

Final Report

**Feeding Ecology of Maturing Sockeye Salmon  
(*Oncorhynchus nerka*) in Nearshore Waters  
of the Kodiak Archipelago**

by

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## Abstract

The diet and feeding behavior of maturing sockeye salmon (*Oncorhynchus nerka*) were investigated during the final marine phase of the spawning migration, immediately prior to re-entry into natal streams. The stomach contents of commercially caught sockeye salmon, migrating through the nearshore waters of the Kodiak Island Archipelago during 1998 and 1999, were examined to determine level of feeding activity and taxa of dominant prey items. Representative samples were collected throughout the majority of the migration (early June to late August) from areas known to be principally migration corridors, and from areas proximate to several natal streams. Dominant prey of sockeye salmon were decapod larvae, Pacific sand lance (*Ammodytes hexapterus*), and the pteropod *Limacina helicina*. Feeding levels and dominant prey varied between areas and within areas over time. Feeding levels for the population appear to gradually diminish, rather than ceasing abruptly, prior to entering freshwater.

## Introduction

The Kodiak Archipelago is located in the western Gulf of Alaska approximately 400 km southwest of Anchorage. The archipelago extends approximately 296 km from the Barren Islands in the north to Tugidak and Sitkinak Islands at the south end. The islands consist of approximately 13,000 km<sup>2</sup> in surface area, with roughly 4,000 km of shoreline. The island group lies 60 km due south of the entrance to Cook Inlet and is separated from the Alaska Peninsula on the west by Shelikof Strait. Kodiak Island proper, at 9,300 km<sup>2</sup>, is the second largest island in the United States.

Five species of Pacific salmon are commercially harvested in Kodiak Archipelago waters. Second only to pink salmon (*Oncorhynchus gorbuscha*) in abundance, sockeye salmon (*O. nerka*) are the economic mainstay of the Kodiak commercial salmon fishing industry. As the principal targeted species of the fishery, sockeye landings accounted for approximately 61% (\$19,014,000) of the total ex-vessel value for salmon in the Kodiak area during the period 1994 to 1998 [ADF&G 1999].

Sockeye salmon are anadromous, typically spending their first one to three years rearing in freshwater lakes, then out-migrating to the marine environment where they will spend another one to three years feeding [Foerster 1968]. During the final spring at sea, as maturing adults, they begin a directed migration back to their natal streams to spawn [French et al. 1976]. The role of the freshwater environment for sockeye salmon production is well understood [Koenings and Burkett 1987; Stockner 1987], but knowledge of marine life history suffers from numerous data gaps, except in the areas of ocean distribution and offshore food web dynamics [Pearcy et al. 1988; Brodeur 1990; Burgner 1991].

An array of research efforts has focused on the feeding ecology of juvenile sockeye salmon in the nearshore marine environment [Brodeur and Pearcy 1990; Landingham et al. 1998] and immature sockeye salmon in offshore Gulf of Alaska waters [Allen 1956; Pearcy et al. 1988; Walker and Myers 1994]. In Brodeur's [1990] review of the feeding habits of salmon, oceanic phase sockeye fed on a variety of organisms including squid, fish, euphausiids, amphipods and pteropods, while maturing sockeye salmon within coastal waters were predominantly zooplanktivores, feeding largely on euphausiids, hyperiid amphipods, and decapod larvae.

The final stages of maturation in salmon are critical to successful reproduction. During the last four months of ocean life, prior to re-entering fresh water, the fish will consume as much food as in all previous months combined, doubling their body weight during the last 5–6 months of life [Brett 1983; Figure 1]. Growth is directed towards both storage of energy reserves and production of gonadal tissue [Brett 1995]. The fish cease feeding at some point during the final stage of the spawning migration, while at the same time undergoing stress associated with changes in osmoregulation, upstream migration and

the partitioning of somatic energy into gonadal growth [Burgner 1991]. At the time of spawning, the fish have depleted a majority of energy stores and die shortly thereafter [Brett 1995]. Perturbations from human activities can increase metabolic demands, decrease prey diversity and reduce prey abundance, adversely affecting growth and available energy stores [Brett 1983; Brett 1995; Higgs et al. 1995].

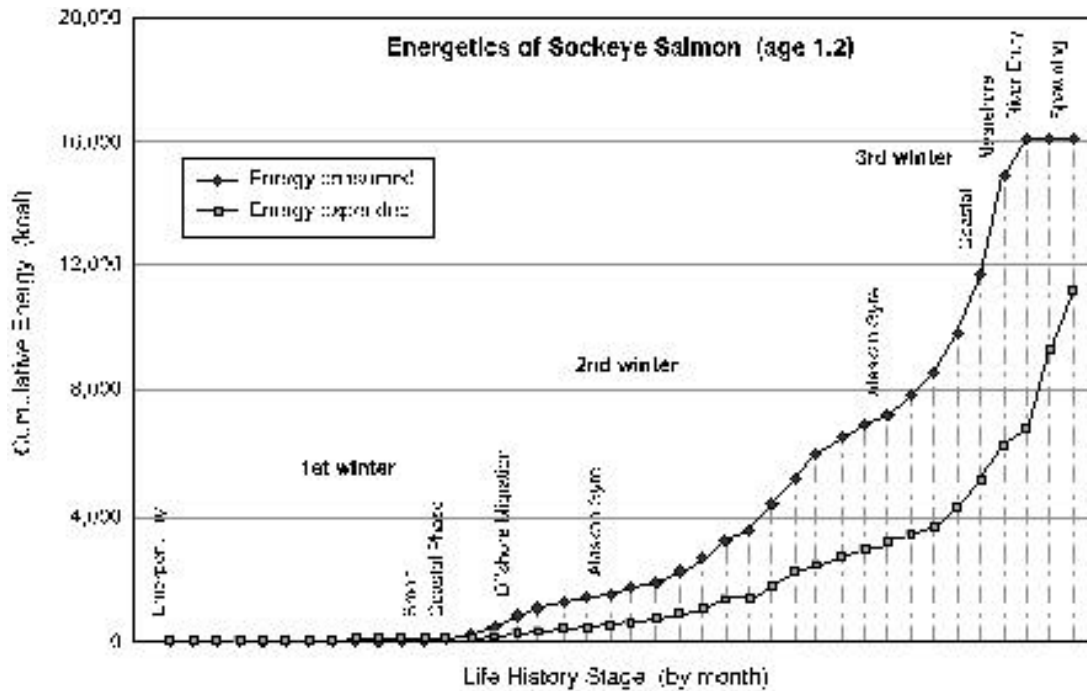


Figure 1. Life energetics of hypothetical age 1.2 Babine Lake sockeye salmon. Adapted from Brett [1983].

Current knowledge of the nearshore feeding ecology of mature sockeye is limited to several research efforts, spanning an area from Oregon to the Sea of Okhotsk, and depicts sockeye salmon as opportunistic feeders. This precludes generalization to other locations, as most studies are site specific [Andrievskaya 1966; Nishiyama 1977; Beacham 1986; Helton 1991]. A recurrent theme in these studies is that euphausiids, fish larvae, decapods and amphipods are the major dietary components of maturing fish in coastal waters. Beacham [1986] reported that for sockeye > 55 cm FL (fork length) sampled from Juan de Fuca Strait (between Washington State and British Columbia), dominant prey (by volume) were euphausiids, amphipods, crab larvae, and mysids. Helton [1991] found that stomach contents of maturing sockeye near Port Moller were dominated by fish larvae, euphausiids and crab zoea. In offshore areas of Bristol Bay, Nishiyama [1977] reported that the diet of maturing sockeye salmon sampled in the “basin” area was comprised of squid, fish larvae, amphipods, and euphausiids, whereas for sockeye from the “continental shelf” area diet was predominately euphausiids. In Andrievskaya’s [1966] research in the coastal waters of the Sea of Okhotsk, squid were the dominant food item in sockeye stomachs, followed by fish, decapod larvae, and euphausiids.

While mature sockeye salmon cease feeding when they near and finally ascend their natal streams to spawn, the environmental cues and timing that lead to feeding cessation are at present not well



understood. The incidence of feeding (proportion of the population actively feeding) varies by time and geographic location. Helton [1991] found that the occurrence of empty stomachs ranged from 16% to 38% in maturing Bristol Bay bound sockeye salmon sampled during June and July 1988–90. In the Juan de Fuca Strait, Beacham [1986] found a 30% occurrence of empty stomachs from maturing sockeye sampled during 1967–1968.

Evaluation of the food web dynamics and feeding habits of mature salmon is necessary to understand potential ingestion pathways for hydrocarbon contamination, especially in areas swept by currents from potential oil exploration and drilling. Kodiak waters make up such an area. Prey taxa, identified in various studies in coastal areas, exhibit varied life history strategies including habitat utilization. Assessment of differences (temporal and spatial) in contamination of these habitats should lead to a more concise evaluation of the impact on sockeye salmon once their prey utilization is known. Identification of feeding incidence and the stage of cessation provides a clearer understanding of contamination potential via ingestion.

Since no published information existed on the diet of maturing sockeye salmon from Kodiak waters, the Alaska Department of Fish and Game (ADF&G) initiated a stomach content study during 1994. The objective was to determine whether commercially harvested sockeye salmon from the east and west sides of the Kodiak Archipelago were feeding and, if so, what were their dominant prey.

In July 1994, stomach samples were collected from the Eastside and Westside sections of Kodiak Island. During early July, a majority (63%) of sockeye salmon sampled were found to be feeding, while in late July the incidence of feeding was sharply reduced to 24%. For both periods combined, an estimated 36% of Eastside and 44% of Westside fish stomachs examined were found to contain food. Of the identifiable prey categories, pooling all areas and periods, sandlance *Ammodytes hexapterus* were found in 26% of feeding sockeye salmon, pteropods *Limacina helicina* in 21%, euphausiids *Thysanoëssa spinifera* in 16%, and crab glaucothoe in 34%. Both time and area effects on feeding incidence and dietary content were found to be significant.

Research areas addressed in the present study include the feeding incidence of maturing fish as they migrate along the nearshore coast, the migration stage of feeding cessation as they approach their natal streams, and the identification of major prey taxa consumed by actively feeding sockeye salmon. The results obtained from the initial study in 1994 indicated that a broader-scale sampling effort, both spatially and temporally, was needed to address these objectives adequately. Unlike some locations such as Bristol Bay, local stocks of sockeye salmon are present in Kodiak waters from May through October, with the majority of catch and escapement occurring in June, July and August. Several major stocks exhibit bimodal run timing, with early run fish present through mid-July and late run fish present mid-July through October. Although the major migration pathways of returning sockeye salmon are well known, variations in migration patterns and timing can occur between years [D. Prokopowich, ADF&G, Kodiak, personal communication]. To provide a comprehensive picture of sockeye feeding behavior, sampling was designed to cover the major nearshore migration areas in the Kodiak Management Area and occurred on a weekly basis during the months of June, July and August. To allow for this scope of coverage, stomach samples were collected from the commercial fleet already fishing in these waters during this time frame.

The North Shelikof Strait lease area is important for maturing sockeye salmon of Kodiak origin, as well as from other regions. Prevailing currents in lower Cook Inlet and Shelikof Strait potentially extend impacts from oil and gas development throughout the inshore areas of the Kodiak Archipelago and the eastern Alaska Peninsula. The results of this research should be applicable to oil and natural gas exploration and development, contingency planning for spill mitigation, as well as establishment of pre-impact baseline measures.

