J. Indian Soc. Coastal Agric. Res. 38(1): 43-49 (2020)

Compensatory Growth Response and Feed Intake Pattern of Indian Major Carps in Confined Aquatic Environment

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Received: 15.10.2019 Accepted: 28.02.2020

Effects of feed restriction on compensatory growth (CG) performance of Indian major carps and their feed intake pattern in a grow-out production system were examined. In this experiment it was found that the magnitude of CG depended on the duration of feed deprivation and the fish deprived and refed cyclically had higher feed intake than that of the control fish, with significantly improved feeding efficiency, during the refeeding periods. This condition along with hyperphagia and improved feed conversion efficiency also helped in the occurrence of CG. Higher performance index (168-174), PSI (240.3-321.2), compensatory growth index (>100%) and per day increment (1.68-2.1) enhanced the overall survival rate (94.3%) and yield (2.86 t ha^{-1}). This infers that occurrence of CG has the potential to enhance growth, productivity and minimize feed input which in turn maintains water quality.

(***Key words:*** *Compensatory growth, Feed intake pattern, Indian major carps, Water quality*)

India's freshwater aquaculture production is mainly carp-based [Indian major carps (IMCs) *viz*., *C. catla, L. rohita and C. mrigala*] contributing over 90% of the aquaculture production. Polyculture of IMCs alone or along with exotic carps at low to moderate stocking density has been realizing a production of 4-10 t ha^{-1} yr^{-1}. However, the success of aquaculture depends heavily on ensuring cost effectiveness during the production process (Mohanty, 2010). It is well known that inappropriate feeding management may lead to over feeding, higher production cost and contamination of aquatic environment, while insufficient feeding leads to poor growth that results in aquaculture business (Mohanty, 2004).

Therefore, an important approach to reduce feed cost in commercial aquaculture is to develop proper feed management and husbandry strategy. One potential way of reducing feed cost is to take advantage of the phenomenon of compensatory growth (CG). According to Jobling (2010), compensatory growth refers to an animal's capacity to grow abnormally rapidly after a period of reduced growth resulting from reduced food availability, or some other unfavorable environmental perturbation. Compensatory growth offers the possibility of improving the growth rates of fish by a careful choice of feeding schedules/protocol in which periods of feed deprivation are followed by periods of satiation feeding. If CG can completely make up for growth lost during starvation, there could be an opportunity to save on fish feed by starving the fish and making up for lost growth when feeding resumes. Using CG is therefore perceived as a way to increase profits in aquaculture operations.

Studies on the CG response of aquatic animals are not only of theoretical value in ecophysiology and evolution, but also important to applications in aquaculture and fisheries resource management. CG following stress is a strategy enabling fish to adjust themselves to a variable inevitable environmental and nutritional stresses that depress the growth and development. Many fishes have the ability to actively regulate their growth as a strategy against negative environmental changes and have the potential to elicit above normal growth rate in recovery periods following stress. CG may follow a period of reduced growth resulting from food restriction or some other unfavorable environmental condition and requires an adaptation period whose duration varies from species to species (Ali *et al*., 2003; Nicieza and Alvarez, 2009). In other words, the degree of recovery seems dependent upon the duration and severity of growth depression (Abdel-Hakim *et al*., 2009; Rubio *et al*., 2010). The extent of CG may be quantified by the "compensatory growth index" which can be calculated as the ratio of the difference between weight variation at the end of restricted and compensatory growth periods, respectively, relative to the variation at the

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end of the restricted growth alone (Fig. 1). A value of 100% indicates full recovery or full compensation, but this is scarcely observed. Generally, the index value range between 50 and 100%. Usually, compensation is improved when the duration of growth restriction is short and is not too severe. Otherwise severely stressed animal and very young animals often fail to express CG.

