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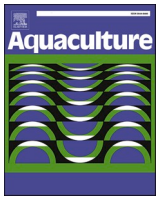

Does nutritional history impact on future performance and utilization of plant based diet in common carp?

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ABSTRACT

This study investigated the possibility to improve the use of plant based feed in common carp (*Cyprinus carpio*), via feeding plant based diet from the early life stage. Fry, obtained from larvae produced by common carp broodstock fed with either of two diets viz. fish based diet (F diet) or plant based diet (P diet), were stocked into six earthen ponds in triplicate. Fry obtained from the F- and P- group were also fed with isoproteic (37% crude protein) and isolipidic (6.5% crude lipid) F- and P- diet respectively, for four months to attain juvenile stage. This early feeding period referred as 'nutritional history F or P', and fish from the respective nutritional histories were denoted as 'F- or P- fish'. After four months, a crossover experiment was initiated with random distribution of F- and P- fish into twelve cages fixed in the pond. Fish in triplicate cages per treatment group were either fed with their original diets or respective complementary diet for six weeks (C- phase). After six weeks, fish reared with complementary diets were switched to their original diet for another six weeks (O- phase). Growth performance, nutrient utilization, gene expression profile (IGF-1, GH and GHR) and protein metabolism enzyme activity were analysed at the end of both C- and O- phase. During C- phase, higher growth performance and improved nutrient utilization in P- fish and F- fish were recorded when they were fed with their original diet (P/F) compared to the complementary diet (F/P). The decreased growth performance and nutrient utilization of F- fish fed with P diet during the C- phase increased again during the O- phase and resumed to a similar growth performance with F- fish fed with F diet; however P- fish could not resume the same growth performance in the O- phase. Expression patterns of IGF-1 and GHR genes in the liver were concomitant with the growth performance. The present study confirms that nutritional history has a significant impact on nutrient utilization during latter life stages, and nutritional programming at early stage may be the strategy for complete replacement of fish based diet with plant based diet in common carp without compromising the growth performance and nutrient utilization. Conclusively, the findings revealed the profound effect of feeding common carp according to their nutritional history on the later performance of the progeny, as well as effective utilization of the plant based diet.

1. Introduction

Aquaculture production in the Central and Eastern Europe (CEE) was 396 thousand MT in 2018, of which 342 thousand MT (86%) was originated from freshwater rearing systems (FAO FishStatJ, 2020). The vast majority (80%) of freshwater fish farming is based on low-production-intensity pond culture, which consists of technologies of polyculture of different carp species, with common carp (*Cyprinus carpio*) being the dominant farmed organism, accounting for 75–80% of pond farming (158 thousand MT in 2018; FAO, 2016). Maximizing production using intensive aquaculture system is most likely the best way to meet this species' expanding market demand. Success of intensive culture practices is highly reliant on the availability of high-quality feeds at reasonable cost. In recent year, intensification of carp production has generated a pressure for the development of suitable fish diet.

Fish meal remained the most important and widely preferred protein

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ingredient for aquaculture feed industry. However, beside high price, there is major concern about the feedstuff's long-term availability for use in fish diets (Sargent and Tacon, 1999). Therefore, from the economic and sustainable point of view, a complete replacement of fish meal is required. Under this scenario, use of plant-based proteins in fish feed represents potential alternatives to fishmeal and fish oil. However, a number of studies had documented that high levels of plant proteins in fish feed can negatively affect growth performance and efficiency of feed utilization (Gatlin et al., 2007; Barrows et al., 2008; Hua and Bureau, 2012; Wacyk et al., 2012), primarily due to the anti-nutritional components. The exclusion of anti-nutritional factors from plant-based diet incurs additional costs which oftentimes restrain the profit margins and may be economically infeasible. Under this scenario where removal of anti-nutritional factor can have limited practical value for commercial fish producers, adapting the fish to plant-based diet rather than amending the diet, can be a promising strategy to promote sustainable feeding strategies in aquaculture.

In this context, research in vertebrates including mammals revealed that metabolic status, and ability to efficiently utilize nutrients during latter stage of life can be permanently influenced by nutritional events during early life stage (Symonds et al., 2009). These types of studies incite new idea to develop strategy to programme metabolism for better utilization of plant based diet during growing stage through application of nutritional programming during early life stage of the cultured fish. Recent study in zebra fish (*Danio rerio*) determined the long term metabolic effect of early nutritional programming with feeding of high carbohydrate diet during first exogenous feeding (Fang et al., 2014). Digestion, transport and metabolism capacity as well as expression of carbohydrate catabolism associated genes in adult fish fed with high carbohydrate diet were found affected without compromise with growth due to nutritional stimulus of high carbohydrate during first feeding (Fang et al., 2014). Similarly, increased acceptance and utilization of plant based diet in rainbow trout (*Oncorhynchus mykiss*) was found after early short-term feeding to fry with same diet (Geurden et al., 2013).

However, developmental plasticity in vertebrates before exogenous feeding stage, allowing the organism to adapt the adverse postpartum conditions (Duque-Guimarães and Ozanne, 2013). Most of the organ development and embryogenesis in fish occurs prior to egg hatching, and is largely dependent on broodstock diet (Fernández-Palacios et al., 2011; Izqquierdo et al., 2000). Although, the relevance of broodstock nutrition for embryonic and larval development has been extensively documented (Fernández-Palacios et al., 2011; Lazzarotto et al., 2015), less is known about the long-term impact of broodstock nutrition on the progeny performance during juvenile or adult phases.

Therefore, the key objective of present work was to examine the effect of total replacement of a fish based diet to a plant based diet on the performance of common carp juveniles, developed from the broodstock with a similar nutritional history. With this objective, the present research also aimed to answer the question whether nutritional history has an impacts on future performance and utilization of diet in common carp?

