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RESEARCH ARTICLE

Optimizing feeding strategies with dry diets to balance growth and reproductive quality in crucian carp (*Carassius carassius*) for conservation-oriented aquaculture

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Abstract. Two commercial dry diets were fed to *Carassius carassius* (L.) juveniles for 60 days at 25°C, each at feeding intensities of 2.0%, 2.5%, or 3.0% of fish biomass per day, to determine the effects of feeding intensity on fish growth, condition factor K, incidence of body deformities, chemical body composition, and gonadal development. Growth of fish and K values were positively influenced by the feeding intensity; likewise fat content in fish bodies. In contrast, ash content was influenced negatively. Intensities of 2.5% and 3.0% resulted in high final incidence of body deformities (range 28.6-76.2%), whereas at 2.0% only 1.9-8.6% fish with deformities were recorded. Gonadal development increased with fish size and feeding intensity, with the most advanced reproductive stages in groups fed at 3.0% biomass/day. Feeding intensity exerted no negative effects on the histological structure of male and female germ cells. However, excessive feeding was associated with a reduced gonadosomatic index (GSI). Our results indicate that feeding at a level slightly below satiation (2.0-2.5% biomass/day) offers the best balance between fish growth, avoidance of body deformities and reproductive readiness. These findings provide guidance for the development of standardized protocols for aquaculture-assisted conservation of *C. carassius*, including stocking programs and captive breeding efforts.

Keywords: fish growth, body deformities, dry diets, feeding intensity, gonadal development

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Introduction

Crucian carp, *Carassius carassius* (L.), is a cyprinid species native to Europe. It typically inhabits still-waters such as ponds, small and shallow lakes, river oxbows and backwaters (Bănărescu 2002, Lusk et al. 2004, Copp et al. 2008, Tarkan et al. 2009, 2011, Sayer et al. 2011). During the 20th century, crucian carp were widely distributed across Central and Northern Europe. However, its ecological status has significantly deteriorated in recent decades. The primary cause of this decline is competitive pressure from closely related invasive Asiatic species, particularly the gibel carp, *Carassius gibelio* (Bloch), and to a lesser extent, the goldfish, *Carassius auratus* (L.). Gibel carp is a strong ecological competitor that outperforms crucian carp in terms of access to food, spawning grounds, and habitat (Sayer et al. 2011, Tapkir et al. 2022). Interspecific hybridization with other Carassius species is also a concern, although it

is considered a secondary threat (Smartt 2007, Copp et al. 2010, Wouters et al. 2012, Olsén and Bonow 2023). Additional factors contributing to the decline include habitat degradation caused by drought, infilling, and terrestrialization (Copp 1991, Wheeler 2000, Sayer et al. 2011), water acidification (Holopainen and Oikari 1992), and broader ecological pressures. As a relatively poor competitor, crucian carp are generally absent from waters with diverse or abundant fish communities.

Consequently, crucian carp populations have declined significantly across most of their native range (Tarkan et al. 2016, Sayer et al. 2020). Despite this trend, the deteriorating status of the species is not fully reflected in formal conservation listings across Europe. For example, *C. carassius* is currently classified as Least Concern (LC) on the IUCN Red List (Freyhof 2024) and is notably absent from the latest national red lists in many European countries, including Poland (Głowaciński 2022), although in 2009 it was classified as vulnerable VU by Witkowski et al. (2009). In contrast, in The Red List of lampreys and fishes of the Czech Republic, the crucian carp is considered as critically endangered species (Lusk et al. 2017), with the highest level of threat in the river basins of the Morava and Oder (Lusková et al. 2008). In Slovakia, it is both legally protected and classified as critically endangered (Hajdú et al. 2023).

England has implemented the first dedicated crucian carp conservation program in Europe, which has already shown promising results (Sayer et al. 2020). In recent years, targeted conservation actions and restocking initiatives have also been introduced – although at a modest scale – in Belgium, Slovakia, and the Czech Republic (Auwerx et al. 2021, Lyach 2022, Hajdú et al. 2023, Šmejkal et al. 2023). All these programs were based on natural pond reproduction; however, restocking with aquaculture-derived material will certainly be necessary in the future. Given the expected reclassification of crucian carp into endangered categories in more European countries (Tapkir et al. 2023), interest in its aquaculture and controlled breeding is growing. Captive rearing of genetically pure stocks, particularly juveniles, in recirculating aquaculture systems (RAS) may become an integral part of conservation strategies. Yet, knowledge regarding optimal rearing conditions under controlled environments remains limited (Myszkowski et al. 2012, Tarkan et al. 2009, Targońska et al. 2012, Cejko and Kucharczyk 2015, Olsén et al. 2018, Sikorska et al. 2018). Most existing data do not specify optimal rearing conditions for this stomachless species (Laurila et al. 1987, Laurila and Holopainen 1990, Żarski et al. 2011, Demény et al. 2012, Sikorska et al. 2018).