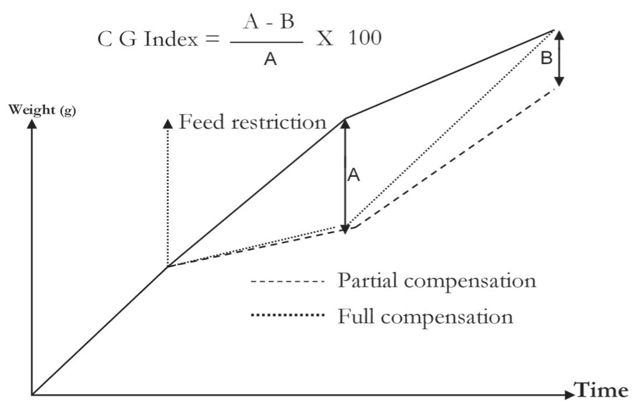

Fig. 1. *CGI a method to estimate catch-up growth*

Most studies on aquatic species have been aimed at examining the potential to use CG to improve production efficiency (Oh *et al*., 2008; Turano *et al*., 2008). However, no work on compensatory growth performance of IMCs in grow-out culture has been reported so far. In this backdrop, an attempt was made to study the effect of cyclic food deprivation and refeeding on the CG performance as well as feed intake pattern of IMCs in a grow-out polyculture system under recommended package of practice.

MATERIALS AND METHODS

Low input-based short-duration fish culture of Indian major carps was undertaken during 2014-16 at ICAR-Indian Institute of Water Management research farm (20° 17′ 30.4″ N, 85° 41′ 32.9″ E), using harvested excess rainwater in small earthen refuge (35 m^2 each) to enhance the growth and production performance. Keeping in view the advantages of compensatory growth, three different feeding protocols (with feeding frequency - 2) with three replications were imposed as treatments (T_1-daily feeding; T_2-every alternate day feeding; T_3-feeding once in two days interval). Pre-stocking refuge preparation included horizontal and longitudinal ploughing followed by application of lime ($CaCO_3$) at the rate of 750 kg ha^{-1}, raw cattle dung (RCD) @ 7000 kg ha^{-1} as basal dose and fertilizer (Urea : Single Super Phosphate :: 1:1) @ 3 ppm. Seven days after pre-stocking refuge preparation, fish fingerlings of IMCs (*Catla catla, Labeo rohita* and *C. mrigala*) were stocked @ 10,000 ha^{-1} with a species composition of 30:30:40 [Mean body weight (MBW) - 38, 24.5 & 32 g for Catla, Rohu & Mrigala, respectively] in each refuge. Supplemental feeding was provided with a ratio of 55:35:10 (rice bran: mustard oil cake: fish meal) at 3.5% of MBW as per feeding protocol. Periodic manuring with RCD at the rate of 500 kg ha^{-1} and liming at 200 kg ha^{-1} were carried out in the refuge at every 15 days interval to maintain plankton population in the confined eco-system. Fish rearing was continued for 120 days.

Most physico-chemical parameters of refuge water such as dissolved oxygen (DO), temperature, pH, turbidity; total alkalinity, total suspended solids, and CO_2 were monitored in-situ once in every 7-days interval between 0700-0800 hours using standard methods (APHA, 1995). Dissolved oxygen (DO) and turbidity were recorded using a Multi-parameter Water Analyzer (YK-611, Yeo-Kal Electronics Pty. Ltd., Australia). NH_4^+ was determined spectrophotometrically with indophenol blue method while chlorophyll-*a* was determined using the acetone extraction method. Primary productivity using "Oxygen method" (APHA, 1995), plankton estimation, nutrient analysis and monthly observations on soil quality (available-N, available-P, organic carbon and pH) were studied using standard methods. Plankton samples were collected at fortnightly intervals by filtering 50 L of water from each unit through a silk net (No. 25, mesh size 64 µm), preserved in 4% formaldehyde (equivalent to 10% solution of Formalin) and later analyzed for quantitative and qualitative estimation. Water exchange/ replenishment were not undertaken during the study period. Sediment samples were collected twice from the refuge during each crop period (*i.e.* before stocking and after harvesting) and analyzed for pH, available nitrogen, available phosphorus and organic carbon using standard methods (Biswas, 1993).

