

Optimal foraging and ontogeny; food selection by *Haplochromis piceatus*

F. Galis and P.W. de Jong

University of Leiden, Department of Organismal Zoology, Division of Ecological Morphology and Department of Population Biology, Division of Ecology. P.O. Box 9516, 2300 RA Leiden, The Netherlands

Summary. We examined the influence of satiation level, prey density and light intensity on food uptake rate through the ontogeny of *Haplochromis piceatus*. Prey handling in the buccal cavity was found to be the main factor limiting prey uptake rate under light circumstances and at a sufficiently high prey density. Food uptake rate per unit body weight of different sizes of *H. piceatus* was equal when feeding on *Chaoborus* but decreased with increasing fish size when feeding on *Daphnia magna*. In choice experiments with *Chaoborus* and *D. magna*, prey selection by *H. piceatus* of all sizes was according to the predictions based on Charnov's 1976 model.

Key words: Optimal foraging – Prey selection – Ontogeny – Cichlids

Since MacArthur and Pianka (1966) and Emlen (1966) published the first optimal foraging models much progress has been made in this approach to behaviour research. Attention has been given to the selection of features to be optimized and the role of constraints (Pulliam 1974; Belovsky 1978; Tinbergen 1980; Werner and Mittelbach 1981; Milinski 1985). Thereby the responsible selective forces are identified (Maynard Smith 1978). Optimization in the foraging behaviour of animals is expected because firstly by minimizing the energy spent to capture prey, an animal will have more energy left for metabolism, growth and reproduction. Secondly by minimizing time spent feeding, an animal will have more time to carry out other activities (Hart 1985). For juvenile fish there are several additional reasons to expect optimization of feeding behaviour. The first is that a high growth rate has a selective advantage when it lowers age at reproductive maturity. The second is that it shortens time spent in vulnerable young stages (Milinski 1985), because mortality rate is for fish usually an inverse function of size (Cushing 1974; Ricker 1979; Taborski 1984). Of course predator avoidance behaviour may be important and may have a negative effect on growth rate since foraging usually occurs in exposed places. In this situation time minimization (Schoener 1971) can be important: *i.e.* food uptake in a minimal time period must be maximal. It elicits the question does extra selective pressure on maximization of food uptake or minimization of time in juvenile stages lead to different feeding efficiencies between adult and juvenile stages?

Offprint requests to: F. Galis

In the last decade much research has been devoted to size selective predation by fish on zooplankton. Some researchers interested in the causation of the size selective predation behaviour have developed and tested models on mechanisms of food selection such as the apparent size hypothesis (O'Brien et al. 1976). Other researchers asked functional questions, examining whether size selective feeding reflects an uptake of prey of optimal sizes. It has been repeatedly suggested that one can choose between an optimality model and a model on mechanisms as if only one of the models can be true (Ranta and Nuutinen 1985; Maiorana 1981; Butler and Bence 1984; Li et al. 1985) and that rejection of one model means support for the other (Butler and Bence 1984). As Tinbergen (1963) has pointed out, the study of behaviour is concerned with four major problems: causation, function (or survival value), evolution and ontogeny. The fields covered by these questions must be distinguished and each provide part of the total explanation. All fields merit equal attention and should be integrated. Functional questions and causal questions are frequently muddled up (Krebs and Davies 1981) as in the case of size selective predation by planktivores. The confusion has been stimulated by the influential article of Gould and Lewontin (1979) who rightly point out the dangers of an exclusively functional approach. However, they are wrong in stating that a causal explanation is more important than a functional one (p. 147). This and their repeated complaint that researchers are not considering alternatives to functional explanations has unfortunately led to the mistaken belief that causal explanations are alternatives to functional ones. Therefore, the aim of an integrated approach has become more remote, although Gould and Lewontin claim to be proponents of this approach. Undoubtedly, there is an interaction between the effect of constraints and the effect of realized optimization of features in organisms (Dennett 1983). To understand the constraints that ontogeny poses on the functioning of organisms we need both a functional and a causal analysis. In this paper we deal with a functional analysis of feeding behaviour in a fish and will follow with a second paper dealing with a functional morphological analysis of changes in the fish's feeding apparatus during ontogeny. This may shed some light on the possibilities and impossibilities of the feeding behaviour imposed by the changing morphology of the growing fish.

We studied a particulate-feeding zooplanktivorous cichlid of Lake Victoria: *H. piceatus* Greenwood & Gee. This species feeds on cladocerans, copepods, insects (mainly

Chaoborus larvae and pupae, van Oyen et al. 1981; Witte 1987) and algae (*Melosira*). In the experiments cladocerans (*Daphnia magna* Straus) and insect larvae (*Chaoborus*) were offered separately and together to individual *H. piceatus*. In single prey experiments, efficiency of the uptake of both prey species was compared for different postbuccal ontogenetic stages of *H. piceatus*. On the basis of these efficiencies, assuming an optimal prey selection, a prediction was made for prey selection when both prey types are simultaneously offered. The empirical results were compared with the predictions of the model.

The model

Charnov's (1976) model was used to predict prey selection. Net rate of energy intake (En/T) in this model is:

$$\frac{En}{T} = \frac{\sum \lambda_i^* E_i^* P_i}{1 + \sum \lambda_i h_i^* P_i}$$

λ_i is the number of prey type i encountered in one unit of search time. E_i^* is the expected net gain in energy from one item of type i . h_i^* is the expected handling time for an item of prey type i . P_i is the probability that the predator attacks an item of type i when one is encountered. En/T is maximized when $P=0$ or 1. If the prey types are ranked by the ratio E_i^*/h_i^* , then the decision whether a prey type i should be eaten is independent of the abundances of those prey types with rank lower than i . A prey type j in the set of prey types eaten has the characteristic that $E_j^*/h_j^* > En^*/T^*$. When two prey types are available this means that the less profitable prey type (2) should not be eaten as long as the abundance of the most profitable prey type (1) is sufficient to meet the dietary needs of the predator: $E_1^*/h_1^* > En^*/T^*$. A similar conclusion was reached by Schoener (1971), Pulliam (1974) and Werner and Hall (1974).

Assumptions of the model

- 1) Prey-type recognition is instantaneous.
- 2) The nutritional needs of the fish impose no constraint on the fish's choice between offered prey types.
- 3) The influence of hunger is ignored.
- 4) The handling time is constant for each prey type and independent of the rate of encounter or the accumulated number of encounters between predator and prey.
- 5) Prey types have equal metabolic costs.
- 6) Mortality risk is equal for all fishes.

