high size-selective mortality during their early marine residence (Bax 1983). High growth rates will quickly move the fish through this critical period of intense predation (Holtby et al. 1990). Juvenile chum salmon collected on the southeastern Bering Sea shelf in late August/early September had an average size of 173 mm FL (Farley *pers. comm.*). In order to achieve these sizes and outgrow the critical period of high predation pressure, juvenile chum salmon appear to allocate the majority of their resources to growth, rather than to the storage of high-energy compounds (Chapter 3).

This study represents the first effort of determining timing of outmigration and distribution of juvenile salmonids in Kuskokwim Bay, western Alaska. While providing the first information on species-specific patterns of outmigration and estuarine habitat use by juvenile salmonids, this study also demonstrates the need for a more thorough understanding of this critical period in the early life of western Alaska salmonids. The large variation in environmental conditions and their potential effects on distribution, growth and survival probability, the spatial and temporal patterns of estuarine distribution of different salmon taxa and the potential for competition and predation between them, and the species-specific seasonal patterns of energy allocation during the estuarine outmigration are only a few of the many areas that are poorly studied. A more thorough understanding of these and other aspects of this critical period in the life of juvenile salmonids may provide some information on mechanisms responsible for regulating population size and on the role of environmental variation.

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List of Tables

	Sampling dates	*Number of stations*
2003		
Cruise 1	June 23 – 26	10
Cruise 2	July 24 - 26	12
Cruise 3	August 26 - 30	8
2004		
Week 1	May 16 - 22	16
Week 2	May 23 - 29	20
Week 3	May 30 – June 5	19
Week 4	June 6 - 12	17 (+4)

Table 1.

Species name	Common name	Cruise 1	Cruise 2	Cruise 3	Total	% Catch
Clupea pallasii	Pacific herring	1	2,034	431	2,466	13.79
Eleginus gracilis	Saffron cod		1		1	0.01
Gasterosteus aculeatus	Threespine stickleback		228	807	1,035	5.79
Hypomesus olidus	Pond smelt		1,261	9,754	11,015	61.62
Lampetra camtschatica	Arctic lamprey	6	1		7	0.04
Lota lota	Burbot		1		1	0.01
Oncorhynchus gorbuscha	Pink salmon	2	2	1	5	0.03
Oncorhynchus keta	Chum salmon	56	12		68	0.38
Oncorhynchus kisutch	Coho salmon	1			1	0.01
Oncorhynchus tshawytscha	King salmon	3	2		5	0.03
Osmerus mordax	Rainbow smelt	212	226	54	492	2.75
Pleuronectes glacialis	Arctic flounder	1			1	0.01
Pungitius pungitius	Ninespine stickleback	49	782	1,949	2,780	15.55
	Total	331	4,550	12,996	17,877	

Table 2.

Scientific name	Common name	Week 1	Week 2	Week 3	Week 4	Total	% Catch
Ammodytes hexapterus	Sand lance	659	4	76		739	2.78
Clupea pallasii	Pacific herring	1				1	0.00
Coregoninae	Whitefish	4				4	0.02
Gasterosteus aculeatus	Threespine stickleback	30	35	19	3	87	0.33
Hypomesus olidus	Pond smelt	894	6,191	3,137	1,565	11,787	44.27
Lampetra camtschatica	Arctic lamprey		1	1	33	35	0.13
Myoxocephalus polyacanthocephalus	Great sculpin	2				2	0.01
Ocella dedecaedron	Bering poacher	2				2	0.01
Oncorhynchus gorbuscha	Pink salmon	19	48	5	4	76	0.29
Oncorhynchus keta	Chum salmon	19	87	81	1,058	1,245	4.68
Oncorhynchus kisutch	Coho salmon	23	82	76	19	200	0.75
Oncorhynchus nerka	Sockeye salmon	1	9	8	20	38	0.14
Oncorhynchus tshawytscha	King salmon			11	39	50	0.19
Osmerus mordax	Rainbow smelt	2,910	4,469	2,818	794	10,991	41.28
Pleuronectes glacialis	Arctic flounder	7			1	8	0.03
Pungitius pungitius	Ninespine stickleback	95	68	1,144	38	1,345	5.05
Others	Unidentified	11	2	0	2	15	0.05
	Total	4,677	10,996	7,376	3,576	26,625	

Table 3.

List of Figures

Figure 1. Kuskokwim Bay study region in western Alaska and station locations (●) sampled in 2003 and 2004 (see table 1 for more information on station location).

Figure 2. Surface plot of Kuskokwim Bay sea surface temperature (SST) in May 15-22, 2004 (A), May 23-29, 2004 (B), May 30-June 5, 2004 (C), and June 6-12, 2004 (D).

Figure 3. Surface plot of Kuskokwim Bay sea surface salinity (SSS) in May 15-22, 2004 (A), May 23-29, 2004 (B), May 30-June 5, 2004 (C), and June 6-12, 2004 (D).

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Figure 7. Mean seasonal CPUE (catch h^{-1} +1 SE) of pink salmon (A) and coho salmon (B) juveniles averaged for station 1-3 by sampling week for 2003 and 2004.

Figure 8. Mean seasonal CPUE (catch h^{-1} +1 SE) of Chinook salmon (A) and sockeye salmon (B) juveniles averaged for station 1-3 by sampling week for 2003 and 2004.

Figure 9. Distribution of juvenile chum salmon CPUE (catch h^{-1} ±1 SE) for May 15-22 (A), May 23-June 23-29 (B), May 30 – June 5 (C), and June 6-12, 2004 (D).

Figure 10. Distribution of juvenile coho salmon CPUE (catch h^{-1} ±1 SE) for May 15-22 (A), May 23-June 23-29 (B), May 30 – June 5 (C), and June 6-12, 2004 (D).

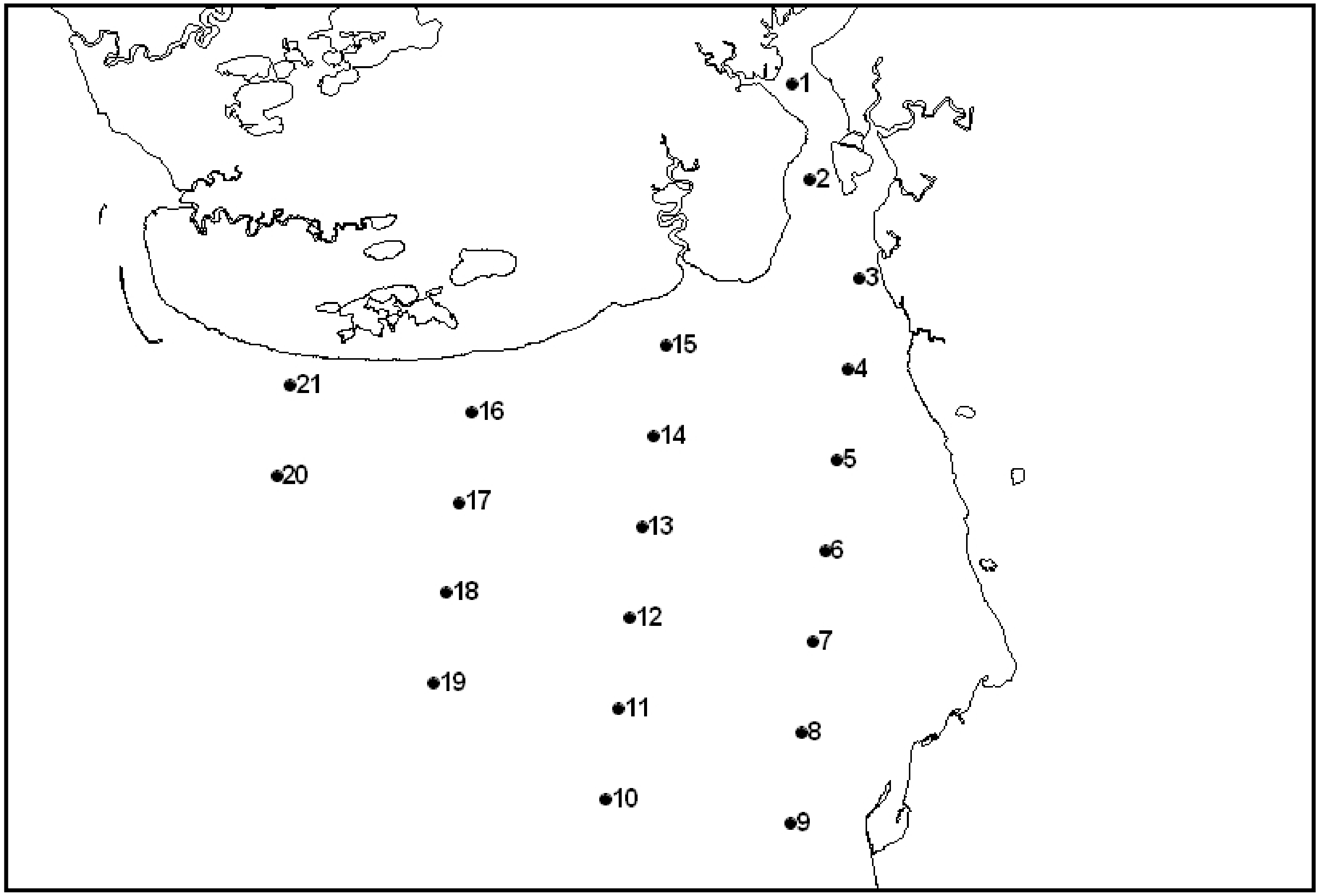
Figure 11. Distribution of juvenile pink salmon CPUE (catch h^{-1} ±1 SE) for May 15-22 (A), May 23-June 23-29 (B), May 30 – June 5 (C), and June 6-12, 2004 (D).

Figure 12. Distribution of juvenile sockeye salmon CPUE (catch h^{-1} ±1 SE) for May 15-22 (A), May 23-June 23-29 (B), May 30 – June 5 (C), and June 6-12, 2004 (D).

Figure 13. Distribution of juvenile Chinook salmon CPUE (catch h^{-1} ±1 SE) for May 15-22 (A), May 23-June 23-29 (B), May 30 – June 5 (C), and June 6-12, 2004 (D).

Figure 14. Frequency distribution of fork length of chum salmon juveniles collected during cruise 1 and 2 in 2003 (n = 59).

Figure 15. Frequency distribution of fork length of chum salmon juveniles collected during week 1 (n=46), week 2 (n=38), week 3(n=98), and week 4 (n=176).



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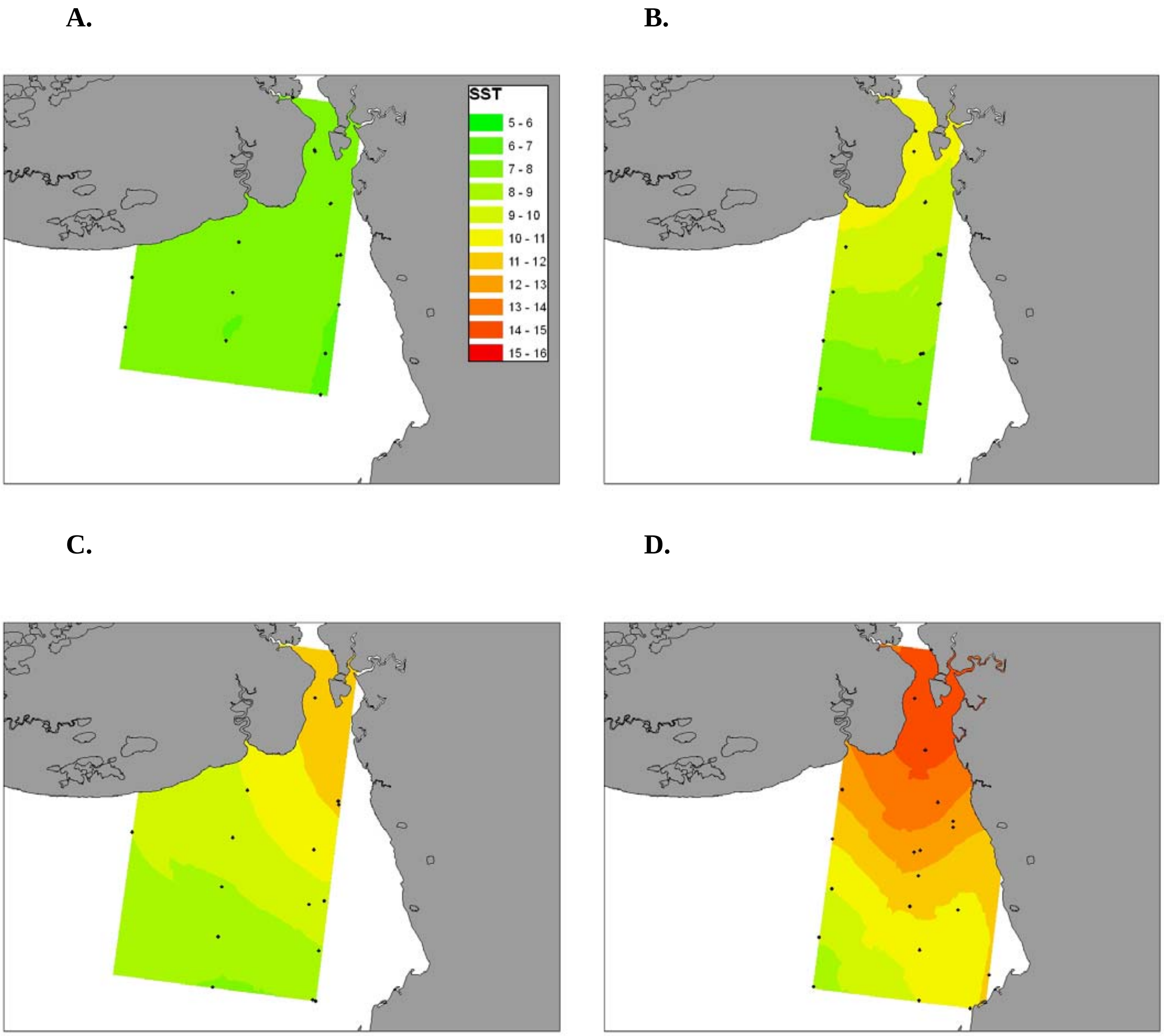

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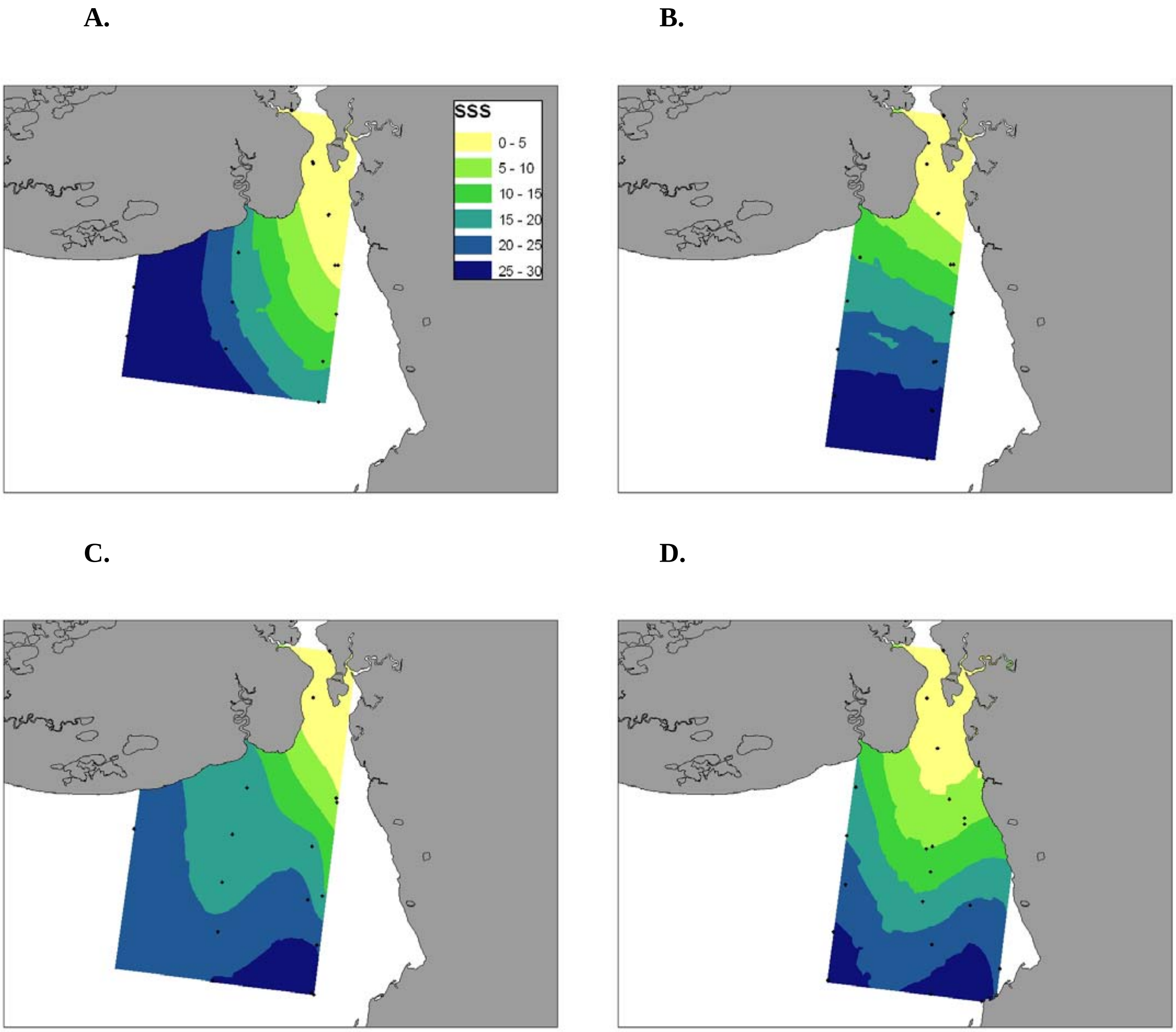

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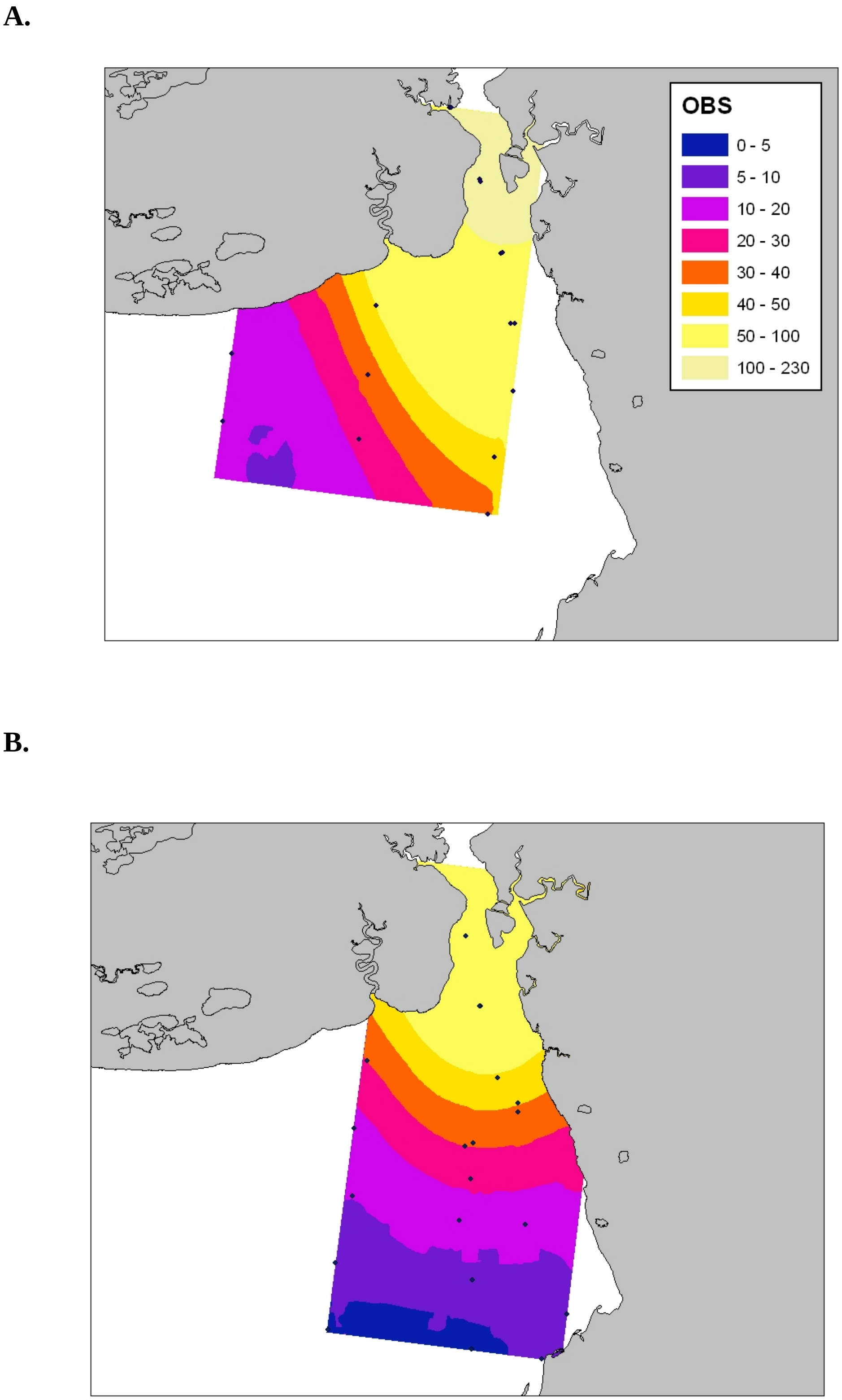

Figure 4

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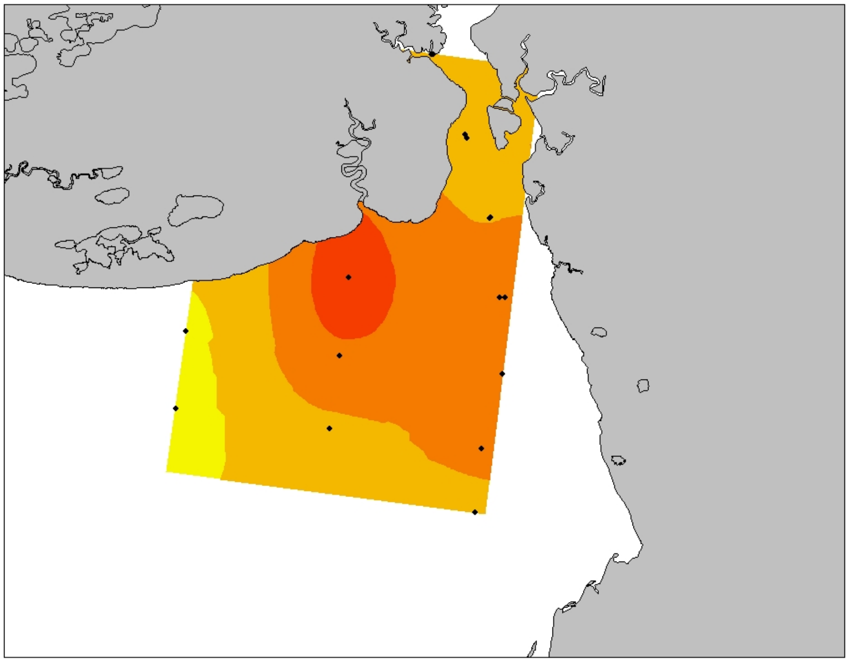

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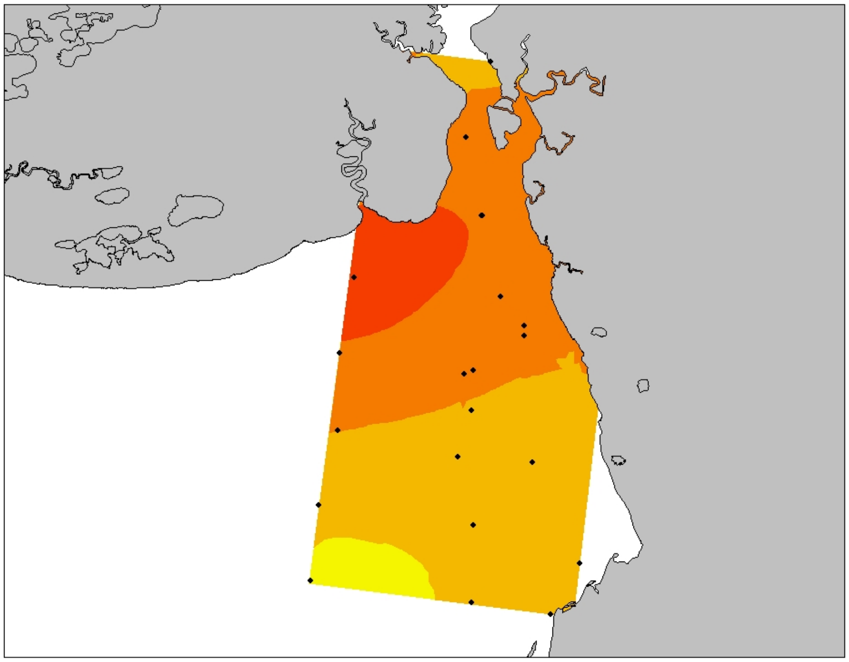

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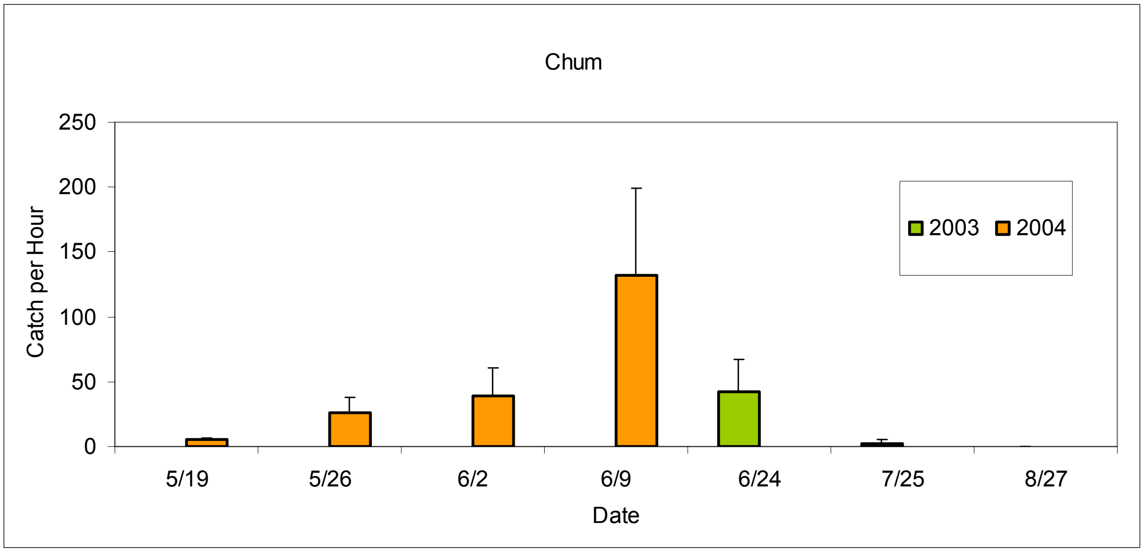
Chum
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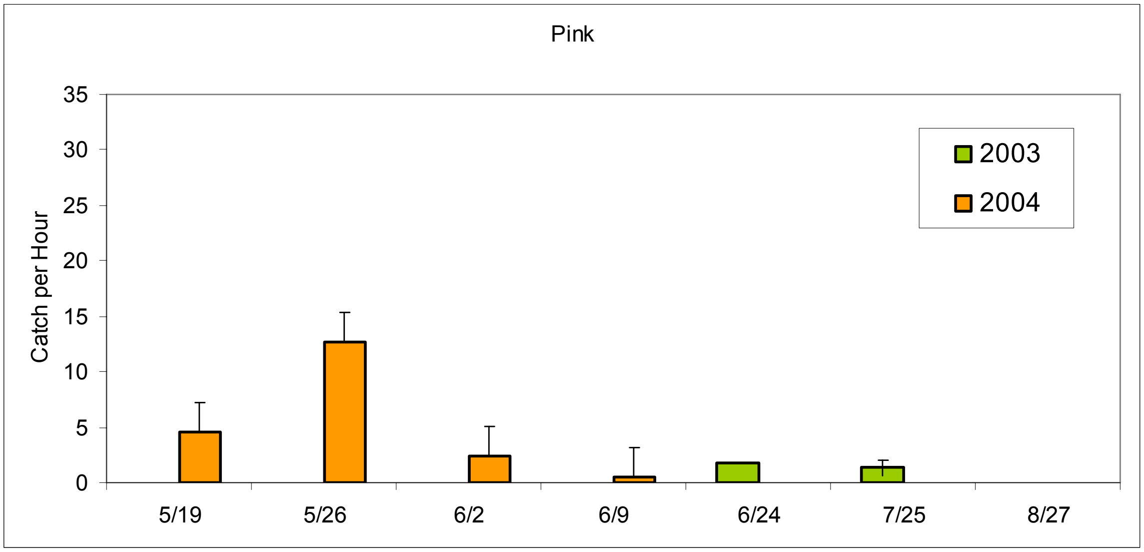
Date

Figure 6.

A.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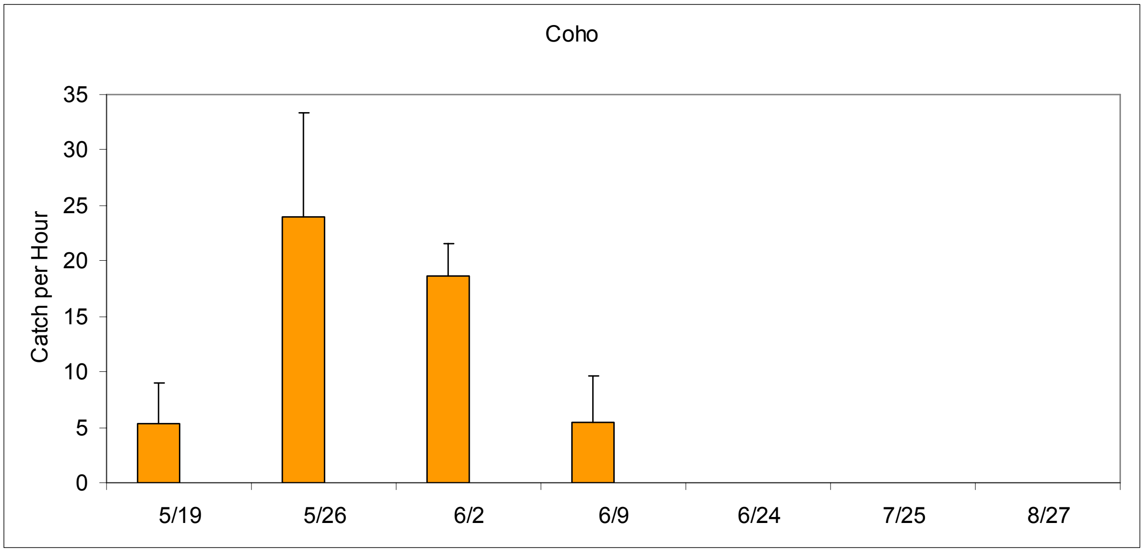
B.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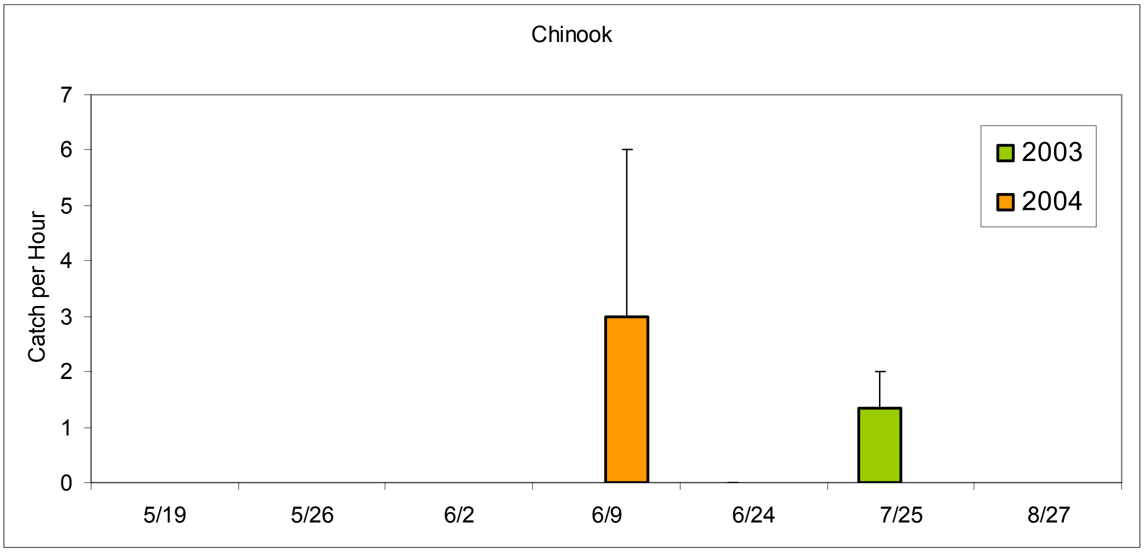
Figures 7.

A.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B.