In particular, information on the optimal feeding regimes for juvenile crucian carp is scarce. Commercial dry feeds are essential in intensive aquaculture; however, they often result in a high incidence of skeletal deformities (Myszkowski et al. 2012, Kasprzak et al. 2019, Sikorska et al. 2023). Furthermore, the impact of these feeds on gonadal development and reproductive potential remains underexplored (Tarkan et al. 2009, Targońska et al. 2012, Żarski et al. 2014, Cejko and Kucharczyk 2015). This is a critical gap, as dietary deficiencies are known to impair gonadal development and affect reproductive capacity (Duray et al. 1994).

Considering these gaps, the present study aimed to assess the effects of feeding crucian carp juveniles with two commercially available dry diets at different intensities under controlled conditions. We evaluated growth performance, external deformities, body chemical composition, and gonadal development. Special attention was paid to the relationship between diet, feeding intensity, and gonadal maturation, which is essential for the effective conservation of the species through aquaculture-based initiatives.

Material and Methods

Fish origin and preparatory proceedings

Crucian carp larvae with confirmed genetic purity (Panicz, unpubl. data), according to the methodology of Hänfling et al. (2005), were obtained from the

Table 1
Proximate composition of the diets used in the experiment

Fish diet	Aller Performa (AP)	Carpco Crumble (CC)
Total lipids (%)	20.0	15.0
Crude protein (%)	45.0	56.0
Fibre (%)	1.5	1.4
Total P content (%)	1.1	1.8
Caloric value (kJ g^{-1})	18.9	16.7

Wet weight basis; data for commercial dry diets according to the manufacturers.

Table 2
Feeding intensity maintained in the experimental groups

	Experimental group					
Daily feeding rate (% fish biomass)	AP 2.0	AP 2.5	AP 3.0	CC 2.0	CC 2.5	CC 3.0
Maximum	2.7	3.3	4.0	2.7	3.3	4.0
Minimum	1.5	1.9	2.3	1.4	1.8	2.2
Mean	2.04	2.55	3.03	2.01	2.50	2.96

commercial fish farm. After transport to the laboratory, they were stocked in flow-through aquaria (V = 40 dm^3) integrated into a recirculation aquaculture system (RAS) at a density of 50 larvae per dm^3. The fish underwent a two-phase pre-experimental rearing process: (1) larval phase (30 days) – this phase lasted from the onset of exogenous feeding to metamorphosis. The larvae were fed ad libitum with live Artemia nauplii for 13 h daily at 25.0°C (±0.5°C); (2) juvenile phase (3 months) – in which the juveniles were reared at 22.0°C (±0.5°C), at a reduced density of 20 fish per dm^3, and fed frozen Chironomidae larvae administered *ad libitum* for 13 h daily.

Experimental design and conditions

The experiment lasted 60 days and involved four-month-old crucian carp juveniles with an initial total length (TL) of 34.0 ± 2.7 mm and body weight (BW) of 0.47 ± 0.11 g (mean ± SD). Only properly developed individuals were selected. Fish were stocked in 18 aquaria (20 dmł each), at a density of 35 individuals per tank, ensuring similar biomass (16.45 ± 0.07 g) and size distribution across tanks.

Six experimental groups were established using two commercially available dry diets (Table 1): Aller Performa 2 (Aller Aqua, Denmark; "AP" groups) and Carpco Crumble (Coppens International, Netherlands; "CC" groups). Each diet was administered at three feeding intensities: 2.0%, 2.5%, and 3.0% of fish biomass per day (mean values; Table 2), resulting in the following treatment groups: AP2.0, AP2.5, AP3.0, CC2.0, CC2.5, and CC3.0. Feeding rations were adjusted every 10 days based on updated biomass per aquarium, determined by the collective weighing of all fish under mild anesthesia. Fish were hand-fed five times daily (08:00, 11:00, 14:00, 17:00, and 20:00) with equal portions. Aquaria were equipped with plastic barriers to prevent feed loss.

Lighting was maintained from 08:00 to 21:00 using fluorescent tubes, with an intensity of ~ 700 lx at the water surface. Each aquarium received a continuous water inflow of 0.4 dm^3 min^{-1}. Water temperature was maintained at 25.0°C (±0.5°C), pH ranged from 7.8 to 8.2, and oxygen saturation was maintained between 69% and 98% (WTW Multi 3430). Total ammonia nitrogen and nitrite levels were monitored every 3-4 days and did not exceed 0.4 mg dm^{-3} and 0.02 mg dm^{-3}, respectively (Slandi LF300).

Sampling and measurements

Every 10 days during the experiment, all fish were examined for the presence of external body deformities (D, %) such as scoliosis, lordosis, head deformities, and bending opercula. At the same time, their BW was determined to adjust the desired daily feeding rates. At the termination of the experiment, TL and BW were measured in all fish from all aquaria. The final condition factor (K) of the fish was calculated using the equation: $K = 10^5 \times BW \times TL^{-3}$, where BW is expressed in grams and TL in millimeters. Fish handling was conducted under mild anesthesia using an 80 mg dm^{-3} water solution of MS-222 (Argent Lab., USA).

