

Compensatory growth and matter or energy deposition in *Vimba vimba* juveniles fed natural food or a formulated diet

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Abstract. *Vimba vimba* (L.) juveniles (initial weight 0.323 g) were fed continuously two contrasting diets, or starved for 7 days, then re-fed. No mortality was observed throughout the experiment. Starved fish lost body weight. During the re-alimentation period compensatory growth occurred on both diets. Full compensation of body wet weight was exhibited only with fish fed natural food. Initial increase of the variability of wet weight was arrested during starvation on both diets. Variability of weight in fish on natural food continued to increase during re-feeding, while on the dry diet the variability stabilised. This can be explained by differences in food particle size distribution between the diets. The observed high value of the condition coefficient is indicative of a combination of high lipids and low mineral content in the body. The fish fed contrasting diets used different strategies in resource allocation during the compensatory phase. *Vimba vimba* fed natural food promoted growth in length, allocating consumed food to structural tissues and increasing water intake. Fish receiving formulated diet first restored energy reserves, then continued to create new structural mass.

Key words: vimba, natural food, dry diet, starvation, growth compensation, tissue chemical composition

Introduction

A migratory fish species vimba, *Vimba vimba* (L.), was commonly distributed in Poland until the late 1960s and had a high commercial value (Wiśniewolski 1987). At present it is vulnerable in the Czech Republic (Lusk et al. 2004), endangered in Austria (Schiemer & Spindler 1989, Schiemer & Waidebacher 1992) and critically endangered in Poland (Witkowski et al. 1999). Ecosystem-centred restitution programmes include, among others, captive breeding and restocking, based on genetic analysis, in order to sustain genetic diversity of the species. The programme for *V. vimba* restitution in Poland assumes mass production of material for stocking (Syech 1996).

Larvae and juveniles of this fish can be successfully reared under controlled conditions (Wolnicki 1996). However intensive feeding of *V. vimba* juveniles with formulated dry diets may result in severe body deformities (Wolnicki 2005). Skeletal malformations have been found to be a common problem in intensive rearing of cyprinid juveniles exclusively on formulated diets under controlled conditions, and have been observed in nase, *Chondrostoma nasus* (L.) (Wolnicki & Myszkowski 1999), crucian carp, *Carassius carassius* (L.) (Myszkowski et al. 2002), lake minnow, *Eupallasella percunurus* (Pallas) (Kamiński et al. 2005) and tench, *Tinca tinca* (L.) (Kamler et al. 2006). This phenomenon is attributed to unsuitable diet composition, including excessive content of lipids (Hassan et al. 1997, Myszkowski et al. 2002, Rennert et al. 2003), poor absorption of minerals from food and phosphorus deficiency (Lall 2002, Roberts 2002) or overfeeding (Wolnicki 2005, Kamler et al. 2006).

In the field many fish experience periods of starvation or food shortage (for example Akiyama & Nose 1980, Paul et al. 1995, reviews in Love 1980, Opuszynski

1983 and Jobling 1994). Compensatory growth (recovery or “catch-up” growth) was defined by Russell & Wootton (1992) as “the ability of a dietary restricted animal to achieve its normal body weight and form by a growth spurt on re-alimentation”. In recent years studies of fish compensatory growth have increased in number both in ecology- and aquaculture-oriented research. From studies on alternating periods of starvation or restricted regimes with those of recommenced feeding the compensatory growth was suggested to be accompanied by an improved efficiency of food utilisation for growth (Miglavš & Jobling 1989a,b, Russell & Wootton 1992, Wieser et al. 1992, review in Jobling 1994, Luquet et al. 1995, Boujard et al. 2000, Qian et al. 2000). However, changes of feeding regime may involve deep changes in body composition, thus compensatory growth, when expressed in terms of wet weight alone, may not give an accurate illustration of the response to feeding conditions (Jobling 1999).

Applying techniques using compensatory growth and elevated food utilisation efficiency have been suggested as promising in aquaculture (Luquet et al. 1995). However, responses of growth and efficiency to feeding disruptions were species-specific, depending on fish size, duration and/or extent of food restriction (Wieser et al. 1992, Jobling 1994, Luquet et al. 1995, Sæther & Jobling 1999), and nutritional history (Boujard et al. 2000). Thus the benefit of the introduction of disrupted-recommended feeding for intensified growth and promotion of food utilisation efficiency is not so clear (Jobling 1994). On the other hand, a question of whether short-term starvation can be used in aquaculture practice to prevent fish overfeeding remains unanswered.

