Diel Catches and Food Habits of Sockeye, Pink, and Chum Salmon in the Central Bering Sea in Summer

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Davis, N.D., K.Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. N. Pac. Anadr. Fish Comm. Bull. No. 2: 99–109.

Keywords: Sockeye salmon, pink salmon, chum salmon, diel catch, diel feeding habits, salmon stomach contents, salmon prey composition, Bering Sea

Abstract: Sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon caught by gillnet in the central Bering Sea were observed for diel changes in prey composition and stomach content weight. Sockeye salmon catches peaked after sunrise, and pink salmon catches increased dramatically between sunset and sunrise. Chum salmon abundance was low, but catches increased after sunrise and in the middle of the day. Sockeye, pink, and chum salmon fed throughout the day and peaks in feeding activity varied. Sockeye feeding increased after sunset, while pink salmon showed two periods of increased feeding activity, one after sunset and another at noon. Chum salmon stomachs contained prey at all times of the day, although there was a peak in feeding activity in the mid-afternoon. Sockeye, pink, and chum salmon stomach contents contained fish during the day, and increased their feeding on euphausiids and copepods during the night. A shift in salmon prey between daytime and nighttime feeding periods suggests that sampling throughout the diel cycle is required to provide an accurate assessment of salmon feeding ecology.

INTRODUCTION

Previous studies of diel changes in immature and maturing salmon food habits in the North Pacific Ocean have included trawling and serial sampling with gillnets in the waters off eastern Kamchatka (Machidori 1968; Ueno et al. 1969; Chuchukalo et al. 1995; Volkov et al. 1995a,b), the Okhotsk Sea (Shimazaki and Mishima 1969; Gorbatenko and Chuchukalo 1989; Chuchukalo et al. 1995; Volkov et al. 1995a, b), Gulf of Alaska (Pearcy et al. 1984), and the Bering Sea (Azuma 1992; Chuchukalo et al. 1995; Radchenko and Chigirinsky 1995). Machidori (1968) reported on experiments using gillnets and concluded that feeding activity of immature and maturing sockeye (*Oncorhynchus nerka*) and chum (*O. keta*) salmon was greater during the day than at night and that light was necessary for salmon feeding. Other studies using shorter sampling intervals have concluded that sockeye salmon feed most actively in late afternoon until midnight (Ueno et al. 1969), and that by morning, sockeye salmon stomachs are empty (Chuchukalo et al. 1995). Alternatively, sockeye salmon have been reported to feed after sunset and continue through the night (Pearcy et al. 1984; Azuma 1992). Results for maturing pink salmon (*O. gorbuscha*) were more varied with experiments indicating intensive feeding immediately after sunrise and sunset (Shimazaki and Mishima 1969), in the evening and shortly after midnight (Ueno et al. 1969), and a somewhat less active feeding period in the mid-morning (Pearcy et al. 1984). In coastal areas off western Kamchatka, maturing pink salmon fed actively during the day and ceased feeding at night (Gorbatenko and Chuchukalo 1989). From earlier studies of immature and maturing chum salmon, active feeding periods have been found immediately after sunrise and sunset (Shimazaki and Mishima 1969; Ueno et al. 1969), and alternatively, chum salmon have been observed to show little or no diel variation in their feeding activity (Pearcy et al. 1984; Azuma 1992). Inconsistency in results suggest that feeding periods of immature and maturing salmon at sea may change in response to several factors including day length, physical characteristics of the water column, and prey availability. However, for salmon food habit surveys to be useful in estimating prey consumption, sampling must be conducted to reflect

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the shifts that might occur in the diel feeding activities (Davis et al. 1998).

In odd years, maturing pink salmon are abundant in the central Bering Sea in the summer, which may contribute to shifts in chum distribution and may indirectly influence the growth of chum salmon (Azumaya and Ishida; this volume). Increased consumption of gelatinous zooplankton by chum salmon has been observed when pink salmon abundance was high in the Bering Sea (Tadokoro et al. 1996). However, no previous study in the central Bering Sea has reported salmon food habits over the 24-hour period for sockeye, pink, and chum salmon. In this study, we conducted gillnet operations throughout the diel period and examined changes in catch, stomach content weight, and prey composition of sockeye, chum, and pink salmon.

MATERIALS AND METHODS

Environmental Conditions

Sea surface temperature (SST), percent cloud cover, and weather conditions were recorded every hour during the 24-hour sampling period (July 11–12, 1997). Sunrise and sunset time and moon phase were also recorded. At noon (local time, GMT+12) a CTD probe was lowered to 1000 m to measure temperature and salinity.

