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**CHIGNIK SALMON STUDIES:
Gastric Evacuation Rate and Daily Ration
of Juvenile Coho Salmon**

by

Gregory T. Ruggerone and Donald E. Rogers

**ANNUAL REPORT
ANADROMOUS FISH PROJECT**

to

National Marine Fisheries Services
Contract no. NA86ABD-0300 and NA87ABD-00300

Project period: 1 July 1986 to 30 June 1988

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TABLE OF CONTENTS

	Page
LIST OF TABLES.....	iii
LIST OF FIGURES.....	iv
PREFACE.....	v
GASTRIC EVACUATION RATES AND DAILY RATION OF PISCIVOROUS COHO SALMON, <i>Oncorhynchus kisutch</i> WALBAUM.....	1
Introduction.....	1
Materials and Methods.....	2
Gastric Evacuation Models and Rates.....	2
Diel Foraging of Coho.....	3
Food Consumption Models and Estimates.....	3
Results.....	4
Gastric Evacuation Models and Rates.....	4
Diel Foraging of Coho.....	8
Food Consumption Models and Estimates.....	13
Discussion.....	13
Gastric Evacuation Models and Rates.....	13
Diel Foraging of Coho.....	18
Food Consumption Models and Estimates.....	18
GASTRIC EVACUATION OF SINGLE AND MULTIPLE MEALS BY PISCIVOROUS COHO SALMON (<i>Oncorhynchus kisutch</i>).....	20
Introduction.....	20
Materials and Methods.....	20
Results.....	21
Discussion.....	22
ACKNOWLEDGMENTS.....	23
REFERENCES.....	24

LIST OF TABLES

Table	Page
1. Summary of regression analyses for each coho stomach evacuation model, including the number of fish utilized in each regression, the initial percent of coho body weight consumed and the initial sockeye (prey) weight	7
2. Summary of regression analyses for the exponential and square root stomach evacuation rate models when the regression was forced through 100% prey remaining at time, $T = 0$	9
3. Comparison of daily meal, and daily ration of a typical coho at two sampling areas during early June 1986 and 1987	15
4. Comparison of average daily meal and number of sockeye fry consumed by coho at two sampling areas during early June 1986 and 1987.....	15
5. Percentage of initial fry weight remaining and experimental conditions during single and multiple meals consumed by coho salmon.....	21

LIST OF FIGURES

Fig.	Page
1. Comparison of exponential decay of a single sockeye salmon fry consumed by coho salmon at 5°C (A), 7°C (B), 10°C (C), and 13°C (D)	5
2. Comparison of exponential decay of two sockeye salmon fry consumed by coho salmon at 5°C (A), 7°C (B), 10°C (C), and 13°C (D).....	6
3. Regression-corrected plots of the relationship between exponential evacuation rate (r_e) of coho salmon and temperature (A) and prey weight (B), and the linear regression of the square root evacuation rate ($r_{.5}$) on temperature (C).	10
4. Estimates of time to reach 90 % evacuation of one or two sockeye salmon fry consumed by coho salmon in relation to water temperature.....	11
5. Estimates of prey weight observed in coho salmon at four sampling locations (A and C) and the resulting estimates of daily meal calculated from the Eggers (1979) method (B and D).....	12
6. Total prey weight consumed by coho salmon and percent of coho containing recently consumed sockeye salmon fry during a 24-h period in early June	14
7. Comparison of exponential evacuation rates (r_e) of fishes in relation to water temperature	17
8. Stomach evacuation of individual prey and total prey of a multiple meal consumed by coho salmon.....	23

PREFACE

This report represents the first step in estimating the consumption of juvenile sockeye salmon by coho salmon in the Chignik Lakes, Alaska. The ultimate goal of the ongoing project will be to estimate the influence of coho predation on the adult returns of sockeye salmon. In the first section, we develop a gastric evacuation rate model that facilitates the conversion of instantaneous stomach content weight of coho observed in the lake to food (i.e., sockeye salmon) consumed per 24 h. The second section examines the gastric evacuation of coho that have consumed sockeye at two time periods rather than a single period. This multiple meal study provides a more realistic approach to gastric evacuation of continuous feeders such as coho and provides a test for the single meal evacuation rate model.

The gastric evacuation rate model developed in this report is presently being applied for the purpose of estimating numbers of sockeye fry consumed by coho during 1985, 1986 and 1987. These results will be summarized in the next annual report, which will also address the role of coho during the recent decline of Chignik Lake (late run) sockeye returns.

ABSTRACT

Effects of temperature and meal size on gastric evacuation rates of juvenile coho salmon (*Oncorhynchus kisutch*) consuming sockeye salmon (*O. nerka*) fry were examined and used in the estimation of daily meal, daily ration, and number of fry consumed by coho in Chignik Lake, Alaska. Evacuation of fry consumed by coho was best described by a negative exponential model (avg. $R^2 = 0.93$). A square root model also provided a good fit (avg. $R^2 = 0.93$), but the Y-intercept deviated more from the expected value than did the Y-intercept of the exponential model. The effect of temperature (T; range = 5°-13°C) and meal size (M.S.; 0.166-0.367 g) on the exponential evacuation rate (r_e , h^{-1}) could be described as:

$$r_e = 0.133 + 0.021(T) - 0.402(M.S.), R^2 = 0.98.$$

Analysis of the diel foraging of coho during early June 1986 and 1987 indicated that coho fed continuously during the 24-h period. Estimates of daily meal and ration of coho calculated by the Eggers (1979) method and the geometric mean of prey weight ranged from 0.224 g (2.1 % BW) to 0.375 g (4.4 % BW) depending on location and year. The Elliott and Persson method (1978) provided similar estimates of food consumption, whereas estimates based on the Pennington method (1985) and square root evacuation of prey differed from the exponential models. Sockeye fry represented 93% of the total prey weight. On the basis of the arithmetic mean of prey weight, the average number of sockeye fry consumed per coho per 24 hours was 3.0 to 3.9 fry.

Gastric evacuation of multiple meals of sockeye salmon fry consumed by juvenile coho salmon were examined and compared with the single meal evacuation rate model developed for the estimation of food consumption by coho in the field. Significant interaction occurred between meals consumed 2 hours apart ($p < 0.001$). Evacuation of the first of two meals (29.9% of initial weight remaining) was significantly faster ($p < 0.05$) than that of a single meal (36.1% of initial weight remaining) after 4 hours, whereas evacuation of the second meal (72.2% of initial weight remaining) was significantly slower ($p < 0.005$) than that of single meal (50.6% of initial weight remaining) after 2 hours. The total weight of the multiple meal remaining after 4 hours in the stomach (0.191 g) was similar to that predicted by the single meal evacuation rate model (0.186 g), indicating that the single meal evacuation rate model is adequate for estimating food consumption of continuously feeding coho in the field.

GASTRIC EVACUATION RATES AND DAILY RATION OF PISCIVOROUS COHO SALMON, *Oncorhynchus kisutch* WALBAUM

Introduction

Predation is believed to be a major source of mortality to juvenile salmon during freshwater residence (Ricker 1941; Neave 1953; Hunter 1959; Peterman and Gatto 1978; Ruggerone and Rogers 1984; Fresh and Schroder 1987). One method of estimating the magnitude of predation involves direct measurement of consumption rates by the predator population. Estimation of consumption, however, is very sensitive to the rate of prey evacuation from the stomach of the predator.

Recently, debate has risen over which mathematical expression best describes the pattern of food evacuation from fishes. Three models have been generally used to describe this relationship:

$$\text{the linear model, } W_t = W_0 - r t; \quad (1)$$

$$\text{the exponential model, } W_t = W_0 e^{-r_e t}; \text{ and,} \quad (2)$$

$$\text{the square root model, } \sqrt{W_t} = \sqrt{W_0} - r_s t; \quad (3)$$

where W_0 is the initial prey weight, W_t is prey weight remaining at time t , and r , r_e , and r_s are the rates of evacuation. Jobling (1981, 1986) suggested that the best evacuation model depends on the prey type consumed by the fish, e.g., piscivorous fishes should have linear or square-root evacuation curves whereas planktivorous fishes should have exponential evacuation curves. In contrast, Persson (1986) argued that food evacuation curves of most fish should be exponential. Although Persson (1986) and Simenstad and Cailliet (1986) have noted that the exponential and square root models are quantitatively similar, investigators have not compared estimates of daily meal (g consumed/24 h) and daily ration (% predator body weight consumed/24 h) calculated from these models. Thus, the effect of applying either the exponential or square root gastric evacuation models to estimate daily food consumption of a predator is not known.

A number of factors may affect the rate of food evacuation from a predator, including temperature, prey size, prey type, predator size and feeding frequency. Temperature appears to have the greatest effect on evacuation rate. Some studies indicate instantaneous evacuation rates (r_e) increase exponentially with temperature (Elliott, 1972; Persson, 1979, 1981; Durbin et al., 1983; From and Rasmussen, 1984), whereas other studies indicate that evacuation rates increase linearly with temperature (Brett and Higgs, 1970; Steigenberger and Larkin, 1974; Worobec, 1984; Ryer and Boehlert, 1983). Some investigators have reported that large prey or meal sizes reduce the instantaneous evacuation rate (r_e) of fish (Steigenberger and Larkin, 1974), whereas other investigators suggest prey weight does not affect evacuation rate (Tyler, 1970; Elliott, 1972; Persson, 1979, 1981). Thus, when estimating *in situ* food consumption of a predator from evacuation rate estimates and

stomach content data, environmental and biological effects on evacuation rates should be known.

