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Food consumption of the three-spined stickleback (Gasterosteus aculeatus L.)

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The daily food consumption of the three-spined stickleback at different temperatures was calculated from determinations of the rate of digestion. The rate of digestion in fish which had taken food in the sea before being caught was compared with that of fish fed in the laboratory either with *Daphnia* or with plankton collected from the sea. Owing to seasonal differences in the food available in nature, determination of the digestion rate in fish that had taken food under natural conditions was found to give a better estimate of the actual food consumption of the three-spined stickleback than feeding experiments. In fish averaging 1.0 g fr.wt. the daily food consumption so calculated was 24.2±7.8 mg (2.4 % of the body fr.wt.) at 10 °C, 48,3±16.3 mg (4.8 %) at 14 °C, and 132.8±28.8 mg (13.3 %) at 18 °C. In fish averaging 1.6 g the respective rates were 100.2±39.7 mg (6.2 %), 186.2±50.4 mg (11.6 %) and 271.2±50.4 mg (16.9 %).

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1. Introduction

Determination of the digestion rate is a practical way to estimate the food consumption of fish (Hunt 1960, Magnuson 1969, Tyler 1970, Davis & Warren 1971, Swenson & Smith 1973, Windell 1978). But results obtained in the laboratory, where the fish have often received unnatural food, are difficult to apply to natural conditions, although they may be applicable to hatchery problems. The feeding ecology of the species should be taken into account when estimating food consumption.

Bajkov (1935) suggested that the rate of digestion should be measured in fish that have fed before being caught. This method avoids errors caused by feeding.

In the present study the daily food consumption of the three-spined stickleback (*Gasterosteus aculeatus* L.) was measured both in fish fed in the laboratory and in those which had fed under natural conditions.

2. Material and methods

The fish were collected with a bag seine from brackish water (S 6 $^{0}/_{00}$) in the archipelago of SW Finland. They were measured from the tip of the snout to the base of the tail, weighed to the nearest 10 mg, and divided into two size classes: 35—45 mm (fresh weight 1.00±0.01 g) and 45—55 mm (1.60±0.03 g). The experiments were started in early June and continued until autumn at different temperatures.

In each experiment, a group of 40—50 recently caught fish of equal size was used. The contents of the alimentary canals of about 10 fish were weighed to the nearest 0.1 mg and the others were put into an aquarium. The temperature was kept the same as in the sea at the time the fish were caught. After 2, 4 and 8 h the contents of the alimentary canals of about 10 fish kept without food were weighed in the same way. The average rate of digestion (%/h) was determined from the data. All the experiments were started at 08.00 — 09.00 hours, when, according to the observations made, the stomachs of the fish were full.

For comparison, the digestion rate was determined from feeding experiments in the laboratory. Before an experiment the fish were kept in the aquarium without food for 2—3 days to become acclimated. They were then fed for 1/2 — 1 h with *Daphnia* (group 1) or with plankton collected from the sea (group 2). The plankton consisted of diatoms (*Melosira* spp., *Chaetoceros* spp., *Thalassiosira* spp.), rotifers (*Synchaeta* spp.), cladocerans and copepods. When feeding was no longer active, the fish were transferred to another aquarium in which no food was available. The contents of the alimentary canals of about 10 fish were weighed immediately after feeding and the remaining fish were taken in batches of 10 after, 2, 4 and 8 h as before. The average rate of digestion was expressed as a percentage.

The daily food consumption was calculated from the data for digestion rates. Food consumption was estimated

Table 1. The rate of digestion, the contents of the alimentary canal in the beginning of the experiment and the daily food consumption at different temperatures (means with standard errors). A = fish which had taken food in the sea. B = fish fed with *Daphnia* in the laboratory. C = fish fed with plankton in the laboratory. *n* = number of fish measured at 0, 2, 4 and 8 h after beginning of the experiment.