Judging from our behavioural observations, assumption (1) seems valid. The validity of assumption (2) is uncertain because we only know the nutritional content of *D. magna* (Vijverberg and Frank 1976) and not of *Chaoborus*. Effects of hunger were avoided in the experiments (assumption 3). Assumption (4) is valid for the food densities used in these experiments (we explain this later). Because we do not know the nutrient composition of *Chaoborus* we cannot conclude anything about assumption (5). In our experiments predators of the fish were absent and therefore assumption (6) is met, but in a situation where predators are important there may be an advantage to feeding on *Chaoborus* because a large amount of food can be ingested at the same time (compared to *D. magna*) after which the fish can process the prey in a safer place with more attention for predators.

Instead of using the net rate of energy intake we calculated the amount of energy ingested and neglected energy costs of the food uptake. We think that this influenced the results very little because Stein et al. (1984) found that for sunfish (*Lepomis microlophus*, size: 130–220 mm) the energy costs of handling prey, which involved crushing molluscs, were only 0.25 to 2.6% of the energetic content of the prey. Using their data we calculated a linear correlation coefficient of 0.95 ($P < 0.05$) between the net energetic reward per unit handling time and the amount of ingested dry mass (not significantly different from energetic content) per unit handling time. In another case, Drost et al. (1987) found that for larval carp (*Cyprinus carpio*) the energy costs of the actual attack are only a fraction of a percent of the energetic content of the attacked prey.

Material and techniques

The predator. *H. piceatus* specimens were caught as juveniles in January 1984 in the Mwanza Bay of Lake Victoria (Tanzania) and were shipped by air to Leiden (For a taxonomic analysis of the Mwanza Gulf population see Witte (1987)). F1-, F2- and F3-generation fishes were used in the experiments, as well as one parent-generation specimen. No significant differences were found between similarly obtained data of F1- and F2-, F1- and F3- and P- and F2-generation fishes (F -test and Mann-Whitney U test; $P < 0.05$). Every week the standard length of the experimental fishes was measured and used to calculate fish volume (a better estimate of fish size) through the following regression line: $Y = 0.282 X + 0.035$ ($r = 0.99$; $P < 0.05$) in which Y is the cube root of fish volume (ml) and X is the standard length (cm). This regression is based on the standard length and volume of 31 fishes of different sizes (2.1–6.0 cm S.L.). Since the specific gravity of a fish approaches unity (Alexander 1958 and 1965; more specifically for cichlids, Hoogerhoud et al. 1973) their weight can be assumed to have the same value as their volume. The experimental fishes were fed zooplankton supplemented with Tetramin when necessary. Care was taken that both prey items used in the experiments, *D. magna* and *Chaoborus* (see below), were regularly and alternately offered to ensure experience, and both to avoid a training bias on one prey item only (Dill 1983) and to avoid long term learning effects (Werner et al. 1981). We found that a carefully balanced diet is particularly important because if only *Chaoborus* larvae are offered for some time large fishes lose any interest in *D. magna* even when no other food is available.

The prey. We chose two prey types that differ considerably in size: with *D. magna* as a substitute for cladoceran prey eaten in the natural environment and fourth instar *Chaoborus* larvae as insect prey. *D. magna* does not occur in Lake Victoria and there *H. piceatus* feeds on *Bosmina longirostris*, *Chydorus* sp., *Moina micrura* and *Diaphanosoma excisum* (Galis unpublished work). However, for many particulate feeders the capture success for different cladoceran species is approximately equal, with the exception of *Diaphanosoma* which is more difficult to capture (but not so much as copepods) (Confer and Blades 1975; Kettle and O'Brien 1978; Drenner et al. 1978; Bohl 1982; Schmidt and O'Brien 1982; Wright and O'Brien 1984). Also the chemical composition of these prey types does not vary much (Vijverberg and

Frank 1976). Therefore we feel that *D. magna* is a reliable substitute for the cladocerans eaten in the lake.

D. magna specimens were reared at the R.I.V.M. (State Institute for Health and Environment). The length (taken as the distance from the tip of the head to the base of the caudal spine) of 25 specimens was measured under a Nikon profile projector V-16A. Two length classes were used in the experiments, 0.9–1.2 mm and 1.2–1.6 mm. Of the smallest size class mean dry weight of 2000 specimens was determined on a Mettler H 54 balance after 10 days drying at 80 C. Mean dry weight was 11.18 μ g. The caloric value of *D. magna* is 5640 ± 60 Cal/g dry weight (Cummins and Wuycheck 1971), therefore one *D. magna* specimen of this size class has an average energy content of 0.26 J.

Because the natural prey species *Chaoborus anomalus* and *C. edulis* do not occur in the Netherlands, a mixture of fourth instar larvae of *C. cristallinus*, *C. pallidus*, *C. flavicans* and *C. obscuripes* was used as insect prey. Thus we ensured a sufficient supply of prey items throughout the year. Mixtures of the above mentioned species of *Chaoborus* larvae can also be easily purchased in aquarium shops. Because they are difficult to distinguish, individual identification of the larvae used in the experiments was not feasible. Since the experiments could be repeated without significantly different results (Wilcoxon matched pairs signed-ranks test, $P > 0.05$) the use of a mixture of species is not problematical. Mean dry weight of 200 larvae, which was determined as described for *D. magna*, is 0.64 mg. The caloric value of *Chaoborus* is 4936 Cal/g (Cummins and Wuycheck 1971), therefore one *Chaoborus* larva has an average energy content of 13.37 J.

Experimental set up and results

Satiation, Series a

Experimental set up. In order to compare the efficiency of food uptake (i.e. food uptake per time unit), the fishes should not be satiated and satiation level should be similar for all fishes. To determine an appropriate experimental duration we did a series of experiments in which we offered 150 *Chaoborus* larvae to an individual *H. piceatus*. After 10, 30, 60, 120 and 180 min the number of larvae eaten was determined either by direct observation or indirectly by counts of remaining larvae. From these data the number of larvae eaten by fishes of several sizes was calculated. Water temperature was maintained at 23 ± 1 C and fishes were starved for 24 h prior to all experiments. The experiments were performed in 40 l aquaria under a light intensity of ± 700 lux. Six *H. piceatus* individuals were used.

