

Mohammad Mustafizur Rahman · Shusaku Kadowaki
Stephen Richard Balcombe · Md. Abdul Wahab

Common carp (*Cyprinus carpio* L.) alters its feeding niche in response to changing food resources: direct observations in simulated ponds

Received: 31 July 2008 / Accepted: 19 September 2009 / Published online: 21 November 2009
© The Ecological Society of Japan 2009

Abstract We used customized fish tanks as model fish ponds to observe grazing, swimming, and conspecific social behavior of common carp (*Cyprinus carpio*) under variable food-resource conditions to assess alterations in feeding niche. Different food and feeding situations were created by using only pond water or pond water plus pond bottom sediment or pond water plus pond bottom sediment and artificial feeding. All tanks were fertilized twice, prior to stocking and 2 weeks later after starting the experiment to stimulate natural food production. Common carp preferred artificial feed over benthic macroinvertebrates, followed by zooplankton. Common carp did not prefer any group of phytoplankton in any treatment. Common carp was mainly benthic in habitat choice, feeding on benthic macroinvertebrates when only plankton and benthic macroinvertebrates were available in the system. In the absence of benthic macroinvertebrates, their feeding niche shifted from near the bottom

of the tanks to the water column where they spent 85% of the total time and fed principally on zooplankton. Common carp readily switched to artificial feed when available, which led to better growth. Common carp preferred to graze individually. Behavioral observations of common carp in tanks yielded new information that assists our understanding of their ecological niche. This knowledge could be potentially used to further the development of common carp aquaculture.

Keywords Food selectivity · Feeding niche · Food resource · Behavior · *Cyprinus carpio*

Introduction

Common carp (*Cyprinus carpio*) is one of the most commercially important and widely cultivated freshwater fish in the world (Biro 1995; Zhou et al. 2003), contributing to 11% of the total world freshwater aquaculture production (FAO 2007). More than 90% of this production comes from Asia (FAO 2007), where common carp is cultured in various pond aquaculture systems. The food resources of different aquaculture systems are highly variable depending on the culture system and nutrient inputs. Many fish change their food selectivity and feeding niche with changing food availability (Hegrenes 2001; Iguchi and Abe 2002). Similarly, common carp might alter its food preference and behavior in response to changing food resources. Although there is some information about diet and feeding behavior of common carp (Adamek et al. 2003; Rahman et al. 2006, 2008a), their feeding niche in aquatic ecosystems under varying food resources is still not fully understood. Better information about how common carp changes its food selectivity and behavior with changing food resources is necessary to understand its ecology and to optimize feeding management.

Direct observation can provide important information on grazing and swimming behavior (Mearns et al. 1987; Smith et al. 1995) and may provide insight into

M. M. Rahman
Aquaculture and Fisheries Group,
Department of Animal Science,
Wageningen University, 338,
6700 AH Wageningen, The Netherlands

S. Kadowaki
Aquatic Resource Science, Faculty of Fisheries,
Kagoshima University, Shimoarata 4-50-20,
Kagoshima 890-0056, Japan

S. R. Balcombe
Australian Rivers Institute, Griffith University,
Nathan, QLD 4111, Australia

M. A. Wahab
Faculty of Fisheries, Bangladesh Agricultural University,
Mymensingh 2202, Bangladesh

Present address: M. M. Rahman (✉)
Aquatic Resource Science, Faculty of Fisheries,
Kagoshima University, Shimoarata 4-50-20,
Kagoshima 890-0056, Japan
E-mail: mustafizu.rahman@yahoo.com
Tel.: +81-99-2864161
Fax: +81-99-2864161

feeding niches in pond ecosystems. This study simultaneously considered gut content and feeding behavior of common carp. The aim of this study was to quantify the effects of different food resources on food selectivity and feeding niche of common carp.

Materials and methods

A 4-week experiment was conducted in six rectangular tanks (size: $2.5 \times 0.4 \times 0.9$ m) at the Fisheries Faculty Field Laboratory, Bangladesh Agricultural University, Bangladesh. In each tank, the 0.4-m sides were constructed using concrete and the 0.9-m sides were from glass, allowing direct observation of fish at any place in the tank. Three treatments, randomly assigned and in duplicate, were compared: tanks with only plankton (P tanks), tanks with plankton and benthic macroinvertebrates (PB tanks) and tanks with plankton, benthic macroinvertebrates and artificial feed (PBF tanks).

