サクラマス幼魚の飽食量と消化速度

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Satiation and Gastric Evacuation in Juvenile Masu Salmon

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The satiation time, the satiation amount and the rate of gastric evacuation for juvenile masu salmon *Oncorhynchus masou* having various sizes were determined at two different water temperatures (16.2–16.8°C and 8.6–9.4°C). When there was an excess of food, the satiation time was less than 60 min, with a tendency to increase with increasing fish size in both water temperatures. The satiation amount was proportional to $W^{0.715}$ (W: fish body weight), independent of the water temperature. A square root model was more suitable for estimating the gastric evacuation rate than an exponential model. The rate of gastric evacuation for high water temperature was greater than that for low water temperature. From the results of statistical analysis of the difference in the regression parameters between the sized groups, the instantaneous rate of gastric evacuation was constant with respect to the fish size, while the evacuation time was longer in the smaller fish, which consumed a larger meal per unit body weight than in the larger fish.

Masu salmon *Oncorhynchus masou* are distributed only on the Asian side of Japan and are centered in the Sea of Japan.[1] At present, the annual catch of this species still remains at the low level of 2000 t, although 5000 t were once landed on the coastal waters around Japan. Recently, a large number of hatchery-reared smolts have been released in order to reverse this decline.[2,3]

The onset of parr-smolt transformations is closely related to the growth or to the growth rate prior to smolt.[4,5] Therefore, promotion of their growth by improving feeding techniques would accelerate the smolting rate. Although some information[6,7] is available on the trophic habitat of this species, comparatively little is known about the food consumption and evacuation. The objective of this study was to examine the time taken for the masu salmon to consume a meal (satiation time), to determine the maximum amount of food consumed within this meal (satiation amount) and their rate of gastric evacuation at two different water temperatures.

Materials and Methods

The feeding experiments were carried out during the period of July 11th to October 16th 1985, using the 0^{+} hatchery-reared masu salmon parr taken from spawner fish which have been reared for generations in the Hokkaido Fish Hatchery's freshwater pond since 1964. Prior to use, the experimental animals were acclimated to laboratory conditions in separate 40 *l* aquaria maintained at the two different experimental water temperatures (16.2–16.8 and 8.6–9.4°C) under running water with the flow rate ranging from 500 to 700 m*l* per min. They were starved for three or four days to ensure that their alimentary tracts were empty.

Satiation Time

Since the amount of food consumed by fish varies with time, in order to obtain a constant value for the food consumption, it is necessary to feed an excess of food to the fish until the cumulative amount of food consumption reaches a constant value.[8] In the present experiment, the time from start of feeding to voluntary cessation was determined as the satiation time according to the definition by Brett.[9]

The fish were divided into three size-matched groups (mean fish dry body weight in mg; 1,685 (N=10), 912 (N=10), 534 (N=12)) at the high water temperature, and into four sized groups (847 (N=8), 441 (N=10), 207 (N=10), and 121 (N=10)) at the low water temperature. The fish of each sized group were fed the weighed amounts of food seven times at intervals of 10 min. The fish were fed a commercial trout feed (crumbles) with about 1.2 mm mean diameter, which had been oven-dried at 60°C for three days to obtain constant weight without loss through volatilization. The proximate composition of the crumble diet (% of dry matter) was as follows: crude protein (>48.0), crude lipid (>3.0), crude fiber (<2.5), crude ash

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(<16.0), and water (<9.0). The uneaten foods were quickly collected by the siphon within 4 min after feeding for 6 min, filtered through a filter with a 0.45 μm (pore size) and oven-dried at 60°C for three days. The crumble diet was considered to lose some of water-soluble ingredients in aquatic conditions. At the preliminary experiment without feeding the fish, however, the recovery of the crumbles determined by the methods above mentioned was 85%, and so the corrected apparent weight of uneaten food was computed by multiplying the actual weight of collected-food by 1.16. Thus, the amount of food taken in at each interval was estimated by the difference between the quantity offered and the apparent amount uneaten.