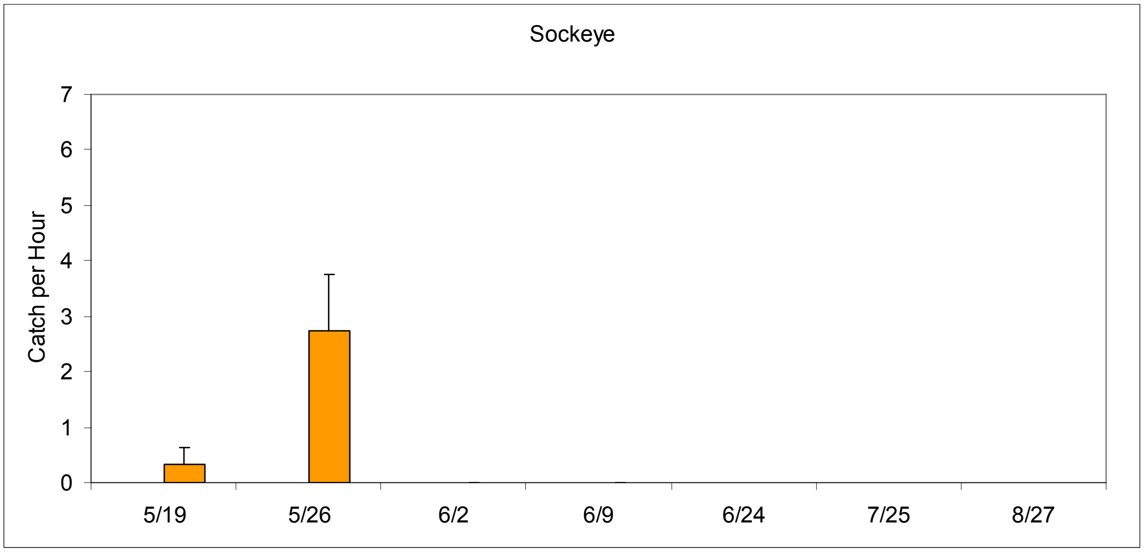
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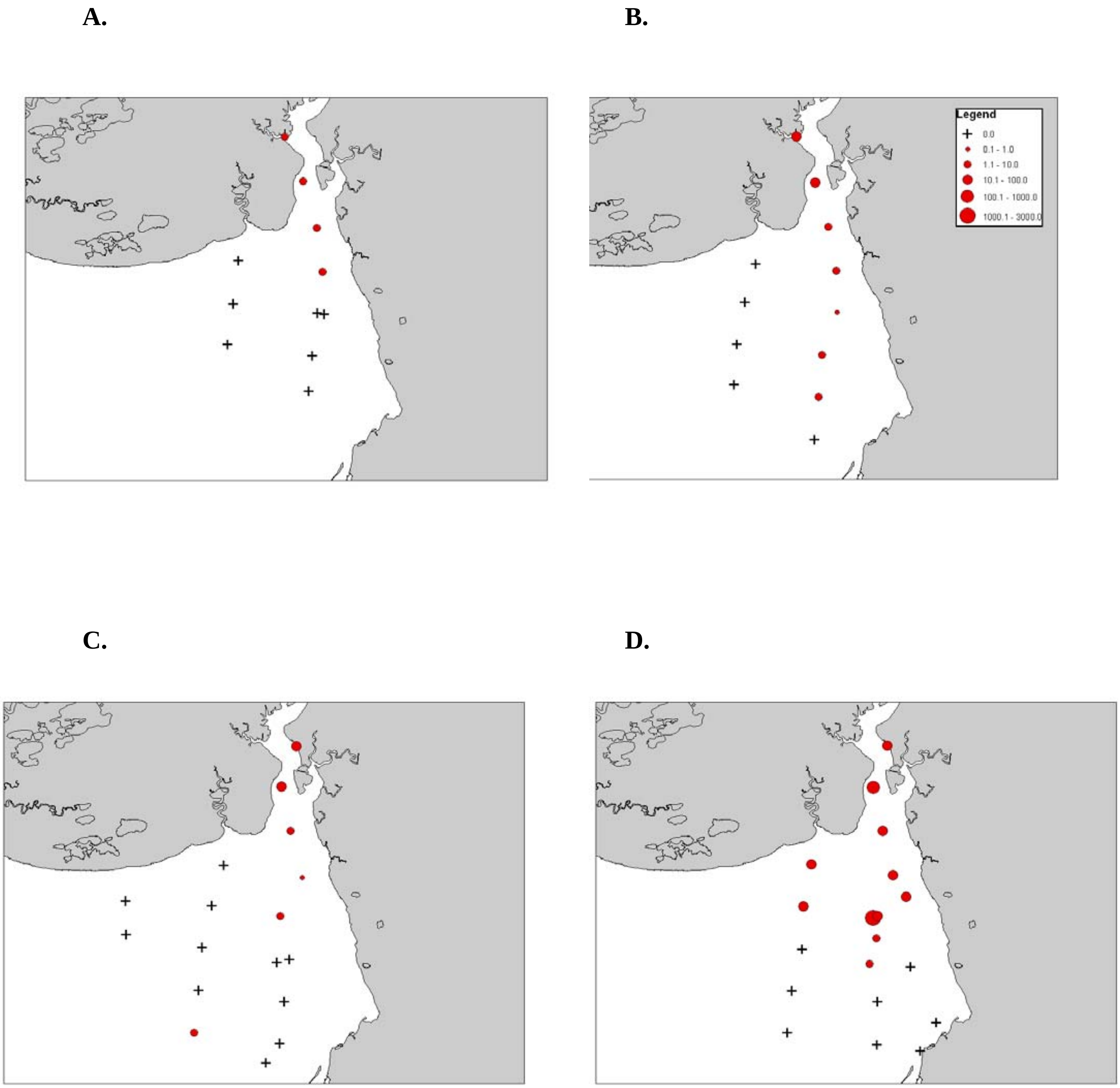
Figure 8.



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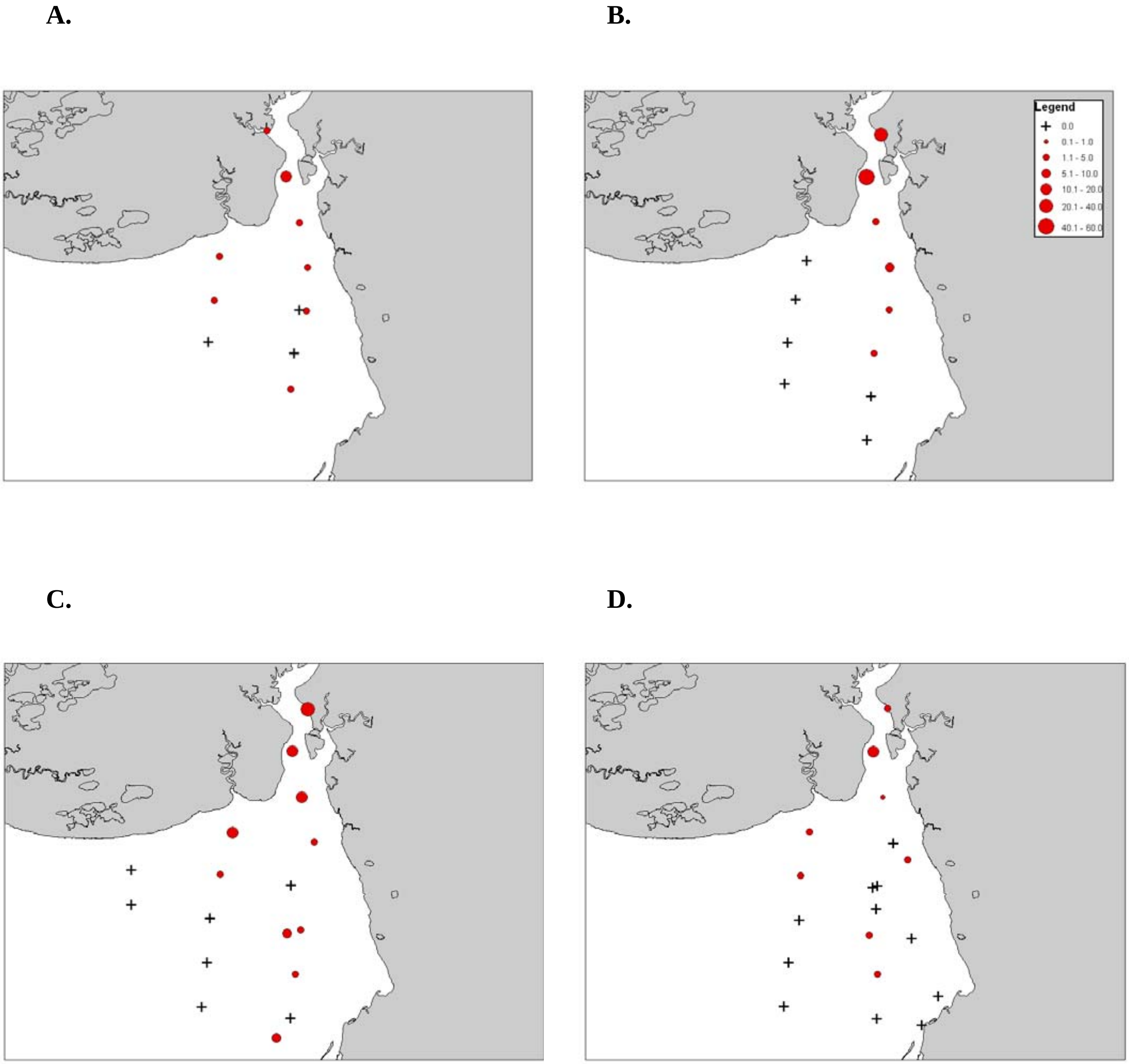

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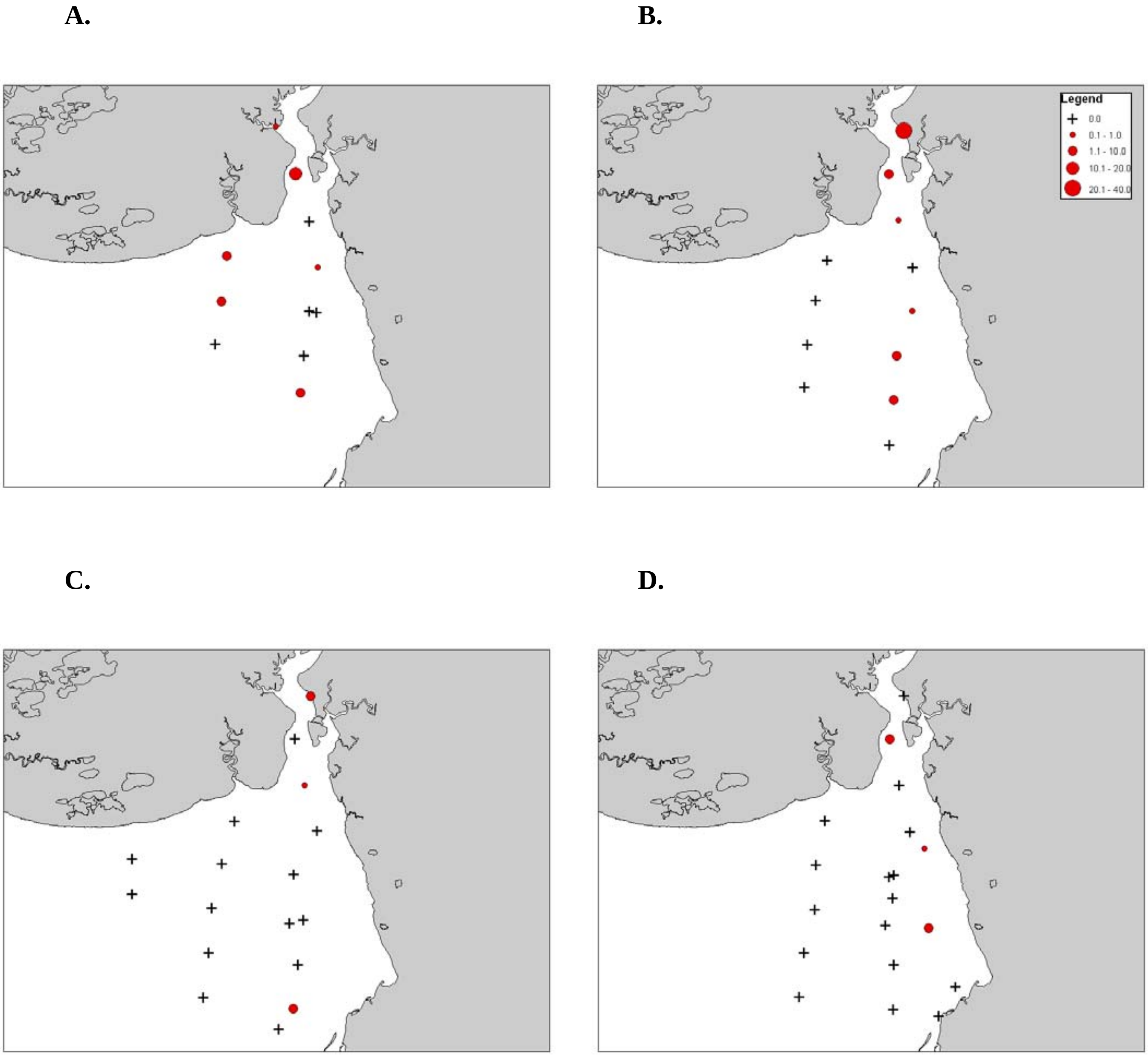

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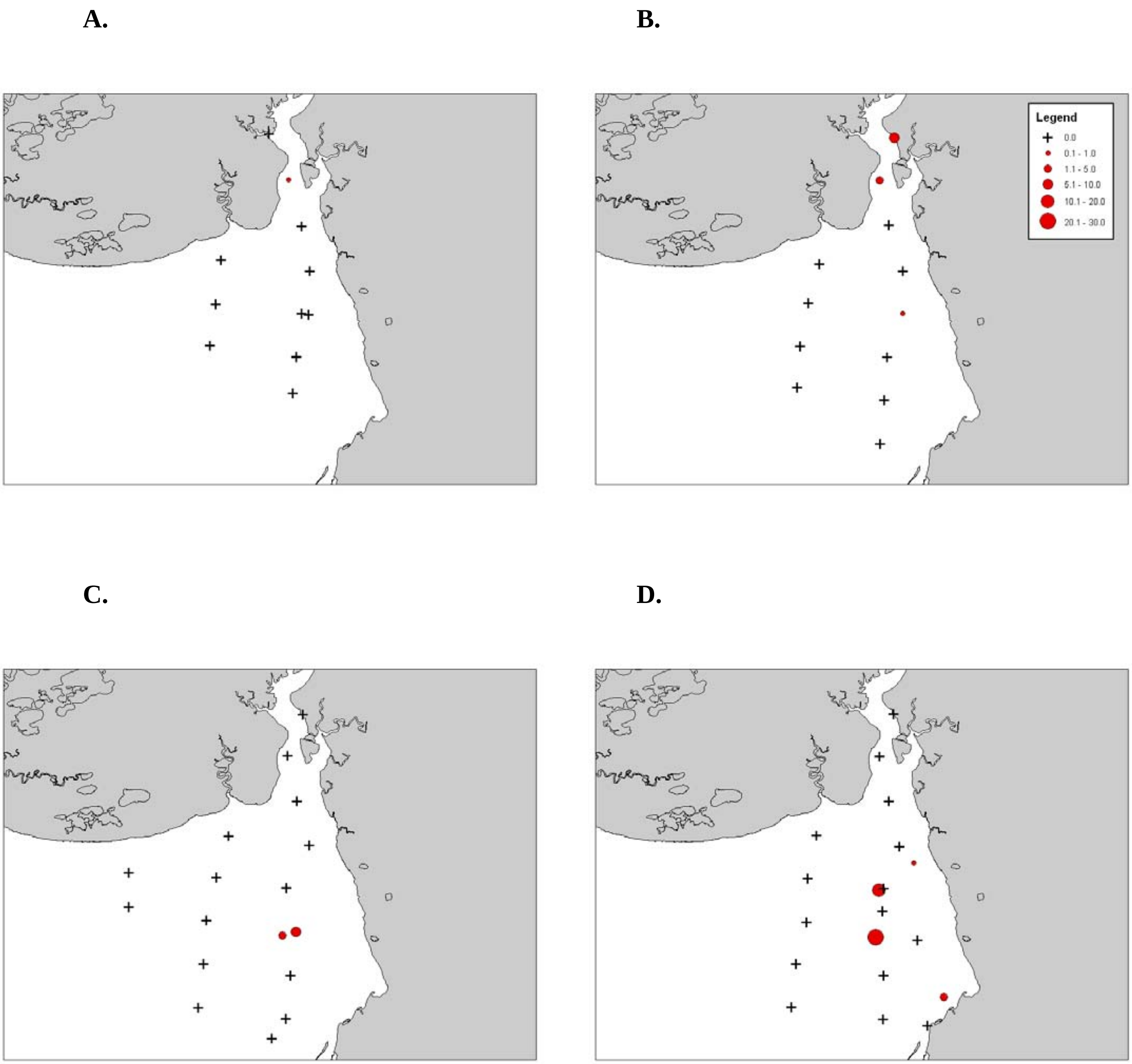

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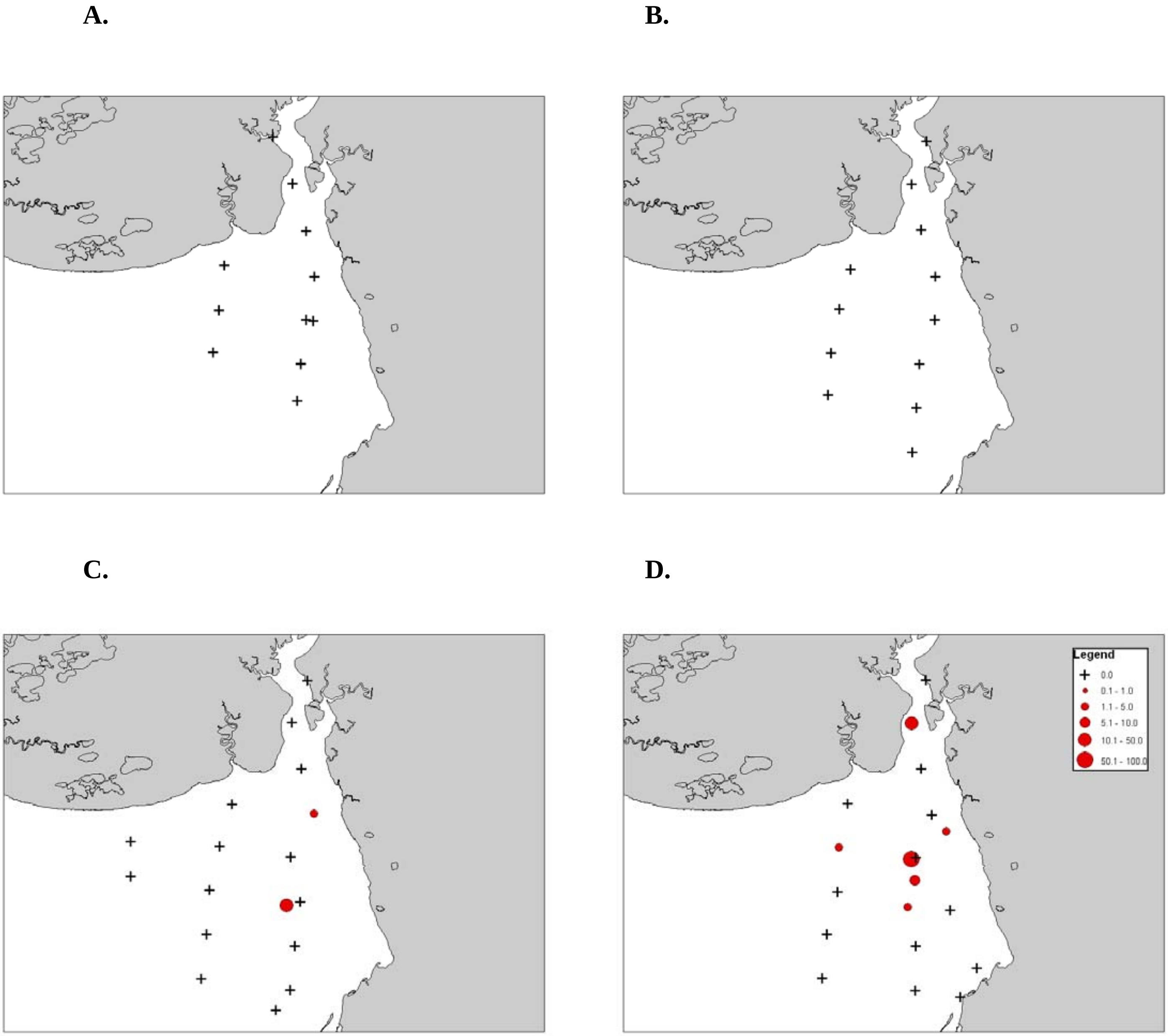

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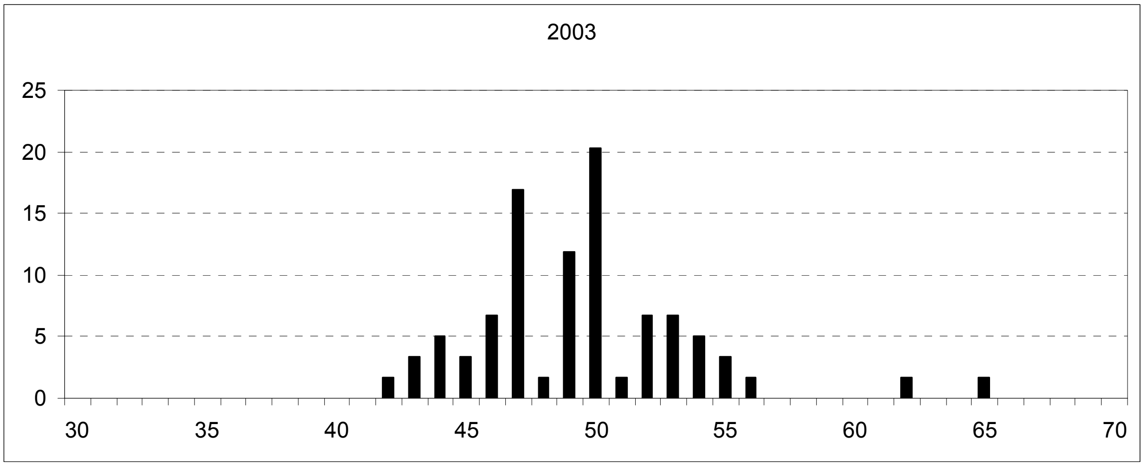

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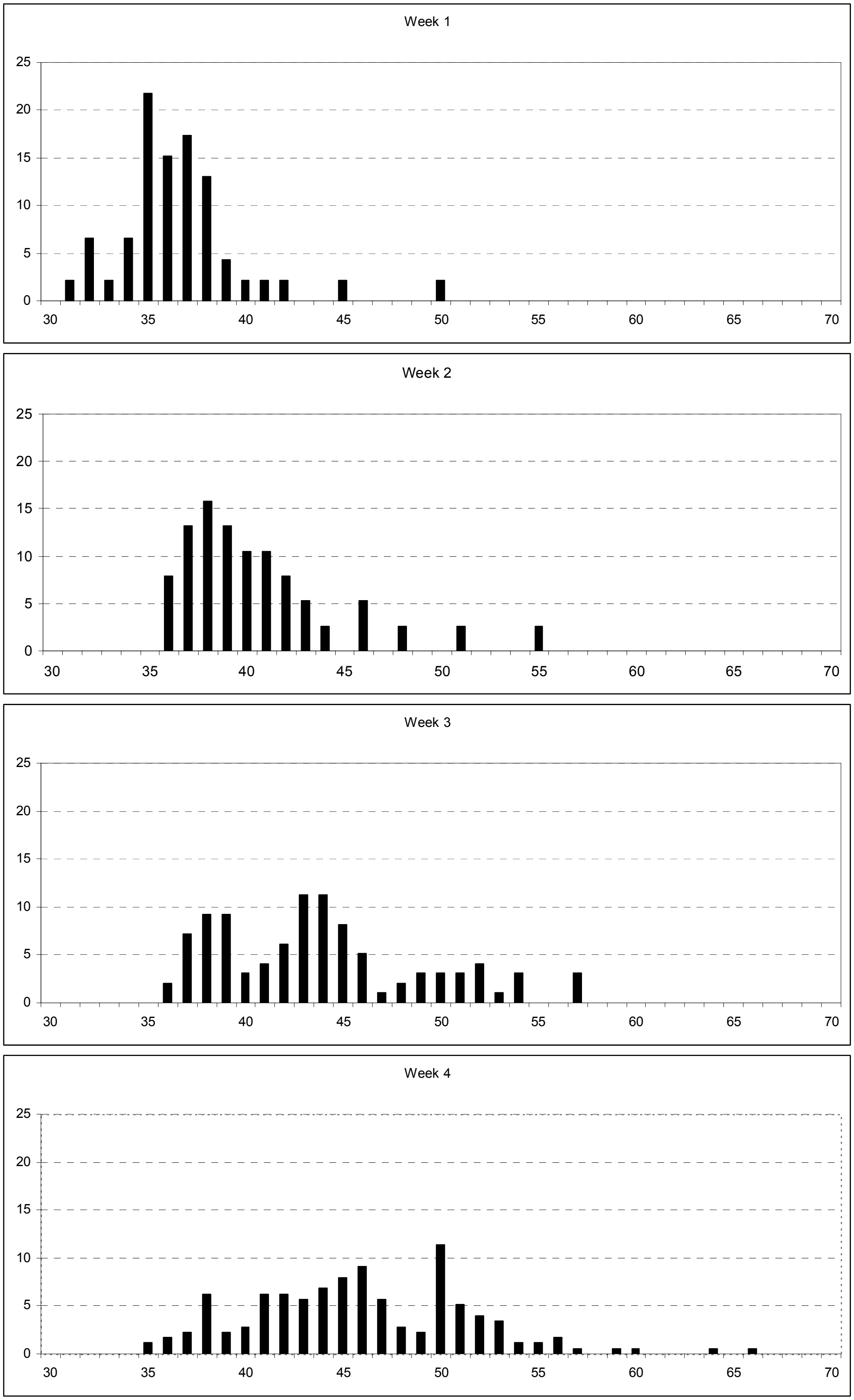
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Figure 15.

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CHAPTER 2 – DIET

Feeding ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Western Alaska

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Abstract

The early estuarine life of juvenile chum salmon (*Oncorhynchus keta*) is a period of high and variable mortality rates. In spite of the potential importance of this period for recruitment success, little is known about the estuarine ecology of chum salmon, particularly of those populations at the northern edge of their distributional range. In this study, juvenile chum salmon from Kuskokwim Bay in western Alaska were sampled in two years, namely in 2003 (N = 59) and in 2004 (N = 311), to examine juvenile feeding success and patterns of prey composition and selection. Feeding success was variable and differed with size, season, salinity, and year. Feeding incidence increased significantly with size and season. Numerical and weight-based feeding intensity increased with size class and week, and was highest in waters with moderate salinity ranging from 5 to 19. Feeding incidence and intensity were lowest for those juvenile chum salmon of the smallest size class that were collected early in the season and in water of 0-4 salinity. Prey composition was similar between years; however, size classes, salinity ranges, and sampling weeks had an effect on prey composition. Drift insects and small calanoid (<2.5mm) and harpacticoid copepods were the primary prey items for juvenile chum salmon within the bay. Calanoids and insects combined made up > 50% of all prey consumed and > 80% of the overall prey biomass for all size classes, salinity ranges, and weeks. No patterns in diel feeding rhythm were detected. With the exception of a positive selection for small calanoid copepods, feeding by juvenile chum salmon in Kuskokwim Bay appeared to be mainly opportunistic.

Introduction

Early marine mortality is thought to be a major factor impacting the population abundance of salmonids (Bakshtanskiy 1964, Healey 1982b, Whitmus 1985, Willette 2001, Willette et al. 2001, Fukuwaka & Suzuki 2002). Dispersal, feeding success, growth, and predation are all believed to be critical elements in survival during the early marine life (Walters et al. 1978). Growth rates during the period of estuarine residence are thought to be associated with recruitment success. Consequently, the analysis of juvenile feeding habits may provide first information about the survival probability of salmonid populations. It is particularly the smaller members of a cohort of juvenile salmon that suffer the highest mortality rates (Ricker 1962, Parker 1971, Simenstad & Salo 1980, Healy 1982b, Simenstad & Wissmar 1984, Pearcy et al. 1989). In Nanaimo estuary, British Columbia, poor feeding conditions were hypothesized as a possible reason for the early emigration of juvenile chum salmon (Healey 1979). Smaller cohorts of juvenile Chinook (*O. tshawytscha*) (Fisher & Pearcy 1995) and chum salmon (Pearcy et al. 1989) had longer residence time in estuaries. Due to the dependence of smaller juveniles on estuaries, an early emigration time may have a negative impact on survival success (Roughgarden et al. 1988).

Pacific salmon are thought to be mainly opportunistic foragers (Healey 1982a). In spite of this, diets seldom reflect the most abundant prey items in the environment (St. John et al. 1992, Schabetsberger et al. 2003), suggesting a trade-off between selection for the most abundant and the energetically most valuable prey items. Both, the amount (Brett 1995) and caloric value (Cho 1983, Higgs et al. 1995) of consumed prey can have a significant impact on juvenile condition and growth rates. Reduced growth rates will extend the period of highest susceptibility to size selective predation, and may ultimately determine year-class strength (Healey 1982b, Willette 2001).

Upon entering the estuaries, juvenile chum salmon are smaller in size than most other Pacific salmon. Estuarine residence is therefore believed to be more essential for the survival of juvenile chum salmon than other salmon species, with the exception of Chinook salmon (Healey 1982a). Common prey items for juvenile chum salmon in estuarine waters are harpacticoid and calanoid copepods, gammarid amphipods, insects, and cladocerans (Feller & Kaczynski 1975, Sibert 1979, Salo 1991, Higgs et al. 1995, Moulton 1997, Landingham et al. 1998). Epibenthic prey species are common in the diets of smaller chum juveniles, while planktonic prey frequent the diets of larger juveniles (Feller & Kaczynski 1975, Wissmar & Simenstad 1988).

Chum salmon returns to the Kuskokwim River have been experiencing low numbers over the last decade (ADF&G 2000). To date, no data are available on the early marine ecology of juvenile chum salmon in Kuskokwim Bay. Changes in the estuarine feeding ecology may contribute to poor marine survival and may ultimately have resulted in poor year-class strength. However, due to the gap in knowledge about this important period, any hypotheses on population regulation in western Alaska chum salmon are difficult to evaluate.

The objectives for this study were to (1) examine the feeding success of juvenile chum salmon from Kuskokwim Bay by size, season, salinity and year, to (2) describe differences in prey composition and selection between years (2003 and 2004), weeks (2004), size classes (2003 and 2004), and salinity ranges (2004), and to (3) examine diel feeding patterns in juvenile chum salmon during their residence in Kuskokwim Bay.

Material and Methods

Study area

Kuskokwim Bay is a large, shallow estuary bordering the southeastern Bering Sea, between Bristol Bay to the Southeast and Norton Sound to the Northwest (Figure 1). The bottom depth throughout much of the bay is between 2 and 6 m. The estuary receives freshwater from the Kuskokwim River, the second largest drainage in Alaska. Estuarine sea surface temperature and salinity indicate a southerly outflow of the Kuskokwim River into the bay with the river plume extending along the eastern estuary shore. Due to the input of the Kuskokwim River, a glacially fed river with a high silt load, much of the bay is very turbid.

Kuskokwim Bay provides a migratory pathway and possibly nursery environment to all five species of Pacific salmon, namely pink (*O. gorbuscha*), chum, sockeye (*O. nerka*), coho (*O. kisutch*) and Chinook salmon.

Field methods

Samples were collected aboard the S/V 'Eileen O'Farrel' in 2003 and the F/V 'Namorada' in 2004. All samples were collected within Kuskokwim Bay, on a station grid of 22 stations. Stations were regularly spaced every 15 minutes of latitude and every 7.5 minutes of longitude. Fish sampling was conducted with a modified Kvichak surface trawl (3.1m height x 6.1m width x 15.0m length) during daylight hours. The Kvichak trawl, traditionally fished between two boats, was equipped with two doors to provide horizontal spread for the net. Floats at the headrope and weights at the footrope provided vertical spread and assured that the net fished at the surface.

In 2003, sampling was conducted during three research cruises, June 23-25, July 24-26 and August 26-30 (Appendix A). In 2004 sampling began May 17 and continued until June 11. Zooplankton was collected with a 1 m^2 NIO Tucker Trawl equipped with 250 µm mesh (2003) or a 0.75 m diameter ring net equipped with 335 µm mesh (2004) fished for 5 minutes at the surface. Both plankton nets were equipped with a flowmeter to record volume of water filtered. Hydrographic data were collected with a SeaBird Electronics SBE-19 Seacat Conductivity-Salinity-Depth (CTD) profiler equipped with a Wetstar fluorometer and a D&A Instruments transmissometer (2004). In 2003, water column turbidity was estimated using Secchi disk readings at each station. In 2004, one 24-hour study was conducted at a single station with fish tows made every five hours for analysis of diel feeding patterns.

After recovery of the trawl, all fish collected were anesthetized in MS-222 prior to handling. Fish treatment followed a protocol approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC # 03-18). All fish were identified to species and counted if the total catch was less than 500 fish. If the total catch exceeded 500 fish, all salmonids were removed and the remainder of the mixed fish was weighed. A random sub-sample of approximately 100 non-salmonid mixed fish was counted, measured and weighed and the total number and catch composition of mixed fish was estimated. All chum salmon juveniles were measured for both standard (SL) and fork length (FL) to the nearest 1 mm and frozen. Non-chum salmonids were identified to species, measured to the nearest 1 mm FL and frozen.

Upon retrieval of the zooplankton net, the net bag was carefully washed down, the cod-end detached and the zooplankton sample preserved in a 10% buffered formalin seawater solution for later analysis.

Laboratory methods

In the lab, juvenile chum salmon were sorted into four 10-mm size classes, namely 30-39 mm FL, 40-49 mm FL, 50-59 mm FL, and ≥ 60 mm FL. Ten individuals from each size class were randomly selected for diet analysis. Wet weight of each fish was measured to the nearest 0.001 g using a Sartorius 300,000g/30,000g scale. Gill raker counts from the first gill arch were used to confirm species identification. Stomachs were dissected and prey items were removed from the cardiac and pyloric section of the stomach for analysis of juvenile diet. The weight of prey contents (mg wet weight) was recorded as the difference between full and empty stomach weights. Fish were considered to have been feeding if their stomachs contained more than a trace of food. Stomach fullness was recorded as (1) empty stomach, (2) trace contents, and (3-6) 25%, 50%, 75%, or 100% full. All prey items were carefully removed, fixed in 10% formalin tap water solution for a minimum of 6 weeks, and preserved in 70% ethanol until diet analysis was performed.

For the diet analysis, stomach contents were identified to the lowest taxonomic level practicable and counted. A Folsom plankton splitter was used when necessary to reduce diet samples to a manageable size (100-200 individuals). Calanoid copepods were separated into large (≥2.5 mm total length TL) and small (<2.5 mm TL) size classes. Average wet weights for taxonomic groups were determined by taking wet weight averages of ≥100 individuals, retrieved from literature (Boldt & Haldorson 2003), or provided by C. Stark (University of Alaska Fairbanks *pers. comm.*).

All zooplankton samples were strained on a 45 µm screen filter and rinsed several times with tap water to remove any trace of formalin. Plankton samples were split into a manageable volume using a Folsom plankton splitter. Prior to splitting the sample, the whole sample was scanned for large, rare items. Detailed species composition of the sample was determined after splitting the sample. Splitting of the sample continued until a total count of 200-500 organisms was achieved. All zooplankton species of one split sub-sample were identified to the lowest taxonomic level and developmental stage possible and counted. Copepods were sub-divided into two groups, namely <2.5 mm TL and ≥2.5 mm TL. For each new taxonomic group, a number of organisms was collected in vials and stored in 70% ethanol solution as voucher specimens for future reference.

Statistical methods

Diet analyses included measures of the quantity of prey consumed and measures of prey composition. Prey quantity was analyzed using mean total number and mean total weight of prey items from all non-empty stomachs, percent body weight (%BW = wet stomach content weight / fish body weight - minus stomach content weight) from all non-empty stomachs, stomach fullness index (Sturdevant et al. 2000), and feeding incidence (calculated as a ratio of empty stomachs to total stomachs). Prey consumption was described by percent number (%N) and percent weight (%W) and percent frequency of occurrence (%FO) of prey categories, from all non-empty stomachs. Each of these three indices portrays a different aspect of the diet of chum salmon juveniles (Hyslop 1980). Percent number and %W were calculated as total number or weight of a given taxon divided by total number or weight of all taxa combined. Percent frequency of occurrence is a non-additive index that is calculated as the proportion of stomachs containing a given prey item (Cortés 1997). Diel feeding habits were analyzed using %BW to account for prey ration (Brodeur & Pearcy 1987).

Prior to statistical testing, all diet data were examined for departures from the assumptions of analysis of variance (ANOVA). Non-normally distributed data were transformed with log (y + 1) for counts and arc-sin square root for percents and proportions to achieve homoscedasticity. A two-way ANOVA was used to test for differences in prey quantity and prey consumption by year, week, size class, and salinity. Since both salinity and week were covariates with size class, a regression of FL and mean total prey number and mean total prey weight was performed and the residual values were used for analysis of variance. Two-way ANOVA was also used for the diel feeding study to test for differences in %BW with time. If significant differences were found a Scheffe's multiple comparison procedure was used to examine pairwise relationships.

Feeding selectivity was estimated using Chesson's α (Chesson 1978):

$$\hat{\alpha}_i = \frac{\dfrac{r_i}{n_i}}{\displaystyle\sum_{j=1}^{m} \frac{r_i}{n_i}}$$

where r_i is the # of food items of type *i* in the consumers diet, n_i is the total # of food of type *i* in the environment, and *m* is total # of prey taxa. Chesson's α was calculated for each individual chum salmon juvenile and averaged for a given length class (Fortier & Harris 1989). Chesson's α is superior to other selectivity indices like Ivlev's, since it provides results that are independent of prey densities in the environment (Chesson 1978, 1983). Assuming Type 1 feeding selection, the results can be statistically tested for significance (Manly 1974):

$$g = \frac{\left(\hat{\beta}_i - \beta_i\right)^2}{\operatorname{var}\left(\hat{\beta}_i\right)^{1/2}}$$

where $\hat{\beta}_i$ is the average alpha, and β_i equals alpha value at which there is no selection (1/k; where k equals the number of prey categories). Since *g* follows a standard normal distribution, significance can be tested using a z-table.

