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RATE OF FOOD DIGESTION BY YELLOW PERCH (PERCA FLAVESCENS) IN RELATION TO SIZE OF PERCH, SIZE AND TYPE OF FOOD, AND TEMPERATURE[1]

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ABSTRACT

Laboratory experiments were performed on the rate of food digestion by yellow perch. Perch were fed single food items of known size, and then sacrificed periodically to determine the amount of food remaining in their stomachs. In an initial experiment, the digestion rate of food which had been inserted forcibly into the esophagus was compared to the digestion rate of food which had been eaten voluntarily. In other experiments, I varied the temperature (7.8, 14.4, 22.2, and 27.2 C), size of perch (9.7, 28.2, 49.1, and 105.8 g), size of food item (0.09 and 1.9% of the weight of the perch), and type of food (fathead minnows and crayfish).

I found that: (1) digestion rate of force-fed food was similar, on the average, to that of food eaten voluntarily; (2) time required for complete evacuation of the stomach was linearily related to temperature on a log-log scale; (3) large perch digested more grams of food per hour than did small perch. However, the amount of time required for evacuation of a meal of the same relative size--2.1% of the weight of the perch--was independent of perch size; (4) a small food item was digested at a slower rate, but in less time, than a large food item; and (5) crayfish were evacuated more slowly than were fish. The yellow perch digested food more rapidly than did the European perch or other species of fish as reported in the literature.

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Introduction

The rate of production in fish, or any other organism, is a complex process determined by the interaction of growth and mortality. Among biologists, growth has received much more attention than has mortality, because it is much easier to study. In the subadult and adult components of natural fish populations in general, and in the yellow perch (*Perca flavescens*) in particular, growth often varies more than does mortality (Ricker, 1958; Schneider, 1971, 1972, 1973a). Consequently, growth affects production to a greater extent.

In order for growth, and thus production, to increase, an increase in the rates of food intake, digestion, absorption, or conversion must take place. Absorption rate is high, 91-98%, for European perch (*Perca fluviatilis*) and for several other species of fish which have been studied (see review by Gerking, 1971). Presumably, absorption rate is high for the yellow perch also. In an earlier paper (1973b) I reported on the rates of food intake and conversion by yellow perch. The digestion rate of perch in relation to temperature, size of perch, size of food, and food type is the subject of the present report.

Methods

Experiments were conducted in the basement of the University of Michigan Museums Annex Building, Ann Arbor, between June 1968 and January 1971. Most of the experimental yellow perch were seined from Sugarloaf Lake, Washtenaw County. After being brought into the laboratory, perch were held in aquaria or large tanks for one or more days to allow some adjustment to their new environment. Few perch would feed readily under these conditions, however, and it was expedient to force feed most of them.

Sufficient time (depending on temperature) was allowed for any food present in the stomach to be evacuated before a digestion experiment was begun. In all tests a single, usually live, food item was used. The food was blotted dry on paper toweling and weighed on a balance accurate to one ten-thousandth of a gram before being offered to a perch. If not eaten voluntarily, the food was force fed by inserting it into the anterior end of the esophagus by means of forceps. Usually the perch would then swallow the food. From 1 to 72 hours later the perch was sacrificed and the food remaining in its stomach was blotted dry and weighed. Digestion rate has been expressed in grams per unit time, and in percent of the initial weight of the food item. Size of food item has been expressed in grams and as a percent of the weight of the perch ("percent meal").

In an initial experiment the digestion rate of 11 perch which has been force fed was compared to the digestion rate of 9 perch which had eaten fathead minnows (Pimephales promelas) voluntarily. Perch weighed 6.2 g, on the average (range 3.6-8.4 g), and minnows averaged 2.3% (range 1.6-4.1%) of the weight of the perch. Temperature averaged 22.2 C.

Digestion rate in relation to perch size was studied next. Examined were 54 perch in 4 size groups: 6-14 g (average 9.7 g), 18-35 g (average 28.2 g), 37-64 g (average 49.1 g), and 87-124 g (average 105.8 g). Fathead minnows, equivalent to 2.1% (range 1.4-2.8%) of the perch weight, served as food. Temperature was 7.8 C.

