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Diel Feeding Habits and Estimates of Prey Consumption of Sockeye, Chum, and Pink Salmon in the Bering Sea in 1997

by

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Abstract

Sockeye, chum, and pink salmon feeding habits were observed over a 24-hour period from gillnet catches in the Bering Sea to examine the diel changes in prey composition and stomach content weight. The largest catches of sockeye, pink, and chum salmon occurred during the time period immediately after sunrise. Sockeye salmon had a strong diel pattern with one peak in stomach content weight (prey weight) during the period immediately after sunset. Pink salmon feeding habits revealed two peaks in prey weight: one after sunset and another at noon. During the night, euphausiids and copepods were important prey of sockeye and pink salmon, and during the day their prey was predominantly fish, squid, and crab larvae. Chum salmon had a peak in stomach content weight that occurred in the middle to late afternoon, when fish were a major component of the diet. Chum salmon diet was most diverse during the night, when they fed on gelatinous zooplankton, euphausiids, pteropods, fish, and appendicularia. Chum salmon fed on gelatinous zooplankton during the day and night. Daily prey consumption (wet weight) was estimated on the basis of stomach content weight and literature values for stomach evacuation rates. At 6-8°C, daily prey consumption was estimated to range from 22 to 27 g/day (1.6-2.0% body weight (BW)/day) for sockeye, 21-26 g/day (1.7-2.1% BW/day) for pink, and 48-59 g/day (2.6-3.3% BW/day) for chum salmon. The sockeye and pink salmon consumption estimates were lower than previous estimates, suggesting poor feeding conditions. Consumption by chum salmon was similar to a previous study at a sea surface temperature of 8.0°, however our consumption estimates were slightly lower than a previous study at cooler water temperatures. Reduction of variability in digestion and consumption estimates would likely result from repetition of diel feeding studies for more than one 24-hour period, sampling in several geographical areas, intensifying the sampling during the times of the day when salmon switch from feeding on one prey type to another and change their feeding intensity, and conducting studies that reveal how salmon move in the water column in relation to their feeding behavior.

Introduction

Since the 1950s, food habits of adult Pacific salmon (*Oncorhynchus* spp.) caught in the offshore waters of the North Pacific Ocean have been surveyed in numerous studies (for example, Andrievskaya 1957, 1966; Allen and Aron 1958; Ito 1964; LeBrasseur 1966; Manzer 1968; Nishiyama 1970, 1977; Kanno and Hamai 1972; Takeuchi 1972; Pearcy et al. 1988; Brodeur 1990; Walker 1993; Davis et al. 1996; Myers et al. 1996; Sobolevksii and Senchenko 1996; Tadokoro et al. 1996). These studies have focused on identifying prey found in salmon stomach contents and describing the prey composition by weight or volume. These studies have provided valuable descriptive information about the diet composition, overlap, and uniqueness of prey among salmon.

However, to provide an essential link between salmon and their forage base, estimates of daily prey consumption are necessary. Establishing the trophic relationship between salmon feeding and prey composition and abundance has been identified as a component of the North Pacific Anadromous Fish Commission Science Plan (NPAFC 1997), and will be important in modeling the effect of historic and future shifts in the productivity of the subarctic North Pacific on the productivity of salmon and other predatory fishes (Brodeur and Ware 1992; Beamish and Bouillon 1993; Hare and Francis 1995; Hallowed and Wooster 1995).

Diel changes in stomach content weight and prey composition add an important temporal component to the study of salmon feeding habits and point to differences in the feeding behavior between the species. Previous diel studies of food habits have included serial gillnet catches of immature and maturing pink (*O. gorbuscha*) and chum *(O. keta)* salmon in the Okhotsk Sea (Shimazaki and Mishima 1969), sockeye (*O. nerka*), chum, and pink salmon in the North Pacific Ocean east of Kamchatka (Ueno et al. 1969), sockeye and chum salmon in the Bering Sea (Azuma 1992), and sockeye, chum, pink, and coho (*O. kisutch*) salmon in the Gulf of Alaska (Pearcy et al. 1984). In general, these studies have shown that salmon are likely to be feeding during both day and night, that prey composition may change during the diel period, and that feeding intensity may change at approximately the time of sunrise or sunset.

There have been several field-based studies of salmon feeding habits that have estimated prey consumption of immature and maturing salmon. Nishiyama (1970, 1977) used a bioenergetics approach (a balanced energy equation, in which the energy consumed equals the energy expended for metabolism, elimination, and growth) to estimate prey consumption for maturing sockeye in the Bering Sea. Davis et al. (1998) also used this approach to estimate prey consumption of sockeye, chum, and pink salmon in the Bering Sea and coho salmon in the North Pacific Ocean. These studies required a specified increase in body weight over a time interval.

Prey consumption can also be estimated from stomach content weight and rate of stomach evacuation by the method of Elliott and Persson (1978), as long as it can be assumed that the rate of evacuation is a function of the current amount of prey the stomach contains. Jobling (1987) suggests that a pulsed (stair-stepped) evacuation rate resulting from physiological feedback mechanisms may be the most accurate representation of digestion, especially for large prey. The digestion rate, α, is a function of both prey type (Jobling 1987) and ambient water temperature. The temperature-dependent nature of α in salmonids has been estimated in laboratory experiments (see Elliott 1972 for brown trout; Suzuki 1993 for a review of salmonid experiments). In addition, shipboard evacuation experiments at ambient ocean conditions have been conducted for chum and pink salmon (Hiramatsu et al. 1996).

The rate of feeding (food intake) may be complex in natural habitats and thus difficult to duplicate under controlled conditions. The inherently stochastic nature of the feeding rate must be summarized in a manner that allows estimation, usually by a continuous, deterministic function (Jarre et al. 1990). Depending on the type of function assumed, different methods have been suggested for estimating feeding rate from regularly timed stomach sampling of a fish population. One method is to assume that during a certain time period a fish population consumes food at a constant rate, while at other times no food is consumed (Jarre et al. 1990). If this assumption is not met, another method that assumes the feeding rate is constant within a single sampling period, but may change between sampling periods can be used (Elliott and Persson 1978). A diet analysis of brown trout in the laboratory indicated that this method gives values +/-15% with sampling intervals of three hours.

