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

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14 **Abstract** We used customized fish tanks as model fish ponds to observe grazing, swimming and conspecific
15 social behaviour of common carp (*Cyprinus carpio*) under variable food resource conditions to assess
16 alterations in feeding niche. Different food and feeding situations were created by using only pond water or
17 pond water plus pond bottom sediment or pond water plus pond bottom sediment and artificial feeding. All
18 tanks were fertilized twice, prior to stocking and two weeks later after starting the experiment to stimulate
19 natural food production. Common carp preferred artificial feed over benthic macroinvertebrates, followed by
20 zooplankton. Common carp did not prefer any group of phytoplankton in any treatment. Common carp was
21 mainly benthic in habitat choice, feeding on benthic macroinvertebrates when only plankton and benthic
22 macroinvertebrates were available in the system. In the absence of benthic macroinvertebrates, their feeding
23 niche shifted from near the bottom of the tanks to the water column where they spent 85% of the total time in
24 the water column and fed principally on zooplankton. Common carp readily switched to artificial feed when
25 available, which led to better growth. Common carp preferred to graze individually. Behavioural
26 observations of common carp in tanks yielded new information that assists our understanding of their
27 ecological niche. This knowledge could be potentially used to further the development of common carp
28 aquaculture.

29

30 **Keywords** Food selectivity . Feeding niche . food resource . Behaviour . *Cyprinus carpio*

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33 Introduction

34

35 Common carp (*Cyprinus carpio*) is one of the most commercially important and widely cultivated freshwater
36 fish in the world (Biro 1995; Zhou et al. 2003), contributing to 11% of the total world freshwater aquaculture
37 production (FAO 2007). More than 90% of this production comes from Asia (FAO 2007), where common
38 carp is cultured in various pond aquaculture systems. The food resources of different aquaculture systems are
39 highly variable depending on culture system and nutrient inputs. Many fish change their food selectivity and
40 feeding niche with changing food availability (Hegrenes 2001; Iguchi and Abe 2002). Similarly, common
41 carp might alter its food preference and behaviour in response to changing food resources. Although there is
42 some information about diet and feeding behaviour of common carp (Adamek et al. 2003; Rahman et al.
43 2006; Rahman et al. 2008a), their feeding niche in aquatic ecosystems under varying food resources is still
44 not fully understood. Better information about how common carp changes its food selectivity and behaviour
45 with changing food resources is necessary to understand its ecology and to optimize feeding management

46 Direct observation can provide important information on grazing and swimming behaviour
47 (Mearns et al. 1987; Smith et al. 1995) and may provide insight into feeding niches in pond ecosystems. This
48 study simultaneously considered gut content and feeding behaviour of common carp. The aim of this study
49 was to quantify the effects of different food resources, on food selectivity and feeding niche of common carp.

50

51 Materials and Methods

52

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

59 The bottom of the tanks of treatments PB and PBF received pond sediment. All tanks were filled

60 with pond water. The heights of the sediment and water column were 10 and 70 cm respectively. The water
61 and sediment were supplied from a central pond. All tanks were treated with agricultural lime (CaCO_3) at a
62 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}
63 (3.1 g tank^{-1}) and triple super phosphate at 16 kg ha^{-1} (1.6 g tank^{-1}) one week before fish stocking and two
64 weeks after starting the experiment. Each tank was stocked with three common carp (90.3-98.7 g) between
65 19:00 and 20:00 h. All common carp were collected from domestic stock. A 30% crude protein formulated
66 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
67 harvesting.

