

## Postprandial metabolic changes in larval and juvenile carp (*Cyprinus carpio*).

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**Summary.** Ammonia-nitrogen excretion and oxygen consumption rates after a meal were followed in carp larvae and juveniles of different sizes, starting from early exogenous feeding and until they had reached about 1 g of body weight. There was an immediate rise in the nitrogen excretion rate after feeding; the amplitude and duration of this increase were affected by body weight (BW) and the amount of nitrogen consumed (NI) and could be described by the equation:  $37.61 \text{ BW}^{-0.311} \text{ NI}^{0.802}$ . Endogenous nitrogen excretion rate and basal metabolic rate were affected by both nutritional status and previous nutritional history. A model used to describe the postprandial nitrogen excretion pattern in young carp fitted well with the experimental data. The different coefficients of the model were affected by body weight.

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### Introduction.

Attempts to feed carp (*Cyprinus carpio*) larvae artificially have met with variable success. The ideal practice suggested (Van der Wind, 1979; Bryant and Matty, 1981) was to offer live food up to a certain stage during the larval period and then to switch to artificial diets. However, some earlier results suggested the possibility of directly weaning carp larvae onto artificial diets (Appelbaum, 1977; Dabrowski, 1982). The notion of « adaptation ages » for weaning during early development of teleosts has been considered to be an artefact (Bryant and Matty, 1981), resulting mainly from lack of sufficient knowledge of the nutritional constraints involved at such stages.

Besides nutritional problems that might be involved, successful early weaning of small-sized larvae onto artificial diets would also depend on feeding strategies and techniques. The proteolytic enzymes of live prey were considered to be an important synergistic factor during the initiation of exogenous feeding because frozen or freeze-dried zooplankton were less efficient growth promoters than live material (Dabrowski and Glogowski, 1977; Van Lukowicz, 1979). But Grabner *et al.* (1981) found that the loss of enzymes from zooplankton treated in these ways was due to the processes of leaching and that stability in water could

be improved, for instance, by pelleting freeze-dried zooplankton. Previously, Ragyanszki (1980) had come to similar conclusions, based on her results on enzyme activities in larvae fed either an artificial diet or live food.

Thus, efforts have been restricted so far to the formulation of diets and to strategies involved in the feeding and culture of small-sized fish larvae. For a closer understanding of the basic metabolic changes occurring during larval development, we thought it would be fruitful to study nitrogen and energy metabolism under laboratory conditions. The present work deals with the development of postprandial patterns of nitrogen excretion and oxygen consumption in carp larvae and juveniles.

### Material and methods.

Eggs of *Cyprinus carpio* obtained by artificial spawning were hatched in the laboratory (20 °C). The wet weight of carp in the experiments ranged from 2 mg (earliest exogenous feeding) to about 1 300 mg. Trials were made at a water temperature of  $23 \pm 1$  °C. Larval and juvenile stages were distinguished according to the recommendations of Balon (1975). The carp were fed daily to excess with freshly collected zooplankton (mainly *Bosmina* sp.) sieved according to the size of the fish.

The postprandial patterns of ammonia excretion and oxygen consumption in carp fed a single meal of limited duration were studied : 1) in zooplankton-fed carp from early exogenous feeding up to a mean body weight (BW) of 900 mg ; 2) in carp transferred to a dry artificial diet (protein content : 64 % dry matter) at 25-mg BW and monitored from a BW of 45 to 1 300 mg ; and 3) in carp fasted or fed a non-protein (NP) diet to measure basal metabolic rate. The NP diet contained 65 % crude starch, 25 % fat and 10 % of a vitamin and mineral premix.

The chamber used for continuous measurement of nitrogen excretion and oxygen consumption was a cylindrical glass column, varying in length and diameter according to the size and number of fish. A peristaltic pump controlled the constant flow of thermoregulated fresh water through the chamber. The water in the metabolism chambers was totally renewed in less than 3 min. All trials were made in triplicate. Sampling and analytical procedures have been described already (Kaushik, 1980 ; Kaushik *et al.*, 1982).

Before each trial, the fish well-adapted to a particular diet (except those receiving the first exogenous meal) were fed that diet for a known period (15 min). The fed fish, whose number varied from 30 to 200 depending on the size, were then introduced into the chamber within less than 2-3 min ; measurement began at  $T_0$  and continued until a constant basal rate was recorded. The protocol used to analyze these postprandial patterns is schematically represented in figure 1. Food consumption rate and fish body weight were also noted in each trial.

