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[Article]

Diel Feeding Chronology, Gastric Evacuation, and Daily Food Consumption of Juvenile Chinook Salmon in Oregon Coastal Waters

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Abstract.—The diel feeding periodicity of juvenile Chinook salmon *Oncorhynchus tshawytscha* was determined from stomachs collected in coastal waters off Oregon in 2000 and 2003. Juvenile Chinook salmon exhibited a diurnal feeding pattern with morning and evening feeding periods. There were differences in the duration and magnitude of the dawn and dusk peaks between the 2 years. Gastric evacuation rates of euphausiid meals were estimated from laboratory experiments at 9.3, 10.7, and 13.9°C. Based on an exponential model, the instantaneous evacuation rates at these three temperatures were 0.0407, 0.0589, and 0.0807 per hour, respectively. The daily ration of juvenile Chinook salmon in Oregon coastal waters in 2000 and 2003 was estimated using three models. Using laboratory-derived evacuation rates, the Elliott and Persson and Eggers models produced daily ration estimates of 2.04% and 2.57% of body weight (BW), respectively, in 2000 and 2.93% and 2.46%BW in 2003. The MAXIMS model, which does not rely on laboratory-derived evacuation rates, produced higher estimates of daily ration (3.84% and 4.28%BW). Our diel feeding chronology, gastric evacuation rate, and daily ration estimates for juvenile Chinook salmon were comparable to those of other juvenile salmonids.

The Chinook salmon *Oncorhynchus tshawytscha* is the largest of the Pacific salmon and lives between southern California and the Bering Strait off Alaska. In addition to its ecological significance, Chinook salmon is culturally and economically important. Over 900,000 Chinook salmon are caught in recreational, subsistence, and aboriginal fisheries in North America per year and between 1 and 2 million fish are harvested commercially per year (Heard et al. 2007). However, as a result of a number of human and natural threats, 7 of the 17 recognized evolutionarily significant units of Chinook salmon on the Pacific coast are listed as threatened and 2 as endangered under the Endangered Species Act (Brodeur et al. 2003; Good et al. 2005). Despite the release of millions of juvenile Chinook salmon per year from hatcheries, adult returns have declined in many areas, including the Columbia River (Heard et al. 2007).

As with other anadromous salmonids, the time when juvenile Chinook salmon first enter the marine environment may be a critical element of their life histories (Pearcy 1992). Much of the ocean mortality occurs in this phase, and survival during this time is an important determinant of subsequent adult populations (Quinn 2005). Rapid growth resulting from high feeding rates may be essential to salmon survival during this critical period. Thus, understanding the feeding ecology of Chinook salmon in the ocean allows us to understand why growth and survival vary under different climate and ocean conditions, which may help better predict and manage salmon populations (Bisbal and McConnaha 1998).

Several studies have examined various aspects of juvenile Chinook salmon feeding ecology, such as variations in feeding intensity (Brodeur 1992), diet and bioenergetics in lake environments (Koehler et al.

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2006), prey selectivity and diel feeding chronology (Schabetsberger et al. 2003), and diel feeding periodicity and daily ration in freshwater populations (Kolok and Rondorf 1987; Sagar and Glova 1988; Principe et al. 2007). While there are estimates of gastric evacuation rate and daily ration for juvenile Chinook salmon in freshwater (Kolok and Rondorf 1987; Sagar and Glova 1988; Principe et al. 2007), to date these parameters have not been estimated for juvenile Chinook salmon once they enter the coastal marine environment. Given the importance of this life history phase to Chinook salmon survival and the major changes that occur in the surrounding environment and physiology between freshwater and the ocean, it is important to attain estimates of the evacuation rate and daily ration for juvenile Chinook salmon in coastal marine waters. Determination of evacuation rate and daily ration has been important in the study of many other fish species, as it is the first step in investigating a range of topics including ration–growth relationships, predator effects on prey populations, habitat assessments, fisheries production, competition, bioenergetics, and broader ecological models like nutrient cycling and energy flow (Doble and Eggers 1978; Godin 1981; Brodeur and Pearcy 1987; Juanes and Conover 1994; Héroux and Magnan 1996; Richter et al. 1999; Hurst 2004; Sturdevant et al. 2004).