Gillnet Operations

Gillnet operations were conducted between 57°33′N, 178°41′W and 57°27′N, 178°20′W in the central Bering Sea (Nagasawa et al. 1997). Eight operations were conducted in a 24-hour period starting at 0600 hrs and ending at 0500 hrs the following day using a surface gillnet (length = 950 m, fishing depth = 0–6 m, mesh size = 115 mm; Table 1). The gillnet set locations were 7.0 to 9.2 km apart. Setting the gillnet required five to six minutes after which it was allowed to soak for two hours. The duration of gillnet retrieval ranged from 16 to 23 min. Although vertical movements of high-seas salmon are different between daylight and dark periods, salmon spend a portion of time at the surface during all periods of the day (Walker et al. 1999, 2000), thereby making it possible for gillnets to catch salmon at the surface throughout the diel cycle. To catch salmon from a narrow range of sizes, a single mesh size was used. The mesh size (115 mm) was selected because it is efficient at catching immature and maturing salmon in the Bering Sea in summer.

Salmon Examination

After each gillnet retrieval, the catch was sorted by species and counted. If the number of individuals per species was greater than 50, the catch was subsampled due to logistical constraints (Table 1). Fork length, and body and gonad weight were measured and a scale sample was collected. The salmon stomachs were removed and frozen individually. After thawing, the stomach samples were weighed on a balance before and after removal of the stomach contents, and the weight of the contents obtained by subtraction. A stomach content index (SCI) was calculated as the ratio of measured prey weight to salmon body weight times 100, and differences in day and night catches and mean weight of stomach contents were compared using chi-square and one-way ANOVA.

Table 1. Salmon catches from eight consecutive gillnet sets on 11–12 July 1997 in the Bering Sea. Sample is the number of salmon sampled for stomach contents. Gillnet set and retrieval time is the local time (GMT+12) when setting and retrieval of the net began. Sunrise time is 03:11 (local) and sunset time is 20:47 on 11 July. Sunrise time is 03:12 on 12 July. Shading indicates periods in darkness.

Set number	SST (°C)	Gillnet set and retrieval time	Sockeye		Pink		Chum		Coho		Chinook		Total	
			Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample
1	8.3	0600–0800	25	25	140	67	6	6	1	1	0	0	172	99
2	8.5	0859–1100	29	29	145	35	10	10	0	0	0	0	184	74
3	8.5	1159–1400	24	24	129	21	26	26	0	0	5	5	184	76
4	8.6	1459–1700	16	16	114	51	5	5	0	0	3	3	138	75
5	8.6	1758–1959	27	27	117	39	9	9	0	0	0	0	153	75
6	8.6	2100–2259	23	23	221	50	9	9	0	0	0	0	253	82
7	8.4	0000–0202	21	21	278	50	9	9	0	0	0	0	308	80
8	8.3	0300–0500	68	50	273	20	20	20	0	0	0	0	361	90
Total			233	215	1417	333	94	94	1	1	8	8	1753	651
% Sampled				92		24		100		100		100		37

Prey composition was determined by separating the stomach contents into twelve prey categories (euphausiids, copepods, amphipods, crab larvae, squid, pteropods, fish, polychaetes, chaetognaths, gelatinous zooplankton, other, and unidentified), and visually estimating the percent volume of each category following the method of Pearcy et al. (1984). Combining less important groups reduced the number of prey categories to eight and the weight of these major prey categories was estimated by multiplying the percent volume of each group by the total measured stomach content weight, assuming the density of all prey was similar.

The degree of digestion was qualitatively described using an index described by Pearcy et al. (1984). Prey were categorized as either fresh, medium, or digested. Fresh prey was intact with no obvious digestion; medium digested prey, such as fish and squid, was missing skin, and euphausiids were opaque; and digested fish consisted of white flesh and bones, and crustaceans were in pieces. Usually digested prey, with the exception of gelatinous forms, was identifiable to prey category. The digestion index was noted as a general guide to the condition of the stomach contents.