In this paper we investigate to what extent *V. vimba* fed natural food or a formulated diet can compensate for growth over a short period of food deprivation. Changes in size variability and condition coefficient were examined, and preferential allocation of different resources to growth were compared between the two diets.

Materials and Methods

Fish

The experimental fish were juvenile *V. vimba*, being pooled offspring of two females and three males. Ovulation was induced by an injection of GnRH analogue Ovopel (Horváth et al. 1997); the males were not stimulated. Larvae were fed *ad libitum* with freshly hatched *Artemia* nauplii from the first feeding (day 4 post hatch) for 17 days, then with a commercial formulated dry diet ASTA 2005 (Pol. Acad. Sci., Poland), supplemented with *Artemia* nauplii for 21 days, and for the subsequent 8 days with ASTA 2005 and frozen, commercially available Chironomidae larvae. At the beginning of the experiment (50 days post hatch) the total length and wet body weight were 36.7 ± 1.57 mm and 0.323 ± 0.041 g, respectively (mean \pm SD). The fish were stocked into eight experimental aquaria. Each aquarium (20 dm³) contained 110 individuals. The stocking procedure (Myszko ws ki et al. 2002) provided the same size distribution in all aquaria.

Experimental procedures

The experiment was designed in parallel with two contrasting diets (Table 1). Two fish groups, each in duplicate, were fed natural food comprised of frozen Chironomidae larvae.

Two other groups, also in duplicate, were fed the dry diet ASTA 2005. This diet proved to cause no body deformities when fed to juvenile cyprinids (Myszowski et al. 2002, Kamiński et al. 2005, Wolnicki et al. 2006). All groups were fed for the first ten days of the experiment (Table 2). Then the duplicate groups CHIR-S and ASTA-S were starved for seven days. When feeding was resumed the fish started to recover from starvation. The two duplicate groups CHIR-F and ASTA-F were fed continuously. The amounts of both diets (Table 2) were provided *ad libitum*. The daily food rations were adjusted every 5 days of the experiment, according to the current fish biomass.

The fish were fed manually at 8:00, 11:00, 14:00, 17:00 and 20:00, in equal portions. Prior to feeding the cubes of frozen Chironomidae larvae were cut into small pieces and thawed in a small volume of water. The aquaria were equipped with a system preventing food from being washed out.

Table 1. Particle size, dry matter, chemical composition and caloric value of Chironomidae and formulated diet ASTA 2005 fed to *V. vimba* juveniles.

Parameter	Chironomidae	ASTA 2005
Particle size (mm)	1–15	0.3–0.5
Dry matter (% wet matter)	19.00	92.68
Ash (% dry matter)	5.15	10.27
Protein (% dry matter)	62.74	48.90
Caloric value (kJ g ⁻¹ dry matter)	25.00	25.50

Facilities and water properties

The aquaria were placed in a raceway and separated with black plastic sheets. Our earlier observations (unpubl. data) suggest social interactions between *V. vimba* from neighbouring aquaria; experimental results might be biased by that behaviour. Aquaria were continuously supplied with water (0.3 dm³min⁻¹) originating from a recirculation system with a polyethylene fluidized bed bio-filter. Light, at an intensity of 750 lx at the water surface, was provided with fluorescent lamps, from 08:00 to 21:00. The aquaria were cleaned of faeces and uneaten food in the evenings. Water temperature, recorded every minute, was kept between 24.4 and 25.8°C, and averaged 25.1 ± 0.1 °C (± SD). The dissolved oxygen level was measured daily and was maintained over 50%. Ammonia and nitrite concentrations remained below 0.1 mg dm⁻³, and 0.02 mg dm⁻³, respectively. Conductivity was between 402 to 428 µS cm⁻¹, and pH between 7.4 and 7.9.

Table 2. Daily doses (% of stock biomass) of two diets: Chironomidae and formulated dry diet ASTA 2005 administered to *V. vimba* four feeding groups. CHIR-F, ASTA-F, continuously fed; CHIR-S, ASTA-S, starved and recovering from starvation.