Proximate composition (total protein, crude fat, ash) was analyzed using AOAC methods (AOAC, 2023). Whole-body samples (~50 g wet weight/sample) were collected at the start (one sample) and end (six samples) of the experiment. Dry diets were also sampled for composition analysis. Fish in the samples were euthanized using an MS-222 overdose. Moisture in samples was determined after drying at 60°C to constant weight in a desiccator over silica gel; fish dry body mass was measured to the nearest 0.0001 g. Dried material was homogenized in an agate mortar, stored at –18°C, homogenized again and dried at 60°C to a constant weight for further analyses. Ash contents were determined from subsamples of 100-150 mg of dry matter after ashing at 450°C in a muffle furnace. Total protein (N × 6.25) was determined with the Kjeldahl method after acid digestion. Total lipid was extracted in a Soxhlet apparatus using hexane, and, upon hexane evaporation, measured gravimetrically to the nearest 0.0001 g.

At the end of the experiment, the state of the fish gonads was examined. The organs were dissected from nine individuals from each experimental group. After dissection, the gonads were weighed, and the gonadosomatic index (GSI) was calculated as follows: GSI (%) = 100 × (gonad weight × body weight^{-1}). As the hepatosomatic index (HSI) is usually used as an indicator of energy reserves in the liver and is related to GSI, we also determined its value using the following formula: HSI (%) = 100 × (liver weight × body weight^{-1}).

For histological analyses, gonadal tissue fragments were fixed in Bouin's solution, dehydrated in ethanol, cleared in xylene, and embedded in paraffin blocks. Sections (4-5 μm) were cut using a rotational microtome RM 2155 (LEICA Microsystems, Wetzlar, Germany), and cross-sections of tissues were stained with hematoxylin and eosin (H&E) (Zawistowski 1986). The nomenclature of cellular structures and germ cells in the analyzed gonads was adapted according to Núńez and Duponchelle (2009) and Brown-Peterson et al. (2011). The stages of crucian carp ovary and testis maturity were determined using the gonad maturity scale developed by Sakun and Bucka (1968). Analyses were performed using a light microscope, LEICA DM 3000, and microimage computer analysis software, LEICA QWin Pro (LEICA Microsystems AG, Heerbrugg, Switzerland).

Statistics

Percentages were angularly transformed (Sokal and Rohlf 1969) before analysis. Data normality was assessed using the Kolmogorov-Smirnov test. Two-way ANOVA was used to evaluate the effects of diet and feeding intensity. Post hoc comparisons for TL, BW, and K were made using Tukey's HSD test at $P \leq 0.05$. Tukey's test for unequal sample size was applied for HSI and GSI.

Results

Fish growth, condition and deformities

No fish mortality occurred throughout the 60-day experiment. Both diet and feeding intensity significantly influenced the final fish BW, K, and D. In contrast, only feeding intensity had a significant influence on the final TL. The largest fish were those fed at the highest feeding intensity in groups AP 3.0 and CC 3.0 (Table 3). The interaction between diet and feeding intensity was not significant. The values

Table 3
Final results of the experiment – growth parameters (BW, TL, condition factor K), incidence of body deformities (D) in juvenile crucian carp fed different diets at different intensity level

	Experimental group						Factor (Two-way ANOVA)		
Parameter	AP 2.0	AP 2.5	AP 3.0	CC 2.0	CC 2.5	CC 3.0	Diet	Feeding intensity	Diet x Feeding intensity
BW (g)	1.57 ± 0.42^{c}	2.51 ± 0.71^{b}	3.62 ± 1.12^{a}	1.62 ± 0.44^{c}	2.62 ± 0.77^{b}	3.70 ± 1.07^{a}	0.003	0.000	0.865
TL (mm)	48.0 ± 3.9^{c}	54.0 ± 4.4^{b}	58.8 ± 5.2^{a}	48.8 ± 4.0^{c}	55.2 ± 4.6^{b}	60.1 ± 4.9^{a}	0.235	0.000	0.937
K	1.39 ± 0.08^{d}	1.55 ± 0.11^{c}	1.73 ± 0.17^{a}	1.37 ± 0.08^{d}	1.52 ± 0.23^{c}	1.66 ± 0.12^{b}	0.000	0.000	0.317
D (%)	8.6 ± 4.9^{d}	28.6 ± 5.0^{c}	58.1 ± 11.6^{b}	1.9 ± 1.7^{d}	38.1 ± 8.7^{c}	76.2 ± 7.2^{a}	0.030	0.000	0.006

Values are means ± SD (n = 3). In rows data with different superscripts differ significantly ($P \leq 0.05$, post-hoc Tukey's HSD test). P values from two-way ANOVA.