In this study, we used field observations of sockeye, chum, and pink salmon feeding habits collected over a 24-hour period from gillnet catches in the Bering Sea to examine the diel changes in prey composition and stomach content weight (prey weight). Observed prey weights and literature values for stomach evacuation rates were used to estimate daily prey consumption of sockeye, chum, and pink salmon. The proportion of the physiological maximum consumption realized by each species according to our consumption estimates (p-value) was compared with the p-values estimated in a previous study (Davis et al. 1998).

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

The 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). The gillnet (length=950 m [19 tans], fishing depth=0 to approximately 6 m, mesh size=115 mm) was set eight times in a 24-hour period starting at 0600 hrs and ending at 0500 hrs (Table 1). The gillnet was set at locations 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.

Salmon Examination

After each gillnet retrieval, the catch was sorted by species and counted. If the number of individuals of a species was greater than 50, that species was subsampled (Table 1). Fork length and body and gonad weight were measured and a scale sample was collected. The salmon stomachs were removed, placed in individual bags, and frozen for laboratory analysis. In the laboratory, the stomach samples were thawed and weighed before and after removal of the stomach contents. Stomach content weight (prey weight) was obtained by subtraction. The general state of digestion of the stomach contents (fresh, medium, digested) was recorded. The stomach contents were examined and separated into general prey categories (euphausiids, copepods, amphipods, crab larvae, squid, pteropods, fish, polychaetes, chaetognaths, and gelatinous zooplankton). Finer taxonomic detail was also recorded for prey where that was possible. The percent volume of each prey category was estimated visually.

Prey weight of each prey category was estimated by multiplying the percent volume of each prey category by the total prey weight, assuming the densities of all the prey categories were similar. The average prey weight by prey category was calculated for each of the eight 2-hour time intervals. Empty stomachs were included in the calculations.

Estimates of Daily Prey Consumption

The method of Jarre et al. (1990) required that we select values for the start and duration of feeding (T_0 and T_{feed}; Fig. 1). We tried to select a feeding period in several ways, including fitting the feeding curve by eye, using the time period with the largest quantity of fresh prey, and examining the residuals or variance in prey weight in each time interval for patterns, as variance in stomach contents increases during feeding.

As an alternative, we used the model of Elliott and Perrson (1978), which makes no apriori assumptions about the daily timing of the feeding period. In this case, the feeding rate was estimated by

$$F = \frac{\alpha \cdot \left(S_t - S_0 e^{-\alpha t}\right)}{(1 - e^{-\alpha t})}$$

Here, F is the feeding rate during the time interval, S_t is the stomach contents measured at the end of the time interval, and S_0 is the stomach contents measured at the beginning. Total consumption C over a time period is simply $F \cdot t$. This method cannot provide an independent estimate of α; however, it makes no assumptions about the feeding rate over time, except that it changes slowly relative to the time interval of measurement.

Using the model of Elliott and Persson (1978), we estimated the mean and standard deviations for F and C for each salmon species between each sampling period by constructing 50,000 bootstrap replicates for S_t and S_0 in each time interval from the stomach contents data. Because this method requires the assumption of α, this procedure used the Elliott (1972) temperature relation empirically determined for brown trout: $\alpha=0.053*e^{0.112T}$, where T is water temperature. The evacuation rate for this estimation was assumed to be Elliott's (1972) value of 0.13 estimated at the SST we observed in the Bering Sea (8.0°C). This value of 0.13 is not significantly different from the values estimated by Hiramatsu et al. (1996) for pink and chum salmon in the same geographical area.

The total consumption over a 24-hour period was estimated for 6°, 7°, and 8°C seawater temperatures found between 0 and 20 meters depth at our sample site. We assumed that the stomach contents in the first time period of day 1 (sampled) was the same as the first time period of day 2 (not sampled) to complete the daily cycle to 24 hours. For each temperature, the mean and standard deviation of the maximum physiological daily consumption was estimated using a bioenergetics model (Hanson et al. 1997) for the body weights of salmon observed in this study. P-values were calculated for each temperature. Estimates of daily prey consumption were divided by the mean value of body weight for each salmon species to calculate the daily consumption as a percentage of body weight.

Results and Discussion

Environmental Conditions

The duration of daylight was approximately 17 hours when these gillnet 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 8.3-8.6°C (Table 1). In the upper 100 m of the water column, the maximum seawater temperature was located at the surface and temperatures decreased to 4.48°C at 100 m (Fig. 2). The minimum temperature was 3.36°C, which was located at a depth of 80 m, 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.

Gillnet Catches

A total of 1753 salmon was caught in eight operations of the gillnet (Table 1). Pink salmon was the most abundant salmon in the catch (81%), followed by sockeye (13%), chum (5%), chinook (1%), and coho salmon (0%). Sockeye, chum, and pink salmon were caught in all eight time periods, however the coho (1) and chinook (8) salmon were caught only in the morning and afternoon time periods. A relatively large catch of pink, chum, and particularly sockeye salmon was obtained during the time period immediately after sunrise (0300-0500 hrs; Table 1). The smallest catch of sockeye salmon occurred in late afternoon (1500-1700 hrs). 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). Chum salmon abundance was low throughout the sampling period, although chum catches increased somewhat shortly after sunrise (0300-0500 hrs) and after the noontime period (1200-1400 hrs). Other studies have shown that gillnet catches of sockeye, pink, and chum salmon were larger during the night than during the day (Taguchi 1963; Takagi 1971; Pearcy et al. 1984; Azuma 1991)

Salmon Biological Characteristics

The average size (length and weight) of pink salmon was the smallest, sockeye size was intermediate, and chum salmon were largest (Table 2). The sockeye salmon were 38% female, predominantly immature (92%), and mostly ocean age .2 (94%) fish. A few ocean age .3 sockeye salmon were caught; there was no catch of ocean age .1 fish. Less than half (47%) of the chum salmon were immature and approximately half (51%) were female. Ocean age .2, .3 and .4 chum salmon were caught, however ocean age .3 was the most abundant age class (61%). Approximately one-third (34%) of the pink salmon were females, and all the fish were maturing ocean age .1.

Comparison of the mean fork length for chum and pink salmon across the diel sampling period showed no significant differences among means using a one-way ANOVA (p-value=0.68 for chum; p-value=0.27 for pink). In contrast, sockeye salmon mean fork lengths were significantly different among time periods (p-value<0.001). Although the Tukey multiple comparisons test was not powerful enough to detect which means were significantly different from one another (p-values >0.50), the greatest difference in mean fork length was between 1500-1700 hrs (mean=517 mm) and 1800-2000 hrs (mean=470 mm; Fig. 3). Variance in the fork length of sockeye salmon was highest in the afternoon gillnet sets (1200-1700 hrs).