The effects of food size and type were examined for perch weighing an average of 10.7 g (range 8.3-17.5 g). Five perch were fed a 0.09% (range 0.03-0.19%) meal of small guppies (*Lebistes reticulatus*). Fathead minnows weighing 1.9% (range 1.4-2.5%) of the weight of the perch were fed to 14 perch, and 7 other perch were fed a 1.5% (range 1.2-2.2%) meal of hard-shelled crayfish. Eight additional perch consumed smaller fathead minnows (average 1.1%, range 0.8-1.3%). Mean temperature was 14.4 C.

To determine the effect of temperature on digestion rate, a 2.1% (range 1.4-4.1%) meal of fathead minnows was selected as a standard. The experiments above supplied data for 7.8 C, 14.4 C, and 22.2 C. An additional experiment was performed at 27.2 C with 6 perch averaging 22.8 g (range 20.6-25.6 g). These 6 perch ate voluntarily.

Results

Voluntary vs force feeding

The digestion rate of perch which had been forced to eat minnows did not differ significantly (95% confidence level) from the digestion rate of perch which had eaten minnows voluntarily (Table 1). The digestion rate of the forced-fed perch was more variable, and due to a low value at 8 hours (0.040 g, 33%) and another at 12 hours (0.076 g, 55%), appeared to be slightly lower. If these two extreme values are deleted (as has been done in subsequent analysis), then the digestion rates of forced- and voluntary-fed perch are quite similar. In subsequent experiments as well, the rates of digestion of some forced-fed perch were clearly lower than expected and, consequently, little or no weight was placed on these points when fitting regression lines to the data.

Effect of perch size

In this experiment perch averaging 9.7, 28.2, 49.1, and 105.8 g were fed a meal of fish 2.1% of their body size. I found that larger perch digested more grams of food per unit time than smaller perch (Table 2). The relationship was linear (Fig. 1). When digestion rate was expressed in relative terms (percent of the initial weight of food digested), it was the same for perch of all sizes. That is, a 2.1% meal was about half digested in 24 hours and completely digested in 72 hours by all perch. Consequently, these data were pooled in subsequent discussion of relative digestion rates.

Effects of meal size and food type

Digestion rate varied with both size of food particle and type of food (Fig. 2). A 0.09% meal of fish was more than 90% digested in 2 hours. A 1.9% meal of fish required 20 hours for the same relative amount of digestion. A meal of crayfish of similar size (1.5%) required 32 hours for 90% reduction. Corresponding absolute digestion rates are 0.0051, 0.0087, and 0.0045 g per hour, respectively.

For all three foods, reduction proceeded slowly at first (especially for crayfish), then rapidly after the integument of the food particle had been broken down. The final stages of digestion were especially slow for guppy and crayfish. Note that in fitting a curve by eye to the data for a fish meal of 1.9% I have assumed that a group of points at 16 to 20 hours are underestimates. This assumption was substantiated by: (1) the additional data for meals of 1.1% and (2) the shape of similar data at other temperatures. Forcing the curve through these points would not have changed the estimates of time required for 50 or 100% digestion appreciably.

Effect of temperature

Percent digestion as a function of time and temperature is graphed in Figure 3. The curves for 7.8 C, 22.2 C, and 27.2 C were drawn with the aid of the points (means) shown; the curve for 14.4 C was taken from Figure 2. Estimates of the time required for 50 and 100% digestion were read from Figure 3 and plotted against temperature in Figure 4.

A curvilinear relationship was found between relative digestion rate and temperature. As temperature increased from 8 to 14 C, digestion time decreased very rapidly. Between 14 and 27 C, the relationship was nearly linear with a 1° increase in temperature reducing the digestion time by 1.2 hours.

Discussion

Force feeding has been used often in experiments on the digestion rate of fishes. The obvious advantage of the technique is that an indefinite period of observation is not required because the time of ingestion is known precisely. The disadvantages of the technique are that digestion may be inhibited in certain fish--especially during the first few hours--and, as Windell (1966) observed also, the resultant estimates of digestion rate will be more variable. With adequate replication, however, satisfactory estimates were obtained in my study and in the experiments by Hunt (1960).