To study the food preference and feed intake pattern of cultured species, gut content analysis, degree of satiation (Mohanty, 2003), frequency, abundance and matrix of dietary overlaps (Johnson, 1999) were carried out. Weekly mean body weight (MBW), survival rate, biomass (kg), feed requirement, % feed used, feed requirement per day and apparent feed conversion ratio (AFCR) was estimated as described by Mohanty (1999). The weekly growth study was carried out sampling prior to feeding, so that the complete evacuation of gut was ensured. Weekly mean body weight (MBW), per day increment (PDI), survival rate (SR%), biomass (kg), feed requirement, % feed used, feed requirement per day and apparent feed conversion ratio (AFCR) were estimated as described by Mishra and Mohanty (2004). Other growth parameters such as performance index (PI) and production-size index (PSI) were estimated as follows:

PI = Per day increment (PDI in g) × Survival rate in % …(1)

PSI = Production in kg ha^{-1} × MBW (g) / 1000 ...(2)

All the data were statistically analyzed using analysis of variance (ANOVA) to test for the effect of treatments (Gomez and Gomez, 1984). Duncan's multiple range test was used to compare all possible pairs of treatment means at 5% level of significance. All statistical analyses were carried out using SAS, Version 9 (SAS Institute, USA).

RESULTS AND DISCUSSION

Environmental variables

Soil analysis shows that textural class is clay having acidic pH (6.6-6.8). The composition of sand, silt and clay was 36.6, 19 and 44.4 % respectively. Organic carbon (%) in soil, available-N and -P in soil (mg 100 g^{-1}) ranged between 0.16-0.19, 7.9-10.1 and 1.28-1.63 respectively at the initial stage of intervention, which improved further (Table 1), with the advancement of crop period. This may be attributed to (1) additional nutrients from fish feed and fish faeces, (2) fish grazing on the photosynthetic aquatic biomass and other components of the system which aids in nutrient recycling (Vromant *et al*., 2004), and (3) minimized N losses (Cagauan, 1995) and increase in P release from the sediment (Breukelaar *et al*., 1994). Significant variation in available-N was recorded among the different treatments (P<0.05) while there was no such variation in soil pH. The sediment characteristics of the different treatments was indicative of a medium productive soil.

Most hydro-biological parameters prevailing in the different treatments were within the optimum ranges for fish growth and survival and did not fluctuate drastically (Table 1). This was probably due to similar levels of inputs in all the treatments in the form of organic manure, inorganic fertilizer and periodic liming. The decreasing trend in dissolved oxygen (DO) was mainly due to fluctuation in plankton density and gradual increase in biomass, resulting in higher oxygen consumption. In the present study, DO level did not drop below 3.3 ppm in any treatment and significantly higher DO was recorded in T_3 (P<0.05).

Total suspended solids (TSS) concentration showed a decreasing trend with the advancement of the rearing period. Cull harvesting in T_1, had no marked influence on the concentrations of dissolved organic matter, NH_4^+, nitrite, nitrate and phosphate (Table 1). The recorded mean values of pH and total alkalinity in different treatments during the experimental period (Table 1) were within the desirable range and maintained due to periodic liming. Water pH and total alkalinity were significantly higher in T_1 (P<0.05) than in T_2, while the concentration of total suspended solid, plankton and chlorophyll-*a* was higher (P<0.05) in T_2 followed by T_1 and T_3. In this experiment, significantly higher plankton density (P<0.05) was recorded in T_2 followed by T_1 and T_3. Phytoplankton was mainly dominated by diatoms and green algae and zooplankton by copepods and rotifers. In all the treatments, average primary production in the first month of cultivation ranged between 87.6-137 mg C m^{-3} h^{-1}, which improved further (407.5 + 38.3 mg C m^{-3} h^{-1}) with the advancement of the rearing period.