Diel Variation in Feeding Habits

The distribution of mean prey weights indicates that salmon fed during all times of the day (Fig. 4).

Sockeye. Sockeye salmon had a relatively strong diel pattern in prey weight (Fig. 5). There was one peak in prey weight immediately after sunset (2100-2300 hrs). The prey during this period was mostly copepods and euphausiids. The proportion of prey weight in a fresh state of digestion was higher during the sunset to early morning hours than in the mid- to late afternoon (Fig. 6). Mean prey weight decreased from mid to late afternoon and was at a minimum before sunset (1800-2000 hrs; Table 3). During daylight fish were consumed, and from late morning until late afternoon crab larvae were an important prey of sockeye salmon. The total number of empty stomachs collected from sockeye were few (n=3) and were scattered among several sampling periods, indicating that sockeye were able to find prey at all times of the day (Table 3).

Pink. There were two peaks in prey weight in the stomachs of pink salmon during the diel period (Fig 5). One peak was at noon (1200-1400) and the other was immediately after sunset (2100-2300 hrs). Euphausiids and copepods were important prey of pink salmon during the night. The daylight peak was composed predominantly of fish, squid, and crab larvae. Pink salmon fed on fish during all time periods. The number of empty stomachs collected from pink salmon was higher than for sockeye and chum salmon (n=22) and empty stomachs were collected from midnight until late afternoon (Table 3, Fig. 6). The high abundance of pink salmon in the sampling area and the relatively large number of empty stomachs collected from pink salmon is suggestive of intra-specific competition for food.

Chum. In every time interval chum salmon had more prey weight in their stomachs than either pink or sockeye salmon (Fig. 5). The diel feeding of chum salmon differed from sockeye and pink salmon in that chum salmon had a strong peak in prey weight in the middle to late afternoon (1500-1700), when fish were a major component of the diet, and showed no peak after sunset. It is unfortunate that the sampling period when the chum salmon prey weight was at a maximum (1500-1700) was also the interval with the smallest sample size (Table 1). The proportion of fish in the chum stomachs decreased from evening through night and then gradually increased again from morning to afternoon. Chum salmon diet was more diverse than those of sockeye and pink salmon. In addition to fish, squid, euphausiids, and copepods, the chum salmon also ate gelatinous zooplankton (medusae, ctenophores, and salps), appendicularians, and pteropods. 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). Chum salmon, like sockeye salmon, had very few empty stomachs (n=2) suggesting chum salmon were able to find food at all times of the day (Table 3).

Results from this study and previous diurnal experiments on high seas salmon feeding habits suggest there is daily variability in salmon feeding patterns and the identity of their prey. A previous study in the central Bering Sea found more empty stomachs than this study; in particular, sockeye salmon had a higher frequency of empty stomachs than chum salmon throughout the day (Azuma 1992), which differs from our results. Results of that study also differed from ours in that sockeye prey weight was greater than that of chum salmon, sockeye prey weight peaked in the period before sunset, and chum prey weight was greatest after sunset. In a study in the Gulf of Alaska, Pearcy et al. (1984) also noted a switch by sockeye and chum salmon to feeding on euphausiids during the night, but neither fed on copepods. Chum salmon were found to increase the diversity of prey fed upon during the night, however fish were not a major component of the diet.

Estimates of Daily Prey Consumption by Salmon

Initial use of the Excel® nonlinear solver found least squares estimates for the parameters $\boldsymbol{R_{feed}}$, $\boldsymbol{T_0}$, $\boldsymbol{T_{feed}}$ and α for each salmon species. However, the 95% confidence interval was large for all parameter estimates, providing no useful information on total consumption. We attempted to reduce the range by selecting values for the start and duration of feeding ($\boldsymbol{T_0}$ and $\boldsymbol{T_{feed}}$). However, none of our methods of visually selecting a feeding period substantially narrowed the range of estimates of total prey consumption.

The difficulty comes from the sensitivity of the model to the estimations of peak time in the feeding curve. Changing the time $\boldsymbol{T_{feed}}$ one hour backwards or forwards changed consumption estimates by as much as ±50%. Sampling more intensively at periods of high feeding rates might provide data for improving this estimation technique by increasing resolution around this peak. However, even more critical was the lack of any distinctly defined peaks followed by troughs in the stomach contents data. This may be due to dissimilar diel feeding periods for different prey in the salmon diet. For example, at night euphausiids and copepods were eaten and during the day fish were a major prey. An approach where parameters are estimated separately for each prey species might be useful in cases such as this, where there are no distinct periods of feeding and non-feeding. Preliminary simulations suggest this might be a productive approach.

The bootstrap estimates of prey consumption (wet weight) between each sampling period based on the evacuation model of Elliott and Persson (1978) indicated highest consumption for sockeye salmon around sunset (17 g between 2000 and 2300 hrs; Table 4). Pink salmon had two high feeding periods, consuming 6.5 g in the early afternoon (1100-1800) and 7.6 g in the evening (2000-2300). Chum salmon were feeding actively in the late afternoon (21.2 g, 1400-1700). Some time periods included negative estimates of prey consumption (Table 4). This may indicate that the evacuation rate selected was too low to account for all the food leaving the salmon stomachs. However, raising the evacuation rate five times above previous evacuation rate estimates did not eliminate the negative values. A more likely explanation may be that salmon with full stomachs move away, or that salmon with empty stomachs move towards the water surface where the gillnet was sampling, thus creating an underestimate of the stomach contents after high feeding periods. Changes in catch rates throughout the day show that such movement may occur (Table 1). Migrating to cooler water while digesting their food conserves greater energy for growth (Murphy 1994). A recent archival tagging study suggests that salmon may have considerable daily up and down movements in the water column (Walker et al. 1998). Until the daily vertical movements of salmon on the high seas are better understood, this factor cannot be included in models used to determine consumption from sampling salmon exclusively at the surface.

