

Rate of gastric digestion in the larvicultural fishes *Aplocheilus lineatus* (Cuv. & Val.) and *Macropodus cupanus* (Cuv. & Val.)

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Abstract. In the larvicultural fishes *Aplocheilus lineatus* and *Macropodus cupanus* investigations on the rate of gastric digestion reveal that interspecific variations are apparent ; however, within the species, digestion rate is not significantly altered by fish size provided the amount of food supplied is sufficient to fill the stomach. Gastric depletion is directly related to temperature, increasing temperature elevating the rate of digestion.

Keywords. Gastric digestion ; larvicultural fishes ; *Aplocheilus lineatus* ; *Macropodus cupanus*.

1. Introduction

The rapid development of insecticidal resistance to pesticides, coupled with a growing concern about environmental pollution has revived an interest in other pest control methods, notably naturalistic ones. In so far as mosquito larvae are concerned, although larvivorous fishes such as *Gambusia affinis* and *Poecilia reticulata* have been utilised in mosquito abatement programmes (Mallars and Fowler 1970; Bay and Self 1972), their indiscriminate releases have led to an alteration of the ecological status quo by their monopolization of the biomass of certain aquatic habitats (Miller 1961; Myers 1965; Hubbs 1972; Bay 1973). This has renewed an interest in the biocontrol potential of indigenous fishes such as *Aplocheilus lineatus* and *Macropodus cupanus*.

The elucidation of the predatory capacity of these fishes necessitates an assessment of their rates of digestion, since these data are essential in the delineation of the relation between feeding motivation and appetite (Miner 1955). Further such data permit an assessment of the rates of energy passage within aquatic food web pathways and the underlying relations controlling growth (Tyler 1970; Molnár *et al* 1967; Fänge and Grove 1979), feeding activity and quantity of food in the stomach (Magnuson 1969), food consumption (Kitchell and Windell 1968; Swenson and Smith 1973) at different temperatures (Elliott 1975a, b; Brett and Higgs 1970), periodicities and feeding frequencies (Swenson and Smith 1973;

Windell 1976), daily rations (Ricker 1946), ration size for fish cultural practices (Brett and Higgs 1970; Elliott 1975c, d) and conversion efficiency (Pandian 1967a, b). Thus, the evaluation of the effects of predation on prey species made possible by this method, renders it an useful tool for a variety of ecological studies (Swenson and Smith 1973).

The rate of digestion for fish is the rate at which food passes from the stomach and digestion is considered complete when the stomach becomes empty of all measurable remains (Windell 1978). The passage of chyme from the stomach to the intestine is dependent on the rate of digestion and hence, depletion rate of food from the stomach/gastric evacuation parallels digestion rate (Tyler 1970). In the present investigation, therefore, the terms gastric digestion, gastric evacuation and gastric depletion are used synonymously, as in Windell (1978).

Available current evidence indicates that among the factors affecting gastric removal rates, none is more potent than ambient water temperature (Windell *et al* 1976); another factor the relevance of which is controversial is the effect of size of the fishes on gastric depletion and thus on the transformation of food by fishes. Hence in the present investigation, keeping other chemical, physical and biological factors (including meal size, meal succession, food digestibility and food particle size) which could significantly influence gastric evacuation rates (Windell *et al* 1976), constant, an assessment of the effects of water temperature of the medium and size of the fishes on the rate of gastric digestion of fishes has been attempted.

2. Materials and methods

Although numerous methods are in vogue for determining the rate of gastric digestion (Fänge and Grove 1979), as recommended by Windell (1968), the serial slaughter method was chosen as the most direct approach, and the wet weight determination of the stomach contents as the simplest, since the food material factor was kept constant.

