THE EFFECT OF TEMPERATURE ON FOOD EVACUATION RATE IN THE PINFISH (*LAGODON RHOMBOIDES*), SPOT (*LEIOSTOMUS XANTHURUS*) AND SILVERSIDE (*MENIDIA MENIDIA*)

D. S. Peters, M. A. Kjelson and M. T. Boyd
National Marine Fisheries Service
Atlantic Estuarine Fisheries Center
Beaufort, North Carolina 28516

ABSTRACT

Alimentary tract evacuation was studied by the serial slaughter method after a single unrestricted feeding on commercial pelletized food. Digestion rate was measured at 6, 12, 18, 24, and 30 C. At the lower temperatures there was a "latent" period immediately following ingestion during which the content of the stomach or alimentary tract did not decline. After adjustment for the "latent" period and logarithmic conversion of the amount of food present, evacuation rates were described by double logarithmic regressions which showed time for complete evacuation as a function of temperature and amount of food. Evacuation rates were also measured at 25 C for natural food consumed by each species and were similar to the rates using artificial food.

INTRODUCTION

Gastric or gastrointestinal evacuation rates are utilized as indicators of digestion rate and are important in studies of fish production, metabolism and energy flow. An organism's daily ration can be calculated from average contents of the gastric or gastrointestinal tract and a corresponding evacuation rate (Bajkov, 1935). In nature, the daily ration provides information on the material and energy flow between trophic levels and is needed as a feeding guide during laboratory experiments on fish growth and metabolism.

Information on food evacuation rates may also help in standardizing measurements of oxygen utilization. Measuring routine respiration at a constant digestive stage rather than at a constant time after feeding will assure including a constant portion of the increased metabolism associated with feeding and digestion.

In fish, digestion rates tend to increase with temperature even near critically high temperatures (Molnar, Tamassy and Tolg, 1967 and Brett and Higgs, 1970), but specific information is needed for estuarine species. Our goals were to determine the specific digestion rate-temperature relations for some estuarine fishes and to compare the digestion rates of natural and commercial foods.

METHODS

Fish were caught with a seine or trawl, acclimated to desired temperatures and fed commercial food. Silverside (*Menidia menidia*, 2-7 g), pinfish (*Lagodon* rhomboides, 15-40 g), and spot (*Leiostomus xanthurus*, 15-40 g), were caught from waters at 10-18°C. They were acclimated to increased temperature at a rate of $<1°$C per day and to reduced temperature at a rate of $<0.5°$C per day. Fish were held in running sea water at salinities between 25 and 30 ppt and temperatures of 6, 12, 18, 24, and 30°C (±0.5°C). The photoperiod was 12-14 hours daily. The food, Purina Trout Chow[1], was 94 percent ash free and had the following tag analysis: protein $>$ 40 percent, fat $>$ 2.5 percent, and crude fiber $<$ 5.5 percent.

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[1] The mention of trade names in this publication does not imply endorsement by the National Marine Fisheries Service.

Prior to each feeding experiment, we starved the fish to clear their guts. In spot and pinfish at lower temperatures, the clearing time was sometimes underestimated so that traces of food remained in the lower gut when feeding occurred. Some fish did not eat, particularly at low temperatures. Including these nonfeeding fish in the experimental treatment would tend to overestimate the digestive rate. Nonfeeding fish were usually identifiable by empty alimentary tracts, full dark green gall bladders and clear intestinal secretions. As evacuation neared completion it became progressively more difficult to distinguish between nonfeeding fish and those in which evacuation was complete. The nonfeeders when recognized were not included in the analysis.

Using Windell's (1971) serial slaughter method we observed the decrease in alimentary tract contents. In silversides, which have no clearly differentiated stomach, total gastrointestinal content was measured. In spot and pinfish, however, the gastric and intestinal contents could be removed separately and gastric and gastrointestinal evacuation rates were determined separately. Sampling occurred periodically from the time of feeding until more than one-half of the sampled fish had empty guts. Stomach or alimentary tract contents at the first sampling periods indicated the amount of food consumed in a single unrestricted meal. The time intervals between samples decreased as temperature increased and ranged from 1-12 hours. Most samples consisted of four to five fish and the total number used at any temperature was between 20 and 145. Both the fish and ingested food were freeze dried and then weighed. Ashfree content of the food was determined by combustion (24 hours at 500° C).