Period (days)	Feeding groups			
	CHIR-F	CHIR-S	ASTA-F	ASTA-S
1-10	19	19	3	3
11-17	19	0	3	0
18-38 or 36*	30	30	5	5

* End of the experiment 38th day for *V. vimba* fed Chironomidae, 36th day for those fed ASTA 2005.

Data collection and analysis

All fish were individually measured to the nearest 0.1 mm total length and 0.01 g weight on days: 1 (beginning of experiment, BE), 10 (beginning of starvation, BS), 17 (end of starvation, ES), and 38 or 36 for fish fed Chironomidae or ASTA 2005 respectively (end of experiment, EE). After measurements fish were returned to the aquaria. On the final day of the experiment all fish were also inspected for the presence of body deformities. Additional measurements (30 fish from each aquarium, returned after measurement) were carried out every 5th day, in order to adjust food rations to the current stock biomass.

All manipulations with fish were performed before 8:00 AM under anaesthesia induced by immersion in 0.4 g dm⁻³ water solution of 2-phenoxyethanol. This treatment had been shown to have no effect on the performance of juveniles of several cyprinids (for example *Vimba vimba*, K a m i ń s k i et al. 2001; *Carassius carassius*, M y s z k o w s k i et al. 2002; *Tinca tinca*, M y s z k o w s k i et al. 2003). In the present experiment we observed that immediately after recovery from anaesthesia fish started feeding.

Condition coefficient (K) was computed following the formula: $K = 10^5 \text{ BW TL}^{-3}$ where BW is wet body weight (g) and TL is total length (mm).

Relative growth rate (% d⁻¹) (R i c k e r 1975, M y s z k o w s k i 1997) was calculated as $\text{RGR} = 100 e^G - 1$; $G = \ln(\text{BW}_{\text{ES}} / \text{BW}_{\text{EE}}) / t$, where BW_{ES} and BW_{EE} are wet body weights at the end of starvation and at the end of the experiment, respectively, and t is duration of the re-alimentation period.

In order to determine hydration of the fish body and chemical composition of whole fish body dry matter, samples of two fish from each experimental group were taken at the beginning of starvation, the end of starvation and the end of experiment. The scales were carefully removed, then the fish were frozen at -18 °C. Their wet weight, and dry weight after drying at 65 °C to constant weight in a desiccator over NaOH, were determined for each fish individually.

Chemical composition of whole fish body dry matter was determined in two fish from each experimental group. The material was homogenised in an agate mortar, and dried at 65 °C to constant weight. Ash percentage in dry matter (A) was determined after ashing two pooled fish in platinum cups at 450 °C for 24 h. Triplicate sub-samples of 3–4 mg each were analysed (C, H, N and S, % dry matter) using an elemental CHNS-O automatic analyser Carlo Erba (1108); sulphanylamine served as a reference. Minimum and maximum coefficients of variation among the triplicate readings in 20 individual fish were: 0.03 to 1.26% for carbon, 0.36 to 2.16% for hydrogen and 0.32 to 3.64% for nitrogen, 3.85 to 23.81% for sulphur.

The oxygen fraction (O, % dry matter) was calculated as $O = 100 - (C + H + N + S + A)$. Caloric value of the dry matter (J mg⁻¹) was calculated from the C, H, S and O fractions using a formula for solid fuels given by the analyser's program (K a m l e r et al. 1994). Protein (% dry matter) was computed using the nitrogen-to-protein conversion factor 5.78 (G n a i g e r & B i t t e r l i c h 1984).

The content of dry matter in wet matter and chemical composition of both diets were determined using the same methods.

Results

During the experiment a 100% survival was observed. No deformed individuals were found in any experimental groups.