The range of prey consumption estimates for sockeye salmon was 21.5 to 26.9 g/day for temperatures from 6° to 8°C (Table 5). For an average size (1330 g) sockeye sampled for this study that is a daily ration of 1.6-2.0% body weight (BW)/day. The estimates for pink salmon were somewhat similar, ranging from 20.6 to 25.7 g/day, or 1.7-2.1% BW/day for a pink salmon weighing 1200 g. Prey consumption estimates for chum salmon were approximately twice the estimates for sockeye and chum salmon, ranging from 47.6 to 59.3 g/day. This consumption estimate is a daily ration of approximately 2.6-3.3% BW/day for the average sized 1820 g chum salmon in this study. Nishiyama's (1970) estimates for the daily prey consumption required for maturing female (41.6 g, wet weight) and maturing male (57.1 g) sockeye salmon returning to Bristol Bay were twice the prey consumption estimated for sockeye in this study. P-values in our study were considerably lower for sockeye and pink salmon than those determined by bioenergetics modeling of data from the same geographical area of the Bering Sea (Davis et al. 1998). Our consumption estimates were approximately half of those estimated by Davis et al. (1998) for immature ocean age .1 sockeye and maturing pink salmon. The estimates of prey consumption by chum salmon are close at 7.0 and 8.0°C, to the estimates for immature ocean age .2 chum salmon in the Bering Sea (Table 5). However, our estimates are lower at 6.0°C.

Our relatively low sockeye and pink salmon prey consumption rates may be due to the overly optimistic ocean growth estimates required by Nishiyama (1970) and Davis et al. (1998) for calculation of their consumption estimates, as was discussed by Davis et al. (1998). Another explanation may be an underestimate of consumption rate after high feeding periods in our study caused by movement of salmon with full stomachs away from the sampling gear. In addition, salmon prey abundance is likely to be patchy on the scale of several kilometers to several hundred kilometers. Our low prey consumption estimates may be due to sampling in an area of low prey abundance. Summer 1997 was an unusual year in the North Pacific for several reasons, including a strong El Nino, unusually warm surface waters in the Bering Sea, and a lower than expected return of Bristol Bay sockeye to the coastal fisheries. If low run size was due, at least in part, to poor ocean conditions in the weeks prior to the fishery, the low consumption rates observed in our study might be symptomatic of poor feeding in the Bering Sea during the summer of 1997. Sampling over several days, at multiple locations within a single year, and in several years may resolve the differences between small-scale prey patchiness and interannual variation in forage conditions.

Recommendations

1. Sampling should be intensified at dawn and dusk when salmon switch prey types. A capture method (such as trawling) that can catch fish in short time intervals (15-30 min) used in areas where salmon are abundant would improve estimates of digestion rates and prey consumption. Trawl gear offers the advantage of being an active capture gear and therefore does not depend on the activity level of foraging and non-foraging fish for their susceptibility to the gear.
2. Repeating a 24-hour experiment for two days and in several different locations would likely reduce the variability in digestion and consumption estimates and be useful in detecting the patchiness of salmon prey abundance. Repeating a diurnal experiment periodically from year to year would provide additional information on interannual variability in salmon food habits. Chum salmon have a diverse diet and, unfortunately for our study, the sample size for chum was low. Repetition of this experiment with improved sample sizes, particularly for chum salmon, would be helpful for improving estimates of digestion and consumption rates.
3. Further analysis of this data should focus on differences in digestion rates and feeding periods of individual prey types, perhaps using simulation models of the variance in stomach contents to more precisely determine feeding periods.
4. A more thorough understanding is required of salmon vertical movements to and from the surface in relation to feeding. This would affect estimates of digestion rates, particularly in the Bering Seas where a vertically migrating salmon would experience a wide temperature range with relatively small vertical movement (20-30 m). Furthermore, if satiated salmon move out of the depth range sampled by the fishing gear and are replaced with salmon with less prey in their stomachs, then prey consumption could be underestimated.

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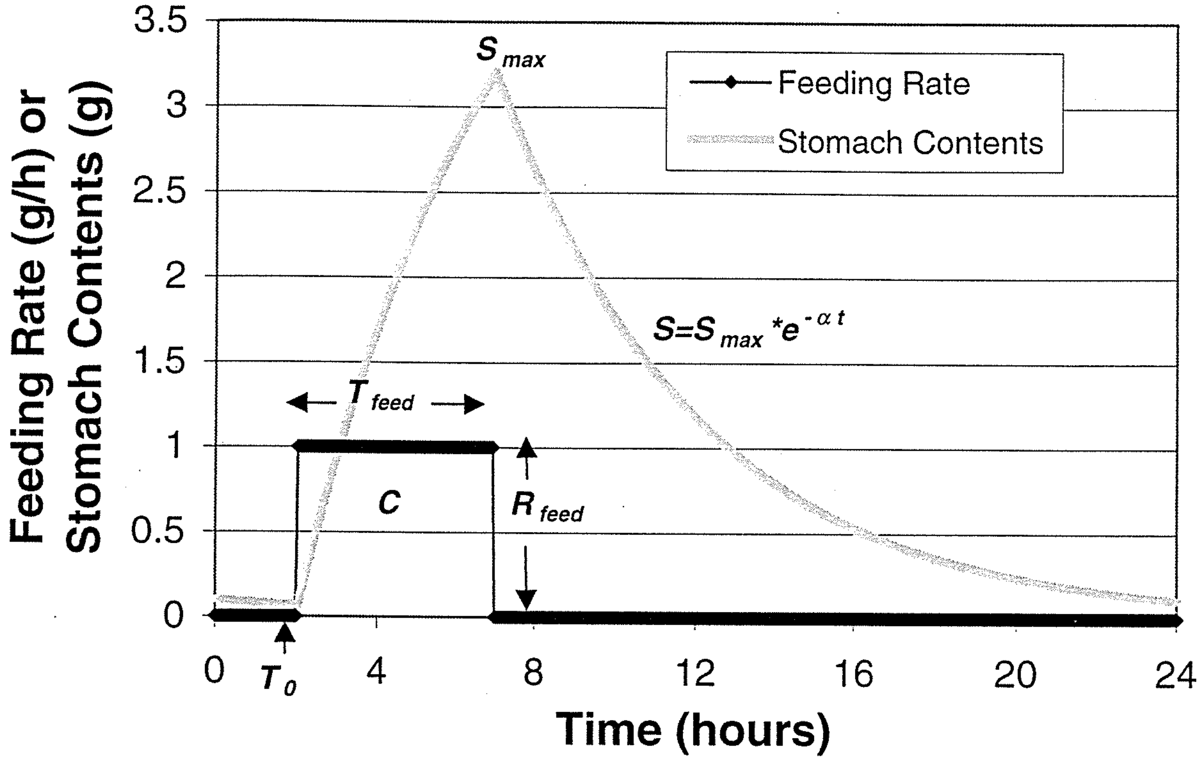

Figure 1. Theoretical relationship between feeding rate, total consumption, and stomach content weight. In this example, a fish feeds on prey at a constant rate (R_{feed}) of 1g/hour for three hours (T_{feed}) between hours 2 (T_0) and 5 of the experiment. Total food consumed (C) is thus 1g/hour * 3 hours = 3 g, the area under the square pulse. However, this quantity must be estimated by measuring the stomach contents, shown by the curved line. The curvature is determined by the evacuation rate α. In order to estimate C using the MAXIMS method (Jarre et al. 1990), estimates of four quantities: T_0, T_{feed}, α, and R_{feed}, are required. In addition, it must be assumed that this pulse occurs as part of a diurnal cycle and the stomach contents are $S_t = S_{(t-24)}$ for any time t. If these assumptions are not met, the method of Elliott and Persson (1978) may provide a better estimation of food consumption because, although their method assumes the feeding rate is constant within a single sampling period, it makes no apriori assumptions about the daily timing of the pulse.