Satiation Amount and Evacuation

The satiation amount and the gastric evacuation rate were measured by examining the contents in the stomach following the serial slaughter. The fish used in this experiment were also divided into three size-matched groups (mean fish dry body weight in mg: 1,729 (N=30), 988 (N=30), 570 (N=35)) at the high water temperature, and into four size-matched groups (1,589 (N=40), 775 (N=60), 463 (N=60), 242 (N=60)) at the low water temperature. The fish of each sized group were fed until satiation on the basis of the results of the experiment on the satiation time, and then initial samples were killed immediately to determine the food consumption. Thereafter the residual fish were starved postprandially through the test period. At intervals after satiation, 3 to 5 individuals were sampled from each aquarium and killed. The sampled fish were weighed, measured and their gastrointestinal tracts taken and cut at the pyloric sphincter. The contents in the stomach were removed and their dry weights determined.

Results

Satiation Time

The food intake estimated at 10 min intervals and the cumulative totals are shown in Fig. 1. The food intake in any sized group diminished markedly on and after the second offering, with a particularly sharp decrease within the samaller sized group at the low water temperature. The cumulative totals which represented an asymptotic curve showed that the time taken to cease feeding had a tendency to increase with increasing fish size. However, it was apparent that fish in any sized group stopped feeding within approximately 60 min. Consequently, the time from the start of feeding to voluntary cessation was estimated at 60 min under the present experimental conditions. Therefore, this feeding time (60 min) was used as the satiation time in the following experiment.

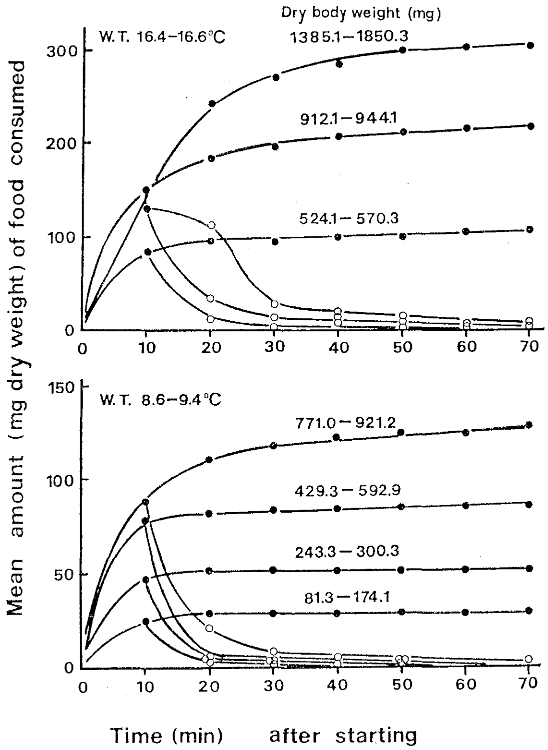

Fig. 1. Changes in food intake (○) estimated at intervals of 10 min and the cumulative totals (●) in different sized groups of juvenile masu salmon.

Satiation Amount and Ratio

The maximum consumption of dry food in a meal (satiation amount) and the ratio of satiation amount to the dry body weight (satiation ratio) were plotted against the dry body weight (W) on a log-logarithmic scale and a semi-logarithmic one, respectively, and experimental equation were obtained using an allometric model ($ln\, S = ln\, a + b\, ln\, W$ or $S = aW^b$) for the satiation amount (S) and an exponential model ($ln\, S_r = ln\, a + bW$ or $S_r = ae^{bW}$) for the satiation ratio (S_r) at two different water temperatures, where a (intercept) and b (slope) are constants (Figs. 2 and 3).