Gradual increases in nitrite, nitrate, and ammoniatowards the later part of the experiment were attributed by intermittent fertilization, increased level of metabolite and decomposition of unutilized feed (Mohanty *et al*., 2004). In general, poor growth performance of cultured species takes place at pH < 6.5 (Mount, 1973) while higher values of total alkalinity (> 90 ppm) indicate a better productive eco-system and increased plankton density reflects higher nutrient

Table 1. *Variations in water and sediment quality parameters in the different treatments*

Parameters	(T_1)	(T_2)	(T_3)
Water quality parameters			
Water pH	7.52 ± 0.17^{ab}	7.63 ± 0.13^{a}	7.31 ± 0.11^{b}
Dissolved oxygen (ppm)	6.1 ± 0.8^{a}	5.1 ± 1.1^{b}	4.9 ± 1.3^{b}
Temperature (°C)	28.7 ± 0.6	28.4 ± 0.5	28.4 ± 0.3
Total alkalinity (ppm)	88 ± 8^{c}	106 ± 7^{a}	94 ± 10^{b}
Dissolved organic matter (ppm)	2.6 ± 0.2^{b}	3.2 ± 0.3^{a}	3.4 ± 0.4^{a}
Total suspended solids (ppm)	177 ± 17^{c}	213 ± 10^{b}	225 ± 13^{a}
NH_4^+ water (ppm)	0.59 ± 0.03^{b}	0.65 ± 0.02^{ab}	0.68 ± 0.03^{a}
Chlorophyll-*a* (mg m^{-3})	22.3 ± 5.3^{c}	36.7 ± 4.1^{b}	41.1 ± 3.2^{a}
Total plankton (units l^{-1})	$0.7x10^4 \pm 1.4x10^{3c}$	$1.4x10^4 \pm 1.3x10^{3b}$	$3.3x10^4 \pm 1.1x10^{3a}$
Nitrite - N (ppm)	0.03 ± 0.00	0.03 ± 0.01	0.04 ± 0.01
Nitrate - N (ppm)	0.36 ± 0.08	0.36 ± 0.09	0.37 ± 0.06
Phosphate - P (ppm)	0.26 ± 0.04^{a}	0.21 ± 0.04^{b}	0.21 ± 0.03^{b}
Sediment quality parameters			
Available-N in soil (mg 100 g^{-1})	20.3 ± 0.3^{a}	19.8 ± 0.2^{b}	19.3 ± 0.3^{c}
Available-P in soil (mg 100 g^{-1})	2.11 ± 0.07^{b}	2.21 ± 0.06^{a}	2.23 ± 0.08^{a}
Organic carbon in soil (%)	0.63 ± 0.01^{a}	0.61 ± 0.01^{b}	0.64 ± 0.01^{a}
Soil pH	6.94 ± 0.07	7.04 ± 0.09	7.01 ± 0.08

All values are mean ± SD. Values with different superscripts in a row differ significantly ($P<0.05$).

status of the water body (Mohanty, 2003). The recorded mean values of pH (7.3-7.6) and total alkalinity (88-106 ppm) in the different treatments were maintained due to periodic liming. Water pH and total alkalinity were significantly higher in T_1 while the concentrations of total suspended solid, plankton and chlorophyll-awere higher in T_2. This agrees with the findings of Frei and Becker (2005) who reported that fish stimulate the growth of phytoplankton and chlorophyll-*a* in integrated rice-fish culture. Plankton density always has a profound effect on water quality having direct relationship with fish production (Yaro *et al*., 2005). Low primary production in the initial phase of rearing was probably due to fixation of nutrient ions by suspended soil/clay particles as well as rich organic matter (Mohanty, 2003).