RESULTS

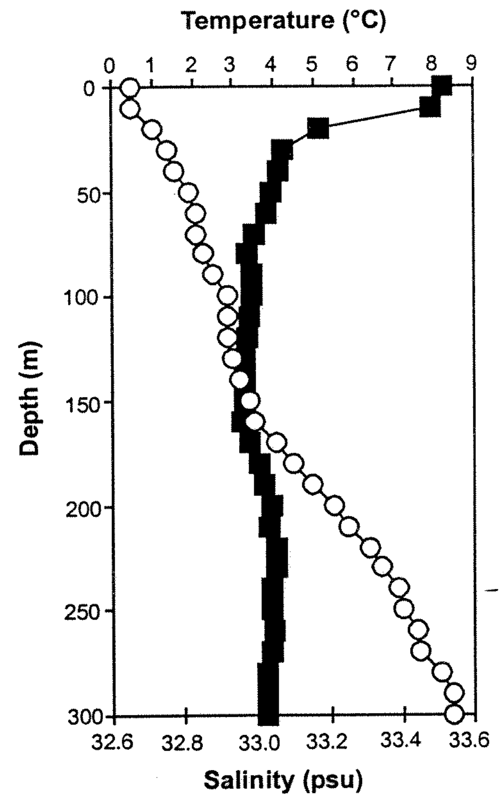
Environmental Conditions

The duration of daylight was approximately 17 hours when these operations were conducted (sunrise = 0311 hrs, sunset time = 2047 hrs). The moon phase was waxing to the first quarter and a continuous 100% cloud cover persisted during the diel period, which included drizzling rain between 2300 and 0200 hrs. Hourly sea surface temperatures ranged from 8.3° to 8.6°C (Table 1). The maximum seawater temperature was located at the surface and temperatures decreased to 4.48°C at 100 m (Fig. 1). The temperature minimum was located at 80 m (3.36°C), and a shallow thermocline was located between 10 and 20 m, where temperatures decreased rapidly from 7.90° to 5.11°C and continued to decrease to 4.23°C at 30 m.

Diel Salmon Catch

A total of 1,753 salmon was caught in eight gillnet operations (Table 1). Pink salmon was the most abundant salmon in the catch (81%), followed by sockeye (13%), chum (5%), chinook (1%), and coho salmon (< 1%). Sockeye, chum, and pink salmon were caught in all eight time periods, but coho (n = 1) and chinook (n = 8) salmon were caught only in the morning and afternoon. A relatively large catch of

Fig. 1. Upper water layer profile of temperature (closed box) and salinity (open circle) in the central Bering Sea at 57°30'N, 178°30'W on 10 July 1997 compiled from conductivity-temperature-depth probe data. Temperature decreased rapidly from 8.3°C at the surface to 4.2°C at 30 m depth.



pink, chum, and sockeye salmon was obtained immediately after sunrise (0300–0500 hrs; Table 1). The smallest catch of sockeye salmon occurred in late afternoon (1500–1700 hrs). Sockeye salmon catches were not independent of day and nighttime gillnet sets (χ^2; p = 0.03; df = 1). More sockeye salmon were caught during daylight and less during the night than would have been expected if catches had been equal in every time period. Pink salmon catches were also small in the afternoon and early evening (1500–2000 hrs) but increased dramatically immediately after sunset and remained at a high level until after sunrise (0300–0500 hrs). Pink salmon catches were not independent of day and night gillnet sets, as few salmon were caught during the day and more at night than would have been expected with equal catches in each time period (χ^2; p = < 0.001; df = 1). Chum salmon catches were relatively small throughout the sampling period, although chum catches increased shortly after sunrise (0300–0500 hrs) and after noon (1200–1400 hrs). The catch of chum salmon was independent of whether the gillnet was fishing during the day or night (χ^2; p = 0.19; df = 1).

Salmon Biological Characteristics

Sockeye salmon in gillnet catches were 62% male, predominantly immature (92%), and mostly ocean age .2 (94%) fish (Table 2). A few ocean age .3 sockeye salmon were caught and there was no catch of ocean age .1 fish. The mean fork length of sockeye salmon was significantly different among time periods (ANOVA; $p < 0.001$; $df = 7$). Although the Tukey multiple comparisons test did not detect which means were significantly different from one another ($p > 0.50$), the greatest difference in mean fork length was in the time interval before and after sunset (1500–1700 hrs, mean = 517 mm; 1800–2000 hrs, mean = 470 mm). However, a comparison of fork lengths of sockeye salmon caught in daytime versus nighttime sets was not significantly different ($p = 0.66$; $df = 1$). Two-thirds (66%) of the pink salmon were males, and all the fish were maturing ocean age .1. There was no significant difference in mean fork lengths among time periods ($p = 0.27$; $df = 7$), or between catches in daytime and nighttime gillnet sets ($p = 0.21$; $df = 1$). Half (51%) of the chum salmon were female and approximately half (53%) were maturing. Ocean age .2, .3, and .4 chum salmon were caught, but ocean age .3 was the most abundant age group (61%). The mean fork lengths of chum salmon caught during each time period were not significantly different, either among time periods ($p = 0.68$; $df = 7$), or between daytime and nighttime catches ($p = 0.81$; $df = 1$). The food habits data were not stratified for predator size because the fork length among individuals of each salmon species was similar between day and nighttime periods.