Results. There was a linear relationship between the number of *Chaoborus* larvae eaten and the volume of the fish over the whole range of experiment times (see Fig. 1a and Table 1). In the first minutes of each experiment the fishes rapidly filled their buccal cavity. After this initial sharp increase the food uptake for all fish sizes used in the experiments was linear from 10 min to three hours (Fig. 1b and Table 2). Thus there are no effects of satiation or depletion on feeding efficiency and consequently the feeding efficiency can be compared for experiments within this time span. This series was not repeated for *D. magna*, but in the exper-

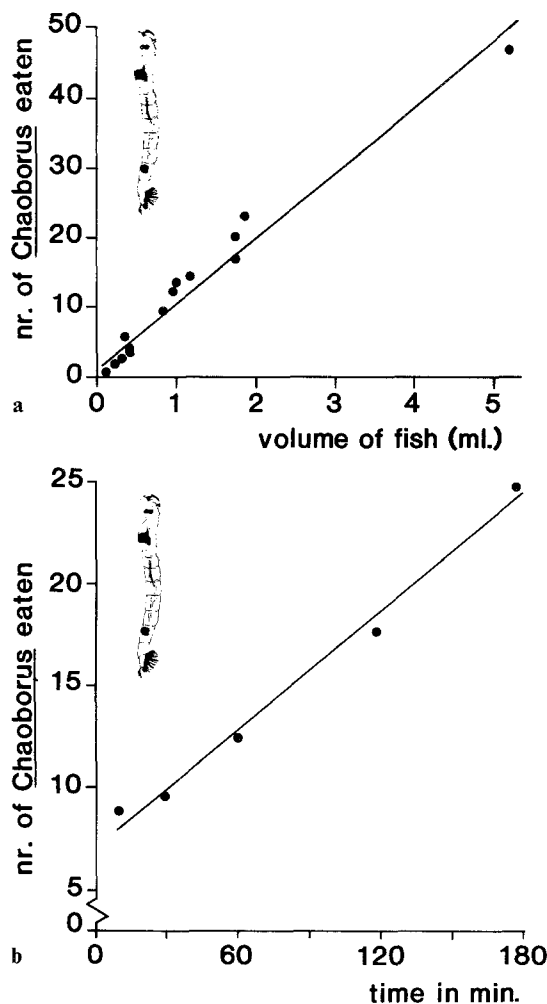


Fig. 1. a Relationship between fish volume and number of *Chaoborus* ingested after 60 min (one example, see table 1). b Relationship between time and number of *Chaoborus* ingested by a fish of 1.07 ml (an example, see Table 2; values indirectly calculated from Table 1)

iments of Series c2 the uptake was found to be linear from 5 min to 50 min (for an example see Fig. 2).

Light intensity and food density, Series b

Experimental set up. To investigate the influence of light intensity and food density on the efficiency of the food uptake, experiments were carried out at various light intensities and with different food densities. The experiments lasted one hour. The number of *Chaoborus* larvae or *D. magna* specimens (smallest size class) eaten was determined indirectly at the end of the experiment by counting the remaining food items in the aquarium. Before all experiments, the fishes were acclimatized to the light intensity of the experiments, for at least four hours. The experiments were performed in 20, 40, 80, 150 and 250 l aquaria. To obtain a homogeneous distribution of *D. magna* in the water column, the walls of the aquaria were blackened. Light intensity was measured with a Lunasix 3 light meter. Six *H. piceatus* individuals were used.

Results. For all densities of *Chaoborus* or *D. magna* offered there were no significant differences between the uptake

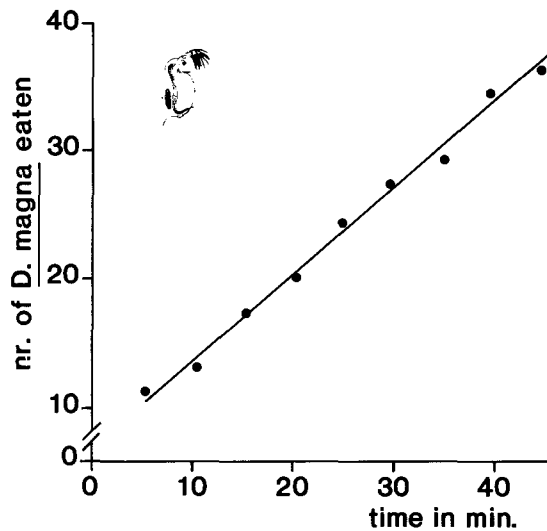


Fig. 2. Relationship between time and number of *D. magna* eaten by a fish of 0.19 ml ($Y=0.65 X+7.28$, $r=0.998$, $P<0.05$)

Table 1. The relationship between fish volume (X) and number of *Chaoborus* ingested (Y)

Experimental time in min	Regression equation	r	p	n
1	$Y=2.05 X+1.61$	0.83	<0.05	42
10	$Y=7.91 X+0.29$	0.98	<0.05	36
30	$Y=8.67 X+0.22$	0.98	<0.05	16
60	$Y=9.43 X+2.42$	0.98	<0.05	15
120	$Y=12.05 X+4.96$	0.98	<0.05	7
180	$Y=14.09 X+9.93$	0.96	<0.05	11

Table 2. The relationship between estimated number of *Chaoborus* ingested (X) and time (Y)

Volume of fish (ml)	Regression equation	r	p	n
0.41	$Y=0.07 X+2.04$	0.99	<0.05	5
0.69	$Y=0.08 X+4.14$	0.99	<0.05	5
1.07	$Y=0.10 X+6.98$	0.99	<0.05	5
1.58	$Y=0.12 X+10.80$	0.99	<0.05	5
2.22	$Y=0.14 X+15.58$	0.99	<0.05	5

rate by *H. piceatus* in very light (700 lux) and in dark (0.09 lux) circumstances (Wilcoxon Matched Pairs Signed-rank test, $P>0.05$, Table 3 and 4). When feeding on *D. magna* in total darkness the uptake rate was lower for all densities than at each light intensity (same test, $P<0.05$). This also held for smaller fishes when they fed on *Chaoborus* (Table 5). For larger fishes, there was no significant difference between uptake rate in total darkness and in light ($P>0.05$) although at the lowest density of 0.1 larva per litre in total darkness, about 40% fewer larvae were eaten.