The slopes (b) on both the satiation amount and the satiation ratio did not differ significantly between the high water temperature and the low water temperature (analysis of covariance with

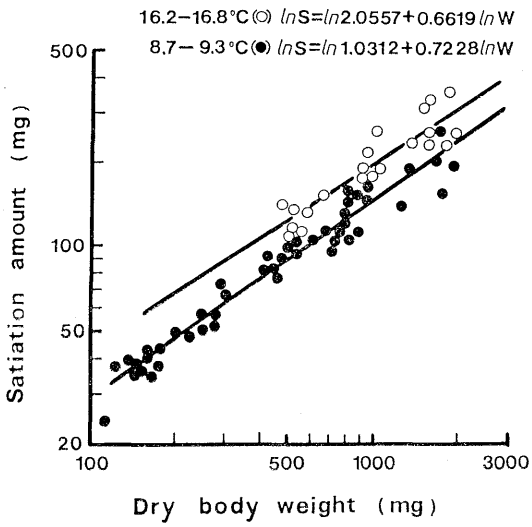

Fig. 2. Satiation amount (S: mg dry weight) in relation to dry body weight (W: mg) of juvenile masu salmon at two differnt water temperatures.

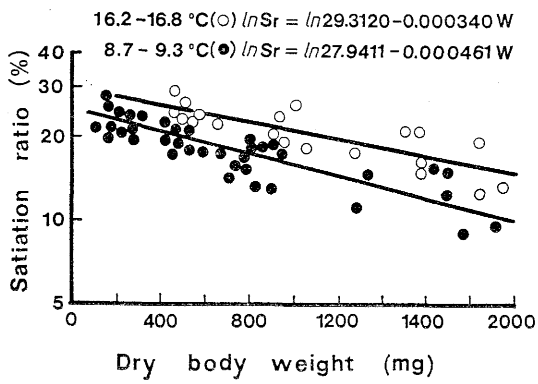

Fig. 3. Satiation ratio (S_r: satiation amount × 100/dry body weight) in relation to dry body weight (W: mg) of juvenile masu salmon at two different water temperatures.

$p=0.05$), however, their intercepts (a) did ($p<0.01$), *i.e.*, the fish with the high water temperature took a significantly larger meal than they did with the low water temperature. In view of these results, each pooled slope was recalculated. Consequently, the satiation amount and the satiation ratio were proportional to $W^{0.715}$ and $e^{-0.424\times10^{-3}w}$, respectively.

Evacuation Rate

The mean values of the individual estimates of contents (dry food × 100/dry fish) in the stomach are plotted against the postprandial time for each sized group under the two different water temperatures in Fig. 4. Although the mean stomach

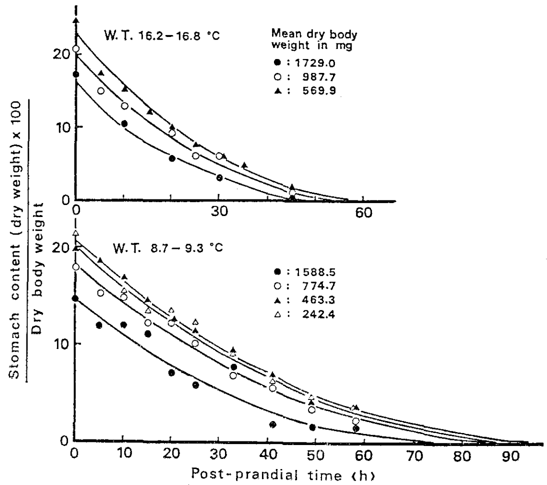

Fig. 4. Changes in mean stomach contents as a percentage of dry body weight with post-prandial time in each sized group at two different water temperatures. Curves are fitted by a square root model.

contents decreased with time, the relationships were not linear. Various non-linear models of gastric evacuation have been proposed[10] and of these a square root model ($\sqrt{S_t}=\sqrt{S_0}+ct$) and an exponential model ($ln\ S_t=ln\ S_0+ct$ or $S_t=S_0e^{ct}$) were considered where S_t is the content remaining in the stomach (expressed as percentage of fish dry body weight) at a specified time after feeding, S_0 is the initial contents (%) in the stomach and is the intercept of the regression line, c is the instantaneous rate of gastric evacuation and is the slope of the regression line, and t is time (h) after feeding. Two curvilinear models were then fitted to the data (Table 1). Using the value of r (correlation coefficient) as indicators of the relative suitability of the models, square root model seems to be more suitable for all the seven data sets. The lines fitted in the square root model were drawn in Fig. 4. It was evident that the rates of gastric evacuation in the high water temperature were greater than those in the low water temperature.