## Objectives

1. Determine the percentage of sockeye salmon that were feeding from three locations known to be migration corridors (Eastside Kodiak, Westside Kodiak, and Alaska Peninsula areas) on a weekly basis during June through August.
2. Determine the percentage of sockeye salmon that were feeding in an area <5 km from their natal stream terminus (Moser–Olga Bay sections) weekly during June through August.
3. Identify and quantify the major prey taxa in sockeye salmon stomachs within the migration corridors and determine if location or period has an effect on prey types utilized.
4. Identify potential mechanisms of indirect effects on sockeye salmon, through prey utilization, due to development in oil and gas lease areas.

## Methods

This study was conducted in conjunction with the existing ADF&G salmon catch sampling program. All sockeye salmon in this study were collected from deliveries of the commercial catch during the 1998 and 1999 fishing seasons. Commercial fishing periods are set in-season by ADF&G, based on estimates of fish abundance and escapement counts. The initial commercial salmon opening begins 9 June and fishing occurs through September. The Kodiak commercial salmon fishing area is comprised of all Alaska statute waters south of 58° 52' N, west of 150° W, north of 55° 30' N, and east of a line extending south from 156° 20' 13' W.

Waters were classified as either migration corridors (no significant sockeye systems, < 20 km distance), terminal harvest areas (waters in vicinity of natal stream mouth) or transition areas (waters intermediate between migration and terminal harvest areas). To facilitate sampling, the boundaries of these study areas corresponded to ADF&G management districts and sections (Table 1). This allowed the use of harvest ticket data to verify date, location and species composition of the delivered catch prior to sampling. Based upon historical catch and tagging studies [Moser 1898; Tyler et al. 1981; Barrett and Nelson 1994], five areas were identified as migration corridors, one as a terminal harvest area, and one as a transition area for inclusion in this study (Figure 2).

Table 1. Study sample areas by classification and corresponding ADF&G descriptions.

Classification	Sample Area	ADF&G District	ADF&G Section(s)	ADF&G Statistical Area(s)
Migration	Westside Kodiak	Northwest Kodiak	Central	254 - 10, 40; 253 - 11, 14, 31 - 35
Migration	Eastside Kodiak	Eastside Kodiak	Sitkalidak, Two-Headed & Seven Rivers	258 - 10 through 70
Migration	Mainland	Mainland	Katmai, Alinchak Bay & Cape Igvak	262 - 60 through 95
Migration	Ayakulik	Southwest Kodiak	Inner & Outer Ayakulik	256 - 10, 15, 20
Migration	Cape Alitak	Alitak Bay	Cape Alitak	257 - 10, 20
Transition	Moser Bay	Alitak Bay	Moser – Olga Bay	257 - 41
Terminal	Olga Bay	Alitak Bay	Moser – Olga Bay	257 - 40

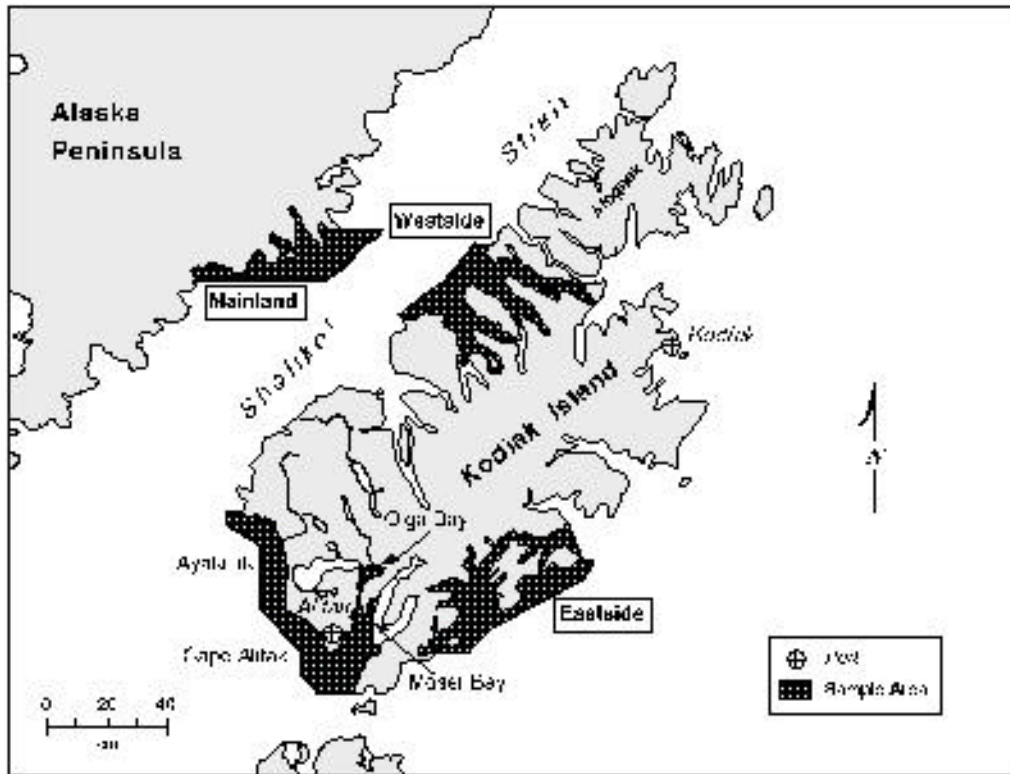


Figure 2. Locations and boundaries of sampling areas. Samples were collected and examined at Alitak.

Stomachs were collected on a weekly basis, dependent upon availability, through the last week of August. Sample periods corresponded to ADF&G statistical weeks (Table 2). Fish were not always available each period for sampling for several reasons, including area closures, inclement weather, and a lack of sockeye in areas open to fishing. Fish were harvested in the five migration areas with purse seines exclusively; the transition and terminal areas are legally restricted to the use of set-gillnets only. Samples consisted of 100 sockeye stomachs (minimum) obtained from a single area and weekly period. All fish were assumed to be mature and of predominately local origin. No prior selection was made for size, condition factor or sex of the fish. Prey were assumed to be equally available to all fish within a single sample. All stomachs were obtained at the Ward's Cove fish processing facility, located in Alitak, Kodiak Island, during the course of normal processing. Plant employees headed the fish and whole, intact digestive tracts (from the esophagus to the pyloric sphincter) were recovered on the processing line immediately after evisceration.

Table 2. ADF&G statistical week and corresponding calendar dates.

ADF&G Statistical Week	Calendar Dates
24	7 Jun – 13 Jun
25	14 Jun – 20 Jun
26	21 Jun – 27 Jun
27	28 Jun – 4 Jul
28	5 Jul – 11 Jul
29	12 Jul – 18 Jul
30	19 Jul – 25 Jul
31	26 Jul – 1 Aug
32	2 Aug – 8 Aug
33	9 Aug – 15 Aug
34	16 Aug – 22 Aug
35	23 Aug – 29 Aug

### **Incidence of feeding**

Stomachs collected from all seven areas were examined for incidence of feeding. The proportion of fish in a sample exhibiting evidence of active feeding was termed incidence of feeding. The digestive tract was incised and examined on site for presence or absence of prey items; stomachs containing prey items, regardless of type or quantity, were classified as feeding. Stomachs without evidence of any food items were classified as non-feeding.

Differences in incidence of feeding within areas and among time periods, and differences among areas during the same time period were tested for significance with contingency tables using log-likelihood (G) statistics [Zar 1996]. Sockeye salmon are physically constrained to migrate sequentially from Cape Alitak through Moser Bay and into Olga Bay on the way to their natal streams (Figure 3). Differences in incidence of feeding among these areas and periods were used to examine the question of feeding cessation.

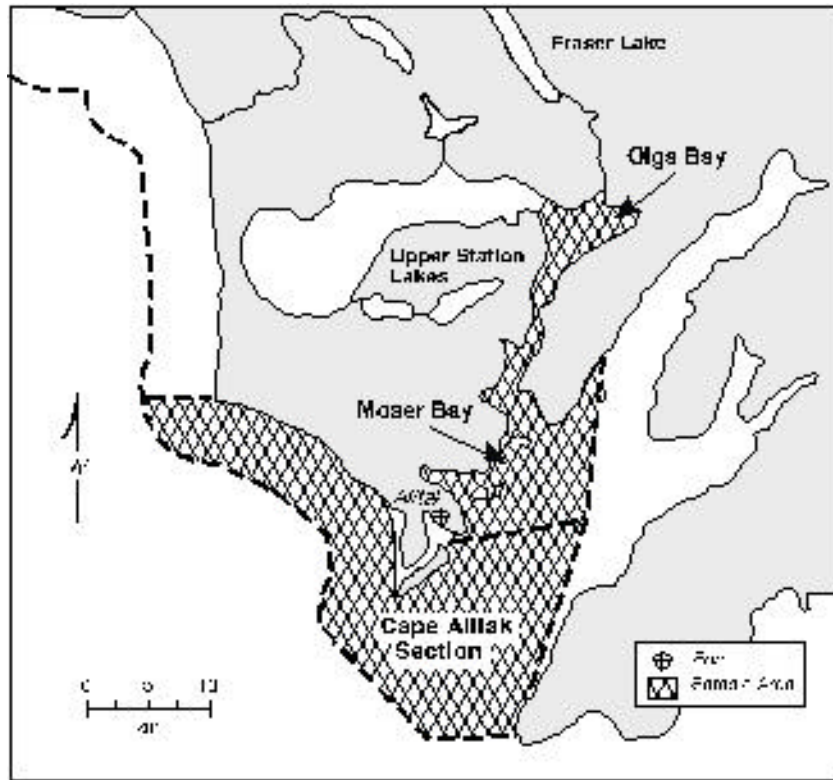


Figure 3. Location of Cape Alitak, Moser Bay and Olga Bay areas. Fraser Lake and Upper Station Lakes are the major sockeye systems in Olga Bay.

### Diet

Prey analysis was performed on samples collected from three migration corridors: the Mainland (Alaska Peninsula), Eastside Kodiak and Westside Kodiak sections (Figure 1). Subsamples of stomachs showing evidence of feeding, based on external characteristics, were collected whole and intact for further analysis of the actual prey items. An attempt was made to collect  $n = 30$  stomachs from each sample. These stomachs were frozen on site and were examined in laboratory facilities located at the University of Alaska Fairbanks. Freezing avoided the use of hazardous chemicals around human food. Similar to other studies [Allen and Aron 1958; Dell 1963], comparative trials early in this project showed that freezing resulted in samples with equal or less degradation than samples preserved with standard fixatives. In the laboratory, stomachs were thawed, weighed whole, opened, and the contents rinsed into a beaker. The empty stomach was re-weighed, with the difference between the whole and empty weights taken as the stomach content weight.

Digestive state of the stomach contents was rated subjectively, on a scale of one to four. A rating of one indicated the contents were largely digested—typically with fish remains consisting primarily of skeletal parts and invertebrate remains consisting of the carapace and detached appendages. A rating of four indicated the remains were fresh and largely undigested—fish had intact skin and fins and invertebrates had all appendages present. The digestion rating was based on the dominant taxa (by volume) found in the stomach.