The bottom of the tanks of treatments PB and PBF received pond sediment. All tanks were filled with pond water. The heights of the sediment and water column were 10 and 70 cm, respectively. The water and sediment were supplied from a central pond. All tanks were treated with agricultural lime (CaCO_3) at a rate of 250 kg ha^{-1} (25 g tank^{-1}), decomposed cow manure at $1,250 \text{ kg ha}^{-1}$ (125 g tank^{-1}), urea at 31 kg ha^{-1} (3.1 g tank^{-1}) and triple super phosphate at 16 kg ha^{-1} (1.6 g tank^{-1}) 1 week before fish stocking and 2 weeks after starting the experiment. Each tank was stocked with three common carp (90.3–98.7 g) between 19:00 and 20:00 hours. All common carp were collected from domestic stock. A 30% crude protein formulated diet was applied daily at $15 \text{ g kg}^{-0.8} \text{ day}^{-1}$ in PBF tanks starting on the day of stocking until the day of harvesting.

The glass walls were covered by bamboo mats to prevent sunlight penetration other than through the water surface as in natural earthen ponds. These bamboo mats were only removed during recording of fish behavior. Each week, 50% of the tank water in each tank was changed with less turbid pond water. During the video recording, if the turbidity levels prevented observations in any part within the tank, the water in the tank was again diluted with less turbid pond water.

Temperature, dissolved oxygen (DO), pH, nitrate nitrogen ($\text{NO}_3\text{-N}$), total ammonia nitrogen (TAN), total nitrogen (TN), phosphate phosphorus ($\text{PO}_4\text{-P}$), and total phosphorus (TP) were determined each week starting on the day of fish stocking until the end of the experiment. Temperature was measured with a centigrade thermometer, DO by the Winkler titration method (Stirling 1985), pH with a Jenway pH meter. TAN and $\text{PO}_4\text{-P}$ were analyzed spectrophotometrically (Stirling 1985). $\text{NO}_3\text{-N}$, TN and TP were determined according to APHA (1998).

Water samples for plankton analysis were collected weekly taking 2–5 l samples from each tank, which were then passed through a $10\text{-}\mu\text{m}$ mesh plankton net. Each concentrated plankton sample was then transferred to a

plastic bottle and diluted to 100 ml with formalin and distilled water to obtain a 5% buffered formalin solution. Quality and quantity of plankton were estimated in a Sedgewick-Rafter (S-R) cell. A 1-ml sample was put in the S-R cell and was left for 10 min to allow plankton to settle. The plankton in ten randomly selected fields in the S-R cell was identified to genus according to the keys of Ward and Whipple (1959), Prescott (1962), Belcher and Swale (1976) and Bellinger (1992) and counted under a microscope. Plankton density was calculated using the formula, $N = (P \times C \times 100)/L$, with N = the number of planktonic organisms per liter of pond water, P = the number of planktonic organisms counted in ten fields, C = the volume of the plastic bottle holding the sample (100 ml), and L = the volume of the tank water sample (l).

In each tank, measured volumes of bottom mud samples were collected at the end of the experiment and washed through a $250\text{-}\mu\text{m}$ mesh size sieve. Benthic macroinvertebrates remaining on the sieve were preserved in 5% buffered formalin solution. Benthic macroinvertebrates were identified using the following keys: Brinkhurst (1971) and Pinder and Reiss (1983). Density was calculated using the formula, $N = Y/A$, with N = the number of benthic organisms (numbers cm^{-3}), Y = total number of benthic macroinvertebrates counted, and A = volume of bottom mud collected (cm^3). The volumes of plankton and benthic macroinvertebrates were calculated according to Rahman et al. (2006).

All behavioral observations were performed in the last week of the experiment by video recording fish activity. Two analogue video cameras (model HEL30K1A000) connected with a Quard (model NB2010S), a video cassette recorder (SANYO, model TLS-9924P), and a TV (SONY, model KV-TG21M80) were used for the recording. The combined camera images covered the entire water volume of each tank. Fish behavior was monitored for a full 24-h period, starting at 08:00 hours with a 15-min recording, which was repeated every 3 h. All video images per tank were analyzed for individual fish behavior by direct observation using “The Observer”, version 4.1 software (Noldus Information Technology, Wageningen, The Netherlands). All behaviors were measured on the basis of total time engaged in every 15-min period and expressed as a percentage of total time. Types of fish behavior quantified in this study included grazing, swimming, and resting (Table 1). The scattering of the fish was also quantified. All behaviors were expressed as the percentage of total time pooled over the whole day.

At the end of the experiment, tanks were drained and all fish were weighed. Specific growth rate (% body weight day^{-1}) was calculated using the formula, $\text{SGR} = [\ln \text{WT}_F - \ln \text{WT}_I] \times 100/T$, with WT_F = average final fish weight (g), WT_I = average initial fish weight (g), and T = duration of the experiment (days).