Daily ration can be calculated by means of a number of different field and laboratory approaches (Adams and Breck 1990; Boisclair and Marchand 1993; Bromley 1994; Héroux and Magnan 1996; Richter et al. 2002). This paper focused on two different approaches to estimate daily ration. The first determined instantaneous evacuation rates in controlled laboratory experiments and then applied these rates to field data of diel stomach fullness to calculate daily ration. This method has been widely applied to a number of salmon and other fish species (e.g., Durbin et al. 1983; Brodeur and Pearcy 1987; Ruggerone 1989), including age-0 Chinook salmon in a lake environment (Principe et al. 2007). Within this general approach, hereafter referred to as the laboratory-derived model, several different formulations have been applied, including the Elliott and Persson (1978) and Eggers (1979) models. The Elliot and Persson model calculates daily ration by summing average stomach fullness from several intervals throughout a 24-h cycle (Schreck and Moyle 1990; Bromley 1994). The simpler Eggers model calculates daily ration based on the assumption of continuous and constant feeding (Schreck and Moyle 1990; Bromley 1994).

In the second approach, called the MAXIMS model, daily ration was estimated from diel field data without independent laboratory determination of gastric evacuation rates (Sainsbury 1986). The MAXIMS model was developed to estimate daily ration from field data through an iterative process of nonlinear regression (Jarre et al. 1991; Richter et al. 1999). It is similar to the Elliott and Persson model in that daily ration is estimated by summing food consumption, which may vary over a diel cycle, over multiple short periods (Richter et al. 2002). Because the MAXIMS model estimates all parameters from field data, it has the advantage of eliminating the need for controlled laboratory experiments.

Estimates of daily ration can vary considerably depending on which method is used, and it is often difficult to compare results from different studies using the various approaches (Héroux and Magnan 1996). While there have been several studies comparing either two or all three of the Eggers, Elliott and Persson, and MAXIMS models (e.g., Boisclair and Leggett 1988; Hayward 1991; Héroux and Magnan 1996; Richter et al. 2002), it is still unclear whether they offer comparable daily ration estimates under a variety of conditions. Owing to this variability and uncertainty surrounding these models, we used all three to estimate juvenile Chinook salmon daily ration.

The purpose of this study was to determine diel feeding chronology, gastric evacuation rate, and daily food consumption in juvenile Chinook salmon collected in Oregon coastal waters offshore from the mouth of the Columbia River. The Columbia River is the largest river on the Pacific coast of North America and is home to the largest runs of Pacific salmon. Most juvenile Chinook salmon migrate out of the estuary and enter the ocean offshore during spring and early summer (Bottom and Jones 1990). Once in the marine environment, juvenile Chinook salmon are diurnal predators, selectively feeding on large, highly pigmented prey items, including fish, amphipods, crab megalopae, and euphausiids (Schabetsberger et al. 2003; DeRobertis et al. 2005; Brodeur et al. 2007). This study will help create a better understanding of juvenile Chinook salmon in this area by providing data on their diel feeding chronology for an interannual comparison with the results of a previous study (Schabetsberger et al. 2003) and by calculating their evacuation rate and daily ration in this area for the first time.

Methods

Diel feeding chronology.—Juvenile Chinook salmon were collected by towing a Nordic 264 rope trawl at the surface during two cruises in June and July 2003 in the coastal marine waters offshore from the Columbia River, Oregon. The FV *Frosti* sampled during daytime on 28–29 June 2003 at approximately hourly intervals

TABLE 1.—Sample sizes, fork lengths, and weights of juvenile Chinook salmon and water temperatures from the three sets of experiments and the field studies conducted offshore from the Columbia River in 2000 and 2003.

	Laboratory			Field	
Variable	9.3°C	10.7°C	13.9°C	2000	2003
Sample size	32	71	59	79	179
Fork length (mm)					
Median	83	84.5	83	122	109
Range	70–100	71–100	66–103	100–250	79–294
Body weight (g)					
Median	5.9	6.5	6.0	16.1	12.6
Range	3.0–11.3	1.6–10.6	2.8–11.5	9.5–191.8	4.9–244.1
Temperature (°C)					
Mean	9.3	10.7	13.9	13.1	12.7
Range	8.9–9.7	10.1–11.5	13.4–14.2	13.04–13.26	9.89–15.88

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from 0800 to 1900 hours (Pacific Daylight Time [PDT]) between 4 and 30 nautical miles (1 nautical mile = 1.85 km) offshore. The FV *Piky* sampled during nighttime on 6 d between 3 June and 18 July 2003, at approximately 2-h intervals from 2130 to 0530 hours PDT between 4 and 25 nautical miles offshore. The prolonged sampling period was necessary to obtain an adequate sample size for each time of day. Data on the numbers and size of fish caught and sea surface temperature are given in Table 1. Throughout the sampling days for both vessels, sunrise occurred at approximately 0530 hours and sunset occurred at about 2100 hours.