Healthy specimens of *A. lineatus* and *M. cupanus* collected from the field were divided into different size groups [1500 ± 200 mg (large), 550 ± 100 mg (medium) and 320 ± 50 mg (small) in the case of *A. lineatus* and 1300 ± 200 mg (large), 550 ± 100 mg (medium) and 300 ± 50 mg (small) in the case of *M. cupanus*] and acclimated to laboratory conditions in aquaria containing well water at a temperature of $27.5 \pm 0.5^\circ\text{C}$, pH of 7.1, salinity of 0.012% and oxygen at near air saturation. However, to explore the influence of temperature on the rate of gastric digestion, the medium-sized specimens of both fishes were further divided into two groups and acclimated to temperatures of $22.5 \pm 0.5^\circ\text{C}$ and $32.5 \pm 0.5^\circ\text{C}$ (in addition to $27.5 \pm 0.5^\circ\text{C}$); all other factors were kept constant. The acclimation period in all groups was an uniform 14 days; during this time the fishes were conditioned to voluntarily consuming an experimental meal of 4th instar *Culex* larvae (reared in the laboratory) by feeding to satiation once daily, after which the excess food was removed. The experimental meal size to be provided during the tests was thus decided by these preliminary observations on the quantity of food required to satisfy voluntary feeding on a once-daily regime basis.

Following the acclimation period, prior to the experiment, a pre-experimental fasting period of 72 hr was initiated to ensure the complete absence of food in the alimentary canal. The experimental fishes were then individually fed the pre-determined measured meal (of 100, 50 and 30 mg in the case of the large, medium and small-sized fishes, respectively). At appropriate time intervals the fishes were sacrificed and the weight of food remaining in the stomach of each was determined, taking care to prevent regurgitation and loss of stomach contents. This serial slaughter was continued until digestion was complete, i.e. the stomach was empty.

3. Results and discussion

Data pertaining to the depletion of food material and the rate of digestion of the different size groups of *A. lineatus* and *M. cupanus* are presented in figures 1 and 2. The results show a curvilinear relationship in all cases; the graphs have, therefore, been drawn utilising the curvilinear relationship $y = ax^b$, where x is the period in hr, y the percentage of food digested and a and b are constants. The rate of digestion is highest in the initial period following consumption, being 59.5%, on an average, at the end of 2 hr in the different size groups of *A. lineatus* and 72.86%, on an average, at the end of 4 hr in the various sizes of *M. cupanus*. The rate of digestion, however, subsequently decreases with increase in time, being 83.3%, 98.83% and 95.4% at the end of 4, 6 and 8 hr after feeding in *A. lineatus*; in *M. cupanus* it is 84.23% and 93.33% at the end of 8 and 12 hr,

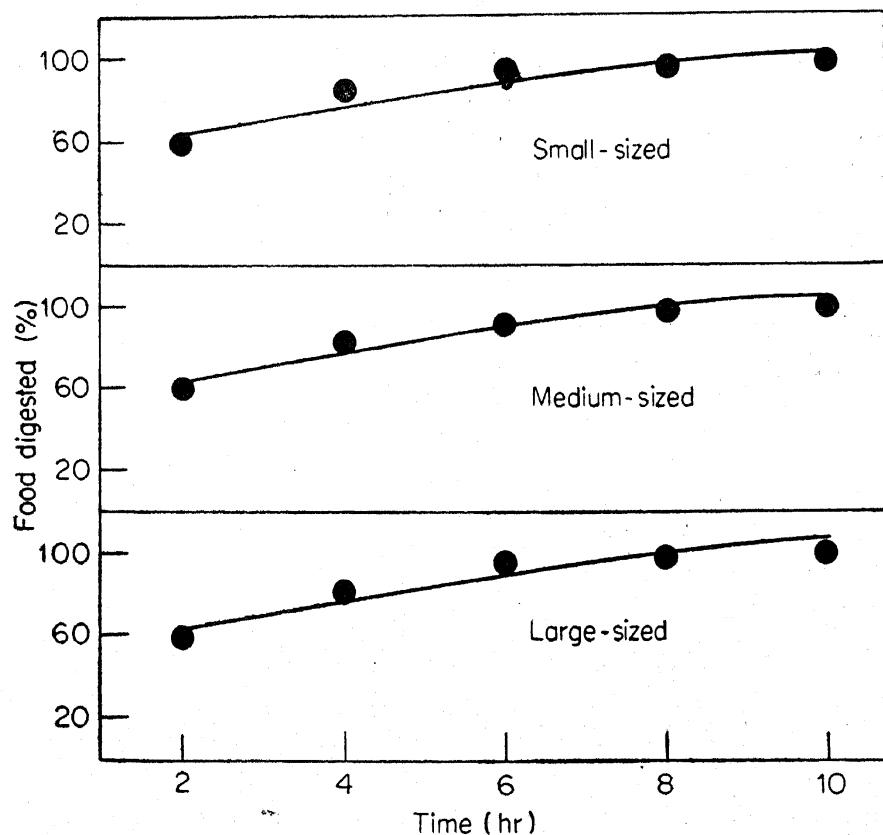


Figure 1. Time course of rate of gastric digestion in different sizes of *A. lineatus*.

