

## Gastric Evacuation and Daily Ration of Naturally Produced Age-0 Chinook Salmon in Lake Ontario

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**Abstract.**—Almost 30 years after natural reproduction of Chinook salmon *Oncorhynchus tshawytscha* was discovered in Lake Ontario tributaries, little is known about the feeding dynamics of these fish after they enter the lake. This study assesses consumption by naturally produced age-0 Chinook salmon as they enter the nearshore region of Lake Ontario after emigrating from the Salmon River, New York, a major U.S. tributary of Lake Ontario. Evacuation rate, estimated as a function of temperature in controlled laboratory experiments, ranged from 0.214/h at 10°C to 0.352/h at 19°C. Diel field sampling for daily ration estimates occurred on three dates in late spring (June 6, 12, and 18, 2001). Although no consistent diel feeding pattern was observed, Chinook salmon maintained an elevated gut fullness value throughout the day and did not feed after dark. Moreover, daily rations (grams [dry weight] of ration per 100 g of dry fish weight), which ranged from 27.54 (SE = 3.07) on June 12 to 33.27 (3.7) on June 6, were high compared with the values obtained in similar studies. Comparisons of daily ration estimates with bioenergetics model estimates showed that juvenile Chinook salmon were consuming prey at or above their maximum estimated daily ration. Daily ring counts of sagittal otoliths confirmed that the Chinook salmon in this investigation were naturally produced. Our results indicate that current food conditions in the nearshore waters of Lake Ontario are suitable for sustaining maximum consumption rates by naturally produced juvenile Chinook salmon that have recently migrated into the lake from spawning tributaries.

Chinook salmon *Oncorhynchus tshawytscha* were originally stocked in the Laurentian Great Lakes during the late 1960s for the purpose of establishing a put-grow-and-take fishery, there being little expectation of natural reproduction in a landlocked, freshwater environment. However, within 10 years of the initial successful stocking efforts in Lakes Michigan and Ontario, natural reproduction of Chinook salmon had been established in some of these lakes' major tributaries (Taube 1974; Johnson and Ringler 1981). By the late 1980s, natural reproduction of Chinook salmon had also been reported in Lakes Superior (Kwain and Thomas 1984) and Huron (Powell and Miller 1990). However, despite the presence of naturally produced Chinook salmon in four of the five Great Lakes, their potential contribution to the angling fishery was largely ignored. In fact, the number of Chinook stocked annually lakewide into Lake Ontario continued to increase rapidly, from

about 100,000 in the late 1960s to about 4.5 million in 1984, in order to meet the demands of the new burgeoning fishery (Jones et al. 1993).

In the early 1980s, evidence of the reduced abundance of alewife *Alosa pseudoharengus*, the preferred prey of Chinook salmon in Lakes Michigan and Ontario, led to concerns about increased stocking levels and the long-term sustainability of Pacific salmon populations. Consequently, many researchers began to examine the survival, growth, and consumption of postsmolt (>4 g) Chinook salmon, coho salmon *O. kisutch*, and steelhead *O. mykiss* occupying the open waters of Lakes Michigan and Ontario. For example, based on a lakewide bioenergetics model of Lake Michigan, Stewart et al. (1981) concluded that Chinook salmon exacted the highest forage demand of all other salmonines stocked in the Great Lakes. Stewart and Ibarra (1991) subsequently presented evidence that the Lake Michigan salmonine community was stressed, based upon finding a decrease in salmonine growth and survival, a shift in diet to less preferred prey items, and an increase in bacterial kidney disease. Similarly, Rand et al. (1994) reported

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that declining prey abundance and prey condition would require Chinook salmon in Lake Ontario to greatly increase consumption rates to sustain high growth rates that had been consistently achieved in previous years. In response to these studies, annual stocking rates of Chinook salmon (i.e., 1.6 million lakewide in 2000) were reduced in Lake Ontario from their mid-1980s peak.

Naturally produced Chinook salmon presmolts (<4 g) out-migrate from the Salmon River (the primary tributary located in U.S. waters) and into Lake Ontario in mid-April and remain in the scoured nearshore regions adjacent to the river's mouth until early July (Johnson and Ringler 1981; Principe 2005). During this brief period Chinook salmon must attain a large enough body size to switch from a nearshore aquatic invertebrate diet to an offshore piscine diet (Johnson 1983; Brandt 1986; Principe 2005), though little is known about this diet transition.