Prey were identified and counted under a dissecting microscope to the lowest practical taxa. The number of each taxa found in each stomach was recorded. In the case of highly digested prey items, counts were made of uniquely identifiable parts, e.g., eye capsules or urostyles. For statistical analysis, prey were assigned to one of seven major categories: fish, pteropod, decapod, amphipod, cumacean, euphausiid or other [Nishiyama 1968; Nishiyama 1977; Pearcy et al. 1984; Beacham 1986; Pearcy et al. 1988; Brodeur and Pearcy 1990]. According to Bowen [1996], large numbers of individual prey species can result in undue emphasis on taxonomic, rather than functional differences between prey items. Use of higher levels of classification is statistically more efficient [Crow 1982]. Due to the several orders of magnitude difference in size of prey items and varying degrees of digestion, weights of individual prey items would be subject to large errors [Berg 1979; Hyslop 1980; Tirasin and Jørgensen 1999] and as such were not recorded.

To assess the adequacy of sample sizes (e.g.,  $n = 30$ ) used in characterizing the breadth of diet, all individual fish diets were pooled into a single unit and sampled randomly. The cumulative number of prey taxa and prey categories accounted for were then plotted against sample size [Landingham et al. 1998; Hurtubia 1973]. This random sampling continued until an asymptote and stability was reached. Ten runs each were made, and the median values were used to assess sample sizes.

Prey contents for each sample were initially characterized using frequency of occurrence (FOcc) and percent composition by number (%N) [Bowen 1996]. Frequency of occurrence is the proportion of fish in a sample that contained one or more items of a particular prey category, and provides a measure of the uniformity of diet selection. It does not indicate dietary importance because a single item is weighted equally to a numerous item. Percent composition by number is the number of items from a prey category expressed as a proportion of the total number of prey items in the sample. Although it does not account for differences in size of prey items, and thus the energy contribution, it does provide a measure of selectivity for a particular prey category. Differences in the degree of feeding among samples were compared using analysis of variance to examine differences in mean prey weights.

Contingency table analysis of prey category counts, using G-statistics, was used to test for overall differences in food habits among areas during the same time period, and within areas across time. Although counts do not necessarily reflect relative importance of prey in the diet, they do indicate differences in the food habits themselves [Crow 1982]. The Kruskal–Wallis procedure, a non-parametric equivalent of one-way ANOVA [Conover 1980], was used to test for area and period effects on utilization of individual prey categories, again using counts. When significant differences were detected, post-hoc comparisons were made using Tukey’s honestly significant difference test [HSD; Zar 1996] at a familywise error rate of  $p = 0.05$ . Bias, due to size differences between prey, is minimal when using counts among similarly sized organisms.

Commonly classified as opportunistic, the question of homogeneity or heterogeneity in feeding strategies, for both the individual and the population, was examined. The diversity of diet for the sampled population ( $H_{pop}$ ) was calculated using the Shannon–Weaver diversity index [Pielou 1975]:

$$H_{pop} = - \sum_{i=1}^n P_{ij} \log P_{ij} \quad (1)$$

where  $P_{ij}$  is the proportion of prey category  $i$  in the  $j$ th predator. The mean individual diversity ( $H_{ind}$ ) was calculated:

$$H_{ind} = \frac{1}{N} \sum_{i=1}^n P_{ij} \log P_{ij} \quad (2)$$

where  $N$  is the total number of predators. When diet is represented by a single prey category,  $H = 0$ . Diversity is at maximum when all prey categories are represented equally. Use of the Shannon–Weaver index provides a relatively objective indication of niche breadth [Marshall and Elliott 1997]. To graphically examine differences in individual versus population feeding habits Tokeshi plots [Tokeshi 1991] were constructed, plotting mean individual diet diversity against group diet diversity (Figure 4).

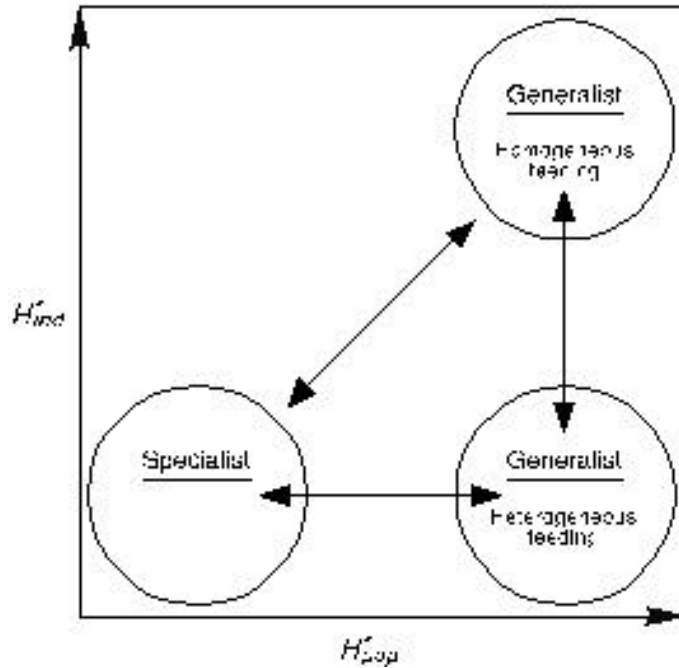


Figure 4. Interpretation of Tokeshi plot. A population with a low individual diversity and a low population diversity corresponds to a specialist, whereas a population with a high individual diversity and a high population diversity indicates a generalist with a homogenous feeding regime.

## Results

### Incidence of feeding

From the seven areas identified for this study, a total of 52 samples were collected in 1998 (Table 3), and 49 in 1999 (Table 4). This represents 11,702 individual sockeye stomachs examined for incidence of feeding. The proportion of fish in any one sample exhibiting evidence of active feeding varied greatly within area and time strata, ranging from 0% to 97% (Figure 5). The highest proportion of fish feeding were found in the Mainland migration corridor samples in 1999, the lowest proportions were during 1998 and 1999 in Olga Bay, the terminal harvest area.

Table 3. Feeding proportions for 1998 samples.

1998	Sample Area	Catch Date(s)	Sample Period	Sample Size	Number Feeding	Proportion Feeding	C.I. (95%)	
							Upper	Lower
<b>Migration Corridors</b>	Ayakulik	14 Jun	25	114	5	0.044	0.090	0.017
	Ayakulik	20–21 Jun	26	114	47	0.412	0.494	0.334
	Ayakulik	27–29 Jun	27	101	42	0.416	0.503	0.333
	Ayakulik	6–9 Jul	28	126	86	0.683	0.751	0.608
	Ayakulik	14–16 Jul	29	113	92	0.814	0.872	0.744
	Ayakulik	27–29 Jul	31	129	77	0.597	0.670	0.521
	Ayakulik	10–11 Aug	33	144	42	0.292	0.360	0.230
	Ayakulik	10–12 Aug	33	120	76	0.633	0.707	0.555
	Ayakulik	18 Aug	34	119	67	0.563	0.640	0.483
	Ayakulik	20 Aug	34	125	82	0.656	0.727	0.580
	Cape Alitak	9–10 Jun	24	117	37	0.316	0.394	0.245
	Cape Alitak	17–18 Jun	25	103	67	0.650	0.729	0.566
	Cape Alitak	28 Jun	27	104	73	0.702	0.775	0.620
	Cape Alitak	6 Jul	28	96	54	0.563	0.649	0.473
	Cape Alitak	16 Jul	29	142	55	0.387	0.459	0.319
	Cape Alitak	20–21 Jul	30	121	47	0.388	0.467	0.314
	Cape Alitak	3–4 Aug	32	116	39	0.336	0.415	0.264
	Cape Alitak	4 Aug	32	110	51	0.464	0.546	0.382
	Cape Alitak	13 Aug	33	124	91	0.734	0.798	0.661
	Cape Alitak	22 Aug	34	125	86	0.688	0.756	0.613
	Cape Alitak	27 Aug	35	112	25	0.223	0.298	0.160
	Eastside	7–8 Jul	28	164	125	0.762	0.816	0.701
	Eastside	14–16 Jul	29	116	86	0.741	0.807	0.666
	Mainland	21–22 Jul	30	157	60	0.382	0.450	0.317
	Westside	20–22 Jun	26	103	69	0.670	0.746	0.586
	Westside	27–28 Jun	27	64	36	0.563	0.668	0.452
	Westside	5 Jul	28	112	85	0.759	0.824	0.683
	Westside	16–17 Jul	29	123	64	0.520	0.597	0.442
	Westside	11–12 Aug	33	138	105	0.761	0.820	0.694
	Westside	16–18 Aug	34	162	45	0.278	0.342	0.220
Westside	25–26 Aug	35	86	11	0.128	0.203	0.073	
<b>Transition Area</b>	Moser Bay	14–15 Jun	25	107	7	0.065	0.119	0.031
	Moser Bay	27–29 Jun	27	86	24	0.279	0.369	0.200
	Moser Bay	5–6 Jul	28	87	19	0.218	0.304	0.148
	Moser Bay	15–16 Jul	29	131	24	0.183	0.248	0.130
	Moser Bay	20–21 Jul	30	112	36	0.321	0.401	0.249
	Moser Bay	27–28 Jul	31	78	4	0.051	0.114	0.018
	Moser Bay	5 Aug	32	123	10	0.081	0.134	0.045
	Moser Bay	10–12 Aug	33	111	24	0.216	0.290	0.154
	Moser Bay	20–21 Aug	34	127	30	0.236	0.306	0.175
	Moser Bay	22 Aug	34	110	41	0.373	0.455	0.296
	Moser Bay	25–27 Aug	35	119	14	0.118	0.178	0.073
<b>Terminal Harvest Area</b>	Olga Bay	14–15 Jun	25	117	0	0.000	0.025	0.000
	Olga Bay	20–21 Jun	26	117	5	0.043	0.088	0.017
	Olga Bay	27–29 Jun	27	73	2	0.027	0.084	0.005
	Olga Bay	6–7 Jul	28	98	4	0.041	0.091	0.014
	Olga Bay	20–21 Jul	30	137	4	0.029	0.066	0.010
	Olga Bay	30 Jul	31	144	14	0.097	0.148	0.060
	Olga Bay	3–4 Aug	32	119	25	0.210	0.281	0.150
	Olga Bay	10–11 Aug	33	104	9	0.087	0.146	0.046
	Olga Bay	20–21 Aug	34	104	11	0.106	0.169	0.060
	Olga Bay	25–26 Aug	35	102	16	0.157	0.228	0.101



Table 4. Feeding proportions for 1999 samples.