In a preliminary trial, the effect of an anesthetic (ethylene glycol mono-phenyl ether,  $0.3 \text{ ml.l}^{-1}$ ) on the nitrogen excretion pattern of carp larvae was also studied. Three groups were tested : 1) fish anesthetized before entering the

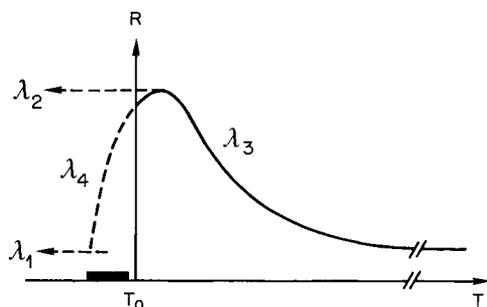


FIG. 1.

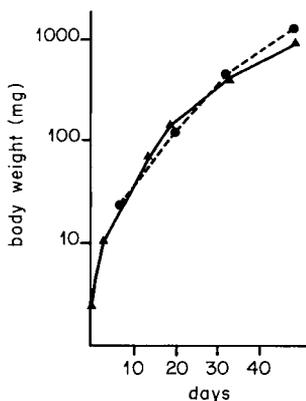


FIG. 2.

FIG. 1. — *Experimental protocol used for measuring metabolic rate (R) against time (T) after feeding.* Before each trial, the larvae were allowed to feed for a given period (black bar). They were then put into a metabolism chamber and measurement began immediately at  $T_0$ . A portion of the ascending part of the exponential curve with slope  $\lambda_4$  before  $T_0$  is hypothetical (see Materials and methods and figures 3 and 4 in Results). Patterns of postprandial rates were fitted using the formula :

$R = \lambda_1 + \lambda_2 (\exp(-\lambda_3 T) - \exp(-\lambda_4 T))$  for intervals of  $T = 15$  min, where  $\lambda_1$  = basal level,  $\lambda_2$  = maximal level,  $\lambda_3$  = instantaneous rate of postprandial decline, and  $\lambda_4$  = instantaneous rate of increase during feeding.

FIG. 2. — *Semi-logarithmic growth curve of carp larvae and juveniles fed either live food ( $\blacktriangle$ ) or artificial food ( $\bullet$ ).* Fish were weaned onto an artificial diet when they reached a mean body weight of 25 mg.

chamber ; 2) fish put in the chamber with anesthetic flowing through for 15 min, followed by slow recovery in fresh water ; and 3) non-anesthetized, sham-treated fish. Groups 1 and 3 responded similarly, while prolonged exposure to the anesthetic affected the postprandial excretion pattern (table 1) and, to a lesser extent, the recovery of the fish as well. We decided to follow procedure 1 which consisted of rapid anesthesia, introduction into the chamber with flowing fresh water, and then analysis.

Endogenous nitrogen excretion (ENE) was estimated either by feeding the fish a NP diet or after a 24-hour fast. Two groups of fish that were initially well-adapted to either the natural diet or the artificial diet were used in this study.

TABLE 1

*Effect of an anesthetic on the different coefficients affecting postprandial nitrogen excretion pattern in zooplankton-fed carp weighing 12.4 mg (Food intake : 4.25 % BW)*

Group*	$\lambda_1^{**}$	$\lambda_2$	$\lambda_3$	$\lambda_4$
1	6.423	260	0.0355	0.3512
2	6.170	215	0.0303	0.3324
3	6.378	290	0.0402	0.3564

\* See Materials & Methods for a description of the groups.

\*\* See figure 1 for a description of the coefficients.

The rate of food passage through the digestive tract was investigated at three different stages : in larvae weighing 10 mg and fed on zooplankton, and in fish of 30 and 200 mg BW that were fed an artificial diet containing a marker (1 %  $\text{Cr}_2\text{O}_3$ ). The remnants of zooplankton in the digestive tract of 10-mg larvae were visually counted and recorded at short intervals after a meal. Carp larvae fed on the artificial diet were sampled at regular intervals after a meal, and whole fish were analyzed for chromic oxide content after acid digestion (Bolin *et al.*, 1952) in a Block digester (Technicon Inc., model BD-40). In the trial on 200-mg fish, the fish were separated into two groups after a marked meal ; one of the groups was fasted and the other was fed the artificial diet without the marker.

Kendall rank correlation coefficients were used for an analysis of trend in time series. Paired t-tests for comparing individual observations in postprandial patterns and other regression analyses were made according to procedures outlined by Snedecor and Cochran (1959) and Draper and Smith (1966). The energy equivalents of oxygen consumption given by Elliott and Davison (1975) were applied to some computations.