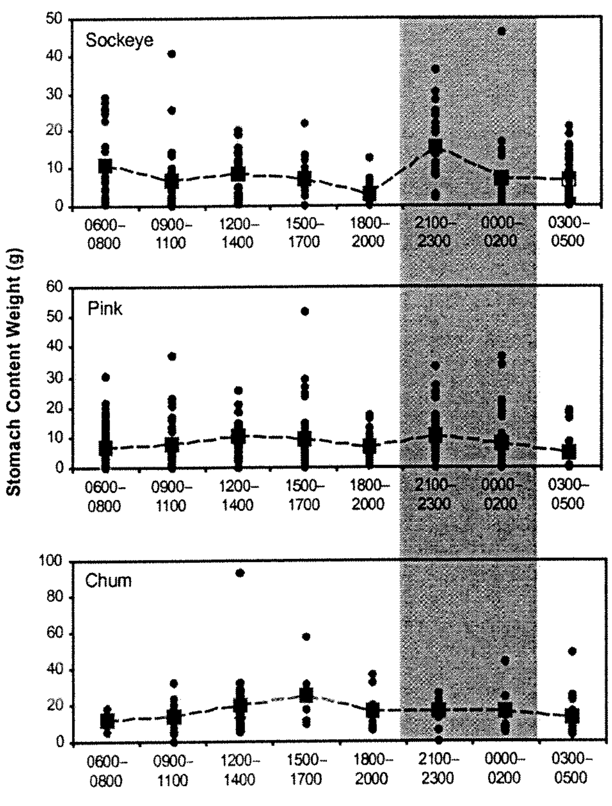
Table 2. Fork length (mm; sd = standard deviation), body weight (g), sex and maturity ratios, and age composition of sockeye, pink, and chum salmon caught in consecutive gillnet sets. Totals are data combined for all time periods. Shading indicates periods in darkness.

Species	Time period	Sample size	Fork length		Body weight		Percent female	Percent immature	Percent ocean age			
			mean	sd	mean	sd			1	2	3	4
Sockeye	0600–0800	25	485	29	1435	316	24	96	0	96	4	0
	0900–1100	29	478	26	1272	218	34	97	0	96	4	0
	1200–1400	24	494	45	1448	444	21	79	0	88	12	0
	1500–1700	16	517	50	1652	702	31	38	0	81	19	0
	1800–2000	27	470	21	1179	143	67	100	0	100	0	0
	2100–2300	23	492	26	1371	272	57	100	0	100	0	0
	0000–0200	21	480	26	1290	264	19	95	0	100	0	0
	0300–0500	50	478	22	1244	181	40	100	0	90	10	0
	Total	215	484	32	1333	336	38	92	0	94	6	0
Pink	0600–0800	67	455	19	1198	154	30	0	100	0	0	0
	0900–1100	35	460	22	1234	167	31	0	100	0	0	0
	1200–1400	21	458	17	1209	134	43	0	100	0	0	0
	1500–1700	51	460	24	1268	190	27	0	100	0	0	0
	1800–2000	39	451	17	1153	135	49	0	100	0	0	0
	2100–2300	50	453	22	1186	169	34	0	100	0	0	0
	0000–0200	50	455	21	1170	166	34	0	100	0	0	0
	0300–0500	20	460	16	1201	153	35	0	100	0	0	0
	Total	333	456	20	1202	165	34	0	100	0	0	0
Chum	0600–0800	6	531	55	1845	592	50	50	0	33	67	0
	0900–1100	10	546	77	2149	1125	50	30	0	40	30	30
	1200–1400	26	526	50	1784	515	42	39	0	24	64	12
	1500–1700	5	569	48	2104	559	40	0	0	20	40	40
	1800–2000	9	533	60	1898	1032	44	67	0	22	67	11
	2100–2300	9	524	38	1629	494	67	67	0	33	56	11
	0000–0200	9	547	50	1862	389	44	44	0	22	78	0
	0300–0500	20	526	43	1667	394	65	60	0	21	68	11
	Total	94	533	52	1822	640	51	47	0	26	61	13

Diel Food Habits of Sockeye Salmon

Stomach contents of sockeye salmon illustrated a diel pattern where prey weight was significantly greater among fish caught during the night than during the day (ANOVA; $p < 0.001$; $df = 1$; Fig. 2). There was one peak in stomach contents weight immediately after sunset (2100–2300 hrs; Table 3). The proportion of stomach contents in a fresh state of digestion was higher during the sunset to early morning hours than in the mid- to late afternoon. Mean stomach content weight decreased from mid-to late afternoon and was at a minimum before sunset (1800–2000 hrs). Few empty stomachs ($n = 3$) were collected from sockeye salmon, regardless of the sampling period, indicating that sockeye were able to find prey during all periods. Sockeye shifted from nighttime feeding on euphausiids and copepods to daytime feeding on fish and crab larvae.