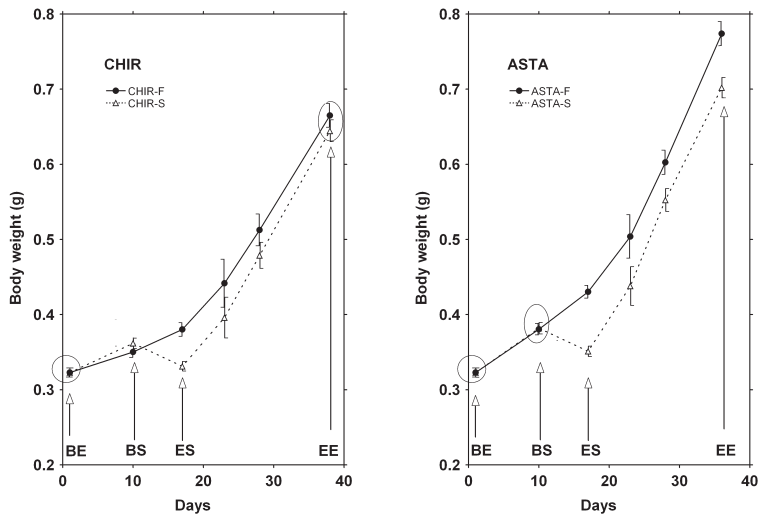


Fig. 1. Growth in wet weight of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA). BE – beginning of the experiment, BS – beginning of starvation, ES – end of starvation, EE – end of the experiment. Vertical lines – 95% confidence intervals. All equal-aged pairs of continuously fed fish and fish recovering from a 7 d starvation differed significantly (Student’s t-test, $P < 0.05$), except the encircled ones.

Fish in both groups, CHIR-S and ASTA-S, exhibited loss of body wet weight during one week of food deprivation (from BS to ES in Fig. 1). During recovery from starvation (from ES to EE) these fish grew faster than the continuously fed ones (CHIR-F and ASTA-F): the RGR values amounted to 3.22% d⁻¹ (CHIR-S), 2.70% d⁻¹ (CHIR-F), and 3.71% d⁻¹ (ASTA-S), 3.14% d⁻¹ (ASTA-F). Thus, compensatory growth was observed on both diets. However, only the chironomid-fed fish displayed a full compensation of body wet weight (encircled

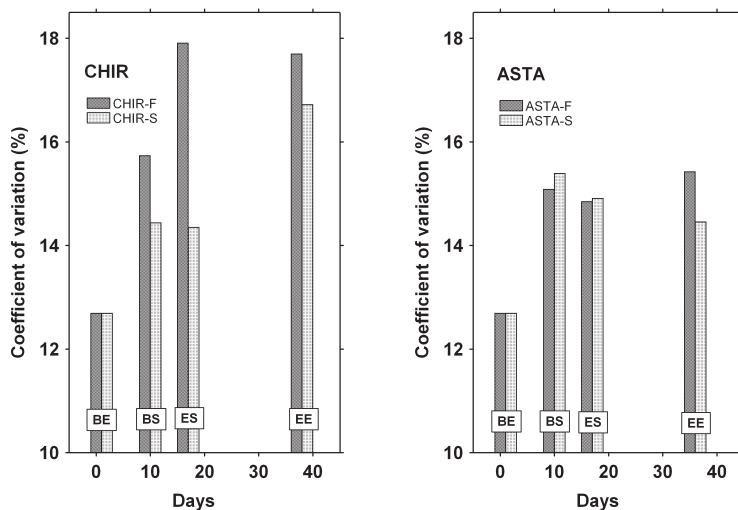


Fig. 2. Time trends in variability of body wet weight (expressed as coefficient of variation = $SD \text{ mean}^{-1} \cdot 100$) in *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA), continuously fed (CHIR-F, ASTA-F) or recovering from starvation (CHIR-S, ASTA-S). Denotations BE, BS, ES and EE as in Fig. 1.