Evacuation rate of natural food was determined in essentially the same manner as for that of commercial food. The fish were caught in a trawl and immediately enclosed in a food-free environment. They were kept at natural water temperature from time of capture until serial slaughter indicated their guts were empty.

RESULTS AND DISCUSSION

Maximum meal size occurred at 24° C in all three species (Fig. 1). Pinfish did not eat or survive at 6° C and were tested at higher temperatures. They ate readily at 34° C, less readily at 35°, and would not eat at 36°. Pinfish survived only one day at 37° C. Salmon also cease feeding about 2° below their lethal temperature (Brett and Higgs, 1970). Silverside feeding showed the same trend as pinfish and spot *i.e.*, continually decreasing average meal size as temperature deviated from the optimum. A similar appetite pattern occurs in salmon (Brett and Higgs, 1970).

The dependent variable, unevacuated food, was expressed as percent of a fish's dry body weight and was entered in regression analysis as $\log_{10}$ (1 + percent of dry body weight in stomach or alimentary tract). Regressions using untransformed data (Hunt, 1960) were also computed but a logarithmic conversion consistently gave a better fit to the data. This relation implies that evacuation rate changes with time and is a constant proportion of the amount of food remaining. Although digestion may have begun at the time of ingestion, evacuation did not. The lag, up to 12 hours, was particularly evident at low temperatures. When lag, defined as the time to begin passage through the pyloric sphincter or time to reach the mid-point of the alimentary tract, was included in the regressions the degree of fit (R^2) increased. No attempt was made to maximize the fit by using values other than the defined lag or less than one hour. Logistic or other models which incorporate a term for the early slow evacuation might be better, but were not tried.

Quadratic regressions summarized the effects of temperature on evacuation time of various meal sizes. The linear regressions discussed above provided estimates of time for complete evacuation of various meal sizes at the test temperatures. These predicted evacuation times were converted to logarithms and related to the logarithms of the corresponding temperature (Molnar, *et al.*, 1967) by a quadratic time-temperature regression (Brett and Higgs, 1970). For example, in pinfish the times required to evacuate 1 percent of body weight was calculated from linear regressions at 12, 18, 24, and 30° C. These four times were used to calculate one of the curves in Fig. 2b. At low temperatures the fish did not eat as much so some predicted values were obtained by extrapolation from the regression coefficients and time for complete evacuation.

As expected, evacuation rates of all three species (regression coefficients, Table 1) increased with temperature to at least 30°C. The time for complete evacuation depended on both the rate of evacuation and the amount of food in the gut (Fig. 2). At temperatures higher than shown in Fig. 2, pinfish intestinal evacuation rate decreased. Considering the temperature-dependent trends of decreasing appetite (Fig. 1) and increasing evacuation rates (Fig. 2), one would expect the pinfish fed at 34 and 35°C to have empty guts a few hours after feeding. However, several days after their last feeding the fish died with stomachs empty but intestines stuffed full. Apparently near-lethal temperature affects evacuation of the stomach and intestine differently.

Evacuation of natural food was measured in each species at 25°C. The fish had food throughout the gut at the time of capture, therefore no lag term was used in the regression equations (Table 2). The natural foods involved were considerably different from the commercial foods. From our observations, pinfish appear to be omnivores, feeding primarily upon crustaceans and detritus. Spot are detrital feeders and silverside are carnivores dependent upon zooplankton. The commercial food contained 4 percent ash while pinfish, spot, and silverside alimentary tract contents were 58 percent, 52 percent, and 20 percent ash respectively. Although the natural and commercial foods had considerable qualitative differences the evacuation time required for both was approximately the same (Table 2). The minor differences noted in the evacuation rates may be due to: (1) the stress of laboratory conditions, (2) different types or sizes of food, (3) small changes of environmental temperature. The importance of a small temperature change was shown in silverside acclimated and fed at 24°C and then accidentally raised to 26°C. This sudden 2° rise decreased evacuation time by 30 percent, almost as much as a 6° rise in acclimation temperature.