In Chignik Lake, Alaska, juvenile coho (*Oncorhynchus kisutch*) are known to consume sockeye salmon fry (*O. nerka*) (Roos, 1960; Ruggerone, unpublished data). Most coho rear in the lake for 1 or 2 years and consume sockeye they as fry emerge from gravel along littoral areas of the lake. As part of a comprehensive study examining the freshwater interactions of these two species, I conducted a study with the following objectives: (1) describe and compare evacuation of prey (sockeye fry) consumed by coho using linear, exponential and square root models of prey evacuation; (2) develop an empirical model to predict evacuation rate upon water temperature, meal size and/or coho size; and (3) estimate daily meal, ration and number of fry consumed by coho based on laboratory estimates of coho evacuation rate and diel sampling of coho foraging in Chignik Lake. Coho utilized in this study were representative of those known to consume sockeye fry in Chignik Lake. The term "evacuation rate" in this paper refers to the slope of the aforementioned models unless noted otherwise.

Materials and Methods

Gastric Evacuation Models and Rates

Laboratory and field studies were conducted during 1986 and 1987 at the Chignik Lakes Research Station located on the south side of the Alaska Peninsula (56°16'N Lat., 158°50'W Long.). Coho were collected with a beach seine and transported to the laboratory where they were anesthetized with MS222, marked with unique fin clips for individual identification, and placed in one of four chambers within an aerated aquarium (504 L). Comparison of percent food weight remaining in fin-clipped and unmarked coho after 1 hour at 5°C and 13°C did not indicate an effect of fin clipping on evacuation rate (2-way ANOVA, N = 23, p = 0.964). Coho (83 - 143 mm; \bar{x} = 105 mm) were allowed to acclimate in the aquarium without feeding for 20-30 h before initiating the stomach evacuation experiments during the following day. Evacuation rates of coho were estimated over a range of water temperatures that commonly occur in the Chignik lakes during spring and summer (i.e., 5.0°C, 7.0°C, 10.0°C and 13.0°C). Each evacuation rate experiment was conducted when lake temperature was similar to that of the experiment in order to minimize the acclimation process of coho. A live sockeye fry of known weight (blot dried to remove excess fluid and weighed to the nearest 1 mg) was introduced to 10-13 marked coho. Typically, one of the coho would immediately attack and consume the fry as it entered the water. This successful coho was identified by the fin clip and the time of fry consumption was recorded. The next fry given to the group of coho was usually consumed by the previously active coho, thus allowing two fry of known weight to be fed to a specific coho within a short period (less than 10 min). Coho were alternately fed one or two fry, then transferred to an adjacent chamber of identical temperature. After a predetermined time, each coho was sacrificed, measured, and weighed. The stomach contents were removed and weighed (nearest 1 mg). Stomach contents of at least three coho were examined at regular intervals throughout the evacuation period until approximately 90% of the original meal was evacuated. Only one sampling period included a coho with an empty stomach and this sample (the last in the series) was removed from analysis, as recommended by Olson and Mullen (1986). From 23 to 66 coho were examined during each of the eight experiments.

Regression analysis was used to describe the relationship between untransformed, log-transformed, and square root-transformed measurements of percent fry remaining and time after ingestion for each temperature (5.0°, 7.0°, 10.0° and 13.0°C) and meal size (1 or 2 fry) category. The adequacy of each evacuation model was assessed through comparisons of the coefficient of determination (R^2), standard error of the regression (S.E.R.), Y-intercept and residual plots. The linear regression models were further tested for deviation from linearity by using an F-test (Neter et al. 1985). Because Y-intercept estimates derived from the regression analyses deviated from the known Y-intercept value of 100%, I forced the regressions through this Y-intercept (Zar 1984). Multiple regression and partial residual analysis (Larsen and McCleary 1972) were used to describe the relationship between evacuation rate and temperature, prey weight and/or predator size.

Diel Foraging of Coho

Sampling of coho for diel food consumption in Chignik Lake was conducted at two locations during early June 1986 and 1987, when most sockeye fry emerge and are available for consumption by coho. At least 11 coho (73-152 mm, $\bar{x} = 100$ mm) were randomly collected from beach seine catches at each location approximately every six hours (1200 h, 1800 h, 2400 h, 0600 h, and 1200 h). Coho stomachs were immediately injected with 50% buffered formaldehyde to reduce the digestion processes, then the entire fish sample was preserved in 10% buffered formaldehyde. At least 48 h were allowed before analysis of the coho stomach contents in order for post-mortem shrinkage of the coho to stabilize (Burgner 1962; Rogers 1964). Coho fork length was then measured and the stomach contents were identified as sockeye fry, insects or other prey (e.g., other fish, spiders, fish eggs or unidentifiable remains) and weighed (nearest 1 mg). Preserved sockeye weight did not differ significantly from live weight (t-test, $N = 80$, $p = 0.825$), thus a correction factor was not utilized. Live length and weight of coho used in the analyses were calculated from preserved measurements. The stage of digestion of the sockeye fry was categorized as none/slight (some skin removed), moderate (most skin removed plus some flesh loss), advanced (most flesh removed) or bones.

Both geometric and arithmetic mean values of total prey weight were calculated. Geometric mean values of prey weight represent typical consumption from the predator or individual perspective when the distribution of prey weight is log-normal (Cochran and Aldeman 1982; Amundsen and Klemetsen 1986). In contrast, arithmetic mean values are preferred when estimating total prey consumption by the coho population, i.e., from the perspective of the prey.

Food Consumption Models and Estimates

Estimates of daily meal, daily ration and number of fry consumed by coho in Chignik Lake were estimated by three food consumption models:

the Elliott and Persson (1978) model,

$$C\Delta_t = \frac{(\bar{W}_t - \bar{W}_{(t-1)}e^{-r_e t})rt}{1 - e^{-r_e t}}, \quad (4)$$

the Eggers (1979) model,

$$C\Delta_{24} = 24 r_e W\Delta_{24}; \text{ and,} \quad (5)$$

the Pennington (1985) model for square root prey evacuation,

$$C\Delta_t = 2r_{.5} \sum_{i=1}^n \frac{W_i}{n} + \frac{\bar{W}_t - \bar{W}_{(t-1)}}{t - (t-1)}; \quad (6)$$

where $C\Delta_t$ is food consumption between sampling periods at time t and $t-1$, \bar{W}_t is average prey weight at time t , W_i is the individual prey weight in a coho at time t , and n is the number of coho. The Elliott and Persson and Eggers models assume prey evacuation is exponential and the Pennington model assumes evacuation is proportional to the square root of prey weight. The Elliott and Persson and Pennington models require that $C\Delta_t$ be summed for each sampling interval over the 24-h period, whereas the Eggers model is calculated from the average prey weight in the stomach during the 24-h period (note that the two noontime periods in 1987 were averaged to provide a single noon estimate).

Coho in Chignik Lake also feed on insects, which may be evacuated slower than sockeye because of their chitinous exoskeleton. *In vitro* comparison of fry and insect digestion using the methods of LeBrasseur and Stephens (1965) indicated fry are digested eight times faster than insects (Ruggerone, unpublished data). Because evacuation of prey in fish stomachs is more complex than in this simple experiment, I estimated a relative evacuation rate for insects based on a comparison of coho evacuation rate of euphausiids (Brodeur and Pearcy 1987) and sockeye fry (this study). The evacuation rate of insects utilized in the daily food consumption estimates of coho in this study was 43 percent of the sockeye fry evacuation rate.

Results

Gastric Evacuation Models and Rates

The relationship between percent prey remaining and time after ingestion for each of four temperature and two prey weight categories indicates good fits by the exponential (R^2 range: 0.82 - 0.97; Fig. 1 and 2) and square root models (R^2 range: 0.87 - 0.97; Table 1). Estimated Y-intercept values of the exponential regressions ($\bar{x} = 96.5\%$ remaining) deviated less from the actual value of 100% than those of the square root regressions ($\bar{x} = 84.6\%$ remaining, Table 1). None of the Y-intercept values estimated by the exponential model were significantly different from the actual value of 100% remaining ($p > 0.05$), whereas two of eight Y-intercept values of the square root model differed significantly. An initial delay in evacuation of fry was not apparent. Residual analysis indicated good fits by both the exponential and square root models (i.e., homoscedasticity and no apparent curvature). In all eight regressions, the linear model provided the poorest fit in terms of R^2 (range: 0.82 - 0.93) and estimated Y-intercept ($\bar{x} = 80.7\%$ remaining). Furthermore, the F-test for linearity indicated that each regression deviated significantly ($p < 0.05$) from a linear curve.