Compensatory growth and yield performance of fish

After 120 days of rearing, the average MBW (g) of Catla, Rohu and Mrigal was 353.2, 276.5 and 278.5 in T_1, 340.2, 283.7 and 270.2 in T_2 and 353.5, 276.7 and 292.5 in T_3. Treatment-wise production, per-day increment, survival rate, apparent feed conversion ratio and feed efficiency (%) is given in Table 2. The elevated FE in T_3 and T_2 was beneficial to water quality and has important cost saving implications providing additional potential for using cyclic feeding in production practices. The improved feed efficiency (FE) with similar MBW in T_3 versus control (T_1) suggests that the cyclic feed regimen was effective in inducing a compensatory growth (CG) response, characterized by increased specific growth rate (SGR). As gut content analysis (GCA) indicated the presence of both plant matter and zooplankton in addition to supplemental feed, it also appears that fish on the cyclic feed regimen may have better used refuge resources by increasing the consumption of natural productivity.

Under different feeding protocols, compensatory growth (CG) response was recorded in both T_2 and T_3. Full compensation (CGI >100%) was recorded in T3 while partial compensation in T_2. In full compensation (T_3) the deprived fish attained the same size at the same age as non-restricted contemporaries (T_1) and regained the weight trajectory shown by control fish

Table 2. *Treatment-wise production performance of Indian major carps*

Treatments	Species	Initial MBW (g)	Final MBW (g)	PDI (g)	SR (%)	PI	PSI	Productivity (t ha^{-1} 150 d^{-1})	AFCR/ FE%
T_1	Catla	38.0	353.2	2.10	91.0	191.1	356.2		
	Rohu	24.5	276.5	1.68	100.0	168.0	240.1	2.83	1.77/ 50.3
	Mrigala	32.0	278.5	1.64	92.3	151.4	265.7		
T_2	Catla	38.0	340.2	2.01	81.8	164.4	297.4		
	Rohu	24.5	283.7	1.73	91.0	157.4	229.4	2.68	1.15/ 70.3
	Mrigala	32.0	270.2	1.59	100.0	159.0	270.9		
T_3	Catla	38.0	353.5	2.10	81.8	171.8	321.2		
	Rohu	24.5	276.7	1.68	100.0	168.0	240.3	2.86	1.39/ 64.2
	Mrigala	32.0	292.5	1.74	100.0	174.0	317.6		

PDI- per day increament; SR- survival rate; PI- performance index; PSI- production size index; AFCR- apparent feed conversion ratio; FE- feeding efficiency

(T_1). The magnitude of CG was species specific and depended on the duration and extent of feed deprivation/ refeeding cycle used (Table 2). The magnitude of CG depended on the duration of feed deprivation. During normal growth/ development, muscle exhibits initially the highest growth rate followed by fat tissue. When growth rates are reduced, there is a coordinate decrease of tissue turnover (viscera > adipose tissue > muscle). Because fat deposition is more affected than protein deposition, the body becomes leaner. If fed at maintenance levels, muscle growth remains close to zero, but fat mobilization continues and visceral weight decreases markedly, leading sometimes to altered body composition (Gurney *et al*., 2003). However, when lean animals are feed-restricted, muscle constitutes the main source of energy, causing a greater protein than fat losses. During severe and prolonged feed restriction, the initial switch from protein to fat mobilization is initially observed but is rapidly followed by combined fat and protein losses. In conclusion, tissues are affected by growth restriction dependent on their metabolic activity. Thus, metabolically very active tissues or organs, such as liver or intestine, show greatest weight losses.