Since evacuation times using commercial food are essentially the same as those with natural food, information on intensity and periodicity of feeding can be used in conjunction with Fig. 2 to estimate daily rations in nature, (Bajkov, 1935). Inherent in Bajkov's method is the assumption that evacuation rate is constant. Brett and Higgs (1970), on the other hand, found that evacuation rate decreases as food content declines. Our data support Brett's position, therefore, we feel that instantaneous evacuation rates which differ at various levels of gut content will produce a more accurate estimate of daily ration.

Using terms as defined in table 1 and $t = X - L$:

$$(1) \quad Y = A + Bt = \log_{10} c$$

where c is 1 plus percent of body weight in the gut

$$(2) \quad c = e2.303(A + Bt)$$

and the instantaneous evacuation rate is

$$(3) \quad \frac{dc}{dt} = 2.303\, B\, e2.303(A + Bt).$$

From evacuation rate studies we obtain $Y = A + Bt$. Then for any gut content observed in a fresh sample, $t=0$, $A = \log_{10} C$ (2) and the instantaneous evacuation rate can be calculated from (3). Using such changing instantaneous evacuation rates to estimate daily ration will result in higher estimates of ration than those obtained assuming a constant evacuation rate.

Table 1. Regression describing evacuation of commercial food in *Lagodon rhomboides, Leiostomus xanthurus*, and *Menidia menidia*. $Y = A + B(X - L)$ where $Y = \log_{10}$ (1 + percent body weight in stomach or alimentary tract), X = hours since feeding and L = hours from ingestion till beginning of evacuation.

Species	Evacuation rate	Temp.	A	B	L
Lagodon rhomboides	Gastrointestinal	12	0.9417	-0.0168	12
		18	0.8719	-0.0216	6
		24	1.0368	-0.0335	2
		30	1.0363	-0.0528	1
	Gastric	12	0.8892	-0.0162	6
		18	0.8638	-0.0271	3
		24	1.0138	-0.0356	1
		30	1.0667	-0.0645	0
Leiostomus xanthurus	Gastrointestinal	6	0.6768	-0.0109	4
		12	0.8277	-0.0266	1.5
		18	0.8958	-0.0267	0
		24	0.9533	-0.0395	0
		30	0.7996	-0.0475	0
	Gastric	6	0.5992	-0.0110	1
		12	0.7823	-0.0311	1
		18	0.8264	-0.0313	0
		24	0.8890	-0.0458	0
		30	0.7306	-0.0553	0
Menidia menidia	Gastrointestinal	6	0.6164	-0.0130	7.5
		12	0.6089	-0.0274	2.5
		18	0.7670	-0.0304	1.0
		24	0.8437	-0.0728	0
		30	0.7093	-0.1024	0

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Table 2. Evacuation of natural food.

	Lagodon rhomboides	*Menidia menidia*	*Leiostomus xanthurus*
Regression equation $Y = \log_{10} (1 + \%$ body weight in gastrointestinal tract$)$ $X =$ hours since capture	$Y=0.388-0.0323X$	$Y=0.312-0.1105X$	$Y=0.557-0.0423X$
Number of fish sampled	59	10	30
Regression estimate of % body weight in gastro-intestinal tract	1.4	1.0	2.6
Estimate of hours for evacuation of natural food	12.0	3.1	13.2
Estimate of hours for evacuation of an equal amount of commercial food (Fig 2 - b, d, and e)	11.0	4.4	13.0