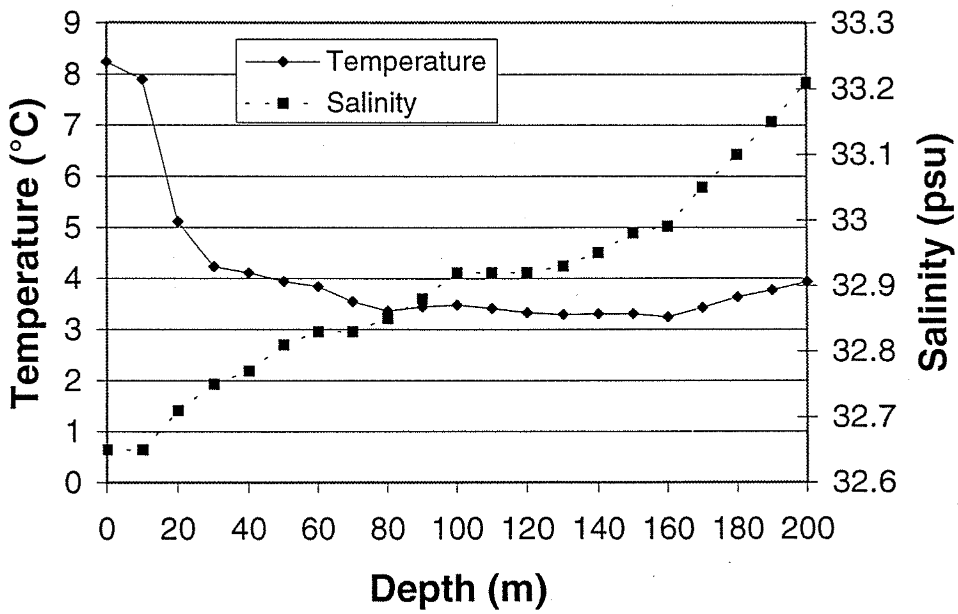

Figure 2. Temperature and salinity profile of CTD data taken at the study location at 57°30'N, 178°30'W on 11 July 1997. Temperature decreased rapidly from 8.3° at the surface to 4.2°C at 30 m depth.

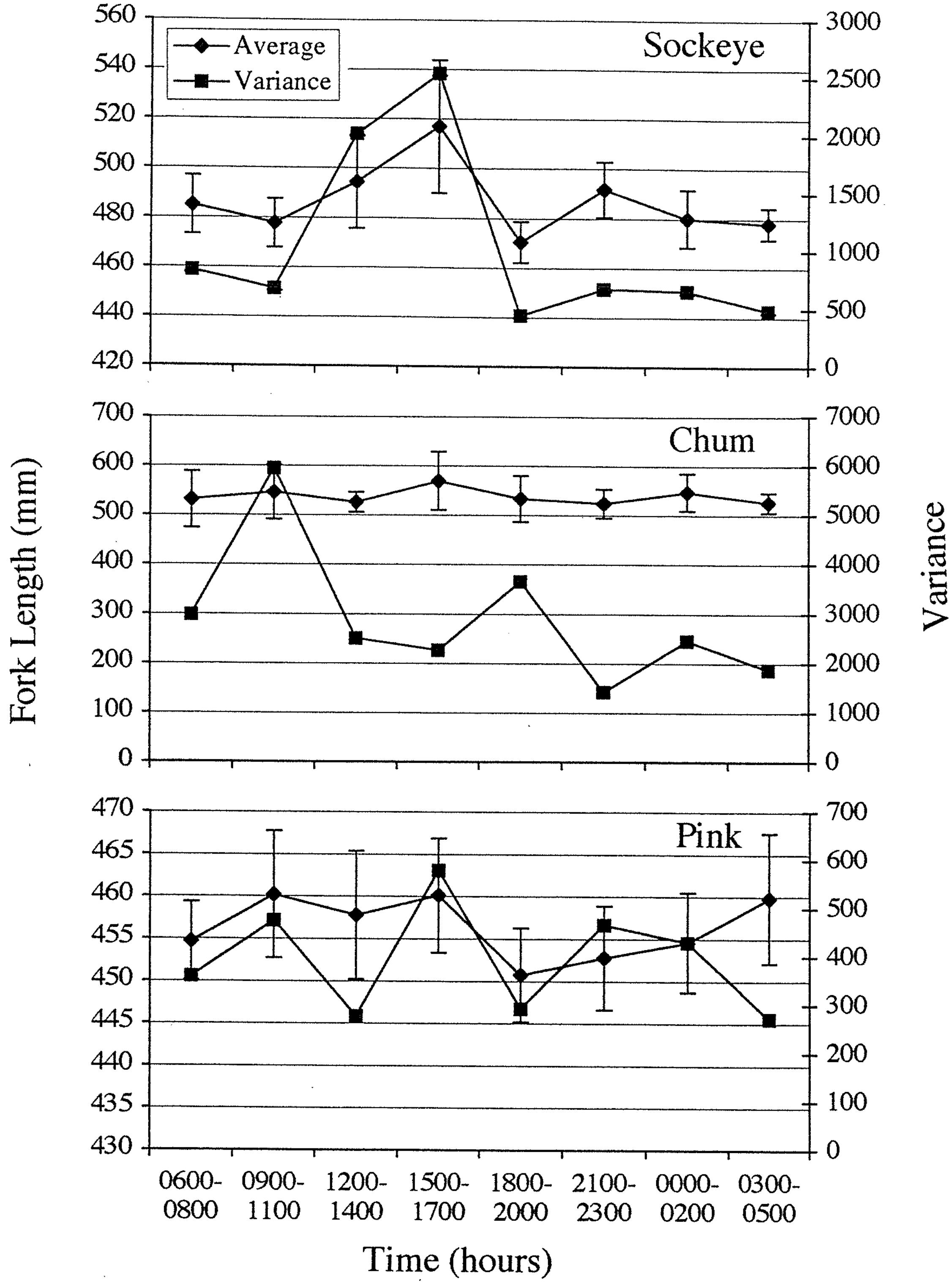

Figure 3. Average fork length (mm) and variance and for sockeye, chum, and pink salmon caught in eight gillnet sets in a 24-hour period. Error bars are 95% confidence interval around the mean value in each time period. Time is the hour of the day (local) the gillnet was in the water.