Up to a density of 10 *D. magna* per litre in light as well as in total darkness, there was a significant positive correlation between prey density and amount of prey consumed by fishes of both size classes (Table 4) (in light, large fish: $r=0.81$, $P<0.05$; small fish: $r=0.99$, $P<0.05$). Above

Table 3. Effect of prey density and light intensity on prey uptake rate, individual experiments. *Chaoborus*

Prey density per litre	Number of <i>Chaoborus</i> ingested at:		
	± 700 lux	± 0.09 lux	0 lux
Fish size: 0.53–0.72 ml			
0.1	7/7	6/7	0/1
0.2	10/10	11/10	1/1
0.35	13/14	13/12	–
0.5	13	14	2/2
1	12	14	4/5
2	14	12	4/4
4	14	13	8/9
Fish size: 1.96–2.22 ml			
0.1	21/24	23/23	13/14/13
0.2	23	22	20/21
0.5	21/24	25/18	19/20
1	19/24	24/23	24/19
2	21	26	22/25
4	25	23	23/24

Table 4. Effect of prey density and light intensity on prey uptake rate, individual experiments. *D. magna*

Prey density per litre	Number of <i>D. magna</i> ingested at:		
	± 700 lux	± 0.09 lux	0 lux
Fish size: 0.53–0.72 ml			
0.66	36/26	30/25	7/6
1.25	50	59	14/17
2.5	79/83	83	43/36
5	118	111	78/69
10	185	195	102/112
15	180	–	116/105
30	168	181	106/115
Fish size: 1.96–2.22 ml			
0.66	148	165	62/50
1.25	235	221	91/82
2.5	313	320	150/161
5	350	354	308/308
10	427	412	327
15	402	390	354/312
30	–	417	309/328

this density there was no increase in amount of consumed prey (in light, large fish: $r=0.03$, $P>0.05$; small fish: $r=0.75$, $P>0.05$); in total darkness, large fish: $r=0.34$, $P>0.05$; small fish: $r=0.22$, $P>0.05$).

Over all *Chaoborus* densities there was a significant positive correlation ($r=0.95$, $P<0.05$) between prey density and amount of prey consumed by the small fishes in total darkness (Table 3). In light, smaller fish initially showed an increase in the number of *Chaoborus* consumed with increasing *Chaoborus* density ($r=0.97$, $P<0.05$), but this levelled off at a density of 0.35 larvae per litre ($r=0.14$, $P>0.05$; see also Table 5). For the large fishes the number of *Chaoborus* consumed in the absence of light increased up to a density of one larva per l ($r=0.67$, $P<0.05$) and remained constant afterwards ($r=0.36$, $P>0.05$).

Table 5. Effect of prey density on prey uptake rate, individual experiments

Volume of fish (ml)	Number of <i>Chaoborus</i> ingested at prey densities of:		
	1 larva/l	2 larvae/l	4 larvae/l
0.36	4	4	5
0.51	8	7	7
0.75	11	11	10
1.25	18	18	21
1.69	26	24	22

Efficiency of prey uptake through ontogeny, Series c

Experimental set up. Three series of experiments were carried out, Series c1 with *Chaoborus* larvae as prey, Series c2 with *D. magna* as prey and series c3 with both species as prey. Six *H. piceatus* individuals were used in series c1, 5 in c2 and 8 in c3.

In the Mwanza Gulf densities of fourth instar *Chaoborus* larvae were found to vary from 0.003 to 0.6 larvae per l (Goldschmidt and Hoogenboezem, unpublished work; Luttik, unpublished work). During the Series b experiments, densities of *Chaoborus* larvae varying from 0.35 to 4 larvae per l did not influence the uptake efficiency of *H. piceatus*, in light, as long as the absolute number of larvae was sufficient to avoid depletion; therefore we chose a density of 2 larvae per l for Series c1, as a convenience.

Akiyama (1977) and Goldschmidt and Hoogenboezem (*in prep.*), found that densities of cladocerans in the Mwanza Gulf vary from 0.21 to 30 individuals per litre. Total densities of cladocerans and copepods varied from 4 to 150 individuals per l. Because densities varying from 2.5 to 30 individuals per l did not influence the uptake efficiency of *H. piceatus* in light (Series b), we chose a density of 30 *D. magna* per l in Series c2 as a convenience. In Series c3 30 *D. magna* and 4 *Chaoborus* larvae per litre were offered because these densities are not limiting prey uptake rate.

Based on the results of Series a an experimental time of 45 min plus the time until the next prey item was caught was chosen for Series c. Because light intensity does not influence prey uptake rate (Series b) we chose a high illumination level to facilitate good observation. The experiments were performed in 20 and 40 l aquaria. The size of the aquaria did not significantly influence the results (Wilcoxon matched pairs signed-rank test, $P > 0.05$). Behavioural observations were made with the help of a behaviour recorder or videorecorder (Sony U-matic).

The following behavioural parameters were measured: 1) Experiment time (see above), which can be divided into search time and handling time. In our experiments search time can be neglected because searching occurred during processing time and therefore did not require extra time (see Discussion). 2) Attack time, the time from the moment the fish approaches a prey until it has taken the prey into its mouth. 3) Processing time, the time the prey spends in the buccal cavity, was indirectly measured as the total processing time divided by the number of prey items eaten minus the last one whose moment of capture determined the end of the experiment. This indirect estimation was necessary because *H. piceatus*, with the exception of very small

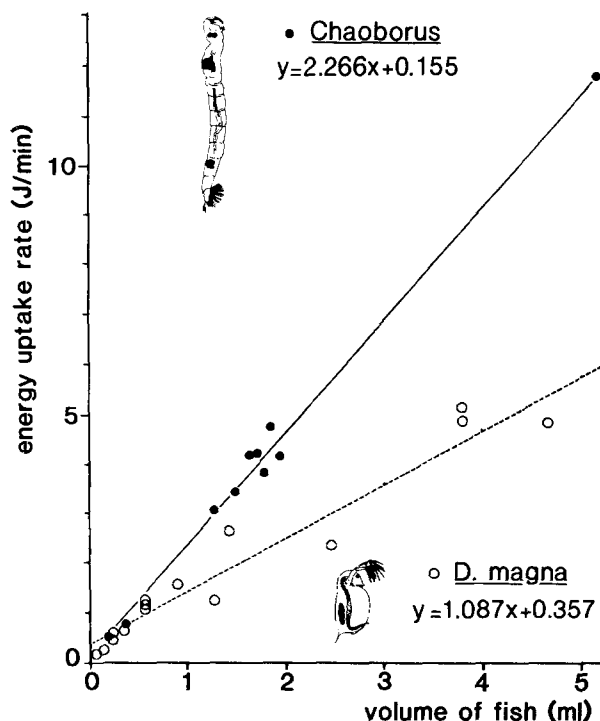


Fig. 3. Relationship between fish volume and rate of energy intake from *Chaoborus* ($r=0.99$, $P < 0.05$) and *D. magna* ($r=0.97$, $P < 0.05$).