Most workers have expressed digestion rate in relative rather than absolute terms. Plots of percent digestion against time have yielded three seemingly different types of curves. Hunt (1960) fitted straight lines to largemouth bass (*Micropterus salmoides*) and warmouth (*Chaenobryttus gulosus*) data. The digestion rate of Florida gar (*Lepisosteus platyrhincus*), on the other hand, declined as digestion neared completion, causing the curve to be convex. This is the type of curve I obtained for yellow perch (Fig. 2) and Windell (1966) reported for bluegill (*Lepomis macrochirus*). A third type of relationship, slightly concave, was obtained for *Megalops cyprinoides* by Pandian (1967a). All three types exhibited an initial period when little reduction occurred. For yellow perch the shape of the relationship appears to be a function of temperature: the regressions changed from convex to near-linear as temperature increased. This was brought about, mainly, by more rapid evacuation during the final stages of digestion. Why this should be true is not apparent.

The relationship between food type and digestion rate has received considerable study yet is not completely clear. In my study, crayfish were digested more slowly than fish in the initial and final phases, and about half as fast overall. Undoubtedly the digestion of crayfish was retarded by their chitinous exoskeletons. Likewise, Pandian (1967b) observed that prawns were digested more slowly than fish, but by only 28%. Earlier, Hess and Rainwater (1939) had reported an inverse correlation between amout of chitin and digestion rate in brook trout (Salvelinus fontinalis) and Seaburg and Moyle (1964) had noted that plants were digested more slowly than animals by bluegill.

Windell (1966), on the other hand, found little difference in the digestion rate of crayfish, oligochaetes, chironomids, mayflies, and darters by bluegills. Dragonfly naiads (with the highest percentage of chitin) took longer to digest but, as Windell pointed out, the results of that experiment were confounded by being conducted at a lower temperature. However, I reexamined his data and found that the effect of lower temperature may have been off-set by smaller meal size--0.6% for dragonflies compared to 0.9-1.7% for the other food organisms. Thus it appears that some difference in digestion rate, albeit small, exists in Windell's data as well.

A better knowledge of the digestion rates of various kinds of foods would be of great practical value. Hess and Rainwater (1939) and Darnell and Meierotto (1962) have already applied information on digestion rate to interpret more precisely the diet of wild fish from the contents of their stomachs. Such knowledge would also be useful for assessing the rate of energy flow through fish in particular, and the aquatic community in general, and for increasing fish production by manipulation of food chains.

Prior to this study on yellow perch, the relationships between size of food, size of fish, and digestion rate have been explored fully only by Pandian (1967a). Several other workers apparently did not control size of fish and food carefully and, consequently, their estimates of digestion rate are of limited value. For perch, I found that a large meal was digested at a faster rate (in terms of weight of food evacuated per hour) and a longer time was required for the stomach to be emptied than for a small meal. The amount of time required for complete digestion was dependent upon the ratio of weight of prey to weight of predator, irregardless of predator size. Supporting evidence for these observations is supplied by Hunt (1960) and Windell (1966) who worked with Florida gar and bluegill, respectively; however, the range in size of these fish was narrow.

Pandian (1967a) obtained slightly different results for Megalops cyprinoides fed a 2% meal of prawns. Rather than being constant, time for complete digestion increased from 6.5 hours to 20.5 hours as fish size increased. However, in terms of grams digested per hour, Megalops showed the same increasing trend as Perca. From Pandian's data I have calculated digestion rates of 15, 33, 59, and 88 mg per hour for Megalops averaging 5.12, 21.15, 51.3, and 90.6 g, respectively. Thus the absolute digestion rate (grams per hour) of both species increased with body size, but Perca increased more rapidly with the result that relative digestion rate (percent) remained constant.

The effect of temperature on the digestion rate of fishes had been investigated previously by Molnár, et al. (1967). They used x-ray equipment to follow the breakdown of force-fed fish in the stomachs of the European perch, pike-perch (L. lucioperca), sheatfish (Silurus glanis) and largemouth bass. They reported that time for complete digestion decreased linearly on a log-log scale as temperature increased. Their data for Perca fluviatilis and mine for Perca flavescens have been plotted in Figure 5. A straight line fits both sets of data reasonably well, except one point (a mean) for P. fluviatilis at 15 C deviates from the line by 25%.