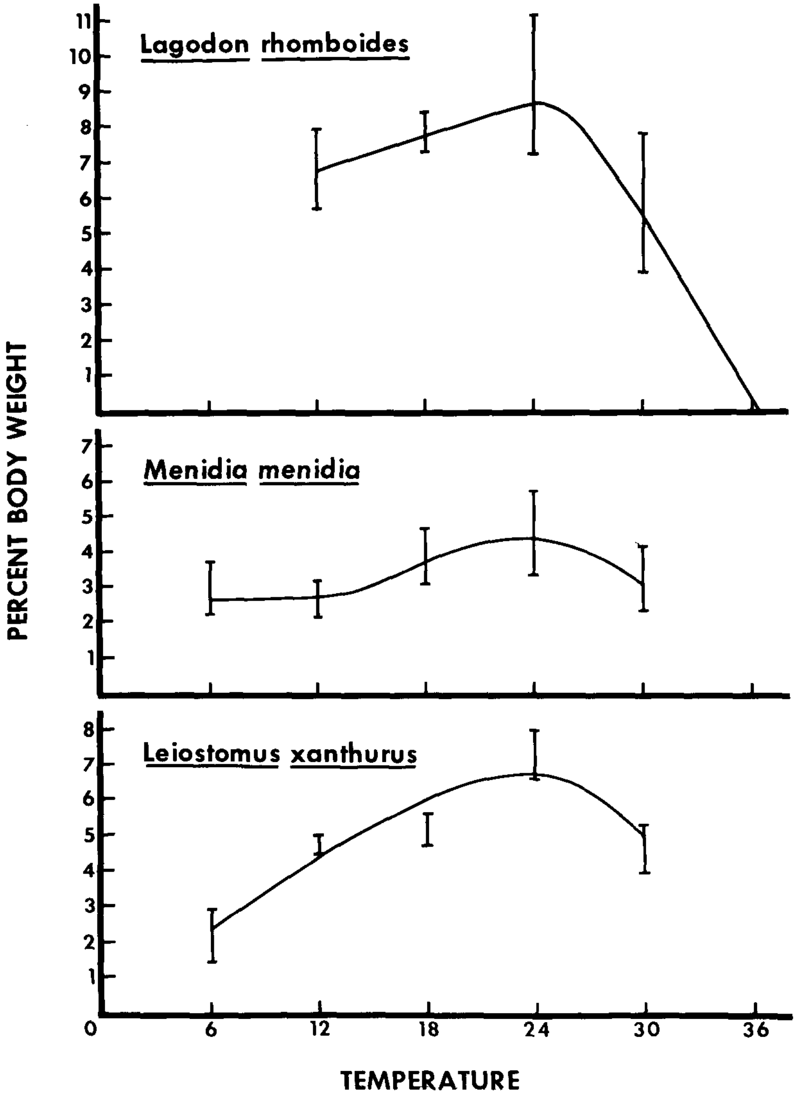

Figure 1. Estimates of food consumed in a single meal at various temperature intervals are geometric mean +one standard error. Curves are fitted by observation.

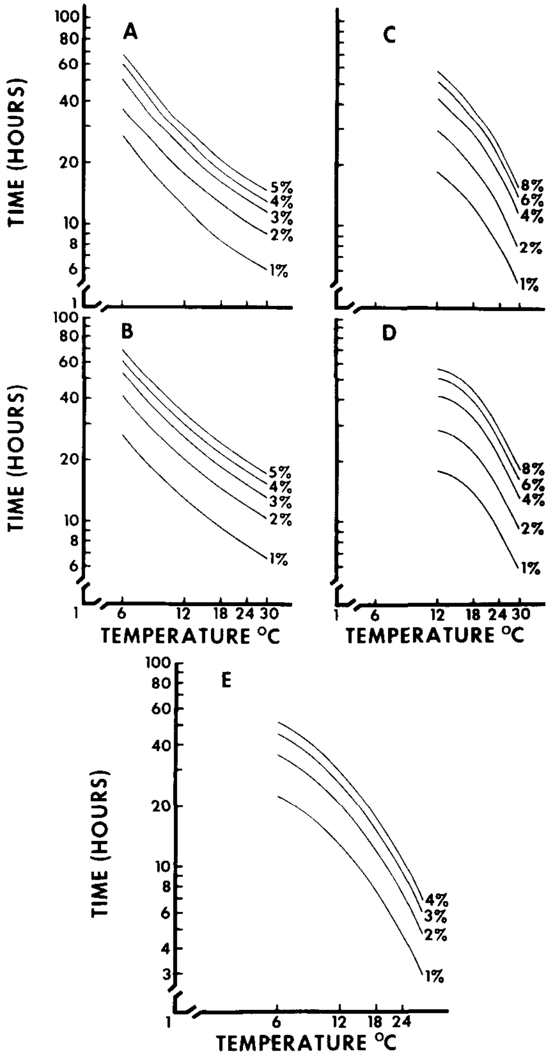

Figure 2. Evacuation time as a function of temperature and meal size (% body wt.). A. *Lagodon* gastric evacuation. B. *Lagodon* gastrointestinal evacuation. c. *Leiostomus* gastric evacuation. D. *Leiostomus* gastrointestinal evacuation. E. Menidia gastronintestinal evacuation.