After weighing, a 5-cm section of the anterior gut of each fish was removed by dissection and preserved in a 10% buffered formalin solution. The contents from each gut were placed into a Petri dish and diluted with 50 ml

of water. A 1-ml sub-sample was transferred by pipette to a S-R cell and allowed to rest for 10 min to allow for settlement of solid particles. The gut contents were quantified by using ten random S-R cells, with contents identified to genus level. We calculated the total organisms in the gut using the following formula, $N = P \times C \times 100$, with N = total number of each organism in a 5-cm gut, P = total number of each organism observed in ten cells, and C = volume (ml) of sample in the Petri dish. Food selectivity was assessed by calculating Chesson's α (Chesson 1983) using the formula, $\alpha_i = r_i / p_i (\sum r_i / p_i)^{-1}$, $i = 1, \dots, n$; where α_i is the selectivity for prey type i , r_i = the relative abundance of prey type i in the fish ration, p_i = the relative abundance of prey type i in the environment, and n = the total number of prey types available. The value of α_i varies between 0 and 1 with $\alpha_i = 1/n$ indicating no selectivity (neutral preference) for prey type i , $\alpha_i < 1/n$ indicating avoidance (negative selection) of a prey type i and $\alpha_i > 1/n$ indicating preference (positive selection) for a prey type i . Because $n = 7$ here, then $1/n = 0.14$. For Chesson's α (selectivity index), 95% confidence intervals were calculated from tank wise selectivity index.

Table 1 Description of behavioral variables of common carp in simulated aquaculture pond conditions

Behavioral element	Variable
Grazing	Grazing in the water column Grazing on the tank wall Grazing on the bottom
Swimming	Swimming in the water column Swimming near the bottom (approximately less than 10 cm from the bottom)
Resting	Resting (motionless)
Social behavior (scattered)	All common carp were more than 10 cm apart

All data were checked for normality and homogeneity of variance before analysis. Only the percent data had to be arcsine-transformed before analysis, but non-transformed data are shown in tables or figures. All water quality and plankton availability data were analyzed through repeated measures one-way ANOVA with treatment as the main factor and time as a sub-factor using the statistical package SAS (version 6.1, SAS Institute Inc., Cary, NC, USA). Because of the scope of the present paper, only the main treatment effects are presented. Gut content, growth parameters, sediment benthic macroinvertebrates availability and behavior data were analyzed using one-way ANOVA with only the treatment factor. Where effects were significant, differences between the means were analyzed by Bonferroni tests for multiple comparisons of means. Bonferroni corrections were also applied to the P -values of the ANOVA main treatment effects.

Results

Water quality, and plankton and benthic macroinvertebrates availability

The difference in food resources and artificial feeding affected all water-quality variables ($P < 0.05$) except temperature and total ammonia nitrogen (TAN) (Table 2). Higher DO, pH, and total alkalinity were observed in P tanks than PB tanks, followed by PBF tanks. The opposite results were observed for $\text{NO}_3\text{-N}$, TN, and TP concentrations. Greater total phytoplankton and zooplankton volumes (in the water) were apparent in the PBF tanks than in the PB and P tanks ($P < 0.05$) (Table 2). The volume of benthic macroinvertebrates in the bottom sediment was also greater in the PBF than in the PB tanks.

Table 2 Water-quality parameters and plankton availability in different treatments based on one-way repeated measure ANOVA

Variable	Error (d.f.)	F -value and probability	Treatment mean \pm 95% confidence intervals		
			Treatment (2 d.f.)	P	PB
Temperature ($^{\circ}\text{C}$)	12	1.05 ns	25.7 \pm 1.0	25.5 \pm 1.1	25.5 \pm 1.2
DO (mg l^{-1})	12	18.81*	7.7 ^a \pm 0.7	6.2 ^b \pm 0.6	4.9 ^c \pm 0.4
pH range	–	–	7.11–8.58	6.92–7.85	6.57–7.69
Total alkalinity (mg l^{-1})	12	11.01*	145 ^a \pm 8	123 ^{ab} \pm 9	108 ^b \pm 8
$\text{NO}_3\text{-N}$ (mg l^{-1})	12	40.32*	0.24 ^c \pm 0.02	0.31 ^b \pm 0.03	0.45 ^a \pm 0.04
TAN (mg l^{-1})	12	4.02 ns	0.12 \pm 0.02	0.13 \pm 0.04	0.19 \pm 0.05
TN (mg l^{-1})	12	41.00*	0.78 ^c \pm 0.11	1.01 ^b \pm 0.10	1.31 ^a \pm 0.13
$\text{PO}_4\text{-P}$ (mg l^{-1})	12	6.01*	0.17 ^b \pm 0.02	0.22 ^{ab} \pm 0.04	0.25 ^a \pm 0.03
TP (mg l^{-1})	12	5.09*	0.48 ^c \pm 0.04	0.61 ^b \pm 0.04	0.86 ^a \pm 0.06
Total phytoplankton ($\text{mm}^3 \text{l}^{-1}$)	12	200.23**	0.24 ^c \pm 0.02	0.33 ^b \pm 0.02	0.55 ^a \pm 0.08
Total zooplankton ($\text{mm}^3 \text{l}^{-1}$)	12	75.10*	0.03 ^c \pm 0.00	0.05 ^b \pm 0.01	0.09 ^a \pm 0.02
Total benthic macroinvertebrates ($\text{mm}^3 \text{cm}^{-3}$)	2	43.381* (1 d.f.)	–	0.14 ^b \pm 0.04	0.46 ^a \pm 0.09