The two regressions differ in both placement and slope--the di gestion rate for P. flavescens being much more rapid at higher temperatures and slightly slower at lower temperatures. The discrepency could be due in part or whole to the size of the meal, or other factors which were not controlled in the experiments. Molnár, et al. did not report the size of the meal or if it was the same for all temperatures, whereas the data for P. flavescens are based on a 2% meal. On the other hand, perhaps the European and American perch do differ to this degree. Differences were reported between the species studies by Molnár, et al., and Hunt (1960) found differences between largemouth bass, warmouth, and Florida gar. The digestion rate of Perca flavescens appears to be more rapid than any of these species and faster than pumpkinseed (Lepomis gibbosus), black crappie (Pomoxis nigromaculatus), or bluegill (Seaburg and Moyle, 1964; Windell, 1967).

Table 1. Average amount of fish in grams and percent (± standard error) digested in 4. 8 and 12 hours at 22. 2 C by forced- and voluntary-fed perch. [N = sample size]

Hours	Voluntary			Forced		
	N	Grams	Percent	N	Grams	Percent
4	3	0.059 ± 0.001	53 ± 7	3	0.045 ± 0.004	38 ± 3
8	3	0.105 ± 0.003	74 ± 5	4	0.090 ± 0.018	65 ± 11
12	3	0.139 ± 0.017	100 ± 0	4	0.126 ± 0.020	80 ± 10

Table 2. Average amount of fish in grams and percent (± standard error) digested in 8, 24, 48, and 72 hours at 7.8 C by perch averaging 9.7, 28.2, 49.1, and 105.8 grams.

Perch used in tests		Hours	Amount of fish digested	
Size, in grams	Number		Grams	Percent
9.7	3	8	0.024 ± 0.006	14 ± 4
	3	24	0.102 ± 0.005	55 ± 3
	4	48	0.162 ± 0.009	86 ± 8
	3	72	0.181 ± 0.008	98 ± 2
28.2	4	8	0.065 ± 0.022	12 ± 4
	4	24	0.232 ± 0.029	49 ± 7
	4	48	0.600 ± 0.048	92 ± 5
	2	72	0.507 ± 0.021	100 ± 0
49.1	3	8	0.212 ± 0.033	19 ± 2
	2	24	0.482 ± 0.030	50 ± 2
	8	48	0.998 ± 0.068	91 ± 4
	4	72	0.862 ± 0.058	93 ± 7
105.8	0	8	-- --	-- --
	2	24	0.968 ± 0.092	48 ± 2
	2	48	2.071 ± 0.340	76 ± 7
	2	72	2.301 ± 0.221	100 ± 0