Results

General feeding patterns

Chum salmon juveniles ranged in size from 42.0 mm to 65.0 mm FL in 2003 and from 31.0 mm to 66.0 mm FL in 2004. There was a significant difference in size with year, with an average size of 49.5 mm FL for chum salmon juveniles in 2003 and 43.5 mm FL in 2004 ($P < 0.05$). Sampling was conducted later in the year in 2003 than in 2004, so the differences in size are possibly the result of seasonal rather than interannual variation. During both years of our study, size of juvenile chum salmon increased with the season. In 2003, juvenile chum salmon from cruise 2 were significantly longer ($P < 0.01$) than cruise 1 juvenile chum salmon (Figure 2). In 2004, average chum salmon FL increased from 36.6 mm to 46.0 mm for week 1 through week 4, with significant differences between all weeks ($P < 0.05$) (Figure 3).

In 2003 and 2004, a total of 412 chum juveniles were examined for their diet. Of these fish, 31 were observed feeding in 2003 (feeding incidence 57%) and 290 in 2004 (81%). During the two years of our study, a total of 25 prey items were identified in the stomachs of chum salmon juveniles (Appendix A). The most important prey categories in terms of abundance and biomass were calanoids, harpacticoids, copepodites, and insects. All other prey taxa, with the exception of cyclopoids, were combined into one category called "other". For the scope of this study, a total of 6 different prey categories were established to describe the diet and 10 categories for description of feeding selectivity (Table 3 & 4). The selectivity index does not accurately represent the major diet items, largely due to the plankton sampling protocol, which did not account for either insects or benthic zooplankton (i.e., harpacticoids).

Interannual diet comparison

Overall, prey quantity was similar between 2003 and 2004. No significant differences were observed in the total average weight and number of prey consumed (Table 1), %BW, and average stomach fullness (Table 2) between 2003 and 2004. However, juvenile chum salmon sampled in 2003 had a higher proportion of empty stomachs (43%) than 2004 juveniles (19%).

Diet composition varied both by number and weight between sampling years (Table 3; Figures 4 & 5). Numerically, diets consisted of small calanoids (60% and 48%), harpacticoids (8% and 16%), cyclopoids (7% and 1%), copepodites (2% and 13%), insects (8% and 16%), and other (12% and 7%) in 2003 and 2004, respectively. Small calanoids and insects made up > 80% of the diet by weight for both years, while other (17% and 5%) and harpacticoids (2% and 6%) made up only a small proportion of the diet by weight in 2003 and 2004, respectively.

Juvenile chum salmon consumed significantly more small calanoid and cyclopoid copepods, but significantly less harpacticoid copepods, copepodites, and insects in 2003 than in 2004 ($P = 0.011$ for insects; $P < 0.01$ for all other prey categories). A significantly greater %W of insects ($P < 0.001$) and copepodites ($P = 0.02$) were consumed in 2004 than in 2003. No significant differences occurred in percentages by weight of small calanoids, harpacticoids, cyclopoids, and other between years.

In 2003, juvenile chum salmon feeding was strictly opportunistic, with no significant selection for any of the prey categories (Table 4). In 2004, positive selection was identified for small calanoids ($P < 0.01$), while all other prey categories had no significant selection results. It should be noted that variance calculations could not be made for many of the prey categories due to absence of a given prey category from either the plankton or the stomach samples.

Weekly diet comparison

In 2004, the average number of prey per stomachs increased from week 1, May 16-22 (109; S.E. = 24.45) to week 4, June 6-12 (226; S.E. = 19.55), with the exception of weeks 2 ($\bar{x}= 28$; S.E. = 6.41) and 3 ($\bar{x} = 108$; S.E. = 13.99) (Table 1). Juveniles consumed significantly more prey during week 4 than in weeks 2 and 3 ($p = 0.001$). Mean total weight of stomach contents also increased from week 1 to week 4, with week 4 fish having significantly higher stomach content weight than weeks 2 and 3 fish ($P < 0.001$). There was an overall increase in average %BW from week 1 (3.3%) to week 4 (4.5%), except for week 2 (2.3%). Average %BW for weeks 1-3 were significantly different from week 4 ($P < 0.05$). Juvenile chum salmon had an average stomach fullness of 50% for all weeks sampled. The proportion of empty stomachs decreased from week 1-4 (Table 2).

In 2004, the diet composition changed with sampling weeks. Generally, small calanoids, harpacticoids, copepodites, and insects were the numerically most important prey categories during each sampling week (Figure 6). However, the composition of small calanoids increased significantly with week, with juveniles in week 4 consuming a significantly higher proportion than juveniles from all other weeks ($P < 0.001$). At the same time, juvenile chum salmon consumed a significantly greater proportion of harpacticoids during week 1 ($P < 0.001$) than weeks 2 and 4, while week 3 juveniles consumed a significantly greater proportion than week 4 juveniles ($P < 0.001$). Insect diet proportions ranged from 27% to 13% for weeks 1 and 4. There were no significant differences with the proportionate abundance of insects between weeks.

The most important prey categories in terms of biomass were small calanoids and insects, although harpacticoids and other made up a small proportion of the diet during week 1 (Figure 7). Small calanoids increased in %W from week 1 (3%) to week 4 (52%), with significant difference between all weeks ($P < 0.05$ for weeks 1 and 2; $P < 0.01$ for all other weeks). Insects made up more than 50% of the overall diet biomass for all weeks, except in the week of June 6-12. Percent weight composition of insects did not differ significantly between weeks.

In 2004, there was variation in prey selectivity between weeks (Table 4). Juvenile chum salmon sampled during weeks 1 and 4, had positive selection values for small copepods ($P < 0.01$ for week 1; $P < 0.05$ for week 4). Gammarid amphipods and isopods had slightly negative selection values for weeks 1 and 4, respectively ($P < 0.01$).

Size class diet comparison

In both years, prey quantity varied with fish size classes. In 2003, the total average number and weight of stomach contents increased with increasing size class (Table 1), although no significant differences were found. Juvenile chum salmon in the 50-59 mm size class fed at a significantly higher %BW than 40-49 mm juveniles ($P < 0.01$; Table 1.2). Juveniles from the 50-59 mm size class had a lower feeding incidence (50%) than the 40-49 mm size class (45%; Table 2).

In 2004, total average number of prey consumed increased from 65 (S.E. = 10.79) to 838 (S.E. = 79.69) for 30-39 mm and ≥60 mm fish (Table 1.1). Juvenile chum salmon of size class 1 consumed significantly less prey than all other size classes ($P < 0.001$).

Average total prey weight also increased significantly with increasing size class ($P < 0.001$; Table 1). The 40-49 mm (4.1%) and ≥60 mm (4.6%) size classes had the highest average %BW's (Table 2), with no significant differences between size classes. Stomachs sampled for 30-39mm thru 50-59 mm juveniles had an average fullness of 50%, but ≥60 mm juveniles averaged 100% stomach fullness. Percent of empty stomachs decreased with increasing size class (Table 2).

In both years of our study, numerical prey composition varied between size classes. In 2003, the most important prey categories numerically were small calanoids, other, harpacticoids, and insects (Figure 8). Significantly more harpacticoids were consumed by 40-49 mm (9%) juvenile chum salmon than 50-59 mm (7%) juveniles ($P<0.01$). Weight-based diet composition also varied with size. In 2003 and 2004, the most important prey categories in terms of biomass were small calanoids and insects (Figures 9 & 11). In 2003, small calanoids and insects combined made up ≥80% of the average diet biomass for 40-49 mm and 50-59 mm juvenile chum salmon (Figure 9). No significant differences were found with the biomass composition of small calanoids or insects ($P = 0.05$) between size classes.

In 2004, consumption of calanoids increased with increasing size class (Figure 10), with 30-39 mm juveniles consuming significantly less small calanoids than all other size classes ($P < 0.001$). Significantly more harpacticoids were consumed by 30-39 mm juveniles than by all other size classes except the ≥60 mm size class ($P < 0.001$; Figure 10). Insects were a numerically important part of the diet composition for 30-39 mm juveniles (19%), and less important for larger juveniles (Figure 10). No significant differences occurred with the numerical composition of insects between size classes.

In 2004, the proportional biomass of small calanoids increased with increasing size class from 21% to 97% (Figure 11). Chum salmon of size class 1 consumed significantly less biomass of small calanoids than juveniles of all other size classes ($P < 0.001$). Percent weight of insects decreased with increasing size class from an average of 55% to 3% (Figure 11). There was no significant difference with %W of insects between size classes.

In 2003 and 2004, selectivity results for size class show small copepods as being the only prey category with a positive selection value (Table 4). All other prey category results indicate opportunistic feeding.

Salinity diet comparison

The quantity of prey consumed by juvenile chum salmon varied with salinity. The highest average total number (420 prey/gut; S.E. = 52.24) and weight of prey (0.045 g/gut; S.E. = 0.005) were consumed in the 15-19 salinity range. Fish in the 0-4 salinity range had the lowest average number and weight of prey per stomach sampled (Table 1) and the highest proportion of empty stomachs (Table 2). Significantly more prey items were consumed in the 5-19 salinity ranges than in freshwater ($P < 0.001$). Juvenile chum salmon in the 0-4 and 10-14 salinity ranges had significantly lower average prey weights than juveniles in the 15-19 salinity range ($P < 0.001$). Juveniles from the 5-9 and 15-19 salinity ranges had the highest average %BW and stomach fullness (Table 2). Significant differences were found in average %BW between the 0-4 and 5-9 salinity ranges and between the 5-9 and 10-14 salinity ranges ($P < 0.001$).

Juvenile chum salmon diet composition also varied with salinity. Small calanoids composed the largest proportion of the diet in stomachs sampled from the 10-14 (90%), and 15-19 (87%) salinity ranges (Figure 12). Fish sampled in the 10-14 salinity range consumed significantly more small calanoids than the 0-9, and 15-19 salinity ranges ($P < 0.01$). Harpacticoids were more numerous in stomachs from the 0-9 salinity ranges (Figure 12), with a significantly higher proportion of harpacticoids being consumed in the 0-4 salinity range than the 5-19 salinity ranges ($P < 0.01$). Copepodites were most numerous in stomachs from the lowest (14%) and highest (20%) salinity ranges (Figure 12). No significant differences were found between salinity range and proportion of copepodites consumed. Insects were more abundant in diets from chum in 0-9 salinity ranges. Chum salmon juveniles in the 0-4 salinity range consumed a significantly higher proportion of insects than juveniles in the 15-19 salinity range ($P < 0.01$), and juveniles in the 5-9 salinity range consumed a significantly higher proportion of insects than juveniles in the 10-19 salinity ranges ($P < 0.01$).

The most important prey categories by biomass were small calanoids and insects, although harpacticoids and other made up a small proportion of the diet by biomass in the 0-4 salinity range (Figure 13). Stomachs sampled from the 15-19 salinity ranges had the highest biomass of small calanoids (Figure 13). Percent weight of small calanoids was significantly higher in stomachs from the 15-19 salinity range than stomachs from the 0-4 and 10-14 salinity ranges ($P < 0.001$). In addition, stomachs from the 10-14 salinity range had significantly higher calanoid weights than those in the 5-9 salinity range ($P < 0.05$). The 0-4 (56%) and 5-9 (74%) salinity ranges had the highest %W of insects. Juvenile chum salmon stomachs from the 0-4 salinity range contained a significantly greater average weight of insects than stomachs from the 15-19 salinity range ($P < 0.001$), and stomachs from the 5-9 salinity range had a significantly greater %W than those from the 10-14 ($P < 0.05$) and 15-19 ($P < 0.001$) salinity ranges.

Juvenile chum salmon exhibited variation in prey selectivity between salinity ranges (Table 4). Small copepods were positively selected for in all salinity ranges except the 0-4 salinity range ($P < 0.01$). Fish eggs had a positive selection value in the 20-29 salinity range ($P < 0.01$). All other prey categories were considered non significant for selection (Table 4).

Diel feeding study

No patterns in diel feeding rhythm were detected. Prey weight appeared to be highest in fish sampled between 1800 and 2300 hours, and lowest during the 0400 hour samples (Figure 14) but no significant differences were found between stomach content weights at different sampling times ($P = 0.067$).

Discussion

Juvenile chum salmon diet in Kuskokwim Bay varied by size, season, salinity, and year, supporting the conclusion that chum salmon during their estuarine early life stage are primarily opportunistic feeders (Healey 1982a). The main dietary items for juvenile chum salmon in Kuskokwim Bay were small calanoid and harpacticoid copepods, and insects. These prey items have also been described as dietary components for juvenile chum salmon in other studies (Mason 1974, Feller & Kaczynski 1975, Sibert 1979, Healey 1991, Moulton 1997, Auburn & Ignell 2000).

While small calanoid copepods were commonly found in the diet of juvenile chum salmon captured in the 0-4 salinity range, these were predominately absent from concurrent plankton samples (unpublished data), possibly indicating that juvenile chum salmon were moving horizontally into waters of higher salinity and prey density to feed. Alternatively, juvenile chum salmon residing in low salinity/high turbidity water of the Kuskokwim River plume may be relying on the effect of the tidal flow to provide them with a supply of small calanoid copepods. Similar dietary differences in juvenile chum salmon due to tidal transport have been reported from Lymm Creek, British Columbia (Mason 1974).

During the earlier sampling weeks juvenile chum salmon were just arriving in the bay. As juvenile chum salmon first entered estuaries, they tended to remain in areas of low salinity for several days, likely slowing the transition from freshwater to water of increasing salinity (Iwata & Komatsu 1984). Early chum salmon juveniles might benefit from residing in the freshwater plume of Kuskokwim Bay. For one, the high turbidity of the river plume could shield early juveniles from predation. Similar mechanisms have been suggested for rainbow smelt (*Osmerus mordax*) in the St. Lawrence River estuary (Dauvin & Dodson 1990). In addition, residing in the lower salinity waters for extended periods may reduce metabolic costs associated with osmoregulatory changes. Alternatively, there may be disadvantages associated with residing in the high turbidity waters. For one, highly turbid waters receive less light penetration which may result in lower plankton abundances and fewer feeding opportunities. Secondly, chum salmon are visual feeders so prey location distances decrease in turbid waters possibly resulting in fewer prey encounters and likely affecting the number of successful feeding attempts (Utne 1997).

Insects appeared to be more important to juvenile chum salmon in Kuskokwim Bay than has been reported for juvenile chum salmon in other studies (Mason 1974, Feller & Kaczynski 1975, Healey 1979, Sibert 1979, Salo 1991), particularly in 2003. The highly turbid waters of upper Kuskokwim Bay may cause this high degree of dependence on drift insects. Highly turbid water has low light penetration, which stunts marine productivity (Kelble et al. 2005) and limits prey location distance (Utne 1997) often resulting in surface oriented feeding. Juvenile chum salmon from Kotzebue Sound and Upper Cook Inlet, both very turbid systems, were found to feed heavily on drift insects (Salo 1991, Moulton 1997).

Harpacticoid copepods were most abundant in the diet of juvenile chum salmon sampled from the 0-4 and 5-9 salinity range. The main harpacticoid taxon found in the diet of juveniles was thought to be *Enhydrosoma sp.* (unpublished data), which is known to inhabit fresh to low salinity waters (Chris Stark, *pers. comm.*). Harpacticoids seemed to contribute less to the diet of Kuskokwim Bay juvenile chum salmon than to chum salmon diets from other studies (Feller & Kaczynski 1975, Sibert 1979, Higgs et al. 1995). However, since the sampling protocol employed for this study did not include benthic sampling, the distribution and abundance of harpacticoid copepods cannot be assessed and compared with patterns of prey composition in juvenile chum salmon.

Consumption rates (%BW) for chum salmon juveniles were higher in Kuskokwim Bay in both years (3.0%-3.8%) than for fish from the Columbia River (1%-2%) (Morgan et al. 2005), but were within the range found for chum salmon from Hecate Strait, British Columbia (2.9%-4.12%; Healey 1991). The most pronounced difference in diet between 2003 and 2004 was the higher proportion of empty stomachs from fish sampled in 2003, even though average stomach fullness and daily consumption rates were similar between years. These results may be an effect of a smaller sample size obtained in 2003 resulting in data unrepresentative of the overall juvenile population. Alternatively, prey fields may have been more sparsely distributed later in the season resulting in a drastic difference in feeding incidence among juveniles in 2003. It is noteworthy though that no other measure of juvenile feeding success (e.g., feeding intensity) differed significantly with sampling year. This might indicate that in 2003 prey was more patchily distributed, with fewer patches allowing a smaller proportion of juvenile chum salmon to feed successfully.

In both years of our study, juvenile chum salmon from Kuskokwim Bay had a drastically greater percentage of empty stomachs in (2003: 43%; 2004: 19%) than juveniles of a similar size from Northern Cook Inlet (1.8%) and Hecate Strait, British

Columbia (0%-3.2%; Healey 1991, Moulton 1997). Average feeding intensity was also lower (2003:116.8 prey/gut; 2004: 154.7 prey/gut) for Kuskokwim Bay juveniles than for juvenile chum salmon of a similar size from Puget Sound (265.8 prey/gut) (Feller & Kaczynski 1975), but higher than for juveniles from Northern Cook Inlet (22.3 prey/gut) (Moulton 1997). However, numerical feeding intensity by itself does not adequately reflect the energetic gain obtained, e.g., juvenile chum salmon from Northern Cook Inlet were feeding predominantly on drift insects and small copepods, similar in size to prey items ingested by chum salmon from Kuskokwim Bay.

In 2004, feeding intensity more than doubled from week 1 to week 4. This increase in the average number of prey per gut could be attributed to the higher water temperatures later in the season (Appendix B). As water temperature increases within the range of tolerable temperatures for fish, their metabolic rates and, thus, energetic costs also increase (Brett 1995). These increased energetic costs can only be met with increases in food supply.

Energy density was lower for juveniles entering the estuary later in the season (Chapter 3). A lower overall condition and higher proportion of empty stomachs may be factors contributing to a lower survival probability of juveniles undergoing offshore migration later in the season. The larger juvenile chum salmon were feeding on mostly small copepods, since no large copepods were available in Kuskokwim Bay (unpublished data). Small copepods have a lower caloric value than insects (Griffiths 1977, Kosobokova 1980, Davis et al. 1998) or large calanoid copepods, which might result in a lower growth rate or energetic loss of the piscine predator.

The diel feeding rhythm of Kuskokwim Bay juvenile chum salmon is uncommon compared to results found from other studies. Juvenile salmonid feeding intensity generally increases after sun rise, remains steady during daylight hours, and decreases as the sun sets. Kuskokwim Bay, being located at such high latitudes, experiences long hours of daylight during the summer months, with few hours of darkness. Extended periods of daylight are likely the reason for the steady feeding rhythm exhibited by Kuskokwim Bay chum salmon juveniles.

In conclusion, Kuskokwim Bay juvenile chum salmon fed on a similar prey spectrum as juvenile chum salmon from other systems. Although there was a higher dependence on drift insects than typically seen in juvenile chum salmon diets, this by itself does not indicate poor condition. However, chum salmon also had a lower than average feeding incidence than juvenile chum salmon from other studies, particularly in 2003, which might indicate a high proportion of fish feeding poorly, particularly those fish emigrating later in the season.

In this study, most juvenile chum salmon were caught in low salinity waters near the river mouth, possibly indicating an area of preference for the juvenile fish. However, concomitant plankton tows indicated that very little zooplankton was available in this low salinity water, suggesting that juvenile chum salmon may either have been subject to suboptimal feeding conditions or that while fish were residing in the low salinity/high turbidity water, they were undertaking feeding excursions or relying on tidal transport to acquire prey.

The large percentage of empty stomachs found in Kuskokwim Bay juveniles compared to juveniles from other systems could be a reason for concern. These results seem to indicate that zooplankton distributions vary interannually and might be patchy within the bay, possibly resulting in highly variable feeding success and mortality rates. Of particular concern would be the smaller chum salmon juveniles entering the bay later in the season during times when water temperatures are elevated and metabolic rates consequently increased. Future research is necessary to further investigate the seasonal and annual differences in condition and survival potential for chum salmon during their estuarine residence in and migration through Kuskokwim Bay.

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List of Tables

Table 1. Mean total weight and number of prey items per juvenile chum salmon stomach for year, size class (mm FL), salinity (2004 only), and week (2004 only). Standard errors are shown in parentheses (n = sample size, n/a = no samples available).

T**able 2.** Percent body weight feeding rate (%BW), percent stomach fullness, and percent empty stomachs of juvenile chum salmon for years 2003 and 2004, size class, salinity range, and week. Values in parenthesis represent standard errors of the mean (n = sample size).

Table 3. Average percent number (%N) and percent weight (%W) prey proportions, and percent frequency of occurrence (%FO) of major prey taxa from juvenile chum salmon diets for year, size class, salinity range, and week. Data were collected from Kuskokwim Bay, Western Alaska (n=sample size).

Table 4. Feeding selectivity values for juvenile chum salmon using Chesson's Selectivity Index (α) for year, size class (mm), salinity range, and week. Weeks 1-4 represent the sampling periods from 5/17-5/24, 5/25-5/31, 6/01-6/07, and 6/8-6/11. The index ranges from 1 (prey selection) to -1 (prey avoidance). Samples were collected from Kuskokwim Bay, Western Alaska, 2004. Values in parenthesis represent the standard error (* and ** and bold type represent significance at the 0.05 and 0.01 confidence level, n=sample size).

Year	**n**	**Mean Total Prey Weight (g)**	**Mean Total Prey #**
2003	54	0.029 (0.003)	116.8 (23.71)
2004	311	0.026 (0.001)	154.7 (11.28)
Size Class			
2003			
30-39	n/a		
40-49	29	0.024 (0.003)	85.0 (22.22)
50-59	25	0.033 (0.004)	160.3 (43.68)
60-69	n/a		
2004			
30-39	89	0.011 (0.007)	65.2 (10.79)
40-49	156	0.027 (0.001)	133.5 (14.22)
50-59	63	0.042 (0.003)	215.2 (30.73)
60-69	3	0.085 (0.016)	838.3 (79.69)
Salinity			
0-4	187	0.021 (0.001)	93.1 (8.14)
5-9	41	0.043 (0.003)	210.6 (32.66)
10-14	27	0.033 (0.002)	247.3 (38.29)
15-19	35	0.045 (0.005)	420.2 (52.24)
20-29	4	0.017 (0.004)	71.8 (35.51)
Week			
1	38	0.012 (0.001)	109.0 (24.45)
2	36	0.011 (0.001)	28.1 (6.41)
3	90	0.021 (0.001)	108.0 (13.99)
4	147	0.037 (0.002)	226.4 (19.55)

Table 1.

Year	**n**	**%BW**	**%Fullness**	**%Empty Stomachs**
2003	54	3.0% (0.003)	50%	43%
2004	358	3.8% (0.001)	50%	19%
Size Class (mm)				
2003				
40-49	29	2.1% (0.003)	50%	45%
50-59	25	3.5% (0.005)	50%	40%
2004				
30-39	111	3.4% (0.002)	50%	26%
40-49	173	4.1% (0.002)	50%	18%
50-59	71	3.7% (0.002)	50%	10%
60-69	3	4.6% (0.013)	100%	0%
Salinity				
0-4	231	3.5% (0.002)	50%	26%
5-9	41	5.5% (0.004)	75%	0%
10-14	28	3.5% (0.002)	50%	4%
15-19	35	4.6% (0.004)	75%	0%
20-29	4	3.1% (0.004)	50%	0%
Week				
1	46	3.3% (0.003)	50%	28%
2	38	2.3% (0.002)	50%	26%
3	108	3.4% (0.002)	50%	19%
4	166	4.5% (0.002)	50%	15%

Table 2.

		Calanoids <2.5mm			Harpacticoids			Cyclopoids			Copepodites			Insects			Other		
Year	**n**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**
2003	54	60%	39%	91%	8%	2%	57%	7%	0%	46%	2%	0%	50%	8%	42%	54%	12%	17%	34%
2004	311	48%	36%	83%	16%	6%	62%	1%	0%	20%	13%	3%	63%	16%	50%	60%	7%	5%	31%
Size Class (mm)																			
2003																			
40-49	29	63%	42%	97%	9%	10%	55%	6%	0%	10%	2%	0%	0%	5%	39%	45%	11%	17%	45%
50-59	25	58%	38%	84%	7%	7%	32%	8%	0%	24%	2%	0%	4%	11%	42%	60%	7%	10%	24%
2004																			
30-39	89	24%	21%	65%	25%	12%	66%	1%	1%	15%	19%	4%	56%	23%	55%	61%	**8%**	7%	28%
40-49	156	53%	39%	88%	13%	3%	65%	1%	0%	23%	12%	2%	69%	14%	51%	62%	7%	4%	31%
50-59	63	67%	47%	92%	10%	4%	52%	1%	0%	22%	6%	0%	68%	12%	43%	59%	4%	5%	37%
≥60	3	88%	97%	100%	0%	0%	0%	0%	0%	0%	11%	1%	100%	0%	3%	33%	0%	0%	0%
Salinity Range																			
0-4	187	33%	28%	78%	24%	9%	77%	1%	1%	20%	14%	2%	57%	20%	56%	63%	7%	4%	32%
5-9	41	68%	25%	90%	6%	1%	66%	1%	0%	49%	2%	0%	54%	22%	74%	90%	1%	1%	17%
10-14	27	90%	68%	100%	0%	0%	30%	0%	0%	11%	4%	0%	78%	1%	27%	48%	4%	5%	33%
15-19	35	87%	80%	100%	0%	0%	17%	0%	0%	3%	8%	0%	89%	1%	9%	23%	4%	10%	46%
20-29	4	44%	14%	75%	0%	0%	0%	0%	0%	0%	20%	0%	75%	4%	53%	75%	33%	33%	50%
Week																			
1	38	3%	3%	32%	36%	19%	71%	0%	0%	8%	21%	5%	50%	27%	62%	68%	13%	11%	42%
2	36	20%	17%	61%	15%	8%	47%	0%	0%	0%	34%	13%	78%	18%	50%	56%	13%	12%	42%
3	90	38%	32%	89%	21%	4%	79%	2%	1%	29%	16%	1%	66%	17%	59%	68%	6%	3%	26%
4	147	72%	52%	97%	8%	3%	53%	1%	0%	23%	3%	0%	62%	13%	42%	55%	4%	3%	29%

Table 3.

Year	**n**	**Fish larvae**	**Fish eggs**	**Copepods (<2.5 mm)**	**Amphipods**	**Cadocerans**	**Ostracods**	**Mysids**	**Shrimp**	**Isopods**	**Bivalves**
2003	44	0.00	0.00	**0.74 (0.017)****	0.00	0.05 (0.082)	0.00	0.00	0.00	0.00	0.2 (0.000)
2004	292	0.00	0.06 (0.276)	0.84 (0.016)	0.01 (0.000)	0.00 (3.950)	0.04 (1.340)	0.02 (0.586)	0.00 (0.000)	0.02 (0.398)	0.02 (0.519)
Size Class											
2003											
40-49	26	0.00	0.00	**0.68 (0.000)***	0.00	0.05 (0.002)	0.00	0.00	0.00	0.00	0.27 (0.000)
50-59	17	0.00	0.00	**0.82 (0.000)****	0.00	0.06 (0.000)	0.00	0.00	0.00	0.00	0.12
2004											
30-39	81	0.00	0.01 (0.004)	**0.85 (0.000)****	0.02	0.00 (0.753)	0.05	0.06 (0.000)	0.00	0.00	0.02 (0.186)
40-49	147	0.00	0.05 (0.007)	**0.85 (0.000)****	0.01 (2.175)	0.01 (0.517)	0.05	0.01 (0.055)	0.00 (0.000)	0.03 (0.206)	0.02 (1.483)
50-59	61	0.00	0.16 (0.008)	0.78 (0.001)	0.02	0.00	0.00	0.01 (19.946)	0.00 (0.000)	0.03 (0.163)	0.00
60-69	3	0.00	0.00	**1.00 (0.000)****	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salinity											
0-4	173	0.00	0.00	0.86 (0.014)	0.02 (0.000)	0.01 (2.005)	0.04 (0.872)	0.04 (0.241)	0.00	0.03 (0.213)	0.02 (0.504)
5-9	39	0.00	0.00	**1.00 (0.000)****	0.00	0.00	0.00	0.00	0.00	0.00	0.04 (10.196)
10-14	27	0.00	0.14	**0.86 (0.000)****	0.00	0.00	0.00	0.00	0.00	0.00	0.000 (0.000)
15-19	35	0.00	0.40	**0.60 (0.000)****	0.00	0.00	0.00	0.00	0.00 (0.000)	0.00	0.00
20-29	4	0.00	**0.025 (0.000)****	**0.75 (0.000)****	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Week											
1	33	0.00	0.03	0.76 (0.157)	0.03 (0.000)	0.00	0.06 (5.629)	0.12 (0.000)	0.00	0.00	0.06 (0.292)
2	33	0.00	0.06	**0.82 (0.000)****	0.00	0.00	0.12 (0.000)	0.00	0.00	0.00 (0.000)	0.03 (1.083)
3	83	0.00	0.01 (0.000)	0.84 (0.015)	0.01 (0.000)	0.02 (2.895)	0.07 (0.334)	0.00 (0.000)	0.00	0.06 (0.419)	0.01 (1.752)
4	143	0.00	0.10 (0.000)	0.86 (0.001)	0.01 (0.000)	0.00	0.00	0.02 (1.858)	0.00 (0.000)	0.01 (0.000)	0.01 (5.325)

Table 4.

List of Figures

Figure 8. Average percent number (%N) prey composition by size class for juvenile chum salmon in Kuskokwim Bay, Western Alaska, 2003. n = 26 for 40-49 mm FL and n = 17 for 50-59 mm FL size class.

Figure 9. Average percent weight (%W) prey composition by size class for juvenile chum salmon in Kuskokwim Bay, Western Alaska, 2003. n = 26 for 40-49 mm FL and n = 17 for 50-59 mm FL size class.

Figure 10. Average percent number (%N) prey composition by size class for juvenile chum salmon in Kuskokwim Bay, Western Alaska, 2004. n = 89, 156, 63, and 3 for the size classes 30-39 mm, 40-49 mm, 50-59mm, and ≥60 mm FL.

Figure 11. Average percent weight (%W) prey proportion for juvenile chum salmon from Kuskokwim Bay, Western Alaska, 2004. n = 89, 156, 63, and 3 for the size classes 30-39 mm, 40-49 mm, 50-59mm, and ≥60 mm FL.

Figure 12. Average percent number (%N) by salinity range for juvenile chum salmon in Kuskokwim Bay, western Alaska, 2004. n = 187, 41, 27, 35, and 4 for salinity ranges 0-4, 5-9, 10-14, 15-19, 20-29.

Figure 13. Average percent weight (%W) prey proportions for juvenile chum salmon from Kuskokwim Bay, Western Alaska, 2004. n = 187, 41, 27, 35, and 4 for salinity ranges 0-4, 5-9, 10-14, 15-19, 20-29.

Figure 14. The relationship between time of day and the average amount of food in stomachs expressed as percent of wet body weight (%BW). Error bars represent ± 1 standard error about the mean. Sample sizes are 18, 25, 11, 13, and 21 for hours 1300-0900.

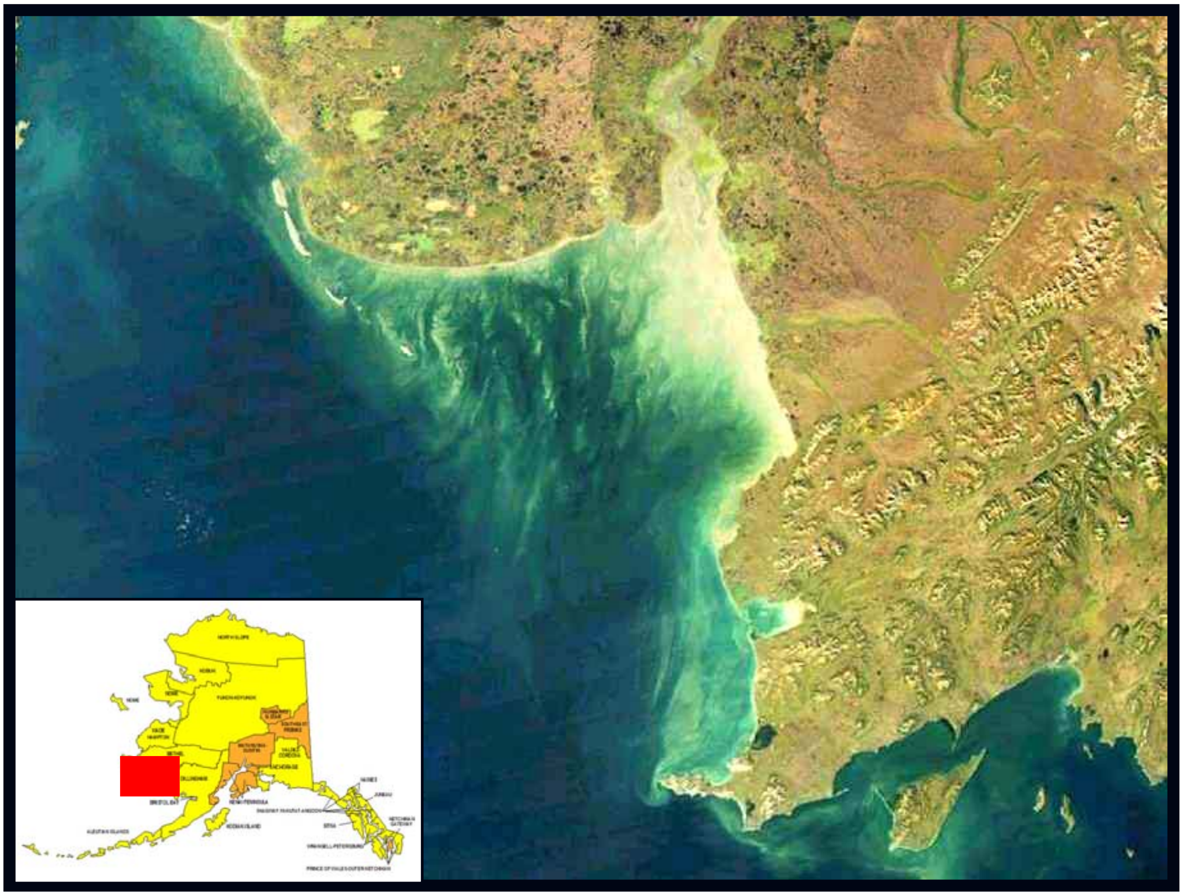
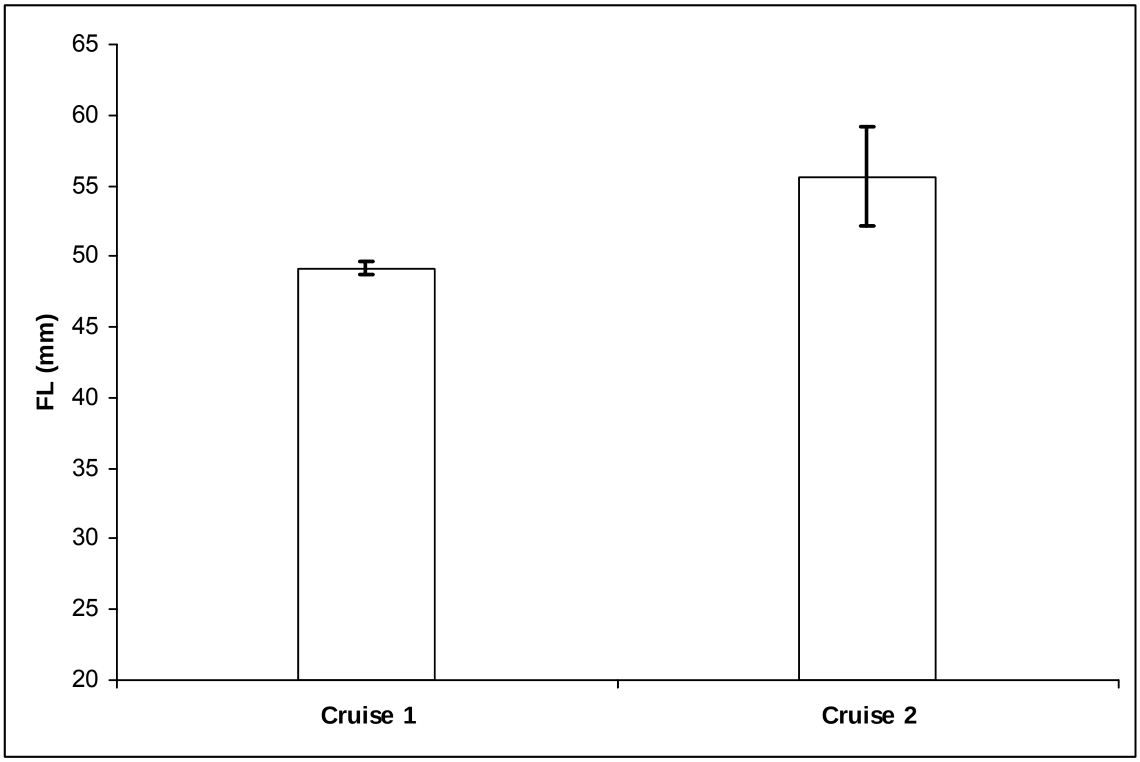

NORTH SLOPE
KOBUK
NOME
NOME
YUKON-KOYUKUK
FAIRBANKS N. STAR
SOUTHEAST FAIRBANKS
WADE HAMPTON
BETHEL
MATANUSKA-SUSITNA
VALDEZ CORDOVA
ANCHORAGE
DILLINGHAM
HAINES
JUNEAU
BRISTOL BAY
KENAI PENINSULA
SKAGWAY-YAKUTAT-ANGOON
KETCHIKAN GATEWAY
ALEUTIAN ISLANDS
KODIAK ISLAND
SITKA
WRANGELL-PETERSBURG
PRINCE OF WALES-OUTER KETCHIKAN

Figure 1.