1999	Sample Area	Catch Date(s)	Sample Period	Sample Size	Number Feeding	Proportion Feeding	C.I. (95%)	
							Upper	Lower
<b>Migration Corridors</b>	Ayakulik	15 – 16 Jun	25	120	57	0.475	0.568	0.383
	Ayakulik	15 – 16 Jun	25	120	42	0.350	0.442	0.265
	Ayakulik	28 – 30 Jun	27	110	80	0.727	0.808	0.634
	Ayakulik	13 – 14 Jul	29	120	96	0.800	0.867	0.717
	Ayakulik	27 – 29 Jul	31	135	71	0.526	0.612	0.438
	Ayakulik	5 – 7 Aug	32	106	49	0.462	0.562	0.365
	Ayakulik	5 – 7 Aug	32	102	44	0.431	0.533	0.334
	Cape Alitak	25 – 26 Jun	26	125	96	0.768	0.839	0.684
	Cape Alitak	25 – 26 Jun	26	106	84	0.792	0.865	0.703
	Cape Alitak	22 Jul	30	135	71	0.526	0.612	0.438
	Cape Alitak	28 Jul	31	109	58	0.532	0.628	0.434
	Cape Alitak	5 Aug	32	127	71	0.559	0.647	0.468
	Cape Alitak	11 Aug	33	108	84	0.778	0.852	0.688
	Cape Alitak	24 Aug	35	160	131	0.819	0.875	0.750
	Eastside	22 – 23 Jun	26	115	54	0.470	0.565	0.376
	Eastside	7 – 9 Jul	28	108	45	0.417	0.515	0.323
	Eastside	8 – 9 Jul	28	110	22	0.200	0.287	0.130
	Eastside	13 – 15 Jul	29	110	71	0.645	0.734	0.549
	Eastside	4 – 5 Aug	32	141	112	0.794	0.858	0.718
	Eastside	13 Aug	33	100	50	0.500	0.602	0.398
	Eastside	14 Aug	33	100	47	0.470	0.572	0.369
	Eastside	17 – 18 Aug	34	104	53	0.510	0.609	0.410
	Mainland	15 – 17 Jun	25	119	72	0.605	0.693	0.511
	Mainland	25 Jun	26	106	99	0.934	0.973	0.869
	Mainland	14 Jul	29	100	97	0.970	0.994	0.915
	Mainland	19 – 22 Jul	30	103	95	0.922	0.966	0.853
	Mainland	27 – 29 Jul	31	108	98	0.907	0.955	0.836
	Westside	17 – 20 Jun	25	120	108	0.900	0.947	0.832
	Westside	23 Jul	30	128	79	0.617	0.702	0.527
	Westside	27 – 30 Jul	31	122	73	0.598	0.686	0.506
	Westside	4 – 7 Aug	32	104	65	0.625	0.718	0.525
	Westside	4 – 7 Aug	32	121	66	0.545	0.636	0.452
	Westside	18 – 19 Aug	34	117	56	0.479	0.573	0.385
<b>Transition Area</b>	Moser Bay	9 – 10 Jun	24	125	77	0.616	0.702	0.525
	Moser Bay	10 Jun	24	125	82	0.656	0.739	0.566
	Moser Bay	22 – 23 Jul	30	124	45	0.363	0.454	0.278
	Moser Bay	27 – 28 Jul	31	125	50	0.400	0.491	0.313
	Moser Bay	3 – 4 Aug	32	120	39	0.325	0.417	0.242
	Moser Bay	11 – 12 Aug	33	149	69	0.463	0.547	0.381
	Moser Bay	22 – 24 Aug	35	140	60	0.429	0.515	0.345
<b>Terminal Harvest Area</b>	Olga Bay	20 – 21 Jun	26	106	11	0.104	0.178	0.053
	Olga Bay	21 Jun	26	105	12	0.114	0.191	0.060
	Olga Bay	26 Jun	26	109	11	0.101	0.173	0.051
	Olga Bay	22 – 23 Jul	30	101	6	0.059	0.125	0.022
	Olga Bay	27 – 29 Jul	31	106	24	0.226	0.318	0.151
	Olga Bay	3 – 4 Aug	32	112	19	0.170	0.252	0.105
	Olga Bay	11 – 12 Aug	33	130	40	0.308	0.395	0.230
	Olga Bay	11 – 12 Aug	33	97	39	0.402	0.507	0.304
	Olga Bay	22 – 23 Aug	35	103	18	0.175	0.262	0.107

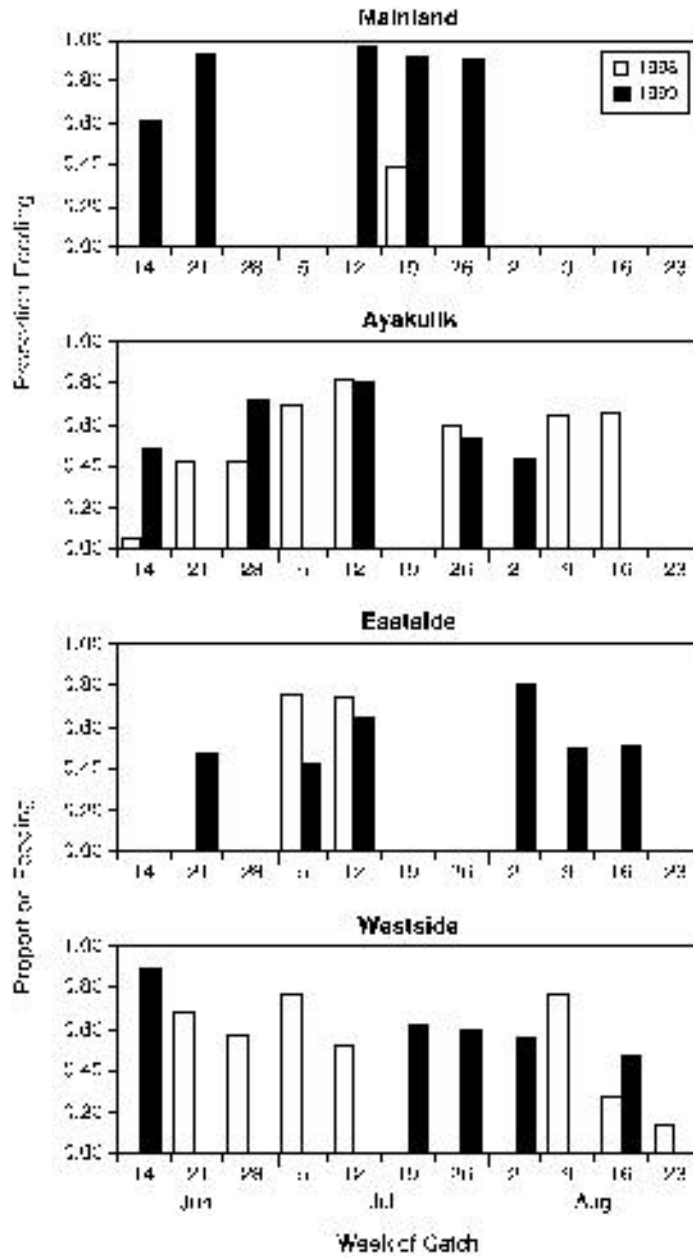


Figure 5. Proportion of feeding sockeye salmon in migration corridors, 1998 and 1999.

In the migration corridors, results of contingency table analysis showed highly significant differences within each area in incidence of feeding during both 1998 (Table 5) and 1999 (Table 6). Only the two sequential samples taken from the Eastside in 1998 were not significantly different. Examining among-area differences in incidence of feeding, during weeks when two or more comparable samples were available, again resulted in highly significant differences in the majority of comparisons made during 1998. In 1999 only the Eastside and Westside areas, during the week of 23–29 August, were not significantly different.

Table 5. Incidence of feeding in migration corridors, with significance testing, 1998. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Period	Ayakulik	Cape Alitak	Eastside	Mainland	Westside	
7 – 13 Jun		31.6%				
14 – 20 Jun	4.4%	65.0%				G = 101.4 p < 0.001
21 – 27 Jun	41.2%				67.0%	G = 14.6 p < 0.001
28 Jun – 4 Jul	41.6%	70.2%			56.3%	G = 17.3 p < 0.001
5 – 11 Jul	68.3%	56.3%	76.2%		75.9%	G = 13.3 p = 0.004
12 – 18 Jul	81.4%	38.7%	74.1%		52.0%	G = 63.4 p < 0.001
19 – 25 Jul		38.8%		38.2%		G = 0.0 p = 0.915
26 Jul – 1 Aug	59.7%					
2 – 8 Aug		46.4%				
9 – 15 Aug	63.3%	73.4%			76.1%	G = 5.4 p = 0.067
16 – 22 Aug	65.6%	68.8%			27.8%	G = 63.2 p < 0.001
23 – 29 Aug		22.3%			12.8%	G = 3.1 p = 0.080
G	= 209.1	= 82.3	= 0.2		= 168.7	
p	< 0.001	< 0.001	= 0.691		< 0.001	

Table 6. Incidence of feeding in migration corridors, with significance testing, 1999. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Period	Ayakulik	Cape Alitak	Eastside	Mainland	Westside	
7 – 13 Jun						
14 – 20 Jun	47.5%			60.5%	90.0%	G = 56.4 p < 0.001
21 – 27 Jun		76.8%	47.0%	93.4%		G = 64.6 p < 0.001
28 Jun – 4 Jul	72.7%					
5 – 11 Jul			20.0%			
12 – 18 Jul	80.0%		64.5%	97.0%		G = 40.2 p < 0.001
19 – 25 Jul		52.6%		92.2%	61.7%	G = 51.1 p < 0.001
26 Jul – 1 Aug	52.6%	53.2%		90.7%	59.8%	G = 54.7 p < 0.001
2 – 8 Aug	46.2%	55.9%	79.4%		54.5%	G = 34.8 p < 0.001
9 – 15 Aug		77.8%	50.0%			G = 17.7 p < 0.001
16 – 22 Aug			51.0%		47.9%	G = 0.2 p = 0.646
23 – 29 Aug		81.9%				
G	= 50.8	= 57.2	= 101.6	= 72.9	= 60.9	
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	

Sockeye salmon moving towards their natal streams through the waters off Cape Alitak, Moser Bay and into Olga Bay exhibited highly significant differences in incidence of feeding within each area during both 1998 (Table 7) and 1999 (Table 8). Comparisons among the three areas during the same weekly time periods also resulted in highly significant differences in all but two weeks (26 July – 1 August and 23–29 August 1998). In most periods, feeding appeared to taper off rather than cease abruptly (Figure 6), with more Cape Alitak fish feeding than Moser Bay fish, and Moser Bay fish generally feeding at a higher rate than Olga Bay fish. Only during three periods in late July and August 1998 did the incidence of feeding in Olga Bay surpass that in Moser Bay.

Table 7. Incidence of feeding as sockeye salmon move towards their natal streams, with significance testing, 1998. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Period	Cape Alitak	Moser Bay	Olga Bay	
7 – 13 Jun	31.6%			
14 – 20 Jun	65.0%	6.5%	0.0%	G = 164.7 p < 0.001
21 – 27 Jun			4.3%	
28 Jun – 4 Jul	70.2%	27.9%	2.7%	G = 101.5 p < 0.001
5 – 11 Jul	56.3%	21.8%	4.1%	G = 73.7 p < 0.001
12 – 18 Jul	38.7%	18.3%		G = 14.1 p < 0.001
19 – 25 Jul	38.8%	32.1%	2.9%	G = 65.1 p < 0.001
26 Jul – 1 Aug		5.1%	9.7%	G = 1.5 p = 0.215
2 – 8 Aug	46.4%	8.1%	21.0%	G = 47.8 p < 0.001
9 – 15 Aug	73.4%	21.6%	8.7%	G = 124.4 p < 0.001
16 – 22 Aug	68.8%	23.6%	10.6%	G = 99.6 p < 0.001
23 – 29 Aug	22.3%	11.8%	15.7%	G = 4.7 p = 0.096
	G = 140.9 p < 0.001	= 59.1 < 0.001	= 55.5 < 0.001	

Table 8. Incidence of feeding as sockeye salmon move towards their natal streams, with significance testing, 1999. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Period	Cape Alitak	Moser Bay	Olga Bay	
7 – 13 Jun		61.6%		
14 – 20 Jun			10.4%	
21 – 27 Jun	76.8%		10.1%	G = 115.9 p < 0.001
28 Jun – 4 Jul				
5 – 11 Jul				
12 – 18 Jul				
19 – 25 Jul	52.6%	36.3%	5.9%	G = 66.2 p < 0.001
26 Jul – 1 Aug	53.2%	40.0%	22.6%	G = 21.9 p < 0.001
2 – 8 Aug	55.9%	32.5%	17.0%	G = 41.3 p < 0.001
9 – 15 Aug	77.8%	46.3%	30.8%	G = 36.9 p < 0.001
16 – 22 Aug		42.9%		
23 – 29 Aug	81.9%		17.5%	G = 113.0 p < 0.001
	G = 57.2 p < 0.001	G = 26.4 p < 0.001	G = 36.1 p < 0.001	