## Results.

Growth rates of carp larvae on the natural diet from first feeding onwards and of carp transferred to an artificial diet at 25-mg size are presented in figure 2. The specific growth rate (SGR) of carp fed a natural diet was  $12.3\% \text{ d}^{-1}$  for the period from the first feeding to the end of the trial. The SGR decreased exponentially as size increased. The instantaneous rate of decrease in SGR with time was  $-4.4\% \text{ d}^{-1}$  ( $r > 0.89$ ). During the first 3 days of feeding, it averaged more than  $50\% \text{ d}^{-1}$ . Carp fed the artificial diet had a mean SGR of  $8.7\% \text{ d}^{-1}$  from 25 mg onwards, and the SGR of carp fed live food during that interval was not much different ( $9\% \text{ d}^{-1}$ ).

### a) *Ammonia excretion*

The postprandial ammonia-N excretion patterns in zooplankton-fed carp larvae of different sizes are presented in figure 3. As larvae were allowed to feed *ad libitum* before analysis, food consumption rates (expressed on a dry matter (DM) basis in % of BW) were variable. Food intake as well as the postprandial peak of nitrogen excretion ( $\lambda_2$ ) tended to decrease as size increased (Kendall rank correlation coefficient : 0.69 ;  $p < 0.05$ ). From a level of  $144 \mu\text{g N.g}^{-1}.15 \text{ min}^{-1}$  of peak rate for larvae feeding for the first time (BW : 2 mg), the maximal rate declined to  $56 \mu\text{g N.g}^{-1}.15 \text{ min}^{-1}$  in 70-mg larvae. The decline from this postfeeding maximal rate was very fast at first (basal rate reached in less than 60 min). In growing larvae, it slowed down gradually and the basal rate was reached progressively later (2-3 h). However, compared with subsequent stages, larvae feeding for the first time showed a slower rate of decline from the maximal rate. Even on the second day of exogenous feeding, postprandial increase and decline was very rapid (observations not included in figure 3). The routine excretion rate after first feeding was about 6 to 8 times higher than that of later stages.

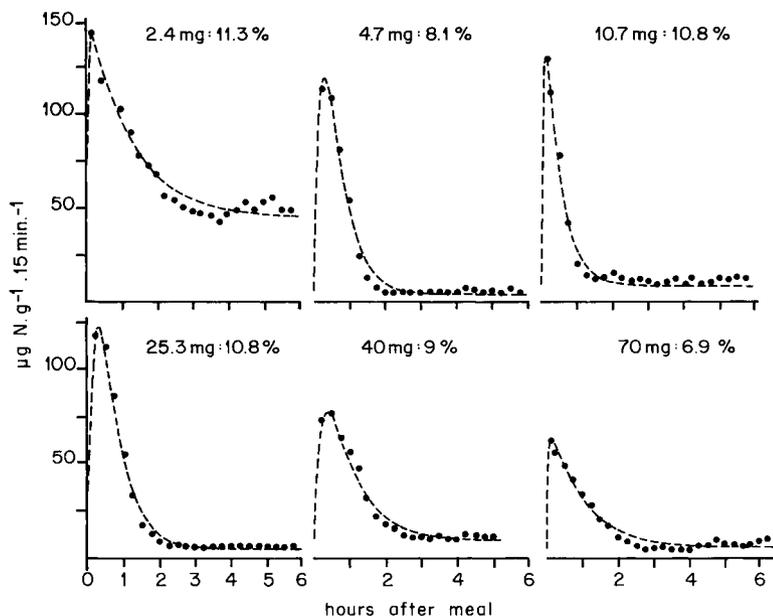


FIG. 3. — Development of postprandial ammonia excretion patterns in carp larvae of selected sizes fed zooplankton. Body weight (in mg) and food intake rate (in % BW on a dry matter basis) are also given. The black dots represent actual observations and the lines the fit obtained using the model described in figure 1.

The patterns of ammonia-N excretion in carp fed zooplankton and those fed the artificial diet are compared in figure 4. The fish used were of the same age but of different body weight. Although care was taken to distribute amounts of artificial diet so as to provide equivalent amounts of nitrogen (in comparison to live food given *ad libitum*), food consumption rates varied. The protein content of zooplankton samples collected daily was also variable ( $59.3 \pm 4.1$  % of protein on a DM basis). Peak rates of ammonia excretion were much lower (less than  $30 \mu\text{g N.g}^{-1}.15 \text{ min}^{-1}$ ) and were observed later (60 to 90 min) as compared to young larvae (15-30 min) (fig. 3). The time of appearance of peak rates ( $T_{\text{max}}$  in min) was affected by body weight (table 2).

Paired t-tests showed that ammonia excretion rates were higher in zooplankton-fed carp than in two (about 100 and 1 000 mg) out of three sizes of carp fed the artificial diet (fig. 4 ;  $p < 0.01$ ). The food consumption rate of 450-mg carp fed the artificial diet (12.9 %) was higher than that of 427-mg fish fed the natural diet (9 %) ; nitrogen excretion rate was also higher.