Daily ration (i.e., food intake per day) provides a measure of the ability of a fish to meet energy requirements for growth and, in the case of juvenile Chinook salmon, to sustain their potential for recruitment into the adult population. Although, an estimate of the daily ration of young salmon in the Great Lakes has not been previously developed, the daily ration of age-0 Chinook salmon in riverine and reservoir habitats has been documented. For example, Sagar and Glova (1988) reported that riverine age-0 Chinook salmon in New Zealand consumed about 8.3% of their dry body weight (DBW) per day, and Koehler et al. (2006) found that naturally produced age-0 Chinook salmon in littoral regions of Lake Washington (Washington State) consumed 58–90% of their maximum daily ration. Both studies concluded that fish at their study sites were well fed and thriving.

Our study was designed to develop comparable data that would reveal the extent to which wild Chinook salmon feed at their maximum daily ration shortly after entering Lake Ontario. Our specific study objectives were to (1) determine gastric evacuation rates for age-0 Chinook salmon at multiple temperatures in the laboratory, and use those results to develop a predictive model of gastric evacuation rates for Chinook salmon captured in the field at various temperatures, (2) estimate the daily ration of naturally produced age-0 Chinook salmon captured in Lake Ontario using a combination of the Eggers (1977) model and the gastric evacuation model, and (3) verify that the Chinook salmon we captured in nearshore waters of Lake Ontario were naturally produced by estimating the number of days since emergence via otolith daily ring counts.

### Study Site

At 18,960 km<sup>2</sup>, Lake Ontario has the smallest surface area of the five Laurentian Great Lakes, but it is second in average depth (86 m; only Lake Superior is deeper). The Salmon River, a large tributary located at the eastern end of Lake Ontario, is well known for large fall salmon runs during which anglers routinely catch Chinook salmon in excess of 17 kg. The headwaters for the Salmon River (watershed area = 738 km<sup>2</sup>) begin in the Tug Hill Plateau, situated just west of the Adirondack Mountains in central upstate New York, after which the main stem flows westward to Lake Ontario. Chinook salmon returning to spawn in the Salmon River can migrate approximately 24 km upstream from Lake Ontario before they reach an impassable dam at the Lower Salmon River Reservoir. Chinook salmon stocked into the Salmon River originate from wild broodstock returning to the Salmon River Hatchery in Altmar, New York. Hatchery fish are typically reared from early November until they are stocked in early June at approximately 80 mm total length. The naturally produced Chinook salmon we captured for daily ration estimation were in less than 1 m of water along the Lake Ontario shoreline, just south of its confluence with the Salmon River (Figure 1). Coarse sand substrate predominated in this sampling area, and little or no available natural or artificial refuge was present to reduce predation. Chinook salmon collected for the evacuation rate component of the study were collected in the Salmon River, approximately 500 m upstream from the lake (Figure 1). Evacuation rates were estimated in controlled laboratory experiments conducted at the Cornell Biological Field Station (CBFS), about 50 km southeast of the Salmon River near Bridgeport, New York.

### Methods

*Gastric evacuation.*—Chinook salmon about 35–70 mm in total length (TL) were collected on June 5, 2001, from the Salmon River using a bag seine (1.2 × 36 m, 0.95-cm mesh in the first 10.7 m of each wing and 0.32-cm mesh in the remainder of the seine). Field water temperature at the time of capture was approximately 14°C. All captured fish were placed immediately into several large plastic bags containing chilled lake water and pure oxygen. The fish were then transported to the CBFS, where approximately 40 individuals were placed in each of four isolated holding bays (each 63 × 55 × 53 cm) contained within two separate temperature-controlled Min-O-Cool raceways (208 × 55 × 53 cm, about 600 L). Each holding bay was covered and divided from the remainder of the raceway with a 1-mm mesh screen. Initial laboratory

