Feeding Ecology of Sockeye and Pink Salmon in the Gulf of Alaska

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Kaeriyama, M., M. Nakamura, M. Yamaguchi, H. Ueda, G. Anma, S. Takagi, K.Y. Aydin, R.V. Walker, and K.W. Myers. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. N. Pac. Anadr. Fish Comm. Bull. No. 2: 55–63.

Keywords: Feeding ecology, sockeye salmon, pink salmon, El Niño event, food niche, stomach content analysis method

Abstract: The feeding ecology of sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon in the Gulf of Alaska was investigated during early summers of 1994–1999. The dominant prey of salmon were squids (mainly *Berryteuthis anonychus*) in the Subarctic Current, and zooplankton (e.g., euphausiids, copepods, and pteropods) in the Alaskan Gyre during 1994–1996 and 1998. Food competition occurred between sockeye and pink salmon. Pink salmon appeared to feed on more diverse prey at a lower trophic level than sockeye salmon. The feeding and growth of sockeye and pink salmon were affected by the El Niño event during spring and summer of 1997.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are distributed widely and grow in oceans, which are typically more productive than freshwaters (Gross 1987). For Pacific salmon, oceanic foraging conditions and food relationships are important to growth. They are omnivorous and opportunistic feeders. Major categories of prey found in stomach contents of Pacific salmon usually include either one or a combination of fish, squid, euphausiids, amphipods, copepods, pteropods, larval crustaceans, gelatinous zooplankton, polychaetes, chaetognaths, appendicularians, ostracods, heteropods, mysids, and shrimps (Pearcy et al. 1988). By switching their diets to micronekton (squid and fish), salmon can sustain themselves through seasons or even years of low zooplankton production (Kaeriyama et al. 1998). Pink salmon (*O. gorbuscha*) fed predominantly on larger food items (squid and fish) in even years and small food items (euphausiids, amphipods, and copepods) in odd years. This relationship suggests a possible feeding interaction with abundance of pink salmon (Ito 1964). The composition of food of sockeye salmon (*O. nerka*) depends on the availability and relative abundance of the food items, which vary with season and location (Burgner 1991).

At the same time, Pacific salmon are selective feeders. In general, chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon tend to feed on large prey (fish and squid), while sockeye, chum (*O. keta*), and pink salmon feed on small prey (zooplankton). Prey selectivity in Pacific salmon is related to inter- and intra-specific differences in functional morphology, physiology, and behavior. In feeding strategy, juvenile chum salmon switch their feeding tactics from "sit-and-waiting" in the river to "wide-foraging" in the sea (Kaeriyama 1986).

Pacific salmon production in the North Pacific Ocean increased dramatically in the late 1970s, possibly owing to enhanced early ocean survival (Pearcy 1992; Pearcy et al. 1999). The increase in the number of salmon has prompted interest in possible density-dependent effects on survival, growth, and production of salmon stocks around the Pacific rim (e.g., Helle 1989; Kaeriyama 1989, 1998). However, the population density-dependent effect on feeding ecology of Pacific salmon has not been proven yet. On the other hand, Pacific salmon runs to some western Alaska river systems were very poor in 1997 and 1998. Sockeye salmon returning to Bristol Bay were smaller than average. Both reduced size and weak

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runs of Bristol Bay sockeye salmon in 1997 and 1998 implied that ocean conditions were unusually poor for growth and survival (Kruse 1998).

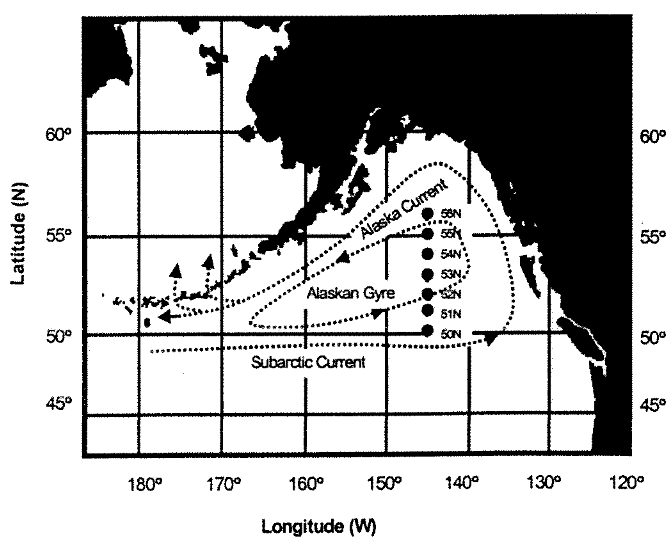
The objective of this paper is to describe the feeding ecology of sockeye and pink salmon in the Gulf of Alaska, and to discuss the basic principles of food and feeding habits, the relationship between feeding ecology and ocean environmental condition, and inter- and intra-specific interaction.