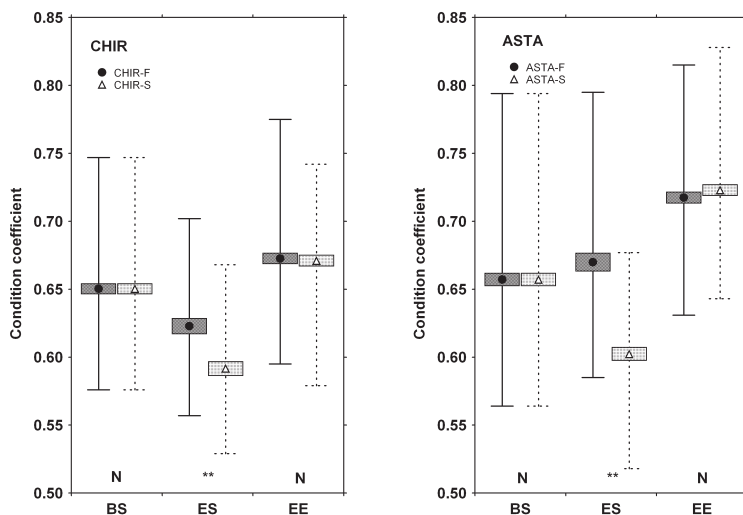


Fig. 3. Condition coefficient of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA). Minimum and maximum values (vertical lines), 95% confidence intervals (boxes) and mean values (circles or triangles) are shown. N – no significant results between continuously fed (CHIR-F, ASTA-F) and recovering from starvation fish (CHIR-S, ASTA-S); Student's t-test, $P > 0.05$, ** - highly significant results (Student's t-test, $P < 0.01$). Denotations BS, ES and EE as in Fig. 1.

points at EE in Fig. 1), while in the ASTA-fed fish the size advantage of the continuously fed fish was maintained until the end of the experiment (Fig. 1).

In the CHIR-F group variability of wet body weight increased with age (Fig. 2). No increase of variability was found in the CHIR-S group during starvation (from BS to ES), but during the re-alimentation period (from ES to EE) the variability almost caught up with

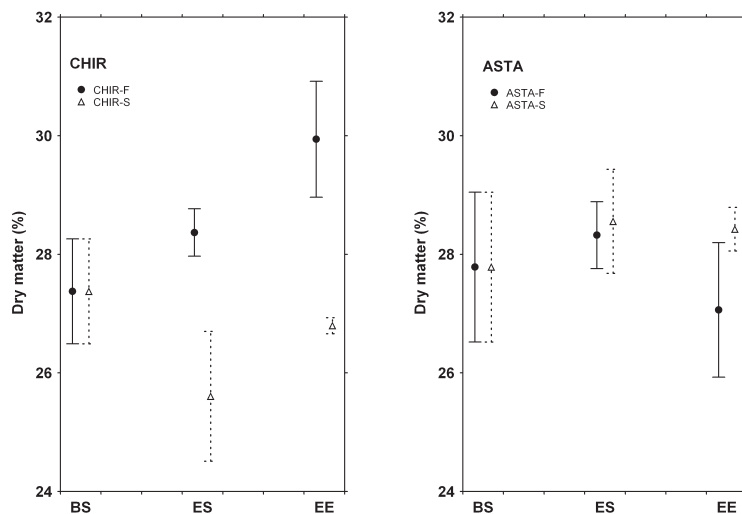


Fig. 4. Percentage of dry matter in wet matter in body of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA), continuously fed (CHIR-F, ASTA-F) or recovering from starvation (CHIR-S, ASTA-S). Minimum and maximum values (vertical lines) and mean values (circles or triangles) are shown. Denotations BS, ES and EE as in Fig. 1.

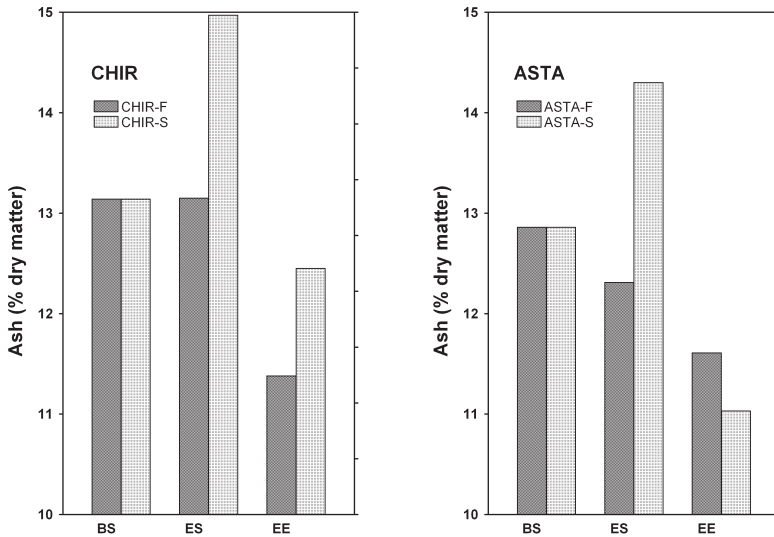


Fig. 5. Ash (% dry matter) in body of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA), continuously fed (CHIR-F, ASTA-F) or recovering from starvation (CHIR-S, ASTA-S). Denotations BS, ES and EE as in Fig. 1.

the CHIR-F group. In the ASTA fed group the variability of body weight increased during the initial 10 days of the experiment only (from BE to BS) and then variability stabilised. Temporal changes of CV were similar in the ASTA-F and ASTA-S groups (Fig. 2).