P, PB, and PBF indicate tanks with plankton, tanks with plankton, and benthic macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

If the effects are significant, ANOVA was followed by Bonferroni post hoc test. Superscripts a, b, and c represent outcomes from the Bonferroni post hoc test. Mean values in same the row with no superscript in common differ significantly ($P < 0.05$). * $P \leq 0.05$; ** $P < 0.01$

ns Not significant

Fish growth and gut content

A higher specific growth rate was observed in the PBF tanks than PB, followed by P tanks (Fig. 1). The volumes of total phytoplankton including all groups in common carp gut were greater in P than PB and PBF tanks ($P < 0.05$), while these gut volumes in PB and PBF tanks were similar (Table 3). The volumes of total zooplankton including all groups (except Copepoda) in common carp gut of P tanks were greater than PB tanks, followed by PBF tanks ($P < 0.05$). Common carp ingested more benthic macroinvertebrates in PB tanks than PBF tanks ($P < 0.01$). The gut contents of common carp in tanks with PBF were mostly identified as artificial food. Despite the volume of plankton and

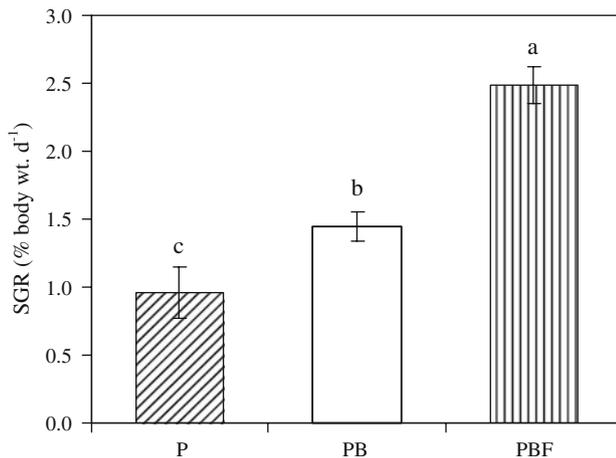


Fig. 1 Effects of treatment on SGR ($F_{2,3} = 99.11$) of common carp based on one-way ANOVA. Treatments with no letter in common are significantly different ($P < 0.05$) based on Bonferroni test. Data are mean \pm 95% confidence intervals. P, PB, and PBF indicate tanks with plankton, tanks with plankton, and benthic macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

macroinvertebrates in common carp gut being higher in the PBF tanks compared to the PB tanks, common carp fed primarily on artificial food.

Common carp did not prefer all groups of phytoplankton in all treatments (Chesson $\alpha < 0.14$; Fig. 2). It preferred (Chesson $\alpha > 0.14$) all groups of zooplankton only in the P tanks and PB tanks. Zooplankton preference of common carp was higher in the P tanks than PB tanks.

Grazing, swimming, and social behavior

Common carp was active during the observations and did not rest, except minimally in PBF tanks (Table 4). Apart from grazing on the tank wall, all grazing and swimming variables were significantly different between treatments ($P < 0.01$). Common carp grazed in the water column more in the P tanks than the PB tanks, followed by PBF tanks ($P < 0.01$). A similar trend was also observed for total grazing. Common carp grazed 3.4 and 5.9 times more in the water column in P tanks than PB and PBF tanks, respectively. Time spent grazing on tank bottoms by common carp was higher in the PB tanks than PBF tanks and followed by P tanks ($P < 0.05$). Time spent grazing on tank bottoms in the PB tanks was 2.2 and 3.8 times higher than the PBF and P tanks, respectively. A significant relationship was observed between common carp's grazing in the water column and the total volume of plankton in common carp gut ($R^2 = 0.95$; $N = 18$; $P = 0.01$; $y = 41.1x + 1.68$, here, y indicates percent time spent for water column grazing by common carp and x indicates total volume of plankton in common carp gut).