°C	Size of fish (mm)	Contents of alim. canal *n*	(fresh weight, mg)	Digestion rate (%/h)	Daily food consumption Fresh weight (mg)	Mean % of body fresh weight
A 10	40.7±0.4	10, 10, 10, 10	20.2±3.1	5.0±1.6	24.2±7.8	2.4
	51.7±0.5	12, 11, 12, 12	78.9±8.3	5.3±2.1	100.2±39.7	6.2
14	42.0±0.3	16, 16, 14, 15	25.2±3.6	8.0±2.7	48.3±16.3	4.8
	50.8±0.3	13, 11, 6, 12	68.7±9.0	11.3±3.0	186.2±50.4	11.6
16	43.1±0.3	10, 7, 7, 9	35.4±3.8	11.8±2.5	100.2±21.6	10.0
18	43.0±0.3	16, 14, 14, 14	37.4±5.9	14.8±3.2	132.8±28.8	13.3
	51.7±0.5	4, 4, 4, 5	74.3±9.7	15.2±2.8	271.2±50.4	16.9
B 10	39.4±0.5	6, 6, 6, 6	23.3±2.1	7.8±2.5	43.6±14.0	4.4
	50.3±0.7	5, 5, 5, 6	60.3±14.8	9.2±3.2	133.3±46.6	8.3
14	39.9±0.2	8, 7, 7, 8	15.8±1.5	13.0±3.1	49.3±11.8	4.9
	55.1±0.6	7, 6, 7, 7	97.4±11.4	13.3±2.0	310.7±46.7	19.4
18	40.9±0.2	10, 10, 10, 10	21.8±1.7	12.6±1.3	65.8±7.0	6.6
	54.0±0.5	7, 6, 6, 6	76.1±8.7	14.3±3.9	261.0±72.0	16.3
C 10	42.4±0.3	10, 10, 10, 9	17.9±2.9	4.0±1.7	17.2±7.3	1.7
18	43.1±0.4	10, 7, 7, 8	15.5±1.7	7.4±2.5	27.6±9.4	2.8

to be equal to the average rate of digestion (Davis & Warren 1971). The contents of the alimentary canals of 34 fish were weighed and dried to constant weight at 60 °C. The dry weight so obtained was 24 % of the fresh weight.

3. Results

3.1. Rate of digestion

The average digestion rates at different temperatures are shown in Table 1.

Figure 1 shows the digestion of food and the emptying of the gut during the 8-h period in the fish fed with *Daphnia* and in those which had taken food in nature. Emptying is expressed as a percentage of the fresh weight of the initial gut contents at the start of the experiment. At 10 and 14 °C the fish fed with *Daphnia* in general digested their food faster than those that had fed in natural conditions. This was true of both size classes.

At 10 °C emptying of the gut was equal in the fish that had taken food in the sea and in those fed with plankton in the laboratory; in the fish fed with *Daphnia* emptying was faster. At 18 °C, in contrast, emptying of the gut was clearly slower in the fish fed with plankton than in the other two groups (Fig. 1).

3.2. Food consumption

The average contents of the alimentary canal at the beginning of the experiment, the daily food consumption calculated from these, and the data for the rate of digestion are shown in Table 1. The consumption curve for the 45—55 mm fish that fed in the sea rises steadily with increasing temperature, but for those fed with *Daphnia* it was higher at 14 °C than at 18 °C (Fig. 2).

4. Discussion

The digestion rate of the nine-spined stickleback (*Pungitius pungitius*) is truly comparable with that of the three-spined stickleback, because the species are closely related and resemble each other in their living habits, and probably in their metabolism as well. For nine-spined stickleback 30 mm in length fed with *Daphnia* at 15 °C, Cameron et al. (1973) give a digestion rate of 13.4 %/h, and the value found here for the three-spined stickleback 40 mm long at 14 °C is 13.0±3.1 %/h.

In fish fed with *Daphnia* and those fed under natural conditions the digestion rates were clearly different. At 10 and 14 °C digestion was faster when the fish had been fed with *Daphnia*, but at 18 °C it was as fast or even faster in the fish that had fed in their natural habitat.

In summer the food of the three-spined stickleback consists of various littoral organisms. The most important groups in the study area are *Corophium volutator, Nereis diversicolor, Gammarus* spp., chironomids and plankton. But in late spring and early summer especially, the food contains large numbers of diatoms (Mankki 1974). In non-herbivorous species plant cellulose retards digestion. This is assumed to be due to the production of digestive enzymes to suit the composition of the diet. Carbohydrases are