Fig. 2. Stomach content weight of sockeye, pink, and chum salmon. Time period is the time of day when the fish was caught. The solid square and dashed line indicate the mean value for each time period. Solid circles represent the value for each fish examined. Shading indicates time periods in darkness.



Diel Food Habits of Pink Salmon

Stomach contents of pink salmon caught during the day and night were not significantly different from one another (ANOVA; $p = 0.07$; $df = 1$; Fig. 2), although there was increased feeding activity after noon (1200–1400) and immediately after sunset (2100–2300 hrs; Table 4). Empty stomachs ($n = 22$) were collected from midnight until late afternoon and the number of empty stomachs collected from pink salmon was higher than for sockeye and chum salmon. Pink salmon fed on fish during all time periods. During the night, euphausiids and copepods were important prey and during the day fish and crab larvae were the predominant prey.

Diel Food Habits of Chum Salmon

There was no significant difference between day and nighttime weight of stomach contents of chum salmon (ANOVA; $p = 0.90$; $df = 1$; Fig. 2). In every sampling period, chum had more prey in their stomachs than either pink or sockeye salmon (Table 5). Unlike the diel feeding of sockeye and pink salmon, chum salmon had an increase of stomach content weight in the middle to late afternoon (1500–1700), when fish were a major component of the diet, and showed no peak in prey weight after sunset. The afternoon period when stomach content weight was at a maximum (1500–1700) was also the time interval with the smallest sample size ($n = 5$) and, therefore, may not have been representative. Chum salmon, like sockeye salmon, had few empty stomachs ($n = 2$), suggesting chum salmon were able to find food at all times of the day. Chum salmon diet was more diverse than that of sockeye and pink salmon. In addition to fish, squid, euphausiids, and copepods, chum salmon also ate gelatinous zooplankton (medusae, ctenophores, and salps), appendicularians, and pteropods. The proportion of fish in chum stomachs decreased from evening through night and then gradually increased again from morning to afternoon. Chum salmon fed on gelatinous zooplankton during the day and night, although it was a less important component of the diet during the early morning daylight hours (0300–0800). Similar to feeding of sockeye and pink salmon, chum salmon increased their feeding on euphausiids during the night.

DISCUSSION

We caught sockeye, chum, and pink salmon at the surface (0–6 m) during each of the six daylight gillnet operations, providing evidence that these species spent some portion of their time at the surface during daylight periods. Previous gillnet studies have

Table 3. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of sockeye salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Sockeye Salmon	Time Period							
	0600–0800	0900–1100	1200–1400	1500–1700	1800–2000	2100–2300	0000–0200	0300–0500
Sample size	25	29	24	16	27	23	21	50
Empty stomachs (%)	0	0	0	6	4	0	0	2
Degree of digestion (%)								
fresh	0	0	0	0	0	83	95	37
medium	72	7	0	6	15	17	5	42
digested	28	93	100	88	81	0	0	18
Stomach content weight								
mean	10.74	6.81	8.52	7.35	3.12	15.60	7.30	6.82
sd	9.24	8.62	5.82	5.20	2.59	8.70	10.21	5.56
SCI								
mean	0.75	0.55	0.63	0.50	0.27	1.15	0.56	0.56
sd	0.68	0.71	0.44	0.34	0.24	0.57	0.72	0.44
Estimated mean weight of major prey categories (g)								
euphausiids	1.4	0.1	0.2	0.0	0.0	3.8	4.0	0.4
copepods	2.6	0.2	0.3	0.6	0.0	10.2	2.0	2.3
crab larvae	0.1	1.2	3.5	4.2	1.2	1.2	0.6	0.1
squid	0.3	0.1	0.2	0.2	0.2	0.2	0.6	0.5
fish	5.7	5.0	4.3	2.3	1.3	0.2	0.1	3.5
other[1]	0.6	0.3	0.1	0.1	0.4	0.0	0.0	0.1
Estimated mean volume of major and minor prey categories (%)								
euphausiids	6.9	2.4	2.5	0.3	0.6	30.1	71.7	10.7
copepods	13.5	2.8	2.2	7.5	0.6	52.7	13.0	20.1
amphipods	5.0	3.7	0.0	0.0	1.3	0.0	1.0	1.2
crab larvae	3.5	34.8	47.4	58.4	34.6	12.9	3.7	0.7
squid	4.7	3.3	1.6	0.9	5.7	2.5	10.0	13.5
pteropods	0.9	0.7	0.1	0.0	0.0	0.0	0.0	2.2
fish	63.6	49.0	45.3	25.3	42.5	1.8	0.6	47.3
polychaetes	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
chaetognaths	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0
gelatinous zooplankton[2]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
other[3]	0.2	4.7	0.1	1.3	10.0	0.0	0.0	2.4
unidentified material	0.8	0.0	0.4	0.0	1.1	0.0	0.0	0.0