Table 4
Ash, fat and protein content in the whole body of juvenile crucian carp fed different diets at different intensity level

	Experimental group						Factor (Two-way ANOVA)		
Component (% w.m.)	AP 2.0	AP 2.5	AP 3.0	CC 2.0	CC 2.5	CC 3.0	Diet	Feeding intensity	Diet x Feeding intensity
Ash	2.70 ± 0.14^{a}	2.27 ± 0.12^{ab}	2.14 ± 0.01^{ab}	2.63 ± 0.02^{a}	2.40 ± 0.22^{ab}	2.12 ± 0.01^{b}	0.446	0.002	0.315
Fat	5.18 ± 0.04e	6.17 ± 0.06^{d}	7.01 ± 0.07^{b}	6.07 ± 0.07^{d}	6.41 ± 0.05^{c}	7.32 ± 0.07^{a}	0.000	0.000	0.000
Protein	12.82 ± 0.15^{c}	12.71 ± 0.17^{c}	12.88 ± 0.01^{c}	12.37 ± 0.09^{d}	15.06 ± 0.06^{a}	13.33 ± 0.04^{b}	0.000	0.000	0.000

Values are means ± SD (n = 3). In rows data with different superscripts differ significantly ($P \leq 0.05$, post-hoc Tukey's HSD test). P values from two-way ANOVA. Data in rows with different superscripts differ significantly ($P \leq 0.05$). Components in the initial fish sample: ash 3.78%; fat 1.61%; protein 13.68%.

of K and the share of D were higher with more intensive feeding with dry diets. The maximum value for K (1.73) and the highest D (76.2%) were determined in groups AP 3.0 and CC 3.0, respectively. Fish exhibiting deformities were observed as early as day 20 in these groups. Both diet and feeding intensity had significant effects on deformities, and the interaction between them was also significant (P = 0.006), indicating that the combined effect of diet and feeding level influences the occurrence of deformities.

Body composition

Chemical analysis of crucian carp bodies showed that both factors tested influenced body contents of fat and protein; however, only feeding intensity influenced ash content (Table 4). The higher was feeding intensity, the lower was ash content and the higher was body fat. The intensity of feeding with Aller Performa did not influence protein content in fish bodies (range 12.71-12.88%), whereas in groups fed Carpco Crumble, significant differences appeared, with a maximum value of 15.06% recorded in group CC 2.5.

Histological analysis of gonads

Histological images of crucian carp gonads after feeding with dry diets at different intensities are presented in Fig. 1 (females) and Fig. 2 (males). No histopathological changes were observed in any of the cross-sections of the ovaries and testes of the examined fish.

In fish fed Carpco Crumble at different intensities, the dominating group was composed of females with ovaries in the previtellogenic stage (II). In groups CC 2.0 and CC 2.5 the ovaries with oogonia and single primary growth oocytes were recorded (Fig. 1A), as well as those advanced in maturity fulfilled by primary growth oocytes separated with clearly visible ovarian lamellae (Fig. 1B).

In fish fed Aller Performa, the stage of advancement in gonadal development in both females and

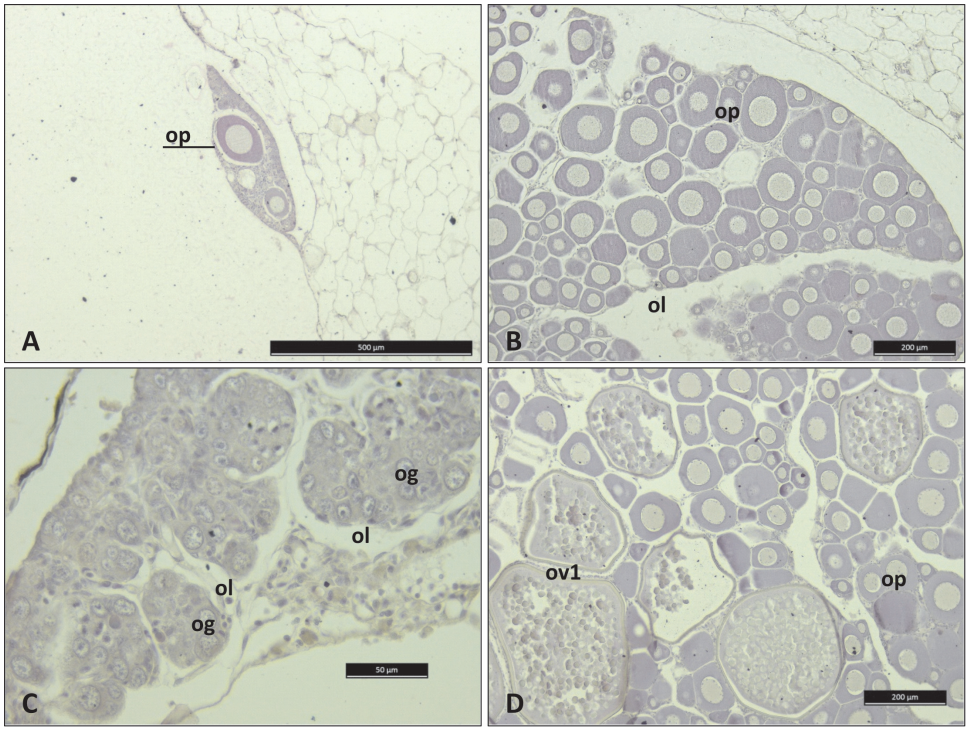

Figure 1. Histological cross-sections of 6-months old crucian carp ovaries: A – I/II stage of maturation in group CC 2.0, B – II stage of maturation in group CC 2.5, C – I stage of maturation in group AP 2.0, D – II/III stage in group AP 3.0. Explanations: og – oogonia, ol – ovarian lamellae, op – previtellogenic oocytes, ov1 – oocytes in the initial phase of vacuolization.