No significant differences between condition coefficient values were found between CHIR-F and CHIR-S as well as between ASTA-F and ASTA-S groups before starvation (BS in Fig. 3). Food deprivation resulted in a significant decrease of condition coefficient

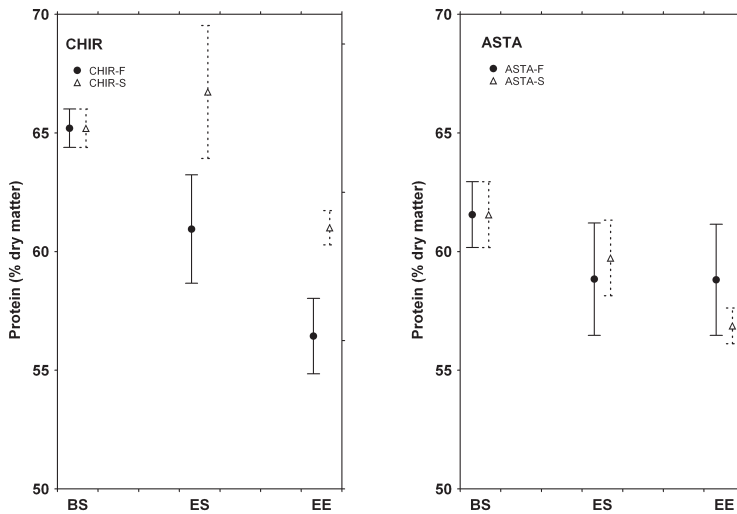


Fig. 6. Protein (% dry matter) in body of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA), continuously fed (CHIR-F, ASTA-F) or recovering from starvation (CHIR-S, ASTA-S). Minimum and maximum values (vertical lines) and mean values (circles or triangles) are shown. Denotations BS, ES and EE as in Fig. 1.

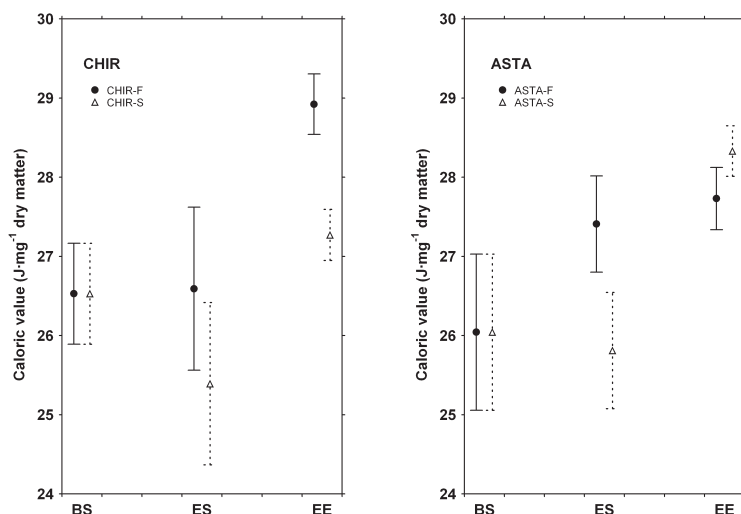


Fig. 7. Caloric value (J mg^{-1} dry matter) in body of *V. vimba* juveniles fed Chironomidae (CHIR) or formulated diet (ASTA), continuously fed (CHIR-F, ASTA-F) or recovering from starvation (CHIR-S, ASTA-S). Minimum and maximum values (vertical lines) and mean values (circles or triangles) are shown. Denotations BS, ES and EE as in Fig. 1.

values (ES), but after re-alimentation (EE) the values in fish recovering from starvation were rapidly restored to the levels recorded in the continuously fed fish. However, additional measurements of 30 fish after five days of refeeding demonstrated that the condition coefficient values in groups fed formulated diet were not significantly different, $K = 0.682 \pm 0.033$ and 0.679 ± 0.025 (mean \pm SD) for ASTA-F and ASTA-S respectively (Student's t-test, $df = 58$, $P = 0.6865$). In contrast, in fish fed natural food the values were different, $K = 0.638 \pm 0.028$ and 0.623 ± 0.028 for CHIR-F and CHIR-S respectively (Student's t-test, $df = 58$, $P = 0.0438$). At the end of the experiment (EE in Fig. 3) in ASTA-fed groups condition coefficients were higher than those in the CHIR-fed groups (Student's t-test, $df = 423$, $P < 0.0001$ for both continuously fed and recovering from starvation groups).