2. Material and methods

2.1. Ethical approval for animal use

All animal research mentioned in this manuscript were carried out in accordance with European Union Council (2010/63/EU) criteria, which were approved by HAKI's Ethical Committee (1/2002) in accordance with Hungarian State law (10/1999. (I.27.); 40/2013. (II.14)).

2.2. Nutritional history of broodstock

Twenty four common carp broodstock (3+ year old) of Research Institute of Fisheries and Aquaculture (HAKI) were randomly selected, transported to the flow-through system of KARAS and distributed in four 2000 L fibre glass tank (six fish/ tank). A 1:1 ratio of males to female was stocked in each group. At the beginning of the trial, mean body weight for broodstock fish were 2.60 ± 0.36 kg. Brood fish were fed either of two isoproteic (30% crude protein) and isolipidic (5% crude lipid) experimental diet (i) fish based diet (F) (16% fish meal and 2.20% fish oil) (EPA + DHA wt% = 11.16) and (ii) plant based diet (P) (without fish meal and fish oil) (EPA + DHA wt% = 0.67) formulated by HALTAP Ltd., Szarvas, Hungary. Broodstock fed with their respective diet (either F- or P- diet) are referred as F- broodstock or P- broodstock. Each diet was dispensed to duplicate tanks randomized with respective dietary treatment. Fish were fed two times a day, a daily ration of 2% initial biomass.

After about 3000 day-degree nutritional trail, hatching was carried out at the KARAS, Ltd. Hatched larvae (3 days post hatch (dph)) were transferred to the earthen manured pond (500m^2) in duplicate groups at a stocking density of 100 larvae/m^2 and grown there for four weeks without any artificial diet. At the end of 28 days survival (%) and growth of larvae were analysed.

2.3. Nutritional history during rearing phase

Fry obtained from both experimental groups were stocked into six earthen pond (1700 m^2) in triplicate at a stocking density of 20,000 fry/ha. Fry produced from F- broodstock and P- broodstock were fed with F-diet or P-diet, respectively, for the next four months to attain the juvenile stage. The isoproteic (37% crude protein) and isolipidic (6.5% crude lipid) experimental diets for rearing phase were formulated according to the nutrient of common carp fry/fingerlings (National Research Council NRC, 2011) (Table 1). This early feeding period is denoted as 'nutritional history F or P' and the fish from the respective nutritional histories are designated 'F- or P- fish'. At the end of rearing phase (four month) growth performance and body composition of juveniles were analysed.

Table 1
Formulation (%) and proximate composition (% dry matter) of the experimental diets used during nursery periods (conversion from fry to juvenile) for 4 months.

Ingredients	Fish based diet (F)	Plant based diet (P)
Fish meal[1]	16.00	0.00
Winter wheat meal[2]	8.88	5.60
Maize[3]	6.00	29.00
Full fat soya[4]	30.00	7.80
Soybean meal[5]	25.47	40.75
Blood meal[6]	5.00	8.00
Yeast[7]	5.00	5.00
Vitamin mineral mixture[8]	2.00	2.00
Fish oil[9]	1.65	0.00
Linseed oil[10]	0.00	1.85
Proximate composition (% dry basis)		
Dry matter	90.65	90.95
Crude protein	37.85	37.35
Crude lipid	6.46	6.83
Ash	6.25	7.61
Gross energy (MJkg^{-1})	18.01	18.11

[1] EUROPROTEIN Ltd. (distributor), Hungary.
[2] GEOMARK Ltd., Hungary.
[3] GEOMARK Ltd., Hungary.
[4] AGRO-TRIÓ Ltd. (distributor), Hungary.
[5] AGRO-TRIÓ Ltd. (distributor), Hungary.
[6] KATECH Ltd., Hungary.
[7] EUROPROTEIN Ltd. (distributor), Hungary.
[8] Vit-Min mix (Cargill Takarmany Zrt.) (quantity kg^{-1}): vitamin A – 1,000,000 IU; vitamin D_3–80000 IU; vitamin E – 5000 mg; vitamin K_3–334 mg; vitamin B_6–200 mg; vitamin C (ascorbic acid monophosphate) – 11,300 mg; Ca – 114 g; P – 78 g; Na – 1 g; Fe – 670 mg; Zn – 1070 mg; Mn – 160 mg; Cu ($CuSO_4$*$5H_2O$) – 200 mg; Se – 20 mg; Lysine – 70 g; Methionine – 198 g.
[9] EUROPROTEIN Ltd., Hungary.
[10] SOLIO Oil Manufactor Ltd., Hungary.

2.4. Crossover experiment

To determine the impact of nutritional history of common carp on change in diet during juvenile stage, a crossover experiment was designed (Fig. 1). Two isoproteic (35% crude protein) and isolipidic (6.5% crude lipid) experimental diets were formulated: (i) F diet – moderate fish based diet and (ii) P diet – plant based diet according to the nutrient requirements of common carp juveniles (National Research Council NRC, 2011). The ingredient composition of both diets is illustrated in Table 2. Both experimental diets were prepared as 4 mm pellets by HALTAP Ltd., Szarvas, Hungary.