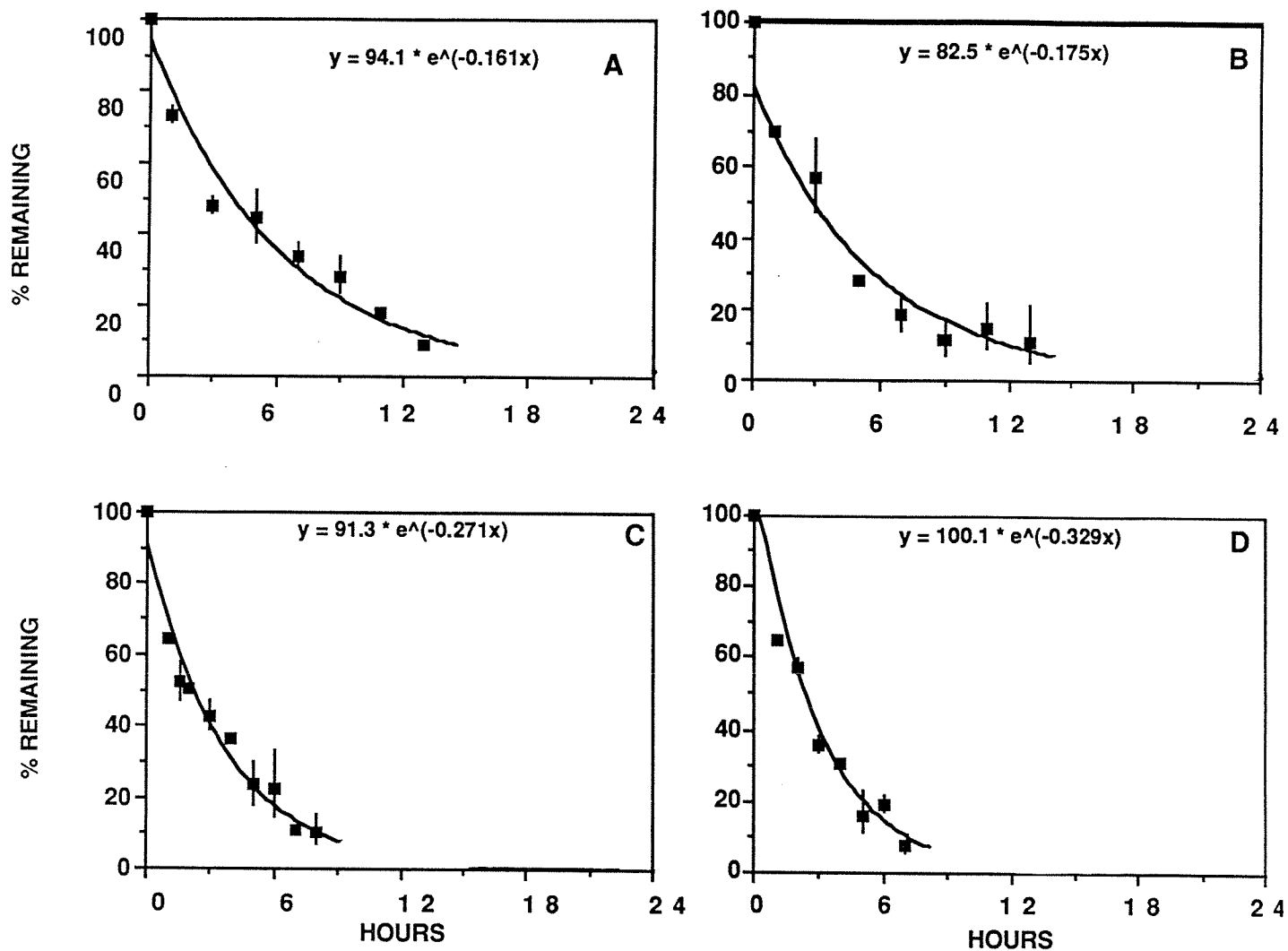


Figure 1. Comparison of exponential decay of a single sockeye salmon fry consumed by coho salmon at 5°C (A), 7°C (B), 10°C (C), and 13°C (D); data are geometric means (\pm SE) for three or more coho.

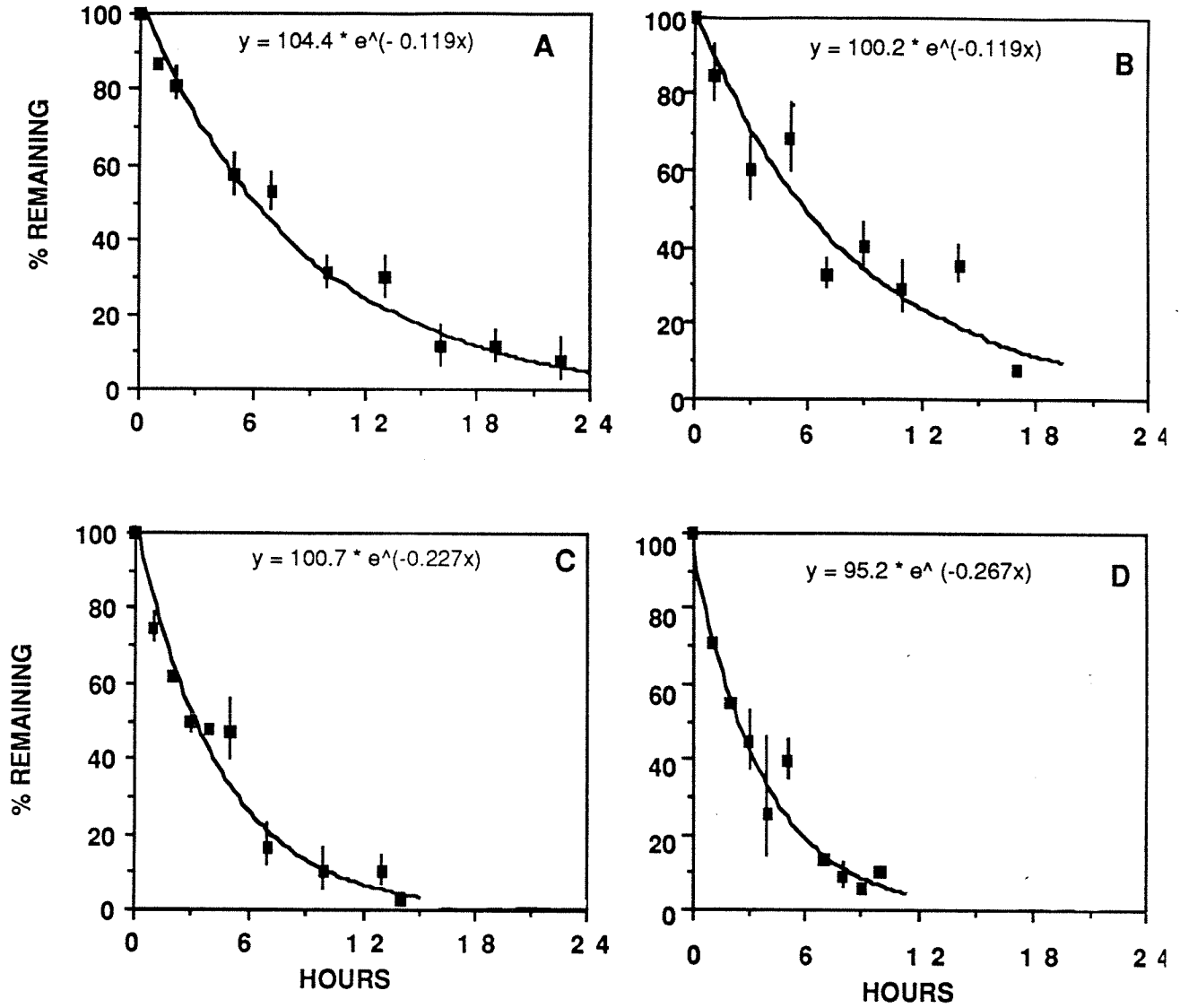


Figure 2. Comparison of exponential decay of two sockeye salmon fry consumed by coho salmon at 5°C (A), 7°C (B), 10°C (C), and 13°C (D); data are geometric means (\pm SE) for three or more coho.

Table 1. Summary of regression analyses for each coho stomach evacuation model, including the number of fish utilized in each regression, the initial percent of coho body weight consumed and the initial sockeye (prey) weight. Forms of the regression models are: linear, $W = a - rT$; exponential, $\ln W = a - r_e T$; and square root, $\sqrt{W} = a - r_{.5} T$, where W is the percentage of the original meal left in the stomach at time, $T = 0$.

Model	Temperature °C	# fish	Initial % BW consumed	Ave. prey wt. (g)	a	r	R ²	Y-intercept	
Linear	5	33	1.52	0.166	81.0*	6.00	0.89	81.0	
	7	23	1.89	0.176	77.8*	6.34	0.82	77.8	
	10	66	1.95	0.175	76.9*	9.49	0.87	76.9	
	13	33	1.80	0.186	82.9*	11.87	0.90	82.9	
	5	30	2.81	0.334	86.7*	4.22	0.93	86.7	
	7	27	3.27	0.367	85.5*	4.65	0.84	85.5	
	10	66	3.19	0.327	77.3*	5.98	0.86	77.3	
	13	36	2.81	0.306	77.5*	8.21	0.85	77.5	
	Exponential	5	33	1.52	0.166	4.54	0.161	0.95	94.1
		7	23	1.89	0.176	4.41	0.175	0.92	82.5
		10	66	1.95	0.175	4.51	0.271	0.97	91.3
		13	33	1.80	0.186	4.61	0.329	0.95	100.1
		5	30	2.81	0.334	4.65	0.119	0.97	104.4
		7	27	3.27	0.367	4.61	0.119	0.82	100.2
10		66	3.19	0.327	4.64	0.227	0.93	103.7	
13		36	2.81	0.306	4.56	0.267	0.92	95.2	
Square Root ¹		5	33	1.52	0.166	9.18*	0.471	0.96	84.5
		7	23	1.89	0.176	8.88	0.507	0.88	78.9
		10	66	1.95	0.175	8.99	0.772	0.95	80.8
		13	33	1.80	0.186	9.35	0.946	0.95	87.4
		5	5	2.81	0.334	9.56	0.336	0.97	91.4
		7	7	3.27	0.367	9.45	0.354	0.87	89.3
	10	10	3.19	0.327	9.11*	0.538	0.94	83.0	
	13	13	2.81	0.306	9.05	0.702	0.92	81.9	

¹The value of $r_{.5}$ used in the square root equation $\sqrt{W}_t = \sqrt{W}_0 - r'_{.5} T$ is $r'_{.5} = r_{.5} \sqrt{W}_0 / \sqrt{100}$. Thus the actual value of $r_{.5}$ at 5°C and prey weight of 0.166 g is 0.019.

*Estimated y-intercept is significantly different ($\alpha = 0.05$) from the original weight at $T = 0$.

Forcing the regressions through the initial value of 100% at $t = 0$ provided the expected result of lowering the evacuation rate when the estimated Y-intercept exceeded 100% and increasing the rate when the Y-intercept was less than 100% (Table 2). Standard errors of the regressions (S.E.R.) of the exponential model ($\bar{x} = 7.48 \%$) were consistently less than that of the square root model ($\bar{x} = 9.97 \%$) after adjusting to common units, indicating that the exponential model provided a better fit. However, because the exponential model was not markedly better than the square root model, I continued to evaluate the square root model so that daily meal and ration estimates based on both models could be compared.