Common carp swam in the water column more in PBF tanks, followed by P tanks and PB tanks. However, the trend of swimming near the bottom by common carp was similar to grazing on the bottom. Common carp swam near the bottom 3.5 and 2.1 times more in the PB

Table 3 Volume (mm^3) of plankton and macroinvertebrates in foregut of common carp based on one-way ANOVA

Variables	Error (d.f.)	<i>F</i> -value and probability	Treatment mean \pm 95% confidence intervals		
			Treatment (2 d.f.)	P	PB
Bacillariophyceae	3	26.67*	0.084 ^a \pm 0.016 (9.8)	0.033 ^b \pm 0.003 (2.2)	0.023 ^b \pm 0.015 (6.9)
Chlorophyceae	3	28.26*	0.081 ^a \pm 0.012 (9.3)	0.032 ^b \pm 0.020 (2.3)	0.011 ^b \pm 0.002 (4.1)
Cyanophyceae	3	64.13*	0.074 ^a \pm 0.011 (8.1)	0.019 ^b \pm 0.008 (1.4)	0.013 ^b \pm 0.005 (4.3)
Euglenophyceae	3	386.78**	0.029 \pm 0.003 (2.3)	0.00	0.00
Total phytoplankton	3	338.27*	0.259 ^a \pm 0.013 (29.4)	0.083 ^b \pm 0.015 (6.0)	0.046 ^b \pm 0.008 (15.2)
Rotifera	3	95.94**	0.180 ^a \pm 0.016 (19.5)	0.089 ^b \pm 0.016 (6.5)	0.024 ^c \pm 0.015 (7.3)
Cladocera	3	64.39**	0.250 ^a \pm 0.016 (28.7)	0.121 ^b \pm 0.047 (8.6)	0.016 ^c \pm 0.000 (5.5)
Copepoda	3	45.97*	0.202 ^a \pm 0.048 (22.4)	0.040 ^b \pm 0.016 (3.1)	0.016 ^b \pm 0.006 (6.5)
Total zooplankton	3	209.37**	0.631 ^a \pm 0.048 (70.6)	0.250 ^b \pm 0.045 (18.1)	0.056 ^c \pm 0.017 (19.4)
Benthic Macroinvertebrates	3	125.18**	0.0	1.062 ^a \pm 0.170 (75.9)	0.195 ^b \pm 0.025 (65.4)
Total natural food	3	61.72**	0.890 ^b \pm 0.035 (100)	1.395 ^a \pm 0.232 (100)	0.298 ^c \pm 0.033 (100)

P, PB, and PBF indicate tanks with plankton, tanks with plankton and benthic macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

Percentage of total food bulks are presented in *parentheses*. ANOVA was performed based on absolute value. If the effects are significant, ANOVA was followed by Bonferroni post hoc test. Superscripts a, b, and c represent outcomes from the Bonferroni post hoc test. Mean values in the same row with no superscript in common differ significantly ($P < 0.05$). * $P \leq 0.05$; ** $P \leq 0.01$

tanks than PBF and P tanks, respectively. Total swimming by common carp was highest in PBF tanks, followed by PB tanks and P tanks.

Common carp showed the highest scattering behavior in P tanks, followed by PB and PBF tanks (Table 4). Time spent scattering was positively correlated with time spent for grazing ($P < 0.01$) (Fig. 3). No aggressive behavior was observed during the observation period.

Discussion

Both sediment bioturbation and artificial feeding influence the biotic and abiotic properties of water by increasing organic matter decomposition, which subsequently increases the N and P concentrations and

decreases DO, pH, and total alkalinity in the water (Hargreaves 1998; Rahman et al. 2008b, 2008c). In this study, PBF tanks were affected by both artificial feeding and bioturbation of the sediment by the fish. In contrast, PB tanks were only affected by the latter. This resulted in comparatively higher N and P compounds and lower DO, pH and total alkalinity in PBF tanks than PB tanks, followed by P tanks. Nutrient concentration stimulated photosynthesis, increasing phytoplankton and zooplankton biomass (Rahman and Verdegem 2007).

In this study, when plankton and benthic macroinvertebrates were available, common carp ignored phytoplankton, strongly selected benthic macroinvertebrates (contributing 76% of the total gut content volume) and weakly selected zooplankton. These results suggest that common carp prefer benthic macroinvertebrates to zooplankton when plankton and benthic macroinvertebrates are provided together. This result is consistent with our earlier study (Rahman et al. 2006) in rohu-common carp bi-culture ponds in which common carp principally ingested benthic macroinvertebrates in the absence of artificial feed. This preference for benthic macroinvertebrates most probably influenced common carp behavior as they spent more time near the bottom of the tanks for grazing and swimming in PB tanks than all other tanks. This indicates that the feeding niche of common carp is largely benthic when only plankton and benthic macroinvertebrates are available in the system. This agrees with the general concept that common carp is a benthivorous fish (Parkos et al. 2003).