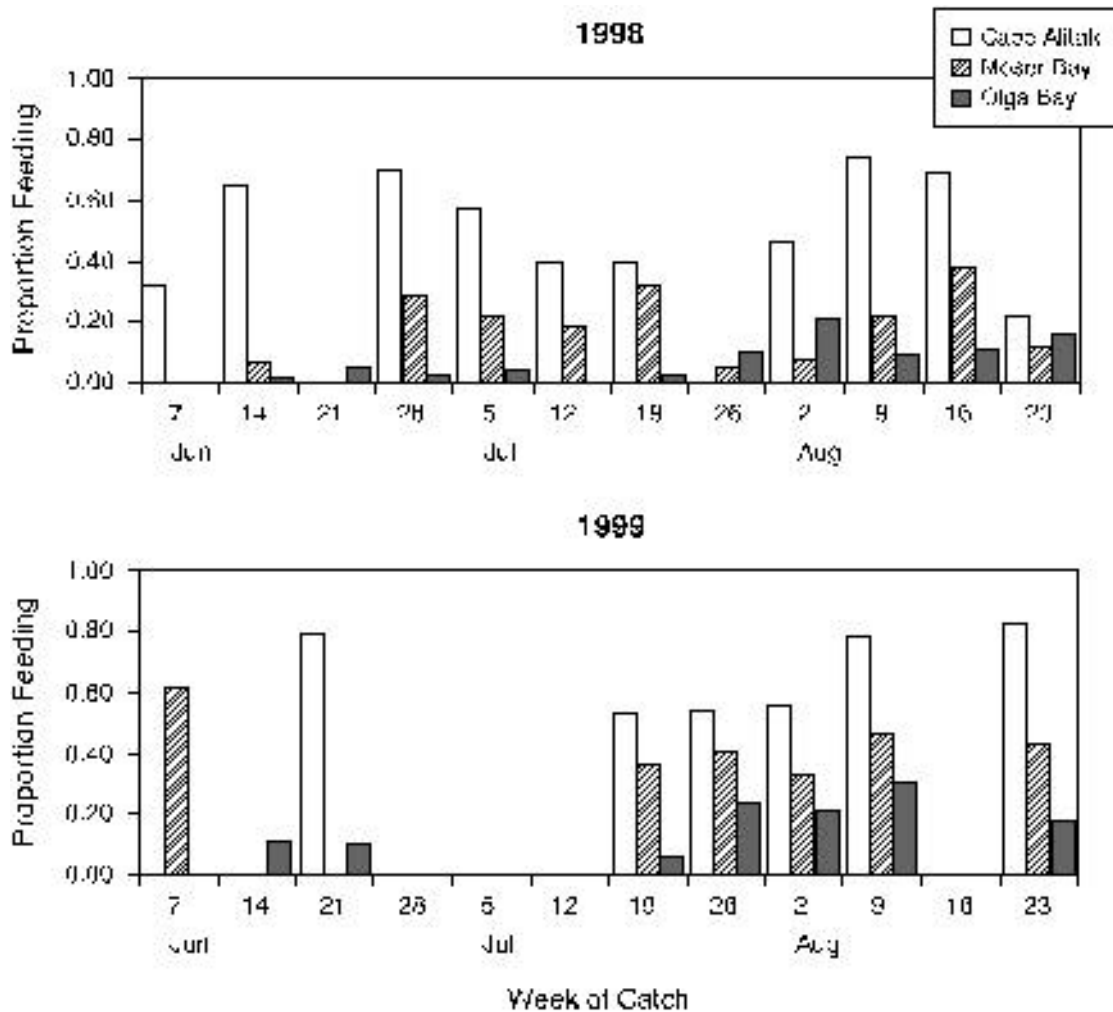


Figure 6. Proportion of sockeye salmon actively feeding as they move towards their natal streams—from Cape Alitak through Moser Bay and into Olga Bay, 1998 and 1999.

The incidence of feeding exhibited a bi-modal pattern in 1998, with greater proportions in late June and mid-August, corresponding to the timing of the dominant early run Fraser Lake stock (June through mid-July) and the late run Upper Station stock (late July through August). Low returns of salmon in 1999 during June and early July resulted in extended fishing closures, and thus a lack of samples during this time period. When the incidence of feeding in these three areas was examined within either the early run (pre-19 July) or late run (post-18 July), early-run Olga Bay fish exhibited no significant differences among time periods in either 1998 (Table 9) or 1999 (Table 10). Early-run and late-run Cape Alitak (1998 and 1999), late-run Olga Bay (1998 and 1999), and late-run Moser Bay (1998) fish were all significantly different when examined among periods. The 1999 late-run Moser Bay fish did not exhibit any significant differences in incidence of feeding.

Table 9. Incidence of feeding of early and late runs, 1998. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Early Run Period	Cape Alitak	Moser Bay	Olga Bay	Late Run Period	Cape Alitak	Moser Bay	Olga Bay
7 – 13 Jun	31.6%			16 – 25 Jul	38.8%	32.1%	2.9%
14 – 20 Jun	65.0%	6.5%	0.0%	26 Jul – 1 Aug		5.1%	9.7%
21 – 27 Jun			4.3%	2 – 8 Aug	46.4%	8.1%	21.0%
28 Jun – 4 Jul	70.2%	27.9%	2.7%	9 – 15 Aug	73.4%	21.6%	8.7%
5 – 11 Jul	56.3%	21.8%	4.1%	16 – 22 Aug	68.8%	23.6%	10.6%
12 – 18 Jul	38.7%	18.3%		23 – 29 Aug	22.3%	11.8%	15.7%
G	= 51.7	= 17.9	= 3.6	G	= 82.4	= 41.2	= 25.4
p	< 0.001	< 0.001	= 0.314	p	< 0.001	< 0.001	< 0.001

Table 10. Incidence of feeding of early and late runs, 1999. G = G-statistic, p = probability. Period is week catch occurred. Percentages are proportion of sockeye salmon with prey in the stomach.

Early Run Period	Cape Alitak	Moser Bay	Olga Bay	Late Run Period	Cape Alitak	Moser Bay	Olga Bay
7 – 13 Jun		61.6%		16 – 25 Jul	52.6%	36.3%	5.9%
14 – 20 Jun			10.4%	26 Jul – 1 Aug	53.2%	40.0%	22.6%
21 – 27 Jun	76.8%		10.1%	2 – 8 Aug	55.9%	32.5%	17.0%
28 Jun – 4 Jul				9 – 15 Aug	77.8%	46.3%	30.8%
5 – 11 Jul				16 – 22 Aug		42.9%	
12 – 18 Jul				23 – 29 Aug	81.9%		17.5%
G			= 0.005	G	= 50.3	= 6.5	= 26.0
p			= 0.945	p	< 0.001	= 0.164	< 0.001

### Prey analysis

For prey analysis, 26 samples were obtained from three areas (Eastside, Westside and Mainland) during the 1998 and 1999 seasons. From a total of 647 stomachs examined, at least 25 taxa are represented by seven prey categories (Table 11). The Eastside and Mainland areas were not well sampled in 1998 due to limited fishery openings and fishing effort, but all three areas were well represented in the 1999 samples (Figure 7).



Table 11. Prey of adult sockeye salmon. Category is the classification used in analyses.

Category		Prey Taxa
<b>Fishes</b>	Ammodytidae	<i>Ammodytes hexapterus</i>
	Gadidae	<i>Gadus</i> spp. unidentified fishes
<b>Decapods</b>		unidentified decapod zoea unidentified decapod decapodid
	Anomura	unidentified anomuran zoea unidentified anomuran glaucothoe <i>Pagurus</i> spp. zoea <i>Pagurus</i> spp. glaucothoe
	Brachyura	unidentified brachyuran zoea unidentified brachyuran megalopa <i>Chionoecetes</i> spp. megalopa <i>Hyas lyratus</i> megalopa unidentified Oregoniinae megalopa <i>Telmessus cheiragonus</i> megalopa <i>Cancer</i> spp. zoea <i>Cancer</i> spp. megalopa unidentified Pinnotheridae zoea
		unidentified euphausiid <i>Thysanoëssa inermis</i> <i>Thysanoëssa spinifera</i> <i>Thysanoëssa</i> spp.
		<i>Diastylopsis dawsoni</i>
<b>Pteropods</b>	Gastropoda	<i>Limacina helicina</i>
<b>Amphipods</b>		unidentified hyperiid unidentified gammarid
	<b>Other</b>	Copepoda
	Mysidacea	unidentified
	Chaetognatha	<i>Sagitta elegans</i>
	Larvacea	<i>Oikopleura</i> spp.
	Crustacea	unidentified
	Fish eggs	unidentified
	Insecta	unidentified

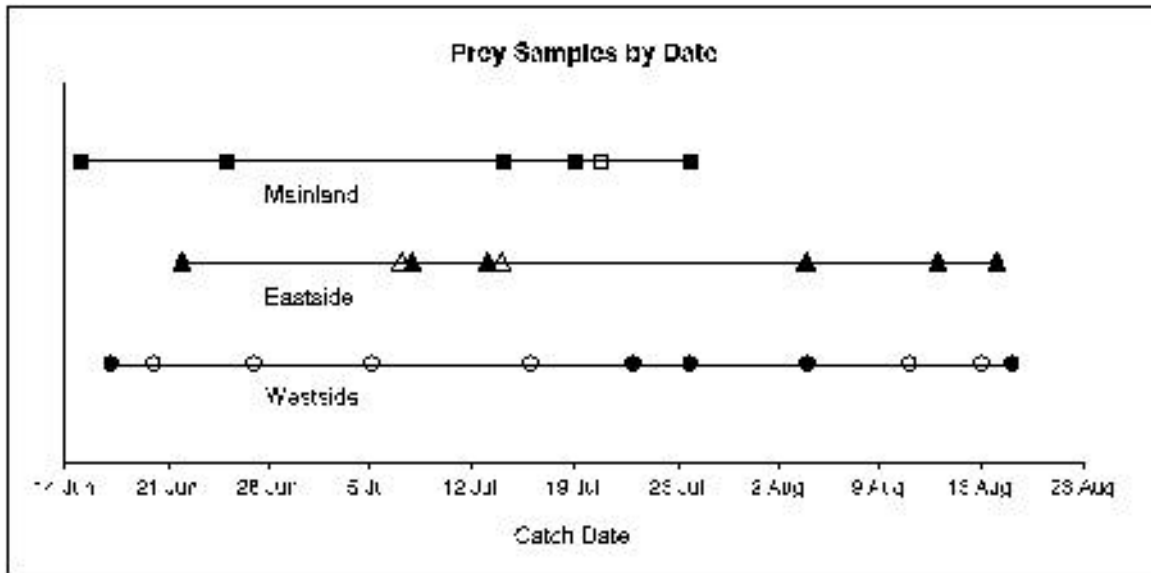


Figure 7. Distribution of sampling effort during 1998 and 1999. Catch date represents the first day fish were caught. Open marker = 1998, solid marker = 1999.