The crossover experiment was begun with random distribution of F- or P- fish into twelve 3 × 3 × 3 m cages (six nylon cages for each group) fixed in one pond. Each cage was stocked with 30 individuals (151.86 ± 9.34 g, mean ± SE, n = 12 cages). Fish in triplicate cages from both groups were either fed with their original diets or shifted to respective complementary diets for 6 weeks, and thereafter, fish sampling was performed (First sampling; C- phase; Fig. 1). Following six weeks of experimentation, fish fed with complementary diets in the remaining cages were fed with their original diet for another six weeks, and second sampling was performed (O- phase). In brief, different treatments were: **FF**: F-fish fed with F diet; **FP**: F-fish fed with P diet; **PP**: P-fish fed with P diet; **PF**: P-fish fed with F diet. A paddlewheel was installed in the pond to ensure continuous aeration and maintain an adequate oxygen level throughout the experiment. Throughout the experiment, each cage's fish were given their corresponding experimental diets twice per day (08.00 h and 16.00 h), at 2.5% of total body weight. Individual fish were weighed at the start of the trial and every other week during the experiment to adjust the feeding level for the next week. Fish were weighed in the morning on specified weigh days after not having eaten for 16 h. Throughout the trial, the water quality was monitored and found within optimum range (temperature 20–22 °C, pH 7.1–8.1, dissolve oxygen 6.7–8.2 mg/L).

2.5. Sampling

During both sampling phase (C- and O- phase), fish in each cage were measured individually to assess growth performance indices including weight gain (%), specific growth rate (SGR), feed conversion ratio (FCR) and protein efficiency ratio (PER). These were calculated based on the standard formulae viz. Weight gain (%) = [(Final weight –Initial weight) / Initial weight] x 100; Specific growth rate (SGR) = (ln initial weight – ln final weight) x 100 / number of trial days; Apparent feed conversion ratio (AFCR) = Total dry feed intake (g)/ wet weight gain (g); Apparent protein efficiency ratio (APER) = Net weight gain (wet weight) / Protein fed. The nutritional contribution of natural fish food organisms was not taken into account, hence FCR and PER are referred AFCR and APER.

Six fish from the beginning stock and three fish from every treatment at the finish of crossover experiment were arbitrarily collected to analyse whole body proximate composition. Another four fish from each cage were sedated, killed with a head blow, and dissected to obtain liver. Liver samples (3–5 g) from two fishes from each cage (N = 6) were instantly frozen in liquid nitrogen and stored in at −80 °C until alanine aminotransferase (ALT) and aspartate aminotransferase (AST) enzyme tests were performed. Similarly, liver samples from two additional fishes from each cage (N = 6) were placed in RNAlater and stored at −80 °C for gene expression assay.

Table 2
Formulation (%), proximate composition (% dry matter) and essential amino acid profile (% crude protein) of the experimental diets used during crossover experiment.

Ingredients	Fish based diet (F)	Plant based diet (P)
Fish meal[1]	14	0
Winter wheat meal[2]	20.5	16.5
Maize[3]	6.5	27.5
Full fat soya[4]	27.5	9.5
Soybean meal[5]	17.5	29.5
Blood meal[6]	5.0	8.0
Yeast[7]	5.0	5.0
Vitamin mineral mixture[8]	2.0	2.0
Fish oil[9]	2.0	0
Linseed oil[10]	0	2.0
Proximate composition (% dry basis)		
Dry matter	91.84	91.71
Crude protein	35.6	34.59
Crude lipid	6.83	6.46
Crude fibre	2.42	2.51
Ash	6.68	4.61
Nitrogen free extract	44.50	47.51
Gross energy (MJkg^{-1})	17.84	17.99
Essential amino acid profile (% crude protein)		
Lysine	5.53 ± 0.03	6.21 ± 0.04
Methionine	1.52 ± 0.01	1.56 ± 0.01
Arginine	4.07 ± 0.03	4.48 ± 0.02
Histidine	3.39 ± 0.01	3.84 ± 0.03
Threonine	3.31 ± 0.02	3.64 ± 0.03
Valine	4.88 ± 0.04	5.89 ± 0.04
Leucine	6.79 ± 0.05	8.47 ± 0.06
Isoleucine	3.39 ± 0.02	3.61 ± 0.01
Phenylalanine	5.08 ± 0.04	5.75 ± 0.04

[1] EUROPROTEIN Ltd. (distributor), Hungary.
[2] GEOMARK Ltd., Hungary.
[3] GEOMARK Ltd., Hungary.
[4] AGRO-TRIÓ Ltd. (distributor), Hungary.
[5] AGRO-TRIÓ Ltd. (distributor), Hungary.
[6] KATECH Ltd., Hungary.
[7] EUROPROTEIN Ltd. (distributor), Hungary.
[8] Vit-Min mix (Cargill Takarmany Zrt.) (quantity kg^{-1}): vitamin A – 1,000,000 IU; vitamin D_3–80000 IU; vitamin E – 5000 mg; vitamin K_3–334 mg; vitamin B_6–200 mg; vitamin C (ascorbic acid monophosphate) – 11,300 mg; Ca – 114 g; P – 78 g; Na – 1 g; Fe – 670 mg; Zn – 1070 mg; Mn – 160 mg; Cu ($CuSO_4$*$5H_2O$) – 200 mg; Se – 20 mg; Lysine – 70 g; Methionine – 198 g.
[9] EUROPROTEIN Ltd., Hungary.
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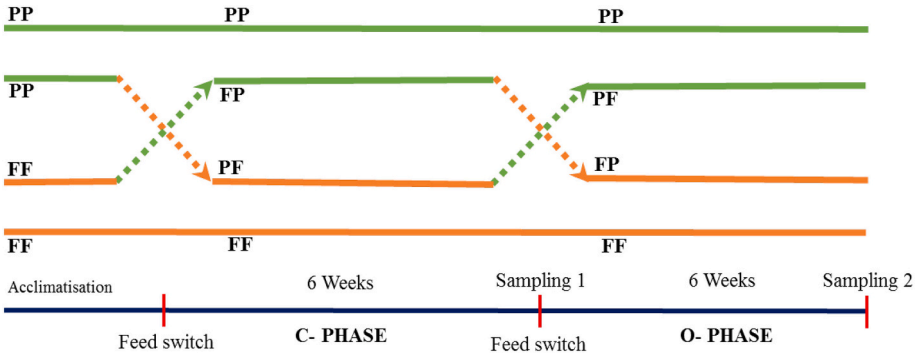

Fig. 1. Design of crossover experiment (**FF**: F-fish fed with F diet; **FP**: F-fish fed with P diet; **PP**: P-fish fed with P diet; **PF**: P-fish fed with F diet.)