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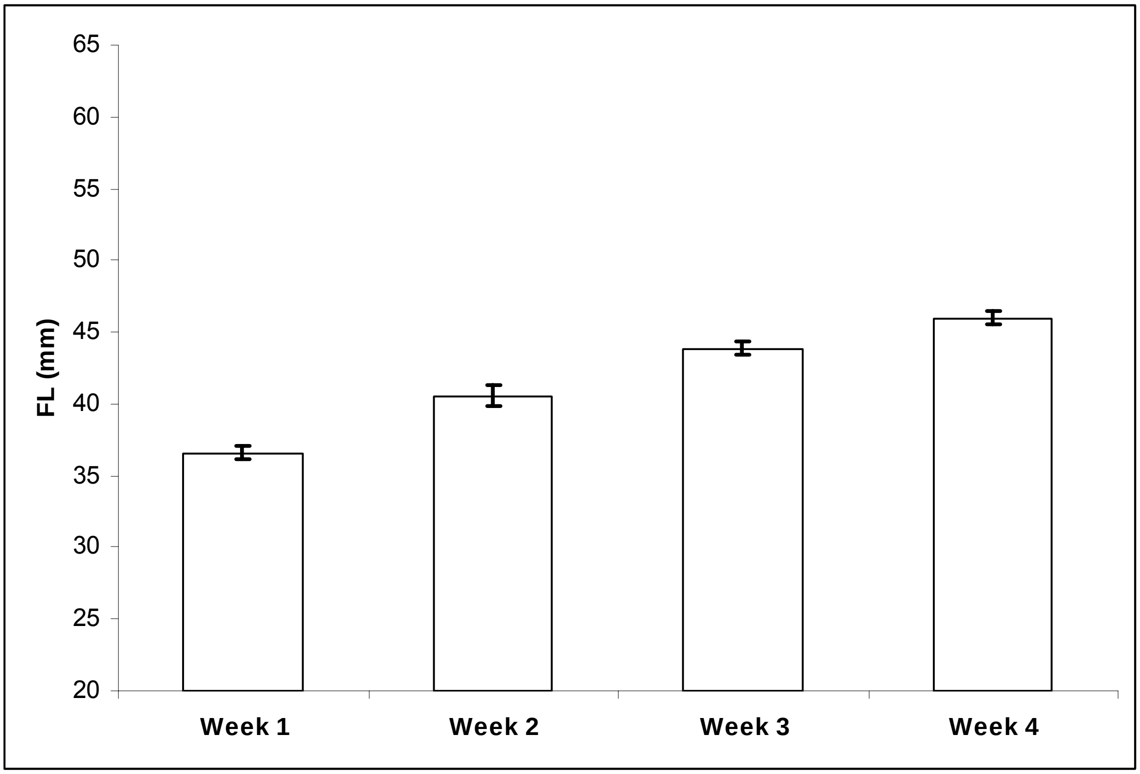

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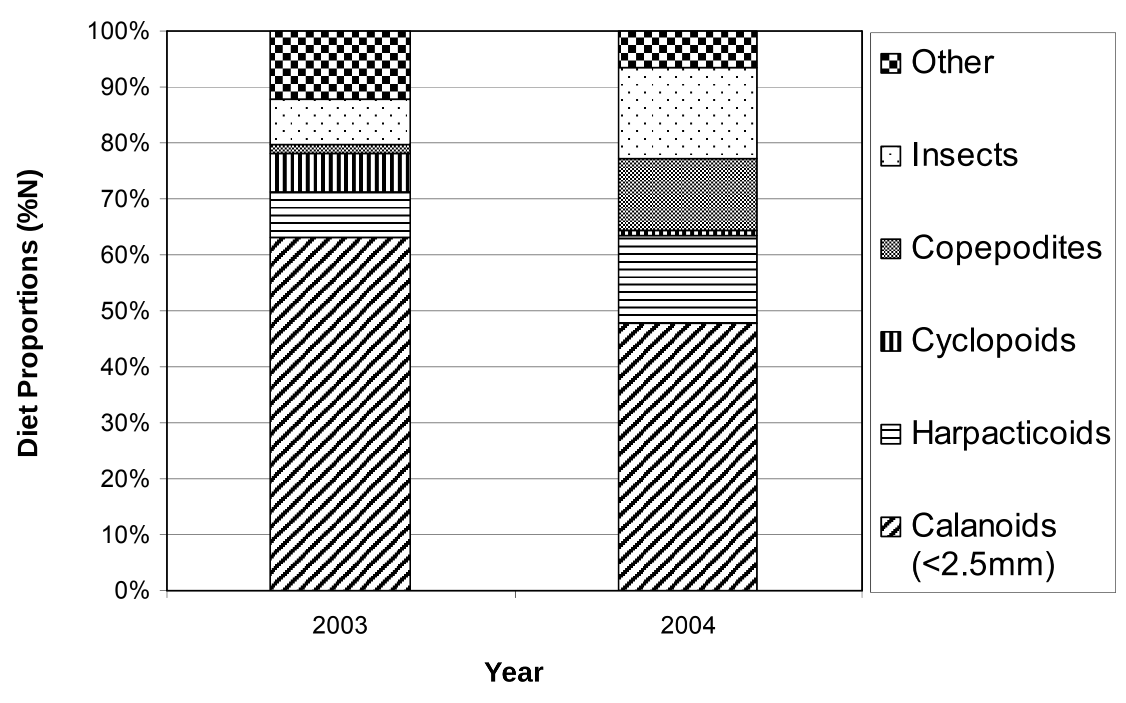
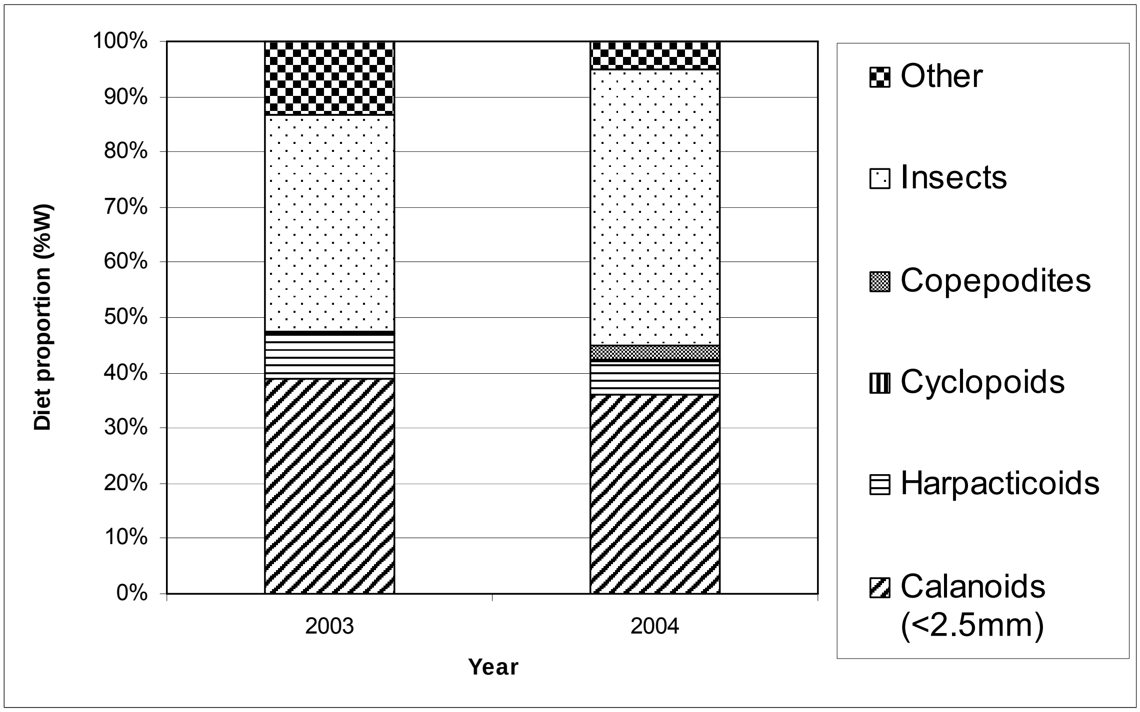

100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Diet Proportions (%N)
2003
2004
Year
Other
Insects
Copepodites
Cyclopoids
Harpacticoids
Calanoids (<2.5mm)

Figure 4.


100%
90%
80%
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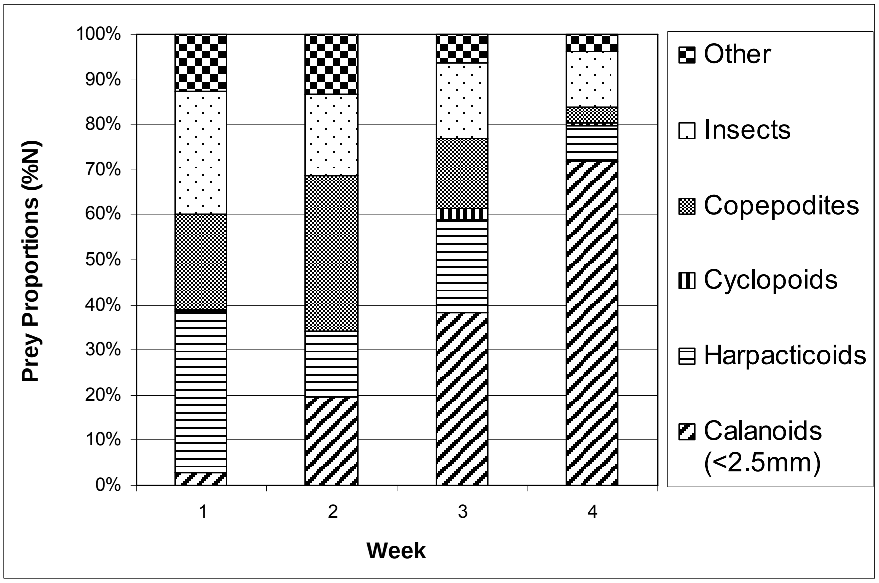
50%
40%
30%
20%
10%
0%
Diet proportion (%W)
2003
2004
Year
Other
Insects
Copepodites
Cyclopoids
Harpacticoids
Calanoids (<2.5mm)

Figure 5.



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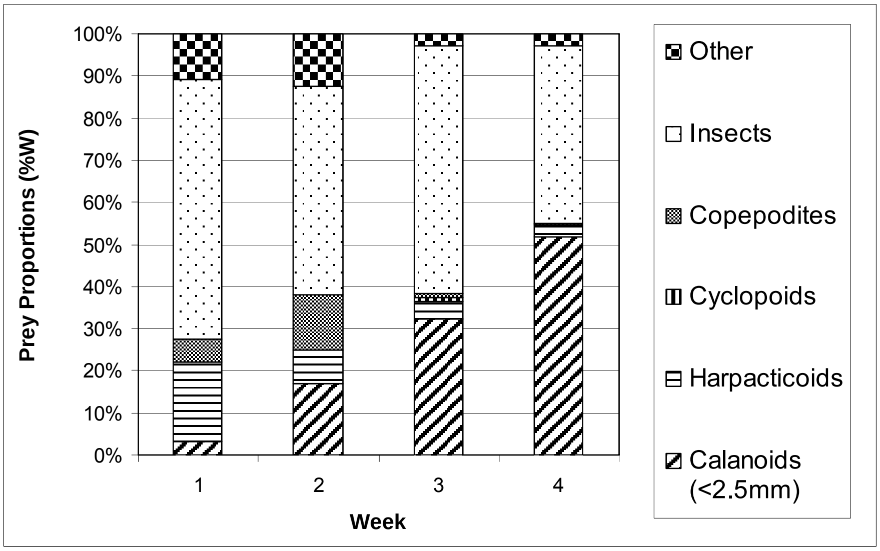

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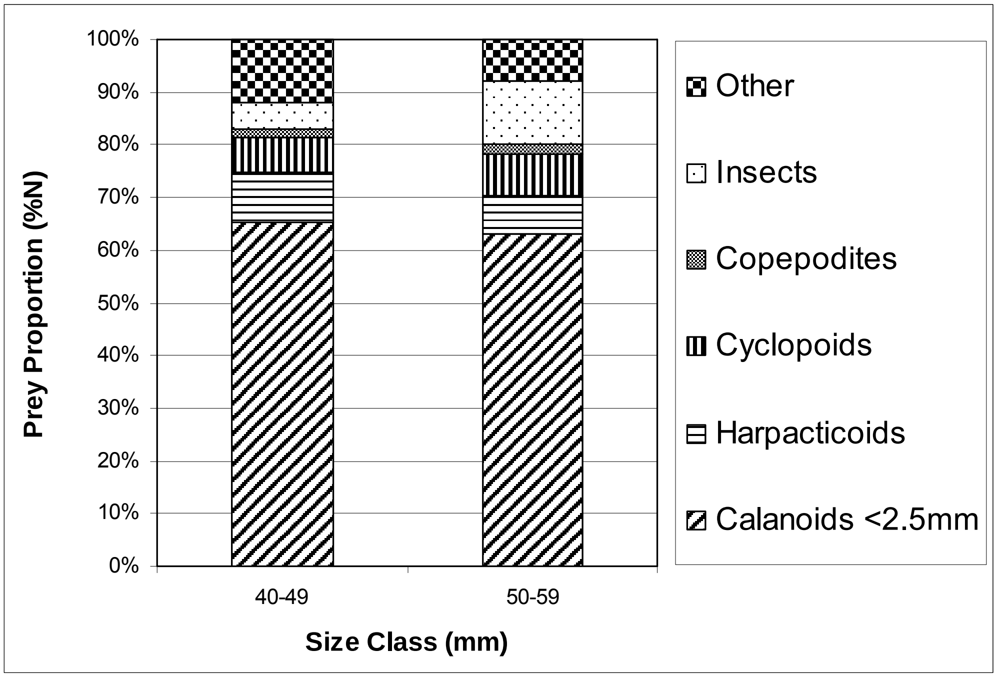

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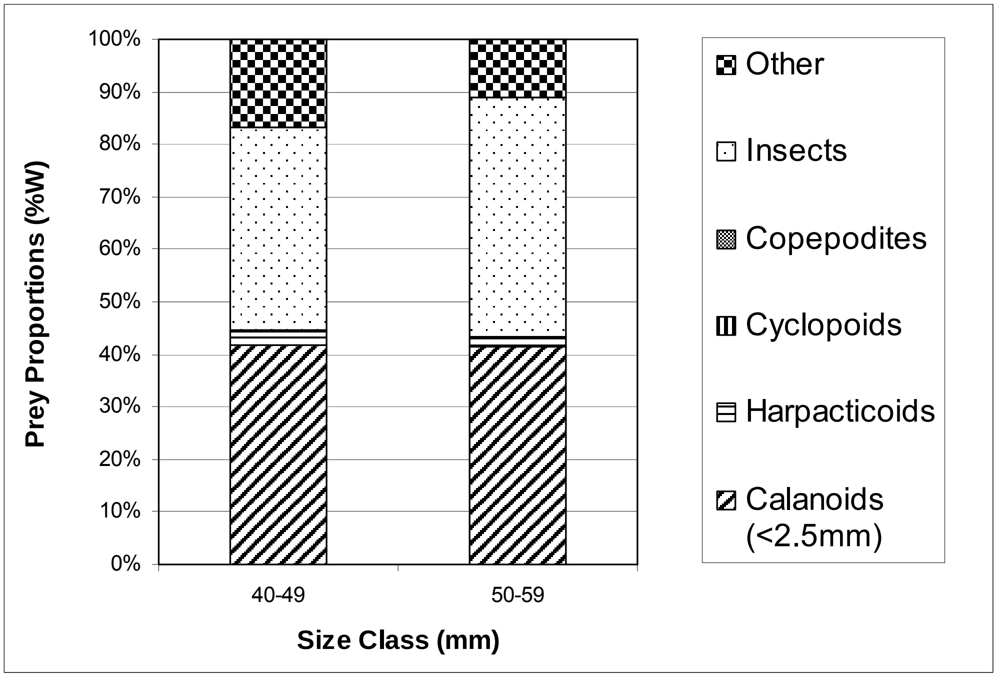

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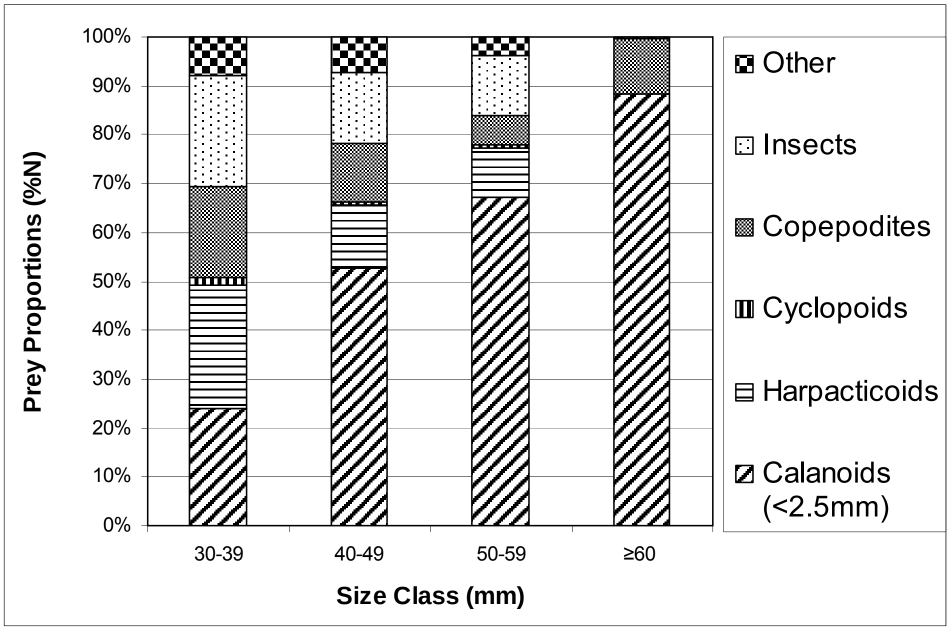
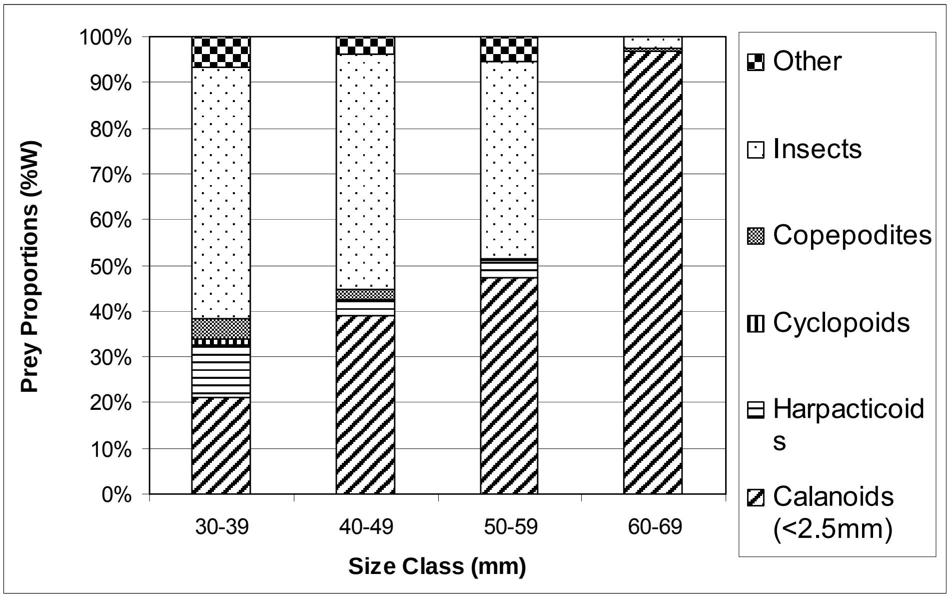


Figure 10.



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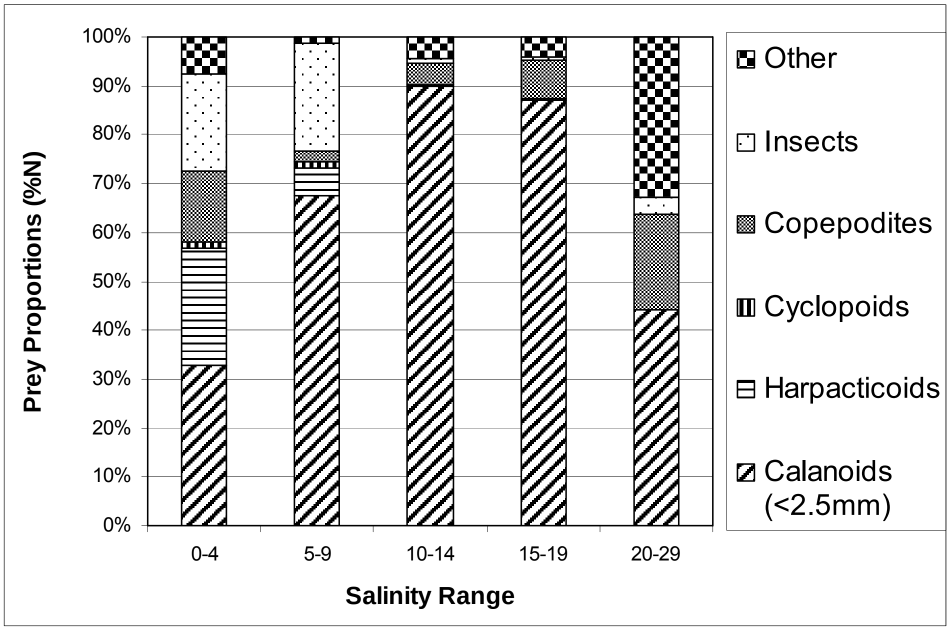

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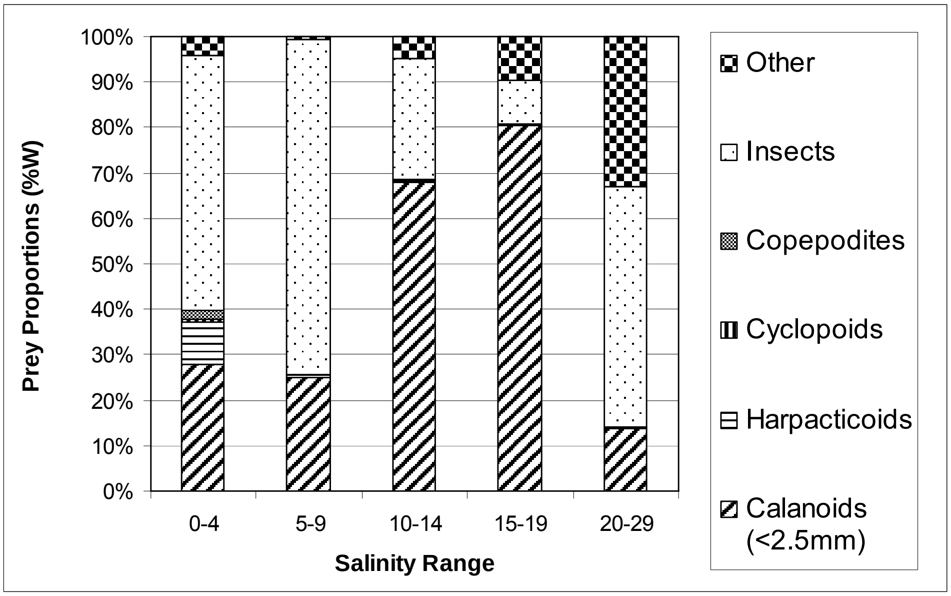

Figure 13.

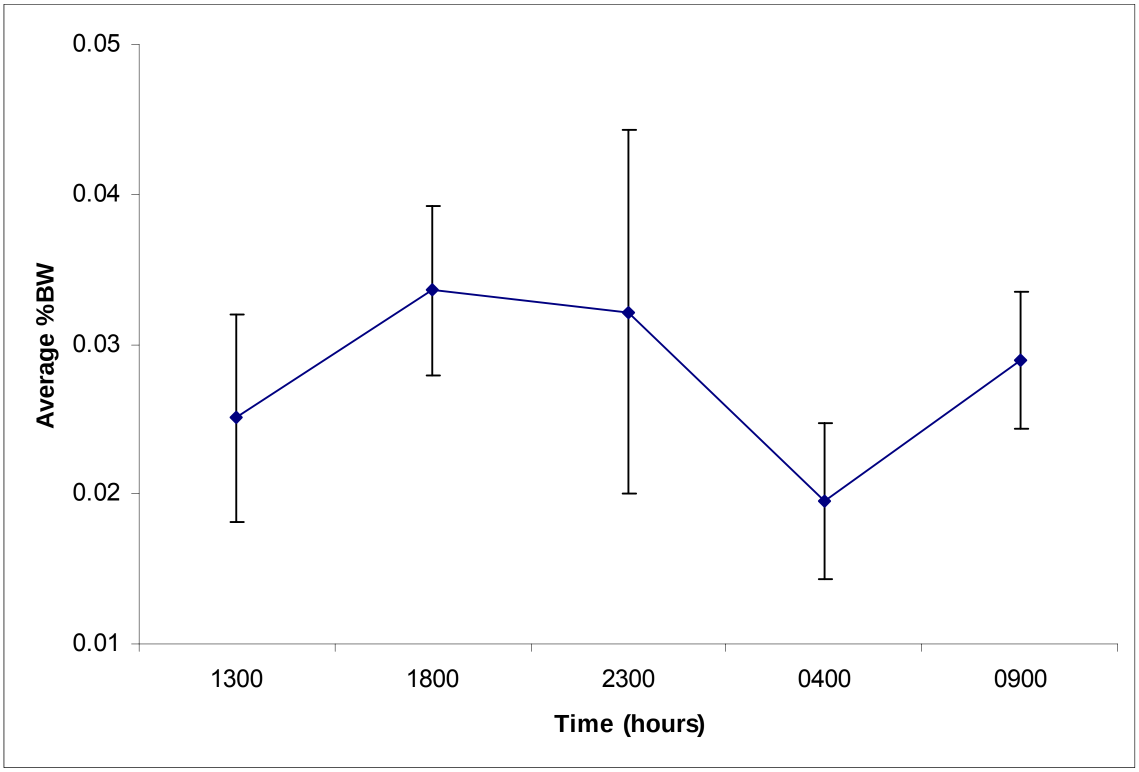
0.05
0.04
0.03
0.02
0.01
Average %BW
1300
1800
2300
0400
0900
Time (hours)

Figure 14.

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Species	**2003**	**2004**
Tortanus	0.52%	0.34%
Psuedocalanus sp.	-	0.63%
Eurytemora	**64.27%**	**44.14%**
Acartia	**13.62%**	**23.39%**
Harpacticoids	**7.43%**	**13.17%**
Cyclopoids	**7.65%**	0.69%
Copepodites	**2.06%**	**11.58%**
Bi-valves	0.38%	0.02%
Fish eggs	0.03%	0.87%
Fish larvae	0.07%	0.00%
UNK. Crust	0.00%	0.49%
Gammarids	0.03%	0.01%
Isopods	0.00%	0.04%
Euphasids	0.03%	-
Cladoceran	0.13%	0.11%
Ostracods	0.00%	0.11%
Shrimp	0.01%	0.05%
Mysids	0.00%	0.04%
Polycheate	0.00%	0.00%
Barnacle Cypris	0.01%	0.00%
Echinoderm	0.00%	0.00%
Nematodes	0.01%	0.09%
Insects	**3.74%**	**4.21%**
Chaetognaths	0.00%	0.00%
Cumacean	-	0.01%

Appendix A.

Year	Cruise	Station	week	Date	Time	Tide	SST	SSS	n
2003	1	1	-	6/23/2003	21:39	ebb	15	1	19
2003	1	2	-	6/24/2003	9:17	ebb	14	4	3
2003	1	X	-	6/24/2003	16:40	flood	-	-	6
2003	1	8	-	6/25/2003	10:45	ebb	14	16	1
2003	1	T1	-	6/25/2003	14:31	ebb	-	-	2
2003	1	T2	-	6/25/2003	16:03	flood	-	-	9
2003	1	T3	-	6/25/2003	17:57	flood	16	1	2
2003	1	T4	-	6/25/2003	19:50	flood	16	0	14
2003	2	1	-	7/24/2003	9:01	ebb	15	1	1
2003	2	12	-	7/26/2003	12:09	ebb	15	0	2
2004	1	1	1	5/17/2004	17:23	low slack	7	0	5
2004	1	2	1	5/18/2004	10:43	flood	6	0	6
2004	2	3	1	5/21/2004	13:48	high slack	8	2	2
2004	2	1	1	5/21/2004	16:30	ebb	9	0	2
2004	2	2	1	5/21/2004	19:30	low slack	9	0	2
2004	2	4	1	5/21/2004	21:58	flood	8	2	2
2004	3	5	1	5/24/2004	13:54	flood	8	14	1
2004	3	4	1	5/24/2004	15:17	high slack	9	6	4
2004	3	3	1	5/24/2004	16:48	ebb	9	3	3
2004	3	2	1	5/24/2004	18:20	ebb	10	0	4
2004	3	1	1	5/24/2004	20:09	ebb	10	0	15
2004	4	1	2	5/28/2004	10:20	ebb	12	0	13
2004	4	2	2	5/28/2004	12:22	ebb	-	-	15
2004	4	3	2	5/28/2004	14:20	flood	11	0	3
2004	4	6	2	5/29/2004	13:16	ebb	8	19	3
2004	4	7	2	5/29/2004	15:01	flood	8	23	2
2004	4	11	2	5/30/2004	12:28	ebb	7	26	2
2004	5	2	3	6/1/2004	11:11	ebb	12	0	15
2004	5	1	3	6/1/2004	12:45	ebb	12	0	25
2004	5	3	3	6/1/2004	13:42	ebb	-	-	4
2004	6	4	3	6/5/2004	12:00	flood	12	5	1
2004	6	20	3	6/5/2004	15:20	ebb	10	17	1
2004	6	3	3	6/6/2004	19:42	ebb	16	1	8
2004	6	1,1	3	6/7/2004	13:23	flood	14	0	18
2004	6	1,2	3	6/7/2004	18:20	ebb	14	0	25
2004	6	1,3	3	6/7/2004	23:21	flood	14	0	11
2004	6	1,4	4	6/8/2004	4:40	high slack	14	0	13
2004	6	1,5	4	6/8/2004	9:36	ebb	14	0	21
2004	6	2	4	6/8/2004	13:14	flood	14	0	21
2004	6	15	4	6/8/2004	17:54	ebb	12	18	19
2004	6	14	4	6/9/2004	7:30	ebb	11	19	12
2004	7	21	4	6/10/2004	14:13	flood	12	15	5
2004	7	20	4	6/10/2004	15:54	flood	12	13	20
2004	7	4	4	6/10/2004	18:06	high slack	13	7	11
2004	7	3	4	6/10/2004	19:23	ebb	14	3	17
2004	7	25	4	6/11/2004	12:26	ebb	13	5	22
2004	7	5	4	6/11/2004	14:23	flood	13	9	3
2004	7	26	4	6/11/2004	15:24	flood	12	12	2

Appendix B.

MANUSCRIPT IS NOT TO BE CITED WITHOUT THE AUTHORS' PERMISSION

Chapter 3 – Energy Density

Patterns in energy density of chum salmon (*Oncorhynchus keta*) during estuarine residence in Kuskokwim Bay, Alaska

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Abstract

The estuarine early life of chum salmon (*Oncorhynchus keta*) is considered to be a period of high and variable mortality rates. In spite of its potential importance, very little is known of this critical period in the life of chum salmon. Chum salmon from Kuskokwim Bay, western Alaska were sampled in two years (2003 and 2004) to evaluate spatial and temporal patterns in their energetic content. For each fish, fork length, wet and dry weights were measured and the mean energy density was determined using bomb calorimetry. Energy density was compared (1) interannually, (2) seasonally, (3) between juvenile size classes, and (4) between salinity ranges.

Mean energy content of chum salmon increased significantly from 2003 to 2004. In 2003, possibly due to low catches of juvenile chum salmon, no significant differences in energy density were found with months, size classes, and salinity ranges. In 2004, energy density decreased significantly from 5,371 cal/g in mid-May to 4,932 cal/g in mid-June. As juvenile chum salmon increased in size, their energy density significantly decreased. The decrease in energy densities from May to June was apparent in all size classes, except for the ≥ 60 mm class. Fish captured in the 0-4 salinity range had significantly higher energy density than those from 15-19 salinity range, but no clear pattern was evident.

The observed decrease in energy content with season and fish size might suggest that juvenile chum salmon were allocating the majority of their energy into growth, rather than the storage of lipids. The significantly lower energy content of chum salmon of similar sizes outmigrating into the bay in June in comparison to May might be the result of higher metabolic costs, possibly due to higher sea surface temperatures. Seasonally increasing energy demands, particularly if not balanced by increasing food supply, could have severe implications for young fish, possibly leading to declines in growth rates and overall survival probability of chum salmon juveniles in Kuskokwim Bay.

Introduction

Fish use a variety of energetic strategies to maximize their condition and their growth potential throughout their lives (Brett 1995). Generally, the energy density of fish increases with increasing fish size (Stewart et al. 1983, Lawson et al. 1998, Trudel et al. 2005, Tirreli et al. 2006). In Pacific salmon, the condition and growth of juveniles during the early estuarine life stages are thought to be important factors in determining overall marine survival success (Holtby et al. 1990).