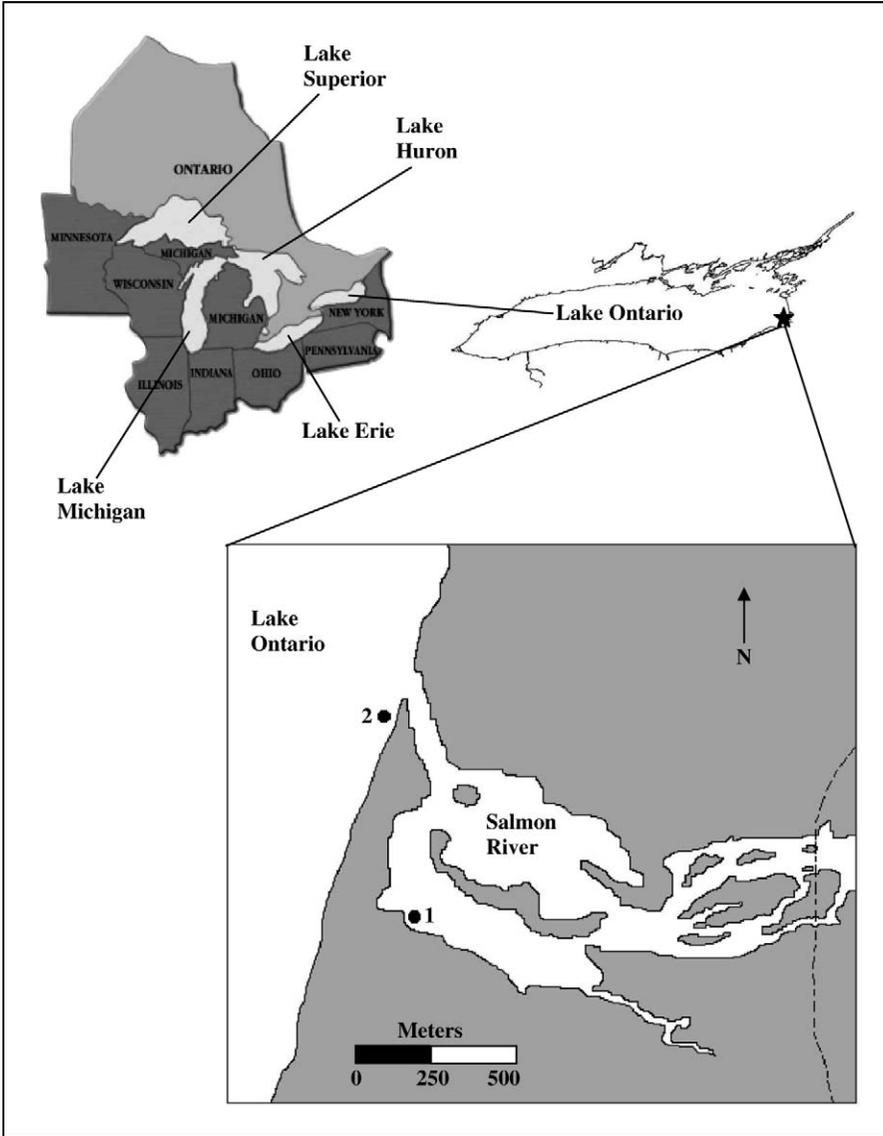


FIGURE 1.—Study sites in the Salmon River, New York. The age-0 Chinook salmon captured at site 1 were used in evacuation experiments, and those captured at site 2 were used to obtain daily ration estimates.

water temperature was 13°C. Surplus Chinook salmon were placed in a separate 1,500-L holding tank at 13°C and were used to replace incidental mortalities from any of the four experimental bays. In addition, a separate 1,500-L tank containing dechlorinated water was used to maintain consistent water levels in the two raceways during the study period.

The water temperatures in both raceways was maintained at 13°C for the first week after the Chinook salmon were placed in the raceway and was then

adjusted by 1°C/d until the respective experimental temperature (i.e., 10, 13, 16, or 19°C) was attained. These experimental temperatures were selected because they approximated the range of water temperatures observed near the mouth of the Salmon River in Lake Ontario from May to June 2000 (i.e., 9–21°C). All fish were acclimated at their respective experimental temperature for approximately 1 week before the feeding trials. During the acclimation period, all fish kept in the laboratory were fed once daily to satiation

with Ziegler Number 3 hatchery crumble acquired from the Salmon River Hatchery. Overall incidental mortality for the duration of the study was less than 10%, of which approximately 65% occurred within 2 d of capture and transfer.

Immediately before the beginning of an evacuation rate trial, the fish in the target holding bay were starved for 48 h. After the starvation period, three fish were randomly sampled from the bay, measured to the nearest millimeter (TL), and dissected to ensure that the complete digestive tract (CDT = stomach + intestine) was empty. Then, from about 0600–0630, the remaining fish from the bay were fed to satiation with freshly thawed adult chironomids (mean body length = 2.9 mm, SE = 0.09) that had been collected from Oneida Lake, New York, before the experiments. This prey type and corresponding size range was selected for these experiments because of the abundance of similar prey in the diet of recently out-migrated Chinook salmon in Lake Ontario (Prince 2005). Immediately after feeding, all uneaten prey items were removed from the bay via a siphon and a dip net. About 30 min after feeding, five fish were randomly sampled from the target bay, measured, and dissected to remove the CDT contents. The CDT contents and the remaining portions of the fish were then dried separately to constant weight at 60°C for 72 h (Bowen 1996). Thereafter, every 4 h another five fish were sampled and dissected until 24 h had elapsed. All dried material was weighed to the nearest 0.0001 g.

