

Behavioral and population-level aspects of intraspecific competition in crucian carp

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We examined experimentally factors influencing intraspecific competition for food in crucian carp *Carassius carassius*, a species prone to stunting under high population densities. Short-term laboratory experiments quantified and compared foraging performances of small fish (60–69.5 mm) in the presence of 1) one similarly-sized small competitor, 2) one large (100–109.5 mm) competitor, or 3) four small competitors whose total biomass was equivalent to the single large competitor. Focal fish obtained significantly more food when competing with one small conspecific than when competing with four small or one large crucian carp. Performances did not differ significantly between the latter two treatments, suggesting comparable impacts can result from different competitive scenarios; however, responsible behavioral mechanisms may have differed. Compared with small fish, large crucian carp consumed food more rapidly, suggesting an exploitative advantage, whereas aggression and interference occurred more frequently within groups of five small fish.

To examine longer-term effects of intraspecific competition, we conducted a 34-d growth experiment in hatchery basins; 10 individually-marked small crucian carp received a pelleted diet in the presence of either 19 additional small fish or six large fish of equal total biomass. Consistent with behavioral experiments, crucian carp held with the two types of competitors did not differ significantly in mass gained or hepatic glycogen stores; however, fish held with large competitors had relatively larger livers.

Our results suggest that the total biomass of competitors is a better predictor of the impact of competition on food intake and growth of crucian carp than is either the size or number of competitors alone. The overall outcome of competition among size-classes is not always predictable from measurements of single factors, e.g., foraging efficiency, but results from complex interactions involving both behavioral mechanisms and population-level phenomena.

1. Introduction

Recently, manipulative approaches have been used very effectively to investigate intraspecific competition in freshwater fishes (e.g., Werner et al. 1983, Persson 1987, Power 1987). Studies of behavioral mechanisms behind these intraspecific interactions have concentrated heavily on either foraging efficiency (Werner 1974, Kislalioglu & Gibson 1976, Paszkowski et al. 1989), or on dominance-based social systems (Magnuson 1962, Rubenstein 1981, Koebele 1985). However, because of the complexities involved in intraspecific interactions within size-structured populations (Ebenman & Persson 1988), studies are needed that integrate fine-scale behavioral processes with larger-scale phenomena.

Crucian carp (*Carassius carassius*) offers an excellent subject for increasing our general understanding of intraspecific competition through laboratory and field experiments. It displays dramatic differences in population density and size-structure in response to varying environmental conditions. In lakes supporting populations of piscivores, population densities are low (<25/ha) but the average crucian carp is large (>200 mm; Hamrin 1979, Piironen & Holopainen 1988). In such water bodies, size-limited predation and interspecific competition appear to be major influences on density and size-structure. (Prejs 1973, Tonn et al. 1989). In contrast, shallow ponds in northern and eastern Europe contain dense populations, with up to 29 000 fish/ha and a predominance of small (<100 mm), short-lived individuals (e.g., Černý 1971, Nikolsky & Shubnikova 1974, Holopainen & Pitkänen 1985, Piironen & Holopainen 1988). Crucian carp is the only fish species found in these ponds, due to its ability to survive hypoxic conditions during winter by anaerobic metabolism of glycogen stored principally in the liver (Holopainen & Hyvärinen 1985, Hyvärinen et al. 1985). Intraspecific competition appears to shape growth and survivorship in these stunted fish; population reductions result in marked increases in growth rate among remaining crucian carp (Nikolsky & Shubnikova 1974, Holopainen & Pitkänen 1985). Changes in population density, and therefore relative food supply, can also be reflected in relative liver size and glycogen content (Tonn et al. 1989); crucian carp's dependence

on glycogen reserves accumulated during the summer to survive periods of winter anoxia means that successful foraging can translate directly into increased fitness.