MATERIALS AND METHODS

Fish Collection

Sockeye and pink salmon were collected from late June to middle July, 1994–1998, in non-selective research gillnet operation aboard the *Oshoro maru*, training vessel of the Hokkaido University, at stations located in 1-degree latitude intervals along a transect 145°W from 50°N to 56°N (Fig. 1). In this area, there are three oceanic regions: the Subarctic Current, Alaskan Gyre, and Alaska Current (Pearcy et al. 1988). Total length and mesh size of gillnet were 2.35–2.50 km (47–50 tans, 50 m/tan) and 48–157 mm, respectively. Gillnet gear was set in the evening, allowed to soak overnight, and was retrieved the following morning. Each fish was weighed to the nearest gram and measured to the nearest millimeter in fork length (FL) on board. Scale samples were collected to determine the age of fish for growth estimation. At each fishing station the CTD model II was lowered to a depth of 3,000 m. The data from the CTD were used to plot temperature isopleths along the 145°W transect.

Fig. 1. Sampling locations in the Gulf of Alaska. Samples were collected from late June 1994 to middle July 1999 in non-selective research gillnet operations aboard the *Oshoro maru*, training vessel of the Hokkaido University.



Stomach Analysis

Stomachs from the esophagus to the pyloric valve were collected from up to 20 fish of each species in each gillnet operation, and preserved in 10% formalin-seawater solution for later stomach analysis in 1997 and 1998. In 1994–1996, fresh stomach contents were used to estimate percent volume of each prey category. This was done in the shipboard laboratory. Stomach contents were classified to 12 taxa (Table 1), then were identified to the lowest identifiable taxon, and counted and weighed by species. We estimated caloric values of each prey in the stomach content using the data provided by Davis et al. (1998).

Table 1. Prey animals and food items of sockeye and pink salmon in the Gulf of Alaska.

Food items	Species
EU Euphausiids	
	Thysanoessa longipes
	Thysanoessa inermis
	Thysanoessa spp.
	Euphausia spp.
	Other euphausiids
CO Copepods	
	Neocalanus cristatus
	Eucalanus bungii
	Other copepods
AM Amphipods	
	Hyperia medusarum
	Hyperia spp.
	Themisto pacifica
	Themisto japonica
	Themisto spp.
	Primno macropa
	Phronima sedentaria
	Other amphipods
DE Decapods	
	Decapods
SQ Squids	
	Berryteuthis anonychus
	Other squids
PT Pteropods	
	Limacina spp.
	Clio spp.
	Clione spp.
FI Fishes	
	Anoplopoma fimbria
	Other fish egg and larva
PO Polychaetes	
	Poloychaetes
CH Chaetognaths	
	Chaetognaths
GE Gelatinous zooplankton	
	Coelenterates
	Ctenophores
	Salps
OT Other animals	
	Halocypridids
	Cumacea
	Octopoda
	Ostracods
	Barnacles
	Debris
UI Unidentified material	

Carbon Isotope Ratio of Salmon Muscle Tissue

Muscles of Pacific salmon were collected from behind the head of 1–3 fish of each species at each station, and frozen on board during early summer sampling in 1999. These samples were thawed and rinsed with distilled water in the laboratory at Hokkaido University. Samples were dried at about 60°C for 24 hours and homogenized. Fat animals tend to possess lower carbon isotope ratios than lean ones (McConnaughey and McRoy 1979). Lipid levels for mature salmon should be considerably higher than for immature salmon (Welch and Parsons 1993). Therefore, lipids were removed from samples to avoid apparent differences in trophic level with maturity of salmon. The carbon isotope ratio was measured by a MAT252/B mass spectrometer fitted with a dual inlet system and double collector. As per convention, the $\delta^{13}C$ isotope values were reported as per mil ^{13}C enrichments relative to PDB standard in the conventional manner:

$$\delta (‰) = 10^3[R(sample)/R(standard)-1],$$

where R is again the ^{13}C : ^{12}C ratio. All marine samples analyzed here produce negative δ values since they are isotopically light (^{13}C-depleted) compared to the standard (McConnaughey and McRoy 1979).

Data Analysis

Stomach contents were analyzed by 5 methods: frequency of occurrence (FO) method, numerical (N) method, volume (V) method, wet-weight (W) method, and the modified index of relative importance (IRI) method (Pinkas et al. 1971). The IRI was used to characterize the diet of each species and to rank prey taxa:

$$IRI = (N + W)\, FO$$

where N is numerical percentage, W is weight percentage, and FO is frequency of occurrence in percent.