The gut fullness ( $F_t$ ) of each fish sampled at time  $t$  was determined using a variation of Boisclair and Leggett's (1988) gut fullness index, that is,

$$F_t = \frac{G_t}{P_t} \cdot 100, \quad (1)$$

where  $G_t$  is the dry weight (g) of the CDT contents and  $P_t$  is the dry weight of the fish.

Several authors (Bajkov 1935; Elliott 1972, 1975; Persson 1979, 1982; Boisclair and Leggett 1988) have demonstrated that in fish with a distinct stomach gut fullness decreases exponentially when fish are deprived of additional food. In mathematical terms,

$$\bar{F}_{(t+1)} = \bar{F}_t e^{-RT}, \quad (2)$$

where  $\bar{F}_t$  and  $\bar{F}_{(t+1)}$  are the mean gut fullness at the beginning and end of time interval  $T$  (4 h), respectively. The evacuation rate,  $R$ , was estimated using multiple linear regression (SAS 1999) as the slope of the relationship between  $\log_e(\bar{F}_t)$  and time (Persson 1979; Boisclair and Leggett 1988).

*Daily ration.*—Although field sampling for daily ration estimates was conducted on five dates, on two

dates (May 21 and June 25, 2001) we captured no Chinook salmon during some of the sampling intervals, so daily ration estimates were calculated for only three dates (June 6, 12, and 18, 2001). Juvenile Chinook salmon were captured using a seine (see above for details). Seining began 30–60 min after sunrise and was subsequently conducted at 4-h intervals for a total of six intervals throughout the diel period. Surface water temperature was measured at the beginning of each sampling interval and the mean daily temperature was then used to estimate the prevailing  $R$  for a given sample date. For each of the three sampling dates, 10 Chinook salmon were retained from each interval for daily ration estimation. Upon capture, the fish were anesthetized using MS-222 (tricaine methanesulfonate) and immediately preserved in 90% ethanol. Within 36 h of capture, CDT contents and fish were dried separately to constant weight at 60°C for 72 h. The  $F_t$  of each fish was determined using equation (1).

Estimates of daily ration ( $\bar{D}$ ) were derived using the Eggers (1977) model, namely,

$$\bar{D} = \bar{F} \cdot R \cdot 24, \quad (3)$$

where  $\bar{F}$  is the mean gut fullness of all fish collected during the sampling date,  $R$  is the evacuation rate, and 24 is the number of hours per day. Sample interval gut fullness data were normalized using an arcsine-square root transformation (Hayward 1991).

The standard error associated with daily ration estimates was calculated with the following equation for multiplying two independent variances (Zar 1999):

$$SE(\bar{D}_C) = \sqrt{\text{var}(\bar{F} \cdot R) \cdot 24}, \quad (4)$$

where  $\bar{D}_C$  is the daily ration estimate at temperature  $C$ . The variance of the product of  $\bar{F}$  and  $R$  is defined by the equation (Zar 1999)

$$\text{var}(\bar{F} \cdot R) = \gamma^2 \text{var}(\bar{F}) + \mu^2 \text{var}(R), \quad (5)$$

where  $\gamma$  is the estimate of evacuation rate at temperature  $C$  and  $\mu$  is the mean gut fullness per day.

To facilitate comparisons of our daily ration estimates with other reported estimates of daily ration for Chinook salmon, we converted our daily ration estimates to units of grams of wet weight per 100 g of wet weight using a dry-to-wet-weight conversion ratio for age-0 Chinook salmon of 0.56 (unpublished data from this study) and a dry-to-wet-weight conversion ratio for prey of 0.15. Similar comparisons to bioenergetics model estimates of maximum possible consumption by juvenile salmon were calculated using model equations and parameters presented by Stewart and Ibarra (1991), which have been subsequently used

in other studies of juvenile Chinook salmon consumption and growth (Beauchamp et al. 1989; Koehler et al. 2006).