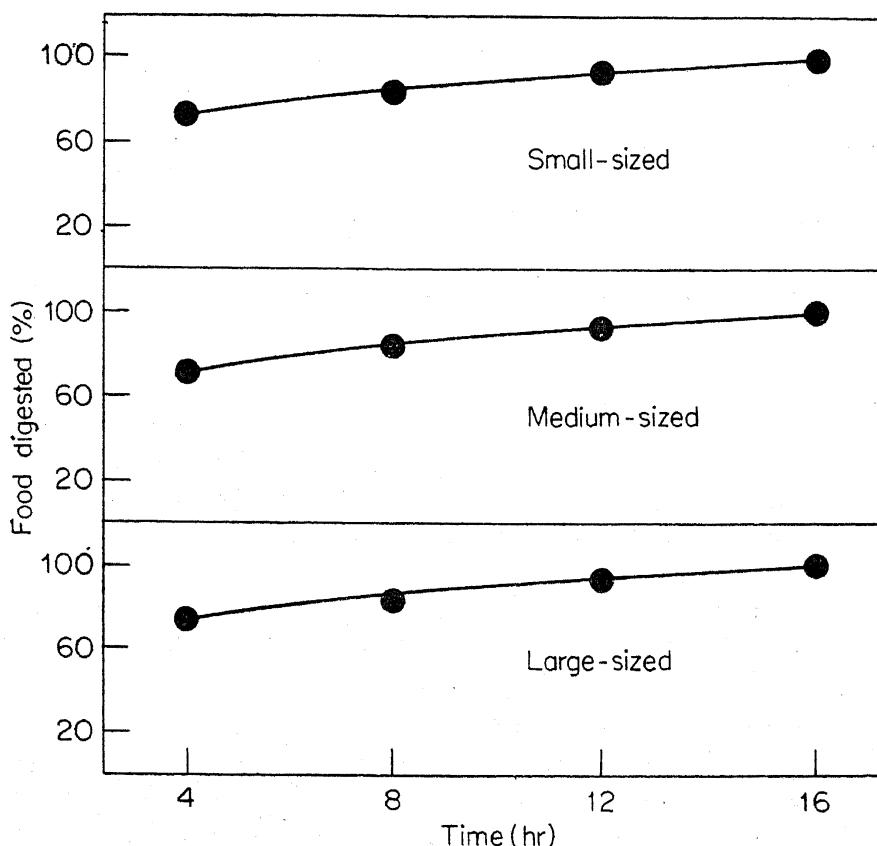


Figure 2. Time course of rate of gastric digestion in different sizes of *M. cupanus*.

respectively, after feeding. 100% evacuation of food from the stomach occurs in 10 hr in the case of *A. lineatus* (at $27.5 \pm 0.5^\circ\text{C}$) and in 16 hr in *M. cupanus* (at the same temperature), regardless of the size of the fish, provided a meal sufficient to satiate the fish was supplied.

The equations obtained in each case are as follows:

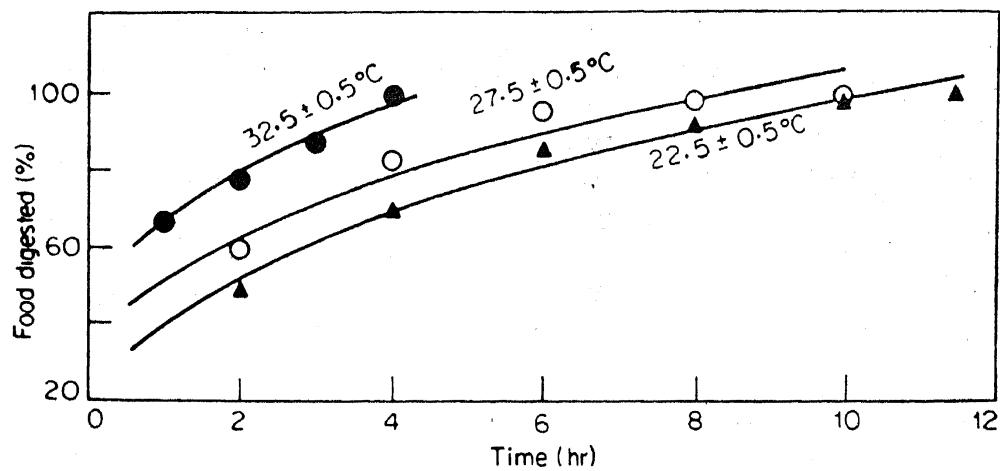
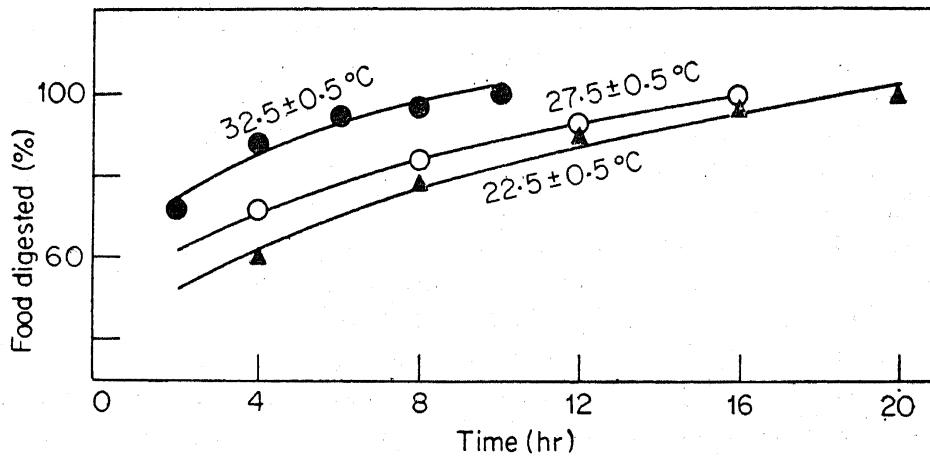
A. lineatus

$$\begin{aligned} \text{Small-sized group} &: y = 50.55 \cdot x^{0.3235} \\ \text{Medium-sized group} &: y = 50.00 \cdot x^{0.3279} \\ \text{Large-sized group} &: y = 48.99 \cdot x^{0.3376} \end{aligned}$$

M. cupanus

$$\begin{aligned} \text{Small-sized group} &: y = 52.64 \cdot x^{0.2302} \\ \text{Medium-sized group} &: y = 51.76 \cdot x^{0.2368} \\ \text{Large-sized group} &: y = 54.13 \cdot x^{0.2191} \end{aligned}$$

The effect of temperature on the rate of gastric digestion is given in figures 3 and 4. Here too, the rate of depletion is highest in the initial period, being 77.6%, 59.6% and 49.4% at the end of 2 hr in *A. lineatus* at $32.5 \pm 0.5^\circ\text{C}$, $27.5 \pm 0.5^\circ\text{C}$ and $22.5 \pm 0.5^\circ\text{C}$, respectively. In *M. cupanus* at the same temperatures it is 88.0%, 72.0% and 60.4% at the end of the initial 4 hr period. Although digestion decreases with increase in time, generally speaking, lower temperatures considerably slow down the rate of gastric digestion while higher temperature

Figure 3. Time course of rate of digestion at different temperatures in *A. lineatus*.Figure 4. Time course of rate of digestion at different temperatures in *M. cupanus*.

hasten it. Interspecific variability was noted for both temperature and size group effects in the two species studied. The completion of digestion occurred within 4 hr at $32.5 \pm 0.5^\circ\text{C}$ and in 12 hr at $22.5 \pm 0.5^\circ\text{C}$ in *A. lineatus* as opposed to the 10 hr period necessary for gastric evacuation at $27.5 \pm 0.5^\circ\text{C}$. In *M. cupanus* gastric digestion took 10 hr at $32.5 \pm 0.5^\circ\text{C}$ and 20 hr at $22.5 \pm 0.5^\circ\text{C}$ as against the 16 hr required for digestion at $27.5 \pm 0.5^\circ\text{C}$.