The Shannon-Wiener formula (H') was used to measure food niche breadth:

$$H' = -\sum p_i \log p_i$$

where p_i is the proportion of the IRI of species i in the stomach.

The simplified Morishita's index (C_H) was used to calculate overlap of food niche between species pairs; values range from 0 (no overlap) to 1 (complete overlap):

$$CH = \frac{2\sum_i^n p_{ij}\, p_{ik}}{\sum_i^n p^2_{ij} + \sum_i^n p^2_{ik}}$$

where p_{ij} and p_{ik} are proportions of the IRI of prey species i found in the predator species j and k, respectively.

To estimate taxonomic similarity between samples from stomach contents, the average linkage clustering method was used (Krebs 1998). Student's t-test and nonparametric Mann-Whitney test were used to compare growth characters and food niche of sockeye and pink salmon in 1997 and 1998 respectively.

RESULTS AND DISCUSSION

Comparison Between Stomach Content Analysis Methods

The prey spectrum of sockeye and pink salmon comprised at least 20 taxa (Table 1). The five taxonomic groups of greatest importance using IRI were squids, calanoid copepods, hyperiid amphipods, euphausiids, and pteropods. In four methods of stomach contents analysis, squids were the most important prey for both sockeye and pink salmon (Tables 2 and 3).

Figure 2 shows the stomach contents of pink salmon in 1998 by stations and by stomach content analysis methods. In the FO (frequency of occurrence) method, percentages of prey species are more evenly spread than in other methods. In the N (numerical) method, small organisms such as copepods were numerous and therefore accounted for high percentages, and large animals such as squid and fish had lower percentages because of small numbers. Results found in both the W (weight) and V (volume) methods were opposite to those in the N method.

While the N method furnishes information about feeding behavior, V and W methods reflect nutritional value of prey. The FO method differs from the two former measures because it is not a quantity of food, but of fish qualified by their diet content (Tirasin and Jørgensen 1999). The IRI was calculated by summing the numerical and weight percentage values, and multiplying by the frequency of occurrence rate (Pinkas et al. 1971). The IRI method assumes that different measures contain substantially independent information, and that the use of compound indices prevents loss of information. Incorporating the different measures was thought to cancel out the biases in individual components and seemed to provide a more accurate description (Tirasin and Jørgensen 1999). Therefore, the IRI method may be the best for evaluating stomach contents.

Table 2. Stomach contents of sockeye salmon in the Gulf of Alaska in 1997 and 1998. FO is frequency of occurrence percentage, N is numerical percentage, W is wet weight percentage of a prey animal per fish, and IRI is percentage of total IRI for all prey taxa. *IRI = (N+W) FO.*

	50N				51N				52N				53N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997																
Euphausiids	0.0	0.0	0.0	0.0	12.5	5.4	0.0	1.1	17.1	3.4	3.8	3.0	17.0	3.9	10.3	6.0
Copepods	9.5	23.0	0.0	3.7	12.5	4.3	0.0	0.9	22.9	92.8	43.0	76.3	21.3	92.2	70.1	85.6
Amphipods	9.5	6.1	0.0	1.0	4.2	1.1	0.0	0.1	22.9	2.8	1.0	2.1	19.1	2.8	1.1	1.9
Decapods	4.8	4.7	0.0	0.4	0.0	0.0	0.0	0.0	2.9	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Squids	42.9	11.3	97.3	77.5	37.5	41.3	100.0	85.5	14.3	0.3	26.1	9.3	12.8	0.2	9.7	3.1
Pteropods	19.0	53.1	0.0	16.8	16.7	43.5	0.0	11.7	14.3	0.5	25.9	9.3	12.8	0.7	0.2	0.3
Fish	9.5	0.9	2.6	0.6	4.2	1.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.1	0.1	0.0	2.1	0.0	0.3	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	4.8	0.9	0.0	0.1	12.5	3.3	0.0	0.7	2.9	0.1	0.0	0.0	14.9	0.2	8.3	3.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998																
Euphausiids	0.0	0.0	0.0	0.0	18.8	10.8	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	15.4	15.4	0.0	2.0	6.3	10.8	0.0	0.8	16.7	93.3	0.5	21.1	0.0	0.0	0.0	0.0
Amphipods	15.4	26.9	0.0	3.6	18.8	8.1	0.0	1.7	16.7	1.9	0.0	0.4	7.7	4.2	0.0	0.2
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	69.2	57.7	100.0	94.4	50.0	67.6	98.0	94.8	58.3	4.3	94.3	77.8	76.9	75.0	100.0	97.4
Pteropods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.4	20.8	0.0	2.3
Fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	0.0	0.0	0.0	0.0	6.3	2.7	2.0	0.3	8.3	0.5	5.2	0.6	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