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

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

79 Water samples for plankton analysis were collected weekly taking 2-5 L samples from each tank,
80 which were then passed through a 10- μm mesh plankton net. Each concentrated plankton sample was then
81 transferred to a plastic bottle and diluted to 100 ml with formalin and distilled water to obtain a 5% buffered
82 formalin solution. Quality and quantity of plankton were estimated in a Sedgewick-Rafter (S-R) cell. A 1 ml
83 sample was put in the S-R cell and was left for 10 minutes to allow plankton to settle. The plankton in 10
84 randomly selected fields in the S-R cell was identified to genus according to the keys of Ward and Whipple
85 (1959), Prescott (1962), Belcher and Swale (1976) and Bellinger (1992) and counted under a microscope.
86 Plankton density was calculated using the formula, $N = (P \times C \times 100)/L$, with N = the number of planktonic

87 organisms per litre of pond water, P = the number of planktonic organisms counted in ten fields, C = the
88 volume of the plastic bottle holding the sample (100 ml), and L = the volume of the tank water sample (L).

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

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

107 At the end of the experiment, tanks were drained and all fish were weighed. Specific growth rate
108 (% body weight day^{-1}) was calculated using the formula, $SGR = [\ln WT_F - \ln WT_I] \times 100/T$, with WT_F =
109 average final fish weight (g), WT_I = average initial fish weight (g), and T = duration of the experiment (days).
110 After weighing, a 5 cm section of the anterior gut of each fish was removed by dissection and preserved in a
111 10% buffered formalin solution. The contents from each gut were placed into a Petri dish and diluted to 50
112 ml with water. A 1 ml sub-sample was transferred by pipette to a S-R cell and allowed to rest for 10 minutes
113 to allow for settlement of solid particles. The gut contents were quantified by using 10 random S-R cells,

114 with contents identified to genus level. We calculated the total organisms in the gut using the following
 115 formula, $N = P \times C \times 100$, with N = total number of each organism in a 5 cm gut, P = total number of each
 116 organism observed in 10 cells, and C = volume (ml) of sample in the Petri dish. Food selectivity was assessed
 117 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
 118 the selectivity for prey type i , r_i = the relative abundance of prey type i in the fish ration, p_i = the relative
 119 abundance of prey type i in the environment, and n = the total number of prey types available. The value of α_i
 120 varies between 0 and 1 with $\alpha_i = 1/n$ indicating no selectivity (neutral preference) for prey type i , $\alpha_i < 1/n$
 121 indicating avoidance (negative selection) of a prey type i and $\alpha_i > 1/n$ indicating preference (positive
 122 selection) for a prey type i . Because $n = 7$ here, then $1/n = 0.14$. For Chesson's α , 95% confidence intervals
 123 were calculated from tank wise selectivity index.

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

133

134 **Results**

135

136 Water quality, and plankton and benthic macroinvertebrates availability

137

138 The difference in food resources and artificial feeding affected all water quality variables ($P < 0.05$) except
 139 temperature and total ammonia nitrogen (TAN) (Table 2). Higher DO, pH and total alkalinity were observed
 140 in P tanks than PB tanks, followed by PBF tanks. The opposite results were observed for $\text{NO}_3\text{-N}$, TN and TP

141 concentrations. Greater total phytoplankton and zooplankton volumes (in the water) were apparent in the
142 PBF tanks than in the PB and P tanks ($P<0.05$) (Table 2). The volume of benthic macroinvertebrates in the
143 bottom sediment was also greater in the PBF than the PB tanks.

144

145 Fish growth and gut content

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

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

157

158 Grazing, swimming and social behaviour

159

160 Common carp was active during the observations and did not rest, except minimally in PBF tanks (Table 4).
161 Apart from grazing on the tank wall, all grazing and swimming variables were significantly different between
162 treatments ($P<0.01$). Common carp grazed in the water column more in the P tanks than the PB tanks,
163 followed by PBF tanks ($P<0.01$). A similar trend was also observed for total grazing. Common carp grazed
164 3.4 and 5.9 times more in the water column in P tanks than PB and PBF tanks, respectively. Time spent
165 grazing on tank bottoms by common carp was higher in the PB tanks than PBF tanks and followed by P tanks
166 ($P<0.05$). Time spent grazing on tank bottoms in the PB tanks was 2.2 and 3.8 times higher than the PBF and
167 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 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 behaviour 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 behaviour 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; Rahman et al. 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

195 preference for benthic macroinvertebrates most probably influenced common carp behaviour as they spent
196 more time near the bottom of the tanks for grazing and swimming in PB tanks than all other tanks. This
197 indicates that the feeding niche of common carp is largely benthic when only plankton and benthic
198 macroinvertebrates are available in the system. This agrees with the general concept that common carp is a
199 benthivorous fish (Parkos et al. 2003).