During refeeding and CG, the secretion of insulin is sharply enhanced and plasma GH concentrations remain high. This situation probably allows more nutrients to be used for growth processes (Hornick *et al*., 2000). Initially, CG is characterized by the deposition of very lean tissue, similar as during feed restriction. This lasts for some weeks. Then protein synthesis decreases, and high feed intake leads to increased fat deposition. In general, CG is a coordinated response to realimentation, initially characterized by high plasma levels of GH. This could be responsible for the accumulation of lean tissue in compensating animals. It was also recorded that, the fish deprived and refed cyclically had higher feed intake than that of the control fish (T_1), with significantly improved FE (64.2-70.3%), during the refeeding periods. This condition along with hyperphagia and improved feed conversion efficiency helped in the occurrence of CG. Individually, SR% of *C. catla* was lower in both T_2 and T_3 as compared to T_1, probably due to feed restriction (nutritional shock) at the initial stage of rearing. However, higher PI (168-174), PSI (240.3-321.2), CGI (>100%) and PDI (1.68-2.1) in T_3, enhanced the overall SR (94.3%) and yield (2.86 t/ha) in comparison to T_2 & T_1. This infers that occurrence of CG has the potential to enhance growth, productivity and minimize feed input which in turn maintains water quality. In both T_1 and T_3, bottom feeders (*C. mrigala*) registered better growth rate than that of *L. rohita* (column feeder) probably due to its superior feed utilizing capability and high degree of tolerance to fluctuations of DO and TSS concentration. Faster growth rate of *C. catla* (surface feeder) and *C. mrigala* (bottom feeder) were attributed to effective utilization of ecological niches and rich detrital food web that was maintained through periodic manuring and fertilization.

Food availability and feed intake pattern of fish

Phytoplanktons and zooplanktons were most preferred food item for *C. catla* and *L. rohita*, while mud and detritus were highly preferred by *C. mirgala* (Table 3). However, quantity-wise most consumed food item was artificial supplemental feed. Omnivorous feeding behavior was observed in case of each species except *C. catla*, while the degree of omnivorous feeding behavior was high in case of *C. mirgala*. Frequency distribution of available food items in the gut content of the cultured fish and prawn species (Table 3) indicated plenty availability of planktonic, periphytic and benthic food to fish and prawn in the rice-field refuge, which can help, reduce the supplemental feed input. Estimated degree of satiation (index of gut fullness) at fingerling stage was high in case of *C. carpio* followed by *C. catla*, (Table 4). Comparative degree of satiation indicated a distinct declining trend form fingerling stage to advanced fingerling stage in case of each species. This was probably due to relatively low nutritional value of the ingested matter (mud and debris) and comparatively less preference to artificial feed at the initial stage of rearing.

ACKNOWLEDGEMENT

Authors would like to thank Director, ICAR-IIWM for facilitating funds and providing helpful comments and suggestions during the experiment. Comments of the anonymous reviewers certainly improved the quality of this manuscript. Further there is no conflict of interest among the authors.

Table 3. *Average % of individual gut content volume (abundance) of fish and % of analyzed species in which mentioned food components were found (frequency)*

Food component	Abundance (%)			Frequency (%)		
	I	II	III	I	II	III
Supplemental feed	49.3$^+$	56.7$^+$	45.8$^+$	77.8	72.2	83.3
Phytoplankton	5.1$^-$	11.2$^-$	2.3$^-$	83.3	94.4	55.6
Zooplankton	4.3$^-$	5.9$^-$	1.4$^-$	83.3	88.8	44.4
Detritus+Mud	15.4$^-$	5.6$^-$	29.1$^+$	22.2	11.1	94.4
Benthos	1.0$^-$	-	12.2$^-$	5.5	-	44.5

I - *L. rohita*, II - *C. catla*, III - *C. mrigala*; $^+$ more than; $^-$ less than

Table 4. *Matrix of dietary overlap(s) and estimated degree of satiation (Fi)of fingerling to advanced fingerling stage of fish*

Species	Matrix of dietary overlap(s)			Estimated degree of satiation (F_i)	
	I	II	III	Fingerling stage	Advanced fingerling stage
C. catla	-	0.70	0.52	5.9 ± 0.5	2.7 ± 0.4
L. rohita	-	-	0.56	5.1 ± 0.3	4.1 ± 0.5
C. mrigala	-	-	-	4.7 ± 0.3	4.2 ± 0.3

I - *C. catla*, II - *L. rohita*, III - *C. mrigala*; $F_i = w \times 100/W$; *where, w - weight of gut content and W - weight of individual fish.*

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