[1]includes amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey.
[2]includes medusae, ctenophores, and salps.
[3] includes appendicularians and mysids.

Table 4. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of pink salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Pink Salmon	Time Period							
	0600–0800	0900–1100	1200–1400	1500–1700	1800–2000	2100–2300	0000–0200	0300–0500
Sample size	67	35	21	51	39	50	50	20
Empty stomachs (%)	4	12	5	4	0	0	10	35
Degree of digestion (%)								
fresh	0	0	0	0	5	70	10	20
medium	30	14	43	14	44	26	54	30
digested	66	74	52	82	51	4	26	15
Stomach content weight								
mean	6.61	7.79	10.33	9.29	6.56	10.64	7.67	4.59
sd	6.61	8.53	6.50	9.07	4.00	6.95	8.46	6.17
SCI								
mean	0.56	0.65	0.85	0.73	0.57	0.90	0.69	0.38
sd	0.56	0.70	0.52	0.66	0.34	0.59	0.64	0.53
Estimated mean weight of major prey categories (g)								
euphausiids	0.1	0.1	1.0	0.0	0.0	1.2	2.7	1.6
copepods	0.4	0.6	0.2	0.5	0.4	3.6	2.7	0.5
crab larvae	0.4	1.6	3.1	3.6	2.1	2.8	0.5	0.0
squid	0.1	0.2	1.5	0.5	0.4	0.7	0.6	0.1
fish	5.5	5.2	4.4	4.6	3.6	2.2	1.0	2.1
other[1]	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.2
Estimated mean volume of major and minor prey categories (%)								
euphausiids	2.1	1.3	6.2	0.5	0.0	10.6	21.9	15.5
copepods	6.9	5.3	1.6	4.4	3.5	27.5	32.5	8.7
amphipods	3.8	0.9	0.9	0.5	1.0	0.4	0.7	2.7
crab larvae	19.3	38.3	31.3	48.9	35.6	30.4	12.5	1.6
squid	3.3	2.6	7.9	3.4	7.3	7.0	4.2	2.1
pteropods	1.4	0.0	0.0	0.1	0.3	0.6	0.0	1.7
fish	58.0	39.9	46.9	38.0	52.2	23.5	16.2	32.9
polychaetes	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
gelatinous zooplankton[2]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
other[3]	0.7	0.0	0.8	0.2	0.1	0.1	2.0	0.0
unidentified material	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0

[1]includes amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey.
[2]includes medusae, ctenophores, and salps.
[3]includes appendicularians and mysids.