2.6. Analysis

2.6.1. Proximate analysis

The AOAC (1995) standard procedures were used to determine the proximate composition of the feeds and fish. After 4 h of drying at 105 °C, the dry matter was measured gravimetrically. Total nitrogen was estimated using the Kjeldahl method, which include the digestion block (KJELDATHERM, Gerhardt, Germany) and the distillation unit (VAPODEST 30, Gerhardt, Germany), and crude protein was calculated by multiplying nitrogen (%) with 6.25. Lipid content was assessed using the Soxhlet (SOXTHERM 2000, Gerhardt, Germany) and diethyl ether (boiling point, 40^0–60 °C) as a solvent. The ash content was estimated after 4 h of combustion at 550 °C. In a GERHARDT Crude Fibre device (Gerhardt, Germany), the crude fibre content of a lipid extracted feed sample was evaluated by digestion with sulphuric acid (0.51 mol/L) and potassium hydroxide (0.89 mol/ L). The difference between 100 and sum of crude protein (%), fat (%), ash (%) and fibre (%) was used to compute nitrogen free extract (NFE). The gross energy value of the experimental diets was determined using Halver and Hardy (2002) formulae. The amino acid content of feed was determined using Official Method (ISO 13903:2005) in the accredited laboratory of the Hungarian Food Chain Safety Office (www.nebih.gov.hu). The essential amino acid contents of the experimental diets are depicted in Table 2.

2.6.2. Protein metabolism enzymes

The activities of protein metabolic enzymes viz. alanine aminotransferase (ALT) and aspartate aminotransferase (AST) in the hepatic tissue were determining using commercially available assay kits (SIGMA-ALDRICH, USA). At 37 °C, one unit of ALT and AST is defined as the quality of enzyme that produces respectively 1.0 mol of pyruvate per minute at 570 nm and 1.0 mol of glutamate per minute at 450 nm.

2.6.3. Gene expression analysis

Liver samples were homogenized, and total RNA were extracted using Promega RNA isolation kit. The quantity and purity of the isolated RNA were determined by Nano-Drop spectrophotometer (Thermo Scientific, Delaware, USA). For all the isolated RNA samples, the OD260/OD280 absorption ratio was greater than 1.95. The denaturing gel electrophoresis (prepared from 1% agarose gel) was performed to evaluate the integrity. 1 μg of RNA was transcribed to cDNA using the Omniscript Reverse Transcriptase cDNA synthesis kit (Qiagen, Germany) as per the manufacturer's instruction. The primer sequences and calculated efficiency of each gene is enlisted in Table 3. The primers sequence of target genes and reference gene were adopted from Sinha et al. (2012) and Sinha et al. (2013), respectively. Brilliant II SYBR Green (Agilent) was used as master mix, and qPCR runs were performed on Mx3000P QPCR System (Agilent Technologies, Belgium) following a four-step experimental run protocol: denaturation, amplification and quantification, melting curve and cooling. Melting curve analysis confirmed the specificity of PCR reactions for tested genes. Moreover, 'no-template' controls were also run for each gene in order to confirm no reagents contamination and no primer–dimer amplification. β-actin has been reported as the most suitable reference gene in common carp (Sinha et al., 2013), and its expression remained highly stable across the samples. Consequently, β-actin was used as endogenous standard to calculate relative expression of the target following standard curve method.

Table 3
PCR primer sequences, accession numbers and calculated efficiency.

Gene	Accession no.	Sequence of primer (5′ → 3′)	Efficiency (%)
Target gene			
Growth hormone	M27000	F: TAACGACTCCTTGCCGC R: TCTACAGGGTGCAGTTGG	114
Insulin-like growth factor-I	AF465830	F: GATGGCAAGTCACCTCC R: GACAAGAGCCAAGCCTG	116
Growth hormone receptor	AY691176	F: GAGCAGGGGTACCAAAC R: GCTGTGAGGGCATATCG	98.2
Reference gene			
β-actin	M24113.1	F: CGTGATGGACTCTGGTGATG R: TCACGGACAATTTCCCTCTC	99.2

The accession number refers to the registered sequence used from Gene bank. F: forward, R: reverse.

2.7. Statistical analysis

All data were subjected to ANOVA using SPSS version 22. Normality of the data was assessed using the Shapiro–Wilk test and homogeneity of variances was verified by Levene's test. Duncan multiple range test was used to see the differences between means at 5% level of significance.