The relationship between rate of sockeye evacuation by coho (forced regression estimate) and temperature, meal size, meal size as a percent of coho weight and coho weight was assessed by multiple regression analysis and partial residual analysis. Temperature (partial $F = 162.1$, $p < 0.001$) and meal size (partial $F = 42.0$, $p < 0.005$) were significantly related to the exponential prey evacuation rate (overall $F = 106.9$, $p < 0.001$). Coho weight (partial $F = 3.0$, $p = 0.158$) and meal size as a percent of coho weight (partial $F = 1.877$, $p = 0.243$) did not add new information. The equation describing the relationship between the exponential evacuation rate (r_e) of coho, temperature (T) and meal size (M.S.) is:

$$r_e = 0.133 + 0.021(T) - 0.402(M.S.); R^2 = 0.98, \quad (7)$$

indicating that evacuation rate increased with temperature but decreased with prey weight. Both temperature and prey weight affected the evacuation rate of coho in a linear fashion as shown in the regression-corrected plots (Fig. 3 a and b). In contrast, only temperature provided significant information for the prediction of evacuation rates based on square root decay of prey ($F = 172.3$, $p < 0.001$). The equation describing the relationship between the square root evacuation rate (r_s) of coho and temperature (T) is:

$$r_s = 0.0045 + 0.0032(T); R^2 = 0.97 \text{ (Fig. 3 c)}. \quad (8)$$

The overall fit of the exponential and square root evacuation rate models, based on R^2 values, is nearly identical, although the exponential model includes the additional variable, meal size.

Based on the exponential evacuation rate model, the number of hours to reach 90% evacuation of a single sockeye fry (0.163 g) required 14 h at 5°C but only 7 h at 13°C, whereas consumption of two fry (0.326 g) by coho required 23 h and 9 h, respectively (Fig. 4). Time to 90% evacuation of sockeye fry was typically 1.5 h less when calculated from the square root evacuation rate model. Prey weight had less effect on time to 90% evacuation at higher temperatures.

Diel Foraging of Coho

Sockeye fry were the dominant prey of coho in Chignik Lake during early June at all locations and at all times of the diel sampling period (Fig. 5). On the average, sockeye fry and insects constituted 88% ($\pm 5\%$ SE) and 9% ($\pm 4\%$ SE), respectively, of the instantaneous diet of coho by weight. Average geometric mean values of total prey weight for the

Table 2. Summary of regression analyses for the exponential and square root stomach evacuation rate models when the regression was forced through 100% prey remaining at time, $T = 0$.

Model	Temperature (°C)	# fish	Ave. prey wt (g)	r	Standardized S.E.R. (%)
Exponential	5	33	0.166	0.168	6.28
	7	23	0.176	0.196	7.75
	10	66	0.175	0.288	4.73
	13	33	0.186	0.329	5.07
	5	30	0.334	0.116	5.96
	7	27	0.367	0.118	13.87
	10	66	0.327	0.223	8.82
	13	36	0.306	0.274	7.39
Square Root	5	33	0.166	0.558	8.83
	7	23	0.176	0.628	13.27
	10	66	0.175	0.955	9.34
	13	33	0.186	1.076	7.74
	5	30	0.334	0.365	7.22
	7	27	0.367	0.401	12.00
	10	66	0.327	0.630	10.84
	13	36	0.306	0.835	10.54

¹The value of b used in the square root equation $\sqrt{Wt} = \sqrt{W_0} - r'.5T$ is $r'.5 = r.5 \sqrt{W_0}/\sqrt{100}$. Thus, the actual value of $r.5$ at 5 °C and prey weight of 0.166 g is 0.023.

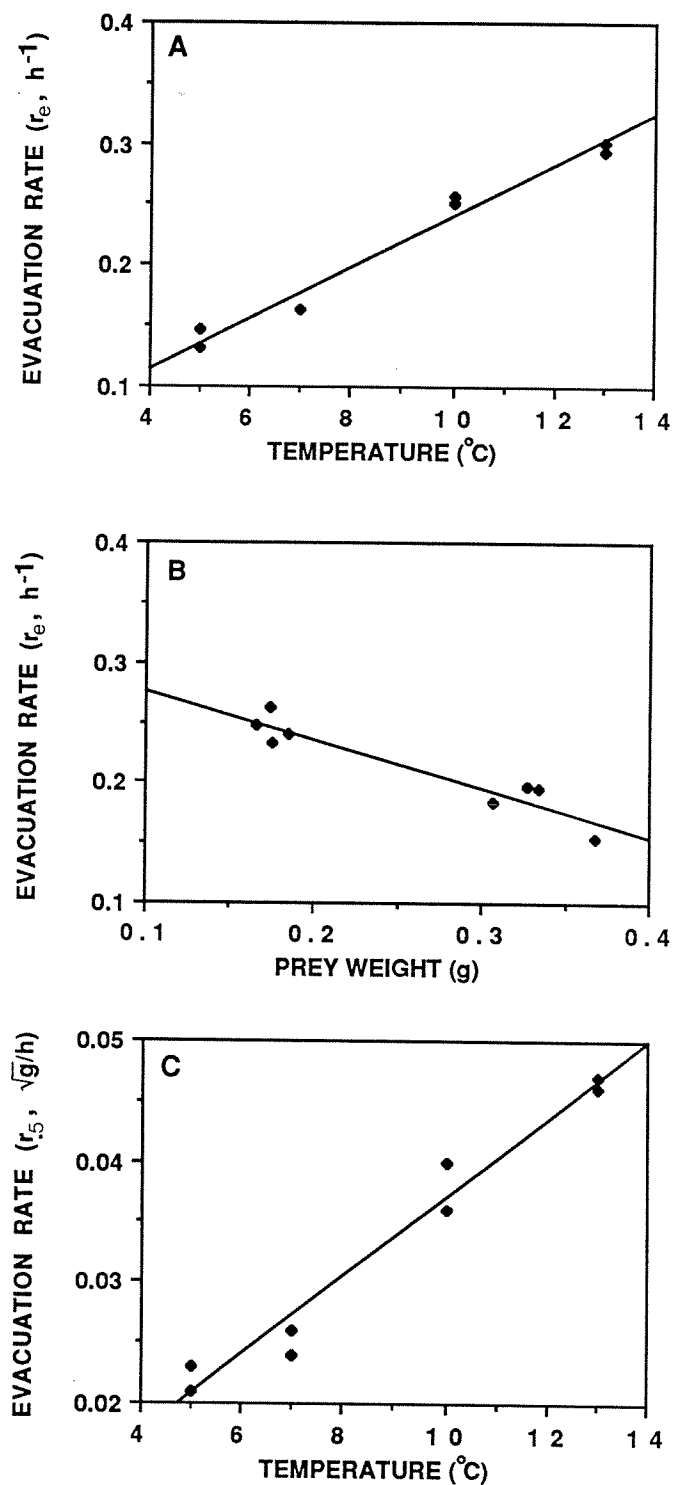


Figure 3. Regression-corrected plots of the relationship between exponential evacuation rate (r_e) of coho salmon and temperature (A) and prey weight (B), and the linear regression of the square root evacuation rate ($r_{.5}$) on temperature (C).