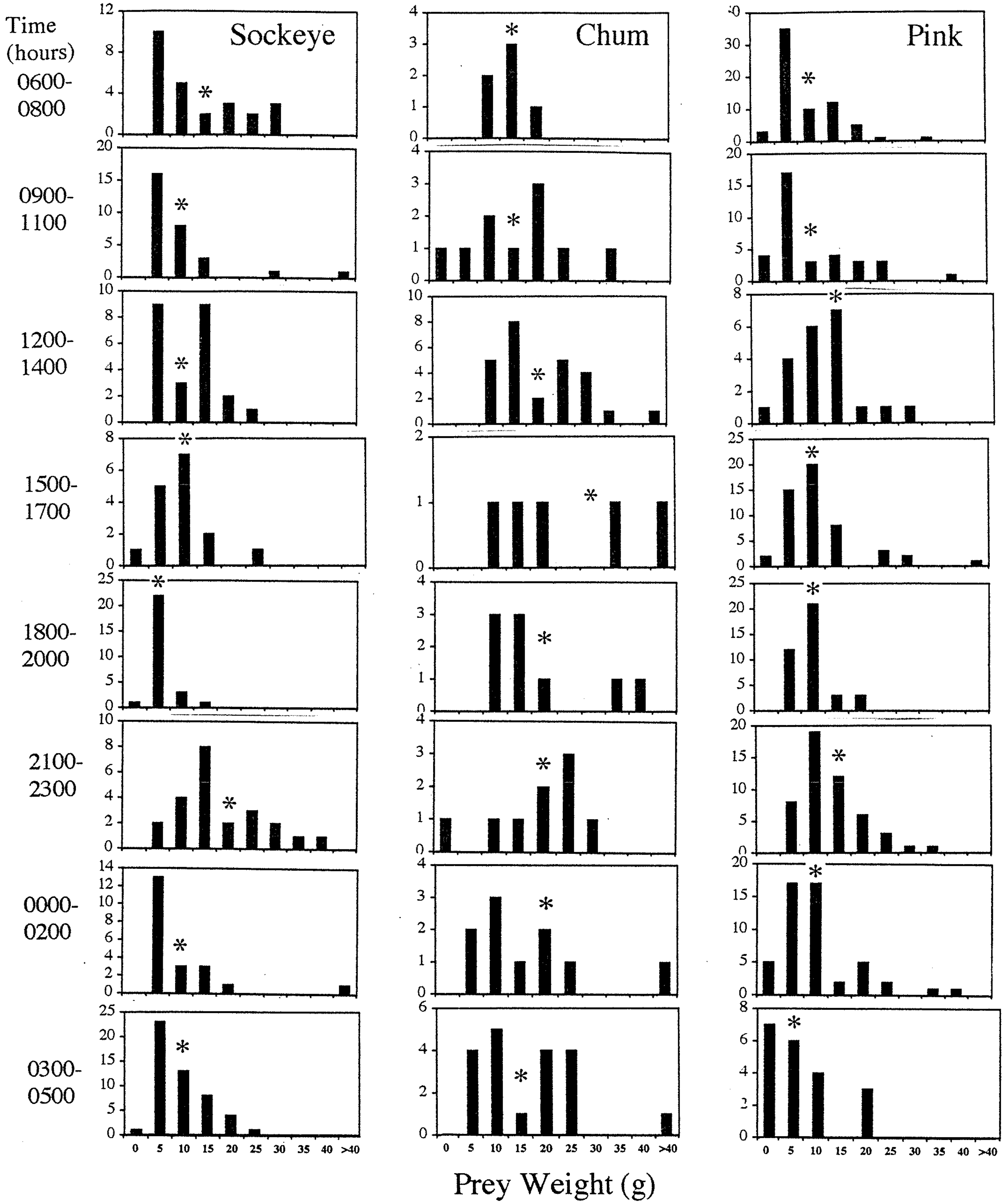

Figure 4. Frequency histograms of prey weight (g) collected from sockeye, chum, and pink salmon stomachs sampled from fish caught in eight gillnet sets over a 24-hour period. Time (hours) is the time period when the salmon were caught. Asterisk indicates the mean prey weight for each time period.