Table 6. Energy uptake rate. *Chaoborus*

Volume of fish (ml)	J/min · gr (x)	Volume of fish (ml)	J/min · gr (x)
0.17	2.89	1.69	2.48
0.36	2.15	1.75	2.18
1.26	2.43	1.82	2.61
1.47	2.35	1.95	2.13
1.62	2.56	5.17	2.28

$r = -0.31$, $P > 0.05$; $x = 2.41$ (sd = 0.06)

individuals, simultaneously processes several prey items in the buccal cavity. The space of the buccal cavity seems to limit the number of prey items that can be ingested (sometimes fishes try to suck additional prey into an already full buccal cavity; the prey item is thereupon released, or, in the case of *Chaoborus*, is sometimes held out of the mouth and is slowly taken into the buccal cavity). 4) Total number of attacks. 5) Percentage of successful attacks. 6) Duration of a successful attack. 7) Total attack time spent per successful attack.

Results: *Chaoborus* larvae (Series c1). Uptake of *Chaoborus* larvae per hour increased with the volume of the fish ($Y = 10.17 X + 0.71$, $r = 0.996$, $P < 0.05$) and thus energy uptake rate increased linearly with volume (Fig. 3). Interestingly, the energy uptake/min.gr body weight is about the same for all ontogenetic stages and is not significantly correlated with body weight (Table 6). During development, *H. piceatus*' success of capture increases: the duration of an attack decreases and the chance of success increases (Fig. 4a and 5a). Success rate is variable and low for the young fishes and invariably high for larger fishes. The increase in the

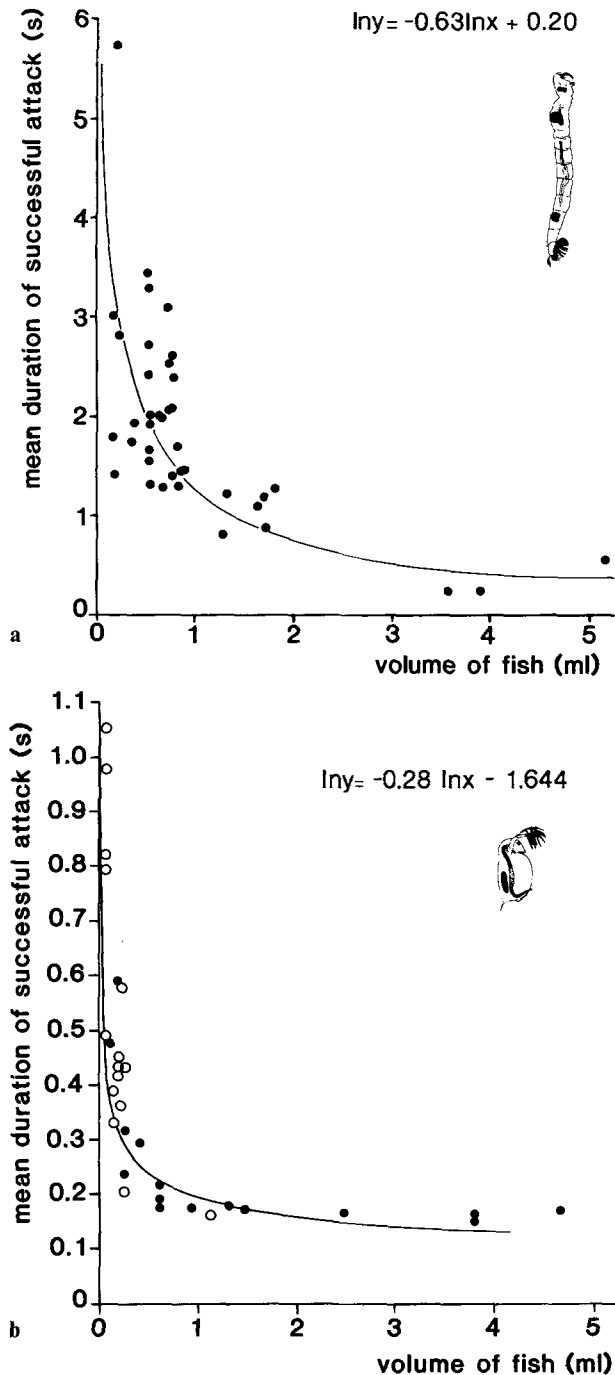


Fig. 4a, b. Relationship between fish volume and mean duration of successful attack on a *Chaoborus* ($r = -0.71$, $P < 0.05$) and b *D. magna* ($r = -0.90$, $P < 0.05$). Black circles represent experiments with *D. magna* of 0.9–1.2 mm. Open circles represent experiments with *D. magna* of 1.2–1.65 mm (not included in the regression analysis)

food uptake with body size of *Chaoborus* is, for a minor part, the result of a decrease in average attack time per larva eaten, but is mostly the result of a decrease in the mean processing time (Fig. 6a) which constitutes on average 99.4% (sd = 0.07) of the handling time per larva.

Results: *D. magna* (Series c2). The results resemble those of *Chaoborus*. The uptake of *D. magna* increases linearly