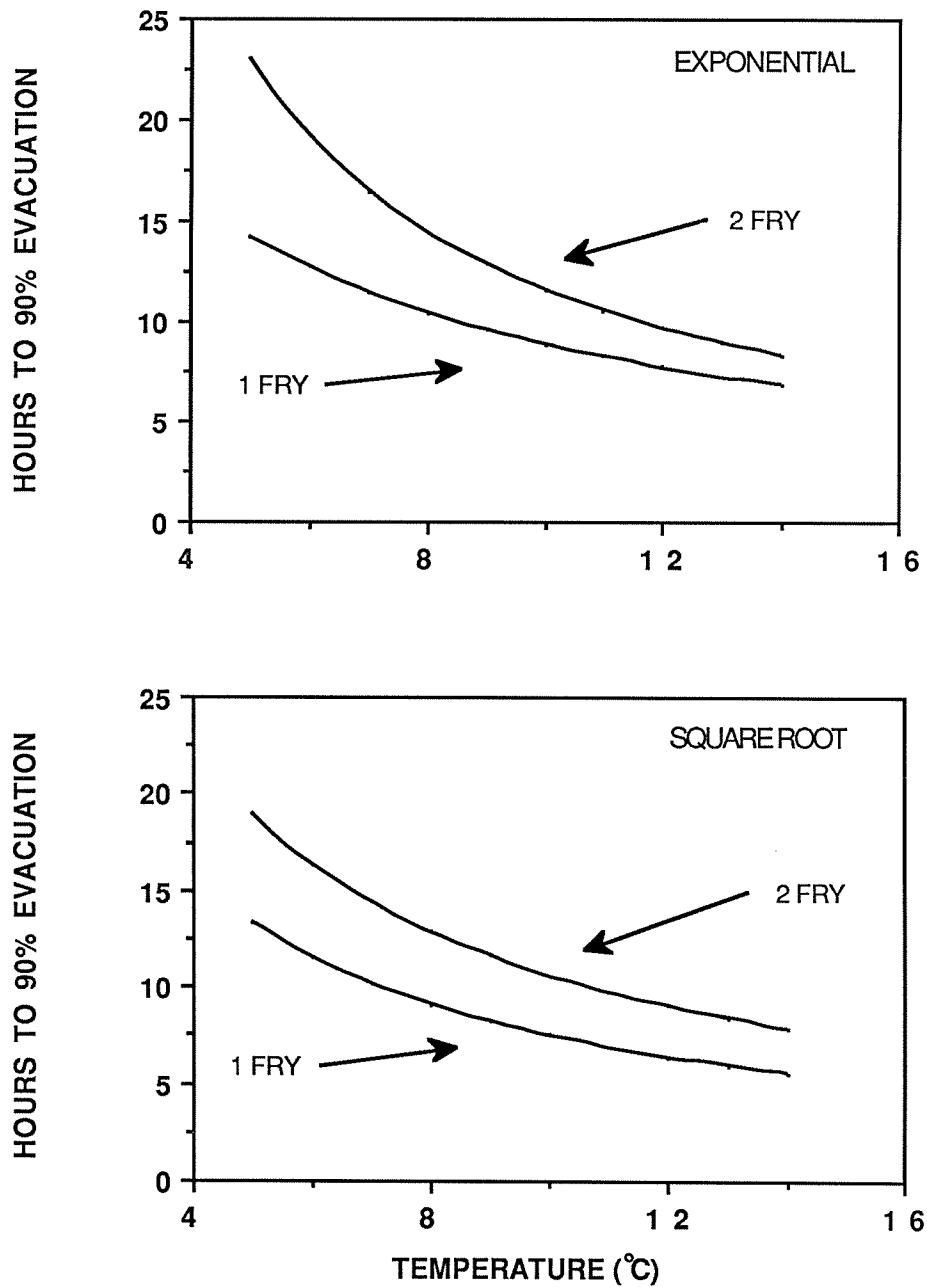


Figure 4. Estimates of time to reach 90% evacuation of one or two sockeye salmon fry consumed by coho salmon in relation to water temperature. Estimates are based on exponential and square root decay rates calculated from equations 7 and 8 and a fry weight of 0.163 g.

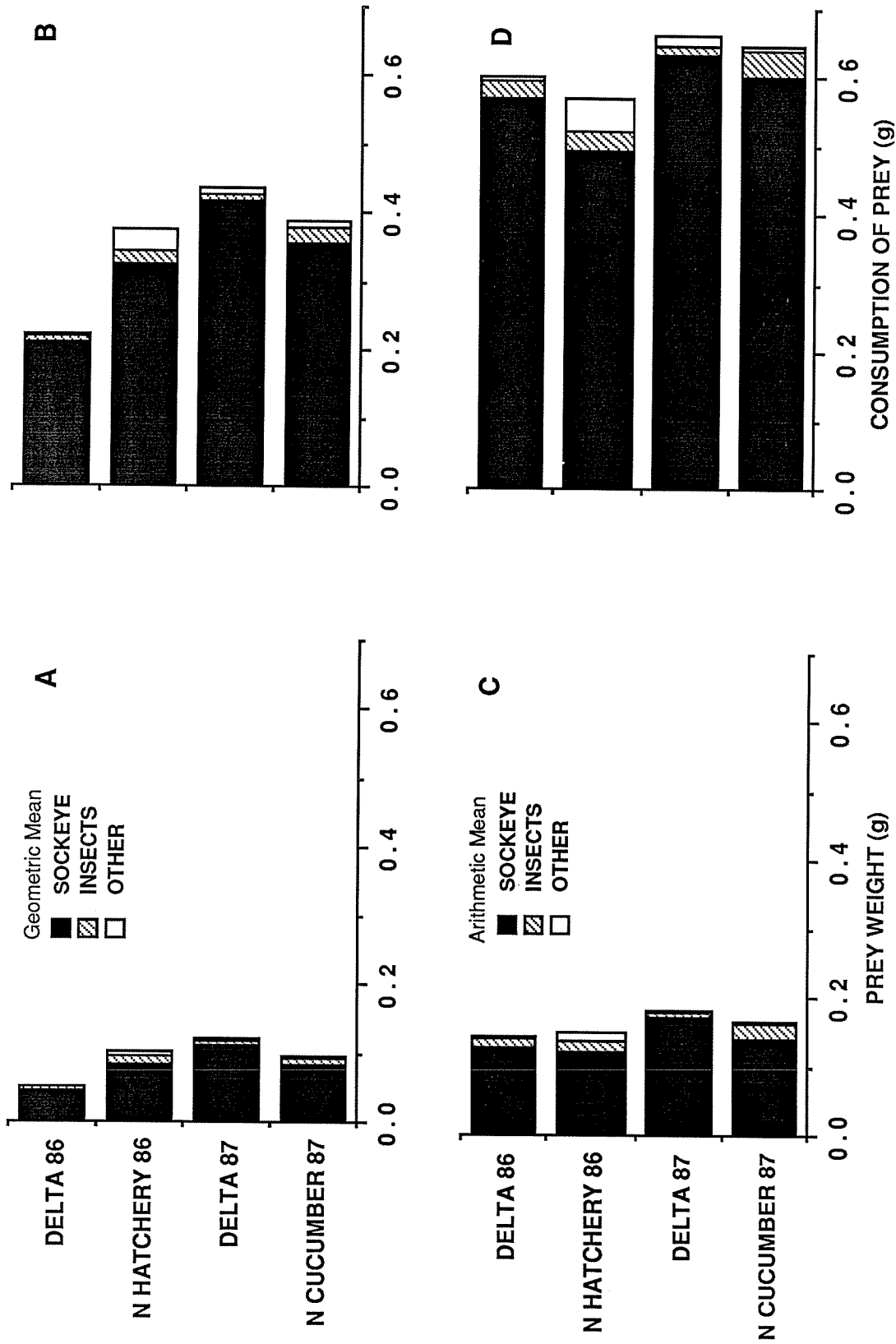


Figure 5. Estimates of prey weight observed in coho salmon at four sampling locations (A and C) and the resulting estimates of daily meal calculated from the Eggers (1979) method (B and D). Note that A and B are based on geometric mean prey weight whereas C and D are based on arithmetic mean prey weight.

24-h period at each sampling location ranged from 0.050 g to 0.120 g (Fig. 5a), whereas the average arithmetic values of total prey weight ranged from 0.143 g to 0.182 g (Fig. 5b). The incidence of coho with empty stomachs was low ($\bar{x} = 5\%$).

Diel changes of coho stomach content weight did not indicate an overall feeding pattern associated with time of day (Fig. 6). As inferred from stomach contents weight and condition, maximum foraging intensity occurred throughout day and night depending on location. On average, 21% of the coho had recently consumed a sockeye fry, although the range in percentage of coho actively feeding on sockeye fry was 0-54% at any given sampling time. The geometric mean of total prey weight also did not indicate feeding periodicity in coho. Within the observed variance, total prey weight generally (14 of 18) did not differ from the sample 6 h earlier, indicating that the coho population tended to feed continuously (Fig. 6).

Food Consumption Models and Estimates

Estimates of coho daily meal and daily ration, based on the geometric mean of total prey weight, were similar for each method of estimation. Estimates of daily meal consumed by a typical coho for all locations averaged 0.356 g (Eggers method), 0.356 g (Elliott and Persson method) and 0.341 g (Pennington method) (Table 3). Daily ration estimates of a typical coho averaged 3.6% (Eggers method), 3.6% (Elliott and Persson method) and 3.4% (Pennington method). Within a given location, differences in daily meal and ration ranged up to 0.065 g or 0.7%, respectively, depending on the method of estimation. Comparison of daily consumption of coho by prey type (based on the Elliott and Persson method) indicated that sockeye fry ($\bar{x} = 0.330$ g or 92.9% of total prey) were the dominant prey of coho during early June (Fig. 6 b and d). Insects (0.014 g or 3.8%) and other prey such as fish, fish eggs and spiders (0.012 g or 3.3%) were of secondary importance.

Estimates of average daily meal and number of sockeye fry consumed by coho were markedly higher when calculated from the perspective of the prey (i.e., calculated from the arithmetic mean of total prey weight; Table 4). However, daily meals calculated by the Pennington method ($\bar{x} = 0.417$ g) were considerably lower than those calculated by the Eggers (0.620 g) or Elliott and Persson method (0.617 g). The number of sockeye fry (0.163 g) consumed by a coho averaged 3.5 fry (Eggers method), 3.5 fry (Elliott and Persson method) and 2.4 fry (Pennington method). Insects (0.023 g) and other prey (0.020 g) were not heavily preyed upon by the coho population during early June relative to sockeye fry (0.574 g) (Fig. 5d).

Discussion

Gastric Evacuation Models and Rates

The exponential prey evacuation model described the depletion of sockeye fry from the stomach of juvenile coho better than the square root and linear evacuation models. Both the exponential and square root models fit the overall evacuation data but the square root model was less satisfactory in describing the rapid prey evacuation immediately after consumption. This result differs from the prediction of Jobling (1981, 1986), who suggested that evacuation of large prey such as fish should follow a linear or square root curve rather than an exponential depletion curve. Jobling based the prediction of a square root or linear evacuation curve on the hypothesis that large prey undergo an initial evacuation delay and