Regression equations were calculated between body weight and/or nitrogen intake and the different coefficients of the model. The coefficients  $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_4$  were significantly related to body weight (table 2). The maximal rate above basal level and the duration of the postprandial peak were affected by both body weight and nitrogen intake. The slope of postprandial decline ( $\lambda_3$ ) was linearly related to maximal rate ( $\lambda_2$ ) with a high degree of correlation ( $r = 0.827$ ). Basal

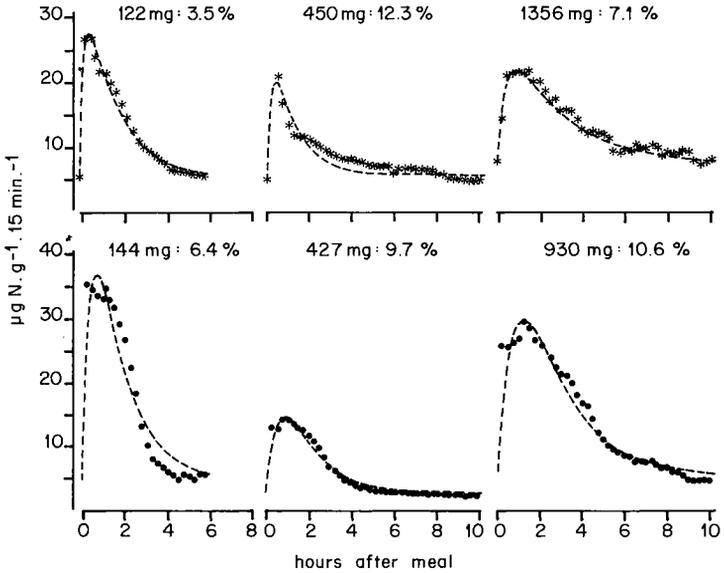


FIG. 4. — Comparison of postprandial ammonia excretion patterns in juvenile carp of selected sizes fed either an artificial diet (\*) or zooplankton (●). Body weight (in mg) and food intake rate (in % BW on a dry matter basis) are also given. The black dots represent actual observations and the lines the fit obtained using the model described in figure 1.

TABLE 2

Relations describing the effect of body weight (BW in mg) and/or nitrogen intake (NI in mg N.g<sup>-1</sup>) on the different parameters of postprandial ammonia excretion rate.  
Regression calculated on log-transformed data

Effect of BW on :

$$\begin{aligned} \lambda_1 &= 21.5022.BW^{-0.3011} ; & r &= -0.687 & a \\ \lambda_2 &= 309.4700.BW^{-0.2300} ; & r &= -0.618 & a \\ \lambda_3 &= 0.0293.BW^{-0.1256} ; & r &= -0.490 & NS \\ \lambda_4 &= 0.4589.BW^{-0.4106} ; & r &= -0.792 & b \\ T_{max}^* &= 11.1758.BW^{0.1843} ; & r &= 0.874 & b \end{aligned}$$

Effect of BW and of NI on :

$$\begin{aligned} \text{Max. rate}^{**} &= 37.61.BW^{-0.311}.NI^{0.802} ; & R^2 &= 0.859 & b \\ \text{Sum rate}^{***} &= 93.38.BW^{-0.117}.NI^{0.751} ; & R^2 &= 0.582 & a \end{aligned}$$

$$\text{Duration of post-prandial rise (min)} = 24.63.BW^{0.210}.NI^{0.680} ; R^2 = 0.605 \quad b$$

a and b : significance at 5 and 1 % levels, respectively.

NS : not significant.

\* : time (in min) after meal when postprandial peak was maximal.

\*\* : peak rate above basal level (ug N.g<sup>-1</sup>.15 min<sup>-1</sup>).

\*\*\* : total postprandial excretion above basal level.

ammonia excretion rate (µg N.g<sup>-1</sup>.h<sup>-1</sup>) was related to body weight (0.196 BW<sup>-0.434</sup> ; r = 0.902).

### b) Urea excretion

Figure 5 shows the postprandial urea-N excretion of carp juveniles weighing about 1 g. These rates in carp fed the different diets diverged significantly from each other in both level (paired t-tests ;  $p < 0.01$ ) and pattern. Mean rates were greater in zooplankton-fed carp than in those fed the artificial diet. For this size of fish, the amount of urea-N excreted as a percentage of the total nitrogen (ammonia + urea) excreted amounted to  $14.5 \pm 2.6 \%$ .