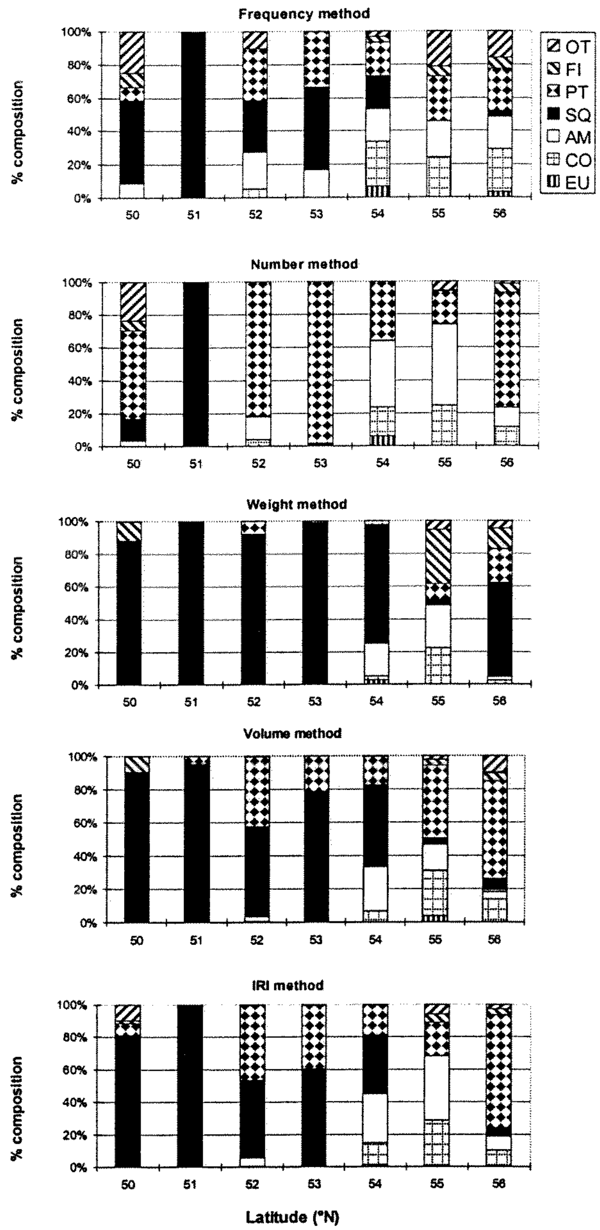
	54N				55N				56N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997												
Euphausiids	14.7	4.7	6.5	3.2	12.5	0.1	0.4	0.1	25.0	59.5	27.0	64.7
Copepods	26.5	91.2	90.1	94.9	28.1	99.3	70.5	90.6	0.0	0.0	0.0	0.0
Amphipods	8.8	0.4	0.9	0.2	21.9	0.4	0.7	0.4	8.3	0.6	0.1	0.2
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.6	0.1	0.2
Squids	5.9	0.1	0.3	0.0	18.8	0.1	23.0	8.2	13.9	0.5	1.6	0.9
Pteropods	14.7	2.8	0.4	0.9	6.3	0.1	0.1	0.0	19.4	31.8	2.6	20.0
Fish	2.9	0.0	0.2	0.0	3.1	0.0	0.0	0.0	5.6	2.6	66.1	11.4
Polychaetes	8.8	0.3	0.9	0.2	3.1	0.0	0.0	0.0	13.9	3.9	2.1	2.5
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	17.6	0.5	0.7	0.4	6.3	0.0	5.3	0.6	5.6	0.4	0.4	0.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998												
Euphausiids	0.0	0.0	0.0	0.0	8.3	0.5	0.0	0.1	8.0	0.7	0.0	0.2
Copepods	25.0	11.0	0.7	5.9	25.0	13.7	0.5	12.7	24.0	1.8	0.2	1.7
Amphipods	21.4	8.8	1.1	4.3	16.7	10.9	0.2	6.6	20.0	24.9	0.2	18.0
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.3	0.0	0.0
Squids	28.6	1.0	94.2	54.5	16.7	0.9	76.2	45.8	12.0	0.4	73.6	31.8
Pteropods	21.4	79.0	3.2	35.3	16.7	19.9	0.3	12.0	16.0	69.2	1.1	40.3
Fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	1.5	0.2	0.5
Polychaetes	0.0	0.0	0.0	0.0	8.3	6.2	17.7	7.1	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	8.3	47.9	5.1	15.7	0.0	0.0	0.0	0.0
Others	3.6	0.1	0.8	0.1	0.0	0.0	0.0	0.0	8.0	1.2	24.7	7.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3. Stomach contents of pink salmon in the Gulf of Alaska in 1997 and 1998. *FO* is frequency of occurrence percentage, *N* is numerical percentage, *W* is wet weight percentage of a prey animal per fish, and *IRI* is percentage of total IRI for all prey taxa. *IRI = (N + W) FO*.