Fish were measured to the nearest millimeter fork length (FL) at sea and then individually labeled and placed in a −20°C freezer until further processing. In the laboratory, fish were thawed slightly and weighed to the nearest 0.1 g (wet weight). The stomachs were removed and contents were lightly blotted with paper towels and weighed to the nearest 0.001 g. Fullness was expressed as the percentage of body weight consisting of food items, standardized for differences in body size (Brodeur and Pearcy 1987), that is,

$$\text{fullness} = (\text{stomach content weight} \times 100) / (\text{total fish weight} - \text{stomach content weight}).$$

Data from a previously published study on the diel feeding chronology of juvenile Chinook salmon conducted 20 nautical miles offshore south of the Columbia River in 2000 were used as a comparison with the 2003 data (Schabetsberger et al. 2003). For this study, the FV *Sea Eagle* sampled on 22–23 June 2000 at approximately 3-h intervals. Juvenile Chinook salmon were collected by towing a 264 Nordic rope trawl at the surface in a similar manner as in the 2003 study (Schabetsberger et al. 2003). In addition, the ingestion rate, evacuation rate, feeding period times, and daily ration were calculated from the 2000 data in the same manner as for the 2003 data, which had not previously been done.

Estimation of evacuation rate.—Juvenile spring Chinook salmon were raised from eggs obtained from Rapid River Hatchery in Riggins, Idaho. Fish were fed a diet of Biodiet moist pellets at the Hatfield Marine Science Center in Newport, Oregon. About 6 months after hatching, approximately 150 fish were transferred to each of three 230-L tanks supplied with a continuous flow of water and switched to a diet of thawed, commercially available euphausiid (*Euphausia pacifica*) pieces. Approximately 1 month before the experiments, smoltification was triggered by acclimating fish to a gradual increase in salinity over the course of several days to a final salinity of approximately 32‰. At least 4 d before the experiments, fish were acclimated to experimental temperatures of 9.3, 10.7, or 13.9°C in either a 230- or 379-L tank with flow-through natural seawater under a similar light regime as they would experience in the wild. Fish were fasted for approximately 36 h before the feeding trial, then fed en masse to satiation on *E. pacifica*. The uneaten portion of food was removed within 10 min.

Five fish were removed 10 min after the introduction of food and sacrificed with an overdose of tricaine methanesulfonate. Thereafter, a sample of fish was removed every 3 h for 27 h at 13.9°C, every 3 h for 33 h at 10.7°C, and every 6 h for 30 h at 9.3°C. Two trials were used for the 10.7°C and 13.9°C experiments to obtain at least five data points at each interval. Once sacrificed, the FL and wet weight of the fish and stomach contents were measured as above. Fullness (%BW) was calculated by the same methods as for the wild fish. The numbers and sizes of fish used at each experimental temperature are given in Table 1.

Data analysis.—For analysis of the diel feeding chronology data, samples were grouped into 3-h intervals over the 24-h period. Samples collected over

multiple days in each sampling were pooled into a single diel cycle to obtain an adequate sample size for each period. Nonparametric Kruskal–Wallis tests were used to test for differences in untransformed fullness data between intervals in 2000 and 2003.

The gastric evacuation rate and daily ration were calculated using two different approaches. For the laboratory-derived model, the general shape of the gastric evacuation function was first determined from the laboratory data with the general evacuation model of Temming and Andersen (1994) using the fraction of the initial meal remaining (Andersen 1998), that is,

$$W_t/W_0 = [1 - b_0 e^{b_1 T}(1-a)t]^{1/(1-a)},$$

where W_0 is the initial meal size (%BW), W_t is the remaining food at time t, T is the temperature, a is the shape parameter of evacuation, b_0 and b_1 describe the temperature dependence of the evacuation rate, and t is time since ingestion (h). The estimated shape parameter a (0.742 ± 0.185 [mean ± SE]) did not differ significantly from 1.0 ($P = 0.17$), indicating that evacuation generally followed an exponential pattern. The exponential evacuation model has been widely used and is directly applicable in daily ration models (Persson 1986; Brodeur and Pearcy 1987; Ruggerone 1989; Héroux and Magnan 1996). Therefore, further analyses were performed by applying an exponential pattern of evacuation in juvenile Chinook salmon according to the function

$$W_t/W_0 = e^{-(b_0 e^{b_1 T})t}.$$

The instantaneous evacuation rate (R) at a specific temperature was determined from the equation $R = b_0 e^{b_1 T}$. Nonlinear regression (Statistica 6.0) was used to fit all model parameters. In addition, an analysis of variance (ANOVA) was used to test for differences in initial meal size between temperatures.