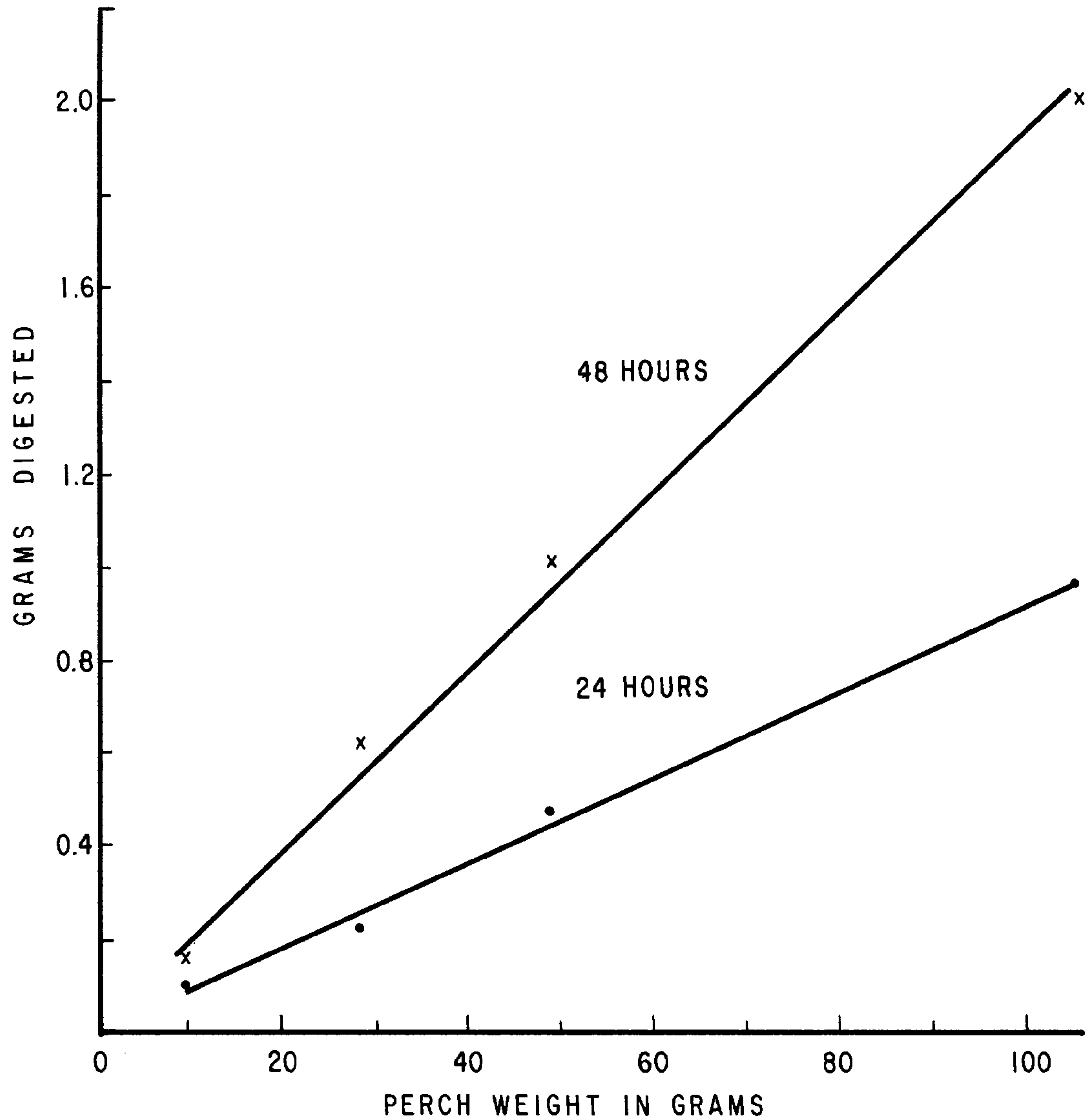

Figure 1. Grams of fish digested by yellow perch in 24 and 48 hours at 7.8 C as a function of perch weight.

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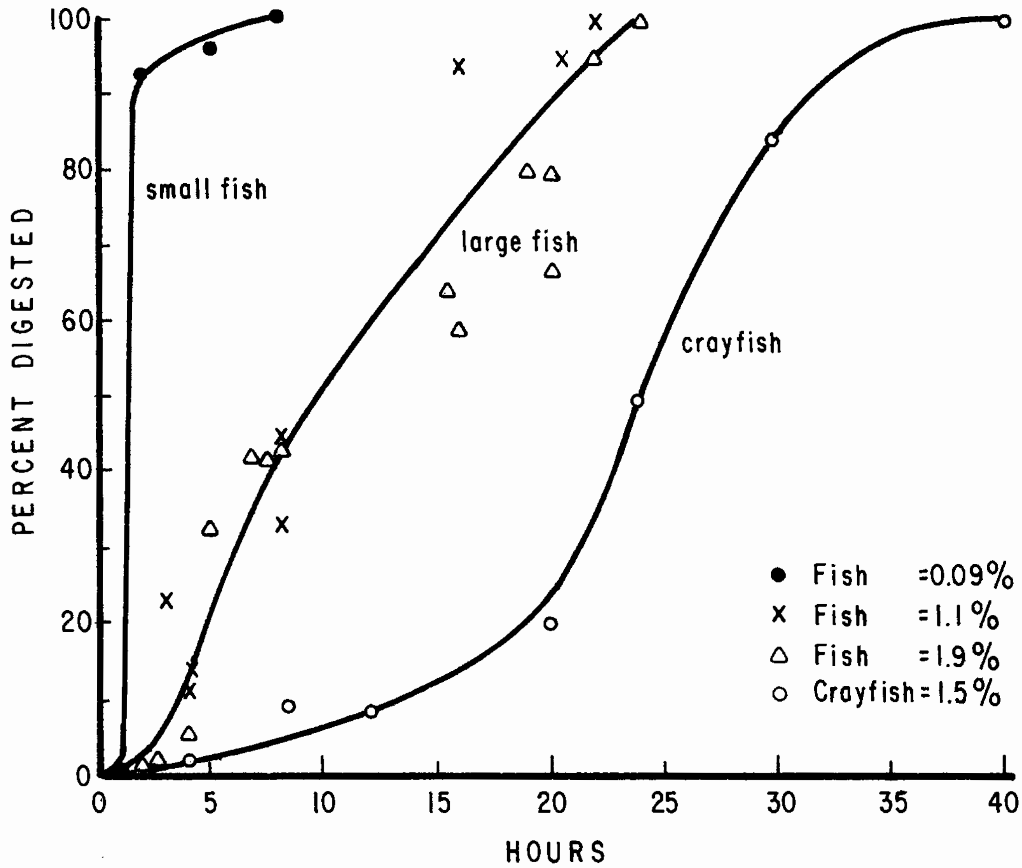