	50N				51N				52N				53N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997																
Euphausiids	-	-	-	-	0.0	0.0	0.0	0.0	20.8	23.0	40.0	29.0	8.8	5.3	10.7	2.3
Copepods	-	-	-	-	0.0	0.0	0.0	0.0	25.0	59.4	47.5	59.0	32.4	85.4	84.8	91.6
Amphipods	-	-	-	-	20.0	2.5	0.4	1.4	16.7	7.4	9.5	6.2	32.4	6.0	2.8	4.7
Decapods	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	-	-	-	-	20.0	3.8	81.0	42.4	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Pteropods	-	-	-	-	20.0	91.8	2.8	47.3	20.8	8.0	2.5	4.8	20.6	3.1	0.8	1.3
Fish	-	-	-	-	20.0	0.6	15.8	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	-	-	-	-	20.0	1.3	0.0	0.6	16.7	2.1	0.5	1.0	5.9	0.2	0.1	0.0
Total	-	-	-	-	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998																
Euphausiids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	4.0	0.1	0.4	0.0	0.0	0.0	0.0
Amphipods	8.3	3.4	0.0	0.4	0.0	0.0	0.0	0.0	22.2	13.8	0.3	5.3	16.7	0.4	0.0	0.1
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	50.0	13.5	88.0	80.6	100.0	100.0	100.0	100.0	31.1	0.4	92.0	48.0	50.0	1.3	98.9	60.1
Pteropods	8.3	53.9	0.2	7.2	0.0	0.0	0.0	0.0	31.1	81.6	7.5	46.3	33.3	98.3	1.1	39.8
Fish	8.3	5.6	11.5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	25.0	23.6	0.3	9.5	0.0	0.0	0.0	0.0	10.4	0.2	0.1	0.0	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

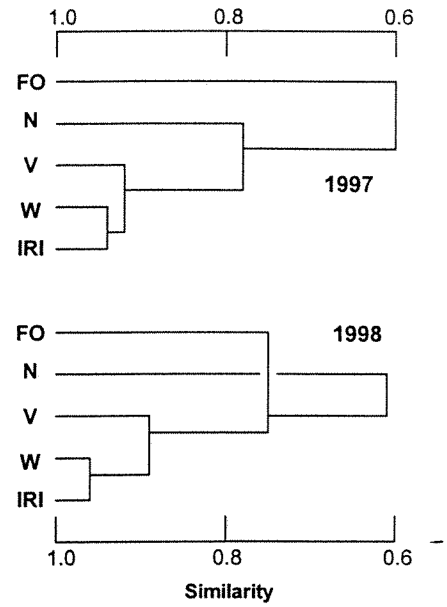
	54N				55N				56N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997												
Euphausiids	23.8	5.1	9.1	6.6	7.5	0.3	0.3	0.1	22.7	24.4	61.6	42.6
Copepods	26.2	86.0	86.9	88.0	22.5	68.7	67.7	73.8	0.0	0.0	0.0	0.0
Amphipods	14.3	0.2	0.3	0.2	22.5	20.6	7.0	15.0	13.6	0.4	0.6	0.3
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	4.8	0.0	1.0	0.1	10.0	0.3	22.3	5.4	4.5	0.0	5.1	0.5
Pteropods	23.8	8.6	2.5	5.2	17.5	6.2	1.7	3.4	25.0	71.0	22.8	51.2
Fish	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	9.1	0.2	4.9	1.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	7.1	0.0	0.1	0.0	20.0	3.9	0.9	2.3	22.7	4.0	4.9	4.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998												
Euphausiids	6.7	6.0	2.7	1.4	0.0	0.0	0.0	0.0	3.2	0.1	0.0	0.0
Copepods	26.7	17.5	2.2	13.1	24.2	24.3	22.3	28.4	25.8	11.1	2.4	10.4
Amphipods	20.0	40.1	20.2	30.1	21.2	49.4	25.8	40.0	19.4	12.1	2.0	8.1
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	20.0	0.6	72.8	36.6	0.0	0.0	3.7	0.0	3.2	0.1	57.7	5.6
Pteropods	20.0	35.6	1.9	18.7	27.3	20.6	9.4	20.5	25.8	70.0	20.6	69.6
Fish	3.3	0.1	0.2	0.0	6.1	0.1	33.2	5.1	6.5	5.5	12.5	3.5
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	3.3	0.1	0.0	0.0	21.2	5.6	5.6	6.0	16.1	1.3	4.7	2.9
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Fig. 2. Stomach contents of pink salmon in the Gulf of Alaska at 145°W longitude in 1998 calculated by five different methods. Number of samples was from 10 to 20 individuals at each station. EU = euphausiids, CO = copepods, AM = amphipods, SQ = squids, PT = pteropods, FI = fish, OT = other species.