Next, the Elliott and Persson and Eggers models were used to estimate daily food consumption (also expressed as %BW) in the field based on the laboratory instantaneous evacuation rate. Since evacuation rates are temperature-dependent, daily rations using these models were calculated using the previously estimated temperature-dependent R interpolated for observed field temperatures of 13.1°C and 12.7°C in 2000 and 2003, respectively. In the Elliot and Persson model,

$$C_t = \frac{(W_t - W_0 e^{-Rt})Rt}{1 - e^{-Rt}},$$

where C_t is the %BW of food consumed during time t. The daily ration is calculated by summing the amount consumed during each time interval over 24 h.

In the Eggers model,

$$C_{24} = W_{24} \times R \times 24 + (W_{t=24} - W_{t=0})$$

where C_{24} is the %BW of food consumed over 24 h, W_{24} is the mean %BW of food consumed over 24 h, $W_{t=24}$ is %BW of food in the stomach at $t = 24$ h, and $W_{t=0}$ is the %BW of food in the stomach at $t = 0$ h.

The second approach used the diel trajectory of stomach fullness to estimate the ration consumed, assuming that feeding is either constant during the feeding periods or inversely dependent on the amount of food in the stomach (Sainsbury 1986; Jarre et al. 1991). Assuming constant feeding with two diel feeding peaks, the MAXIMS model (2.1) run with SAS (version 9.1) software was applied to the 24-h stomach content field data to determine evacuation rates, ingestion rates, and feeding periods (Richter et al. 1999). The change in stomach contents (S) can be modeled as

$$dS/dt = J - R \times S,$$

where J is the ingestion rate. Daily ration was then calculated using the equation (Richter et al. 1999),

$$C_{24} = J(T_{f1} + T_{f2} - T_{r1} - T_{r2})$$

where T_{f1} is the end of the first feeding period, T_{f2} is the end of the second feeding period, T_{r1} is the beginning of the first feeding period, and T_{r2} is the beginning of the second feeding period.

Results

Diel Feeding Chronology

Juvenile Chinook salmon in the coastal waters off Oregon exhibited statistically significant differences in stomach fullness throughout a 24-h period in both 2000 and 2003 (Kruskal–Wallis test: $P < 0.001$). In 2000, fullness was lowest at 0142 hours, whereas in 2003 fullness was highest at 1930 and 2230 hours (Figure 1). In both years there were two feeding periods, yet there were differences in the duration and timing of the feeding periods. Based on the MAXIMS model, in 2000 the first feeding period occurred in the early morning before dawn and lasted over 7 h, while the second feeding period began in the late afternoon and lasted over 2 h (Table 2). Conversely, in 2003 the first feeding period began just after dawn and lasted approximately 2 h, while the second feeding period began in late afternoon and lasted until sunset (Table 2). As previously reported by Schabetsberger et al. (2003), fullness (as %BW) in 2000 was significantly greater in the morning hours than in the afternoon and evening. Conversely, in 2003 fullness was significantly higher during the two periods just after sunset than during any other 3-h period (Kruskal–Wallis test: $P < 0.001$).

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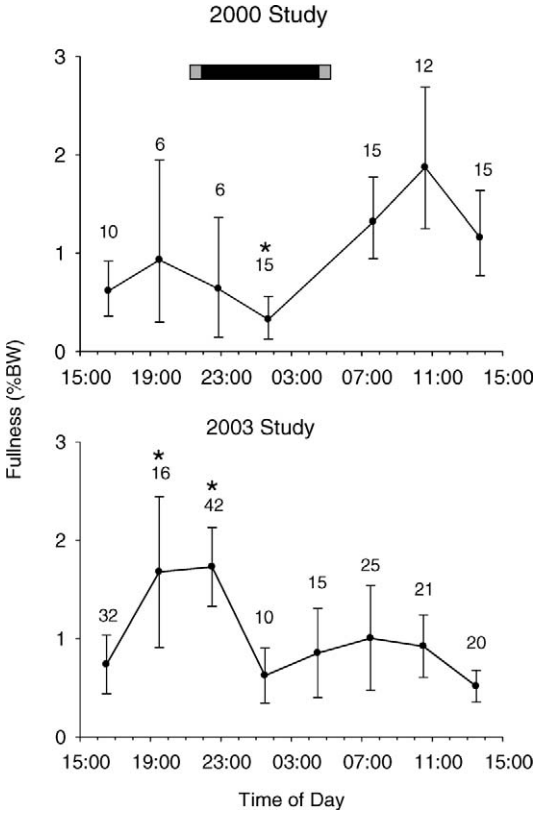

FIGURE 1.—Relationships between time of day and stomach fullness in juvenile Chinook salmon in 2000 (Schabetsberger et al. 2003) and 2003. The dots indicate means, the thin vertical lines 95% confidence limits. Points with asterisks above them were significantly different from all points without asterisks (Kruskal–Wallis test; $P < 0.05$). Sample sizes are shown above the points. The bar on top indicates the times of twilight (gray) and darkness (black).