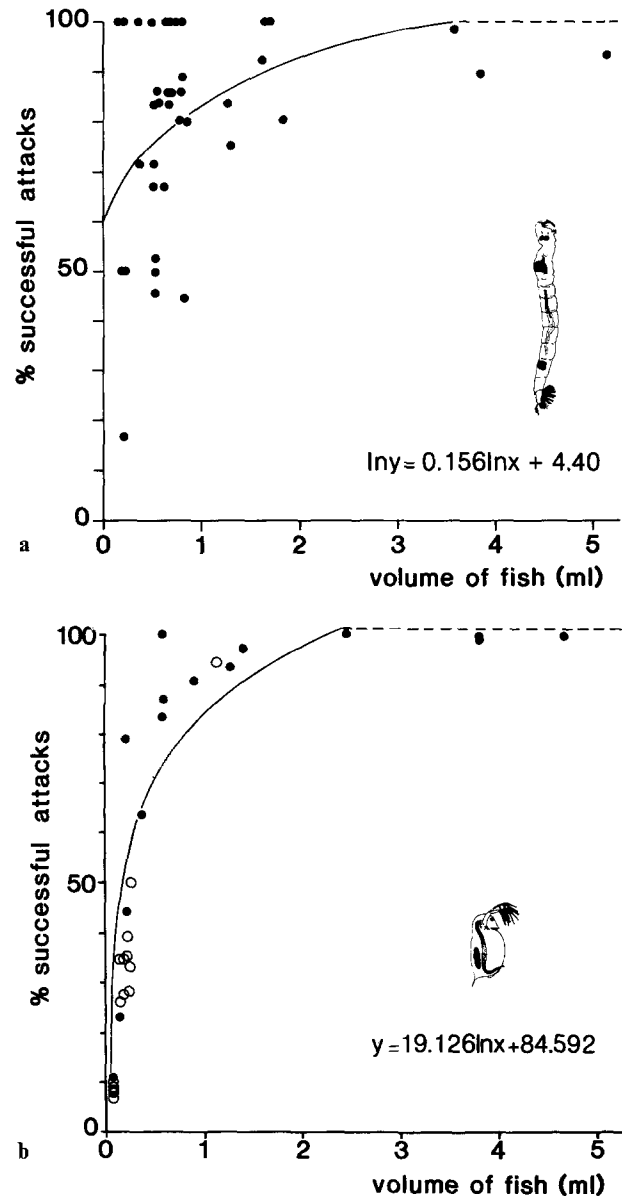


Fig. 5a, b. Relationship between fish volume and percentage of successful attacks on a *Chaoborus* ($r = 0.41$, $P < 0.05$) and b *D. magna* ($r = 0.87$, $P < 0.05$). Black circles represent experiments with *D. magna* of 0.9–1.2 mm. Open circles represent experiments with *D. magna* of 1.2–1.65 mm (not included in the regression analysis)

with volume of the fish ($Y = 4.119 X + 1.353$, $r = 0.97$, $P < 0.05$) and thus the energy uptake rate per min (Fig. 3). However the uptake of energy/min.gr body weight does not remain constant as is the case with *Chaoborus* but decreases (Table 7). Again, the duration of an attack decreases with size (Fig. 4b) and the percentage of successful attacks increases (Fig. 5b). The variation for young fishes is much lower than in experiments with *Chaoborus* (compare Figs. 4a, 4b, 5a and 5b). Though processing time (Fig. 6a) again constitutes most of the handling time, attack time is relatively more important, especially for small fish. From a fish volume of 0.06 to 1.26 ml the percentage of attack

Table 7. Energy uptake rate. *D. magna*

Volume of fish (ml)	J/min.gr	Volume of fish (ml)	J/min.gr
0.06	2.62	0.90	1.76
0.13	1.87	1.26	0.96
0.20	2.83	1.41	1.87
0.22	2.14	2.45	0.97
0.36	1.80	3.79	1.27
0.56	1.98	3.79	1.35
0.56	2.30	4.68	1.02
0.56	1.93		

$r = -0.74, P < 0.05 (Y = -28 X + 2.16)$

time decreases from 10.46% to 1.16%. From 1.26 to 4.68 ml the percentage attack time increases to 5.16% but this is probably a measuring error, since the attacks are too short (less than 0.2 s) for a reliable measurement with our behaviour recorder.

Prediction for the mixed-prey experiment (Series c3). With increasing fish size, the regression lines for energy yield per time unit of *D. magna* and *Chaoborus* are different

(Fig. 3). Up to 0.49 ml there is no significant difference in energy uptake for both prey (*F*-test, $P > 0.05$). Above 0.49 ml the difference is significant and increases with fish size. According to Charnov's model (1976) fishes larger than 0.49 ml should specialize entirely on *Chaoborus* because E_2^*/h_2^* (*D. magna*) $< En^*/T^*$. Fish smaller than 0.49 ml should generalize and take *D. magna* and *Chaoborus* as encountered because $E_2^*/h_2^* = E_1^*/h_1^*$ (*Chaoborus*) = En^*/T^* .

Results of the mixed-prey experiments (series c3). Figure 7 shows that fish smaller than 0.49 ml ate both *Chaoborus* and *D. magna* as predicted: the percentage of *Chaoborus* in the prey eaten varies from 7.7 to 60. It is 60% for a fish of 0.46 ml and 87.5% for a fish of 0.49 ml. Because a *Chaoborus* larva contains 50 times more energy than a single *D. magna*, even when *Chaoborus* makes up only 8% of the items eaten it still provides 81% of the total energy intake (Fig. 8). Fish larger than 0.49 ml ate mainly *Chaoborus* as predicted and virtually all ingested energy is derived from this prey. The energy uptake rate in these experiments did not differ from those in which only *Chaoborus* larvae were eaten (*F* test, $P > 0.05$). If we assume similar handling times for *D. magna* in mixed- and single-prey experiments, the handling times of *Chaoborus* larvae and the number of attacks on *Chaoborus* larvae per time unit do