In fish fed Chironomidae the content of dry matter in wet matter increased during the experiment in CHIR-F group (Fig. 4). Starvation resulted in a dramatic drop of the dry matter percentage, and after re-alimentation the compensation response failed to be induced. In fish fed ASTA 2005 the dry matter content did not respond to starvation and re-alimentation (Fig. 4).

Table 3. Interrelationships between condition coefficient, dry matter (% wet matter), ash (% dry matter), protein (% dry matter) and caloric value of dry matter (Cal. val., J mg^{-1}) in *V. vimba* juveniles fed Chironomidae or ASTA 2005 – pooled data. Coefficients of determination (r^2) are shown in the upper right part of the table, significance shown in the lower left part. N non significant result, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Negative (-) or positive (+) relationships are shown.

Parameter	Condition coefficient	Dry matter	Ash	Protein	Cal. val.
Condition coefficient	X	0.15	0.88	0.41	0.65
Dry matter	N	X	0.33	0.58	0.43
Ash	_-***	N	X	0.61	0.87
Protein	_*	_*	+**	X	0.64
Cal. val.	+**	+*	_-***	_*	X

Mineral content decreased with age in fish continuously fed both diets (Fig. 5). Starvation-induced increase of ash percentage in dry matter was observed in both, CHIR-S and ASTA-S groups, while re-alimentation resulted in a decrease of relative content of minerals, especially in the ASTA-S group (Fig. 5). Protein percentage in dry matter (Fig. 6) exhibited a similar pattern, while caloric value of dry matter showed opposite tendencies (Fig. 7).

Interrelationships between minerals, protein and caloric value were confirmed to be strong (Table 3). Condition coefficient and dry matter percentage correlated positively with caloric value, and negatively with ash and protein.

Discussion

Wieser et al. (1992) found juveniles of three cyprinid species fed *Artemia* nauplii unable to fully compensate for the loss of body weight after starvation lasting 7 to 28 days. In contrast, full compensation for body weight growth in cyprinid fishes fed formulated diets was reported for gibel carp, *Carassius auratus gibelio* (Bloch) (Xie et al. 2001) and Eurasian minnow, *Phoxinus phoxinus* (L.) (Zhu et al. 2001). It is generally agreed that strength and duration of a compensatory growth response in fish depends on an array of factors and is species-specific. Our study demonstrated, however, that compensatory growth responses may differ within a species depending on diet. Full compensation of body wet weight occurred only in fish fed natural food, but no complete compensation was observed in those fed formulated diet (Fig. 1). Better compensation of wet weight in the CHIR-S group (Fig. 1) was partly due to a higher water intake (Fig. 4). Data on inter-specific differences in the compensatory growth response depending on diet quality have not been available.

Small fish have small mouth gapes, thus they can ingest only small prey, while the large mouth gape of large individuals allows them to ingest both small and large prey (Lass 1980, Bergot & Kestemont 1995). Larger individuals are more favoured in food acquisition. They eat more and grow faster, and feeding hierarchies are formed, especially under restricted food supply (Jobling & Koskela 1996, Sæther & Jobling 1999). This disparity often results in an increase in an inter-individual body size variation with age (review in Jobling 1999). Increase in fish size variation with time was seen in the group of *V. vimba* fed continuously with Chironomidae (Fig. 2), a food of a wide range of particle sizes (1–15 mm, Table 1). During starvation fish did not compete for food, thus increase of size variability in the CHIR-S group during starvation was arrested, but upon return to adequate feeding variability increased again (Fig. 2). In contrast to Chironomidae, particles of the formulated diet ASTA 2005 were smaller and less variable in size (Table 1). During the initial 10 days of the experiment the smallest individuals could have difficulties in handling the largest ASTA 2005 particles. Thus inter-individual differences in availability of diet particles might be reflected in heterogeneous growth (Fig. 2). All sizes of the ASTA 2005 particles could have been available to all individuals following further growth. Variability of body size remained unchanged and similar in fish fed formulated diet continuously (ASTA-F) and those recovering from starvation (ASTA-S in Fig. 2). Summing up, our results suggest that disparity in growth among individuals is a response to restricted food availability. It is suggested that both aspects of food availability, quantitative (mean number of particles per consumer, Jobling & Koskela 1996, Sæther & Jobling 1999) and qualitative (food particle size distribution) are of importance.