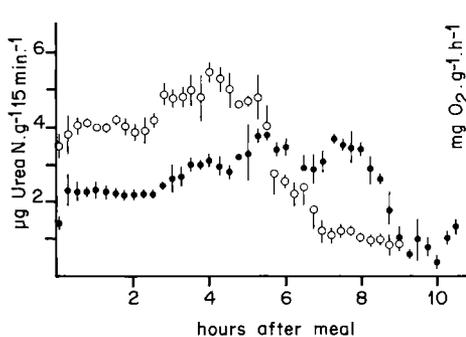


FIG. 5.

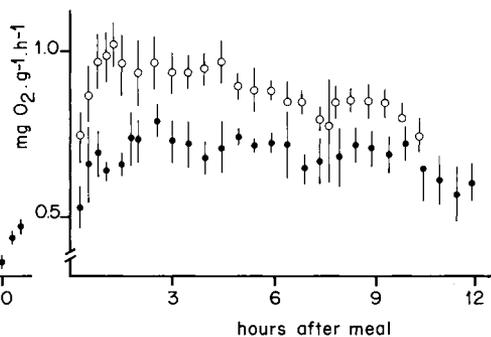


FIG. 6.

FIG. 5. — Urea nitrogen excretion pattern in carp juveniles weighing 1 g and fed either zooplankton (○) or an artificial diet (●). Vertical bars represent standard deviations.

FIG. 6. — Oxygen consumption pattern in juvenile carp (BW :  $\approx 1$  g) fed zooplankton (○) or an artificial diet (●). Vertical bars represent standard deviations.

### c) Oxygen consumption

No consistent variation in postprandial oxygen consumption patterns could be demonstrated in larvae ; mean consumption rates are presented in the upper part of table 3. A slight decrease in mean  $O_2$  consumption rate with body size was shown ( $p < 0.05$ ). The routine metabolic rate was also affected by body size ( $1.55 BW^{-0.123}$  ;  $r = -0.953$ ).

A comparison of oxygen consumption rates (see lower part of table 3) between the two groups showed differences in both mean and basal rates. A definite postprandial pattern of  $O_2$  consumption was noted only in juveniles weighing nearly 1 g (fig. 6). Mean consumption rate was higher when live food was offered than when the artificial diet was given. The routine prefeeding rate of  $O_2$  consumption was not attained even 12 h after the meal.

### d) Endogenous nitrogen excretion

At each point in time, paired t-tests were used to compare the rates of endogenous nitrogen excretion (ENE) between live-fed carp and those on the artificial diet ; a significant difference ( $p < 0.01$ ) was found between the two groups, irrespective of the method of ENE measurement. Table 4 shows the intragroup variability of the mean hourly ENE rate. Fasted fish excreted much

TABLE 3

Mean oxygen consumption rate ( $\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) of carp larvae and juveniles fed either the zooplankton (Z) or the artificial diet (A) and basal metabolic rate at given stages

Body Weight (mg)	Diet	O <sub>2</sub> consumption (Mean $\pm$ s.d.)		Basal rate <sup>a</sup> (Mean $\pm$ s.d.)	
2.02	Z <sup>b</sup>	1.62	0.17	1.42	0.20
2.44	Z <sup>b</sup>	1.42	0.08	1.20	0.10
3.24	Z	1.91	0.27		
7.32	Z	1.16	0.09		
10.74	Z	1.01	0.08		
25.30	Z	1.41	0.21	1.07	0.09
32.90	Z	1.27	0.19	1.01	0.10
70.00	Z	1.43	0.06	0.99	0.05
144	Z	1.12	0.07	0.76	0.10
128	A	0.97	0.09	0.82	0.39
427	Z	0.90	0.04	0.73	0.11
450	A	0.86	0.02	0.59	0.08
930*	Z	0.89	0.12	0.70	0.06
1360*	A	0.68	0.10	0.52	0.07

a : basal metabolic rate =  $1.55 \cdot \text{BW}^{-0.123}$ ;  $r = -0.953$ .

b : first-feeding larvae.

\* : see figure 6 for postprandial patterns.

TABLE 4

Oxygen consumption ( $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) and nitrogen excretion ( $\mu\text{g N} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) rates of carp under conditions of fasting (F) or non-protein (NP) feeding (Mean  $\pm$  s.d.)

Treatment	BW (mg)	O <sub>2</sub> consumption	N excretion	Ratio of fat/protein utilized in terms of :	
				energy	mass
Z to NP	168	1.07 $\pm$ 0.07	24.48 $\pm$ 2.08	3.17	1.89
A to NP	168	1.19 $\pm$ 0.09	16.68 $\pm$ 3.20	5.73	3.43
Z to F	179	0.89 $\pm$ 0.03	35.64 $\pm$ 7.92	1.43	0.85
A to F	230	1.07 $\pm$ 0.09	39.28 $\pm$ 3.20	1.64	0.98

more than carp fed the non-protein diet. On the other hand, oxygen consumption rate was higher in fish fed the non-protein diet, again with a difference between those adapted to live food and those adapted to the artificial diet.