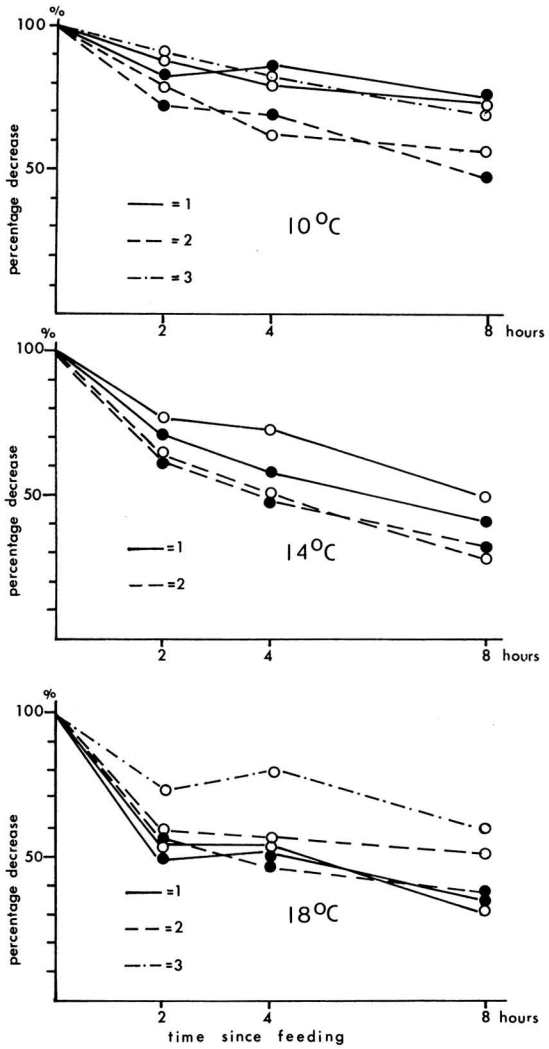

Fig. 1. The digestion of food at different temperatures. Percentage decrease in weight is given. ∅ = 35—45 mm, • = 45—55 mm. 1 = fish which had taken food in the sea. 2 = fish fed with *Daphnia* in the laboratory. 3 = fish fed with plankton in the laboratory.

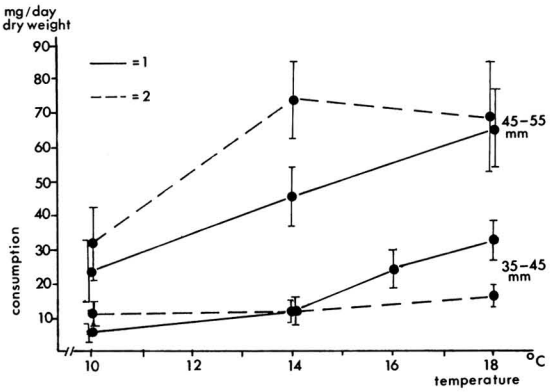

Fig. 2. The daily food consumption of the three-spined stickleback at different temperatures. (means with standard errors). 1 = Fish which have taken food in the sea. 2 = fish fed with *Daphnia* in the laboratory.

secreted more copiously in herbivores, whereas proteases are quantitatively more important in carnivores (Kapoor et al. 1975). The three-spined stickleback is not a pure herbivore and the algae in its food may retard the rate of digestion. Hence, if food consumption is calculated from the digestion rate as determined from feeding experiments with purely animal food, the values obtained for the energy requirement of the species will be too high. In early summer the digestion rate was lower (7.4±2.5 %/h) in fish acclimated at 18 °C and fed with plankton from the sea than in fish fed with *Daphnia* (12.6±1.3 %/h) or those fed in the sea (14.8±3.2 %/h) at the same temperature. The reason for this is that when the water tempterature rises to 18 °C later in summer, the plankton contains few algae and the food consists only of animals. Thus seasonal changes in the quality of the food have to be taken into account when the food consumption of a species is determined from its digestion rate.

The amount consumed depends on the feeding activity of the fish, as well as on the digestion rates. In feeding experiments the difficulty often lies in how to induce the fish to feed voluntarily and in a natural way in captivity. Among the fish of the 35—45 mm size class, the stomach contents were clearly smaller in the group fed with *Daphnia* than in those which had taken food in the sea at 18 °C, which accounts for the very slight rise in the curve for food consumption. In the same way the fish fed with plankton had low consumption rates because their stomach contents were small; in addition their digestion rates were slow because of the algae given in the food.

In the 45—55 mm size- class the values of the stomach contents were higher at 14 °C than at other temperatures, and between 14 and 18 °C the slope of the consumption curve was descending instead of ascending (Fig. 2). Fish with empty stomachs take food very greedily and their feeding activity diminishes only if food is available continuously (Hotta & Nakashima 1969). Thus fasting before determination of the digestion rate affects the feeding behaviour of the fish and they may take more food than normally.

Krokhin (1957) determined the food consumption of the three-spined stickleback by the respiration method. The daily food consumption of an adult fish at 14 °C was estimated as 0.23 g and at 11 °C as 0.17 g. In the present study the daily food consumption of a fish of 1.6 g at 14 °C was 0.19±0.05 g and at 10 °C 0.10±0.04 g, so the results are very similar in spite of the different methods used.

Determination of the digestion rate from fish which have fed in the sea proved to be a practicable method for estimating the food consumption of the three-spined stickleback. It is easier to determine the digestion rate when there is no need to feed the fish, and at the same time feeding is regulated by all the factors that operate in the environment at a certain time and the food is the natural food of the species.

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