Environmental factors, such as water temperature can have dramatic impacts on growth rates of juvenile Pacific salmon. Water temperature affects the rate of metabolism in ectothermic animals such as fishes (Brett 1995) and controls the rate of biochemical reactions, potentially causing fluctuation in metabolic rate (Fry 1971). As water temperature increases within the range of tolerable temperatures for fish, their metabolic rates and, thus, energetic costs also increase. These increased energetic costs can only be met with increases in food supply. While maximum growth potential for juvenile sockeye salmon (*Oncorhynchus nerka*) was determined at 15˚C, it was noted that maximum growth rates could only be achieved with adequate food availability (Brett 1995).

Within estuaries zooplankton abundance and distribution is often patchy and dependent on environmental variables such as water temperature and salinity, as well as phytoplankton abundance (Carlotti & Radach 1996). In addition, caloric content of zooplankton can vary greatly with taxonomic group, seasonally or even spatially (Costa et al. 2006). Consequently, the diet composition of juvenile salmon may be an important factor in understanding energetic requirements and their effects on maximizing growth and survival in fish (Cho 1983, Higgs et al. 1995). For example, a study on energetics of juvenile chum salmon (*O. keta*) in Washington estuaries, found prey energy levels to peak in early March and then decline through the remainder of the outmigration of chum salmon (Wissmar & Simenstad 1988); this decline in food supply is likely to have an effect on growth and thus survival probability of juveniles passing through the estuaries later in the season. Maximizing growth is especially important for chum salmon and pink salmon (*O. gorbuscha*), since they enter estuaries at a very small size, which makes them highly susceptible to size-selective mortality (Parker 1971, Simenstad and Salo 1980, Healy 1982b, Simenstad and Wissmar 1984).

Chum salmon from the Kuskokwim River have been experiencing extremely low escapement numbers over the last decade; to date, the reasons for these low returns are unknown (ADF&G 2000). However, since only little information is available on the ecology of chum salmon from Kuskokwim River and even less on the early estuarine ecology of juvenile chum in Kuskokwim Bay, it is difficult to assess the validity of hypotheses regarding population regulation of chum salmon in this watershed. Poor condition and inadequate growth of Kuskokwim Bay chum salmon juveniles may be contributing to poor marine survival and ultimately affecting stock abundance. The energy density of juvenile salmonids can be viewed as a predictor of their overall condition, thus allowing the assessment of the productivity of their estuarine habitat.

The overall goal of this study is to evaluate patterns in energy density of chum salmon juveniles during their estuarine residence in Kuskokwim Bay. Specifically, juvenile chum salmon from Kuskokwim Bay were examined for differences in energy content by (1) year, (2) within and between sampling months, (3) between juvenile size classes, and (4) between salinity ranges. A better knowledge of patterns of condition and energetic trends may increase our understanding of the importance of the estuarine residence for chum salmon juvenile and may allow an evaluation of factors responsible for year-class strength in Kuskokwim River chum salmon stocks.

Materials and Methods

Field Methods

This study was conducted in Kuskokwim Bay, a large, shallow bay in Western Alaska (Figure 1). Large parts of Kuskokwim Bay are extremely shallow, with depths between 2 and 6 m. Kuskokwim Bay provides migration and possibly nursery habitat for five species of Pacific salmon, namely pink, chum, sockeye, coho (*O. kisutch*) and Chinook salmon (*O. tshawytscha*).

Samples were collected in two years, aboard the S/V 'Eileen O'Farrel' in 2003 and the F/V 'Namorada' in 2004. All samples were collected on a station grid of 22 stations. Fish sampling was conducted during daylight hours with a modified Kvichak trawl (3.1 m height x 6.1 m width x 15.0 m length). The Kvichak trawl, traditionally fished between two boats, was equipped with two doors to provide horizontal spread for the net. Floats at the headrope and weights at the footrope provided vertical spread and assured that the net fished at the surface.

In 2003, sampling was conducted during three research cruises, June 23-25, July 24-26 and August 26-30 (Appendix A). In 2004 sampling began May 17 and continued until June 11. At every station, hydrographic data were collected with a SeaBird Electronics SBE-19 Seacat Conductivity-Salinity-Depth (CTD) profiler equipped with a Wetstar fluorometer and a D&A Instruments transmissometer (2004). In 2003, water column turbidity was estimated using Secchi disk readings at each station.

After recovery of the trawl, all fish collected were anesthetized in MS-222 prior to handling. Fish treatment followed a protocol approved by the University of Alaska Fairbanks Animal Care and Use Committee (IACUC # 03-18). All fish were identified to species and counted if the total catch was less than 500 fish. If the total catch exceeded 500 fish, all salmonids were removed and the remainder of the mixed fish was weighed. A sub-sample of approximately 100 non-salmonid mixed fish was counted, measured and weighed, and the total number and catch composition of mixed fish was estimated. All chum salmon juveniles were measured for both standard (SL) and fork length (FL) to the nearest 1 mm and frozen. Non-chum salmonids were identified to species, measured to the nearest 1 mm FL and frozen.

Laboratory Methods

In the lab, juvenile chum salmon were sorted into 10 mm size classes, namely 30-39 mm FL, 40-49 mm FL, 50-59 mm FL, and ≥ 60 mm FL. Ten individuals from each size class were randomly selected for analyses of diet (Chapter 1) and energy density. Wet weight of each fish was measured to the nearest 0.001 g using a Sartorius 300,000g/30,000g scale. Gill raker on the first gill arch were counted to confirm species identification. Both saggital otoliths were removed for later analysis of age and microchemistry. The stomachs were removed and all prey were carefully emptied and fixed in 10% formalin tap water solution. The empty stomach was returned into the body cavity in order to retain all body tissue for the analysis of energetic body content. Whole fish weight minus otoliths and stomach contents was measured to the nearest 0.001 g. Processed fish were placed in whirl-pak bags and stored in a freezer at -27 ºC for later processing. Prior to being placed in a bomb calorimeter, the frozen juveniles were placed in a freeze dryer (VirTis, Freezemobile 12) at -60 °C until weight stabilization occurred, confirming minimal moisture content of the sample. Each individual was homogenized using a mortar and pestle. A sub-sample of each juvenile fish was pressed into a 0.15 g pellet. Pellets were weighed immediately after pressing. For juvenile chum salmon less than 0.15 g, all body tissue was used in the pellet. A semimicro Parr 1425 calorimeter was used to measure caloric content. Methods used for bomb calorimetry followed the Parr manual (Parr Instrument Co. 1994). Sulfuric and nitric acid formation was disregarded in calculations used for energy density because they are considered insignificant (Parr Instrument Co. 1994).

Statistical Methods

A two-factor analysis of variance (ANOVA) was used to compare energy density by sampling month, size class, and salinity range. Normal probability plots and one-sample Kolmogorov Smirnoff tests were used to test for normality of the data. Scheffe's multiple comparison tests were used to examine pairwise relationships if significant differences were detected. Since fish length (size classes) covaries with month and salinity range, fork length was regressed against energy density, and the resulting residuals were used for ANOVA's to test for differences in energy density of size classes by month and salinity. Linear regressions were conducted to assess the relationships between energy content and juvenile chum salmon fork length, energy content and % dry mass, and log-transformed fork lengths and log-transformed dry weights.

Results

General

A total of 350 juvenile chum salmon were analyzed for their energy density, with 59 juveniles from 2003 and 291 fish from 2004. Fish ranged in FL from 42 mm to 65 mm (mean = 49 mm, SD = 3.3) in 2003 and from 31 mm to 66 mm (mean = 44 mm, SD = 6.0) in 2004. Fish weight ranged from 0.55 g to 2.47 g wet weight and 0.04 g to 0.68 g dry weight in 2003 and from 0.17 g to 2.36 g wet weight and 0.03 g to 0.51 g dry weight in 2004.

In 2003 and 2004, dry weight was a function of fish length (Figure 5 A & B). The regressions for both years were:

2003: $\log(DW)\,[g] = 2.2892 * \log(FL) - 12.944 \quad r^2 = 0.7939; n = 59$
2004: $\log(DW)\,[g] = 3.7235 * \log(FL) - 16.167 \quad r^2 = 0.9532; n = 291$

Monthly Comparisons

Energy density of juvenile chum salmon varied with season (Figure 2). In 2003, energy densities appeared to decrease slightly from late-June (4,751 cal/g) to late-July (4,709 cal/g), with no significant differences between sampling months. In comparison, in 2004, energy densities decreased significantly from mid-May (5,371 cal/g) to mid-June (4,932 cal/g). Significant differences were found within and between all months except early and mid-June ($p \leq 0.01$). Average sea surface temperature (SST) within Kuskokwim Bay fluctuated from 7 °C in May to 15°C in July (Figure 2).

Size Class Comparisons

In both years, energy density varied with juvenile chum salmon size class (Figure 3A and B). In 2003, energy density appeared to increase from 4,724 cal/g to 4,862 cal/g for juveniles in the 40-49 mm FL and ≥ 60 mm FL size classes. However, differences in energy density between size classes in 2003 were not significant. In 2004, energy density decreased significantly with increasing size class. Juvenile chum salmon in the 30-39 mm FL range had significantly higher energy density than all other size classes

($p<0.001$), except the ≥ 60 mm FL class ($p=0.055$). In addition, energy density of juvenile chum salmon was lower for each size class between sampling months (Figure 4). Juvenile chum salmon energy densities in May were significantly higher than in June for the 30-39 mm ($p < 0.001$), 40-49 mm ($p < 0.001$), and 50-59 mm ($p < 0.01$) size classes.

No significant relationship was found between energy density and FL for both years (Figures 6A and B). Energy density and percent dry mass had no relationship in 2003 ($r^2 = 0.01$) and 2004 ($r^2 = 0.03$).

Salinity Range Comparisons

In 2003, all chum salmon juveniles were captured within the 0-5 salinity range. Therefore, no patterns of energy density with regard to salinity could be examined for this year. In 2004, energy density significantly varied in fish sampled at different salinities ($P < 0.01$) (Figure 7). Highest energy densities occurred in juvenile chum salmon from the 0-4 salinity range (5060 cal/g). Juveniles sampled in the 0-4 salinity range had significantly higher energy densities than juveniles from the 15-19 salinity range ($P < 0.05$).

Discussion

The observed decreasing energy density with increasing size of juvenile chum salmon and time within Kuskokwim Bay is not consistent with results from other studies. In contrast, many studies demonstrate an increase in energy density with increasing fish size (Stewart et al. 1983, Lawson et al. 1998, Trudel et al. 2005, Tirelli et al. 2006) and season. Further indication that Kuskokwim Bay juvenile chum salmon have different energy expenditures while in estuaries is the poor correlation found between energy density and % dry mass. Percent dry mass was found to be strongly correlated with energy density in juvenile coho and Chinook salmon (Trudel et al. 2005).

Juvenile chum salmon of similar size entering Kuskokwim Bay in May had higher energy density than those entering the Bay in June. A likely explanation for this energetic difference is the increased water temperatures in June compared to May

(Chapter 2). As waters temperatures increases, so do the metabolic rates of ectothermic fish such as salmon, causing energy reserves to be utilized at a higher rate (Brett et al 1969, Brett 1995). Energy density has been found to be closely correlated with % lipid content in juvenile salmonids (Brett 1995, Trudel et al. 2005). Unless enough food is available to satiate the increased metabolic demand, juvenile energy density and growth rate will decline. Kuskokwim Bay juvenile chum salmon fed at a higher percent body weight per day during June than May (Chapter 2), suggesting temperature as the main factor responsible for lower energy densities in June. While energy densities of juvenile chum salmon were similar to those values observed for juvenile chum salmon of a similar size in Icy Straight, southeast Alaska (Orsi et al. 2004), it should be noted that average SST was higher in Kuskokwim Bay than in Icy Straight (Chapter 1).

Prey type, due to varying chemical make-up, can affect the bioenergetics of salmonids (Cho 1983, Higgs et al. 1995). Kuskokwim Bay juveniles fed almost entirely on small copepods and insects in 2003 and 2004 (Chapter 2). In May of 2004, insects made up a greater portion of the diet than in June. Insects have a higher energy density (4,531.8 J/g wet wt) than small calanoids (3810.7 J/g wet wt) (Griffiths 1977, Kosobokova 1980, Davis et al. 1998). Switching from a small copepod and insects diet to a mostly small copepod diet during times when water temperatures were elevated may have led to decreased energy densities in June relative to May.

Juvenile chum salmon, of Kuskokwim Bay origin, caught along the Southern Bering Sea shelf in August-October of 2002 averaged 188 mm FL (Farley et al. 2005), indicating that juveniles more than doubled in size from early July to August-October in 2003. In addition, the same Bering Sea juveniles had energy densities of 4,998 cal/g dry weight. These energy density values compared to those of juvenile chum salmon within Kuskokwim Bay, suggest that shortly after leaving the bay changes in energy expenditures are occurring possibly as a result of changing physiological conditions, resulting in an increase in energy density with size. Alternatively, fish with lower energy density might have been removed from the population, with fish collected on the Bering Sea shelf representing the survivors. It should be noted that juvenile chum salmon collected in Bering Sea surveys are not necessarily the same fish as those observed in Kuskokwim Bay in June and July.

Although very few studies have been conducted regarding the energy density of juvenile chum salmon during their residence in estuaries, energetic strategies are likely to be different for juvenile chum salmon as they enter the marine environment at a smaller size than most other Pacific salmon species with the exception of pink salmon. The need for maximum growth rate to decrease their vulnerability to size selective mortality and the physiological stress of osmoregulatory changes further impact their energetic demand. It is apparent that smaller juveniles have higher energy densities than larger juveniles, which is likely the result of lipid storage from yolk reserves. These lipid reserves appear to be quickly allocated towards somatic growth. Since 1 g of lipid has almost double the caloric value of 1 g of protein, the outcome is a lower energy density with increasing size. The caloric value of prey is lower for larger juveniles as they switch to a strictly small calanoid diet (Chapter 1). As temperature increases, the rate at which lipid reserves are utilized also increases. Therefore, fish entering the estuary later in the season, of a similar size as those entering earlier, have lower energy densities. This could pose concern as metabolic rates are higher and a higher number of empty stomachs were found in late entering juveniles (Chapter 1). Further research is needed on outmigrating Kuskokwim Bay chum salmon that more closely examines their ecology and survival probability of these juvenile as they move into off-shore waters.

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Figure 1. Kuskokwim Bay, Western Alaska. Sample area for the 2003 and 2004 research cruises.

Figure 2. Comparison of juvenile chum salmon energy density by sampling period and sea surface temperature (SST) in Kuskokwim Bay. Error bars represent ± 1 S.E. about the mean. Sample size is 11, 71, 182, 27, 56, and 3 for mid May until late July.

Figure 3A. Comparison of energy content between juvenile chum salmon of different size classes from Kuskokwim Bay, 2003. Error bars represent ± 1 S.E. about the mean. Sample sizes are 30, 27, and 2 for the 40-49 mm thru 60-69 mm size classes.

Figure 3B. Comparison of energy content between juvenile chum salmon of different size classes from Kuskokwim Bay, 2004. Error bars represent ± 1 S.E. about the mean. Sample sizes are 90, 132, 66, and 3 for the 30-39 mm thru 60-69 mm size classes.

Figure 4. Comparison of energy content between juvenile chum salmon of different size classes from Kuskokwim Bay. Error bars represent ± 1 S.E. about the mean. Sample sizes are 58, 21, and 3 for the 30-39 mm thru 50-59 mm size classes in May, and 32, 11, 63, 3 for the 30-39 mm thru 60-69 mm size classes in June.

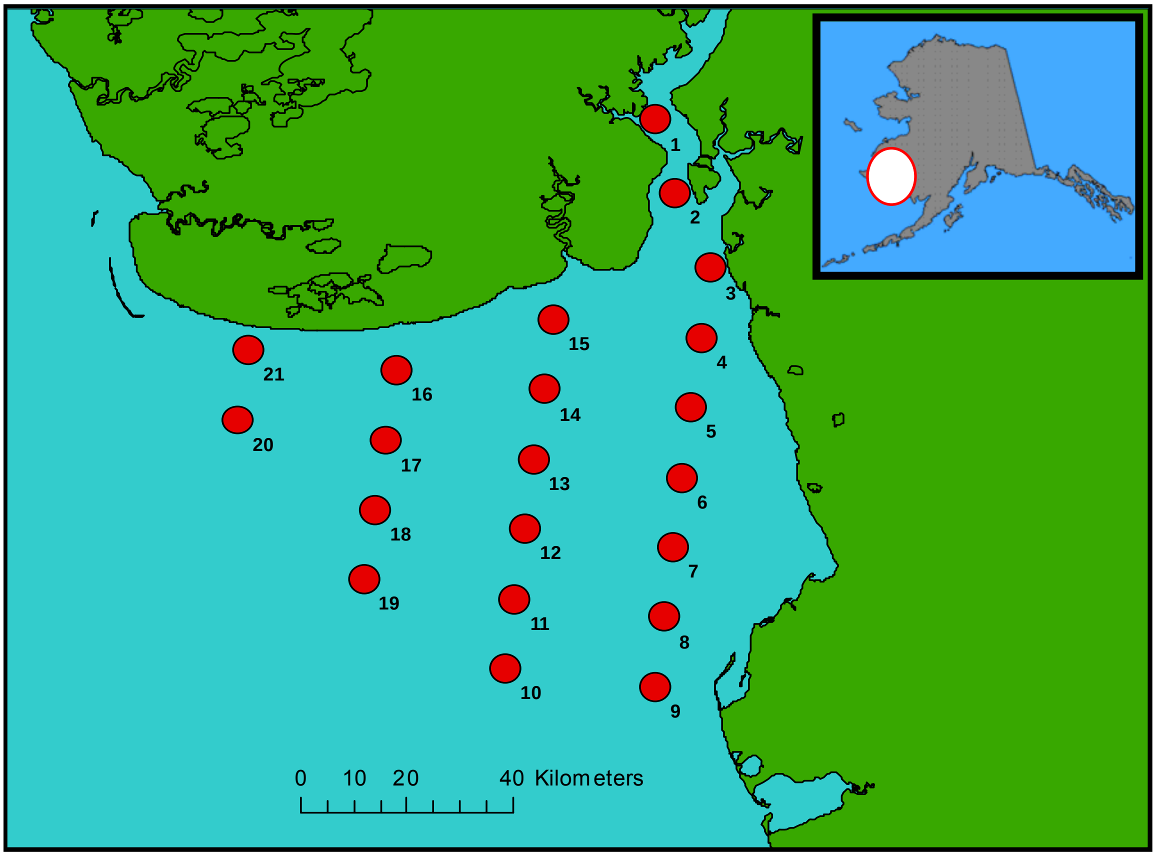
Figure 5A. Linear regression of natural log of dry weight versus natural log of fork length for juvenile chum salmon from Kuskokwim Bay, 2003 (n = 59).

Figure 5B. Linear regression of natural log of dry weight versus natural log of fork length for juvenile chum salmon from Kuskokwim Bay, 2004 (n = 291).

Figure 6A. Linear regression of energy content versus fork length for juvenile chum salmon from Kuskokwim bay, 2003 (n = 59).

Figure 6B. Linear regression of energy content versus fork length for juvenile chum salmon from Kuskokwim bay, 2004 (n = 291).

Figure 7. Comparison of energy content for juvenile chum salmon at different salinity ranges from Kuskokwim bay, 2004. Error bars represent ± 1 S.E. about the mean. Sample sizes are 164, 41, 28, 35, 4 for the 0-4 thru 20-29 salinity ranges.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4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
0 10 20 40 Kilometers

Figure 1.

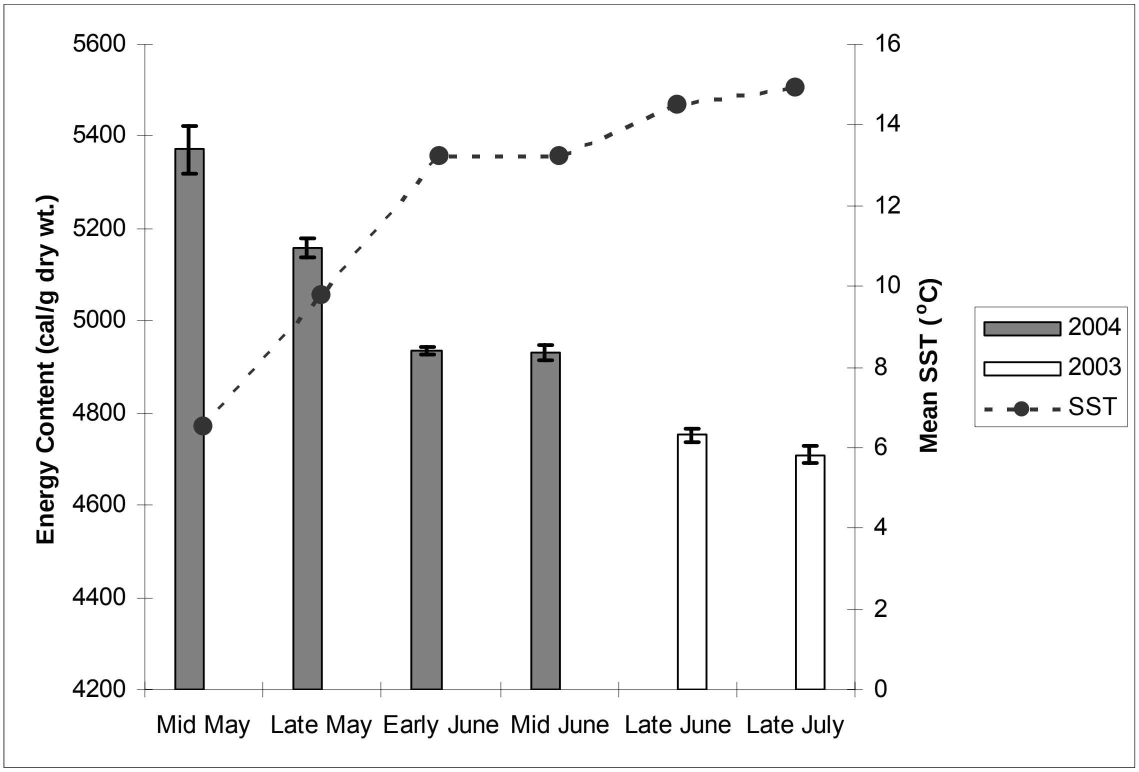
Energy Content (cal/g dry wt.)
5600
5400
5200
5000
4800
4600
4400
4200
Mean SST (°C)
16
14
12
10
8
6
4
2
0
Mid May
Late May
Early June
Mid June
Late June
Late July
2004
2003
SST

Figure 2.

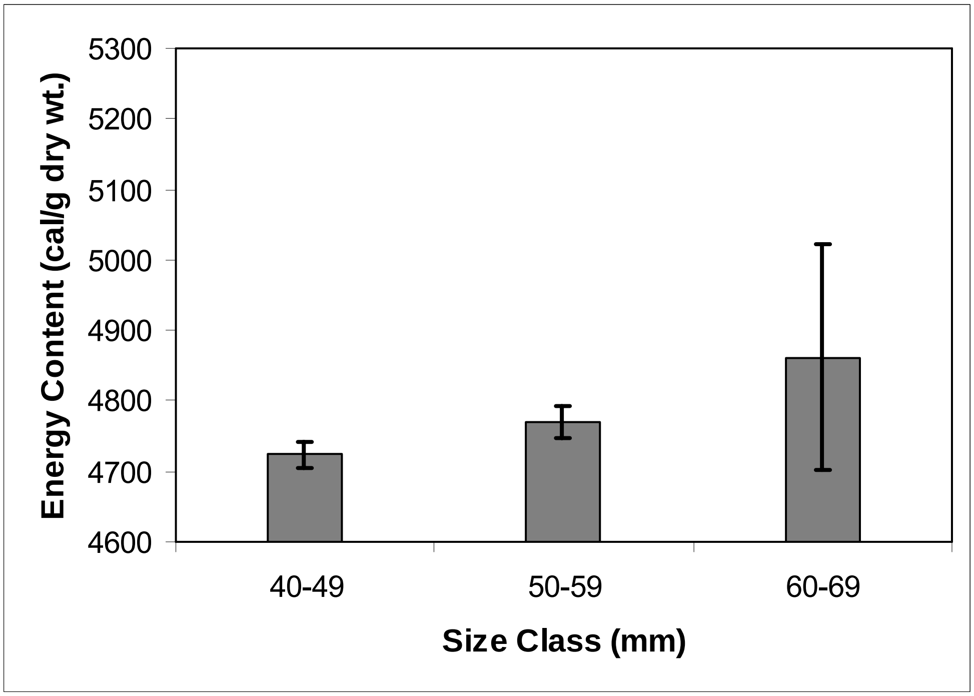

Figure 3A.

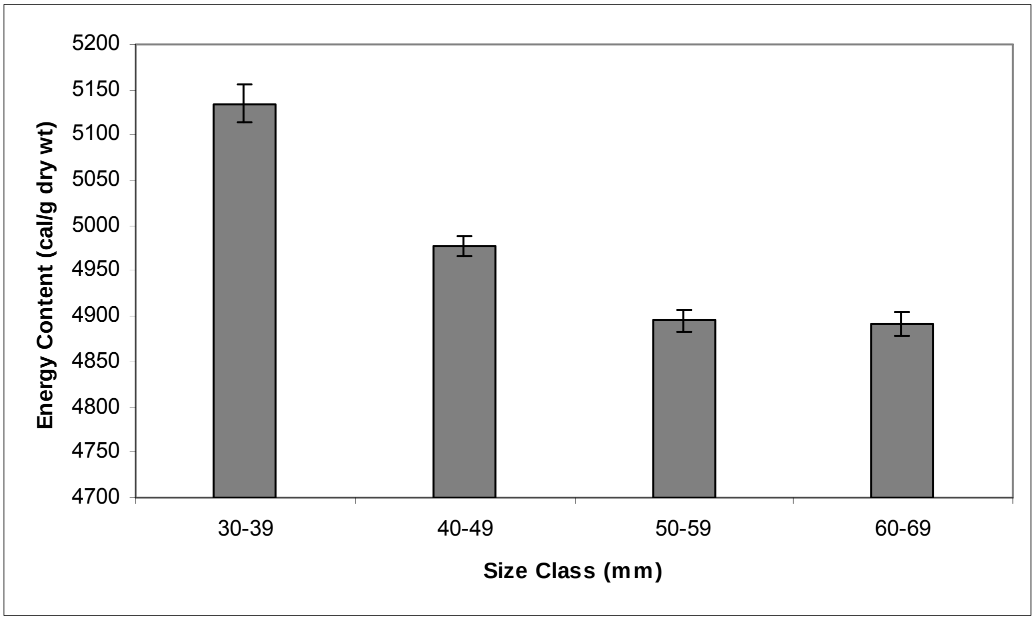

Figure 3B.

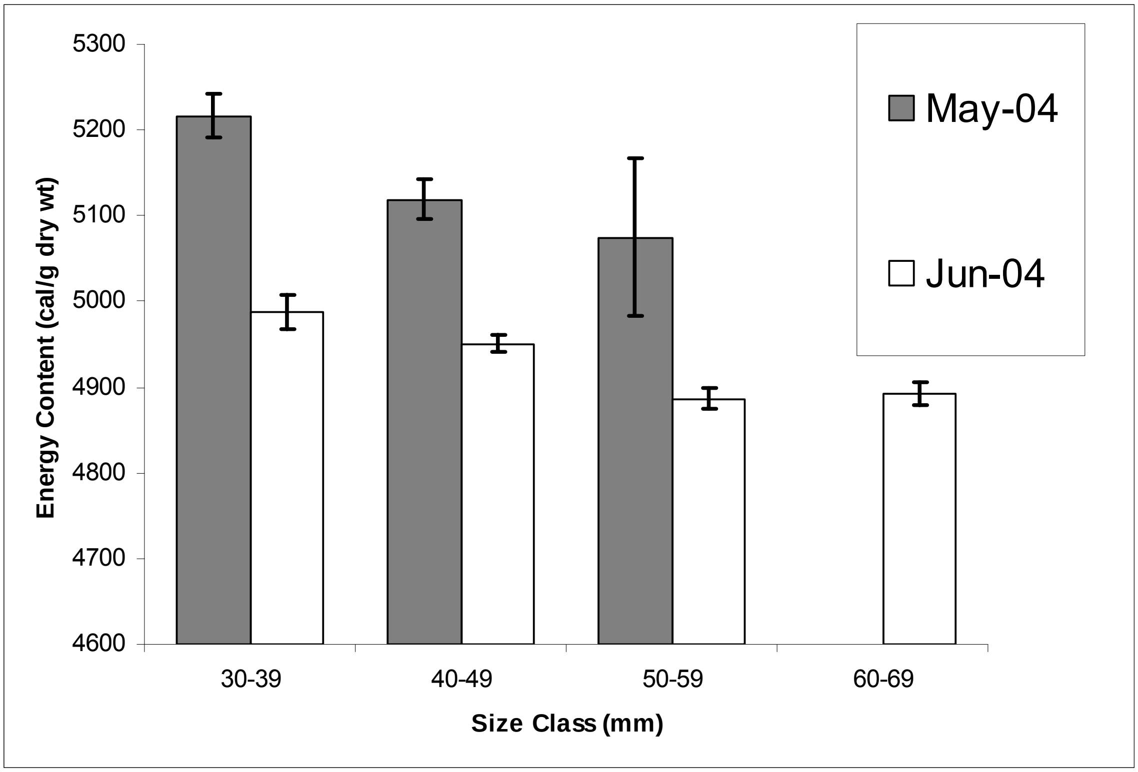
5300
5200
5100
5000
4900
4800
4700
4600
Energy Content (cal/g dry wt)
30-39
40-49
50-59
60-69
Size Class (mm)
▨ May-04
☐ Jun-04

Figure 4.

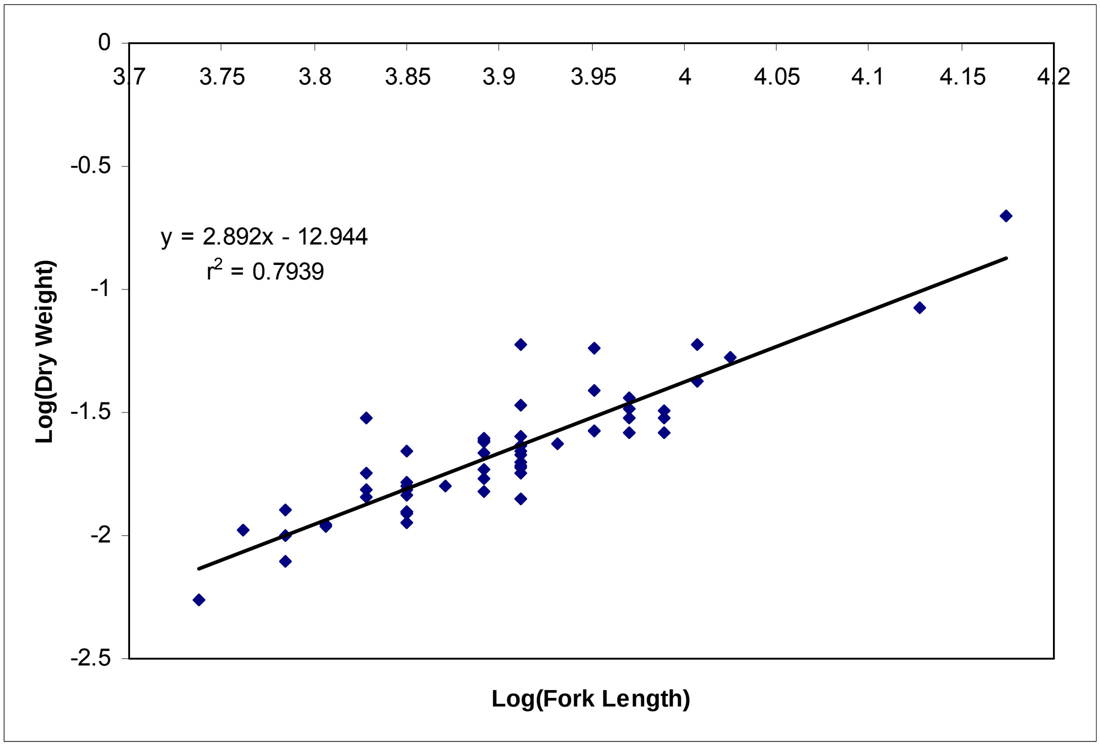

Figure 5A.

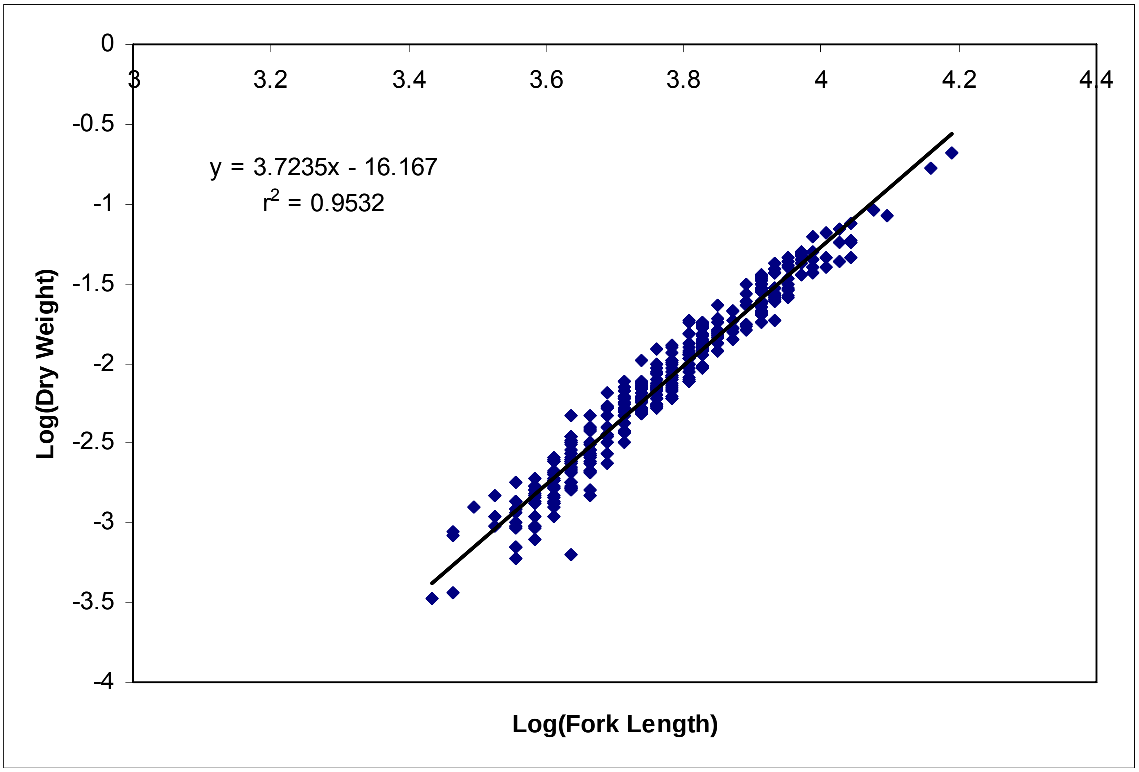

Figure 5B.