Figure 2. Relative digestion rate (percent) as a function of meal size (prey fish = 0.1%, 1.1%, and 1.9% of the perch weight) and food type (fish compared to crayfish) at 14.4 C.

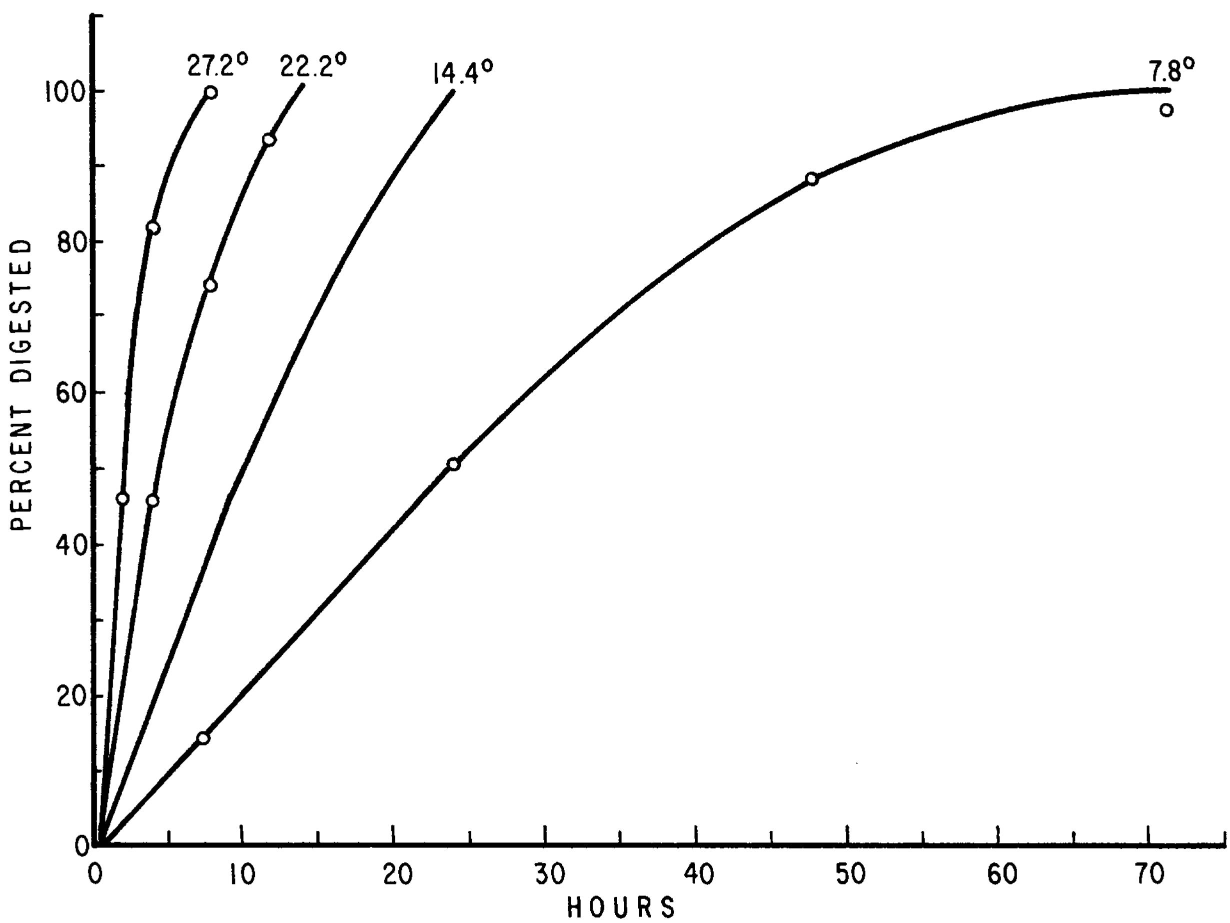

Figure 3. Relative digestion rate (percent) of a 2.1% meal of fish at 7.8, 14.4, 22.2, and 27.2 C. Three of the curves are based on means; the fourth curve (for 14.4 C) is copied from Figure 2 (large fish).