*Origin verification.*—To verify that the Chinook salmon used in this study were naturally produced, an additional 15 fish were retained for otolith analysis on each of the three daily ration collection dates. Individual emergence dates were estimated for each fish by counting daily growth rings on one sagittal otolith via a compound microscope at 40× magnification. Otoliths were attached to microscope slides, sulcus side up, using heated Crystal-bond plastic adhesive and then gently wet-sanded with fine-grit sandpaper until flat (approximately 2–3 min; Neilson and Geen 1986). Each otolith was counted four times by a single reader and the mean of the four counts was considered as the number of days since emergence.

**Results**

*Gastric Evacuation*

Although every attempt was made to control for fish length among the four experimental temperatures, incidental fish growth that occurred between the first temperature treatment (10°C) and the last temperature tested (19°C) resulted in a significant difference in fish lengths among the four temperature groups (analysis of variance:  $F_{3, 24} = 92.50, P < 0.0001$ ). Follow-up group contrasts using a Tukey’s Studentized range test showed that fish lengths did not differ between 10°C (mean, 50.8 mm TL) and 13°C (51.5 mm). However, the mean fish lengths for the 16°C (56.2 mm) and 19°C groups (67.7 mm) were significantly different from those of all other groups ( $P < 0.05$ ). Thus, the collinearity between fish length and temperature (i.e., as temperature increased, fish length also increased) made it impossible to consider length as an additional independent variable (Zar 1999). Therefore, any effect of length on evacuation rate could not be determined from this experiment.

Estimates of  $R$  ranged from a low of 0.214/h at 10°C to a peak of 0.352/h at 19°C (Figure 2). Moreover, there was a significant overall difference among evacuation rates across all four temperatures (multiple comparison test for slopes; GLM method:  $F_{3, 20} = 3.08, P = 0.05$ ). Because there was no significant difference in  $y$ -intercepts among the four temperature treatments ( $P > 0.05$ ), the  $y$ -intercepts were assumed to be equal in the evacuation rate model.

The general linear model used to predict  $R$  for Chinook salmon in this study was

$$\log_e \bar{F} = 1.7052 - (0.0193 \cdot C) \cdot t, \quad (6)$$

where  $C$  is the prevailing temperature during the

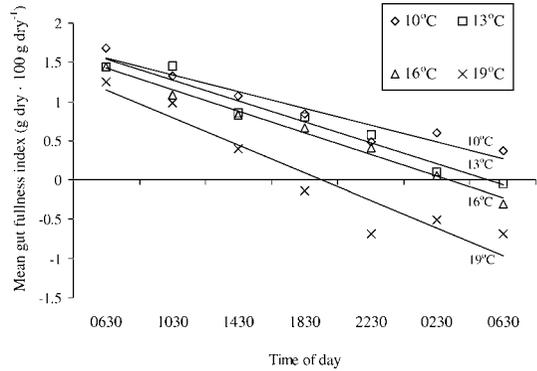


FIGURE 2.—Mean gut fullness index of age-0 Chinook salmon at four temperatures during 24-h laboratory evacuation rate experiments.

sampling period and  $0.0193 \cdot C$  is the slope ( $R$ ) of the relationship between the natural log of gut fullness ( $\log_e [\bar{F}]$ ) and time  $t$  ( $F_{1, 26} = 315.05, P < 0.0001, R^2 = 0.99$ ).

*Daily Ration*

The mean water temperature at field collection sites ranged from 15°C to 19°C, and the mean fish length increased from 52.2 to 64.4 mm TL over the sampling period (Table 1). Back-transformed mean gut fullness values ranged from 3.48 g dry contents (DC) per 100 g dry body weight ( $DBW_{100}$ ) on June 18 to 4.78 g DC/ $DBW_{100}$  on June 6, and individual contrasts using a Tukey’s Studentized range test showed that the peak gut fullness value on June 6 was significantly different ( $P < 0.05$ ) from the other two sample dates. Moreover, gut fullness varied significantly with both date ( $F_{2, 162} = 38.46, P < 0.0001$ ) and time of day ( $F_{5, 162} = 12.12, P < 0.0001$ ), while nonsynchronous diel variability in gut fullness among dates was indicated by the significance of the interaction term ( $F_{10, 162} = 5.49, P < 0.0001$ ). Gut fullness varied with time of day on June 6 ( $F_{1, 58} = 7.16, P < 0.01$ ) and June 18 ( $F_{1, 58} = 20.90, P < 0.0001$ ), whereas June 12 showed no significant diel trend ( $P > 0.05$ ), indicating that on two of the dates (June 6 and June 18) the Chinook salmon displayed a true peak feeding period between 0600 and 1000 hours (Figure 3).