3. Results

3.1. Performance of larvae during nursery phase

Larvae obtained from the F- broodstock recorded significantly ($P < 0.05$) higher body weight at 28 dph compared to the larvae obtained from P- broodstock (Fig. 2A). However, at 28 dph, survival (%) of larvae was not significantly affected by the nutritional history of broodstock (Fig. 2B)

3.2. Performance of fish during rearing phase

Growth performance of common carp fry during rearing phase is depicted in Table 4. F- fish registered significantly ($P < 0.05$) higher

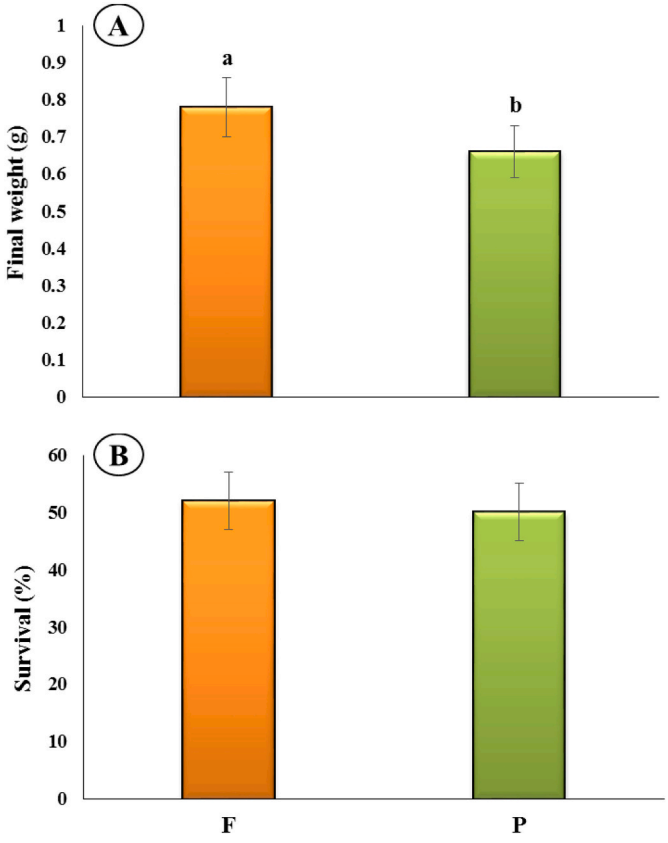

Fig. 2. Final weight [A] and survival (%) [B] of common carp larvae after 28 days of hatching from F- and P- broodstock (mean ± SE). Mean values with different letters represent significant difference ($P < 0.05$).

Table 4
Growth performance (mean ± SE) of fry fed with experimental diets for 4 months.

	F	P
Final Weight (g)	77.9 ± 27.6[a]	62.2 ± 12.0[b]
Survival (%)	79.0 ± 3.0	75.0 ± 2.0
SGR	3.37 ± 0.05	3.33 ± 0.12
AFCR	1.63 ± 0.11[b]	1.91 ± 0.08[a]
CF (g. cm^{-3})	1.70 ± 0.1	1.80 ± 0.1

Significant differences ($P < 0.05$) are represented by mean values with different letters.

final weight compared to P- fish, however, SGR was similar for both groups. Significantly ($P < 0.05$) higher AFCR was recorded in P- fish group compared to F- fish group.

3.3. Crossover trial

3.3.1. Performance of fish at the end of C- phase

The growth performance of the different treatments during C- phase of the crossover trial is given in Table 5. Percentage weight gain and SGR were similar ($P > 0.05$) in P- fish fed with P diet (PP) and F- fish fed with F diet (FF). Change to their complementary diet significantly ($P < 0.05$) decreased the growth performance of juveniles (PF/FP). The growth performance of P- fish fed with fish meal based diet (PF) was significantly ($P < 0.05$) decreased compared to F- fish fed with the plant based diet (FP). Better nutrient utilization in terms of lower AFCR and higher APER was registered in juveniles fed with their original feed (PP/FF) compared to their complementary diet (PF/ FP). However, similar ($P > 0.05$) AFCR and APER were found among fish fed with either of their complementary diet.

3.3.2. Fish performance at the end of O- phase

Change in the diet from complementary to their original diet (O- phase) registered significant change in the growth performance due to different treatment groups (Table 5). At the end of O- phase, weight gain (%) and SGR of PP group was significantly ($P < 0.05$) higher compared to PF groups, however no difference ($P > 0.05$) was noted between FF and FP group. The PF group displayed significantly ($P < 0.05$) lower growth performance compared to all other treatment groups i.e. PP, FF and FP group. Remarkably ($P < 0.05$) highest AFCR and lowest APER were found in PF group compared to PP, FF and FP groups. However, similar ($P > 0.05$) AFCR and APER were recorded in PP, FF and FP groups.

3.3.3. Proximate composition of whole body

The whole body composition of fish at the end of C- and O- phase is presented in Table 6. Differences among different treatments during C- and O- phase were not significant for whole body crude protein and ash content. Fish fed with F diet registered significantly higher crude lipid content compared to those from the P diet during both C- and O- phase. A reverse relation of moisture and crude lipid content was evident but no significant difference in the whole body moisture content was observed among different treatments.

3.3.4. Expression of growth associated gene

Hepatic IGF-I gene expression level was significantly down-regulated in P- fish fed with F diet (PF) compared to P diet (PP) and F- fish fed with P diet (FP) compared to F diet (FF) (Fig. 3A). Both, during the C- phase as well as the O- phase, IGF-I mRNA expression level was similar ($P > 0.05$) between P- fish fed with P diet (PP) and F- fish fed with F diet (FF). Relative to the PP group, a 2.59 fold and 2.38 fold reduction ($P < 0.05$) in IGF-I transcript level was observed in PF group during C- phase and O- phase respectively. Similarly, relative to FF group, a 2.17 fold reduction ($P < 0.05$) in IGF-I transcript level was registered in FP group during C- phase, which became again similar ($P > 0.05$) during the O- phase.

P-fish fed with P diet (PP) and F- fish fed with F diet (FF) displayed similar ($P > 0.05$) GHR mRNA expression levels during both the C- phase and O- phase (Fig. 3B). Significant reduction in GHR mRNA expression level were seen for P- fish fed with the F diet (PF) with a 4.18 fold lower expression than in P- fish fed with P diet (PP) and for F- fish fed with P diet (PF) with 3.38 fold lower expression than in F- fish fed with F diet (Fig. 3B). The drop in the GHR mRNA transcript level of FF-PP group during C- phase became similar ($P > 0.05$) to the FF group during O- phase, however PF group registered 2.84 fold lower expression than in PP group.