Many fish shift to less profitable foods when preferred food sources become depleted (Balcombe et al. 2005; Balcombe and Humphries 2006), which can affect foraging, swimming and social behavior. This concept is also true for common carp. In this study, common carp increased its preference for zooplankton, which was a very dominant food (contributing more than 70% of the total gut content volume) in the absence of benthic macroinvertebrates. The zooplankton dependency re-

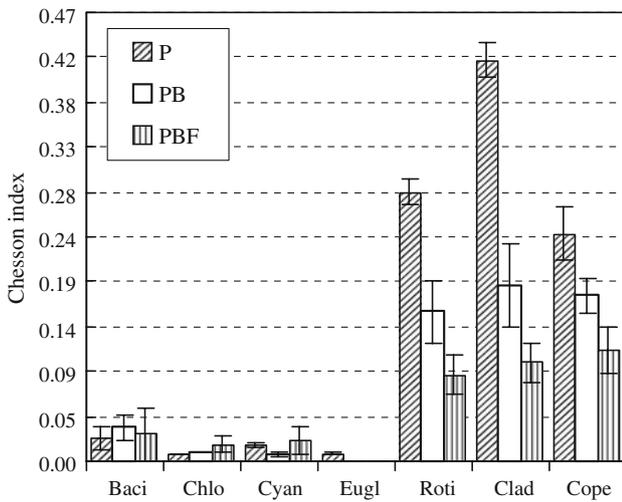


Fig. 2 Chesson selectivity index (mean ± 95% confidence intervals) of common carp in different groups of plankton under different treatments. Baci, Chlo, Cyan, Eugl, Roti, Clad, and Cope indicate Bacillariophyceae, Chlorophyceae, Cyanophyceae, Euglenophyceae, Rotifera, Cladocera, and Copepoda, respectively

Table 4 Grazing and swimming, resting, and social behavior of common carp in different treatments based on one-way ANOVA

Variable	Error (d.f.)	F-value and probability	Treatment means ± 95% confidence intervals		
			Treatment (2 d.f.)	P	PB
<i>Grazing, swimming, and resting</i>					
Grazing in the water column	3	155.97**	39.6 ^a ± 5.7	12.7 ^b ± 0.7	7.2 ^c ± 0.4
Grazing on the wall	3	0.84 ns	0.8 ± 0.4	0.5 ± 0.2	0.7 ± 0.3
Grazing on the bottom	3	58.71*	6.3 ^c ± 0.4	24.2 ^a ± 3.9	10.8 ^b ± 1.2
Total grazing	3	84.49*	46.7 ^a ± 3.9	37.5 ^b ± 3.5	18.6 ^c ± 1.1
Swimming in the water column	3	113.51**	45.0 ^b ± 3.0	33.3 ^c ± 1.6	64.0 ^a ± 3.6
Swimming near bottom	3	166.75**	8.3 ^c ± 0.9	29.2 ^a ± 1.9	14.0 ^b ± 2.0
Total swimming	3	61.22*	53.3 ^c ± 3.9	62.5 ^b ± 3.5	77.9 ^a ± 2.6
Resting (motionless)	3	186.32**	0.0	0.0	3.4 ± 0.5
<i>Social behavior (Scattered)</i>					
	3	74.15*	76.0 ^a ± 6.6	62.6 ^b ± 3.2	41.9 ^c ± 2.0

P, PB, and PBF indicate tanks with plankton, tanks with plankton and benthic macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

Results are based on the percent duration of time for any given behavior. If the effects are significant, ANOVA was followed by Bonferroni post hoc test. Superscripts a, b, and c represent outcomes from the Bonferroni post hoc test. Mean values in the same row with no superscript in common are significantly different * $P \leq 0.05$; ** $P < 0.01$; ns, not significant