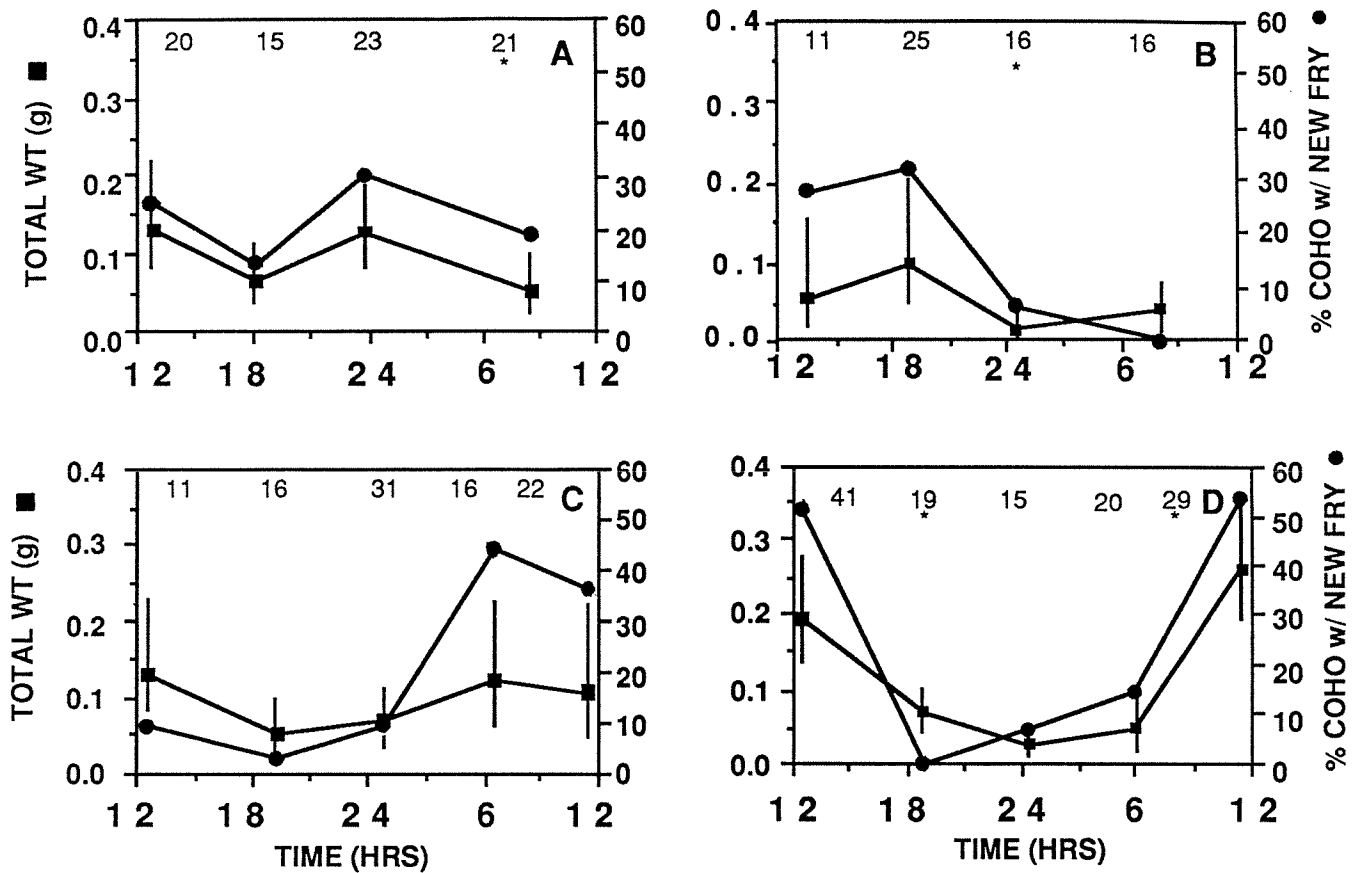


Figure 6. Total prey weight consumed by coho salmon (geometric mean \pm 95 % C.I.) and percent of coho containing recently consumed sockeye salmon fry during a 24-h period in early June; sampling locations are N. Hatchery Beach, 1986 (A), Delta Beach, 1986 (B), N. Cucumber Beach, 1987 (C), and Delta Beach, 1987 (D); numbers above data are number of coho examined and asterisk (*) indicates total weight is significantly different from previous value (ANOVA, $p < 0.05$).

Table 3. Comparison of daily meal, and daily ration of a typical coho at two sampling areas during early June 1986 and 1987. Estimates are calculated from geometric mean values of total prey weight using the Elliott and Persson, Eggers, and Pennington daily meal and ration models.

Location	Temperature (°C)	Daily meal (g)	Daily ration (% body wt.)
Delta 1986			
Elliott and Persson	7.5	0.211	1.9
Eggers	7.5	0.224	2.1
Pennington	7.5	0.268	2.4
N Hatchery 1986			
Elliott and Persson	5.8	0.363	4.3
Eggers	5.8	0.375	4.4
Pennington	5.8	0.316	3.7
Delta 1987			
Elliott and Persson	7.2	0.500	4.6
Eggers	7.2	0.435	3.9
Pennington	7.2	0.438	4.0
N Cucumber 1987			
Elliott and Persson	7.2	0.350	3.4
Eggers	7.2	0.388	3.7
Pennington	7.2	0.341	3.3

Table 4. Comparison of average daily meal and number of sockeye fry consumed by coho at two sampling areas during early June 1986 and 1987. Estimates are calculated from arithmetic mean values of total prey weight using the Elliott and Persson, Eggers and Pennington daily meal models.

Location	Temperature (°C)	Daily meal (g)	Equivalent number of fry
Delta 1986			
Elliott and Persson	7.5	0.549	3.2
Eggers	7.5	0.602	3.5
Pennington	7.5	0.371	2.1
N Hatchery 1986			
Elliott and Persson	5.8	0.559	3.0
Eggers	5.8	0.569	3.0
Pennington	5.8	0.360	1.9
Delta 1987			
Elliott and Persson	7.2	0.699	4.1
Eggers	7.2	0.661	3.9
Pennington	7.2	0.481	2.8
N Cucumber 1987			
Elliott and Persson	7.2	0.661	3.7
Eggers	7.2	0.647	3.7
Pennington	7.2	0.456	2.6

require more time to be completely evacuated or reach a given percent evacuation than small prey. This is in opposition to the exponential model, which assumes time to a given percent evacuation stage is constant regardless of prey or meal size. Although the exponential model provided the best fit for coho by accurately describing the initial rapid decay of fry, meal size (single or double meal) significantly affected the time to a given percent evacuation. The decline in evacuation rate after a double meal may be related to negative feedback processes caused by the emptying of energy-rich food into the upper intestine (Jobling, 1986). Presumably, the negative feedback mechanism facilitates control of absorption efficiency, although absorption efficiency has been reported to decrease with greater ration size in some fishes (Solomon and Brafield 1972; Elliott 1976; Windell et al. 1978) but remain constant in others (Beamish 1972; Kelso 1972; Charles et al. 1984; Sampath 1984). The reduced surface/volume ratio of two fry overlapping in the stomach also may have caused reduced evacuation. The reduction of evacuation rate with a doubling of meal size does not support the hypothesis of Persson (1981, 1986), who suggested a single exponential model should adequately describe prey evacuation of most fishes unless an initial lag phase was apparent.

The results of evacuation experiments on piscivorous fish have not shown one model type to be superior to other models. Investigators have utilized linear (Olson and Boggs 1986; Vonracek 1987), square root (Jobling 1982), and exponential models (this study; Steigenberger and Larkin 1974; Persson 1981; Brodeur 1984) to describe the evacuation of fish prey. A second degree polynomial (Magnuson 1969) and a power curve (Beyers et al. in press) have also been utilized to describe the evacuation of food from piscivorous fishes, although an exponential function could have replaced the polynomial function (Elliott and Persson 1978) and the power function was similar to the square root function. Meal sizes utilized in these studies were relatively large, except for the study by Persson (1981), indicating that the effect of large meal size on the pattern of evacuation is not the same for all piscivores.

The exponential evacuation rate (r_e) of coho in this study increased linearly with temperature and may be related to meal size, energy content and nutritious value of sockeye fry. I have replotted the data from other studies that have calculated evacuation rates at several temperatures (Fig. 7). Sockeye salmon (Brett and Higgs 1970), squawfish (*Ptychocheilus oregonensis*) (Steigenberger and Larkin, 1974) and other fishes have exponential evacuation rates that also increased linearly with temperature, whereas trout (*Salmo* spp.; Elliott 1972; From and Rasmussen 1984), perch (*Perca* spp.; Persson 1979, 1981; Boisclair and Leggett 1988) and roach (*Rutilus rutilus*; Persson 1982) exhibited an exponential increase in evacuation rate with temperature. An exponential increase in instantaneous evacuation rate with temperature indicates that the range in food weight passed through the pylorus will be greater than if temperature affects evacuation rate linearly. At high temperatures, fish that exhibit an exponential increase in evacuation rate would have relatively large amounts ($g\ hr^{-1}$) of food entering the intestine, which could reduce absorption efficiency. However, most studies indicate absorption efficiency is not reduced at high temperatures (Kelso 1972; Davies and Massey 1977), rather absorption efficiency in some fishes may be reduced at low temperatures (Elliott 1976; Windell et al. 1978). It may be that the greater enzyme activity at high temperatures (Smit 1967) compensates for faster evacuation of food. Absorption efficiency may also be controlled through a negative feedback mechanism between the stomach and intestine (Jobling 1986), which could explain the differences in the relationship between evacuation rate and