The equations obtained in each case are as follows:

A. lineatus

$$\text{At } 32.5 \pm 0.5^\circ\text{C} : y = 65.79 \cdot x^{0.2813}$$

$$\text{At } 27.5 \pm 0.5^\circ\text{C} : y = 50.00 \cdot x^{0.3279}$$

$$\text{At } 22.5 \pm 0.5^\circ\text{C} : y = 39.26 \cdot x^{0.4009}$$

M. cupanus

$$\text{At } 32.5 \pm 0.5^\circ\text{C} : y = 64.21 \cdot x^{0.2031}$$

$$\text{At } 27.5 \pm 0.5^\circ\text{C} : y = 51.76 \cdot x^{0.2368}$$

$$\text{At } 22.5 \pm 0.5^\circ\text{C} : y = 39.64 \cdot x^{0.3184}$$

Slight variations in water temperature, previous thermal history of the fish, size of the experimental animals, size of the experimental meal in relation to volume, weight and fullness of the stomach, and type of quality of food items consumed afford interpretive complications (Windell 1976) in addition to those arising from variations in techniques and methodology used to gather data; method of feeding (i.e., individual/group, voluntary/forced) may induce handling effects, and length of the fasting/food deprivation period may affect digestion rate (Windell 1967; Ishiwata 1969; Tyler 1970; Brett 1971; Jones 1974; Sarokon 1975). Thus, comparison of much of the available data is hindered.

3.1. Pattern of gastric digestion

The pattern of gastric depletion both in *A. lineatus* and *M. cupanus* was as follows: immediately on consumption, digestion commenced and 72% and 83% of the food material was digested in *M. cupanus* and *A. lineatus* respectively within the initial 4 hr period. The remaining food was evacuated in 10 hr in *A. lineatus* and 16 hr in *M. cupanus*. The complete evacuation period in *M. cupanus* thus compares fairly closely with values of 16–19 hr reported for other larvivorous fishes such as *Gambusia* at temperatures of 24–25°C by Hunt (1960). Nicholls (1931) working on the North American topminnow, *Fundulus heteroclitus* stated that 100% evacuation took place in 12.5–8.5 hr at intermediate temperatures (10–18°C); these values are not dissimilar to those obtained for *A. lineatus*, a close relative, at intermediate temperatures in the tropics. The relatively high rate of digestion (seen in *A. lineatus* as opposed to *M. cupanus*) probably reflected the more effective digestion process of the fish (McKone 1971).

The pattern of digestion in *A. lineatus* and *M. cupanus* differed in the initial phase from that found by Windell (1966) in *Lepomis macrochirus*. The latter hold their stomach contents for a time until a certain degree of liquefaction occurs; after this initial period, a period of high digestive activity takes place during which the major portion of the food material is digested and evacuated. The final phase, in both cases, is a very slow digestion rate period, during which the small quantity of food remaining in the stomach is slowly digested, probably since as stated by Kionka and Windell (1972) near the end of gastric emptying less digestible remains such as chitin form the bulk of the residuum.

The pattern found here has been explained by Steigenberger and Larkin (1974) as resulting from an initial period of hydrolysis of food, which increased its weight, supported by the fact that "standard regression techniques overestimated the amount of food fed and gave a higher estimate of the rate of digestion than constrained regression". Again, Fänge and Grove (1979) assert that the initial delay following the intake of a meal is variable and may be affected by temperature or food item (Jones 1974). The pattern of digestion observed in *A. lineatus* and *M. cupanus* is supported by Tyler (1970) who stated that greater quantities of digested food moved out of the stomach in the first few hours than towards the end of digestion. Perhaps the best explanation for the variation in findings is given by Brett and Higgs (1970) who stated that factors like enzyme secretion, differences in substrate relation, enzyme saturation, etc. would influence the rate of gastric digestion between species and between diets.

3.2. Effect of body size on depletion rates

Although numerous gastric evacuation rate studies have been conducted, few experiments have been designed to determine the relationship between evacuation time and size of the fishes; the available work, further, fails to clarify the effect of size of the fishes on digestion (Hunt 1960; Tyler 1970).