### Sample size

In random sampling from pooled stomach content data, only 18 of 28 prey taxa (64%; the median of 10 random samples) were represented at a sample size of  $n = 30$  stomachs, the target sample size for this study (Figure 8). By increasing the sample size to  $n = 200$ , 25 of 28 prey types (89%) were represented. In contrast, when sampling prey categories rather than individual prey taxa, all seven prey categories were present at a sample size of  $n = 22$ . By using prey categories rather than individual taxa in analyses, diet breadth could be adequately characterized with a smaller sample size than that used in this project.

### Digestive state

Overall digestive state for all samples was  $\bar{x} = 2.5$ , indicating relatively recent feeding. Digestive state ranged from a minimum  $\bar{x} = 1.9$  for Eastside samples during 22–23 June 1999 to a maximum of  $\bar{x} = 3.53$  for Mainland samples captured on 25 June 1999. There were no significant differences between areas when samples were pooled over 1998 and 1999 ( $F = 1.003$ ;  $p = 0.367$ ; Table 12).

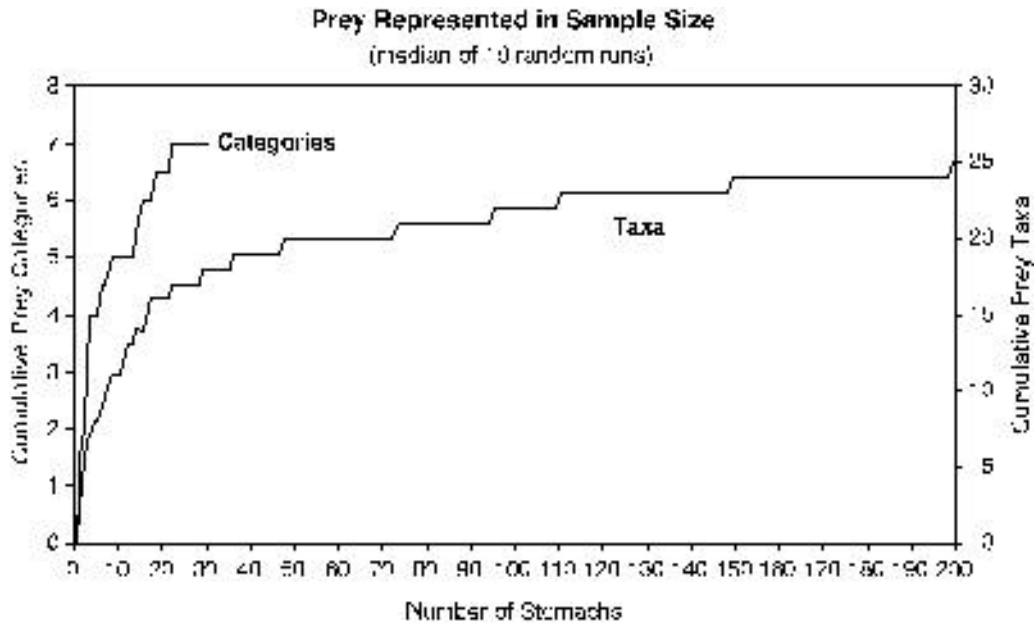


Figure 8. Cumulative prey taxa and categories represented from pooled stomach contents as a function of sample size. Line represents the median value of 10 random runs.

Table 12. Digestive state of stomach contents from each area with samples pooled by year. Digestive state was subjectively rated for each stomach examined, on a scale of 1 to 4. A score of 1 = highly digested; 4 = minimal digestion. UCI = upper 95% confidence interval; LCI = lower 95% confidence interval.

Year	Area	n	Mean	LCI (95%)	UCI (95%)	Median
1998	Mainland	30	2.5	2.1	2.9	2.8
1999	Mainland	142	2.6	2.5	2.7	3.0
1998	Eastside	55	3.1	2.9	3.3	3.0
1999	Eastside	136	2.2	2.0	2.3	2.0
1998	Westside	124	2.4	2.3	2.6	2.5
1999	Westside	160	2.6	2.5	2.7	3.0

### Stomach content weight

Overall mean weight for total stomach contents was  $\bar{x} = 8.15$  g, ranging by sample from  $\bar{x} = 4.19$  g (Westside, 27–28 June 1998) to a maximum of  $\bar{x} = 21.49$  g (Mainland, 19–22 July 1999). The minimum weight for an individual stomach with prey was 0.12 g and the maximum individual weight was 65.98 g. (Table 13). Stomach content weights exhibited a log-normal distribution and were transformed prior to analysis with ANOVA.

Table 13. Mean, minimum and maximum stomach content weights (g). UCI = upper 95% confidence interval; LCI = lower 95% confidence interval.

Year	Area	Catch Date	n	Mean Content Wt (g)	LCI (95%)	UCI (95%)	Minimum (g)	Maximum (g)
1998	Mainland	21–22 Jul	30	12.24	6.78	17.71	0.52	53.99
1999	Mainland	15–17 Jun	29	6.90	5.34	8.47	1.20	16.86
		25 Jun	30	9.34	7.39	11.28	4.73	24.89
		14 Jul	30	10.15	7.62	12.68	1.38	29.32
		19–22 Jul	23	21.49	12.59	30.40	0.81	65.98
		27–29 Jul	30	14.25	10.94	17.57	2.05	34.50
1998	Eastside	7–8 Jul	26	13.30	8.29	18.31	0.20	47.99
		14–16 Jul	29	8.65	6.67	10.63	1.48	21.16
1999	Eastside	22–23 Jul	11	7.10	2.88	11.31	1.30	20.75
		7–9 Jul	20	6.93	3.69	10.18	1.07	23.56
		13–15 Jul	28	8.70	3.30	14.09	0.41	55.68
		4–5 Aug	30	6.19	4.51	7.88	1.39	21.09
		13–14 Aug	34	5.59	4.28	6.90	1.45	18.30
1998	Westside	17–18 Aug	17	5.07	3.68	6.46	1.43	10.86
		20–22 Jun	17	5.73	2.43	9.04	0.15	23.69
		27–28 Jun	14	4.19	2.21	6.18	0.12	13.67
		5 Jul	30	7.30	4.56	10.03	0.14	29.50
		16–17 Jul	20	5.99	4.07	7.91	0.81	19.68
1999	Westside	11–12 Aug	30	5.97	4.61	7.32	1.10	13.66
		16–18 Aug	14	4.75	2.74	6.76	0.28	10.54
		17–20 Jun	30	6.30	4.72	7.88	0.98	18.61
		23 Jul	30	4.90	3.74	6.05	0.53	12.19
		27–30 Jul	30	8.62	5.21	12.03	0.98	41.27
		4–7 Aug	29	4.37	2.78	5.96	0.84	16.81
		4–7 Aug	27	5.31	3.68	6.94	0.34	15.21
		18–19 Aug	14	7.78	2.41	13.16	1.02	32.13

Sample data were initially pooled by area over both 1998 and 1999 (Mainland,  $\bar{x} = 12.06$  g; Eastside,  $\bar{x} = 7.80$  g; Westside,  $\bar{x} = 6.01$  g) and showed the effect of area to be highly significant ( $F = 35.67$ ,  $p \ll 0.001$ ). Post-hoc comparisons of the three areas using Tukey's HSD test showed all three to be significantly different ( $p < 0.01$ ) in terms of fullness by weight. When examined for year and area effects, area ( $F = 23.36$ ;  $p \ll 0.001$ ) and the interaction with year ( $F = 6.33$ ;  $p = 0.002$ ) were highly significant. The interaction effect was due to a decrease in mean weights in the Eastside samples and an increase in weights in the Mainland samples in 1999. Year effect was not significant.

Tests of between area differences in 1998 were hampered by the small number of samples obtained from the Mainland and Eastside. The 1999 samples were well balanced among areas and the results of a one-way ANOVA for 1999 weights were highly significant ( $F = 34.78$ ;  $p \ll 0.001$ ). Tukey's HSD showed that stomach content weights from the Mainland area differed significantly ( $p \ll 0.001$ ) from the Eastside and Westside areas, which were not significantly different from each other. The mean weight of stomach contents in 1999 Mainland samples ( $\bar{x} = 12.02$  g) was nearly twice that found in the Eastside ( $\bar{x} = 6.56$  g) and Westside ( $\bar{x} = 6.08$  g) areas.

Within each area, only the Mainland samples exhibited highly significant differences among periods ( $F = 3.98$ ;  $p = 0.002$ ). Tukey's HSD showed this was due to the high 19–22 July 1999 ( $\bar{x} = 21.49$  g) and

27–29 July 1999 ( $\bar{x} = 14.25$  g) values in comparison to the low 15–16 June ( $\bar{x} = 6.90$  g) weights. Mean stomach content weights were positively correlated with higher incidence of feeding ( $r^2 = 0.212$ ,  $p = 0.02$ ,  $n = 26$ ).

### Prey composition

Overall, the principal prey of sockeye salmon were decapod larvae, pteropods and fish (Figure 9). Pteropods were comprised exclusively of *L. helicina* and fish were predominately (86% by number) Pacific sandlance, of which 94% were < 70 mm FL. In the Eastside and Westside areas, when pooled over the course of the season, decapod larvae were both the most frequently occurring and numerous prey item (Table 14). In Mainland samples pteropods and fish were the most frequently occurring prey, with decapods and pteropods the most numerous.

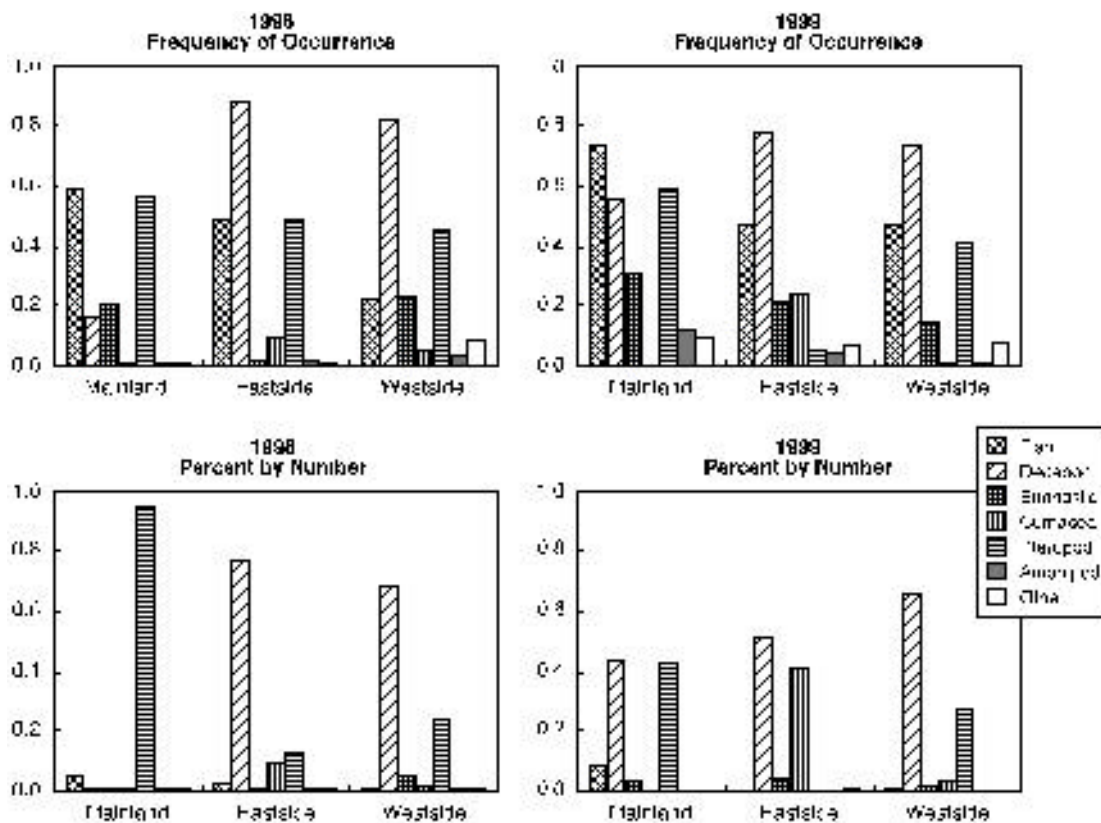


Figure 9. Overall frequency of occurrence and percent by number for sockeye prey items, 1998 and 1999.