The pattern for the GH gene expression among different dietary treatment was similar ($P > 0.05$) during both C- phase and O- phase (Fig. 3C).

3.3.5. Protein metabolism enzyme activity

Hepatic activities pattern of the two main enzymes (ALT and AST) associated with the amino acid catabolism are shown in Fig. 4 (A & B). During the C- phase, activities of ALT and AST were significantly ($P > 0.05$) inhibited in P- fish and F- fish fed with their complementary diet compared to original diet. In contrary, activities of ALT and AST were similar ($P > 0.05$) between FF, FP and PP group.

4. Discussion

It is well anticipated that a limitation in the constant supply of fish meal and fish oil will restrict the further improvement of aquaculture industry. Therefore, any progress in the whole replacement of fish based diet to plant based diet will contribute the sustainability of aquaculture. To address these issues, this study explored how nutritional history of the developing embryo, through the broodstock diet, can influence the performance of the progeny, particular when juveniles are reared with plant based diet. This also assists determining if these plants based dietary ingredients can have an impact on the metabolism later in the life.

Our results revealed a profound effect of broodstock feeding on the later performance of the progeny. Total replacement of fish meal (FM) and fish oil (FO) to plant meal and plant oil (Linseed oil, LO) in the broodstock diet, markedly reduced the total body weight of 28 dah larvae, denoting a negative effect on growth performance of larvae. Likewise, many authors have shown the influence of broodstock nutrition on the quality of larvae hatching (Lavens et al., 1999; Izquierdo et al., 2015; Lazzarotto et al., 2015). Notably, the viability of fry was related to their HUFA content itself which was a function of the diet supplied to turbot broodstock (Lavens et al., 1999). In agreement,

Table 5
Growth performance of juveniles during crossover experiment.

	C- phase				O- phase			
	FF	FP	PP	PF	FF	FP	PP	PF
Weight gain (%)	95.16 ± 4.27[a]	79.56 ± 2.59[b]	92.54 ± 7.59[a]	69.60 ± 1.32[c]	62.86 ± 2.03[p]	65.09 ± 3.97[p]	61.41 ± 2.56[p]	53.77 ± 3.98[q]
SGR	1.63 ± 0.06[b]	1.43 ± 0.03[b]	1.60 ± 0.09[a]	1.29 ± 0.01[b]	1.19 ± 0.03[p]	1.22 ± 0.04[p]	1.16 ± 0.02[p]	1.05 ± 0.02[q]
AFCR	1.03 ± 0.11[b]	1.24 ± 0.04[a]	1.06 ± 0.05[b]	1.37 ± 0.02[a]	1.26 ± 0.04[q]	1.22 ± 0.07[q]	1.25 ± 0.05[q]	1.55 ± 0.03[p]
APER	2.71 ± 0.13[b]	2.34 ± 0.06[b]	2.73 ± 0.13[a]	2.05 ± 0.03[b]	2.24 ± 0.05[q]	2.41 ± 0.07[p]	2.32 ± 0.06[pq]	1.82 ± 0.04[r]

Significant differences ($P < 0.05$) are represented by mean values with different letters.
FF: F-fish fed with F diet; **FP**: F-fish fed with P diet; **PP**: P-fish fed with P diet; **PF**: P-fish fed with F diet.

Table 6
Proximate composition (% wet weight basis) in whole body of common carp during crossover experiment.

	C- phase				O- phase			
	FF	FP	PP	PF	FF	FP	PP	PF
Moisture	76.52 ± 0.37	77.40 ± 0.65	77.45 ± 1.46	76.84 ± 0.98	75.99 ± 0.37	76.98 ± 0.76	77.82 ± 0.09	77.95 ± 0.49
Crude protein	15.10 ± 0.24	15.20 ± 0.62	15.04 ± 1.02	15.14 ± 0.82	16.01 ± 0.20	15.31 ± 0.15	15.03 ± 0.13	14.86 ± 0.40
Crude lipid	4.15 ± 0.33^{a}	2.90 ± 0.46^{ab}	2.50 ± 0.58^{b}	3.82 ± 0.35^{ab}	3.90 ± 0.37^{p}	3.75 ± 0.58^{p}	3.03 ± 0.13^{q}	3.13 ± 0.10^{q}
Ash	2.33 ± 0.10	2.43 ± 0.13	3.08 ± 0.12	2.49 ± 0.17	2.29 ± 0.09	2.24 ± 0.10	2.52 ± 0.15	2.23 ± 0.13

Significant differences ($P < 0.05$) are represented by mean values with different letters.
FF: F-fish fed with F diet; **FP**: F-fish fed with P diet; **PP**: P-fish fed with P diet; **PF**: P-fish fed with F diet.