In continuously fed fish an increase of caloric value of dry tissue with age was observed (Fig. 7), reflecting an increasing lipid deposition in older fish (J o b l i n g 1999). Proportions of ash (Fig. 5) and protein (Fig. 6) in dry matter showed ontogenetic changes opposite to caloric value. It has been almost invariably found that in the sequence from lean fish, through fairly fatty fish, fatty fish and to very fatty fish, the content of dry matter (% of wet matter) and lipids (% dry matter) increase, whereas percentage of ash and protein in dry matter decreases (L o v e 1980, K o ł a k o w s k a & K o ł a k o w s k i 2000). Such inter-relationships between biochemical indices were also found in *V. vimba* (Table 3). It is noteworthy that condition coefficient (a morphometric index) was found to correlate with biochemical indices: positively with caloric value, but negatively with protein and, very strongly ($r^2 = 0.88$) negatively with minerals. Also, an increase in condition coefficient and a corresponding increase in caloric value were reported for yellowfin sole, *Pleuronectes asper* (Pallas) ($r^2 = 0.84$, P a u l et al. 1995) and *Tinca tinca* ($r^2 = 0.95$, K a m l e r et al. 2006). A high condition coefficient was associated with low mineral levels ($r^2 = 0.96$) and with body deformities in *T. tinca* fed a commercial formulated diet Futura (K a m l e r et al. 2006). In summary, condition coefficient is a non-invasive index which can be used for making repeated measurements of the same individuals. A high condition coefficient is indicative of a combination of high lipids and low mineral content in the body, which, along with body deformities, may be a response to unsuitable feeding. The absence of body deformities in ASTA 2005 fed fish was found in the present study, but other formulated diets, although of similar composition, often produced deformed cyprinid juveniles (K a m i ń s k i et al. 2005, K a m l e r et al. 2006, W o l n i c k i et al. 2006)

Chironomids are a food relatively low in minerals (ca. 5% of dry matter) compared with the dry diet ASTA 2005 (ca. 10%) (Table 1). However, an elevated content of minerals in the bodies of fish fed Chironomidae compared with those fed dry diet (Fig. 5) suggests a poor utilisation of total minerals from the dry diet. An understanding of this difference is not possible without identification of individual minerals.

The ASTA-S group quickly and completely recovered from the loss of energy reserves during starvation, while the CHIR-S fish showed an incomplete restoration of energy stores (Fig. 7). Two speculative explanations of this difference can be proposed. First, higher availability of particle sizes of the formulated diet might promote hyperphagia, thus a rapid restoration of energy reserves. The second explanation involves the lipostatic model for the control of food intake (K e n n e d y 1953, J o b l i n g & J o h a n s e n 1999). In the ASTA-S group lipid accumulation took place rapidly during recovery growth (Fig. 7). In contrast, in the CHIR-S group lipid accumulation was slower but body wet weight was completely restored (Fig. 1). J o b l i n g & J o h a n s e n (1999) hypothesised that the rate with which lipids are deposited in the body has a regulatory role during compensatory growth.

Taken together, fish fed different diets used different strategies in resources allocation during the re-alimentation phase. *Vimba vimba* fed chironomid larvae allocated consumed food to structural tissues rather than to energy stores, increased water intake, and promoted growth in length. In contrast, fish receiving formulated diet first restored energy reserves, building up body fat tissue what was reflected in rapid increase of condition coefficient during first five days of re-alimentation. Then the fish continued to create new structural mass. Results obtained in the present study suggest that imposing of a short-term starvation-refeeding regime to *V. vimba* juveniles would not lead to production of higher quality fish in a shorter time neither on natural food nor on a high quality formulated diet.

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