The slopes (c) did not differ significantly between sized groups at both water temperatures (analysis of covariance with $p=0.05$), but their intercepts (S_0) did ($p<0.01$) *i.e.*, the small fish took a significantly larger meal per unit body weight than did the large fish, but the instantaneous rate of gastric evacuation was constant with respect to the fish size. Therefore, a common regression parameter was recomputed by pooling the sums

Table 1. Relationships between contents (S_t) as percentage of dry body weitght remaining in the stomach and post-prandial time (t: h) of each sized group at two different water temperatures. Data are applied to both a square root model ($\sqrt{S_t}=\sqrt{S_0}+c\cdot t$) and an exponential model ($ln\ S_t=ln\ S_0+c\cdot t$)*

a) High water temperature (16.2−16.8°C)

Mean dry body weight (mg) with S.D. of each sized group	$\sqrt{S_t}=\sqrt{S_0}+c\cdot t$			$ln\ S_t=ln\ S_0+c\cdot t$		
	S_0	c	r	S_0	c	r
1729.0±176.3	16.2949	−0.0771	−0.998	25.8756	−0.0551	−0.964
987.7± 92.0	19.7545	−0.0761	−0.986	26.0730	−0.0670	−0.936
569.9± 65.4	22.4600	−0.0774	−0.989	22.7781	−0.0813	−0.973

b) Low water temperature (8.7−9.3°C)

Mean dry body weight (mg) with S.D. of each sized group	$\sqrt{S_t}=\sqrt{S_0}+c\cdot t$			$ln\ S_t=ln\ S_0+c\cdot t$		
	S_0	c	r	S_0	c	r
1588.5±204.0	14.9089	0.0510	−0.937	17.9125	−0.0470	−0.919
774.7± 84.9	18.4530	0.0478	−0.990	21.0816	−0.0353	−0.976
463.3± 59.0	20.5200	0.0465	−0.990	22.5537	−0.0305	−0.978
242.4± 47.1	20.1287	0.0463	−0.985	12.9990	−0.0304	−0.985

* S_0 c, and r represent initial contents (%) in the stomach, instantaneous rate of gastric evacuation, and regression coefficient (indicator as the relative suitability of the models), respectively.

Table 2. Revised regression formulae for gastric evacuation fitted to each sized group at two different water temperatures using the result of analysis of covariance*

Water temperature (°C)	Mean dry body weigh (mg) of each sized group	$\sqrt{S_t}=\sqrt{S_0}+c\cdot t$	
		S_0	c
16.2–16.8	1729.0	16.2643	−0.0769
	987.7	19.8925	
	569.0	22.3615	
8.7– 9.8	1588.5	14.3050	−0.0479
	744.7	18.4831	
	463.3	20.8411	
	242.4	20.4955	

* Pooled slopes (c) at both water temperature were recalculated because of no significant difference between the slopes of regression formulae for each sized group, and then intercepts (S_0) also performed using the pooled slope. S_t, S_0, and c represent contents (%) remaining in the stomach at time t(h), initial contents (%) in the stomach, and instantaneous rate of gastric evacuation, respectively.

of squares and the sums of products for all groups. The results of recalculation are summarized in Table 2.