Gastric Evacuation Rate

As expected at lower temperatures, the mean meal size voluntarily consumed by fish in the evacuation experiment was significantly lower and more variable at 9.3°C (3.31%BW) than at 10.7°C (6.68%BW) and 13.9°C (5.41%BW) (ANOVA; $P = 0.009$), resulting in the appearance of greater variation in the evacuation rate data (Table 3, Figure 2).

As determined by applying an exponential model to each temperature, the instantaneous evacuation rate parameter of juvenile Chinook salmon increased with increasing temperature between 9.3°C and 13.9°C (Table 3). With a near doubling in R between 9.3°C and 13.9°C (0.043 versus 0.083 per hour), the time to 90% evacuation decreased from 54 to 28 h. The overall relationship between R and temperature was described in the evacuation model by the equation $R = b_0 e^{b_1 T}$, where b_0 was 0.0134 ± 0.0046 (mean ± SE) and b_1 was 0.130 ± 0.0293.

TABLE 2.—MAXIMS model estimates of ingestion and evacuation rates and beginning and ending times of feeding periods for juvenile Chinook salmon in field studies from 2000 and 2003 offshore from the Columbia River. Times are expressed in terms of the 24-h clock.

Parameter	2000	2003
Ingestion rate (%BW/h)	0.402 ± 0.051	0.535 ± 0.191
Instantaneous evacuation rate (per hour)	0.168 ± 0.032	0.178 ± 0.080
Beginning of first feeding period	0252 ± 0022	0604 ± 0058
End of first feeding period	1037 ± 0040	0827 ± 0105
Beginning of second feeding period	1654 ± 0027	1539 ± 0054
End of second feeding period	1842	2116 ± 0123

Daily Ration

Estimates of daily ration based on the Elliott and Persson and Eggers models were lower than those based on the MAXIMS model by 1–2%BW (Table 4). The Elliott and Persson and Eggers models produced daily ration estimates of 2.04%BW and 2.57%BW, respectively, in 2000 and 2.93%BW and 2.46%BW in 2003. By contrast, the MAXIMS model produced daily ration estimates of 3.84%BW in 2000 and 4.28%BW in 2003.

Discussion

Both the 2000 and 2003 diel feeding data suggest that juvenile Chinook salmon are diurnal predators with feeding peaks around either dawn or dusk. This diel pattern of crepuscular peaks in prey consumption is similar to that of other juvenile salmon in a range of environments, including riverine Chinook salmon (Sagar and Glova 1988), coho salmon *O. kisutch* in coastal waters (Brodeur and Pearcy 1987), pink salmon *O. gorbuscha* in two marine bays (Godin 1981), sockeye salmon *O. nerka* in an urban lake (Doble and Eggers 1978), and chum salmon *O. keta* in marine waters (Sturdevant et al. 2004).

Comparing the 2000 and 2003 diel feeding patterns shows the variability in the timing and duration of diurnal peaks. In 2000, the low stomach fullness in the middle of the night suggests that the highest feeding

TABLE 3.—Initial %BW consumed, r^2 value of exponential evacuation curve, and evacuation rate of juvenile Chinook salmon from laboratory experiments at three temperatures.

Variable	9.3°C	10.7°C	13.9°C
Initial %BW consumed	3.31	6.68	5.41
Exponential r^2	0.45	0.81	0.89
Evacuation rate per hour (SE)	0.0407 (0.008)	0.0589 (0.003)	0.0807 (0.004)