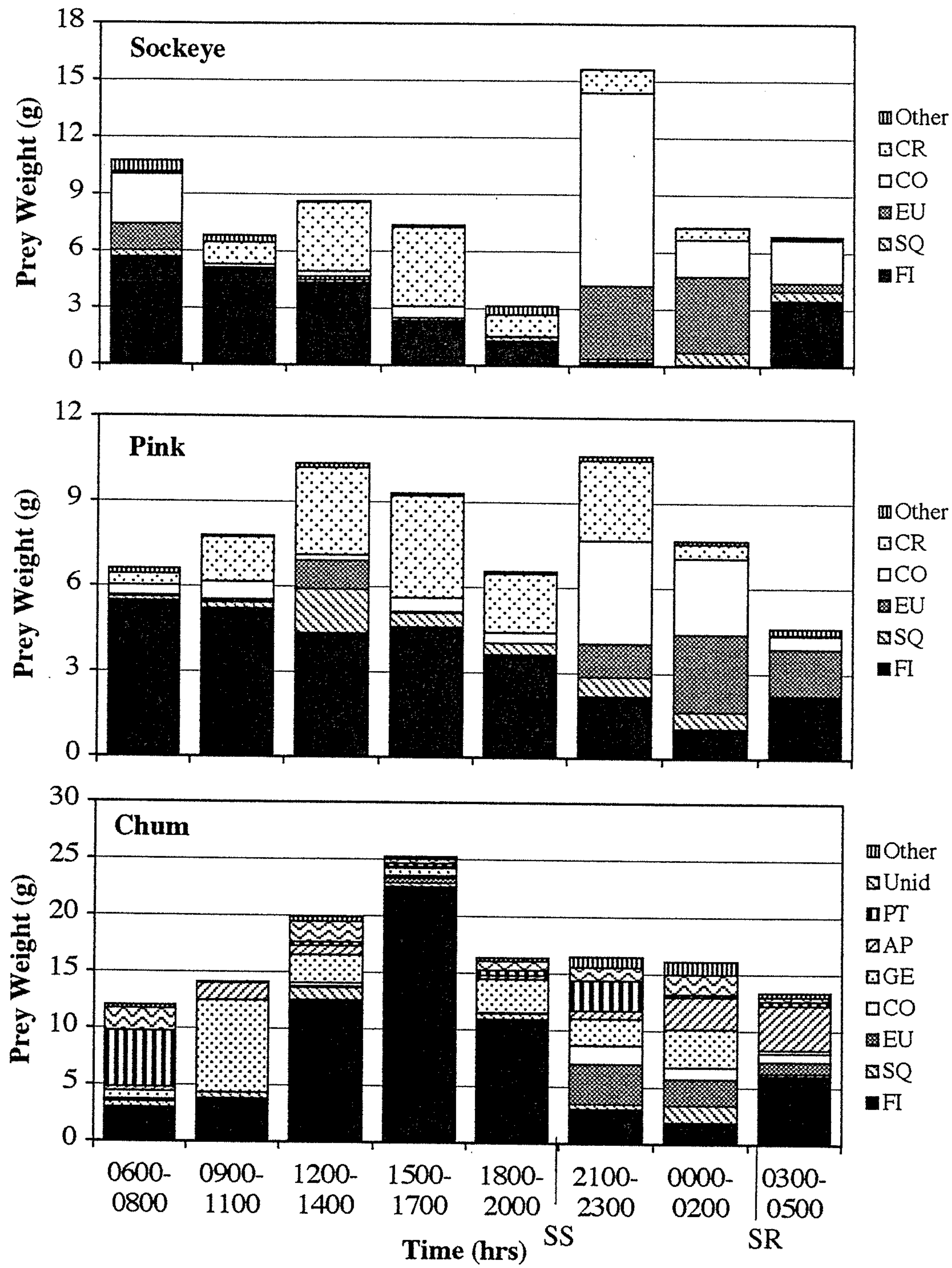

Figure 5. Mean weight (g) of each prey category observed in stomach contents of sockeye, pink, and chum salmon caught over a 24-hour period. Time (hrs) is the time period when the salmon were caught, SR=sunrise, SS=sunset. Prey categories include FI=fish, SQ=squid, EU=euphausiids, CO=copepods, CR=crab larvae, GE=gelatinous zooplankton (medusae, ctenophores, and salps), AP=appendicularians, PT=pteropods, Unid (chum)=unidentified prey, Other (sockeye and pink)=amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey; Other (chum)=amphipods, crab larvae, polychaetes, chaetognaths, mysids.

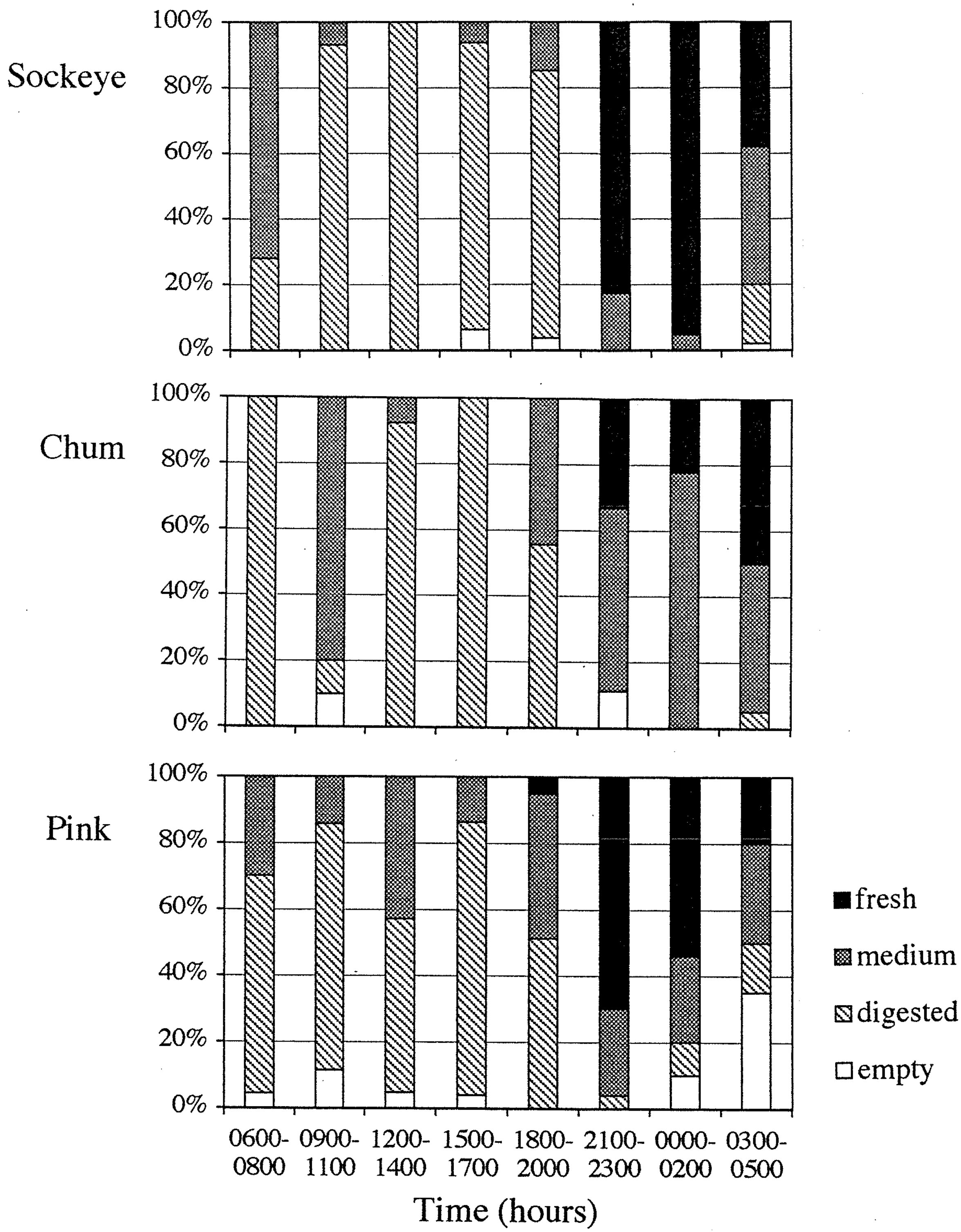

Figure 6. Degree of digestion observed in stomachs sampled from sockeye, chum, and pink salmon caught over a 24-hour period shown as percent frequency in each time period. Each stomach sample was assigned to one of four categories: empty, fresh, medium, or digested. Time (hours) is the time period when the salmon were caught.