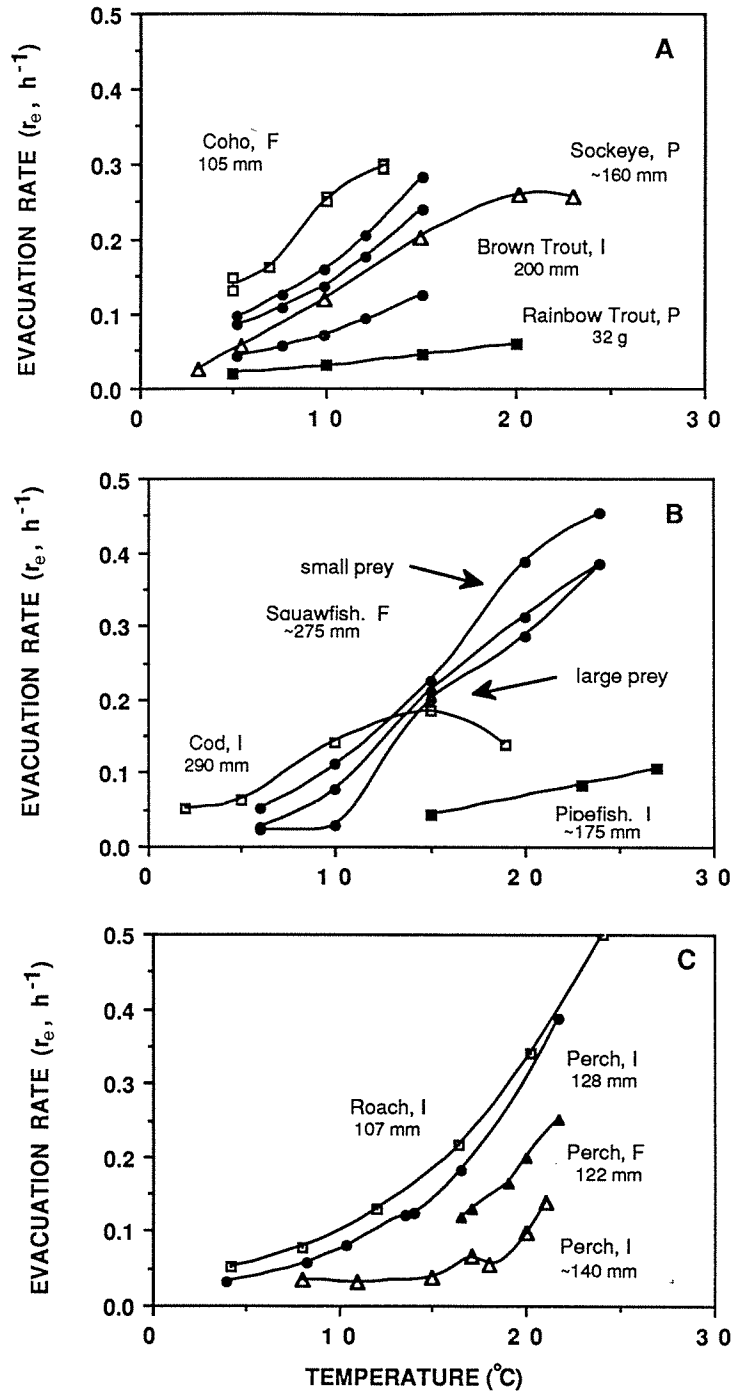


Figure 7. Comparison of exponential evacuation rates (r_e) of fishes in relation to water temperature. Prey types indicated as F = fish, I = invertebrates, and P = formulated pellets; mean predator size is indicated below common name. Lines are drawn by computer interpolation. Sources of information: (A) Brett and Higgs 1970; Elliott 1972; From and Rasmussen 1984; this study; (B) Tyler 1970; Steigenberger and Larkin 1974; Ryer and Boehlert 1983; (C) Persson 1979, 1981, 1982; Boisclair and Leggett 1988.

temperature shown in Figure 7. The exponential relationship reported by Elliott (1972), Persson (1979, 1981, 1982), and Boisclair and Leggett (1988) involved small invertebrates or fish larvae, which presumably have low energy content (Jobling, 1986) and would be evacuated rapidly. From and Rasmussen (1984) reported an exponential relationship after feeding trout with a relatively low-fat (10.4% dry wt) fish pellet, whereas Brett and Higgs (1970) reported a linear relationship after feeding salmon a relatively high-fat fish pellet (14% dry wt).

The exponential evacuation rate of coho appears to be considerably higher than those reported for many other fishes (Fig. 7; also see reviews by Magnuson 1969; Fänge and Grove 1979; Durbin et al. 1983), although direct comparison is hindered by differences in prey size, prey type, predator size, temperature, model type and experimental methods. I suggest that the high evacuation rate of coho matches their life history pattern, which apparently maximizes the potential intrinsic rate of increase through aggressive foraging habits and rapid growth prior to reaching maturity after 2 or 3 years. Observation of few empty stomachs in freshwater (5%, this study) and in marine waters (Brodeur and Pearcy 1987) during the day indicate that coho continually search for food when conditions such as light level permit. Associated with this aggressive feeding behavior is a high metabolism and growth rate. After 12.5 or 25 months in freshwater and 14 months at sea, coho return to Chignik at approximately 3.7 kg (non size-selective purse seine fishery), or an average growth of 8.8 g per day at sea. Coho smolts at Chignik are considerably larger than sockeye smolts of the same age, indicating greater food consumption by juvenile coho. However, the consumption of food, which leads to a high growth rate, is related not only to food availability but to rapid processing of food (Vahl 1979; Pandian and Vivekanandan 1985). Hunt (1960) reported that the evacuation rate (% BW hr⁻¹) of largemouth bass (*Micropterus salmoides*) was 1.5 x that of warmouth (*Chaenobryttus gulosus*) and 2.4 x that of gar (*Lepisosteus platyrhincus*) and suggested that the species differences in evacuation rate were related to the activity level and daily food consumption of the fish. Thus, the high evacuation rate of coho appears to be related to the coho life history pattern of high intrinsic rate of increase, which is a result of rapid growth and aggressive foraging behavior in habitats where food availability is high.

Diel Foraging of Coho

There was no apparent trend in the feeding periodicity of coho in Chignik Lake. The maximum weight of food in the stomachs of coho varied from one location to another and occurred throughout the diel period. In contrast, Brodeur and Pearcy (1987) reported that young coho at sea fed primarily during crepuscular periods. Apparently, coho at Chignik feed opportunistically whenever prey are available, which includes most of the 24-h period since nights during mid-June are relatively short (approximately 3-4 h). Amundsen and Klemetsen (1986) also reported the lack of diel feeding periodicity by arctic char at high latitudes during the season of minimal darkness.

Food Consumption Models and Estimates

Continuous feeding by fish has been shown to accelerate the evacuation of earlier prey items and could cause underestimation of food consumption when based on single meal evacuation experiments (Noble 1973; Corazza and Nickum 1983). However, multiple meal experiments (Ruggerone, in review) utilizing juvenile coho consuming sockeye fry

indicated that the evacuation of subsequent meals are reduced, resulting in the evacuation of a total combined meal that can be reliably estimated from single meal experiments. Thus, the evacuation rate models developed in this study, which were based on single meal models (1 or 2 fry), can be used to estimate food consumption of coho in the field.

The square root model (Pennington method) utilized in calculating daily meal and ration of coho provided lower consumption rates relative to the exponential models (Eggers method and Elliott and Persson method) when the arithmetic mean prey weight was utilized. One reason for this difference is that the Pennington model is dependent on the average square root of prey weight, whereas the exponential models are calculated from average prey weight. The curvilinear nature of the square root function causes the Pennington method to estimate relatively low food consumption when prey weight in the fish stomach is high. This result is especially evident when comparing coho food consumption estimates based on relatively small geometric and relatively large arithmetic mean prey weights. At low stomach content weight, the Pennington method will produce food consumption estimates that are higher than the exponential methods. For example, the geometric mean stomach content weight of coho at Delta Beach in 1986 was low (0.050 g) and the resultant estimate of food consumption was greater when calculated by the square root model than the exponential models. Thus, the pattern of prey evacuation should be carefully analyzed in order to minimize errors in estimating food consumption. The Elliott and Persson and the Eggers models provided similar estimates of food consumption. Boisclair and Leggett (1988) also reported similar food consumption estimates of perch based on these two methods, although they also concluded that the Eggers model was less sensitive to changes in sampling frequency and number of fish examined. Amundsen and Klemetsen (1986) argued that the Eggers model is more reliable when prey weight estimates are variable and generally not significant between sampling periods.

The daily ration estimates of coho in Chignik during early June ranged from 2.1-4.4% BW day⁻¹ based on the Eggers method. This estimate is similar to that of young coho (2.4-3.7% BW day⁻¹) foraging in coastal waters (Brodeur and Pearcy 1987), although these fish inhabited warmer water and were larger. The daily ration of coho in Chignik Lake was estimated during peak emergence of sockeye fry, which occurs in early June, then declines in late June and is complete by late July. Individual coho consumed a large number of sockeye fry during early June, indicating that the coho population, on average, consume many sockeye fry during their peak emergence. Subsequent sampling of coho foraging during late June and July indicates continued, although reduced, consumption of sockeye fry and a large population of coho (Ruggerone, in prep.), indicating that coho could markedly influence sockeye abundance in Chignik Lake.

GASTRIC EVACUATION OF SINGLE AND MULTIPLE MEALS BY PISCIVOROUS COHO SALMON (*Oncorhynchus kisutch*)

Introduction

Gastric evacuation rates of fishes are often estimated in the laboratory and used together with stomach contents of field-caught fish to estimate daily meal or ration. Laboratory procedures for estimating evacuation rates usually involve serial observations of the decline of a single meal through time. However, a number of studies have indicated that evacuation rate of a given meal is accelerated when followed by an additional meal (Rozin and Mayer 1964; Laurence 1971; Noble 1973; Corazza and Nickum 1983). Unless the evacuation rates of subsequent meals are reduced, the evacuation rate of a total multiple meal (i.e., the sum of meals consumed at different times) may be underestimated by observing evacuation of a single meal through time (Noble 1973). Examination of the evacuation rate of multiple meals is important to studies of food consumption in the field, especially those concerned with continuously feeding fish.

Recent studies by Persson (1984) and Talbot et al. (1984) indicated interference between the evacuation of consecutive meals consumed by fish. These investigators demonstrated that evacuation rate of the first of two meals consumed by perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and Atlantic salmon (*Salmo salar*) was faster than a single meal, but that the evacuation rate of the second meal was slower than that of a single meal. Persson also demonstrated that the total food remaining in the stomach of perch or roach after a multiple meal could be accurately estimated by applying evacuation rates of a single meal. These studies involved fish consuming small prey such as zooplankton, algae, or formulated pellets. Evacuation of larger prey, such as other fish, may have different characteristics than small prey (Jobling 1986).