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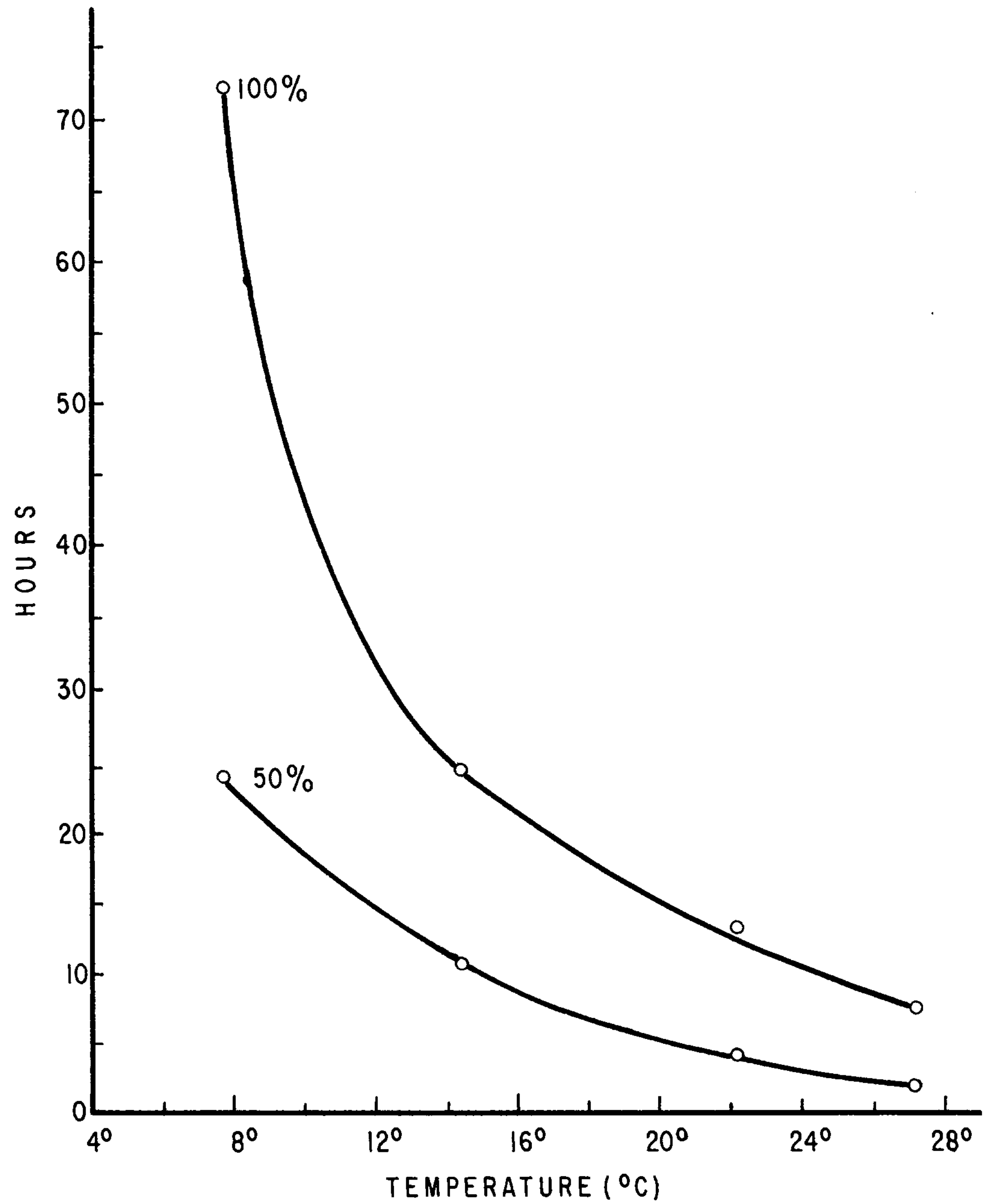

Figure 4. Time required for 50% and 100% digestion of a 2.1% meal of fish as a function of temperature.