The similarity between the five methods results in similar outcomes for the stomach contents of sockeye salmon collected in 1997 and 1998 (Fig. 3). The most similar pair was the IRI and W methods. The results from the N and FO methods were very different from the IRI method. To evaluate the feeding ecology of salmon, we therefore mainly used the IRI method, but depending on the situation also employed the W method.

Fig. 3. Dendrograms of stomach contents of sockeye salmon from the Gulf of Alaska in 1997 and 1998. Degree of overlap and cluster analysis between stomach content analysis methods were calculated by the simplified Morishita's index and the average linkage within group. IRI = index of relative importance method, W = weight method, V = volume method, N = numerical method, FO = frequency of occurrence method.



Comparison of Feeding Ecology Between Sockeye and Pink salmon

We investigated the carbon isotope ratio of Pacific salmon in the Gulf of Alaska during summer in 1999 (Fig. 4). Trophic levels of nekton-feeders (e.g., coho and chinook salmon, and steelhead trout) were higher than those of plankton-feeders (e.g., sockeye, pink, and chum salmon). In the Gulf of Alaska, sockeye salmon appear to be positioned between coho and pink salmon, with the potential for significant trophic competition to occur (Welch and Parsons 1993). Our results indicate that the trophic level of sockeye salmon was higher than the trophic levels of pink and chum salmon in the southern stations (the Subarctic Current; 50–53°N). However, there was no difference in trophic level among these three species at the northern stations (the Alaskan Gyre; 54–56°N).

We calculated the breadth and overlap of feeding niche of sockeye and pink salmon based on the Shannon-Wiener formula and the simplified Morishita index, respectively (Table 4). The high degree of food niche overlap between sockeye and pink salmon indicates that their food niche may be the same. Sockeye salmon ate more large prey (e.g., squid) than pink salmon (Figs. 5–6). The breadth of the food niche of pink salmon was wider than that of sockeye salmon in both years, although not significantly so (U-test; $p > 0.05$).

Fig. 4. Carbon isotope ratios of Pacific salmon collected in the Gulf of Alaska (145°W) during early summer of 1999. Symbols are means for various species, bars indicate standard error. Number of samples was from one to three individuals of each species in each station.

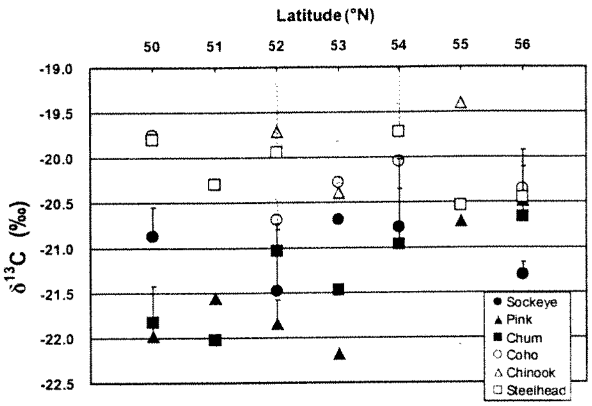


Table 4. Breadth (Shannon-Wiener index) and overlap (simplified Morishita's index) of food niche between sockeye and pink salmon in the Gulf of Alaska, 1997–1998.

Station	1997 Overlap	1997 Breadth Sockeye	1997 Breadth Pink	1998 Overlap	1998 Breadth Sockeye	1998 Breadth Pink
50N	-	0.719	-	0.978	0.254	0.696
51N	0.724	0.520	1.017	0.998	0.265	0.000
52N	0.895	0.838	1.034	0.682	0.580	0.887
53N	0.995	0.610	0.372	0.810	0.127	0.678
54N	0.995	0.258	0.462	0.813	1.004	1.373
55N	0.963	0.362	0.875	0.309	1.541	1.368
56N	0.827	1.019	0.936	0.783	1.344	1.071
Ave	0.900	0.618	0.783	0.768	0.731	0.868
SD	0.099	0.266	0.265	0.231	0.569	0.477

These results suggest that there is a potential for food competition between sockeye and pink salmon. Pink salmon appear to feed on more diverse prey at a lower trophic level than sockeye salmon.