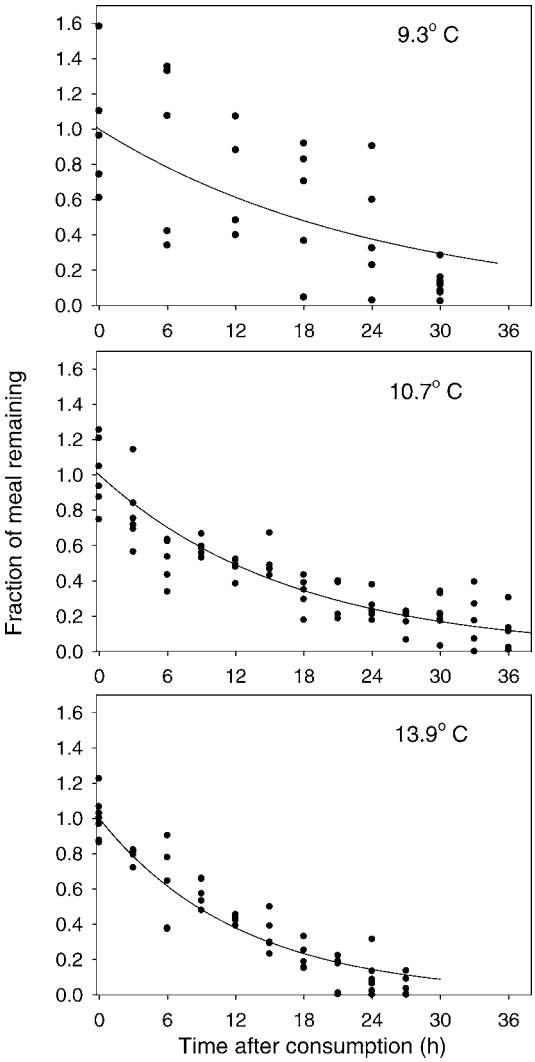

FIGURE 2.—Gastric evacuation patterns of juvenile Chinook salmon fed commercially available euphausiid pieces at 9.3, 10.7, and 13.9°C. The lines represent the exponential evacuation model fit to the data at each temperature.

intensity occurred in the morning hours, with a gradual decrease in stomach fullness throughout the remainder of the day despite a second smaller feeding period in the afternoon (Schabetsberger et al. 2003). In contrast, in 2003 the peak fullness occurred in the two periods around sunset, suggesting the highest feeding intensity occurred around dusk, with a smaller feeding period in the morning. In addition, the morning and evening feeding periods occurred at slightly different times across the 2 years (Table 2). As in the 2003 study, Brodeur and Pearcy (1987) found that juvenile coho salmon exhibit the most distinct increase in feeding

TABLE 4.—Daily ration (%BW) of juvenile Chinook salmon examined in field evacuation studies from 2000 and 2003 offshore from the Columbia River using three different models.

Model	2000	2003
MAXIMS	3.84	4.28
Elliott and Persson	2.57	2.46
Eggers	2.04	2.93

period during the evening hours. Among salmonids, the timing of crepuscular feeding peaks is highly variable, suggesting that factors such as prey availability and feeding motivation of the fish are important (Godin 1981). Specifically for juvenile Chinook salmon, light intensity is a significant variable affecting the level of feeding intensity (Brodeur 1992). Several other factors, including differences in temperature and diet composition, may help explain some of the observed variability between 2000 and 2003. The diet composition was only partially quantified for the 2003 fish, but based on the analyzed stomachs juvenile Chinook salmon ate similar prey items in 2000 and 2003. However, in 2000 they seemed to be slightly more reliant on euphausiids and hyperiid amphipods, whereas in 2003 they were slightly more reliant on fish.

The instantaneous evacuation rates obtained from the laboratory are similar to those found for a variety of other fish species within their normal temperature ranges (He and Wurtsbaugh 1993). Specifically with regard to other juvenile salmon, laboratory-based estimates found in this study were lower than estimates for slightly larger juvenile coho salmon obtained by similar methods (Brodeur and Pearcy 1987). This is consistent with the observation that coho salmon have higher evacuation rates than most other fishes (Ruggerone 1989). The present estimates were similar to field-based estimates reported for juvenile Chinook salmon in freshwater at similar sizes and temperatures (Kolok and Rondorf 1987), but somewhat lower than those found for smaller juvenile salmonids in freshwater (Doble and Eggers 1978; Sagar and Glova 1988; Principe et al. 2007). However, direct comparisons of evacuation rates are difficult due to the multitude of factors that influence them (Ruggerone 1989).

In laboratory experiments, the gastric evacuation rate of juvenile Chinook salmon increased with increasing temperature. Compared with other variables, temperature seems to have the greatest effect on gastric evacuation, and this pattern has been widely observed for a variety of marine and freshwater fishes (Brett and Higgs 1970; Tyler 1970; Elliott 1972; Doble and Eggers 1978; Durbin et al. 1983; Brodeur and Pearcy 1987; He and Wurtsbaugh 1993; Bromley 1994;

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Temming and Herrmann 2001). The general relationship between gastric evacuation and temperature is exponential, described by the equation $R = b_0 e^{b_1 T}$ (Bromley 1994). For marine fishes, b_0 can vary significantly according to food type, whereas b_1 appears to be fairly constant at around 0.115 (Durbin et al. 1983), which is similar to the b_1 value of 0.130 from this study.