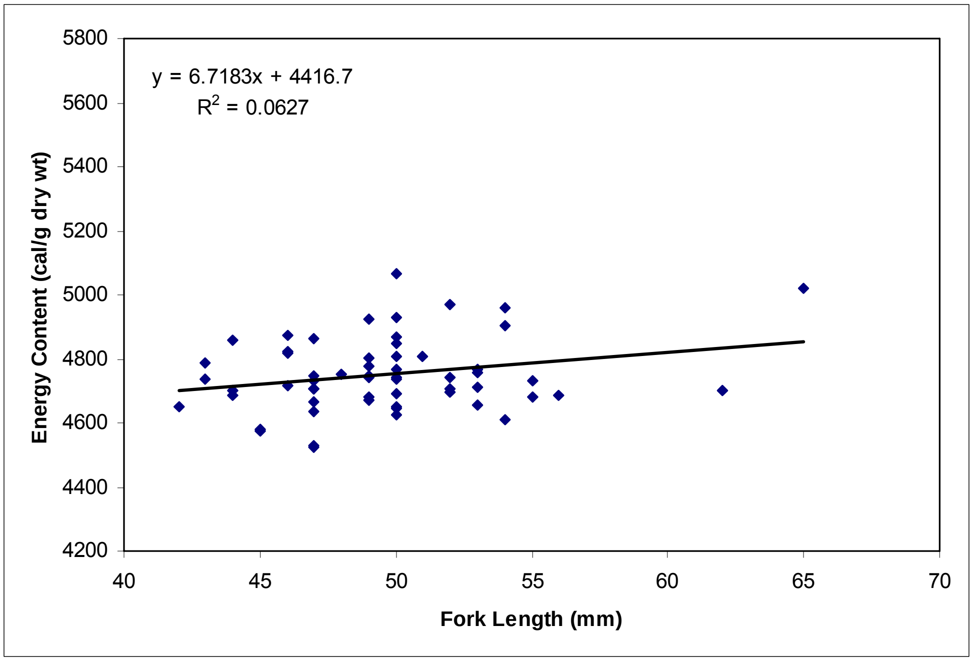

Figure 6A.

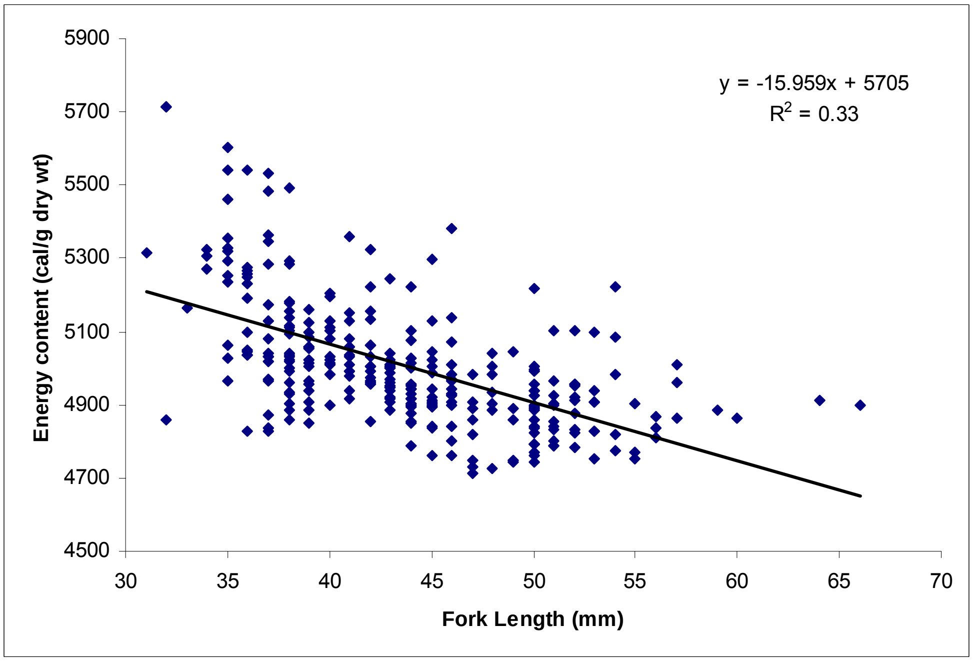

Figure 6B.

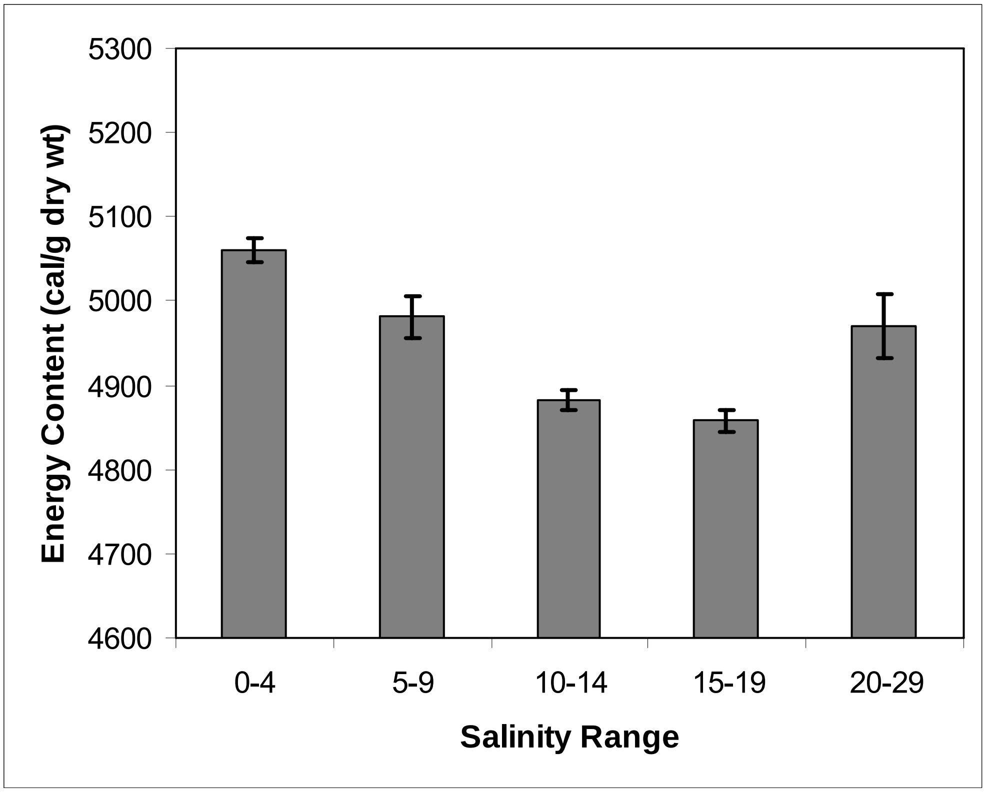
Energy Content (cal/g dry wt)
5300
5200
5100
5000
4900
4800
4700
4600
0-4
5-9
10-14
15-19
20-29
Salinity Range

Figure 7.

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CHAPTER 4 – AGE AND DURATION OF SALTWATER RESIDENCE

Age and duration of saltwater residence of juvenile chum salmon (*Oncorhynchus keta*) captured in Kuskokwim Bay, Alaska.

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Abstract

Age and duration of residence in saltwater habitats of juvenile chum salmon (*Oncorhynchus keta*) captured in Kuskokwim Bay, Alaska was examined using otolith microstructure and microchemistry. Juvenile chum salmon were captured from stations distributed throughout the bay and across a salinity gradient from 0 to 26. To determine the age of fish, we counted presumed daily increments from the emergence check to the edge of the otolith. Post-emergence ages ranged from 12 to 44 d and was weakly correlated with standard length ($r^2 = 0.31$, $n = 192$, $p < 0.001$). There was no relation between post-emergence age and salinity ($r^2 = 0.009$, $n = 192$, $p = 0.19$) indicating that fish of all ages were distributed among salinity habitats. Dates of emergence were back-calculated and ranged from 19 April to 24 May with a median date of 6 May. Otolith strontium-to-calcium ratios (Sr/Ca) were examined to determine the timing of saltwater entry. Fifty otoliths collected over time and across the full salinity gradient were examined, but the freshwater to saltwater transition could only be identified on 8 otoliths that were collected from 3 stations over a period of 2 d. Duration of residence for these fish ranged from 8 to 18 d. Identification of the freshwater to saltwater transition was not identified in the other 42 otoliths due to possible interference from maternally inherited effects and the apparent short duration of residence in freshwater and Kuskokwim Bay habitats.

Introduction

Estuaries are believed to serve as critical habitat for salmonids as they migrate from freshwater to the marine environment (Healey 1982). The transition from freshwater to marine phase is a critical period of high and variable mortality in the life history of salmonids (Pearcy 1992). In chum salmon (*Oncorhynchus keta*), mortality rates initially following ocean entry may range as high as 38-49% per day in Puget Sound (Bax 1983), 3-25% per day in coastal waters off the coast of Japan (Fukuwaka & Suzuki 2002), or an average of 8.1% per day in the first 21 days in southeast Alaska (Wertheimer & Thrower *in press*). Reasons for these high and variable mortality rates are assumed to be food limitation (Salo 1991) and size-selective predation pressure (Beamish & Mahnken 2001). However, only little is known about the early marine ecology of juvenile chum salmon from western Alaska.

Estuary and nearshore dependence differs among salmonid specie species. In comparison to most other salmonids, chum salmon enter the estuaries at a comparatively small size and remain longer in brackish water habitats of estuaries or river plumes (Healey 1982, Simenstad et al. 1982, Fukuwaka & Suzuki 1998). Thus, the period of estuarine residency might be particularly important for chum salmon juveniles because rapid growth and subsequent larger size might substantially reduce the risk of intense size-selective predation pressure in the marine environment. The length of time juvenile salmonids spend in estuarine habitats is a critical to understand the role of estuaries as rearing habitats.

We used otolith microchemistry and microstructure to determine duration of residence in estuary habitats exhibited by juvenile chum salmon as they migrated through Kuskokwim Bay, Alaska. We used counts of presumed daily increments between the emergence check and edge of the otolith to determine age of fish captured in Kuskokwim Bay. Second, we used otolith strontium-to-calcium ratios (Sr/Ca) to determine the transition from freshwater riverine habitats to saltwater estuarine habitats and presumed daily increments to determine the duration of residence in saltwater before capture. Strontium, an element with binding characteristics similar to calcium, is substituted for calcium in the calcium carbonate matrix of the otolith at levels relative to the concentration of strontium in the environment. Because the concentration of strontium is greater in saltwater compared to freshwater, examination of Sr/Ca ratios across the otolith of a fish will describe the chemical life history of that fish and identify times spent in fresh and saltwater (Campana 1999, Zimmerman 2005).

Materials and Methods

Sample Collection and Otolith Preparation

Juvenile chum salmon were collected from sample sites throughout Kuskokwim Bay between 17 May and 11 June 2004. This sampling period was divided into four statistical weeks: 17 May to 24 May, 25 May to 31 May, 1 June to 7 June, and 8 June to 11 June. Although surveys were also conducted in 2003, we focused this study on samples collected in 2004 due to greater sample sizes and distribution among salinity environments encountered in that year. Fish were frozen in the field and transported to the laboratory for analysis. After thawing, standard length was measured for each fish and otoliths were removed and stored dry in plastic vials. One sagittal otolith from each fish was mounted sulcus side down with Crystal Bond 509 on a microscope cover slip attached on one edge to a standard microscope slide. The otolith was then ground with 2000-grit sandpaper in the sagittal plane to the level of the nucleus. The mounting medium was heated and the otolith turned sulcus side-up. The otolith was then ground with 2000-grit sandpaper in the sagittal plane to the level of the primordia, polished with 12000-grit polishing cloth, and further polished with a slurry of 0.05 μm alumina paste.

Age of fish

To determine fish age, otoliths were examined using transmitted light at a magnification of 300x. Increment counts were made from the assumed point of emergence to the edge of the otolith. The emergence check was defined at the point of transition from very dark and irregularly spaced increments to much more weakly expressed and regularly spaced increments as described by Martin et al. (1987). Martin et al. (1987) referred to this point as the hatch check but analysis of their data suggests that this transition corresponds to the time that fish emerge from the gravel rather than hatching. Data from our lab indicate that chum salmon eggs hatch in the fall or winter and remain in the gravel until late spring. Since Martin et al. (1987) reported "post-hatch" increment counts for chum salmon collected in the Yukon River delta of only 11 to 44 increments, it is improbable that these could be days since hatch as reported and more likely correspond to days since emergence. Based on this analysis we chose to identify this check as an emergence check. Post-emergence increment counts were assumed to be the age of the fish in days. Date of emergence was back-calculated for each fish by subtracting the number of post-emergence increments from the date of capture.

Duration of saltwater residence

To determine the time of transition between freshwater and saltwater, we measured Sr/Ca ratios along one transect from a primordium to the edge of the otolith. A sub-sample of 50 chum salmon otoliths were selected from the across the salinity gradient to confirm this technique was sufficiently successful to warrant analysis of all samples. These otoliths were mounted on a petrographic slide for microprobe analysis. The slide containing several otoliths was rinsed with deionized water, air dried, and coated with a 400 Å carbon layer. Elemental analysis was conducted with a JEOL 8900 Electron Microprobe at the USGS Menlo Park Laboratory. A 10 µm focused beam was used to measure Sr and Ca concentrations at points along the primordia to edge transect. Analytical conditions and analysis followed the methods of Zimmerman & Nielsen (2003) and Zimmerman (2005). Strontiantite and calcite were used as standards for Sr and Ca, respectively. Each element was analyzed simultaneously and a counting time of 40 s was used to maximize precision (Toole & Nielsen 1992).

Transects of otolith Sr/Ca were plotted to determine the timing of transition from freshwater to saltwater. The timing of this transition was defined as the point at which otolith Sr/Ca increased from expected freshwater values to expected saltwater values based on the laboratory rearing results of Zimmerman (2005). Otolith increments after this inflection point were assumed to indicate the number of days spent in saltwater before capture. In addition to chum salmon otoliths, a juvenile Chinook salmon (*O. tshawytscha*) was analyzed for comparison of Sr/Ca transects.

Results

The age of fish ranged from 12 to 44 days post-emergence (Figure 1). There were significant differences in mean age among sampling weeks (ANOVA: $F_{[3,188]} = 26.37$, $P < 0.0001$). Mean age (± s.d.) steadily increased each week from 19.5 ± 4.1 d in week 1, 25.5 ± 9.1 d in week 2, 26.9 ± 6.4 d in week 3, to 31.5 ± 7.3 d in week 4. Age of fish was weakly correlated with standard length (Figure 2: $r^2 = 0.31$, $n = 192$, $P < 0.001$). There was no relation between post emergence age and salinity ($r^2 = 0.009$, $n = 192$, $P = 0.19$). Back-calculated dates of emergence ranged from 19 April to 24 May (Figure 2). Median back-calculated date of emergence varied among sampling weeks

Analysis of otolith Sr/Ca was not entirely effective in determining the transition from freshwater to saltwater as expected. Of the 50 chum salmon otoliths examined, the transition from freshwater to saltwater (as indicated by increasing otolith Sr/Ca) could be identified on only eight samples (Figure 3). For example, in Figures 4A and 4B, otolith Sr/Ca is elevated in the first points and declines to approximately 0.001. The data in Figure 4A represent the otolith Sr/Ca transect of a 35 mm standard length juvenile collected at a salinity of 0. As such, it was unlikely that this fish had migrated to saltwater and no increase in Sr/Ca is evident. Similarly, Figure 4B presents data from a 40 mm standard length juvenile, but this individual was collected from a salinity of 12. An increase in otolith Sr/Ca at the end of this transect should be expected unless the fish had spent no time in elevated salinity. Figures 4C, 4D, and 4E present otolith Sr/Ca transect data from samples collected at a salinity of 5, 5, and 12, respectively. These transects are characterized by increased Sr/Ca (~ 0.0018) representing maternal signals, followed by a brief period of lower Sr/Ca (~ 0.0010) representing freshwater growth; the transects conclude with an increase in Sr/Ca associated with transition to saltwater. The eight otoliths that indicated a transition to saltwater were collected at three stations on 10 and 11 June (Table 1). Salinity at these stations ranged from 5 to 15 (Table 1). Back-calculated date of saltwater entry for these fish ranged from 26 May to 3 June and duration of saltwater residence (prior to capture) ranged from 8 to 18 d (Table 1). The otolith transect of a Chinook salmon juvenile collected at a salinity of 12 is characterized by a distinct increase in Sr/Ca at the edge of the otolith corresponding to transition to saltwater (Figure 5).

Discussion

Based on analysis of otolith microstructure and microchemistry, it appears that juvenile chum salmon do not rear in Kuskokwim Bay for extended periods. This finding is confirmed by our sampling throughout the bay that indicates chum salmon use of intermediate salinity habitats (i.e., 0 to 24) Kuskokwim Bay is restricted a brief period of time between the middle of May and end of June (Chapter 1). Within that time frame, the longest duration of residence that we estimated using otolith microchemistry and microstructure was 18 d. Similarly, chum salmon juveniles of the Fraser and Nanaimo Rivers of British Columbia are reported to spend up to three weeks rearing in estuarine habitats (Healey 1982). Further sampling is needed to confirm these values with an emphasis on gathering larger sample sizes from higher salinity habitats (i.e., > salinity of 14).

We originally intended on determining the timing of saltwater entry for all fish using otolith microchemistry followed by counts of otolith increments to determine duration of saltwater residence. After analyzing a sub-sample of otoliths, it became clear that otolith Sr/Ca could not be used to determine this transition with any consistency. Progeny of anadromous salmonids are characterized by elevated Sr/Ca ratios in the core of the otolith (Kalish 1990, Zimmerman & Reeves 2002). The chemistry of these regions is primarily influenced by elements deposited in yolk precursors that form when the mother is still at sea. As a result, anadromous salmonids such as chum salmon are characterized by elevated Sr/Ca ratios in the primordia and core of the otolith. It does not appear that chum salmon spend enough time in freshwater to grow beyond this maternally influenced region. In contrast, Chinook salmon rear in freshwater for one winter before migrating to saltwater and otolith regions associated with this period are characterized by lower Sr/Ca ratios (Figure 5).

Our estimates for the timing of emergence represent the first data concerning this life history event in the Kuskokwim River watershed and will be useful in planning further research in riverine habitats. Further work is needed to confirm this timing across multiple years, environmental conditions, and locations. Continued sampling in Kuskokwim Bay can provide a convenient location to collect fish and if coupled with genetic stock identification, these estimates could be refined to determine emergence timing among stocks within the watershed.

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Zimmerman CE, Reeves GH (2000). Population structure of sympatric anadromous and non-anadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Can J Fish. Aquat Sci 57:2152-2162

List of Tables

Otolith ID	Capture Date	Post-emergence Increments	Emergence Date	Saltwater increments	Saltwater entry date
316	10 June	25	16 May	7	3 June
323	10 June	34	7 May	13	28 May
331	10 June	25	16 May	8	2 June
335	11 June	23	19 May	11	31 May
340	11 June	35	28 April	18	24 May
350	11 June	47	25 April	16	26 May
355	11 June	44	28 April	12	30 May
356	11 June	27	15 May	12	30 May

Table 1.

List of Figure

Figure 1. Post-emergence otolith increment frequency for chum salmon captured in (A) week 1 – 17 to 24 May, (B) week 2 – 25 to 31 May, (C) week 3 – 1 to 7 June, and (D) week 4 – 8 to 11 June from Kuskokwim Bay, Alaska in 2004.

Figure 2. Relationship between standard length (mm) and number of post-emergence otolith increments of chum salmon captured in Kuskokwim Bay, Alaska in 2004.

Figure 3. Frequency distribution of chum salmon by back-calculated date of emergence for (A) all fish captured in 2004, and fish captured in (B) week 1 – 17 to 24 May, (C) week 2 – 25 to 31 May, (D) week 3 – 1 to 7 June, and (E) week 4 – 8 to 11 June from Kuskokwim Bay, Alaska in 2004.

Figure 4. Transects of otolith Sr/Ca ratios beginning in a primordium and concluding at the edge of the otolith of juvenile chum salmon captured in Kuskokwim Bay, Alaska in 2004. The arrow indicates the transition from freshwater to saltwater.

Figure 5. Transect of otolith Sr/Ca ratios beginning in a primordium and concluding at the edge of the otolith of a juvenile Chinook salmon captured in Kuskokwim Bay, Alaska in 2004. The arrow indicates the transition from freshwater to saltwater.

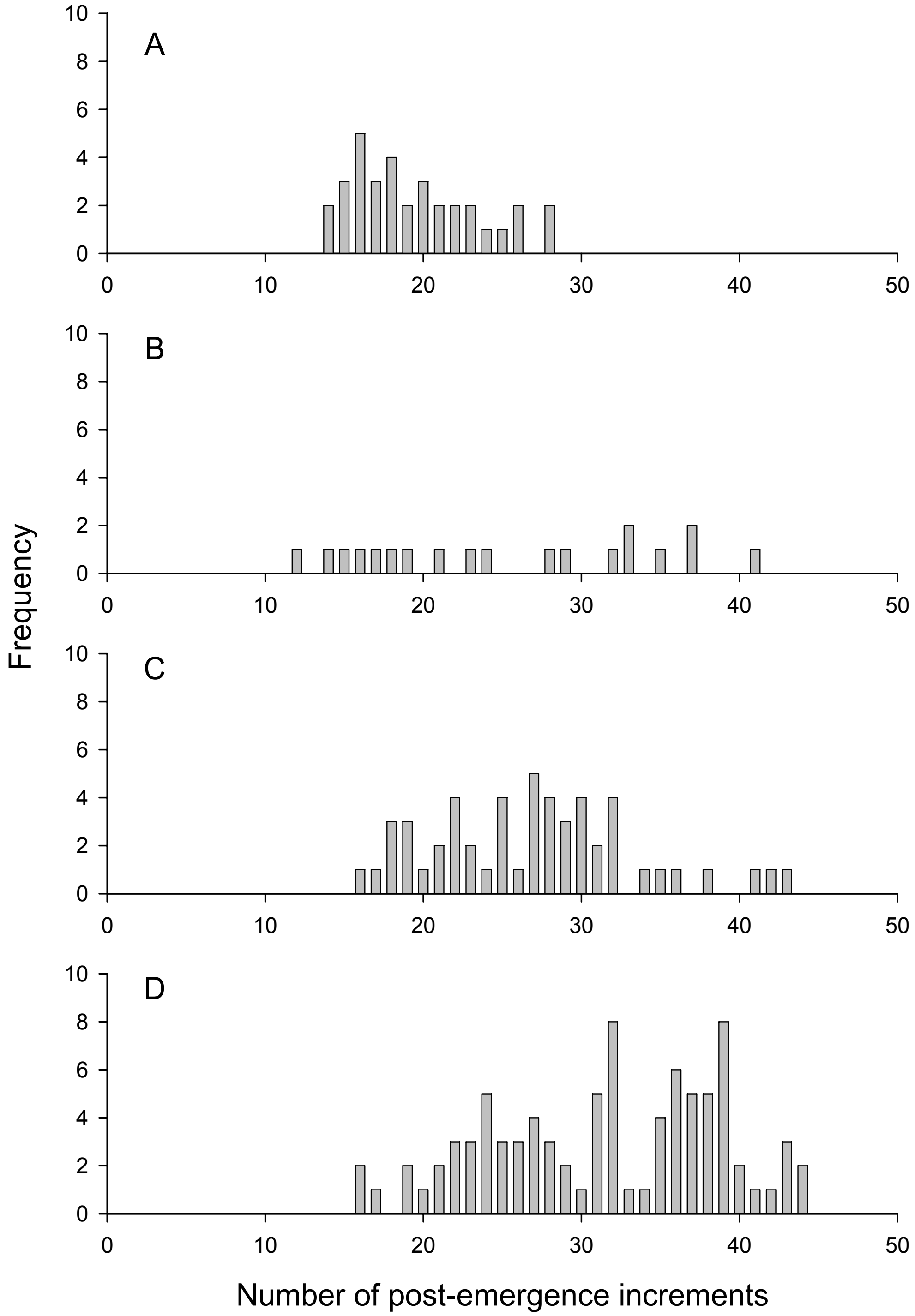
A
B
C
D
Frequency
0
2
4
6
8
10
0
10
20
30
40
50
Number of post-emergence increments

Figure 1.

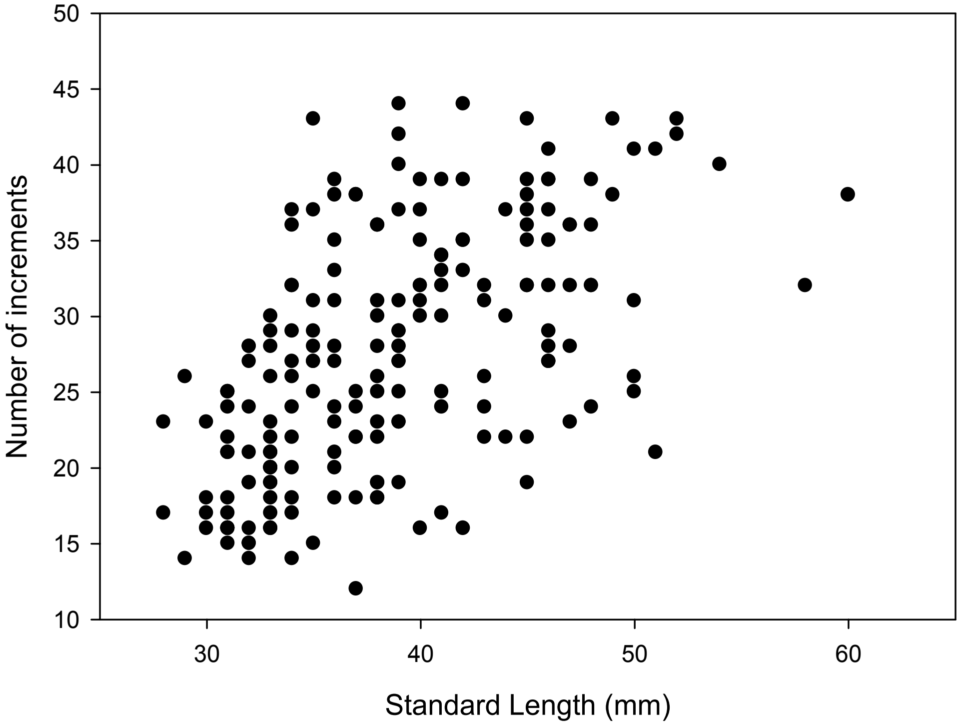
Number of increments
50
45
40
35
30
25
20
15
10
30
40
50
60
Standard Length (mm)

Figure 2.

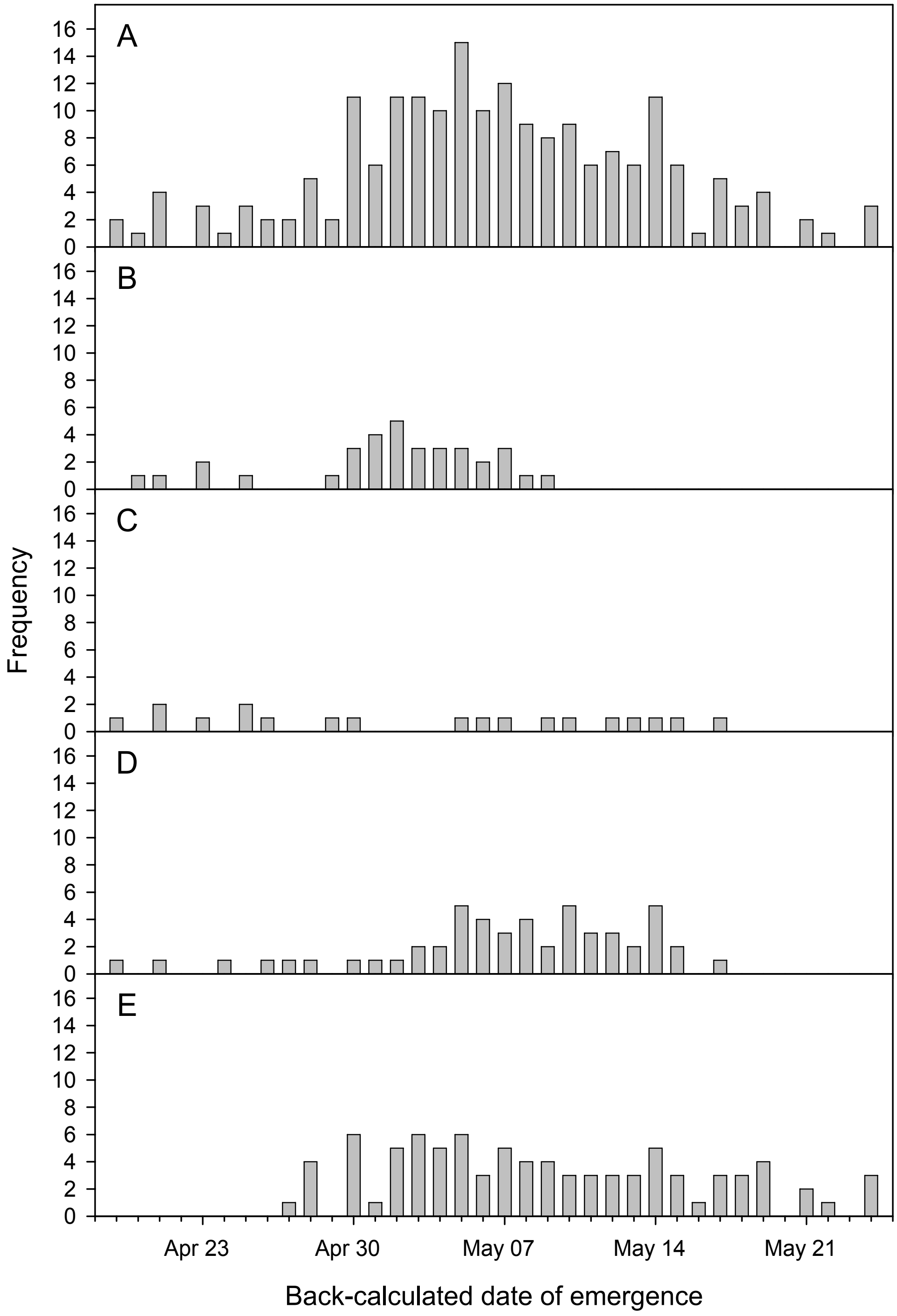
A
B
C
D
E
Frequency
0
2
4
6
8
10
12
14
16
Apr 23
Apr 30
May 07
May 14
May 21
Back-calculated date of emergence

Figure 3.

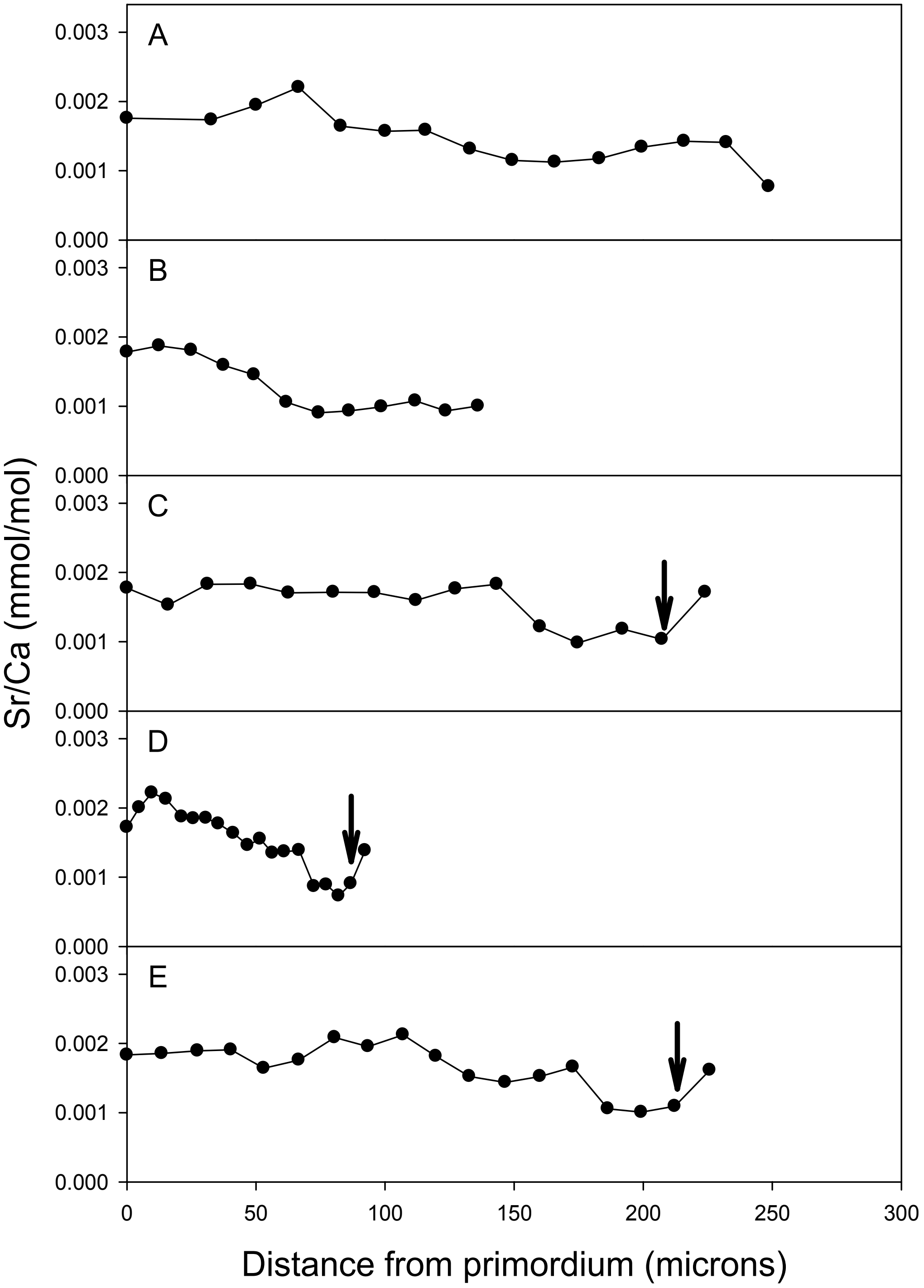
A
B
C
D
E
0.003
0.002
0.001
0.000
Sr/Ca (mmol/mol)
0
50
100
150
200
250
300
Distance from primordium (microns)

Figure 4.

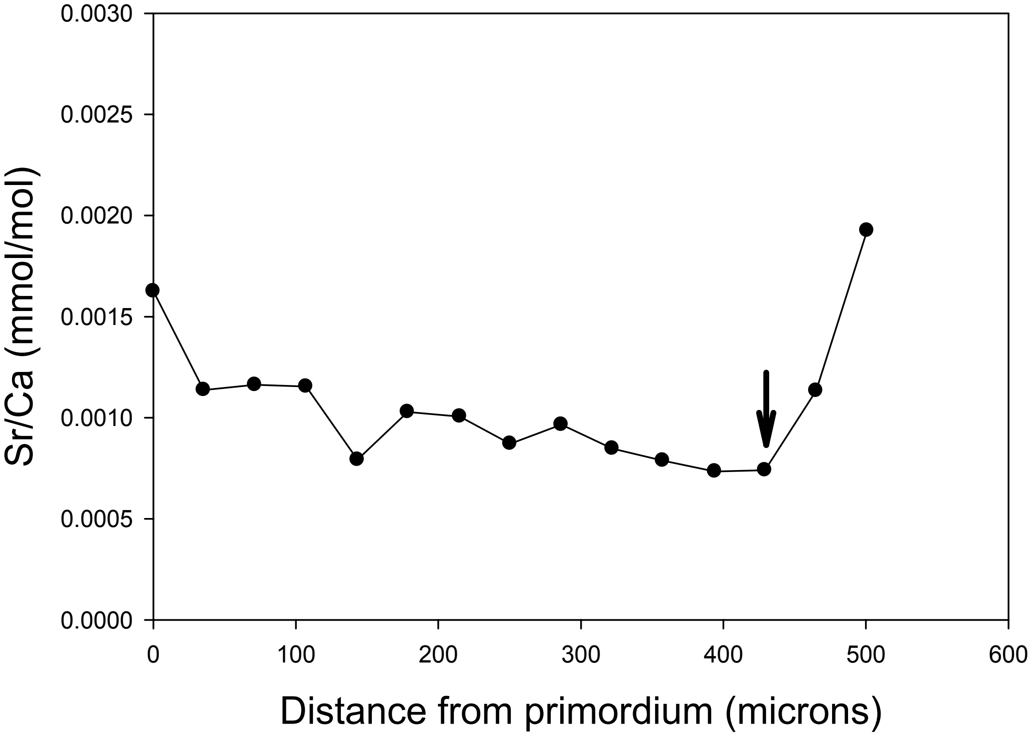
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
Sr/Ca (mmol/mol)
0
100
200
300
400
500
600
Distance from primordium (microns)

Figure 5.