Daily ration ranged from 27.54 g of dry ration (DR) per  $DBW_{100}$  (SE = 3.07) on June 12 to 33.27 g DR/ $DBW_{100}$  (3.70) on June 6 (Table 1). Scheffé’s (1953) multiple contrasts revealed that daily ration on June 6 was significantly greater than on June 12 ( $P < 0.05$ ), but all other paired contrasts revealed no significant differences in daily ration among dates ( $P > 0.05$ ).

Comparisons of our three daily ration estimates with

TABLE 1.—Sampling conditions and data used to estimate daily ration (grams of dry ration per 100 g dry fish weight) for Chinook salmon collected near the mouth of the Salmon River, New York, in June 2001;  $\bar{F}$  = mean gut fullness (grams dry contents per 100 g dry fish weight);  $R$  = gastric evacuation rate; and  $\bar{D}$  = daily ration. Standard errors are shown in parentheses.

Sampling date	Temperature (°C)		Number of fish sampled per interval	Mean total length (mm)	$\bar{F}$	$R$	$\bar{D}$
	Mean	Range					
Jun 6	15	13–17	10	52.23 (1.50)	4.78 (0.183)	0.290 (0.016)	33.27 (3.70)
Jun 12	17	14–19	10	59.48 (2.13)	3.49 (0.116)	0.329 (0.019)	27.54 (3.07)
Jun 18	19	18–20	10	64.37 (1.46)	3.48 (0.141)	0.368 (0.021)	30.72 (3.43)

bioenergetics model estimates of maximum daily consumption by juvenile salmon converted to wet weight units showed that on all three dates the juvenile Chinook salmon in nearshore waters of Lake Ontario were consuming prey at or above their maximum estimated daily ration: 1.04 g wet contents per 100 g wet body weight on June 6, 0.86 g on June 12, and 0.96 g on June 18. Observed daily ration estimates equaled bioenergetics model estimates of maximum consumption rate on two sampling dates (June 12 and 18) and exceeded the bioenergetics model estimate for June 6.

#### Origin Verification

Evaluation of sagittal otoliths revealed that the estimated date since emergence of Chinook salmon in Lake Ontario in 2001 ranged from February 27 to March 26, the majority emerging between February 28 and March 20. Because the emergence period of the

2001 stocked Chinook salmon originating from the Salmon River Hatchery was approximately November 1–10, 2000 (D. Bishop, New York State Department of Environmental Conservation, personal communication), we concluded that all Chinook salmon captured for daily ration estimation in 2001 were naturally produced.

#### Discussion

Although our predicted evacuation rate at 15°C for Chinook salmon was greater than that obtained by Kolok and Rondorf (1987) for Chinook salmon at 14°C, our estimate was close to those observed by Elliott (1975) for juvenile brown trout *Salmo trutta* at 15°C and by Doble and Eggers (1978) for sockeye salmon *O. nerka* at 8.5–16°C (Table 1). One possible explanation for this difference is that in our study evacuation rates were estimated, as were Elliott's (1975), using controlled laboratory feeding experiments on fish that had been living in tanks for several weeks. Conversely, Kolok and Rondorf (1987) estimated evacuation rate from experiments conducted in the field, which could have resulted in lower estimates. This could have occurred because freshly captured fish are often highly stressed, which tends to suppress evacuation rate (Swenson and Smith 1973; Thorpe 1977). Moreover, it is unlikely that our decision to use CDT instead of stomach contents for evacuation rate estimation resulted in a high evacuation rate estimate. On the contrary, we used the CDT for the express purpose of limiting the probability of missing a feeding period and, thus, overestimating evacuation rate (Boisclair and Marchand 1993). If anything, our gastric evacuation rates should have been lower than other studies that used only stomach contents to estimate evacuation rates because the CDT evacuation time is slower than that of the stomach (Persson 1979; Boisclair and Leggett 1988).