Likewise, temperature had an effect on the meal size when fed to satiation. The initial meal size in evacuation experiments at 9.3°C was almost half that observed at 10.7°C and 13.9°C. Similarly, in fingerling sockeye salmon at 5°C the maximum average stomach content decreased by one-half compared with that at 15–17°C (Brett and Higgs 1970). The low initial meal size, high variability in meal size, and slower digestion rate at 9.3°C are consistent with expectations for observations made at the low end of a species' thermal range (Hurst and Conover 2001), and 9.3°C is low for juvenile Chinook salmon off the coast of Oregon (Brodeur et al. 2004; Fisher et al. 2007).

The major difference between the daily ration models used is that the MAXIMS model derives estimates of gastric evacuation rate and daily ration purely from field data, as opposed to the Elliott and Persson and Eggers models, which also use laboratory-derived evacuation rates. The evacuation rate obtained from the laboratory experiments was lower than that estimated using the MAXIMS model (0.0589 at 10.7°C and 0.0807 at 13.9°C versus 0.178 for 2000 and 0.168 for 2003, respectively). Higher estimates of field evacuation rates compared with laboratory-derived rates have previously been reported (Rindorf 2004).

Several factors have been shown to affect gastric evacuation rate in fishes, including fish size, prey type, meal size, and meal frequency (Durbin et al. 1983; Persson 1984; Ruggerone 1989; He and Wurtsbaugh 1993; Bromley 1994). Generally, within a species the absolute evacuation rate is faster in larger fish, but the relative evacuation rate is slower (Bromley 1994). However, in many studies, including those with salmonids, fish size did not significantly affect the gastric evacuation rate (Elliott 1972; Doble and Eggers 1978; He and Wurtsbaugh 1993; Bromley 1994). Fish size is a confounding variable in our study, in that the laboratory fish were slightly smaller than the ocean-caught fish. The faster evacuation rate determined from the larger field fish is consistent with the expectation that evacuation rate increases with fish size. At the same time, however, whether fish size significantly affected gastric evacuation rate in this study cannot be determined due to the difference in methods used between the laboratory and field fish studies.

Likewise, prey type also affects gastric evacuation rates (Elliott 1972; Kolok and Rondorf 1987; Bromley 1994). In general, fishes digest soft-bodied prey more rapidly than prey with exoskeletons (Bromley 1994), and this relationship holds true for salmon (LeBrasseur and Stephens 1965; Sturdevant et al. 2004). While the fish in the laboratory were fed only euphausiids, juvenile Chinook salmon in coastal waters feed on other prey items as well, including amphipods, decapods, and larval and juvenile fish (Schabetsberger et al. 2003; DeRobertis et al. 2005; Brodeur et al. 2007). Although Chinook salmon did feed on euphausiids in both the 2000 and 2003 field collections, fish seemed to be the dominant prey in their diets. Thus, the lower evacuation rates observed in the laboratory could be because euphausiids are digested more slowly than other prey items consumed in the field.

Multiple meals and meal size also seem to affect evacuation rates, but there is conflicting evidence as to their relationships (Bromley 1994). Several studies have found that the evacuation rate of a meal is increased by the consumption of a second meal (Persson 1984; Ruggerone 1989). However, recent observations with Atlantic cod *Gadus morhua* found that evacuation rate was decreased by the consumption of a second meal (Andersen and Beyer 2007). Likewise, while most studies show that the evacuation rate increases with increasing meal size, several others found either no relationship or the opposite relationship (Bromley 1994). Even though the precise relationship between multiple meals and meal size and evacuation rate cannot be determined for our study, they are important variables to consider when comparing laboratory-derived and field-derived rates.

Alternatively, the differences between the estimated rates of evacuation and consumption between the Elliott and Persson and MAXIMS models could be the result of overestimation of the evacuation rate in the latter. While an appealing tool for the estimation of consumption rates, the MAXIMS model has been criticized for poor estimation of the evacuation parameter (Richter et al. 2002). A less recognized consideration of the MAXIMS model is that the feeding and evacuation rates are not independent (and actually covary), being derived from the same set of stomach fullness observations. Hence, expected levels of sampling error in field collections can have a marked influence on the estimation of rates.