Table 5. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of chum salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Chum Salmon	Time Period							
	0600–0800	0900–1100	1200–1400	1500–1700	1800–2000	2100–2300	0000–0200	0300–0500
Sample size	6	10	26	5	9	9	9	20
Empty stomachs (%)	0	10	0	0	0	11	0	0
Degree of digestion (%)								
fresh	0	0	0	0	0	33	22	50
medium	0	80	8	0	44	56	78	45
digested	100	10	92	100	56	0	0	5
Stomach content weight								
mean	12.03	14.06	19.86	25.20	16.36	16.47	16.10	13.35
sd	4.34	9.73	16.75	19.90	11.00	8.62	11.99	11.28
SCI								
mean	0.74	0.73	1.04	1.24	0.83	1.07	0.85	0.77
sd	0.50	0.48	0.54	0.99	0.32	0.64	0.50	0.52
Estimated mean weight of major prey categories (g)								
euphausiids	0.2	0.0	0.1	0.4	0.0	3.5	2.3	1.0
copepods	0.0	0.0	0.3	0.2	0.1	1.6	1.0	0.7
squid	0.5	0.5	1.1	0.3	0.5	0.5	1.5	0.3
pteropods	4.9	0	0.3	0.3	0.4	2.6	0.3	0.4
fish	3.0	3.8	12.5	22.6	10.9	3.0	1.9	6.0
gelatinous zooplankton[1]	0.7	8.2	2.5	0.7	2.9	2.3	3.4	0.3
appendicularians	0.4	1.5	0.8	0.1	0.3	0.7	2.8	3.9
other[2]	2.3	0.0	2.2	0.6	1.1	2.1	2.9	0.7
Estimated mean volume of major and minor prey categories (%)								
euphausiids	1.7	0.0	0.8	1.4	0.0	17.8	16.1	7.3
copepods	0.8	0.1	2.5	1.4	0.3	10.0	8.1	5.2
amphipods	0.8	0.1	0.1	0.0	0.0	3.3	6.7	2.8
crab larvae	0.0	0.0	2.3	2.0	0.6	0.0	0.0	0.0
squid	4.2	3.5	5.0	2.0	3.9	3.3	6.7	3.2
pteropods	40.8	0.3	2.0	1.0	2.8	13.9	3.3	3.1
fish	16.7	14.5	57.9	83.2	68.0	15.6	7.8	32.3
polychaetes	1.7	0.1	0.2	0.0	0.0	1.1	0.6	0.0
chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
gelatinous zooplankton[1]	7.5	52.4	14.0	4.0	17.8	12.8	25.0	2.5
other[3]	6.7	19.0	4.2	1.0	4.4	3.3	13.9	41.0
unidentified material	19.2	0.0	11.0	4.0	2.2	7.8	13.4	2.8

[1]includes medusae, ctenophores, and salps.
[2]includes amphipods, crab larvae, polychaetes, chaetognaths, mysids, and unidentified prey.
[3]includes appendicularians and mysids.

generally shown that catches were generally higher during the night than during the day (Taguchi 1963; Manzer 1964; Takagi 1971; Pearcy et al. 1984; Azuma 1991). Based on these studies, it was hypothesized that perhaps salmon remained at depth during the day (Taguchi 1963; Manzer 1964). Although no consistent diel pattern was shown for short duration tracking of sockeye, pink, and chum using ultrasonic tags (Ogura and Ishida 1995), recent archival tag data recovered from salmon released on the high seas and recovered after many days in the coastal areas of Alaska and Japan have corroborated that salmon generally remain at the surface (< 10 m) during the night and, therefore, are susceptible to capture by gillnets (Wada and Ueno 1999; Walker et al. 2000). During the day, these data have shown that salmon swimming behavior by depth is highly variable because the fish are making continuous dives and ascents from the surface to a depth of approximately 50 m, or more (Walker et al. 2000). This behavior makes them vulnerable to capture by gillnets in the daytime when salmon return to the surface between dives.

Our results showed that sockeye salmon have a diel rhythm to their food habits with a peak in feeding activity in the evening after sunset (2100–2300 hrs). Earlier studies have reported a diel pattern to sockeye salmon feeding, where the most active feeding time was in the late afternoon before sunset until midnight (Ueno et al. 1969), or late in the evening (Pearcy et al. 1984; Azuma 1992). Azuma (1992) observed a secondary feeding period in the morning soon after sunrise (0400–0600 hrs), as did we (0600–0800 hrs). In our study in the central area of the Bering Sea, we noted a distinct change in the prey composition over the diel period from euphausiids and copepods in sockeye salmon stomachs collected at night to a striking predominance of fish and crab larvae in stomach contents sampled during the day. Pearcy et al. (1984), sampling in the Gulf of Alaska, likewise observed a shift in sockeye salmon prey composition from euphausiids at night to amphipods during daylight periods. In the western Bering Sea, Chuchukalo et al. (1995) observed that sockeye salmon fed primarily on euphausiids and squids at night and the proportion of copepods, hyperiid amphipods, and pteropods increased during the day.

We observed a pattern in pink salmon food habits characterized by two peaks in feeding intensity, one at night after sunset, and another at mid-day. Earlier studies have observed that pink salmon have a diel rhythm to their food habits, and feeding activity increased immediately after sunset and continued through the night (Shimazaki and Mishima 1969; Ueno et al. 1969; Pearcy et al. 1984). In the Bering Sea, we observed that at night pink salmon decreased the proportion of fish and increased the proportion of euphausiids and copepods in their stomach contents. Shimazaki and Mishima (1969) saw no evidence of a switch in prey types between day and night in the Okhotsk Sea. However, in the Gulf of Alaska there was a clear increase in feeding on euphausiids during the night (Pearcy et al. 1984).