Table 14. Frequency of occurrence and percent composition by number of prey categories; areas pooled by year. An entry of “–” indicates a value < 1%.

Frequency of Occurrence		Prey Category						
Year	Area	Fish	Decapod	Euphausiid	Cumacea	Pteropod	Amphipod	Other
1998	Mainland	60%	17%	20%	–	57%	–	–
	Eastside	49%	89%	2%	9%	49%	2%	–
	Westside	22%	83%	23%	5%	46%	3%	8%
1999	Mainland	74%	56%	32%	–	59%	12%	10%
	Eastside	47%	78%	22%	25%	5%	4%	7%
	Westside	56%	74%	15%	1%	41%	1%	8%
overall		51%	71%	21%	7%	40%	5%	7%

Percent Composition by Number								
Year	Area	Fish	Decapod	Euphausiid	Cumacea	Pteropod	Amphipod	Other
1998	Mainland	5%	–	–	–	94%	–	–
	Eastside	1%	77%	–	9%	13%	–	–
	Westside	–	69%	5%	1%	24%	–	–
1999	Mainland	10%	44%	3%	–	43%	–	–
	Eastside	–	52%	5%	41%	–	–	1%
	Westside	1%	66%	2%	3%	28%	–	–
overall		3%	59%	3%	11%	23%	–	–

Prey use varied between areas, and within each area between periods. Only fish and decapods were found in all samples. Fish percent composition by number (%N) was greatest in the Mainland area in July 1999 with the percent frequency of occurrence (FOcc) approaching 100% (Table 15). In June 1999 FOcc for fish in Mainland sockeye diets varied from 7% to 72% while FOcc for decapods and pteropods fell in July from high June levels. Although fish occurred in all Eastside and Westside samples, %N values in these areas were always low, varying from < 1% to 5% (Table 16).

Table 15. Frequency of occurrence (percent) of prey categories for individual samples. An entry of “–” indicates a value < 1%.

Frequency of Occurrence (percent)				Prey Category						
Year	Area	Catch Date	n	Fish	Decapod	Euphausiid	Cumacea	Pteropod	Amphipod	Other
1998	Mainland	21 – 22 Jul	30	60%	17%	20%	–	57%	–	–
1999	Mainland	15 – 17 Jun	29	72%	69%	31%	–	86%	28%	10%
		25 Jun	30	7%	80%	30%	–	90%	10%	–
		14 Jul	30	97%	27%	23%	–	53%	–	20%
		19 – 22 Jul	23	100%	22%	35%	–	22%	4%	–
		27 – 29 Jul	30	100%	73%	40%	–	37%	17%	17%
1998	Eastside	7 – 8 Jul	26	65%	85%	4%	15%	35%	–	–
		14 – 16 Jul	29	35%	93%	–	3%	62%	3%	–
1999	Eastside	22 – 23 Jun	11	45%	73%	36%	–	27%	–	9%
		7 – 9 Jul	20	42%	47%	16%	47%	–	10%	10%
		13 – 15 Jul	28	92%	58%	–	35%	8%	–	11%
		4 – 5 Aug	30	57%	100%	30%	10%	7%	10%	–
		13 – 14 Aug	34	18%	91%	23%	21%	–	–	12%
1998	Westside	17 – 18 Aug	17	25%	81%	37%	37%	–	6%	–
		20 – 22 Jun	17	31%	69%	25%	12%	69%	–	25%
		27 – 28 Jun	14	36%	57%	29%	–	71%	–	–
		5 Jul	30	30%	93%	20%	13%	80%	7%	13%
		16 – 17 Jul	20	10%	85%	25%	–	60%	–	–
1999	Westside	11 – 12 Aug	30	7%	93%	13%	–	–	7%	7%
		16 – 18 Aug	14	29%	77%	43%	–	–	–	–
		17 – 20 Jun	30	47%	67%	17%	–	90%	3%	23%
		23 Jul	30	47%	57%	13%	–	47%	–	–
		27 – 30 Jul	30	73%	87%	27%	–	37%	–	13%
1999	Westside	4 – 7 Aug	29	55%	72%	17%	–	17%	–	7%
		4 – 7 Aug	27	48%	81%	7%	7%	30%	4%	–
		18 – 19 Aug	14	79%	86%	–	–	–	–	–

Table 16. Percent composition by number of prey categories for individual samples. An entry of “–” indicates a value < 1%.

Percent Composition by Number				Prey Category						
Year	Area	Catch Date	n	Fish	Decapod	Euphausiid	Cumacea	Pteropod	Amphipod	Other
1998	Mainland	21 – 22 Jul	30	4%	–	–	–	94%	–	–
1999	Mainland	15 – 17 Jun	29	4%	14%	4%	–	76%	–	–
		25 Jun	30	–	55%	2%	–	43%	–	–
		14 Jul	30	41%	13%	4%	–	41%	–	–
		19 – 22 Jul	23	54%	21%	15%	–	9%	–	–
		27 – 29 Jul	30	15%	77%	2%	–	5%	–	–
1998	Eastside	7 – 8 Jul	26	4%	76%	–	19%	2%	–	–
		14 – 16 Jul	29	–	77%	–	5%	17%	–	–
1999	Eastside	22 – 23 Jun	11	2%	69%	11%	–	16%	–	1%
		7 – 9 Jul	20	–	1%	–	97%	–	–	–
		13 – 15 Jul	28	3%	–	–	94%	–	–	2%
		4 – 5 Aug	30	–	94%	3%	2%	–	–	–
		13 – 14 Aug	34	–	71%	6%	20%	–	–	3%
1998	Westside	17 – 18 Aug	17	–	53%	21%	26%	–	–	–
		20 – 22 Jun	17	4%	76%	6%	–	14%	–	–
		27 – 28 Jun	14	2%	13%	–	–	84%	–	–
		5 Jul	30	2%	54%	–	6%	38%	–	–
		16 – 17 Jul	20	–	46%	5%	–	48%	–	–
1999	Westside	11 – 12 Aug	30	–	98%	2%	–	–	–	–
		16 – 18 Aug	14	–	60%	40%	–	–	–	–
		17 – 20 Jun	30	1%	58%	–	–	41%	–	–
		23 Jul	30	2%	43%	8%	–	47%	–	–
		27 – 30 Jul	30	4%	42%	9%	–	45%	–	–
		4 – 7 Aug	29	1%	85%	3%	–	11%	–	–
		4 – 7 Aug	27	–	71%	–	8%	20%	–	–
		18 – 19 Aug	14	5%	95%	–	–	–	–	–

Decapods were found in all samples, with euphausiids and pteropods occurring in all Mainland samples and nearly all Eastside and Westside samples. Decapods always outnumbered euphausiids, with the highest decapod %N found in the Westside and Eastside area diets. Cumaceans occurred primarily in sockeye sampled from the Eastside. In early July 1999 cumacean FOcc ranged from 35% to 47% and %N from 94% to 97%. Cumaceans occurred in only three Westside samples; there were no cumaceans in any Mainland stomachs. In those Westside samples, the cumacea %N ranged from < 1% to 8%. Although amphipods (approximately 80% gammarids) occurred in nearly half the samples obtained, they were always < 1% by number. Taxa in the category “other” (primarily unidentified crustaceans) were also found in approximately half the samples, but rarely accounted for more than 1% of prey items by number.

Contingency table analysis, using the number of prey items in each category, showed highly significant differences in patterns of overall prey usage. The categories “amphipod” and “other” were not included in those tests to avoid the confounding effect of sparse data. For both 1998 and 1999 all tests of differences within areas / between periods, and between areas, resulted in p-values < 0.001.

Patterns in consumption of individual prey categories were tested for within- and between-area differences using the Kruskal–Wallis ANOVA by ranks. In examining areas pooled by year, only the



category “other” was not significantly different between areas. Tests of all remaining categories showed highly significant differences ( $p < 0.001$ ) between areas.

Post-hoc comparisons among these pooled areas (by prey category), using Tukey’s HSD, show the greatest number of significant comparisons occurred in the decapod category (Table 17). Within-year comparisons of decapod consumption were non-significant only for Eastside and Westside sockeye in 1998 and 1999, all other comparisons being significantly different. Fish consumption differed significantly between years within both the Westside and Mainland areas. In 1998 the Westside area had significantly lower fish consumption than the Mainland and Eastside areas; in 1999 the Mainland area had higher fish consumption than the Westside and Eastside areas.

Table 17. Results of Tukey’s HSD test comparing overall prey usage between areas. n.s.: not significant at  $p = 0.05$ , \*:  $p < 0.05$ .

		1998			1999		
		Mainland	Eastside	Westside	Mainland	Eastside	Westside
<b>Fish</b>	<b>1998</b>	Mainland					
		Eastside	n.s.				
		Westside	*	*			
	<b>1999</b>	Mainland	*	*	*		
		Eastside	n.s.	n.s.	n.s.	*	
		Westside	n.s.	n.s.	*	*	n.s.
<b>Decapod</b>	<b>1998</b>	Mainland					
		Eastside	*				
		Westside	*	n.s.			
	<b>1999</b>	Mainland	*	*	*		
		Eastside	*	*	*	*	
		Westside	*	*	*	*	n.s.
<b>Euphausiid</b>	<b>1998</b>	Mainland					
		Eastside	n.s.				
		Westside	n.s.	n.s.			
	<b>1999</b>	Mainland	n.s.	*	n.s.		
		Eastside	n.s.	n.s.	n.s.	n.s.	
		Westside	n.s.	n.s.	n.s.	n.s.	n.s.
<b>Pteropod</b>	<b>1998</b>	Mainland					
		Eastside	n.s.				
		Westside	n.s.	n.s.			
	<b>1999</b>	Mainland	n.s.	n.s.	n.s.		
		Eastside	*	*	*	*	
		Westside	n.s.	n.s.	n.s.	*	*

In 1998 there were no significant differences among areas in pteropod consumption. In contrast, in 1999 all between-area comparisons were significantly different. Within-area/between-year differences in pteropod consumption were significant only for Eastside sockeye. Euphausiid consumption appears to be relatively uniform in all within-year/between-area, and between-year/within-area tests. The significance of this prey category in the initial Kruskal–Wallis test is due only to differences between the Eastside

1998 and Mainland 1999 sockeye. Cumacean consumption was not significantly different between years for any area, and in 1999 only the Eastside sockeye differed from Mainland and Westside sockeye.

Period effects on prey consumption were tested for each area by year (Table 18). Due to the small number of samples, the 1998 Eastside area (only two sequential samples) and the 1998 Mainland area (one sample) were not included. In all areas the effect of period on prey consumption was most notable for decapods and pteropods. Only in the 1998 Westside samples did period not have a significant effect on fish consumption. Overall, the most pronounced effect of period, found in the majority of prey categories tested, occurred in the 1999 Eastside samples.