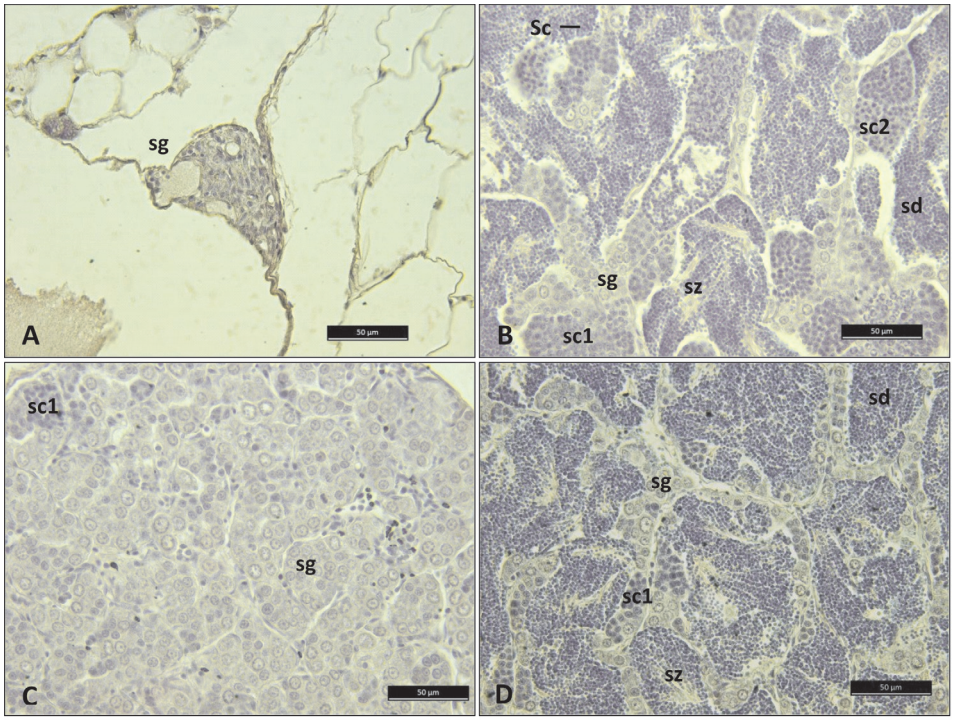

Figure 2. Histological cross-sections of 6-months old crucian carp testes: A – I/II stage of maturation in group CC 2.0, B – III/IV stage in group CC 2.0, C – II stage of maturation in group AP 2.0, D – IV stage of maturation in group AP 3.0. Explanations : Sc –Sertoli cell, sd – spermatid, sg – spermatogonia, sc1 – primary spermatocyte, sp2 – secondary spermatocyte, sz – spermatozoid.

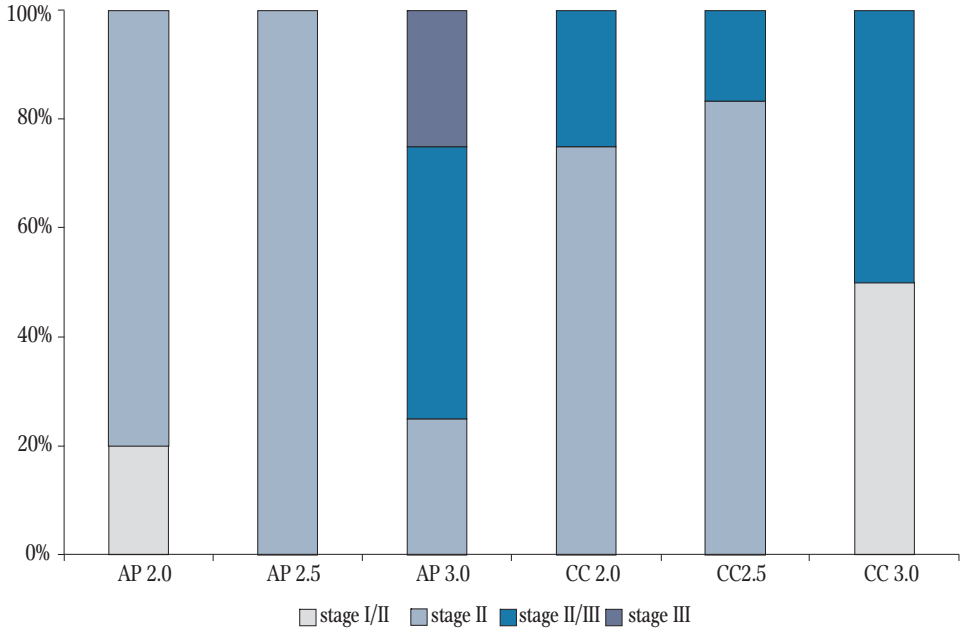

Fig. 3A. Stages of gonadal maturation in 6-months old crucian carp females at the end of the experiment.