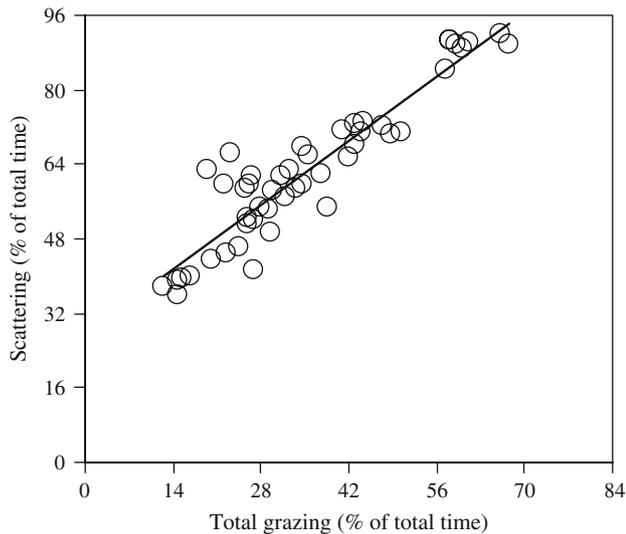


Fig. 3 Relationship between scattering (% of total time) and grazing (% of total time) behavior of common carp ($R^2 = 0.87$; $n = 48$; $P = 0.01$; $y = 0.99x + 27.4$, y percent time spent for scattering by common carp and x percent time spent for total grazing)

sulted in a behavioral shift from benthic grazing and swimming to activities mostly in the water column with 85% of the total time recorded spent in the water column. This result was further supported by the positive relationship between common carp's grazing in the water column and the total volume of plankton in common carp gut. Thus, common carp shifted its feeding from the bottom of the tank to the water column in absence of benthic macroinvertebrates.

When artificial food was supplied with plankton and benthic macroinvertebrates, common carp ingested the lowest volume of phytoplankton, zooplankton, and benthic macroinvertebrates. Although the volume of artificial feed in common carp gut was not directly measured, microscopic observation indicated that common carp mostly ingested artificial feed in PBF tanks. The gut contents of common carp in PBF tanks clearly suggested that common carp preferred artificial feed to benthic macroinvertebrates, followed by zooplankton. This result agrees in part with Spataru et al. (1980) and Schroeder (1983), who observed that common carp naturally depend on plankton and benthic macroinvertebrates but when artificial feed is applied, they will readily accept artificial feed.

Fish would need less time and energy to ingest readily available artificial feed than to ingest the same volume of plankton by sucking water and/or benthic macroinvertebrates by digging bottom sediment. Artificial food preference of common carp resulted in the lowest total grazing and highest total swimming time and highest growth rate in PBF tanks. Similar effects of artificial feed on total grazing and swimming time of common carp were observed in our earlier study (Rahman et al. 2008a), in which common carp was stocked in rohu tanks. This indicates that common carp can modify their

feeding and behavior in the presence of other fish, thus making them a valuable species not only for monoculture but also for polyculture.

Regardless of where fish live, they may exhibit either scattering or shoaling during grazing, which varies among species, food habits, and food resources (Breder 1959; Morgan 1988). In this study, conspecific scattering behavior of common carp was dependent on both food resources and grazing. The relationship between grazing and scattering time of common carp indicated that common carp preferred to graze individually. Therefore, lower grazing in the presence of artificial feed resulted in less time spent scattered and more time swimming.

In conclusion, common carp was confirmed to be benthivorous in their general behavior, which was linked to their feeding ecology where they exhibited a preference for benthic macroinvertebrates over zooplankton. This fish readily switched to artificial feed when it was available. Common carp can also change its grazing, swimming, and conspecific social behavior in response to changing food resources. There is further research potential to examine whether common carp can shift its food selectivity and feeding niche when interspecific (with other benthivorous fish) and/or intraspecific (mixture of same species, including different size classes at high density) competition exists. Knowledge gained from such research could benefit common carp mono- and polyculture management.

Acknowledgments We gratefully acknowledge the European Commission for financial support through Pond-Live project. Special thanks to Dr. Marc Verdegem, Aquaculture and Fisheries Group, Department of Animal Science, Wageningen University, The Netherlands, for his cooperation during conducting this experiment. This experiment complied with the current law of Bangladesh.

References

- Adamek Z, Sukop I, Rendon MP, Kouril J (2003) Food competition between 2+ tench (*Tinca tinca* L.), common carp (*Cyprinus carpio* L.) and bigmouth buffalo (*Ictiobus cyprinellus* Val.) in pond polyculture. *J Appl Ichthyol* 19:65–169
- APHA (1998) Standard methods for the examination of water and waste water. American Public Health Association, Washington, DC
- Balcombe SR, Humphries P (2006) Diet of the Western carp gudgeon (*Hypseleotris klunzingeri* Ogilby) in an Australian floodplain lake: the role of water level stability. *J Fish Biol* 68:1484–1493
- Balcombe SR, Bunn SE, Davies PM, McKenzie Smith FJ (2005) Variability of fish diets between dry and flood periods in an arid zone floodplain river. *J Fish Biol* 67:552–1567
- Belcher H, Swale S (1976) A beginner's guide to freshwater algae. Institute of Terrestrial Ecology, Natural Environmental Research Council, London
- Bellinger EG (1992) A key to common algae. The Institute of Water and Environmental Management, London
- Biro P (1995) Management of pond ecosystems and trophic webs. *Aquaculture* 129:373–386
- Breder CM Jr (1959) Studies on social groupings in fishes. *Bull Am Mus Nat His* 117:397–482
- Brinkhurst RO (1971) A guide for the identification of British Aquatic Oligochaeta. Freshwater Biological Association, Kendal

- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304
- FAO (2007) Fishstat plus (v. 2.30). FAO, Rome
- Hargreaves JA (1998) Nitrogen biochemistry of aquaculture ponds. *Aquaculture* 166:181–212
- Hegrenes S (2001) Diet-induced phenotypic plasticity of feeding morphology in the orange spotted sunfish, *Lepomis humilis*. *Ecol Freshw Fish* 10:35–42
- Iguchi K, Abe S (2002) Territorial defense of an excess food supply by an algal grazing fish, ayu. *Ecol Res* 17:373–380
- Mearns KJ, Ellingsen OF, Doving KB, Helmer S (1987) Feeding behaviour in adult rainbow trout and Atlantic salmon parr, elicited by chemical fractions and mixtures of compounds identified in shrimp extract. *Aquaculture* 64:47–63
- Morgan MJ (1988) The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. *Anim Behav* 36:1317–1322
- Parkos JJ III, Santucci VJ Jr, Wahl DH (2003) Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Can J Fish Aquat Sci* 60:182–192
- Pinder LC, Reiss F (1983) The larvae of Chironomidae (Diptera: Chironomidae) of the Holarctic region. In: Wiederholm T (ed) Chironomidae of the Holarctic Region. *Entomol Scand Suppl* 19:293–437
- Prescott GW (1962) Algae of the western Great Lakes area. Wm C Brown Co, Inc, Iowa
- Rahman MM, Verdegem MCJ (2007) Multi-species fishpond and nutrients balance. In: van der Zijpp AJ, Verreth AJA, Tri LQ, van Mensvoort MEF, Bosma RH, Beveridge MCM (eds) Fishponds in farming systems. Wageningen Academic Publishers, Netherlands, pp 79–88
- Rahman MM, Verdegem MCJ, Nagelkerke LAJ, Wahab MA, Milstein A, Verreth JAJ (2006) Growth production and food preference of rohu *Labeo rohita* (H.) in monoculture and in polyculture with common carp *Cyprinus carpio* (L.) under fed and non-fed ponds. *Aquaculture* 257:359–372
- Rahman MM, Verdegem MCJ, Nagelkerke LAJ, Wahab MA, Verreth JAJ (2008a) Swimming grazing and social behaviour of rohu *Labeo rohita* (Hamilton) and common carp *Cyprinus carpio* (L.) in tanks under fed and non-fed conditions. *Appl Anim Behav Sci* 213:255–264
- Rahman MM, Verdegem M, Nagelkerke L, Wahab MA, Milstein A, Verreth J (2008b) Effects of common carp *Cyprinus carpio* (L.) and feed addition in rohu *Labeo rohita* (Hamilton) ponds on nutrient partitioning among fish, plankton and benthos. *Aquacult Res* 39:85–95
- Rahman MM, Verdegem MCJ, Nagelkerke LAJ, Wahab MA, Verreth JAJ (2008c) Relationships among water quality, food resources, fish diet and fish growth in polyculture ponds: a multivariate approach. *Aquaculture* 275:108–115
- Schroeder GL (1983) Sources of fish and prawn growth in polyculture ponds as indicated by delta C analysis. *Aquaculture* 35:29–42
- Smith IP, Metcalfe NB, Huntingford FA (1995) The effects of food pellet dimensions on feeding response by Atlantic salmon (*Salmo salar* L.) in a marine net pen. *Aquaculture* 130:167–175
- Spataru P, Hephher B, Helevy A (1980) The effect of the method of artificial food application on the feeding habits of carps (*Cyprinus carpio* L.) with regard to natural food in ponds. *Hydrobiologia* 72:171–178
- Stirling HP (1985) Chemical and biological methods of water analysis for aquaculturists. Institute of Aquaculture, University of Stirling, Stirling
- Ward HB, Whipple GC (1959) Freshwater biology. Wiley, New York
- Zhou JF, Wu QJ, Ye YZ, Tong JG (2003) Genetic divergence between *Cyprinus carpio carpio* and *Cyprinus carpio haematopterus* as assessed by mitochondrial DNA analysis, with emphasis on origin of European domestic carp. *Genetica* 119:93–97