200 Many fish shift to less profitable foods when preferred food sources become depleted (Balcombe et
201 al 2005; Balcombe and Humphries 2006), which can affect foraging, swimming and social behaviour. This
202 concept is also true for common carp. In this study, common carp increased its preference for zooplankton,
203 which was a very dominant food (contributing more than 70% of the total gut content volume) in the absence
204 of benthic macroinvertebrates. The zooplankton dependency resulted in a behavioural shift from benthic
205 grazing and swimming to activities mostly in the water column with 85% of the total time recorded spent in
206 the water column. This result was further supported by the positive relationship between common carp's
207 grazing in the water column and the total volume of plankton in common carp gut. Thus, common carp shifted
208 its feeding from the bottom of the tank to the water column in absence of benthic macroinvertebrates.

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

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

222 rohu tanks. This indicates that common carp can modify their feeding and behaviour in the presence of other
223 fish, thus making them a valuable species not only for monoculture but also for polyculture.

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

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

238

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243

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245

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307

308 **Figure legends**

309

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

314 **Fig. 2** Chesson selectivity index (mean $\pm 95\%$ confidence intervals) of common carp in different groups of
315 plankton under different treatments. Baci, Chlo, Cyan, Eugl, Roti, Clad and Cope indicate Bacillariophyceae,
316 Chlorophyceae, Cuanophyceae, Euglenophyceae, Rotifera, Cladocera and Copepoda, respectively

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

320

321 **Table 1** Description of behavioural variables of common carp in simulated aquaculture pond conditions

Behavioural 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 behaviour (scattered)	All common carp were more than 10 cm apart

322

323

324 **Table 2** Water quality parameters and plankton availability in different treatments based on one-way repeated
 325 measure ANOVA. P, PB and PBF indicate tanks with plankton, tanks with plankton and benthic
 326 macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

Variable	Error (d.f.)	F-value and probability	Treatment Means $\pm$ 95% confidence intervals		
		Treatment (2 d.f.)	P	PB	PBF
Temp. ($^{\circ}$ C)	12	1.05 ns	25.7 ± 1.0	25.5 ± 1.1	25.5 ± 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
Tot. Alk. (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 ± 0.02	0.13 ± 0.04	0.19 ± 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.)	-	$0.14^b \pm 0.04$	$0.46^a \pm 0.09$

327 If the effects are significant, ANOVA was followed by Bonferroni post hoc test. Superscript a, b and c
 328 represent outcomes from the Bonferroni post hoc test. Mean values in same the row with no superscript in
 329 common differ significantly ($P < 0.05$). * $P \leq 0.05$; ** $P < 0.01$; ns, not significant

330

331 **Table 3** Volume (mm³) of plankton and macroinvertebrates in foregut of common carp based on one-way
332 ANOVA. P, PB and PBF indicate tanks with plankton, tanks with plankton and benthic macroinvertebrates
333 and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

Variables	Error (d.f.)	F-value and probability	Treatment Means $\pm$ 95% confidence intervals		
		Treatment (2 d.f.)	P	PB	PBF
Bacillriophyceae	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)

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

Table 4 Grazing and swimming, resting and social behaviour of common carp in different treatments based on one-way ANOVA. P, PB and PBF indicate tanks with plankton, tanks with plankton and benthic macroinvertebrates and tanks with plankton, benthic macroinvertebrates and artificial feed, respectively

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

Results based on the percent duration of time for any given behaviour. If the effects are significant, ANOVA was followed by Bonferroni post hoc test. Superscript 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

345 Fig. 1

346 Fig. 2

349 Fig. 3