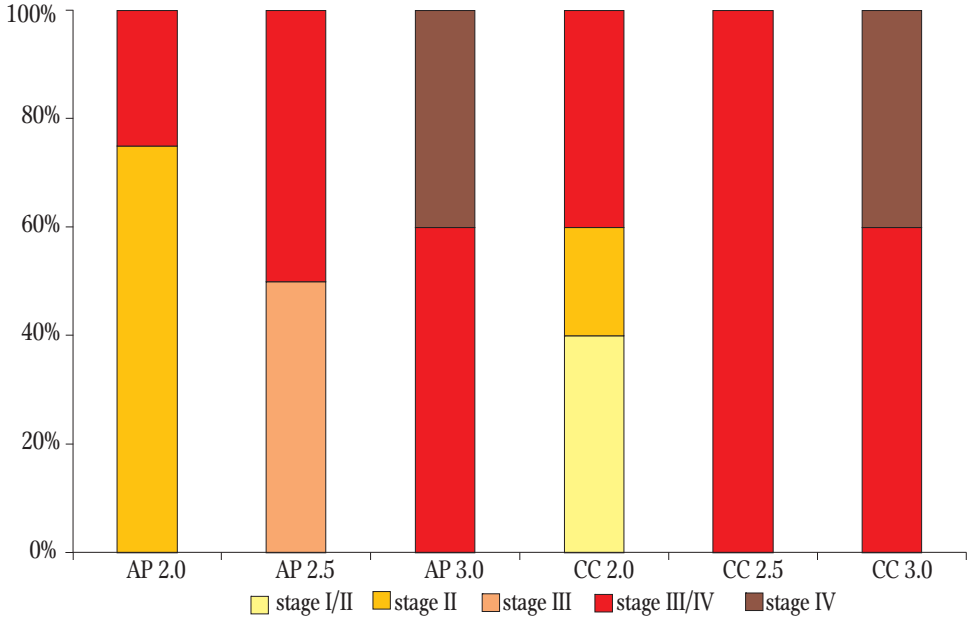

Fig. 3B. Stages of gonadal maturation in 6-months old crucian carp males at the end of the experiment.

males was related to the feeding intensity and thus to the size of the fish (Fig. 3A-3B). In group AP 2.0 dominating (80%) were females with ovaries in II stage of development, although gonads in I/II stage were also found, with visible oogonia grouped into oval nests, separated by ovarian lamellae as shown in Fig. 1C. The II stage was also reached by all females from group AP 2.5. In females from group AP 3.0 ovaries were most often in II/III and even III stage of development, where beside primary vitellogenic oocytes few secondary vitellogenic oocytes were also found (Fig. 1D).

In males fed diet CC, the stage of gonadal development was affected by feeding intensity and fish size (Fig 3B, Table 3). In group CC 2.0 males in I/II, II as well as III/IV stage (Fig. 2A-2B, Fig. 3B) were found, whereas in group CC 3.0 in testis all germ cells of the spermatogenesis pathway, including

Table 5
Final HSI and GSI values in female and male crucian carp fed different diets at different intensity level

	Experimental group						Factor (Two-way ANOVA)		
Parameter	AP 2.0	AP 2.5	AP 3.0	CC 2.0	CC 2.5	CC 3.0	Diet	Feeding intensity	Diet x Feeding intensity
Females									
n	5	5	4	4	6	4			
HSI	6.64 ± 0.95 ^{a}	7.21 ± 1.45^{a}	8.23 ± 0.58^{a}	8.21 ±1.83^{a}	8.25 ± 0.76^{a}	8.35 ± 1.31^{a}	0.058	0.336	0.466
GSI	1.57 ± 0.50^{b}	2.01 ± 0.52^{ab}	2.09 ± 0.26^{ab}	2.38 ± 0.90^{ab}	3.08 ± 0.44^{a}	1.70 ± 0.90^{b}	0.045	0.055	0.049
Males									
n	4	4	5	5	3	5			
HSI	7.03 ± 1.24^{b}	7.98 ± 0.95^{ab}	9.19 ± 1.63^{ab}	8.40 ± 2.69^{ab}	9.24 ± 2.11^{a}	8.40 ± 1.9^{b}	0.419	0.444	0.395
GSI	0.37 ± 0.23^{b}	1.34 ± 0.69^{ab}	0.65 ± 0.32^{b}	1.28 ± 0.40^{ab}	2.17 ± 0.35^{a}	1.27 ± 0.51^{ab}	0.000	0.001	0.769

Values are means ± SD. In rows data not shearing the same superscript letter differ significantly ($P \leq 0.05$, post-hoc Tukey's test for unequal n). P values from two-way ANOVA. Data in rows with different superscripts differ significantly ($P \leq 0.05$).

Table 6
Incidence of deformities in crucian carp juveniles fed commercial dry diets at different intensities at 25°C

Dry diet	Feeding intensity (% fish biomass daily)	Deformities (%)	Source
Aller Performa (Aller Aqua)	2.0	8.6	present paper
	2.5	28.6	
Carpco Crumble (Coppens)	2.0	1.9	present paper
	2.5	38.1	
Aller Futura (Aller Aqua)	2.5	64.0	Sikorska et al. 2023
Aller Futura (Aller Aqua)	3.5	87.0	Kamiński et al. 2021
Carpco Crumble (Coppens)	3.5	74.0	
Carp Starter (Aller Aqua)	4.0	36.0	Myszkowski et al. 2012
Eel (Trouw)	4.0	62.7	
Commercial dry diet X	4.0	36.0	Kasprzak et al. 2019
Commercial dry diet Y	4.0	60.0	

spermatozoa, were observed, what corresponded to III/IV or IV stage of testis maturity.