We observed that chum salmon stomachs contained relatively large volumes of prey at all times of the day, and there was a peak in feeding in the mid-afternoon. Earlier diel experiments on chum salmon have shown varied results regarding the period of the day when feeding is most active. Feeding indices of chum salmon collected after sunset and sunrise were greater than those for chum collected during the day and night in the Okhotsk Sea and in the North Pacific off eastern Kamchatka (Shimazaki and Mishima 1969; Ueno et al. 1969). Pearcy et al. (1984) found no suggestion of diel periodicity of stomach fullness in chum salmon. The chum they observed fed predominately on salps in the afternoon and euphausiids from sunset until mid-day. Azuma (1992) concluded that the peak time for chum salmon feeding was in the morning, and that chum salmon were adapted to quickly digest large volumes of relatively non-nutritious prey organisms. The most interesting observation in our study was that chum salmon collected during the day were feeding substantially on fish. Unfortunately, our catch of chum salmon was small, but we speculate that chum salmon may shift their behavior from feeding predominantly on gelatinous zooplankton to fish during the day, thereby substantially increasing the caloric and nutritious quality of their diet.

The qualitative digestion index is well established in previous high seas salmon food habits studies (Pearcy et al. 1984; Azuma 1994). However, there is an inherent problem associated with using this index. There is only one value (fresh, medium, or digested) assigned to each stomach and a problem arises when the contents of the stomach are not at the same stage of digestion. This can happen when there are large and small prey items present in one stomach, when prey is in different locations in the stomach (front to back), when prey is positioned in the exterior or interior of the food bolus, and when prey of different digestibility are located in one stomach sample (for example, euphausiids digest more quickly than hyperiid amphipods). We reported the digestion index to provide a general qualitative description of the condition of the prey in the stomachs in each time period. Development of a more comprehensive and objective measure of the level of digestion would be a useful contribution for future studies of salmon food habits.

If we assume that salmon feed actively only at night on zooplankton and fish, and that fish is present in salmon stomach contents during the day because fish is digested more slowly than zooplankton; then we would expect stomach content weight to decrease over succeeding daylight hours until it reached a minimum before sunset. However, this was not our result. In this experiment, stomach content weight is actually higher in daylight than dark periods for chum salmon, and sockeye and pink salmon have at least one daylight time period when there is about the same amount of food in the stomachs as during the dark periods. These results suggest that fish were feeding throughout the 24-hour period, whenever prey was available. Nighttime competition for euphausiids may be intense, particularly when pink salmon are abundant, and when the period of darkness is short during summer at high latitudes. Therefore, a daytime switch to feeding on fish by sockeye, pink, and chum salmon may be a mechanism to decrease competition for food.

Our results emphasize that daily periods of increased feeding activities are different for each salmon species and that the prey composition shifts between day and night feeding periods. Although studies of salmon food habits that rely on sampling at one time of day highlight the difference in prey composition between salmon species, this type of study may fall short of examining the full spectrum of prey species taken by salmon predation. Therefore, sampling salmon throughout the diel cycle is required to provide an accurate assessment of salmon feeding ecology. Future investigations of diel feeding of salmon would benefit if sampling were intensified at dawn and dusk, when sockeye, pink, and chum salmon switch from feeding on fish during the day to zooplankton and squid at night. A diel trawl study using a short tow duration could sample a wide portion of the water column, increase the number of samples collected within a 24-hour period, and substantially reduce the time fish are held in the fishing gear digesting their meals. Further insight into the temporal variability of salmon diel feeding habits would be gained by repeating diel experiments in locations where these studies have been previously conducted and expanding these experiments to other seasons.

ACKNOWLEDGMENTS

We are grateful to Captain Yoshiyuki Hayasaka and the crew of the *Wakatake maru* for their fishing repetitive gillnet sets and careful sample collection. The help of Kazuya Nagasawa (National Research Institute of Far Seas Fisheries, Fisheries Agency of Japan) and Yuka Uwano (Dept. Aquat. Restoration Ecology, Tohoku University) was essential in data collection. Katherine Myers and Robert Walker (Fisheries Research Institute, University of Washington) made helpful comments during the study and on drafts of the manuscript, and we thank two anonymous reviewers for their thoughtful comments. The Fisheries Agency of Japan provided financial support for sampling and the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service (NOAA Contract Nos. 50ABNF700003 and 50ABNF000008) provided support for the U.S. authors.

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