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CHAPTER 5 – BIOENERGETICS MODELING

A bioenergetic evaluation of habitat quality experienced by juvenile chum salmon in Kuskokwim Bay, Alaska, during the 2004 smolt migration

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Abstract

Juvenile chum salmon migrate seaward from the Kuskokwim River through Kuskokwim Bay in May and June. The freshwater to marine transition by juvenile salmon is a period of high mortality when faster growth promotes higher survival. We used spatially-explicit foraging/bioenergetic modeling to assess the growth potential of Kuskokwim Bay habitats for outmigrating juvenile chum salmon in 2004, based on an intensive field sampling program in that year. We modeled growth potential for small and large juveniles based on zooplankton abundance, water temperatures and water clarity on three cruises that occurred early, near the middle (mid), and late in outmigration. Kuskokwim Bay had three distinct habitats: 1) inshore, with high turbidity and low salinity; 2) transition, an area of less turbidity and higher salinity just seaward of the front marking the edge of the river plume; 3) offshore, less turbid water typical of the nearshore Bering Sea. Growth potential was always near zero or negative in the inshore habitat, and was low in the other habitats in the early period. In the mid and late periods growth potential was highest in the transition zone, due to relatively clear water and high zooplankton abundance there. Highest growth potential occurred in the late period, as the highest temperatures occurred then. Outmigrating juvenile chum salmon must transit the inshore zone where foraging conditions apparently are always very poor, due to very high turbidity. Consequently, it is important that they encounter favorable foraging when they move out into the transition habitat where high abundance of zooplankton, especially small copepods, combined with less turbid water, allowing them to compensate for the growth deficits they incur inshore. The timing of outmigration relative to development of a zooplankton bloom in the transition zone may be an important factor in growth and survival of juvenile chum salmon from the Kuskokwim River.

Introduction

Chum salmon (*Oncorhynchus keta*) are an important commercial and subsistence resource in the Kuskokwim River watershed of western Alaska. Chum salmon runs have declined since 1998, resulting in fishing restrictions and closures of commercial and subsistence fisheries in the Kuskokwim and other western Alaska rivers. The causes of these declines are unknown; however, there is widespread recognition that returns of mature salmon to their natal streams are strongly affected by mortality of juveniles during their early marine residence. The transition from freshwater to marine habitats is a period of high mortality in the life history of salmonids (Pearcy 1992). In chum salmon, the period of early marine residence is marked by daily mortality rates that range as high as 38 – 49 % in Puget Sound (Bax 1983) and 25% in coastal waters of Japan (Fukuwaka & Suzuki 2002). Much of this early marine mortality is probably due to size-dependent predation; consequently, growth during the early marine period is thought to be an important variable affecting overall survival. Beamish & Mahnken (2001) have hypothesized that for juvenile salmon the first fall and winter in marine waters may be a second stage of high mortality, as individuals that fail to achieve some threshold of size and energy storage at the end of their first summer will experience high levels of mortality. Both hypothesized mortality mechanisms are size-dependent, and would be affected by growth rates during the first summer in marine habitats.

Juvenile chum salmon leave freshwater and enter estuaries at a small size relative to many other anadromous salmonids. In western Alaska, they enter estuaries in May and June (Chapter 1, Merritt & Raymond 1983). Their diets while in nearshore habitats include taxa that are part of detritus-based food webs, such as harpacticoid copepods and in part terrestrial prey, such as insects, and prey that are part of planktonic food webs (Sibert et al. 1977, Pearcy et al. 1989, Salo 1991). Variation in growth rates while in nearshore habitats will be a function of feeding success and water temperatures.

Spatially-explicit foraging and bioenergetic models provide an integrative approach to evaluating the effects of prey availability and physical conditions on growth potential of fishes (Ney 1990, Brandt et al. 1992, Brandt & Hartman 1993). These models are constructed by linking a foraging model that estimates predator consumption with a bioenergetic model that estimates growth based on consumption (from the foraging model) and water temperature. Spatially-explicit foraging/bioenergetic models have been used to assess habitat quality of fishes (e.g. Mason et al. 1995, Luecke et al. 1999) including chum salmon (Perry et al. 1996). In these applications, habitat quality is defined by growth potential, expressed as a daily weight-specific growth increment (growth increment as a proportion of body weight). The daily growth increment is generated based on an estimate of daily consumption, and a set of physiological sub-models that are temperature, body-size, and ration dependent (Brandt et al. 1992, Hanson et al. 1997).

Daily consumption is estimated with a foraging model based on an encounter rate with prey. The encounter rate is typically a function of fish swimming speed, distance at which predator perceives prey, and prey density. For zooplanktivorous fishes a modified version of the Gerritson & Strickler (1977) model is typically used, with swimming speed of prey removed from the model, as the swimming speed of the prey is very low relative to the predator (Lueck et al. 1999). Satiation may be included in the foraging model at high prey encounter rates by adding a functional response model that incorporates prey handling times; the Holling (1959) disk equation is often used.

The bioenergetic model is an energy-balance model in which total energy consumption (C) must satisfy the net gain or loss of weight (G), plus metabolic costs (M) and waste losses (W) in the standard mass-balance equation:

$$G = C - (M+W)$$

The model operates on a daily time step, producing estimates of daily growth increments based on body size, prey consumption, and thermal experience of the predator. The Wisconsin bioenergetic model (Hanson et al. 1997) is the most widely used bioenergetic component in spatially-explicit modeling; it was developed to address ecological questions associated with salmonid populations in the Great Lakes.

We used a spatially-explicit foraging/bioenergetic modeling approach to evaluate the quality of the estuarine nearshore habitat for juvenile chum salmon off the mouth of the Kuskokwim River. Specifically, we address two questions:

1. Does quality of the estuarine habitat for migrating chum salmon juveniles change during the period of outmigration?
2. Is there geographic variation in the quality of the estuarine habitat, and, if so, do spatial patterns in habitat quality vary seasonally?

Methods

We modeled growth potential of juvenile chum salmon off the mouth of the Kuskokwim River in 2004. Most data required for the models were collected in a field program that began May 17 and continued until June 11. All samples were collected within Kuskokwim Bay, on a grid of 22 stations (Figure 1). Stations were regularly spaced every 15 minutes of latitude and every 7.5 minutes of longitude. Fish sampling was conducted with a modified Kvichak surface trawl (3.1m height x 6.1m width x 15.0m length) during daylight hours. Zooplankton was collected with a 0.75 m diameter ring net equipped with 335 µm mesh, fished for 5 minutes at the surface. The plankton net was equipped with a flowmeter to record volume of water filtered. Hydrographic data were collected with a SeaBird Electronics SBE-19 Seacat Conductivity-Salinity-Depth (CTD) profiler equipped with a Wetstar fluorometer and a D&A Instruments transmissometer.

Foraging Model Configuration

Our foraging model was the Gerritson & Strickler (1997) model, with swimming speed of the prey set at zero:

$$S_{(vol)} = pi * V * R^2$$

Where $S_{(vol)}$ is the search volume, R is the reaction distance of the predator to the prey, and V is the swimming speed of a juvenile chum salmon. Fish swimming speed was based on experimental studies by Brett & Glass (1973) and was set at three times fork length. Reaction distance for fish in clear water (NPU = 0.3) was set at 30cm, and was reduced based on the turbidity measured at each station. The proportional reduction in clear water R was based on the empirical model of Miner & Stein (1996):

$$R_{(prop)} = 0.472\ R^{-0.624}$$

Where $R_{(prop)}$ is the proportional reduction in maximum R (30 cm) and NTU is the NTU value measured at a station, we used the mean NTU value in the upper 5 meters.

Satiation was included in the foraging model by adding a functional response model that incorporates prey handling times. We used the Holling Type II functional response model (Holling 1959) with handling time set at one second for all prey types, based on the handling time observed for small Kokanee (freshwater sockeye salmon, *Oncorhynchus nerka*) feeding on *Daphnia* (Stockwell & Johnson 1997). If the foraging model daily ingestion was greater than the maximum daily consumption from the bioenergetic model, it is assumed that the fish were satiated and did not feed continually. The daily consumption in these cases was set at the maximum from the bioenergetic model. The consumption rate output from the foraging model was the number of prey ingested hourly. Those prey consumption rates were converted to weight of prey, using literature values of typical prey weights for each category. The hourly ingestion weights were then expanded to a daily ingestion, assuming the fish could forage for 16 hours a day.

Bioenergetic Model Configuration

The Wisconsin Bioenergetic Model with the metabolic sub-models for juvenile pink and sockeye salmon (Hanson et al. 1997) were used in all model runs. The inputs required for the model are:

1) Wet weight of fish (g)
2) Energy density of fish (joules/g wet wt)
3) Composition of fish diet (proportion by weight)
4) Daily consumption of prey (g/day)
5) Prey energy density (joules/g wet wt)
6) Water temperature (˚C)

1) Fish weights were estimated from a length/weight model constructed from the lengths and weights measured in the laboratory on fish we collected during the 2004 field program.
2) Energy density was the mean value measured for fish in each sampling period by bomb calorimetry (Chapter 3).
3) Diet composition was estimated from proportions of zooplankton in the consumption estimates generated by the foraging model.
4) Daily consumption was input from the foraging model described above.
5) Prey energy densities and mean weights were taken from the literature.
6) Water temperatures were measured at each station in 2004; we used the mean value in the upper 10 m as the model inputs.

Model Runs

We ran the foraging/bioenergetic models on juvenile chum salmon for three cruises in 2004, selected to evaluate the growth potential early (17 – 18 May), near the middle (28 – 31 May), and late (5 – 9 June) in the outmigration period. For each cruise we ran the model for small fish (3 cm) and large fish (6 cm) at each station.

Foraging Model Inputs

Zooplankton abundance. Zooplankton densities were calculated based on numbers in samples and volume filtered measurements. We used the same taxonomic categories as were used in the fish diet analyses, and collapsed rare items into a single category (Tables 1 – 3).

Water Clarity. Turbidity, measured in NTU units, was highly variable among stations, with very turbid water at stations in the plume of the Kuskokwim River (Table 4).

Bioenergetic Model Inputs

Fish Weights. Wet weights of 3 cm and 6 cm fish from the length/weight model were about 0.3 g and 1.8 g, and the energy densities of fish for each size and cruise are summarized in Chapter 3.

Fish Diets. Diet composition based on encounter rates with zooplankton were generally similar to observed diets (Chapter 2), with heavy reliance on small copepods (Tables 5 – 7); although other prey were important when those were abundant, such as the use of fish eggs at stations outside the river plume in the late cruise (Table 7).

Prey Weight and Energy Content. Prey energy densities and average prey weights (Table 8) were gathered from literature sources, including Hanson et al. (1997), Boldt & Haldorson (2002), and Davis et al. (1998).

Water Temperature. Temperatures in the upper water column warmed substantially from the early to late cruise, and were usually warmest in the river plume and nearshore stations (Table 9).

Results

Foraging Model

The volume of water searched per hour was highly variable among stations on each cruise, and also varied strongly among cruises (Table 10). The highly variable search volumes were a consequence of the variation in water clarity (Table 4). At nearshore stations, water clarity was very low due to the turbid plume of the Kuskokwim River. On all three cruises we modeled, water clarity and search volumes increased to the south in the transitions from stations 5 – 7 on the eastern-most transect, and stations 11 – 14 on the next transect to the west (Table 10).

Prey consumption rates were strongly influenced by volumes searched and by the abundance of planktonic prey items. The numbers of prey consumed per hour varied extensively among stations on each cruise, typically with low consumption rates at nearshore stations influenced by the turbid plume of the Kuskokwim River (Figures 2 - 4). The highest consumption rates usually were found in the transition zone, due both to increased search volumes (Table 10) and relatively high abundance of zooplankton, especially small copepods (Tables 1 – 3).

Bioenergetic Model

Bioenergetic model runs produced spatial patterns that were generally consistent among the three cruises, with reduced growth and daily rations where high turbidity and/or low zooplankton abundance occurred, especially at nearshore stations (Tables 11 – 13, Figures 5 - 7). The proportion of maximum daily ration (P) at each station (Tables 11 – 13) is an indicator of how well the fish were foraging at each station, a value of 1 indicates the fish were satiated and had achieved their maximum growth possible at that temperature. In all three cruises, stations near the mouth of the Kuskokwim River had very low P-values, daily rations and growth potential (Tables 11 – 13, Figures 5 – 7).

Addressing our two questions:

1) Does quality of the estuarine habitat for migrating chum salmon juveniles change during the period of outmigration?

   Yes. Overall, the first cruise had the lowest growth potential, whereas conditions on the second and third cruises resulted in relatively high growth potentials, and a relatively high number of stations where fish were growing at their maximum rates (P = 1). On the third cruise the growth potential was typically higher at those stations with maximum growth because water temperatures (Table 9) were highest then.

2) Is there geographic variation in the quality of the estuarine habitat, and, if so, do spatial patterns in habitat quality vary seasonally?

   Yes and no. There was a very consistent spatial pattern in growth potential, with negative or very low values in the stations just seaward of the river mouth. This was the dominant geographic pattern, and it persisted throughout the sampling period.

Discussion

As juvenile chum salmon migrate out of the Kuskokwim River and through Kuskokwim Bay, they traverse an estuary where physical and biotic conditions are highly variable, and where those conditions affect their foraging and growth. During the 2004 outmigration; turbidity, temperature, and zooplankton abundance varied spatially in a very consistent pattern that appears driven by the interaction of the river's freshwater plume with marine waters just offshore. For the purpose of interpreting our modeling results, we view Kuskokwim Bay as comprised of three zones, namely (1) an inshore estuarine zone with highly turbid water under the influence of the river plume, (2) a transition zone associated with a front between the nearshore zone and more marine conditions further offshore, and (3) an offshore zone with lower turbidity and temperature/salinity more characteristic of nearshore Bering Sea water.

The inshore zone affected by the river plume was always highly turbid. On the first cruise there was little temperature difference across the transition zone between offshore and inshore, turbid water; however, by the time of the third cruise a strong temperature differential had also been established, with relatively warm water in the inshore zone. The transition zone was marked by a frontal boundary along a southeast to northwest line that crossed our station grid between stations 5 – 7 and 12 – 14 (Figure 1). Small copepods were the dominant taxa among the zooplankton, and during the second and third cruise they were strongly aggregated in the transition zone.

There was also a strong element of temporal variability in physical and biotic conditions in the study area, especially in water temperature (Table 9) and zooplankton abundance (Tables 1 – 3). There was a marked increase in temperature at inshore stations between the first and second cruises, and a steady increase in temperature at stations further offshore over all three cruises. Zooplankton increased most sharply between the first and second cruises, with resultant high densities in the transition zone during cruises two and three.

The growth potential of juvenile chum salmon was strongly influenced by turbidity, zooplankton abundance, and temperature. During the entire outmigration period, the area outside the river mouth (Stations 1–4) was typified by very low or negative growth potential. That area had a combination of conditions that were detrimental to feeding and growth. Near the river mouth, very high turbidity and low zooplankton abundance resulted in very low consumption estimates from the foraging model; and, especially in the last two cruises, elevated water temperatures imposed increased metabolic energy demands in the bioenergetic model. In sharp contrast to the river-influenced inshore zone, the transition zone just seaward of the frontal boundary had relatively good foraging and growth, due to increased water clarity and high abundance of small copepods, most notably after the first cruise. During the last two cruises, the growth potential of juvenile chum salmon seaward of the inshore zone was often the maximum rate allowed by water temperature.

The timing of the smolt migration into Kuskokwim Bay by juvenile chum salmon may affect their survival. It seems likely that the inshore zone will always be very turbid, with resultant poor foraging conditions for zooplankton prey. The negative growth estimates we found for the inshore area may be typical, and are consistent with the decreasing energy content with increased size we observed in juvenile chum salmon (Chapter 3). In that case, development of favorable foraging conditions in the transition zone would be an important factor in growth and size-related mortality during the initial marine life history of these fish. In 2004, transition zone zooplankton densities, especially density of small copepods, increased markedly between the first and second cruises, with associated improvement in growth potential in that zone. If outmigration of chum salmon occurred earlier than development of the zooplankton bloom in the transition zone, those fish may not be able to recover energetically from the stress of crossing the inshore zone. The timing of events in freshwater river watersheds and in marine plankton production systems may be driven by different mechanisms, and those mechanisms probably are influenced by large-scale climate forcing. Juvenile salmon could be negatively affected if freshwater and marine systems respond differently to climate forcing. If, for example, climate warming were to cause earlier spring break-up in river watersheds without a similar shift to earlier plankton production, juvenile chum salmon would probably smolt earlier in the spring and encounter poor foraging and growth conditions in marine habitats. As they say, timing is everything.

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Table 10. Volumes (m^3) of water searched per hour by juvenile chum salmon of 3 cm and 6 cm fork length (FL), based on foraging models for Kuskokwim Bay on three cruises in 2004.

Table 11. Weight-specific growth rates, daily ration and P (proportion of maximum daily consumption) from bioenergetic model runs for juvenile chum salmon of 3 cm and 6 cm fork length (FL) at stations sampled on cruise K04-1.

Table 12. Weight-specific growth rates, daily ration and P (proportion of maximum daily consumption) from bioenergetic model runs for juvenile chum salmon of 3 cm and 6 cm fork length (FL) at stations sampled on cruise K04-4.

Table 13. Weight-specific growth rates, daily ration and P (proportion of maximum daily consumption) from bioenergetic model runs for juvenile chum salmon of 3 cm and 6 cm fork length (FL) at stations sampled on cruise K04-6.

Station	Fish Larvae	Fish Eggs	Copepods (<2.5 mm)	Cladocerans	Echinoderm Larvae	Polychaetes	Polychaete Larvae	All Other
K1	0.55	0.00	2.06	0.48	0.00	0.00	0.00	1.22
K2	0.48	0.00	2.98	0.23	0.00	0.01	0.00	1.26
K3	0.04	0.00	1.32	0.00	0.00	0.00	0.00	0.02
K4	0.48	0.00	5.34	0.01	0.00	0.03	0.00	0.02
K5	0.16	0.00	188.94	0.00	0.00	0.42	0.84	0.43
K6	0.02	0.07	221.82	0.00	0.00	0.03	0.00	0.07
K7	0.04	0.00	2.30	0.00	0.00	0.00	0.05	0.03
K13	0.00	30.02	22.99	0.19	40.15	1.71	50.16	0.76
K14	0.00	0.21	55.91	0.00	4.15	0.32	9.46	0.01
K15	1.09	0.22	610.29	0.87	13.91	8.70	6.95	7.82
K16	0.00	6.99	74.60	0.00	4.90	1.40	10.26	2.68
K17	0.05	22.90	120.00	0.00	50.53	13.42	878.67	6.32

Table 1.

Station	Fish larvae	Fish eggs	Eggs (<1mm)	Copepods (<2.5mm)	Cladocerans	Echinoderm Larvae	Polychaetes	Polychaete Larvae	All Other
K1	0.00	0.00	0.00	26.76	8.00	0.00	0.03	0.00	0.00
K2	0.00	0.00	0.00	6.43	1.13	0.00	0.00	0.00	0.39
K3	0.00	0.00	0.00	6.88	0.23	0.00	0.00	0.00	1.77
K4	0.00	0.00	0.00	219.32	0.00	0.00	0.00	0.00	0.00
K5	0.00	0.00	0.00	7991.68	0.00	0.00	0.00	0.00	0.00
K6	0.00	0.00	0.00	894.01	4.51	0.00	0.00	6.01	0.00
K7	0.04	0.00	2.77	10.83	0.00	0.00	0.00	0.64	0.21
K8	0.03	0.00	29.42	4.55	0.00	0.00	0.00	0.01	0.05
K11	0.00	30.48	0.00	0.38	0.00	0.01	0.00	0.32	0.31
K12	0.00	52.55	0.00	8.74	0.00	1.71	0.00	12.05	0.00
K13	0.00	5.09	0.00	48.49	0.22	1.11	0.22	129.10	0.68
K14	0.05	0.00	0.00	1000.28	0.00	1.70	0.00	15.31	0.01
K15	0.00	0.00	0.00	1473.49	0.00	25.14	5.80	17.40	0.00
K16	2.32	8.80	5.09	337.10	0.00	5.56	35.19	268.57	5.79
K17	4.44	76.48	0.00	34.96	0.00	211.95	2.19	537.52	0.00

Table 2.

Station	Fish larvae	Fish eggs	Copepods (<2.5mm)	Cladocerans	Echinoderm Larvae	Polychaetes	Polychaete Larvae	Barnacle nauplii	All Other
K1	0.22	0.00	9.28	1.31	0.00	0.03	0.00	0.00	0.09
K2	0.01	0.00	17.75	0.08	0.00	0.00	0.01	0.00	0.07
K3	0.00	0.00	63.90	1.18	0.00	0.00	0.00	0.00	0.50
K4	0.03	0.00	8.03	0.00	0.00	0.00	0.00	0.00	0.02
K7	0.00	13.71	10.46	0.05	0.00	0.01	8.42	0.02	0.03
K8	0.00	42.57	27.08	1.30	0.00	0.00	3.43	0.00	0.33
K11	0.01	91.58	25.40	0.07	0.00	0.02	6.04	0.02	0.05
K12	0.01	96.85	122.97	23.82	2.97	0.07	31.93	0.00	0.07
K13	0.87	18.32	80.48	2.91	14.43	0.83	99.36	0.14	0.17
K14	0.12	2.21	1070.37	4.92	0.00	2.95	74.77	0.74	0.00
K15	0.38	0.25	1424.02	0.75	1.00	0.25	9.51	0.00	0.02
K20	0.19	0.13	218.64	0.13	0.44	0.00	0.69	0.06	1.17
K21	0.01	0.01	10.23	0.01	0.00	0.00	0.06	0.01	0.01
K22	16.10	5.08	295.25	0.15	0.00	0.58	0.00	12.18	0.87
K23	0.03	2.04	56.75	2.34	0.00	0.11	0.27	1.66	0.22
K24	0.01	3.13	2.94	0.03	0.00	0.02	0.95	0.03	0.03
K25	0.04	0.00	604.92	0.00	0.00	0.00	0.00	0.00	0.14

Table 3.

Station		**Cruise**	
	K04-1	**K04-4**	**K04-6**
K1	87.8	22.9	43.7
K2	148.5	22.9	115.2
K3	74.6	74.5	110.9
K4	44.4	23.0	22.2
K5	101.7	23.7	
K6	45.2	8.7	
K7	7.4	3.6	3.3
K8		2.3	3.9
K11		3.2	2.8
K2		5.6	3.3
K13	5.9	7.1	8.2
K14	17.8	16.0	16.8
K15	52.8	33.9	13.0
K16	4.9	20.1	
K17	2.7	4.2	
K20			16.0
K21			6.9
K22			9.6
K23			3.1
K24			5.3
K25			23.0

Table 4.

Station	Fish Larvae	Fish Eggs	Small Copepods (< 2.5 mm)	Cladocerans	Enchinoderm Larvae	Polychaetes	Polychaete Larvae	All Other
K1	0.12	0.00	0.49	0.11	0.00	0.00	0.00	0.28
K2	0.10	0.00	0.60	0.05	0.00	0.00	0.00	0.25
K3	0.03	0.00	0.95	0.00	0.00	0.00	0.00	0.01
K4	0.08	0.00	0.91	0.00	0.00	0.01	0.00	0.00
K5	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00
K6	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
K7	0.02	0.00	0.95	0.00	0.00	0.00	0.02	0.01
K13	0.00	0.21	0.16	0.00	0.28	0.01	0.34	0.01
K14	0.00	0.00	0.80	0.00	0.06	0.00	0.14	0.00
K15	0.00	0.00	0.94	0.00	0.02	0.01	0.01	0.01
K16	0.00	0.07	0.74	0.00	0.05	0.01	0.10	0.03
K17	0.00	0.02	0.11	0.00	0.05	0.01	0.80	0.01

Table 5.

Station	Fish Larvae	Fish Eggs	Other Eggs	Small Copepods (< 2.5 mm)	Cladocerans	Echinoderm Larvae	Polychaetes	Polychaete Larvae	All Other
K1	0.00	0.00	0.00	0.77	0.23	0.00	0.00	0.00	0.00
K2	0.00	0.00	0.00	0.81	0.14	0.00	0.00	0.00	0.05
K3	0.00	0.00	0.00	0.78	0.03	0.00	0.00	0.00	0.20
K4	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
K5	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
K6	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00
K7	0.00	0.00	0.19	0.75	0.00	0.00	0.00	0.04	0.01
K8	0.00	0.00	0.86	0.13	0.00	0.00	0.00	0.00	0.00
K11	0.00	0.97	0.00	0.01	0.00	0.00	0.00	0.01	0.01
K12	0.00	0.70	0.00	0.12	0.00	0.02	0.00	0.16	0.00
K13	0.00	0.03	0.00	0.26	0.00	0.01	0.00	0.70	0.00
K14	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.02	0.00
K15	0.00	0.00	0.00	0.97	0.00	0.02	0.00	0.01	0.00
K16	0.00	0.01	0.01	0.50	0.00	0.01	0.05	0.40	0.01
K17	0.01	0.09	0.00	0.04	0.00	0.24	0.00	0.62	0.00

Table 6.

Station	Fish Larvae	Fish Eggs	Small Copepods (< 2.5 mm)	Cladocerans	Echinoderm Larvae	Polychaetes	Polychaete Larvae	Barnacle Larvae	All Other
K1	0.02	0.00	0.85	0.12	0.00	0.00	0.00	0.00	0.01
K2	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00
K3	0.00	0.00	0.97	0.02	0.00	0.00	0.00	0.00	0.01
K4	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00
K7	0.00	0.42	0.32	0.00	0.00	0.00	0.26	0.00	0.00
K8	0.00	0.57	0.36	0.02	0.00	0.00	0.05	0.00	0.00
K11	0.00	0.74	0.21	0.00	0.00	0.00	0.05	0.00	0.00
K12	0.00	0.35	0.44	0.09	0.01	0.00	0.11	0.00	0.00
K13	0.00	0.08	0.37	0.01	0.07	0.00	0.46	0.00	0.00
K14	0.00	0.00	0.93	0.00	0.00	0.00	0.06	0.00	0.00
K15	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.00
K20	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.01
K21	0.00	0.00	0.99	0.00	0.00	0.00	0.01	0.00	0.00
K22	0.05	0.02	0.89	0.00	0.00	0.00	0.00	0.04	0.00
K23	0.00	0.03	0.89	0.04	0.00	0.00	0.00	0.03	0.00
K24	0.00	0.44	0.41	0.00	0.00	0.00	0.13	0.00	0.00
K25	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 7.

	Fish Larvae	**Fish Eggs**	**Other eggs**	**Small Copepod**	**Cladocerans**	**Echinoderm Larvae**	**Polychaetes**	**Polychaete Larvae**	**All Other**
Energy Density	5300	6000	6000	3810	2515	2500	3000	2500	3000
Weight	0.001	0.0001	0.00001	0.00003	0.00007	0.00005	0.001	0.00005	0.001

Table 8.

	Cruise		
Station	**K04-1**	**K04-4**	**K04-6**
1	6.57	11.5	14.5
2	6.44	11.5	14.1
3	6.46	10.7	15.6
4	6.34	9.8	12.1
5	6.24	9.2	
6	6.32	8.3	
7	6.80	7.8	9.2
8		7.5	8.5
11		6.9	8.4
12		7.3	9.0
13	6.19	8.2	9.9
14	6.35	9.2	11.1
15	7.95	9.5	12.2
16	8.46	9.6	
17	7.58	9.0	
20			10.2
21			9.4
22			11.0
23			11.4
24			10.0
25			11.7

Table 9.

	3 cm FL			6 cm FL		
	Cruise			Cruise		
Station	**K04-1**	**K04-4**	**K04-6**	**K04-1**	**K04-4**	**K04-6**
K1	0.08	0.41	0.18	0.15	0.83	0.37
K2	0.04	0.41	0.05	0.08	0.83	0.11
K3	0.09	0.09	0.06	0.19	0.19	0.11
K4	0.18	0.41	0.43	0.36	0.82	0.85
K5	0.06	0.39		0.13	0.79	
K6	0.18	1.38		0.35	2.74	
K7	1.68	4.16	4.67	3.37	7.98	9.34
K8		7.22	3.69		14.43	7.37
K11		4.86	5.60		9.95	11.19
K12		2.37	4.53		4.86	9.06
K13	2.22	1.76	1.49	4.44	3.87	2.98
K14	0.56	0.64	0.60	1.12	1.35	1.20
K15	0.14	0.25	0.83	0.29	0.56	1.67
K16	2.84	0.48		5.69	1.09	
K17	5.91	3.40		11.82	6.81	
K20			0.64			1.28
K21			1.84			3.67
K22			1.21			2.43
K23			4.95			9.91
K24			2.56			5.12
K25			0.41			0.82

Table 10.

		Cruise K04-1 3 cm FL			Cruise K04-1 6 cm FL	
Station	**Specific Growth**	**Daily Ration**	**P**	**Specific Growth**	**Daily Ration**	**P**
K1	-0.009	0.008	0.024	-0.009	0.003	0.013
K2	-0.011	0.004	0.013	-0.009	0.001	0.007
K3	-0.014	0.001	0.002	-0.010	0.000	0.001
K4	-0.009	0.007	0.021	-0.009	0.002	0.012
K5	0.001	0.023	0.073	-0.005	0.008	0.04
K6	0.027	0.063	0.202	0.004	0.021	0.109
K7	-0.006	0.012	0.039	-0.008	0.004	0.021
K13	0.150	0.308	1	0.090	0.188	1
K14	0.035	0.080	0.258	0.006	0.026	0.139
K15	0.151	0.278	0.829	0.045	0.090	0.441
K16	0.183	0.343	1	0.110	0.210	1
K17	0.125	0.330	1	0.074	0.202	1

Table 11.

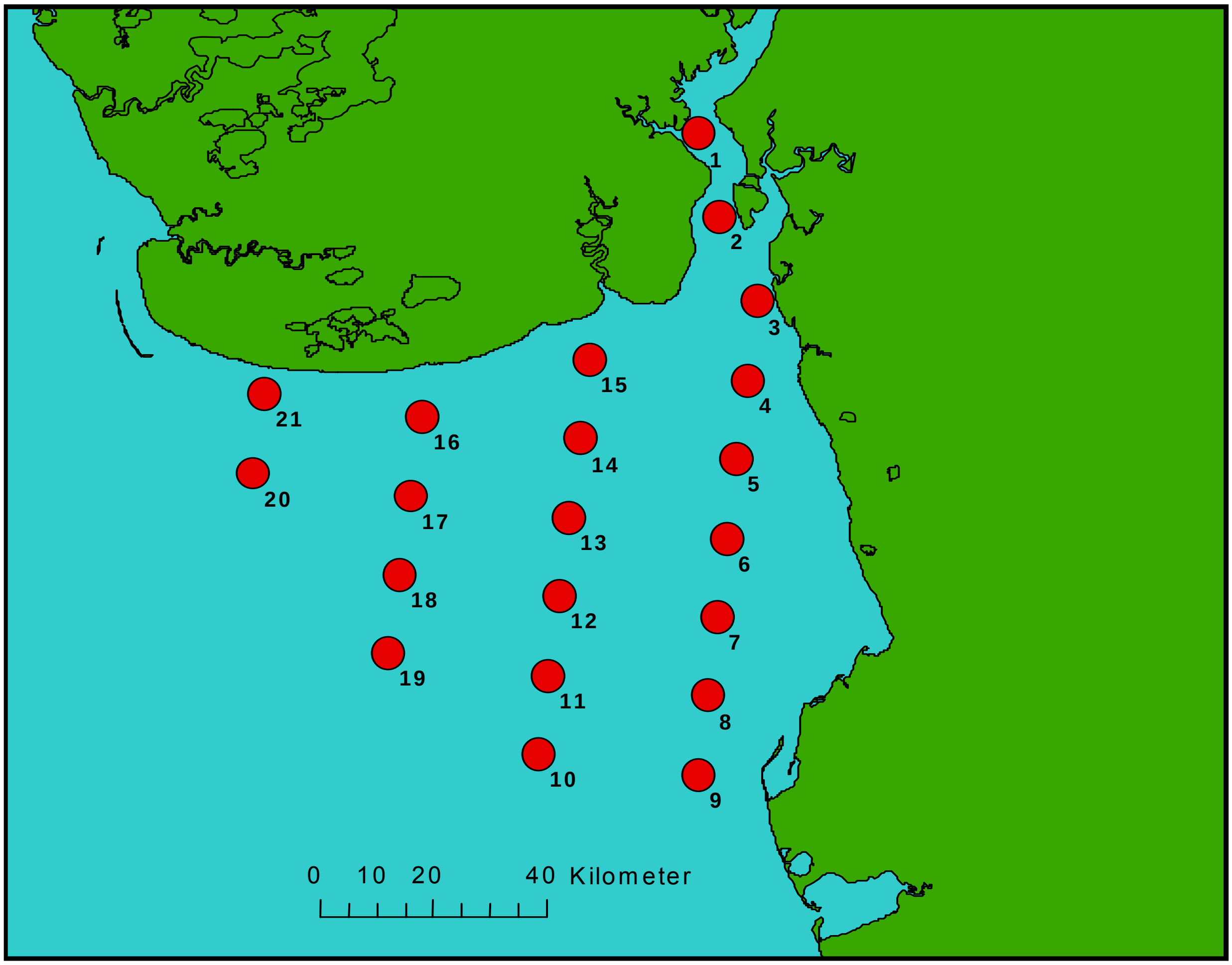
	K04-4 3cm FL			K04-4 6 cm FL		
Station	**Specific Growth**	**Daily Ration**	**P**	**Specific Growth**	**Daily Ration**	**P**
K1	-0.005	0.030	0.081	-0.011	0.010	0.044
K2	-0.014	0.014	0.038	-0.014	0.005	0.021
K3	-0.015	0.010	0.027	-0.014	0.003	0.015
K4	0.070	0.140	0.389	0.015	0.046	0.209
K5	0.192	0.352	1	0.115	0.216	1
K6	0.185	0.341	1	0.111	0.208	1
K7	0.080	0.137	0.410	0.018	0.043	0.207
K8	0.157	0.182	0.553	0.044	0.057	0.278
K11	0.279	0.320	1	0.171	0.198	1
K12	0.244	0.326	1	0.148	0.200	1
K13	0.139	0.339	1	0.083	0.208	1
K14	0.190	0.352	1	0.114	0.216	1
K15	0.191	0.356	1	0.110	0.209	0.959
K16	0.164	0.357	1	0.098	0.218	1
K17	0.139	0.350	1	0.083	0.214	1

Table 12.

	K04-6 3 cm FL			**K04-6 6 cm FL**		
Station	**Specific Growth**	**Daily Ration**	**P**	**Specific Growth**	**Daily Ration**	**P**
K1	-0.027	0.007	0.018	-0.022	0.003	0.011
K2	-0.029	0.002	0.004	-0.022	0.001	0.003
K3	-0.030	0.008	0.019	-0.025	0.003	0.01
K4	-0.020	0.007	0.017	-0.017	0.002	0.009
K7	0.223	0.352	1	0.103	0.165	0.765
K8	0.250	0.344	1	0.150	0.210	1
K11	0.270	0.342	1	0.163	0.209	1
K12	0.217	0.350	1	0.130	0.214	1
K13	0.166	0.361	1	0.099	0.220	1
K14	0.189	1.063	1	0.116	0.228	1
K15	0.202	0.381	1	0.120	0.233	1
K20	0.142	0.263	0.722	0.039	0.084	0.38
K21	0.003	0.033	0.092	-0.007	0.011	0.05
K22	0.203	0.372	1	0.121	0.227	1
K23	0.199	0.375	1	0.098	0.189	0.826
K24	0.033	0.068	0.187	0.003	0.022	0.102
K25	0.199	0.373	0.988	0.056	0.117	0.506

Table 13.