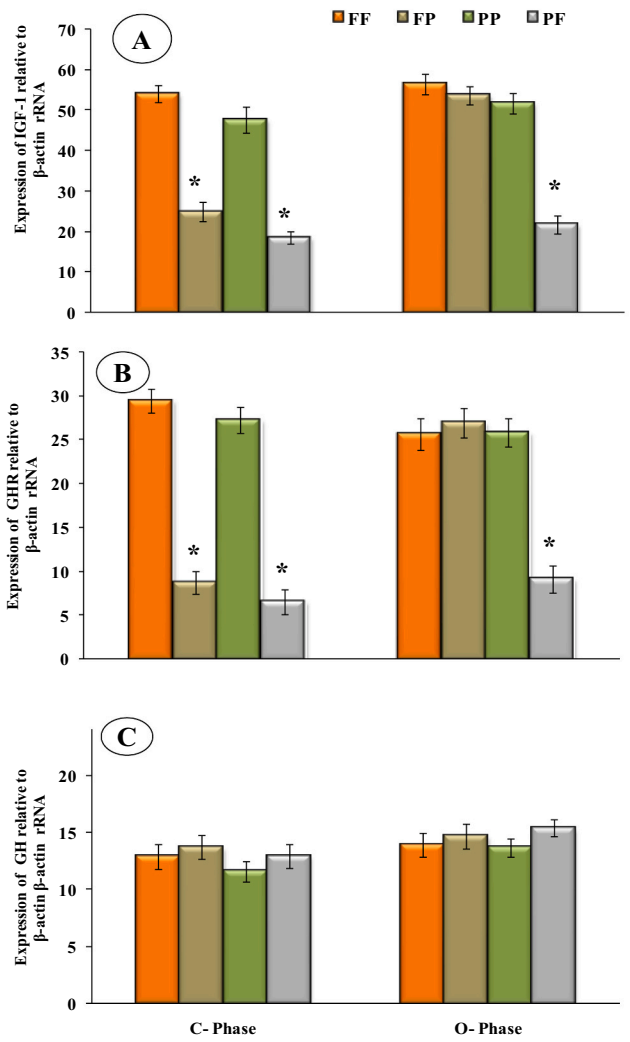

Fig. 3. IGF-1, Growth hormone receptor (GHR) and Growth hormone (GH) gene expression (mean ± SE). Mean values with asterisk (*) having significant difference (P < 0.05) with others.

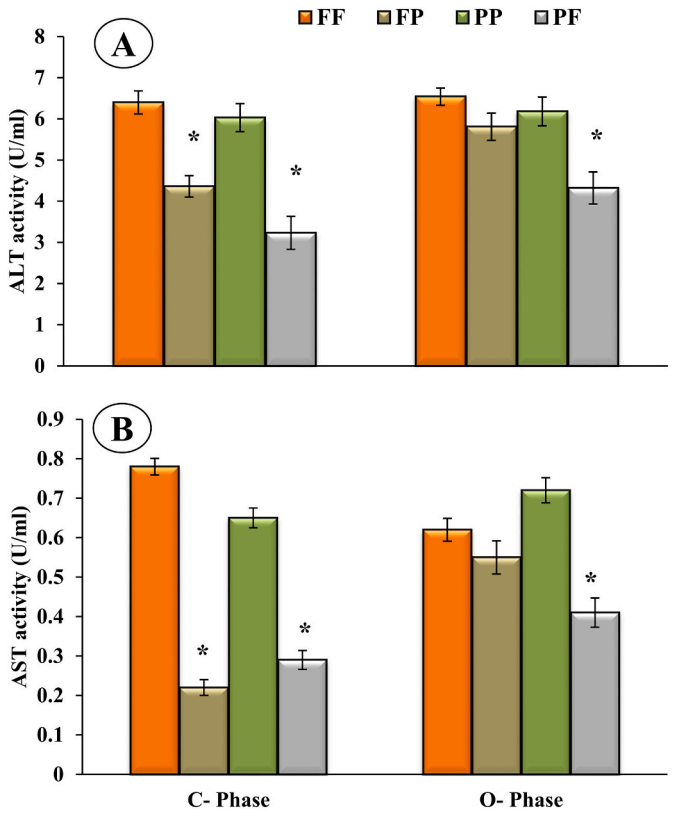

Fig. 4. ALT and AST enzyme activities during crossover experiment (mean ± SE). Mean values with asterisk (*) having significant difference (P < 0.05) with others.

nutrition in mammals through parental diet promoted changes in adults' weight gain performance, metabolic capacity and immune competency (Sinclair et al., 2016). Moreover, complete replacement of FO (rich in HUFA) with LO (rich in 18:3n − 3) inhibited expression of Δ6D gene in 15 dah larvae of gilthead sea bream, which was further reflected in the reduction of growth (Izquierdo et al., 2015). Lazzarotto et al. (2015) also found that total replacement of fish meal by plant ingredients in the diet of rainbow trout reduced ova size and resulted in decrease in survival rate at all stage at first spawning.

Fry is a critical developmental stage of many fish species including carp. Fry are the transitional stage between the dependence on yolk sac for nutrition followed by natural food and then shift to artificial feeds. In the present study, fry from F- broodstock fed with F-diet and from P-broodstock fed with P-diet, growth rate (SGR) and condition factor (CF) of fry form both parents were very similar, however, final weight of fry from F- broodstock was higher compared to fry from P- broodstock. This confirms that higher final weight of fry (F- fish) after 4 months of rearing period was due to higher weight gain of larvae obtained from F-broodstock compared to P- broodstock during nursery rearing (28 dph) and feeding of diet to larvae according to their nutritional history.