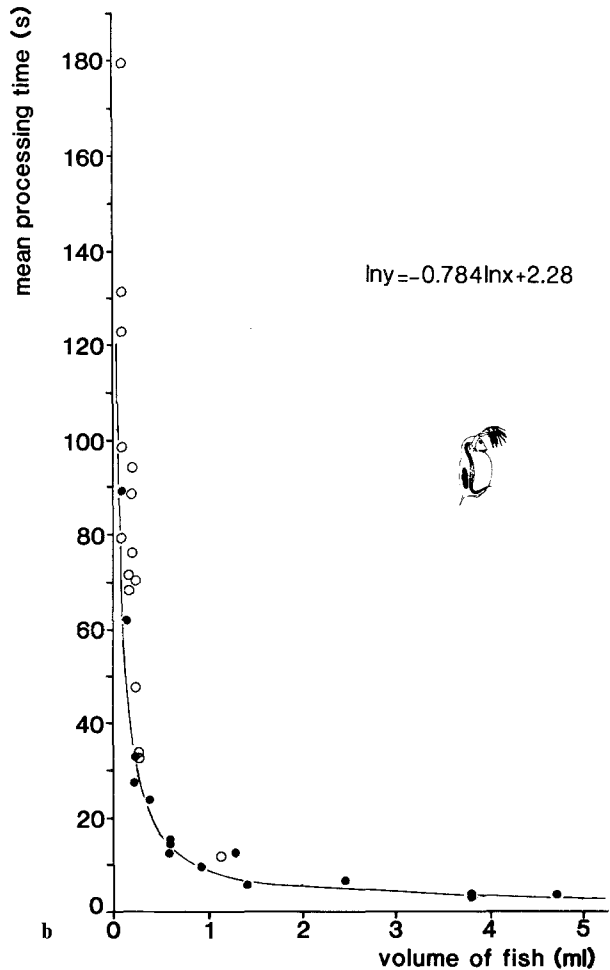
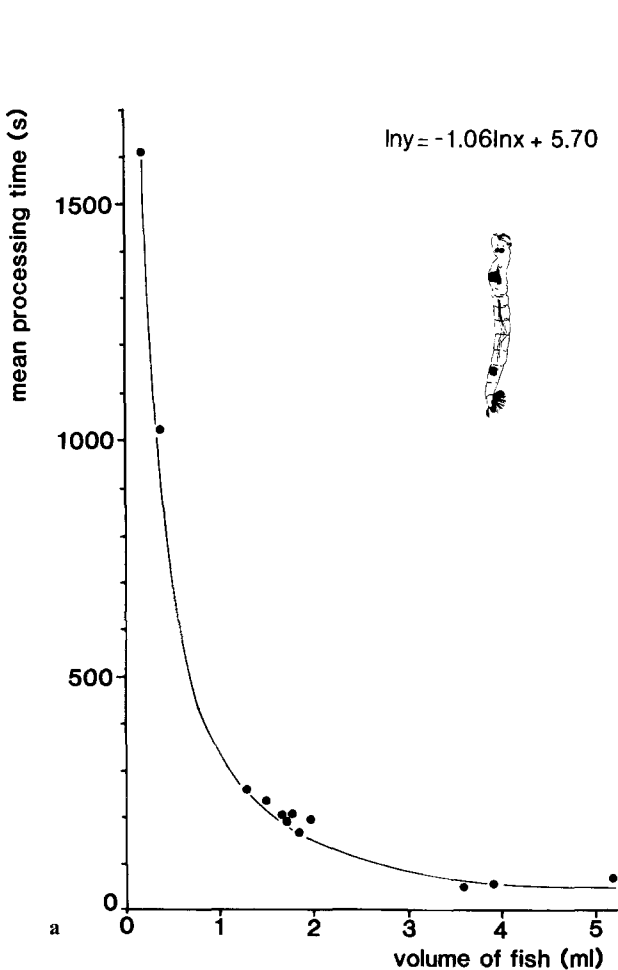


Fig. 6a, b. Relationship between fish volume and mean processing time for **a** *Chaoborus* ($r = -0.996, P < 0.05$) and **b** *D. magna* ($r = -0.80, P < 0.05$). Black circles represent experiments with *D. magna* of 0.9–1.2 mm. Open circles represent experiments with *D. magna* of 1.2–1.65 mm (not included in the regression analysis)

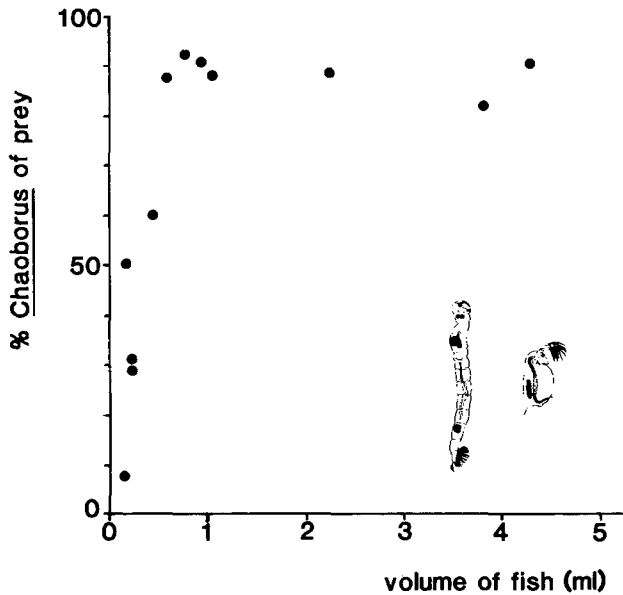


Fig. 7. Relationship between fish volume and percentage *Chaoborus* of ingested prey in mixed-prey experiments

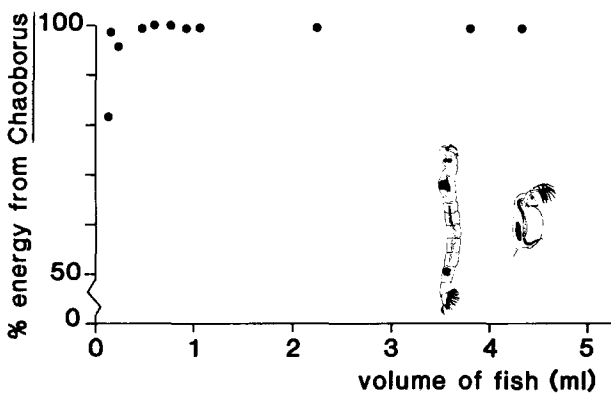


Fig. 8. Relationship between fish volume and the percentage of ingested energy that is derived from *Chaoborus* in mixed-prey experiments

not significantly differ from those of Series c1 (only *Chaoborus* as prey, F test, $P > 0.05$).

Discussion

Which factors influence prey uptake rate by *H. piceatus*?

Satiation level does not influence uptake rate. Preliminary experiments indicate that if an excess of food is offered, satiation does eventually occur. Stomach content analyses (Witte, unpublished work and Galis, unpublished work) indicate, however, that satiation is not a likely event in nature. Light intensity also does not influence uptake rate, except that in total darkness uptake rate is lower in most circumstances; at lower prey densities, uptake rate is influenced by density, and in the case of smaller fish in total darkness, prey density is limiting at all *Chaoborus* densities. At higher prey densities the food uptake rate is not density-dependent but is almost exclusively limited by processing time. Hence we believe it is limited by the capacity of the fishes to store food in the buccal cavity and by the speed