List of Figures



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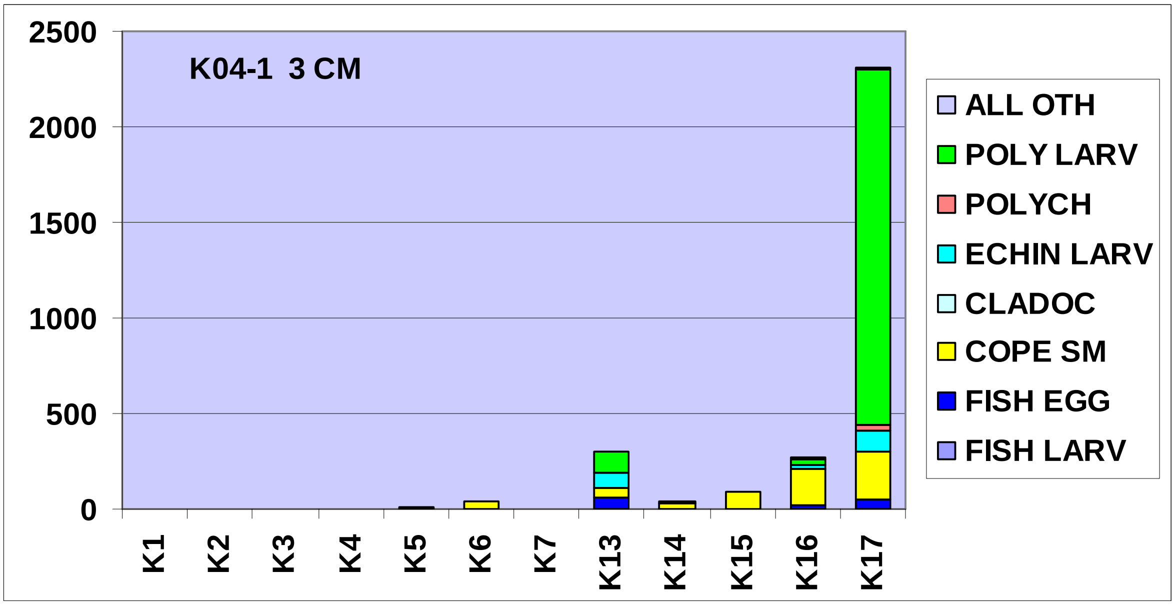
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CLADOC
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FISH EGG
FISH LARV

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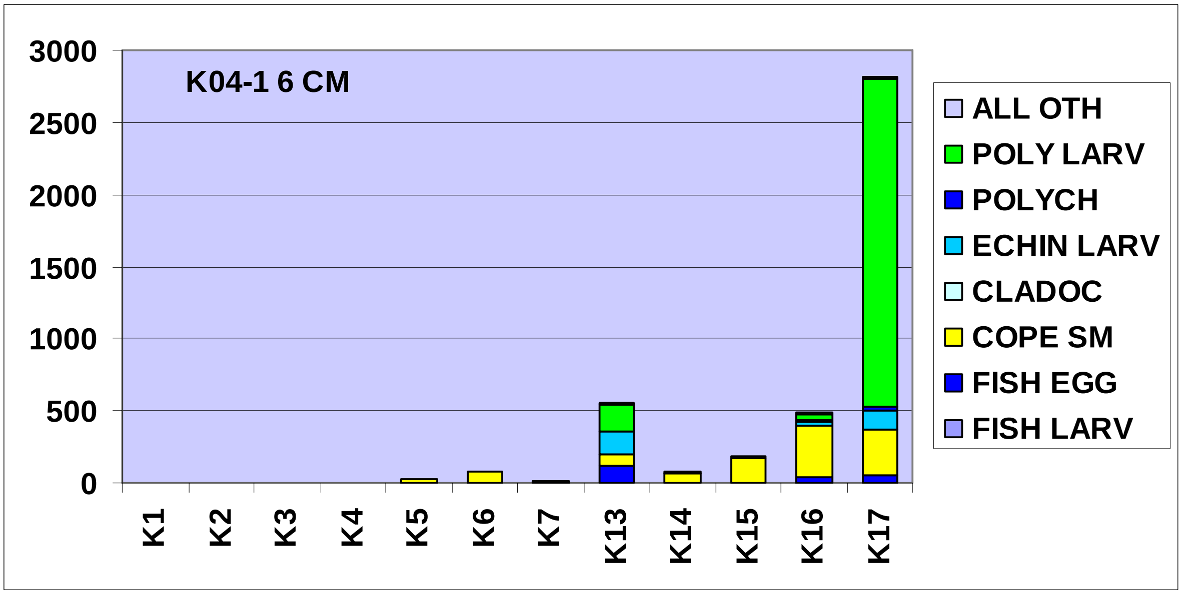
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Figure 2.

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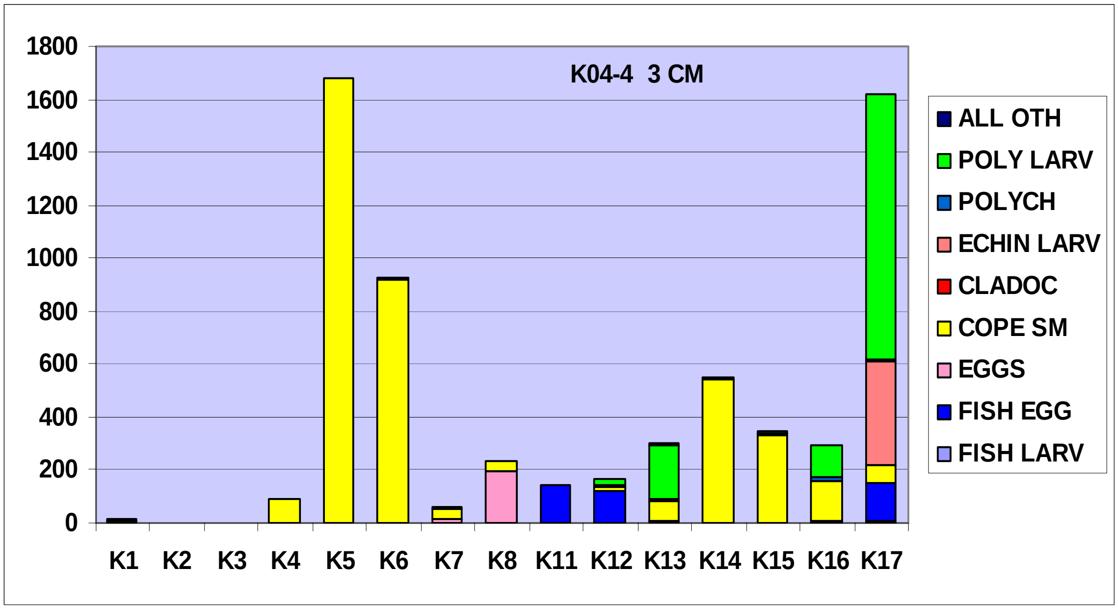
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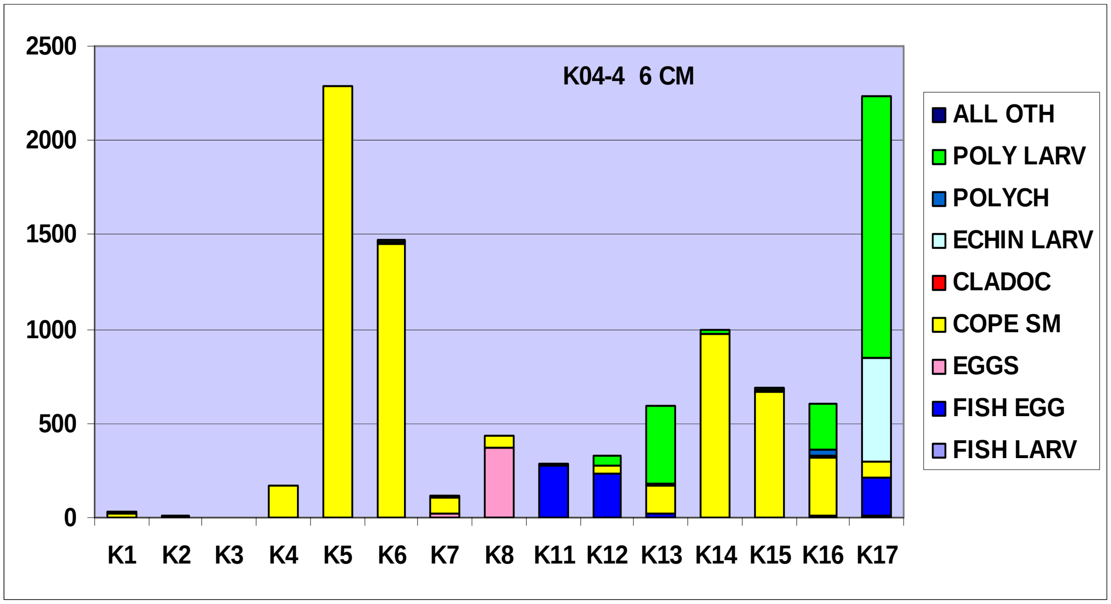
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Figure 3.

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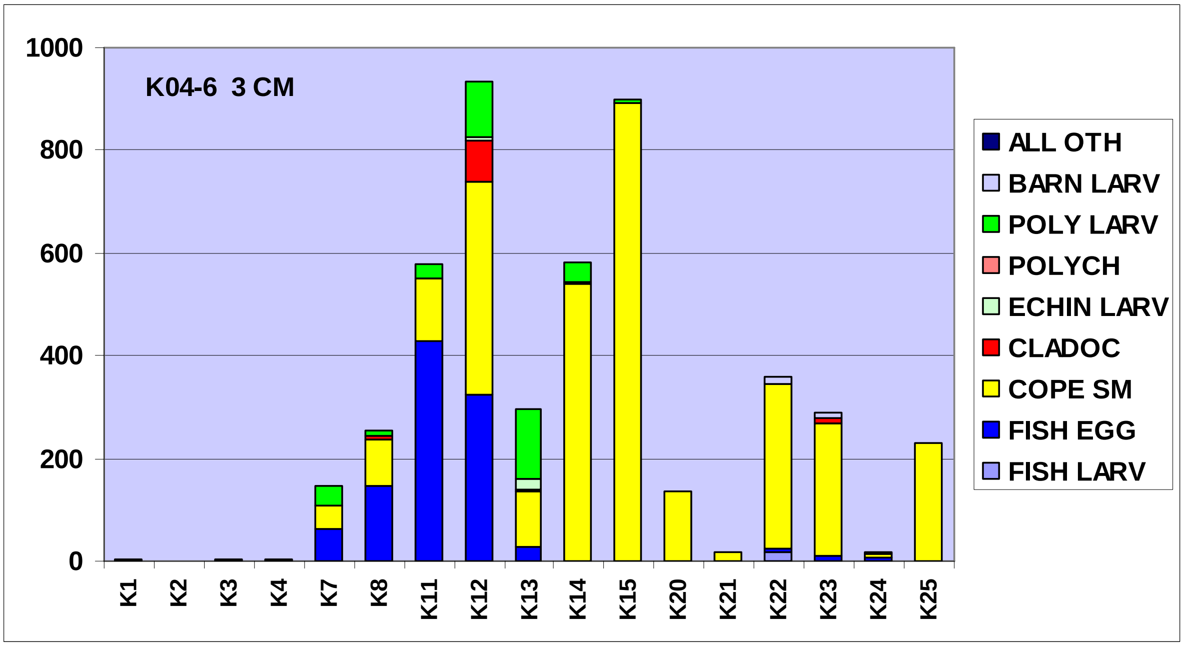
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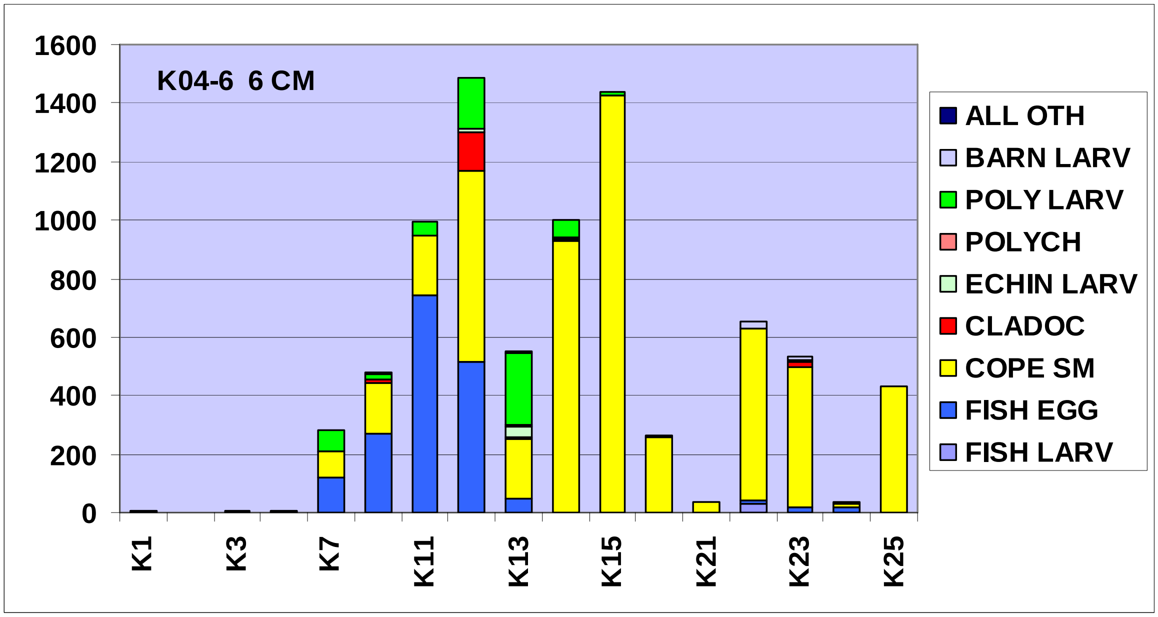
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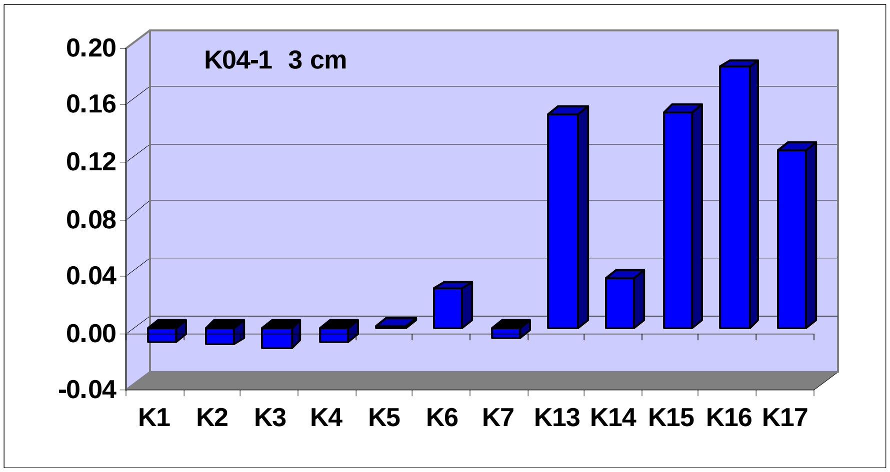
Figure 4.

A.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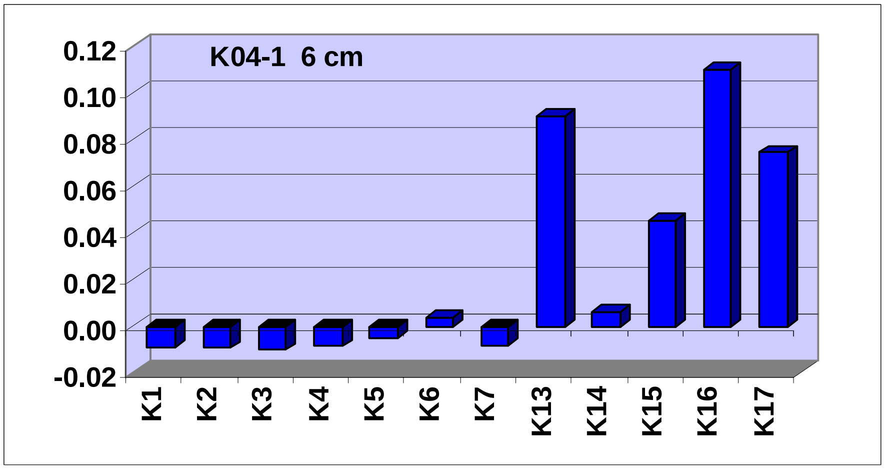
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Figure 5.

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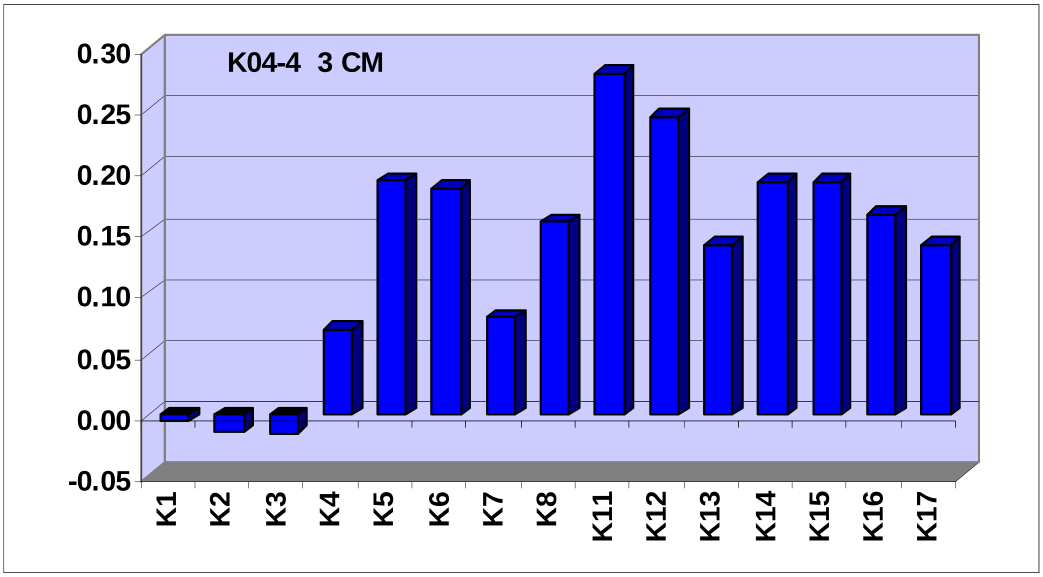
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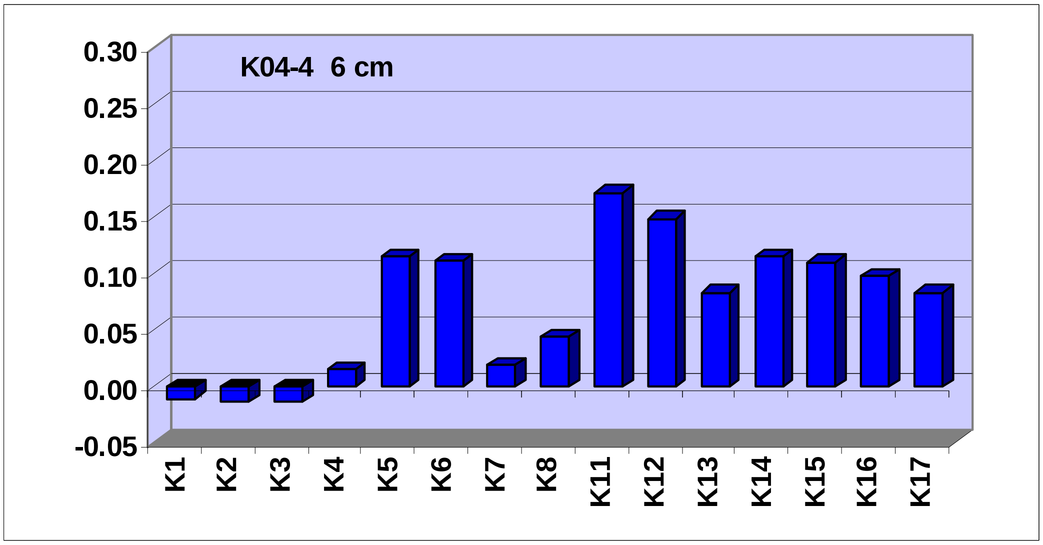
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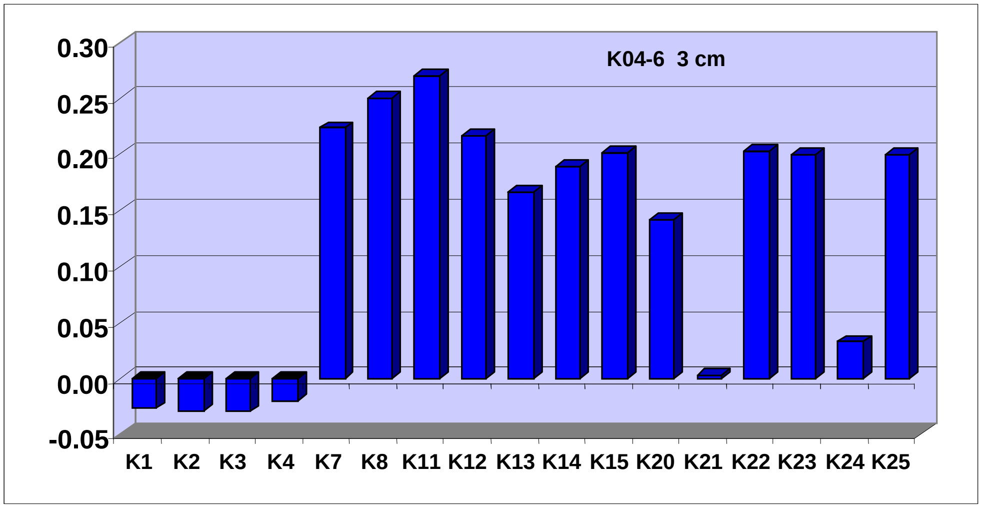
Figure 6.

A.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B.

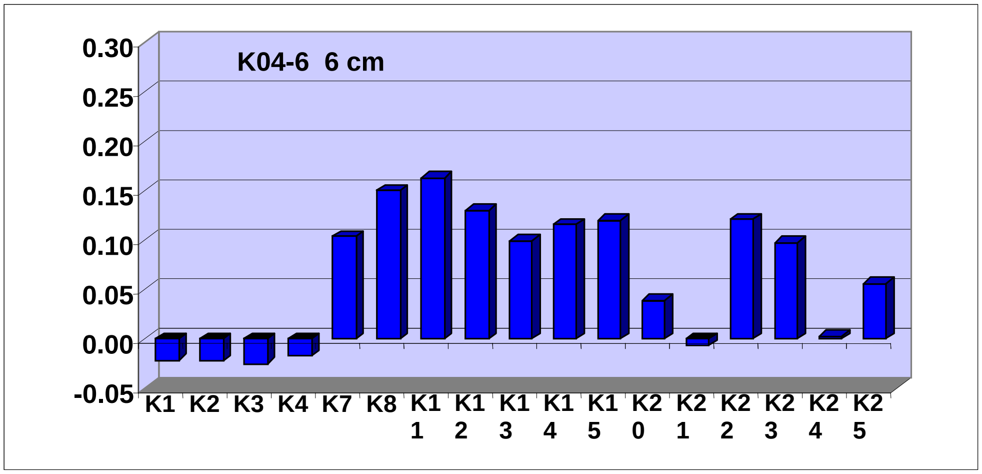
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Figure 7.

CONCLUSIONS

Juvenile salmonids were collected in 2003 and 2004 in Kuskokwim Bay, Alaska. In the two years of the study, all five species of juvenile Pacific salmon were collected with a modified Kvichak surface tow-net. Chum salmon (*Oncorhynchus keta)* were the most abundant salmonid taxon by nearly one order of magnitude, followed by coho salmon (*O. kisutch*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*), and sockeye salmon (*O. nerka*) in order of their abundance (Chapter 1). No sockeye salmon were collected in 2003, and they made up only 0.14% of the total catch of salmonids in 2004. Combining data from both study years, we determined an estuarine residence period for chum salmon juveniles from the middle of May until late July; no chum salmon were caught in August. Environmental conditions, particularly sea surface temperature (SST) changed remarkably during the juvenile outmigration, with uniformly low temperatures of 7˚C in May, increasing to SST as high as 15.6˚C in June. In May, distribution of juvenile chum salmon was confined primarily to the waters of the river plume, with fish leaving the plume towards the later part of their outmigration, indicating that they were using the river plume as a staging area to adjust to higher salinity water and possibly as a nursery area to protect them from visual predators (Thorpe 1994, Miner & Stein 1996). During their residence in Kuskokwim Bay, chum salmon juveniles were apparently growing in size, increasing from a mean fork length (FL) of 36.6 mm in May 16-22 to 45.9 mm FL in June 6-12, 2004 (Chapter 1).

Juvenile chum salmon appeared to switch their diet from primarily insects and harpacticoid copepods in the mouth of Kuskokwim River to small pelagic cyclopoid and calanoid copepods further in the estuary (Chapter 2). A similar composition of chum salmon diet was observed in Puget Sound (Duffy 2003). Chum salmon elsewhere apparently rely on a detritus-based food web (Sibert et al. 1977, Salo 1991). Several studies have indicated the predominance of small harpacticoid copepods in the diet of chum juveniles during their residence in estuaries (Healey 1979, Landingham 1982).

While in Kuskokwim Bay, most juvenile chum salmon were caught in low salinity waters near the river mouth and concomitant plankton tows indicated that very little zooplankton were available in this low salinity water. This may suggest that chum salmon fry may either have been subject to suboptimal feeding conditions or may have used the low salinity/high turbidity water for protection from predation pressure and as a staging area to adapt to higher salinity waters, while undertaking feeding excursions or relying on tidal transport to acquire prey (Chapter 2). Compared to other systems, chum salmon were characterized by a large percentage of empty stomachs, possibly suggesting that zooplankton might be patchily distributed within the bay, likely resulting in highly variable feeding success and growth rates.

In Kuskokwim Bay, juvenile chum salmon exhibited a loss in energy density that was coupled with an increase in fork length and weight, indicating the conversion of energy-rich storage tissue into growth (Chapter 3). This pattern is contrary to those reported from other areas. In addition, chum salmon caught during BASIS surveys in late September/early October, were not only significantly larger, but also had substantially elevated energy content (Farley *pers. comm.)*. It was also noteworthy that juvenile chum salmon that entered the bay later in the middle of June had a lower energy density than fish of the same size that entered the bay in the middle of May. This reduced energy density may be an effect of increased metabolic rates at higher sea surface temperature, raising questions about survival probability of different juvenile salmon migratory cohorts.

Juvenile chum salmon captured in Kuskokwim Bay ranged in age from 12 to 44 days (post emergence). Using these ages, the dates of emergence of chum salmon in the Kuskokwim watershed were calculated to be between 19 April and 24 May (Chapter 4). This represents the first estimate of emergence timing in this region. Because juvenile chum salmon were predominantly encountered in low salinity waters, we were unable to determine duration of residence in higher salinity habitats using otolith microchemistry. For the few fish that were characterized by movement to higher salinity habitats, duration of residence ranged from 8 to 18 days. Coupled with seasonal catch data, it appears that juvenile chum salmon in Kuskokwim Bay spend less than 30 days in areas characterized by salinities less than 24.

Models of juvenile chum salmon growth potential in Kuskokwim Bay indicated marked spatial and temporal variations in habitat quality, determined by variability in water clarity, zooplankton abundance, and water temperature (Chapter 5). Spatially, the bay appears comprised of three zones: 1) an inshore zone comprised largely of river plume with highly turbid water, 2) a transition zone associated with a front between the inshore zone and more marine conditions further offshore and 3) an offshore zone with lower turbidity and temperature/salinity more characteristic of Bering Sea water. Inshore, water clarity and zooplankton abundance were always very low, whereas SST was typically warmer than further offshore, especially early in the season. The transition zone typically had fairly clear water and elevated zooplankton abundance after the early phase of outmigration, with SST increasing steadily from early to late outmigration. The offshore zone had highest water clarity, with increases in zooplankton and water temperature during the outmigration period.

During the entire outmigration period, the inshore zone was typified by very low or negative growth potential (Chapter 5). That area had a combination of conditions (high turbidity, low zooplankton, and high temperature) that were detrimental to feeding and growth. The transition zone had relatively good foraging and high growth potential after the early period of outmigration, due to good water clarity and high abundance of small copepods. The offshore zone had relatively high growth potential, especially late in the outmigration period when increased water temperatures resulted in higher growth in the bioenergetic model. After the early period, growth potential of juvenile chum salmon seaward of the inshore zone was often a maximum rate allowed by water temperature. The model results confirm field observations that indicate that timing of outmigration may be an important factor in early marine growth of chum salmon juveniles in Kuskokwim Bay.

This study represents the first research effort on the estuarine ecology of juvenile chum salmon in Kuskokwim Bay, western Alaska. Results obtained from this study include information on timing of emergence and outmigration of chum salmon, species-specific patterns of estuarine distribution, chum salmon diet, energy density, and age, as well as first results of bioenergetic modeling of chum salmon juvenile growth potential in Kuskokwim Bay. Our results indicate that timing of outmigration may be of essential importance for condition, growth, and subsequent survival probability of juvenile chum salmon. This study also demonstrates the need for a more thorough understanding of this critical period in the early life of western Alaska salmonids. The large variation in environmental conditions and their potential effects on distribution, growth and survival probability, the spatial and temporal patterns of estuarine distribution of different salmon taxa and the potential for competition and predation between them, and the species-specific seasonal patterns of energy allocation during the estuarine outmigration are only a few of the many areas that are poorly studied. A more thorough understanding of these and other aspects of this critical period in the life of juvenile salmonids may provide some information on mechanisms responsible for regulating population size and on the role of environmental variation, which may be of particular importance in front of changing climatic condition as recently observed in the Bering Sea.

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Thorpe JE (1994) Salmonid fishes and the estuarine environment. Estuaries 17(1A):76-93

PUBLICATIONS

Peer-reviewed and limited distribution publications

1. Burril SE, Hillgruber N, Zimmerman CE (2006) Estuarine ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska. Proceedings of the 22nd Northeast Pacific Pink & Chum Salmon Workshop, Ketchikan, Alaska, pp 91-97

2. Zimmerman CE, Hillgruber N, Burril SE, St. Peters MA, Wetzel JD (2005) Offshore marine observation of willow ptarmigan including water landings, Kuskokwim Bay, Alaska. Wilson Bull 117(1): 12-14

Publications in preparation, submitted or pending

1. Hillgruber N, Zimmerman CE, Burril SE (*in prep*) Timing of outmigration and distribution during estuarine residence of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska
2. Burril SE, Hillgruber N, Zimmerman CE (*in prep*) Feeding ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, western Alaska.
3. Burril SE, Hillgruber N, Zimmerman CE (*in prep*) Patterns in energy density of chum salmon (*Oncorhynchus keta*) during estuarine residence in Kuskokwim Bay, Alaska.
4. Zimmerman CE, Hillgruber N, Burril SE, Wang S (*in prep*) Emergence timing and duration of estuarine residence of juvenile chum salmon captured in Kuskokwim Bay, Alaska.
5. Haldorson LJ, Hillgruber N, Burril SE, Zimmerman CE (*in prep*)
6. Zimmerman CE, Hillgruber N (*in prep*) Distribution of sticklebacks in Kuskokwim Bay, Alaska

OUTREACH

Conference presentations

1. Hillgruber N, Burril SE, Zimmerman CE (2007) Early marine ecology of uvenile salmon in Western Alaska: estuaries, bays, and deltas. Sustainability of the Arctic-Yukon-Kuskokwim salmon fisheries. What do we know about salmon ecology, management, and fisheries? February 2007, Anchorage, Alaska
2. Hillgruber N, Zimmerman SE, Burril SE (2007) Distribution, condition, and age of chum salmon (*Oncorhynchus keta*) juveniles in Western Alaska. Marine Science in Alaska: 2007 Symposium. January 2007, Anchorage, Alaska
3. Hillgruber N, Zimmerman CE (2006) Distribution of sticklebacks in Kuskokwim Bay, Alaska. 33rd Meeting of the Alaska Chapter, American Fisheries Society, November 13-16, 2006, Fairbanks, Alaska
4. Peterson V, Hillgruber N (2006) Seasonal distribution of pond smelt (*Hypomesus olidus*) and rainbow smelt (*Osmerus mordax*) in Kuskokwim Bay, Alaska. 33rd Meeting of the Alaska Chapter, American Fisheries Society, November 13-16, 2006, Fairbanks, Alaska. (Poster)
5. Hillgruber N, Burril SE, Zimmerman CE, Haldorson LJ (2006) Estuarine ecology of juvenile chum salmon in Kuskokwim Bay, Alaska. Juneau Center, SFOS UAF Friday Seminar Series, February 24, 2006.
6. Hillgruber N, Burril SE, Zimmerman CE, Haldorson LJ (2006) Estuarine ecology of juvenile chum salmon in Kuskokwim Bay, Alaska. UAF Student Chapter of the American Fisheries Society, University of Alaska Fairbanks, Fairbanks, Alaska. February 2, 2006.
7. Zimmerman CE, Hillgruber N (2006) Distribution of sticklebacks in Kuskokwim Bay, Alaska. 5th International Conference on Stickleback Behavior and Evolution. 30 July/August 2006, Anchorage, Alaska. (Poster)
8. Zimmerman CE, Hillgruber N, Burril SE, Haldorson LJ (2006) Estuarine ecology of juvenile chum salmon in Kuskokwim Bay, Alaska. Marine Science in Alaska: 2006 Symposium. January 2006, Anchorage, Alaska.

9. Hillgruber N, Zimmerman CE, Burril SE (2005) Timing of outmigration and distribution during estuarine residence of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska. 135th Annual Meeting, American Fisheries Society, September 2005, Anchorage, Alaska.
10. Hillgruber N, Zimmerman CE, Burril SE (2005) Timing of outmigration and distribution during estuarine residence of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska. 29th Annual Larval Fish Conference. July 11-14, 2005, Barcelona, Spain.
11. Burril SE, Hillgruber N, Zimmerman CE (2005) Estuarine ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Alaska. 22nd Northeast Pacific Pink & Chum Salmon Workshop. February 23-25, 2005, Ketchikan, Alaska.
12. Burril SE, Hillgruber N, Zimmerman CE (2004) Feeding ecology and energy density of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay. 31st Meeting of the Alaska Chapter, American Fisheries Society, November 14-18, 2004, Sitka, Alaska.

OTHER OUTREACH

1. Board readies salmon research project. Biologists search for causes of diminishing salmon numbers. Katrina Baldwin. The Tundra Drums, June 26, 2003, p 6
2. Discussion with regional representatives concerning research activities in Kuskokwim Bay, Christian Zimmerman, Kuskokwim Fishery Recourses Coalition, March 18, 2004.
3. Presentation of research activities in Kuskokwim Bay and discussion with regional representatives, Christian Zimmerman, Kuskokwim Interagency Planning Meeting, March 30, 2005.
4. Presentation of preliminary research activities and results, Christian Zimmerman, Kuskokwim Interagency Planning Meeting, November 2, 2005.
5. Provided PowerPoint presentations to Doug Molyneaux for inclusion in presentations at local venues throughout the Kuskokwim River watershed, Ongoing.

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