The Effect of the El Niño Event on the Feeding Ecology and Growth of Sockeye and Pink Salmon

Squids, mostly *Berryteuthis anonychus*, dominated the stomach contents of sockeye salmon by both W and IRI methods in the Subarctic Current from 1994 to 1998. An exception was 1997, when squids and copepods were the most important prey. In the Alaskan Gyre, squids had the highest or second-highest percentages from 1994 to 1996 and 1998. In 1997, however, squids were rarely observed in the stomachs of sockeye salmon, and copepods were their most important prey (Fig. 5). Pink salmon also showed a similar pattern, although their diet was much more diverse (e.g., copepods, pteropods, and amphipods) than that of sockeye salmon (Fig. 6).

Fig. 5. Mean percent composition of stomach contents of sockeye salmon in the Subarctic Current (50–53°N 145°W) and the Alaskan Gyre (54–56°N 145°W) of the Gulf of Alaska during early summer from 1994 to 1998. Number of samples was from 10 to 20 individuals at each station. The mean percent composition evenly weighted for stations is shown by the volume method in 1994–1996, and by the IRI method in 1997 and 1998. EU = euphausiids, CO = copepods, AM = amphipods, DE = decapods, SQ = squids, PT = pteropods, FI = fish, PO = polychaetes, GE = gelatinous zooplankton, OT = other species.

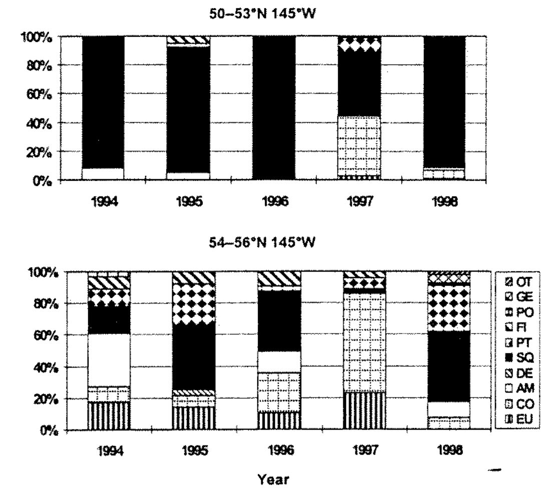
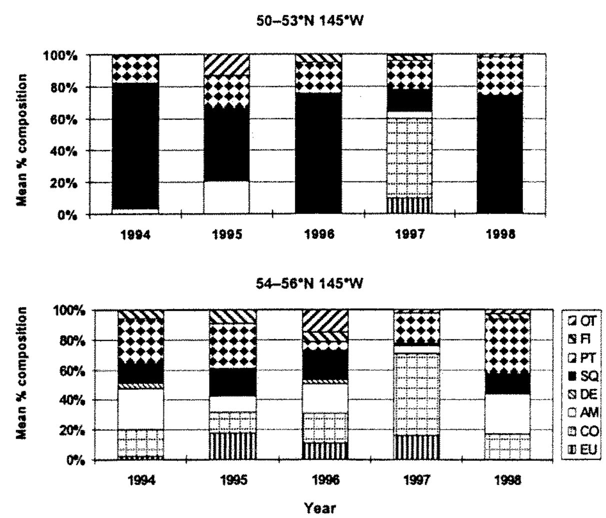


Fig. 6. Mean percent composition of stomach contents of pink salmon in the Subarctic Current (50–53°N 145°W) and the Alaska Gyre (54–56°N 145°W) of the Gulf of Alaska during early summer from 1994 to 1998. Number of samples was from 10 to 20 individuals at each station. The mean percent composition evenly weighted for stations is shown by the volume method in 1994–1996, and by the IRI method in 1997 and 1998. EU = euphausiids, CO = copepods, AM = amphipods, DE = decapods, SQ = squids, PT = pteropods, FI = fish, OT = other species.



The degree of food niche overlap between sockeye and pink salmon was higher in 1997 than in 1998, and the breadth of food niche of both species was lower in 1997 than in 1998 although not significantly so (U-test; $p > 0.05$; Table 4).