Estimates of daily ration for juvenile salmon have been somewhat variable. Godin (1981) estimated daily rations of 6.6 and 13.1%BW for pink salmon fry in two bays on the British Columbia coast. Similarly, Sagar and Glova (1988) estimated a daily ration of 8.3%BW for juvenile Chinook salmon in a riverine system. However, daily ration decreases with increasing body

size (Doble and Eggers 1978), and the smaller size of the pink salmon fry (mean FL, 42.1–44.0 mm) in Godin's (1981) study and the juvenile Chinook salmon (mean FL, 58.7–73.6 mm) in Sagar and Glova's (1988) study relative to our juvenile Chinook salmon (Table 1) could account for our lower daily ration estimates.

A number of other studies reported salmonid daily rations closer to our estimates. For juvenile coho salmon in a lake environment, Ruggerone (1989) estimated daily ration to be between 2.1 and 4.4%BW depending on location and year, based on the Eggers and Elliott and Persson models. Similarly, Brodeur and Pearcy (1987) estimated the daily ration of juvenile coho salmon in the coastal marine environment to be approximately 2.4 or 3.7%BW, depending on temperature, using the Elliott and Persson model. Healey (1991) found the daily ration for juvenile pink and chum salmon to be 2.91–4.12%BW and that for juvenile sockeye salmon to be 1.24–2.33%BW in Hecate Strait, British Columbia. For juvenile sockeye salmon in Lake Washington, Doble and Eggers (1978) estimated daily rations to be 0.62–4.41%BW, depending on the size of the fish and the water temperature. Overall, our daily ration estimates of between 2.04% to 4.28%BW for juvenile Chinook salmon offshore of the Columbia River fit within the normal ranges of daily ration estimates for other juvenile Pacific salmon in a range of environments.

In our study, daily ration estimates varied between the laboratory-derived models and the MAXIMS model, making a brief comparison of these models useful. The Elliott and Persson model is the most commonly used and is generally considered to be accurate (Hayward 1991). Because it accounts for variance in stomach fullness throughout the diel cycle, it is best suited to filter feeders and grazers, which demonstrate feeding periodicity (Richter et al. 2002). By contrast, the applicability of the Eggers model to fishes that do not meet its key assumption of continual feeding has been debated in the literature. The Eggers model may be simpler and more robust, provide lower variance, and allow for lower sampling frequency than the Elliott and Persson model (Boisclair and Leggett 1988; Boisclair and Marchand 1993; Héroux and Magnan 1996). However, Hayward (1991) found the Eggers model to be susceptible to several sources of bias. Consequently, it may overestimate daily ration, particularly at longer sampling intervals and at medium and high ration levels, thus, decreasing its utility compared with the Elliott and Persson model (Hayward 1991). In our study, the Elliott and Persson and Eggers models produced comparable daily ration estimates despite observed feeding periodicity, corroborating the findings of several others (Boisclair and Leggett 1988; Ruggerone 1989; Bromley 1994; Richter et al. 2002). Due to the aforementioned advantages of the Eggers model, it may be used in place of the Elliott and Persson model in many circumstances.

The main advantage of the MAXIMS model over the other two is that it does not rely on controlled laboratory studies to determine gastric evacuation rates (Richter et al. 1999). Due to the expenses associated with laboratory work and the difficulty with simulating natural conditions, this is a particularly important consideration. At the same time, however, it may not accurately estimate the evacuation parameter and is highly influenced by the expected levels of sampling error (Richter et al. 2002). Whereas the MAXIMS model has provided comparable estimates to laboratory-derived models in the past (Richter et al. 2002), in our study the MAXIMS model provided higher estimates of daily ration.

Since higher evacuation rates lead to higher estimates of daily ration, one reason for the discrepancy in our estimates between the laboratory-derived models and the MAXIMS model is the difference in evacuation rates. However, since it is unclear whether the MAXIMS model overestimated or the laboratory-derived models underestimated daily ration, we cannot conclude which model is most accurate. Both are feasible, although the difficulty in adequately simulating field conditions in the laboratory led to many confounding variables. Owing to the high variability in estimates, reporting a range of possible rates seems best, although recognizing the biases associated with each model is an important first step in providing accurate daily ration estimates.

In conclusion, juvenile Chinook salmon in the coastal marine environment exhibit a crespuscular feeding pattern and daily ration similar to that of other juvenile salmonids. In addition, the Elliott and Persson and Eggers models provided comparable estimates of daily ration while the MAXIMS estimates were slightly higher. The estimates of the daily ration and gastric evacuation rates seemed to be affected by method (laboratory or field data), temperature, predator size, and prey type, as has been noted for other fish species. The gastric evacuation rates and daily rations we obtained can be used to infer about the variability in feeding ecology of juvenile Chinook salmon to better understand the factors that regulate growth and survival of this species.

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