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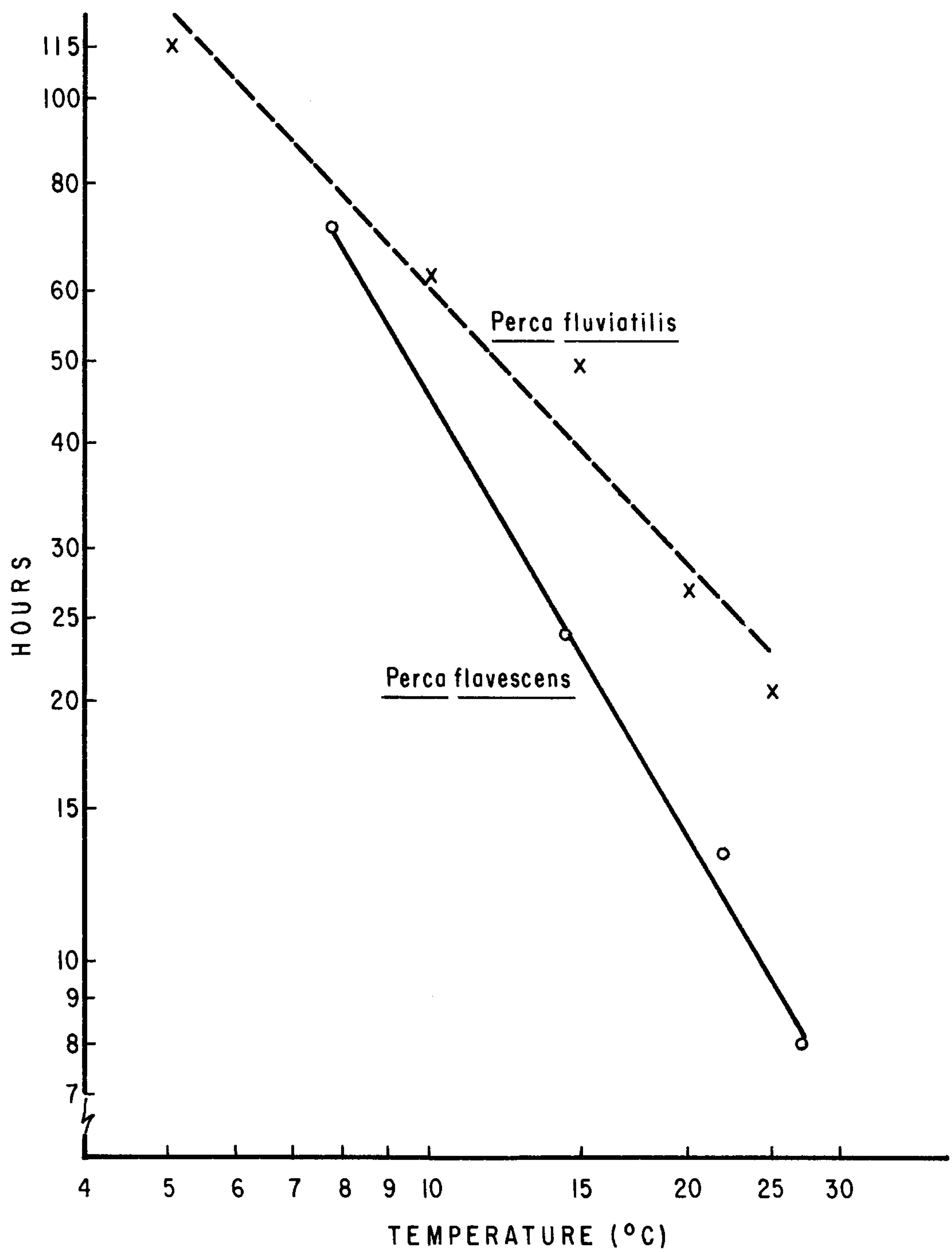

Figure 5. Time required for 100% digestion by Perca flavescens (this study) and Perca fluviatilis (Molnár, et al., 1967), as a function of temperature. Plotted on log-log scale. -145

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