In Chignik Lake, Alaska, juvenile coho salmon (*Oncorhynchus kisutch*) have been shown to feed continuously on sockeye salmon fry (*O. nerka*), as indicated by few empty stomachs throughout the diel period and observations of fry at various digestion stages (Ruggerone, in review and this report). The objectives of this investigation were to assess the interaction of multiple fish meals consumed by juvenile coho salmon on the gastric evacuation of individual meals and to evaluate an evacuation rate model (Ruggerone, in review and this report) for predicting the evacuation rate of multiple meals consumed by coho.

Materials and Methods

Gastric evacuation experiments on coho consuming sockeye fry were conducted during June 1987 at the Chignik Lakes Research Station located on the south side of the Alaska Peninsula (56°15'N Lat.; 158°50'W Long.). Details of the experimental procedures have been described by Ruggerone (in review and this report). Coho were collected with a beach seine from Chignik Lake (9.0°C) and transported to the laboratory where they were anesthetized with MS222, marked with unique fin clips for individual identification, and placed in one of four chambers within a aerated, constant temperature (10°C) aquarium (504 L). Previous studies did not indicate an effect on evacuation rate caused by fin clipping

(Ruggerone, in review and this report). Coho were allowed to acclimate in the aquarium without feeding for 20-30 hrs before initiation of the stomach evacuation experiments during the following day. Coho were fed either a preweighed (nearest 0.001 g) sockeye fry (live) or a multiple meal consisting of an additional fry 2 hours after the first meal (Table 5). Stomach contents of coho consuming a multiple meal were analyzed 4 hours after ingestion of the first meal (2 hours after the second meal). Each fry of the multiple meal was weighed separately. Coho consuming a single fry were sacrificed and analyzed for remaining fry weight at 2 or 4 hours after ingestion, corresponding to the same evacuation times of coho consuming multiple meals. Twenty coho were utilized in each of the three meal type categories.

Analysis of variance (2 x 2) and the Tukey multiple comparison test (Zar 1984) were used to assess the interaction of individual fry evacuation rate in multiple meal consumption. If fry evacuation from coho was independent from other meals, then percent weight remaining (geometric mean) from the first and second fry of a multiple meal should be similar to that of a single meal after equal time in the stomach.

The exponential gastric evacuation rate of coho has been shown to decrease with greater single meal size; therefore actual evacuated weight of the multiple meal was compared with estimates based on the following weight-dependent evacuation model (Ruggerone, in review and this report):

$$\text{Evacuation Rate (r)} = 0.133 + 0.021(\text{Temp.}) - 0.402(\text{Prey Wt}).$$

The estimated evacuation rate (r) was used in the exponential decay model, $W_t = W_0 e^{-rt}$, to estimate prey weight (W_t) remaining 2 or 4 hours (t) after consumption of the initial meal (W_0).

Results

Analysis of variance indicated significant interaction between the first and second fry consumed during a multiple meal (N = 80, F = 28.5, p < 0.001). The interaction effect resulted from the rapid evacuation of the first of two fry (29.9% of initial weight remain-

Table 5. Percentage of initial fry weight remaining and experimental conditions during single and multiple meals consumed by coho salmon (N = 20 coho per condition).

Meal type	Hours of evacuation	Coho wt (g)	Initial prey wt (g) ¹	Percent Remaining	
				Mean ¹	95% C.I.
Single	2	10.5	0.176	50.6	47.3 -54.1
Multiple (2nd of two meals)	2	9.8	0.183	72.2	69.2 -75.4
Single	4	9.8	0.177	36.1	31.5 -41.3
Multiple (1st of two meals)	4	9.8	0.185	29.9	25.5 -35.1

1 - Geometric mean.

ing) compared to that of a single fry (36.1% of initial weight) after 4 hours of evacuation, and the slow evacuation of the second fry of the multiple meal (72.2% of initial weight) compared to that of a single fry (50.6% of initial weight) after 2 hours of evacuation (Table 5). Comparison of single and multiple meal mean values indicated significant differences 2 hours ($q = 6.730$, $p = 4$, $P < 0.005$) and 4 hours after ingestion ($q = 3.989$, $p = 4$, $P < 0.05$).

Comparison of the actual fry weight remaining with that calculated from the exponential evacuation model also indicated that evacuation of the first meal was markedly increased by the second meal, whereas evacuation of the second meal was reduced by the first meal (Fig. 8). The total weight of the multiple meal at 4 hours (0.191 g; 51.9% of initial weight) was similar to that predicted by the evacuation model (0.186 g; 50.5% of initial weight).

Discussion

The results of this study on piscivorous coho salmon support the findings of Persson (1984) and Talbot et al. (1984), who reported that multiple meals consumed by herbivorous, planktivorous and pellet-fed fishes interact and substantially alter the evacuation rate of individual prey items. The evacuation of the first fry consumed by coho was accelerated by a subsequent meal, whereas evacuation of the second fry was reduced by the first meal. A potential mechanism for the interaction between meals consumed by coho may be related to the slower decay observed in fry near the foregut relative to the pylorus area where enzymes apparently accumulate as a result of gravity. The first of two fry consumed by coho was located next to the pylorus, whereas the second fry was usually adjacent to the first fry but separated from the pylorus area. Thus, the reduced evacuation of the second meal may be related to its distance from the pylorus, whereas the accelerated evacuation of the first meal may be related to its proximity to the pylorus and the greater peristaltic activity and enzyme secretion caused by the larger total meal size following the second meal.

Although previous studies indicated concern over the effect of subsequent meals on the evacuation rate of a given meal (Noble 1973), the result of meal interaction in coho was equivalent to that predicted by the single meal evacuation model. Persson (1984) also reported that the negative interaction of multiple meals consumed by perch and roach enabled accurate prediction of total meal weight based on a single meal evacuation curve. Elliott (1972) reported that multiple meals of zooplankton consumed by brown trout (*Salmo trutta*) were evacuated independently, and that evacuation of multiple meals could be estimated from single meal experiments. Several other investigators have reported accurate prediction of evacuation of multiple meals (El-Shamy 1976; Persson 1981, 1982). However, Tyler (1970) reported that the evacuation rate for cod (*Gadus morhua*) underestimated total food remaining after consumption of multiple meals and suggested this result was caused by starving the cod for 3-4 days prior to the experiment. Although these studies indicate evacuation of multiple meals consumed by herbivorous, planktivorous, and piscivorous fish can be accurately predicted by single meal evacuation models, additional studies are needed before such a generalization can be applied to all fishes.

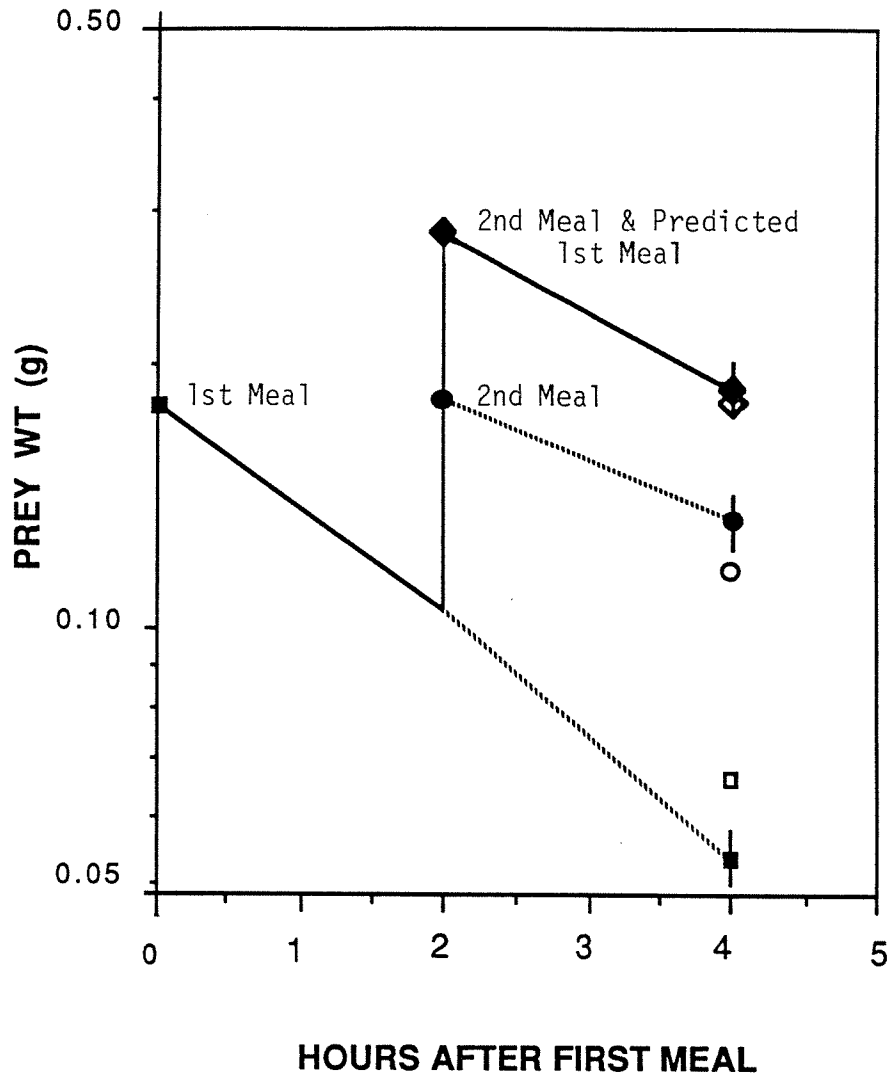


Figure 8. Stomach evacuation of individual prey (■, ●) and total prey (◆) of a multiple meal consumed by coho salmon. The unfilled symbols, (□, ○, ◇) represent expected fry weight calculated from the single meal evacuation model. Values are geometric means \pm 95% C.I.

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