Discussion

Before the food consumption and the evacuation rate are investigated, the time required to reach satiation should be assessed. Salmonids have been shown to require up to an hour to reach satiation, for example, *Salmo gairdneri* with a single sized group[11] *Oncorhynchus nerka* with a wide difference in size[9] and *Salmo trutta* with sizes less than 100 g in wet body weight.[12] Assuming an equal and unlimited opportunity to feed, the satiation time in the present study is in approximate agreement with those of other salmonids.

Brett[9] found no relationship between the body weight and satition time. However, in the present study the satiation time increased with increasing fish size as reported by Elliot.[12] The difference in the experimental techniques used may be one of the possible reasons for this apparent fundamental difference in response, namely the consequences of feeding a single food item as opposed to the broadcast feeding of pellets.[13]

It is well known that the logarithm of the food consumption is linearly related to the logarithm of individual weight.[12,14−16] The maximum weight of food consumed in a meal (satiation amount) was

Table 3. Regression formulae for the rate of gastric evacuation as a function of dry body weight (W: mg) and post-prandial time (t: h)*

Water temperature (°C)	$\sqrt{S_{tw}}=a\cdot e^{bw}+c\cdot t$		
	a	b	c
16.2–16.8	5.6525	−0.0002122	−0.0769
8.7– 9.3	4.9473	−0.0002122	−0.0479

* These formulae were derived by substituting $a\cdot e^{bw}(=S_r)$ for S_0 because S_0 (initial stomach contents: %) in square root model ($\sqrt{S_t}=\sqrt{S_0}+c\cdot t$) for gastric evacuation is equivalent to S_r (satiation ratio: %). S_{tw} and c represent contents (%) in the stomach at time $t(h)$ and instantaneous rate of gastric evacuation. a and b are constants.

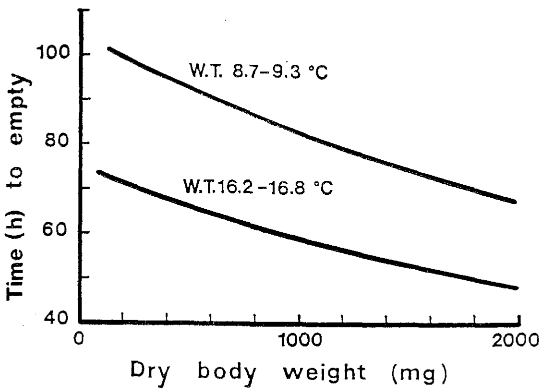

Fig. 5. Relationship between time (h) taken for emptying and dry body weight of juvenile masu salmon at two different water temperatures estimated by using the regression formulae shown in Table 3.

shown to be proportional to $W^{0.75}$ for *Salmo trutta*[12] and *Oncorhynchus nerka*.[9] The weight exponent, 0.72 obtained for juvenile masu salmon is similar to the value of 0.75.

The values of the intercept (S_0) in the equation for the evacuation, summarized in Table 2, estimate the mean satiation ratio (S_r). Using the results of the equation of the satiation ratio relative to dry body weight, it is possible to express the rate of gastric evacuation (S_{tw}) as a function of the individual dry body weight (W: mg) and the post-prandial time (t: h) as shown in Table 3. Then, the time taken for emptying in different sized fish is also easily derived from their equations and the relationship between the gastric emptying time and the body weight is represented in Fig. 5. Kitchell and Windell[17] found that the time taken for emptying of pumpkinseed sunfish *Lepomis gibbosus* was approximately constant regardless of stomach fullness, *i.e.*, the evaculation rate increases in protion to meal size. When fish were fed a given percentage of body weight, it has been shown that as stomach evacuation was faster for the smaller fish, the evacuation time was shorter in the smaller fish.[18–20] On the other hand, in the present study, since the small fish took a larger meal as percentage of body weight than the larger fish, the evacuation time was longer in the smaller fish. This tendency is in agreement with the results for juvenile Atlantic salmon *Salmo salar* with post-prandial starvation.[21] Therefore, it can be concluded that the rate of gastric evacuation in the satiated juvenile fish is constant, independent of fish size.

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