In contrast to our expectations, we found that the Chinook salmon collected from nearshore waters of Lake Ontario did not exhibit a regular diel feeding pattern. However, the observed decline in gut fullness after dusk for all three sampling dates indicates that

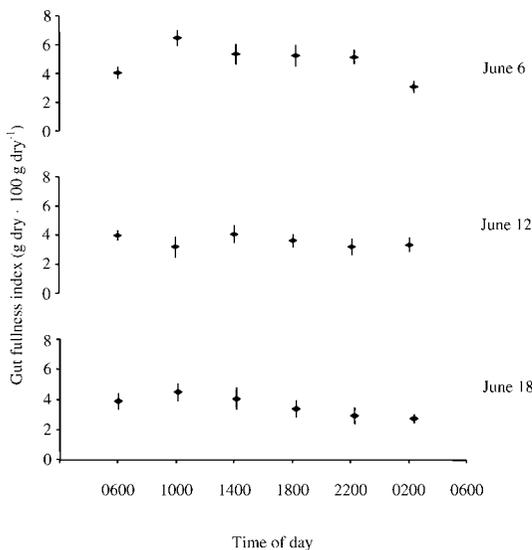


FIGURE 3.—Mean gut fullness index of age-0 Chinook salmon during three 20-h intervals in June 2001. Error bars represent 95% confidence intervals.

TABLE 2.—Published estimates of evacuation rate and daily ration in various age-0 salmonine fishes.

Study	Species	Approximate wet weight of fish (g)	Evacuation rate (per hour)	Temperature (°C)	Daily ration estimate (% of dry weight)
Davis and Warren (1968)	Chinook salmon	0.6		10	20
Brett (1971)	Sockeye salmon	4			17
Elliott (1975)	Brown trout	1	0.283	15	16.4
Doble and Eggers (1978)	Sockeye salmon	1.2–2 <sup>a</sup>	0.466	10.5–16	
Doble and Eggers (1978)	Sockeye salmon	2.1–3.2 <sup>a</sup>	0.329	10.5–16	
Doble and Eggers (1978)	Sockeye salmon	≤3.2 <sup>a</sup>	0.267	8.5–10	4.4
Healey (1979)	Chum salmon	0.5–1.3		10–15	4.4–18
Sagar and Glova (1988)	Chinook salmon	4	0.152 <sup>b</sup>	14	8.3
This study (June 6)	Chinook salmon	2.4	0.290	15	33.3

<sup>a</sup> Estimated with the following regression from Ruggerone and Rogers (1992) treating weight ( $W$ ) as a function of length ( $L$ ):  $W = 0.00001888(L^{2.896})$ .

<sup>b</sup> From Kolok and Rondorf (1987).

age-0 Chinook salmon occupying nearshore waters in Lake Ontario ceased feeding after dark. This finding concurs with many other studies that have found that young salmonines are primarily sight feeders, either feeding most actively during the day (e.g., Walsh et al. 1988; Angradi and Griffith 1990) or in a crepuscular fashion (e.g., Sagar and Glova 1988; Riehle and Griffith 1993).

Our estimate of daily ration (27.5–33.3% of DBW) for age-0 Chinook salmon in Lake Ontario exceeded estimates obtained by most other studies of small salmonine fishes (Table 2). For instance, Sagar and Glova (1988) found that Chinook salmon living in New Zealand rivers consumed about 8.3% of their DBW per day. Similarly, Doble and Eggers (1978) concluded that young sockeye salmon occupying the limnetic regions of Lake Washington, in the Pacific Northwest, only consumed about 4.4% of their DBW per day. However, several key differences were present between our study and these two examples, namely, the size of our fish, the average gut content of our fish, and the evacuation rate used to estimate daily ration.

For example, Sagar and Glova (1988) evaluated Chinook salmon that were larger than our fish (4 g versus 2.4 g), as were the fish used by Doble and Eggers (1978; ≤64 mm fork length and ≤3.2 g; Table 2). It has been well documented that daily ration decreases substantially as a function of fish size. For example, Brett (1971) estimated a daily ration of about 17% of DBW for a 4-g juvenile sockeye salmon but only 4.3% for a 216-g fish. Similarly, Elliott (1975) found that a 1-g brown trout consumed about 16.4% of its DBW per day, whereas a 200-g brown trout would consume only 4.8% of its DBW.

Furthermore, in both the Sagar and Glova (1988) and the Doble and Eggers (1978) studies, estimates of daily ration were based on a much lower evacuation rate than we found (Table 2). For example, increasing evacuation rate twofold and using the same gut fullness value

would increase daily ration twofold. Although it is difficult to confidently identify reasons for differences in estimated evacuation rate between these previous studies and our estimates, we note that Doble and Eggers (1978) reported a wide variety of evacuation rate estimates as a function of season, temperatures, and fish length. These details make it difficult to simply compare our evacuation rate estimates to theirs, yet we are confident that our laboratory protocols resulted in a gastric evacuation rate that was representative of our sampled population.