at which the food is processed and passed from the buccal cavity into the esophagus. If the storage capacity of the stomach had been limiting, we would have expected a deflection in the food uptake curves at the moment the storage capacity was reached. The density of *Chaoborus* and *D. magna* probably has only a limited influence on the uptake rate because *H. piceatus* can swim towards novel prey, while processing previously caught food items. In the dark, when eyes cannot be used and the lateral line system may play a role in food detection, search time is more important. *H. piceatus* is a rather efficient feeder in the dark. In its turbid lake, *H. piceatus* feeds at low light intensities and may even feed in total darkness, since it feeds day and night (Witte, unpublished work). Especially around the new moon, when full-grown fourth instar *Chaoborus* larvae most frequently occur (Hoogenboezem and Goldschmidt, unpublished work) little light penetrates to a depth of 2 to 7 meters where most juvenile *H. piceatus* occur (Witte 1987). Even less light if any will reach a depth of 6 to 11 meters where most adults occur (Witte 1987). Therefore, the capacity to feed without optical aid is important. The atherinid *Xenomelaniris venezuelae*, a particulate feeding planktivore, is also able to catch *Chaoborus* larvae (and pupae) in complete darkness and maintains its size-selective feeding pattern (Unger et al. 1984). However it does not feed on cladocerans and copepods in the dark. The common bream *Abramis brama* can eat *D. magna* at light intensities approaching 0 lux, though at about half the rate as in light (Townsend and Risebrow 1984). Also the minnow, *Phoxinus phoxinus*, is able to capture *D. magna* in the absence of light with a similarly reduced efficiency (45% of the capture rate in light, Harden Jones 1956). It is possible that the lateral line system is involved in the feeding of other visually foraging planktivorous fish. The lateral line system may have been unjustly excluded from mechanistic models of feeding, such as the apparent size model (O'Brien et al. 1976).

How good is the fit with the model?

The results of the mixed-prey experiments are in agreement with the predictions of Charnov's model based on the results of the single prey experiments, except that fishes larger than 0.5 ml never totally exclude *D. magna*. Similar partial preferences that are not predicted by the model are reported from many studies (e.g. Werner and Hall 1974; Krebs et al. 1977; Elner and Hughes 1978 and Krebs et al. 1983 for a summary). Krebs and McCleery (1984) summarize four different explanations that have been proposed in the literature for this partial preference:

- 1) *Discrimination errors*. It is not likely that *H. piceatus* mistakes *D. magna* for fourth instar *Chaoborus* larvae which are more than fifty times larger. Observations support this hypothesis.
- 2) *Long-term learning effects*. These were avoided in our experiments because *H. piceatus* quickly learns to handle *D. magna* and *Chaoborus* and the fishes were sufficiently experienced prior to the experiments.
- 3) *Runs of bad luck*. Because food density had so little influence on the uptake rate in light, this is not a likely explanation.

4) *Simultaneous encounters*. Waddington and Holden (1979), see also Waddington (1982) developed an optimal diet model that predicts partial preferences if more than one food item can be perceived at the same time by the predator. This simultaneous perception indeed applies to our experiments and therefore we calculated the partial preferences that should be shown towards *Chaoborus* larvae in our experiments, assuming an average swimming velocity of twice the standard length per second (this velocity is well within the range of swimming speeds observed for the similarly sized insectivorous *H. angustifrons* and *H. elegans*, Galis and Smit 1979). The model predicts that a 0.22 ml fish should show a partial preference for *Chaoborus* larvae of 14.97% and a 5.17 ml fish a partial preference of 36.05%. Doubling the fish's velocity has little influence on the predicted preference (a decrease of 0.5%). These predictions are far less accurate in describing our results than the model of Charnov. The reason for the inaccuracy is that the food density is important in the model of Waddington and Holden whereas in our experiments food density does not influence the uptake efficiency of *H. piceatus*.

Other possible explanations for partial preference mentioned in the literature, such as prey recognition time (Hughes 1979), crypsis of the prey (Erichson et al. 1980) and short-term learning (McNair 1980 and 1981) are also not applicable to our results. It could be that a small intake of *D. magna* is necessary for nutritional reasons.

Apart from this small deviation from the model of Charnov, his model predicts the behaviour of *H. piceatus* remarkably well. The model, however, did not agree with Persson's (1985) findings. Persson found that *Perca fluviatilis* feeds more efficiently on *Chaoborus* than on *D. magna* when offered separately, as is the case for *H. piceatus* specimens larger than 0.5 g. However, *P. fluviatilis* generalizes when both prey items are simultaneously offered. According to Persson this is due to the inability of *P. fluviatilis* to simultaneously cope with prey species exhibiting different anti-predation behaviour. Behavioural observations show that *H. piceatus* employs the same feeding technique for *Chaoborus* and *D. magna*. This may explain the difference with *P. fluviatilis*. Like *H. piceatus* several molluscivorous cichlids show an optimal prey choice (Hoogerhoud 1987; Slootweg, unpublished work).

Food choice in nature. Stomach content analyses of wild-caught *H. piceatus* show a positive relationship between the size of the fish and the percentage of fish that have eaten insects (mainly *Chaoborus* larvae and pupae, Witte, unpublished work; Galis, unpublished work). These differences in diet are probably due to differential food selection since ontogenetic series were selected from each catch. The preference of *H. piceatus* for insects increases with the size of the fish. This agrees well with our laboratory data which show that during growth the selection of *Chaoborus* instead of *D. magna* becomes increasingly more profitable. The possible effects of competition and predation have not been investigated, but partitioning of food among ontogenetic stages will lead to decreased intraspecific competition.

Does ontogeny pose constraints on uptake efficiency?

When feeding on *Chaoborus*, the efficiency of food uptake by *H. piceatus*, measured as energy per unit time per gram

body weight, is equal for individuals differing as much as thirty times in body weight (0.17–5.17 g). Although considerable allometric changes take place during ontogeny, for all fish sizes the same energetic reward per gram body weight exists. These unexpected results seem to contradict in this case the enormous importance attributed to the constraints posed by ontogeny on the optimal performance of animals by e.g. Gould and Lewontin (1979).

When *H. piceatus* feeds on *D. magna*, the energetic reward per unit body weight decreases with increasing body weight because the processing time per ingested Joule does not decrease as much as the body weight increases ($\ln Y = -0.77 \ln X + 3.6$, $r = 0.98$, $P < 0.05$; Y = total processing time/total ingested energy; X = body weight). The diminished reward per gram body weight can be due to size constraints *per se*. Another possibility is that the need of the fish to grow while continuing to function is constraining the reward rate. If the latter is true adaptive peaks would be expected interspersed with less adaptive stretches. It seems more likely that the diminished reward is due to a size constraint *per se* since the number of *D. magna* ingested per unit time linearly increases with the volume of the fish and is not irregular. However a functional morphological analysis of the processing apparatus is necessary to answer this question, and to further understand the equal reward observed for all sizes of *H. piceatus* when feeding on *Chaoborus*. Such a functional morphological analysis is currently under way and will hopefully lead to a fruitful synthesis of ecology and functional morphology of food uptake during ontogeny.

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