Effect of nutritional history on the development of fishes has been studied through nutritional programming in different fishes viz. gilthead sea bream (Izquierdo et al., 2015), rainbow trout (Geurden et al., 2013; Lazzarotto et al., 2015), Atlantic salmon (Clarskon et al., 2017), yellow Perch (Kemski et al., 2018) and zebrafish (Kwasek et al., 2020). In these studies, nutritional programming was probed through early short term subjection of fry to a plant-based diet and use of the same diet when offered at a later life stage. Similarly, in our study, a crossover experiment was conducted through switch-over in the diet of P-fish and F-fish. During the complementary phase, higher growth performance in P-fish

and F-fish was recorded when they fed with their original diet (P-diet/ F-diet) compared to complementary diet (F-diet/ P-diet). As mentioned earlier, fish meal based diet generally leads to a higher fish growth performance in comparison to those fed with plant based diet; however similar growth performance registered in the present highlights the association between early life feeding history and long-term effects on feed utilization. Nutritional programming improves growth and plant protein utilization in pre-adult stage of zebrafish (Kwasek et al., 2020). Geurden et al. (2013) reported that acceptance and utilization of the same diet improves when provided at a later life stage. They documented that juvenile rainbow trout which in general have low capacity to utilize dietary carbohydrates, can be adapted to efficiently mobilize dietary carbohydrate with a beneficial long-term effect on growth performance by early first-feeding with a high level of carbohydrates diet. During C-phase of the crossover experiment, growth performance of P- fish fed with its complementary diet was lower than the F- fish fed with its respective complementary diet. This reflects the higher ability of F-fish to adapt the change in diet during latter stage of life than the P-fish.

Similar growth performance of PP group and FF group continued during O- phase also. In tilapia, the effects of early nutritional intervention stimulus can permanently modify the metabolic efficiency later in the life (Kumkhong et al., 2020). Accordingly, present results also reflect that fish fed with plant based diet during early stage utilize same diet equally as fish fed with fish meal based throughout from early stage. However, the decreased growth performance and nutrient utilization of FP group during C- phase resume similar growth performance with FF group after fed with their original diet during O- phase. On the contrary, the reduced growth performance of PF group during C- phase did not resume the growth performance of PP group during O- phase i.e. after fed with their original diet. These results signify that fish having a nutritional history of fish meal based diet are more plastic to adapt with change in feed compared to fish having nutritional history of plant based diet.

The utilization efficiency of P diet was greater in P- fish relative to F-fish and vice versa during C- phase, which was reversed after change in diet from complementary diet to original diet during O- phase. This explains the diet specificity for the feed efficiency response (Geurden et al., 2013). Prenatal flavour experiences improve acceptance and enjoyment of similar-flavoured food throughout weaning and later life stages in humans (Mennella et al., 2001; Mennella et al., 2004). Along with that, the digestive and adaptive capacities of the gastrointestinal tract of new-born mammals are ontogenetically adapted to the food it may receive at birth (Schmitz, 2000). In rainbow trout Balasubramanian et al. (2016) reported that feed preference and acquisition of flavour of the plant diet during latter stage of life depends on the early plant diet exposure. Likewise, in the same fish species, Geurden et al. (2007) found that hyperglucidic stimulus at onset of feeding had a long-lasting impact on carbohydrate digestive enzyme at the juvenile stage. In line with these findings, our study also demonstrated the profound effect of nutritional history on feed efficiency as well as protein utilization during latter life stage, signifying a positive physio-biochemical changes induced by the first feeding.

Furthermore, the activities of protein metabolism enzymes (ALT and AST) in liver were reduced with the change in diet from original to complementary diet during C- phase, which indicates the decreased utilization of dietary protein due to alteration in diet from their early feeding history. The reduced ALT and AST activities of FP group increased after resume of their original diet (F diet), however PF group could not retain the enzyme activities after resume of their original diet (P diet). This illustrates the flexible nature of F-fish, which retain the performance after resume of diet according to their early feeding history.

Growth is a composite process that primarily controlled by the GH/IGF-I axis. This axis is also an important signal for nutrient partitioning (Beckman and Dickhoff, 1998). In the present study, the expression patterns of growth regulating hormones and receptors genes, such as GH, IGF-I, GHR were studied. Because GH and IGF-I both have metabolic functions, it's reasonable to assume that dietary changes are the primary regulator of GH/IGF-I axis in fish. IGF-I is predominantly produced in the hepatic tissue and directly stimulates the organ growth by facilitating growth-promoting actions of GH. On target tissues, including liver, the actions of GH are triggered by interactions with GH receptor (GHR). We documented that hepatic IGF-I and GHR expression was down-regulated as fish fed with their complementary diet compared to early feeding history, which paralleled well with the results of growth performance. Apparently, the decreased transcript level of GHR/IGF-I axis genes in FP group during C- phase and PF group during both C-phase and O- phase might be responsible for the lower growth rate. The decline in growth rate in these treatments is also allied to the decrease in the binding ability of GH to the hepatic GH receptors associated with the subsided GHR gene expression level (Kumar et al., 2017). This results in a reduction of IGF-I synthesis (or mRNA transcript) since there is a diminished signal from the GHR. Duan (1998) also reported that IGF-I is the principal anabolic agent accountable for tissue growth in fish, and change in IGF-I gene expression can moderately account the growth rate variation. In the present study, although there was a quite good correlation with the growth rate, alterations in gene expression do not necessarily translate into corresponding changes in functional protein. In future studies, investigation of these hormones/proteins at the translational level will be considered.

5. Conclusion

In brief, our study documents that feeding to common carp according to their previous nutritional history improves acceptance and utilization of the same diet when offered at a later life stage. Growth performance and nutrient utilization were decreased due to change in diet from original diet (as per nutritional history) to complementary diet. The decreased growth performance was linked to the down-regulation of hepatic GHR/IGF-I axis genes. The activity of hepatic protein metabolism enzymes (ALT and AST) was positively correlated with the growth performance and protein utilization efficiency. In conclusion, the present study demonstrates that common carp can be adopted to utilize a plant based diet in place of fish based diet more efficiently after an early nutritional intervention. Present study confirms that nutritional history influences nutrient utilization during juvenile stage, and nutritional programming at early stage may be the strategy for total replacement of fish based diet with plant based diet in common carp without compromising with the growth performance and nutrient utilization. Conclusively, the results displayed the profound effect of feeding common carp according to their nutritional history, on the later performance of the progeny and the effective utilization of plant based diet.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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