#### e) Evacuation rate

Fifty percent of the ingested zooplankton was evacuated in small larvae (BW : 10 mg) within practically 45 min after feeding. The evacuation rates, expressed in terms of percentage of food remaining in the alimentary tract, were related to time, and exponential models fitted. The coefficients of these models for different sizes of fish are given in table 5. The rate of emptying declined with increase in size. In juveniles weighing 200 mg, marker evacuation rate was slightly slower in fed carp than in fasted ones.

TABLE 5

Evacuation rate in carp larvae. Gut fullness (S %) expressed as an exponential function of time (T in min) :  $S \% = A e^{-\lambda T}$  and the correlation coefficients (r)

BW (mg)	A	$\lambda$	r <sup>a</sup>
10*	107.092	- 0.0152	- 0.863
30**	114.420	- 0.0048	- 0.904
200**			
fed	94.106	- 0.0020	- 0.890
fasted	91.721	- 0.0026	- 0.952

\* : zooplankton-fed larvae.

\*\* : larvae fed an artificial diet with marker incorporated.

a : correlation coefficients were significant (P < 0.01).

## Discussion and conclusions.

It is evident that ingested nitrogen was absorbed very rapidly by carp larvae and juveniles, and that ammonia excretion quickly reached a peak between 15 and 90 min after a meal. Postfeeding impulses of ammonia excretion have been described in bigger fish, including carp (Brett and Zala, 1975 ; Kaushik, 1980). The duration of this immediate postprandial rise (very short in young larvae) lasted longer as the fish grew and was also affected to a great extent by nitrogen intake.

On the first day of feeding, the routine level of excretion was extremely high compared to that on subsequent days, showing very inefficient utilization of ingested nitrogen by larvae feeding for the first time. If maintained, this rate of  $160 \mu\text{g N.g}^{-1}.\text{h}^{-1}$  at the first exogenous feeding would amount to a total daily loss of nearly 36 % of body nitrogen stores. That this increased basal rate is due to inefficient utilization of ingested nitrogen (in the first meal) is evident from the fact that unfed larvae of this size (2 mg) and age (160 degree-days) excrete much less ( $30 \mu\text{g N.g}^{-1}.\text{h}^{-1}$  ; Kaushik *et al.*, 1982). At this stage, computation (Elliott and Davison, 1975) shows that the oxygen consumed is used primarily for protein oxidation.

This high routine rate of excretion decreased very rapidly and, even in larvae weighing 4.7 mg, the pattern of nitrogen excretion was comparable to that observed at later stages. It might have been interesting to follow the patterns after every meal on the first day of exogenous feeding.

The initially high growth rates of larvae fed live food and the later decline in SGR are comparable to the observations of several authors (Bryant and Matty, 1980 ; Hogendoorn, 1980). The carp were weaned onto an artificial diet when they weighed only 25 mg and growth rates were almost identical with the artificial or the natural diet. The high food consumption rates were somewhat similar to those described by Bryant and Matty (1981). Patterns of nitrogen excretion did not differ between the two types of diets. According to Ragyanszki (1980), the digestive tract of carp larvae contains proteolytic activity even immediately after hatching, and there is no difference in activity between larvae fed live food or artificial food.

Peak rate of nitrogen excretion after the meal was more affected by the amount of nitrogen consumed than by body weight (table 2). Although variable, the protein content of fresh zooplankton did not differ much from that of the artificial diet employed. Variability in the gross biochemical composition of live food is an unavoidable natural phenomenon (Yurkowski and Tabachek, 1979). But the greatest differences in nutritional quality have not been observed in the protein or amino acid fraction but in the fatty acid composition of live food (Watanabe *et al.*, 1978 ; Watanabe, 1979).

Oxygen consumption rate seems to be affected by the type of diet employed. The fat/protein ratio utilized, which would explain the oxygen consumed by the fish, also declined with increasing size, especially in juveniles fed the artificial diet. Both routine nitrogen excretion and oxygen consumption rates were also affected by body weight.