Pandian (1967a, b) and Jobling *et al* (1977) found digestion rate varied inversely with size in *Megalops cyprinoides* and *Limanda limanda*; larval *Micropterus salmoides* fed zooplankton evacuated more rapidly than adults (Laurence 1971). Noble (1973) working on *Perca flavescens* stated that a slower rate of gastric evacuation in larger fish might reflect the effects of greater amounts of food in their stomach.

As opposed to this, Swenson and Smith (1973), experimenting with fishes of different sizes which consumed similar meals showed that larger fish could digest a meal faster. However, when meal size was expressed in mg consumed per gram body weight, percentage values of digestion were not influenced by fish size.

Therefore, meal size probably accounts for the variability in digestive rates associated with fish size (Molnár *et al* 1967; Windell and Norris 1969; Swenson and Smith 1973) since in as much as stomach capacity increases proportionately with fish size, effects of size of fish on evacuation rate are confounded with the effects of meal size (Windell 1978). In the present investigation a full meal, sufficient to satiate the fish was fed to each size group; the resultant regression coefficients indicate that the rates of digestion by different sizes of the fish are not significantly different. This is supported by Steigenberger and Larkin (1974) who state that there are no consistent differences in the rate of digestion by different sizes of the fish.

The digestion curve is adequately, in all sizes, represented by a straight line as depicted by Hunt (1960), Magnuson (1969), Pandian (1967a, b), Daan (1973), Swenson and Smith (1973), Jones (1974) and not by an exponential curve (citations in Fänge and Grove 1979).

3.3. Effect of temperature on depletion rates

Available literature on the effect of temperature on gastric evacuation rates can be classified into those dealing with low, intermediate and high ambient water temperatures. However, Windell (1978) considers 1-9°C as low water temperatures, 10-18°C as intermediate and 19-30°C as high water temperatures, probably based on data collected in the temperate zone. In the tropics, ambient water temperature ranges are different, and $27 \pm 2^\circ\text{C}$ is often noted. The ranges on either side of this do not go so low or high as in the temperate zone; hence the experimental values of $22.5 \pm 0.5^\circ\text{C}$ and $32.5 \pm 0.5^\circ\text{C}$ were chosen as the minimum and maximum ranges of temperature which prevail in the natural habitat of the species experimented with—i.e. *A. lineatus* and *M. cupanus*. However, whatever the ranges, the environmental temperature significantly affects the rate of processing of food (Fänge and Grove 1979).

Time for 100% gastric evacuation at different temperatures varies with species, ranging from 158 hr at 1°C in *Pleuronectes platessa* (Edwards 1971) to 7 hr at 9°C in *Ctenopharyngodon* species (Hickling 1966) and 3-4 hr in *Gambusia affinis*

at 30° C (Sokolov and Chvaliova 1936); the last value is close to that of *A. lineatus* at 32.5° C, as is the 3 hr value of *Fundulus heteroclitus* at 30° C (Nicholls 1931).

Generally for most species, the rate of gastric evacuation is greatly depressed at low temperatures (Brett and Higgs 1970) and this is borne out by this investigation. A 5° C change in temperature produces much greater effects at low temperatures than at high temperatures (Molnár *et al* 1967). As the water temperature rises from low to intermediate, gastric evacuation rates increase accordingly. The importance of this lies in the fact that related processes such as appetite, food intake, absorption and conversion efficiency increase roughly in the same proportion (Windell 1978).

Data from studies on high temperatures clearly indicate that gastric evacuation tends to increase with rising temperature as in this investigation, reaching a maximum as the general limit of species temperature tolerance is approached; it may cease or alter at that stage (Molnár and Tolog 1962; Smit 1967; Molnár *et al* 1967; Brett and Higgs 1970; Tyler 1970; McKone 1971; Steigenberger and Larkin 1974). However data collected at this region is subject to high variability (Tyler 1970; Windell 1978).

Although the growth rate has been repeatedly shown to be characterized by an optimum temperature, digestion rate does not display a distinct optimum (Brett and Higgs 1970; Elliott 1972). However, the possibility of temperature and metabolic compensation for seasonal temperatures has been offered by Smit (1967), Molnár *et al* (1967) and Brett and Higgs (1970).

Thus, data on digestion rates are interrelated with other feeding processes; altogether, they can lead to predictions on growth and production rates not only in fish populations but also in aquatic ecosystems.

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