In 75% males from group AP 2.0 the testes were in II stage of development (Fig. 2C, Fig. 3B), where dominating type of generative cells were spermatogonia, located in formulated spermatic lobules. This stage of gonadal development was reflected in the low GSI index (Table 5). In gonads of males from group AP 3.0 the process of spermatogenesis was more advanced. On histological cross-sections a few spermatogonia, primary and secondary spermatocytes, spermatids, including spermatozoa were visible, what corresponded to III/IV or IV stage of testes development (Fig. 2D).

In crucian carp females mean values of HSI ranged from 6,64 to 8.35, and no significant difference was found among the groups (Table 5). In males significant differences in HSI were found between groups CC 2.5, where the value was the highest, and groups AP 2.0 and CC 3.0, where it was the lowest and ranged from 7.03 to 8.40. For female GSI index, significant differences were found only between the extreme values found for groups AP 2.0 and CC 3.0 (minimum) and group CC 2.5 (maximum). A similar situation was found among males, with a minimum GSI in groups AP 2.0 and AP 3.0 and a maximum in group CC 2.5.

Discussion

Feeding intensity vs. growth and deformities

The sources of knowledge on the effects of juvenile crucian carp feeding on dry formulated feeds are surprisingly scarce, although the species is increasingly becoming a subject of interest for scientists. Crucian carp, like other cyprinid species, are stomachless, which excludes acidic digestion in the alimentary tract and considerably limits the fish's ability to utilize the components included in dry diets. This particular biological feature makes early life stages of crucian carp very difficult to rear under controlled conditions with the use of exclusively dry formulated diets (Żarski et al. 2011, Demény et al. 2012, Myszkowski et al. 2012, Łączyńska et al. 2016, Kamiński et al. 2021). In contrast to the growth of dry feed-fed juvenile crucian carp, which can be satisfactory, as in the present study, the main and unsolved problem remains the high incidence of body deformities. According to Sikorska et al. (2023), among common cypriniforms crucian carp belongs to large group of species of relatively high susceptibility to external deformities, which is considerably higher as compared to other native to Europe cyprinids as common carp *Cyprinus carpio* L. and barbel *Barbus barbus* (L.). Body deformities are species- and diet-specific traits, resulting primarily from the poor utilization of phosphorus from dry diets, which are the major source of this macromineral (Ogino et al. 1979, Hertrampf and Piedad-Pascual 2003). Intensive feeding with dry diets, especially those with a high lipid content, often leads to the mass appearance of deformities in fish (Wolnicki 2005). Deformities are usually accompanied by low body ash content and high fat deposits in the fish body, the latter being expressed as an elevated condition factor (Wolnicki 2005, Kamler et al. 2012). It should be stressed that external deformities do not occur in fish fed exclusively natural food at any intensity of the feeding (Kamler et al. 2006).

The available data indicate that the incidence of deformities is generally dependent on the intensity of feeding with a particular dry diet; that is, more intensive feeding induces deformities in more fish (Kamler et al. 2006). The results of the present study are in agreement with those obtained in earlier feeding trials with juvenile crucian carp under comparable experimental conditions. As shown in Table 6, feeding with the feed used in the present experiment (Carpco Crumble) or with other commercial dry diets always resulted in deformities, and their incidence was found to be diet- and feeding intensity-dependent. This problem is particularly evident when fish receive a dry diet at a level of approximately 2.5% of fish biomass per day or higher. It should be noted that the value of approximately 2.5% is accepted as being close to the level of satiation in several cypriniform species (Wolnicki 2005, Kamler et al. 2006, 2008, Wolnicki et al. 2009, Myszkowski et al. 2010).

Taking into account all the above, the question arises what feeding intensity might be regarded as safe for fish in terms of incidence of deformities. It is noteworthy that in the present experiment deformities appeared even at the lowest intensity of feeding of merely 2.0% of fish biomass, so below satiation level. Since the susceptibility to deformities among cypriniform species is different (Sikorska et al. 2023), their safe level of feeding intensity has also to be different. Such susceptible species as crucian carp seem to require strongly restricted feeding with dry formulated feeds, below the satiation level, limited to less than 2% of their biomass per day. Under such conditions, fish would not be endangered with external deformities; however, their growth would be considerably slower than that under conditions closer to the satiation level.