Table 1. Summary of 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 (local) is 03:11 and sunset time is 20:47 on 11 July. Sunrise time is 03:12 on 12 July.

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

Table 2. Description of biological characters of sockeye, chum, and pink salmon caught in eight gillnet sets in a 24-hour period. Data are combined for all time periods. N=total number of fish examined for biological characters and stomach content analysis, Fl=fork length (mm), BW=body weight (g).

Species	N	Mean FL (sd)	Mean BW (sd)	Percent Female	Percent Immature	Percent Ocean Age 1	2	3	4
sockeye	215	484 (32)	1333 (336)	38	92	0	94	6	0
chum	94	533 (52)	1822 (640)	51	47	0	26	61	13
pink	333	456 (20)	1202 (165)	34	0	100	0	0	0

Table 3. Number of empty stomachs, and the mean prey weight (g) and SCI for sockeye, chum, and pink salmon analyzed for stomach content analysis. Time period is the time of day when the fish were caught. SCI is the ratio of prey weight to body weight times 100. Values for prey weight and SCI include all fish, including those with empty stomachs.

Time Period	Sockeye			Chum			Pink		
	Number Empty (%)	Prey Weight (sd)	SCI (sd)	Number Empty (%)	Prey Weight (sd)	SCI (sd)	Number Empty (%)	Prey Weight (sd)	SCI (sd)
0600-0800	0 (0)	10.74 (9.24)	0.75 (0.68)	0 (0)	12.03 (4.34)	0.74 (0.50)	3 (4)	6.61 (6.61)	0.56 (0.56)
0900-1100	0 (0)	6.81 (8.62)	0.55 (0.71)	1 (10)	14.06 (9.73)	0.73 (0.48)	4 (11)	7.79 (8.53)	0.65 (0.70)
1200-1400	0 (0)	8.52 (5.82)	0.63 (0.44)	0 (0)	19.86 (16.75)	1.04 (0.54)	1 (5)	10.33 (6.50)	0.85 (0.52)
1500-1700	1 (6)	7.35 (5.20)	0.50 (0.34)	0 (0)	25.20 (19.90)	1.24 (0.99)	2 (4)	9.29 (9.07)	0.73 (0.66)
1800-2000	1 (4)	3.12 (2.59)	0.27 (0.24)	0 (0)	16.36 (11.00)	0.83 (0.32)	0 (0)	6.56 (4.00)	0.57 (0.34)
2100-2300	0 (0)	15.60 (8.70)	1.15 (0.57)	1 (11)	16.47 (8.62)	1.07 (0.64)	0 (0)	10.64 (6.95)	0.90 (0.59)
0000-0200	0 (0)	7.30 (10.21)	0.56 (0.72)	0 (0)	16.10 (11.99)	0.85 (0.50)	5 (10)	7.67 (8.46)	0.69 (0.64)
0300-0500	1 (2)	6.82 (5.56)	0.56 (0.44)	0 (0)	13.35 (11.28)	0.77 (0.52)	7 (35)	4.59 (6.17)	0.38 (0.53)

Table 4. Prey consumption (g) of sockeye, pink, and chum salmon estimated by time interval. The feeding start and end time is when the gear was removed from the water from one sampling period to the next. Mean and standard deviation (std. dev.) are estimated from 50,000 bootstrap estimates. The stomach evacuation rate is the value (0.13) Elliot (1972) estimated for brown trout at 8.0°C.

Species	Feeding start time (hr)	Feeding end time (hr)	Estimated prey consumed (g)	
			Mean	Std. dev.
Sockeye	5	8	7.8	5.2
	8	11	-0.6	5.8
	11	14	5.1	3.6
	14	17	2.1	3.2
	17	20	-2.5	1.4
	20	23	17.0	4.8
	23	2	-4.1	9.0
	2	5	2.2	4.1
Pink	5	8	4.1	2.2
	8	11	4.2	3.4
	11	14	6.5	4.1
	14	17	2.6	3.6
	17	20	0.4	1.7
	20	23	7.6	1.6
	23	2	0.6	2.7
	2	5	-0.5	3.6
Chum	5	8	6.0	8.0
	8	11	7.1	14.3
	11	14	12.2	20.9
	14	17	21.2	103.2
	17	20	-3.6	61.5
	20	23	7.3	18.8
	23	2	6.7	25.9
	2	5	2.1	18.5

Table 5. Estimates for daily consumption (g/24 hr) based on our data, the daily physiological maximum consumption (Cmax; g/24 hr) as determined from a bioenergetics model (Hanson et al. 1997), and the p-value (proportion of the maximum consumption realized by our estimate of consumption) are given for sockeye, pink, and chum salmon. Mean and standard deviation (std dev) of consumption rates are estimated from 50,000 bootstrap estimates for all time periods combined. P-values calculated from this study and from a previous study (Davis et al. 1997) are shown.

Temper-ature	Estimated daily consumption (g/24 hr)						Maximum daily consumption (g/24 hr)						P-Values					
	Sockeye		Pink		Chum		Sockeye		Pink		Chum		Sockeye		Pink		Chum	
(°C)	mean	std dev	mean	std dev	mean	std dev	mean	std dev	mean	std dev	mean	std dev	this study	previous study	this study	previous study	this study	previous study
6	21.5	6.2	20.6	4.9	47.6	18.3	40.0	7.3	37.3	3.7	65.0	16.3	0.54	0.88	0.55	0.91	0.73	0.82
7	24.0	6.2	22.9	4.9	53.0	18.4	42.3	7.7	39.4	3.9	68.6	17.2	0.57	0.86	0.58	0.84	0.77	0.80
8	26.9	6.2	25.7	4.9	59.3	18.5	44.3	8.0	41.3	4.1	71.8	18.0	0.61	0.84	0.62	0.83	0.83	0.80