The drop in postprandial N-excretion rates to the prefeeding level corresponds to the rate of evacuation of foodstuffs from the digestive tract in larval carp, as suggested by Brett and Zala (1975) in bigger sockeye salmon, *Oncorhynchus nerka*. However, transit rate ( $\lambda$ : table 5) was slightly slower with either natural or artificial diets compared to the rapid decline in the N-excretion rate ( $\lambda_3$  of the model : see table 2 for its relation to BW). The anterior portion of the developing digestive tract undoubtedly plays a major role in the breakdown and absorption of nitrogen. However, Iwai (1969) demonstrated the absorption of protein macromolecules through pinocytotic processes exclusively in the posterior gut of carp larvae and juveniles, but suggested that breakdown of part of the protein and absorption of amino acids might occur in the mid-gut. Another possible explanation for this slight discrepancy between transit rate and excretion might be that the marker evacuation rate does not truly represent the rate of evacuation of foodstuffs from the digestive tract of young carp. The appearance of peak excretion at successively later intervals after feeding also indicates the development and increased differentiation of the digestive tract in growing larvae. De Silva and Weerakoon (1981) found that complete gut evacuation of zooplankton in grass carp (*Ctenopharyngodon idella*) larvae and juveniles (60-360 mg) took place rapidly between 4 and 7 h at 28 °C. Mathematical models of the rate of food passage through the alimentary tract of fish have been described by Jobling (1981). Recently, Fauconneau *et al.* (1982) developed a four-compartment model to describe transit in rainbow trout. In a stomachless teleost, *Blennius pholis*, Grove and Crawford (1980) found a common instantaneous rate of 0.006 for fish varying in size from 1 to 30 g and at 16 °C. However, our results show that this instantaneous rate in carp larvae and juveniles decreases with increasing size.

The immediate rise in ammonia-N excretion rate might also be due partly to an increase in activity, not related directly to deamination processes as observed in the case of blood ammonia levels in rainbow trout (*Salmo gairdneri*), where after a meal there is an immediate but short peak, followed later by a greater rise (Fauconneau and Luquet, 1979). But the postprandial rise of nearly 10 times the prefeeding level with an immediate decline would reflect the rapid utilization of nitrogen, resulting, in a very high growth rate at such young stages, rather than

any increase in activity. Under such conditions, a fast of one day can be considered to represent the basal metabolic rate, and the results on ENE rate (table 4) underline the importance of the nutritional status of the animal as well as its previous nutritional history. Under non-protein feeding conditions, more exogenous fat substrates are available to satisfy energy demands with a reduction in endogenous nitrogen excretion.

More fat was utilized by carp adapted to the artificial diet than by those fed regularly on live food under endogenous metabolic conditions. This difference in nitrogen metabolism is reflected as well in the slightly improved specific growth rate of carp fed the artificial diet (fig. 2).

Differences in the level and pattern of urea excretion in carp fed the different diets (fig. 5) also suggest that carp fed the artificial diet excrete a greater proportion of waste nitrogen in the form of ammonia than carp fed the natural diet. This probably reflects a difference in the biochemical utilization of protein from the two sources. A greater output of ammonia as an end-product of nitrogen catabolism would potentially have some practical significance in recirculated systems. Furthermore, as the peak ammonia excretion rate of growing larvae reflects well the amount of nitrogen consumed (partial correlation coefficient between maximal rates and nitrogen intake with fixed body weight was 0.92), these rates could well be a practical criterion for estimating feed intake in very young larvae fed artificial diets.

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**Résumé.** *Métabolisme post-prandial chez les larves et juvéniles de la Carpe (Cyprinus carpio).*

L'évolution de l'excrétion ammoniacale et de la consommation d'oxygène après un repas a été suivie chez les larves et juvéniles de la Carpe, du début de leur alimentation exogène jusqu'à un poids moyen de 1 g. Nous avons observé une augmentation immédiate du taux d'excrétion azotée après le repas : la durée de cette augmentation et son amplitude ont été liées au poids vif et à la quantité de l'azote ingérée. Une comparaison entre animaux recevant du zooplancton frais et ceux nourris avec un aliment artificiel a également été effectuée. L'excrétion de l'azote endogène et le métabolisme de base ont été influencés par l'état (jeûne, alimentation non protéique) et l'antécédent (alimentation naturelle ou artificielle) nutritionnels des poissons. Un modèle a été utilisé pour décrire l'évolution post-prandiale de l'excrétion ammoniacale et les différents coefficients de ce modèle ont été affectés par le poids vif des poissons.

## Références

- APPELBAUM S., 1977. Geeigneter Ersatz für Lebendnahrung von Karpfenbrut ? *Arch. Fisch. Wiss.*, **28**, 31-43.
- BALON E. K., 1975. Terminology of intervals in fish development. *J. Fish. Res. Board Can.*, **32**, 1663-1670.
- BOLIN D. W., KING R. P., KLOSTERMAN W. W., 1952. A simplified method for the determination of chromic oxide (Cr<sub>2</sub>O<sub>3</sub>) when used as an inert substance. *Science*, **116**, 634-635.