Feeding vs. development of gonads in females and males

In our study, the female-to-male ratio was very similar (1.17:1.00); however, in natural populations of crucian carp, the sex ratio is more in favor of females (Szczerbowski et. al. 1997). It is generally known that fish gonadal development and fertility are greatly influenced by the diet and nutrients such as vitamins A,

C and E as well as protein, lipid and carbohydrate levels (Memis and Gün 2004, Zhou et al. 2022), although other factors as for example photothermic conditions are also very important. Some effects of nutrients, such as proteins and lipids, and the influence of feed ration size on gonad maturation have been documented in some fish, such as tilapia, *Oreochromis niloticus* (L.) (Gunasekera and Lam 1997, Al-Hafedh et al. 1999), seabream *Sparus aurata* L. (Fernández-Palacios et al. 1997), and rohu *Labeo rohita* (Hamilton) (Khan et al. 2005). However, we still have limited knowledge about the optimal nutritional requirements and the effects of feeding intensity for gonadal development of many fish species, although it has already been shown that the rate of gonad development and the onset of fish maturation can be manipulated by the diet (Cerdá et al. 1994, Izquierdo et al. 2001, Çek and Yilmaz 2009). Generally, restricted feeding during the early stages of fish ontogeny delays the first maturation age, and a quantitatively restricted food supply during the stages of oocyte differentiation reduces the number of eggs (Luquet and Watanabe 1986). Much less is known about the effects of intensive feeding and/or overfeeding on gonadal development. In the present work, the advancement of gonad development in females and males depended on the intensity of feeding and, consequently, on the size of the fish. Interestingly, feeding with dry diets at the highest intensity did not have a detrimental effect on the gonads (no histopathological changes), although it had a clear negative effect on the incidence of body deformities and fat content in the fish body. However, it is worth considering indirect indicators, such as GSI and HSI.

Many researchers have indicated ovary maturation based on HSI, GSI, and the proportion of oocyte stadia (Prakash 2022). The GSI shows the proportion of body tissue devoted to gamete production and can be an appropriate indicator for gonadal development and gonad expenditure (Zhou et al. 2022), providing a quantitative basis for assessing fish gonadal development potential. Liver plays an important role in the gonadal development, because during gonadal maturation vitellogenin and zona radiata proteins are synthesized by hepatocytes and then transported through the bloodstream to the ovaries by means of receptor-mediated pinocytosis (Rizzo and Bazzoli 2020). Therefore, HSI reflects the involvement of the liver in vitellogenesis. Generally, HSI values are higher during maturation and lower values are observed when the gonads are in the ripened stage (Hismayasari et al. 2015).

The hepatosomatic index is also used in fisheries science as an indicator of energy reserves in the liver (Hismayasari et al. 2015, Sharma and Ram 2020), and in our study, higher feeding intensity with dry diets resulted in higher HSI values in female and male crucian carp. In turn, gonadosomatic index was generally higher in females than in males (Table 5). Moreover, in most cases, the GSI values were higher in groups fed dry diets at higher feeding intensities. However, in females fed both dry diets at the highest intensity (3% of fish biomass), the GSI value was clearly lower than that at medium feeding intensity. Especially since similar situation was observed also in males from groups CC 3.0, it may suggest negative effects of overfeeding (probably excessive fat deposits in the fish body negatively affected the ratio of gonad weight to somatic weight).

Generally, in our experiment significant differences in the GSI index were found in different experimental groups, which were certainly related to the feeding intensity and final size of the fish. The highest values of GSI index, i.e. 2.17% and 3.08% for males and females respectively, were recorded in group CC 2.5 with medium level of feeding intensity. Also in Aller Performa-fed fish the highest values of GSI were found in group with the medium intensity of feeding. This may suggest that this level of feeding intensity is the optimum for the rate of gamete development. Feeding intensity had generally no negative effect on the histological structure of male and female germ cells in crucian carp. Likewise, no histopathological changes were observed in the cross-sections of the ovaries and testes.

Implications for aquaculture-based conservation and restoration programs

In light of the shrinking range of this species and insufficient conservation efforts (Sayer et al. 2020,

Auwerx et al. 2021, Lyach 2022, Hajdú et al. 2023), our research may serve as a foundation for future conservation programs for crucian carp, based on habitat restoration and the production of stocking material under aquaculture conditions. Recent efforts in countries such as England and Slovakia have shown promising results (Sayer et al. 2020, Hajdú et al. 2023); however, there is still a need to develop more comprehensive conservation protocols, particularly in areas concerning the production of stocking material, juvenile care, and gonadal development. Our findings indicate that feeding intensities of 2.0-2.5% biomass/day are optimal for maintaining healthy growth, low deformity rates, and proper gonadal development and maturation. This provides a key element in designing effective restocking programs and breeding initiatives related to the reintroduction and restoration of genetically pure populations across Europe, which will contribute to the conservation of *C. carassius*.

Conclusions

Juvenile crucian carp can be effectively and safely reared under controlled conditions using commercial dry diets, provided that the average feeding intensity is limited to 2.0-2.5% of fish biomass per day i.e. slightly below the satiation level. Although growth may be slower under such a restricted regime, the resulting individuals exhibit high biological quality: low deformity rates, favorable body composition, and appropriate gonadal development. These make dry-feed-reared juveniles suitable candidates for use in aquaculture-assisted conservation and restocking programs. Our findings provide essential insights for the development of captive breeding protocols aimed at restoring genetically pure *C. carassius* populations in Central Europe. Given the scarcity of applied studies in this field, our work makes a significant contribution toward establishing standardized methodologies for active species conservation.

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