Finally, the mean daily gut fullness for age-0 Chinook salmon in the New Zealand river where Sagar and Glova (1988) conducted their study was about 2.4 g DC/DBW<sub>100</sub>, far lower than the range of gut fullness values found in this study (3.5–4.8 g DC/DBW<sub>100</sub>). Similarly, the daily meal (milligrams dry weight) calculated for sockeye salmon in the Doble and Eggers' (1978) study (21.2 mg for fish ≤64 mm fork length) was about one-third of that of our Chinook salmon of similar size (65.4 mg on June 6; mean = 52.2 mm TL). Although some of the difference in gut fullness could be due to our use of the slightly heavier CDT contents—rather than solely using stomach contents (as in Sagar and Glova 1988)—that cannot explain the large difference between our results and those of Doble and Eggers (1978), in which they used both the cardiac and pyloric stomach contents to estimate daily ration.

Chinook salmon in nearshore waters of Lake Ontario consumed prey at or above their maximum estimated daily ration, based on comparisons of daily ration estimates with bioenergetics model estimates of maximum daily consumption. Although one of the daily ration estimates from fish collected in the field exceeded the bioenergetics model estimate (June 6), the model estimate on this date and other dates are imprecise because they lacked complete information regarding the dry : wet weight ratio and energy content

of juvenile salmon and their prey. Nevertheless, this comparison provides a clear indication that Chinook salmon at our study sites were eating at a level near their maximum possible consumption rate. This comparison is consistent with the observation that juvenile wild and hatchery Chinook salmon entering Lake Washington fed at consumption rates approaching the maximum daily ration, as estimated by a bioenergetics model (Koehler et al. 2006). The Lake Washington fish also exhibited exceptional growth compared with Chinook salmon from other studies (Koehler et al. 2006). Although we could not conclusively evaluate growth of individual Chinook salmon in our study, two pieces of evidence suggest that growth in the nearshore environment of Lake Ontario was similar to that reported by Koehler et al. (2006): (1) we observed consistent increases in mean fish length within our nearshore field surveys (15 mm within a 35-d period, May 21 to June 25), and (2) an otolith-derived estimate of postemergence growth (which inevitably included growth before entering Lake Ontario) showed that Chinook salmon in our study exhibited a mean growth rate of 0.65 mm/d ( $SD = 0.018$ ; Principe 2005).

Our results suggest that the nearshore waters of Lake Ontario provide abundant food for juvenile Chinook salmon as they migrate into the main lake from spawning tributaries in May and early June. Although our conclusion regarding prey availability is based on observed daily ration, other researchers have suggested that low daily rations with young salmonines result from limited food supply (e.g., Healey 1979; Godin 1981). Diet evaluations of age-0 Chinook salmon collected during the course of this study showed that these fish fed primarily on mature chironomids and that only 1% of fish captured during May and June had empty stomachs (Principe 2005). Koehler et al. (2006) found a similar diet preference by age-0 Chinook salmon first entering the littoral regions of Lake Washington; they fed primarily upon chironomid pupae before switching to a diet of daphnia when these zooplankters became abundant in June.

High consumption rates of young Chinook salmon entering the nearshore environment of Lake Ontario would enhance the survival of these fish, allowing them to quickly attain a large enough size to emigrate offshore, thus escaping nearshore predation and improving their ability to consume piscine prey, such as alewives and rainbow smelt *Osmerus mordax*. These conditions could help sustain the establishment of naturally reproducing Chinook salmon populations in Lake Ontario, thereby raising further questions about the ability of management agencies to regulate Chinook salmon abundance by adjusting hatchery

production and the ability of managers to re-establish native fish communities within this lake in the face of extensive wild production of nonnative salmonine predators. Our study results also show that naturally produced Chinook salmon in Lake Ontario are able to consume prey at their maximum consumption rate when first entering the lake, indicating that hatchery fish are not reducing these prey resources when they enter the main lake at about the same time of year.

Since the stocking of Pacific salmon in Lake Ontario began over 30 years ago, significant ecosystem changes have occurred that could ultimately affect the success of Chinook salmon in Lake Ontario. Specifically, Mills et al. (2003) observed declines in both algal photosynthesis and epilimnetic zooplankton production, declines in the abundance of some native benthic prey, behavioral shifts in fish distribution, and dramatic increases in water clarity. Although these food web alterations lead to predictions of an ultimate reduction in the growth and production of Pacific salmon in Lake Ontario (O'Gorman et al. 1997), our results indicate that current food conditions in the nearshore waters of the lake can sustain maximum consumption rates by the juvenile Chinook salmon that have recently migrated into the lake from spawning tributaries.

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