- BRETT J. R., ZALA C. A., 1975. Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (*Oncorhynchus nerka*) under controlled conditions. *J. Fish. Res. Board Can.*, **32**, 2479-2486.
- BRYANT P. L., MATTY A. J., 1980. Optimisation of *Artemia* feeding rate for carp (*Cyprinus carpio* L.) larvae. *Aquaculture*, **21**, 203-212.
- BRYANT P. L., MATTY A. J., 1981. Adaptation of carp (*Cyprinus carpio*) larvae to artificial diets. I. Optimum feeding rate and adaptation age for a commercial diet. *Aquaculture*, **23**, 275-286.
- DABROWSKI K. R., 1982. Further study on dry diet formulation for common carp larvae. *Riv. ital. Piscicult. Ittiopatol.*, **17**, 11-39.
- DABROWSKI K., GLOGOWSKI J., 1977. Studies on the role of proteolytic enzymes in digestion processes in fish. *Hydrobiologia*, **54**, 129-134.
- DE SILVA S. S., WEERAKOON D. E. M., 1981. Growth, food intake and evacuation rates of grass carp, *Ctenopharyngodon idella* fry. *Aquaculture*, **25**, 67-76.
- DRAPER N. R., SMITH H., 1966. *Applied regression analysis*. John Wiley and Sons, Inc., New York.
- ELLIOTT J. M., DAIVSON W., 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia*, **19**, 195-201.
- FAUCONNEAU B., CHOUBERT G., BLANC D., BREQUE J., LUQUET P., 1982. Influence of environmental temperature on flow rate of foodstuffs through the gastrointestinal tract of rainbow trout (soumis à publication).
- FAUCONNEAU B., LUQUET P., 1979. Influence d'une élévation de température sur l'évolution de l'aminocidémie et de l'ammoniémie après un repas chez la truite arc-en-ciel (*Salmo gairdneri* R.). *Ann. Biol. anim. Bioch. Biophys.*, **19**, 1063-1079.
- GRABNER M., WIESER W., LACKNER R., 1981. The suitability of frozen and freeze-dried zooplankton as food for fish larvae : a biochemical test program. *Aquaculture*, **26**, 85-94.
- GROVE D. J., CRAWFORD C., 1980. Correlation between digestion rate and feeding frequency in the stomachless teleost, *Blennius pholis* L. *J. Fish Biol.*, **16**, 235-247.
- HOGENDOORN H., 1980. Controlled propagation of the African catfish, *Clarias lazera* (C & V). III. Feeding and growth of fry. *Aquaculture*, **21**, 233-241.
- IWAI T., 1969. Fine structure of gut epithelial cells of larval and juvenile carp during absorption of fat and protein. *Arch. Histol. Jap.*, **30**, 183-199.
- JOBLING M., 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *J. Fish Biol.*, **19**, 245-257.
- KAUSHIK S. J., 1980. Influence of nutritional status on the daily patterns of nitrogen excretion in carp (*Cyprinus carpio* L.) and rainbow trout (*Salmo gairdneri* R.). *Reprod. Nutr. Dévelop.*, **20**, 1751-1765.
- KAUSHIK S. J., DABROWSKI K., LUQUET P., 1982. Patterns of nitrogen excretion and oxygen consumption during ontogenesis of carp (*Cyprinus carpio*). *Can. J. Fish. Aquat. Sci.*, **39**, 1095-1105.
- RAGYANSZKI M., 1980. Preliminary investigations on the proteolytic digestive enzymes of carp fry. *Aquacult. hung.*, **2**, 27-30.
- SNEDECOR G. W., COCHRAN W. G., 1959. *Statistical methods*. Iowa State Univ. Press, Iowa, USA, 534 p.
- VAN DER WIND J. J., 1979. Feeds and feeding in fry and fingerling culture. *EIFAC Tech. Pap.*, **35**, Suppl. 1, 59-69.
- VON LUKOWICZ M., 1979. Experiments on first fuding of carp fry with alevin and freeze-dried fish. *EIFAC Tech. Pap.*, **35**, Suppl. 1, 94-102.
- YURKOWSKI M., TABACHEK J. L., 1979. Proximate and amino acid composition of some natural fish foods. In J. HALVER K., TIEWS, *Finfish nutrition and fishfeed technology*, vol 1, 435-448, Heenemann GmbH & Co., Berlin.
- WATANABE T., 1979. Nutritional quality of living feeds used in seed production of fish. *Proc. 7th Japan-Soviet Joint Symp. Aquaculture*, Sept 1978, pp. 49-57.
- WATANABE T., ARAKAWA T., KITAJIMA C., FUJITA S., 1978. Nutritional evaluation of proteins of living feeds used in seed production of fish. *Bull. jap. Soc. sci. Fish.*, **44**, 985-988.
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