Table 18. Effect of period on prey contents. n.s: not significant at  $p = 0.05$ , \*:  $0.05 < p < 0.01$ , \*\*:  $p < 0.01$ .

Year	Area	Fish	Decapod	Euphausiid	Cumacea	Pteropod	Amphipod	Other
1998	Westside	n.s.	**	n.s.	n.s.	**	n.s.	n.s.
1999	Mainland	**	**	n.s.	n.s.	**	*	n.s.
	Eastside	**	**	**	**	**	n.s.	n.s.
	Westside	*	*	n.s.	n.s.	**	n.s.	**

### Diversity

The maximum potential diversity value ( $H_{max}$ ) for any sample, given equal consumption of the seven prey categories, is  $H = 0.85$ . Measurements of diversity in samples (Table 19) ranged from  $H = 0.047$  to  $H = 0.509$  for the pooled population ( $H_{pop}$ ) and  $H = 0.015$  to  $H = 0.260$  for the mean individual ( $H_{ind}$ ). The largest values for  $H_{pop}$  and  $H_{ind}$  occurred in the 1999 Mainland samples, with the lowest values occurring in the 1998 Westside samples. In only the two July 1999 Eastside samples did the values of  $H_{ind}$  exceed  $H_{pop}$ .

Table 19. Shannon–Weaver diversity indices ( $H$ ) for mean individual and pooled samples.  $H_{min} = 0.0$ ;  $H_{max} = 0.85$ .

Year	Area	Catch Date	n	H pooled	H individual
1998	Mainland	21 – 22 Jul	30	0.106	0.074
1999	Mainland	15 – 17 Jun	29	0.348	0.198
		25 Jun	30	0.337	0.099
		14 Jul	30	0.505	0.161
		19 – 22 Jul	23	0.509	0.144
		27–29 Jul	30	0.336	0.260
1998	Eastside	7 – 8 Jul	26	0.312	0.135
		14 – 16 Jul	29	0.295	0.088
1999	Eastside	22 – 23 Jun	11	0.402	0.188
		7 – 9 Jul	20	0.066	0.118
		13 – 15 Jul	28	0.130	0.207
		4 – 5 Aug	30	0.134	0.086
		13 – 14 Aug	34	0.327	0.072
		17 – 18 Aug	17	0.451	0.149
1998	Westside	20 – 22 Jun	17	0.347	0.176
		27 – 28 Jun	14	0.223	0.095
		5 Jul	30	0.422	0.210
		16 – 17 Jul	20	0.377	0.089
		11 – 12 Aug	30	0.047	0.024
		16 – 18 Aug	14	0.298	0.015
1999	Westside	17 – 20 Jun	30	0.330	0.134
		23 Jul	30	0.437	0.127
		27 – 30 Jul	30	0.470	0.212
		4 – 7 Aug	29	0.235	0.132
		4 – 7 Aug	27	0.345	0.052
		18 – 19 Aug	14	0.085	0.075

No clear trends over time were apparent for any area. There was a significant correlation between  $H_{pop}$  and  $H_{ind}$  ( $r^2 = 0.19$ ;  $p = 0.03$ ). When values of  $H_{ind}$  were plotted against  $H_{pop}$  all sample areas tended to cluster in the region corresponding to a specialist feeding mode with a heterogeneous diet (Figure 10).

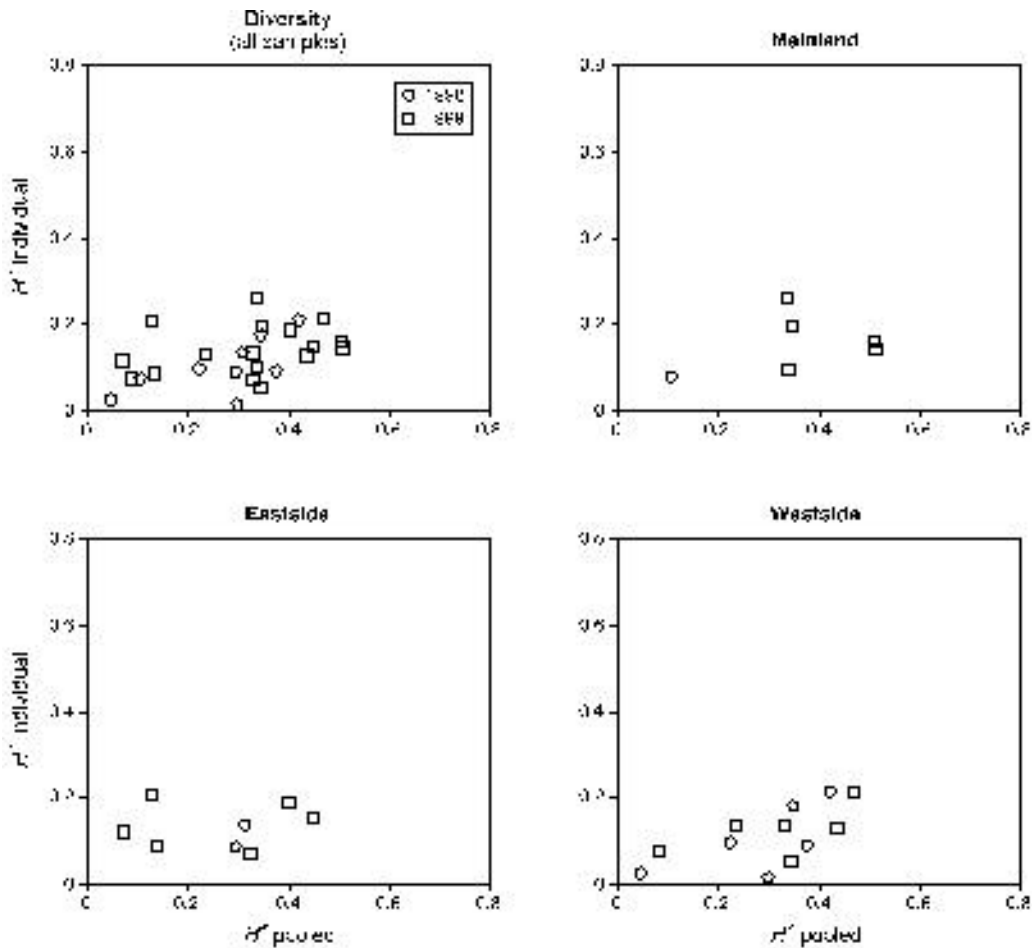


Figure 10. Tokeshi plots of Shannon–Weaver diversity indices ( $H'$ ) of diet, contrasting mean individual and pooled-sample values.  $H_{min} = 0.0$ ;  $H_{max} = 0.85$ .

## Discussion

Sockeye in the nearshore waters function as both filter and particle feeders. The feeding behavior of sockeye salmon, as they enter the final stages of their homeward migration, is neither uniform nor easily characterized. This study allowed for a fairly comprehensive examination of this behavior in the nearshore environment, and the results point to significant spatial and temporal variation in the incidence of feeding, the amount consumed and the types of prey eaten.

Most of the sockeye in the Mainland area are a substantially greater distance from their natal streams than those caught in the vicinity of Kodiak Island. It was the feeding behavior for these fish that was most noticeably different from all other sample areas. The high levels of incidence of feeding, greater mean stomach content weights, and reliance on sandlance as prey contrasted sharply with fish caught adjacent to Kodiak Island. The diets of migrating sockeye in the Westside and Eastside areas were characterized by consumption of zooplankton (principally larval decapods). However, the diets in these two areas contrasted in the other types of zooplankton eaten; Westside sockeye utilized pteropods extensively while

Eastside sockeye were unique in consuming relatively significant numbers of cumaceans. These differences could be due either to selective feeding or contrasts in the available prey base.

For the Westside and Eastside areas the low individual dietary diversity and appearance of sequential layering of one dominant taxa in stomachs suggest sockeye in these areas are exploiting concentrated prey patches. The fish had low individual diversity relative to population diversity. By looking at several feeding areas we could see a breadth of feeding habits not evident in any one location.

Copepods, and to a lesser extent euphausiids, were conspicuous in their absence. Larval decapods were consistently abundant, with the broad range of decapod species found indicating that these organisms function as a preferred prey type independent of individual taxa. Although not directly sampled for this project, four other species of salmon (pink, *O. gorbuscha*; chum, *O. keta*; coho, *O. kisutch*; Chinook, *O. tshawytscha*) were caught in the same areas during the same time periods and examined concurrently with these sockeye. Subjective observations during this investigation were that sockeye appeared to be the least piscivorous of the five species of salmon. Chinook salmon stomachs in particular were often distended to the point of bursting with sand lance, leading to the conclusion that sand lance were also readily available to, but ignored by, sockeye in the Kodiak Island areas.

In all areas though, sockeye feed on organisms that utilize a variety of different habitats. The potential exists for hydrocarbon transport from either sediments or the water column. In addition, filter feeding necessitates some indiscriminate filtering of the water column, as evidenced by the occasional piece of pumice, grass or feather found in stomachs. If sockeye are exploiting hydrographic features that concentrate zooplankton prey [Pingree et al. 1978], these may also be areas that concentrate hydrocarbons. The published evidence is not clear on the degree to which migrating salmon avoid hydrocarbons in the water [Weber et al. 1981; Martin et al. 1989; Purdy 1989]. In the study areas the fish are making a directed migration through coastal waters. If they are preferentially exploiting prey in areas that also concentrate contaminants, avoidance of these areas (and thus their preferred prey) would have an unknown, but likely detrimental, effect on sockeye reproductive fitness. Likewise, deleterious impacts on the prey base itself (changes in abundance, size or species composition) may increase intra- and inter-specific competition, reducing rations, due to the limited scope of these areas.

Incidence of feeding appears to taper off rather than cease abruptly, as does quantity of prey consumed, as sockeye near their natal streams. This is evidenced by the progressive decreases in stomach contents as fish moved from Cape Alitak through Moser Bay and into Olga Bay. The early-run sockeye in Olga Bay are predominately bound for the Fraser Lake system, with the stream mouth proximate to the fishery. There was a small but significant increase in incidence of feeding for Olga Bay sockeye as the late-run Upper Station stock entered the area. The Upper Station system lies approximately 20 km from the Olga Bay fishery.

Higher levels of feeding are associated with greater distances or travel time from natal streams, indicating that non-local sockeye would be at greater risk of contamination via ingestion than local fish. The further from their natal stream, the larger the meal size and the greater number of fish actively feeding in a population. We conclude that sockeye proximate to their natal stream would be at the least risk, as feeding has nearly ceased.

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## Study Products

Quarterly reports starting July 1998.

Annual reports for 1998–1999, 1999–2000.

Presentations at CMI Annual Research Reviews on 23 February 1999 and 9 March 2000.

Poster presentation, Alaska Chapter – American Fisheries Society annual meeting, Kodiak, 9–11 November 1999.

Seminar – Minerals Management Service, Anchorage, 30 November 1999.

35-mm slides representative of fieldwork submitted to MMS.

Final report: Tyler, A.V., C.O. Swanton and B.C. McIntosh. 2001. Feeding Ecology of Maturing Sockeye Salmon (*Oncorhynchus nerka*) in Nearshore Waters of the Kodiak Archipelago OCS Study MMS 2001-059, University of Alaska Coastal Marine Institute, University of Alaska Fairbanks, 34 p.

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