The Gulf of Alaska was affected by the El Niño event in 1997 (Freeland 1998). In 1997, early-July mean sea surface temperature (SST: 12.4°C) was 2.5°C warmer than in the other years (Fig. 7). The caloric value of prey consumed in 1998 was higher than that in 1997, because in 1998 pink salmon fed predominately on squids which provided higher potential energy than zooplankton (Fig. 8). The body weight and condition factor of both species plus fork length for sockeye salmon were significantly higher in 1998 than in 1997 (*t*-test; $p < 0.05$; Table 5). Returning Bristol Bay sockeye salmon were smaller than average in 1997–1998 (Kruse 1998). Typically, smaller fish are associated with strong runs: density-dependent growth or changes in marine environmental conditions are commonly postulated as causes (Helle and Hoffman 1995). The combination of smaller body size and weak runs of Bristol Bay sockeye salmon in 1997 and 1998 implies that ocean conditions were unusually poor for growth and survival (Kruse 1998). Therefore, these results suggest that the salmonid feeding ecology in 1997 was affected by the El Niño event, which resulted in the difference in annual growth of both species.

Fig. 7. Vertical profile of seawater temperature (°C) of the surface layers in the Gulf of Alaska (145°W) in early July from 1996 to 1998.

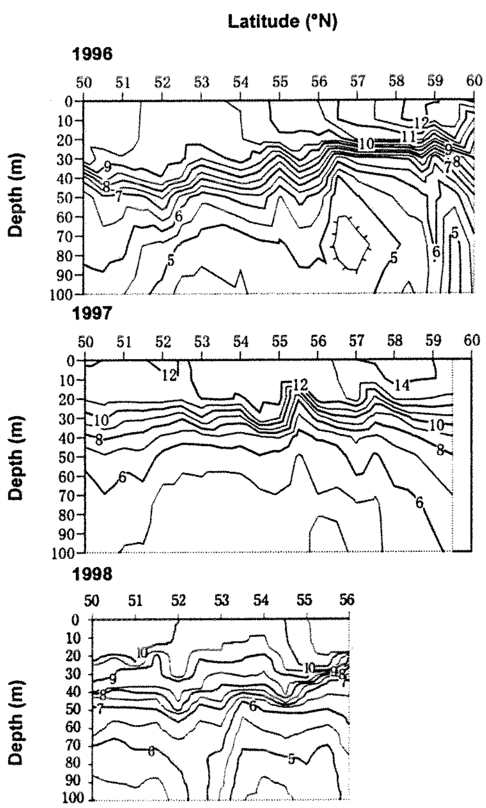


Fig. 8. Caloric value of organisms in stomach contents of pink salmon caught in the Gulf of Alaska (145°W) during early summer of 1997 and 1998. The caloric value was estimated from each prey weight in stomach contents of pink salmon using the data provided by Davis et al. (1998). EU = euphausiids, CO = copepods, AM = amphipods, SQ = squids, PT = pteropods, FI = fish, OT = other species.

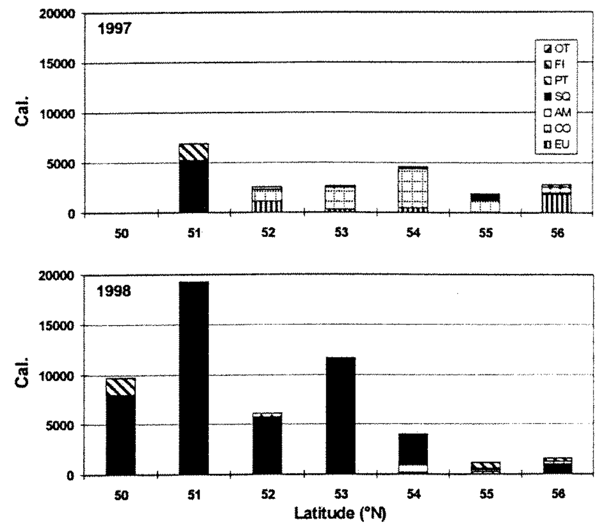


Table 5. Fork length, body weight, and condition factor of sockeye and pink salmon in the Gulf of Alaska, 1997–1998. The P indicates result of *t*-test comparison between 1997 and 1998 in each growth character.

	1997			1998			P
	Mean	SD	No	Mean	SD	No	
Sockeye salmon							
Fork length (mm)	564	51	674	571	62	586	0.019
Body weight (g)	2367	667	674	2579	699	586	<0.001
Condition factor	12.9	1.5	674	13.4	1.5	586	<0.001
Pink salmon							
Fork length (mm)	480	37	228	484	29	581	0.159
Body weight (g)	1374	316	228	1433	350	581	0.023
Condition factor	12.2	0.9	228	12.4	1.4	581	0.008

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