Our study examined effects of intraspecific competition on the behavior and growth of crucian carp, focussing on the smaller fish that predominate in densely populated, monospecific ponds. We addressed the following questions in a series of laboratory experiments:

- 1) How does body size affect foraging performance?
- 2) How does the size and number of competitors affect foraging performance?
- 3) What are the behavioral mechanisms behind foraging performances under different competitive regimes?
- 4) Do patterns seen in short-term foraging experiments agree with trends in growth and glycogen reserves seen in longer-term trials?

2. Materials and methods

2.1. Foraging performances without competitors

To provide baseline information for our competition studies, we conducted laboratory experiments to determine the relative foraging performances (exploitative abilities) of two size-classes of crucian carp feeding on a standardized food item in the absence of potential competitors. Trials were conducted in July 1986 and 1987 at the Central Fish Culture Station for Eastern Finland, Enonkoski.

Small (63.5–71 mm total length, TL) and large (100–109 mm) crucian carp were captured from local lakes and held in stock tanks for several days; during this time fish were introduced to the experimental food, Tess Elite Plus 2.0 trout food (max. diam. of each pellet = 1 mm). After this acclimation period, individual fish were measured, introduced singly into glass aquaria (61 × 40 × 40 cm in 1986, 44 × 39 × 39 cm in 1987), and fed 0.1 g of pellets 24 h before their first trial. Water temperature was 22°C and the laboratory was well-lit with natural and artificial light.

During a trial, 0.1 g of Tess Elite Plus 2.0 was scattered evenly across the surface of an experimental aquarium; most pellets sank rapidly. An observer timed how long it took the fish to find and handle all of the pellets (ca. 33). Handling could be a prolonged process, often involving more than one pellet simultaneously (see Paszkowski et al. 1989); feeding was considered complete when all pellets were consumed and fish resumed normal breathing and swimming. Feeding trials were conducted once per day per fish and a total of three trials were conducted on each experimental fish, usually on successive days. If no trial was run on a particular day, the fish was simply fed 0.1 g of pellets without observation. Data were collected on 10 small and 10 large crucian carp.

For analysis, we used the median value of the three trials as the foraging performance for an individual crucian carp. Performances of small and large crucian carp were compared with a Mann-Whitney *U*-test (Sokal & Rohlf 1981). Medians and 95% confidence intervals reported for foraging performance without competitors, as well as medians reported for foraging experiments with competitors and growth experiments, were calculated using Wilcoxon point estimates of the center based on Walsh averages (Hollander & Wolfe 1973).

2.2. Foraging performance with competitors

These trials were designed to measure the food intake of individual small (60–69.5 mm TL, 3.3–5.2 g) focal crucian carp foraging under three competitive regimes:

- 1) with one other small (60–69.5 mm) crucian carp (referred to as the “one-small-competitor” or ISC treatment),
- 2) with one other large (100–109.5 mm, 14.0–17.8 g) crucian carp (referred to as the “one-large-competitor” or ILC treatment), and
- 3) with four other small (60–69.5 mm) crucian carp whose total biomass equalled that of a large competitor (referred to as the “four-small-competitors” or 4SC treatment).

Trials were conducted during July–August 1987; laboratory conditions and general proce-

dures were as described previously, except that glass observation tanks were either $92 \times 38 \times 38$ cm or $92 \times 38 \times 42$ cm. Six groups of fish, two of each treatment type, were assembled at a time. Fish were measured and one small fish in each group was randomly assigned the role of focal fish. All focal fish, the second small fish in ISC trials, and one of the four small fish in 4SC trials were marked by clipping a small notch in the upper or lower lobe of the caudal fin. Fish were introduced to an observation tank 24 h before a round of trials began; a few hours after introduction they were given 25 pellets (ca. 0.08 g) of Tess Elite Plus 2.0.

A trial consisted of presenting a group with 50 pellets (ca. 0.15 g) of Tess Elite Plus 2.0 by scattering them evenly over the water's surface. An observer followed the focal fish until all pellets were taken up; for most trials, a second observer similarly followed the marked small competitor or the large competitor. If no food was eaten in 15 min, all pellets were removed and the trial repeated later that same day. Data were recorded as the number of pellets eaten by the observed fish during each 1-min interval; the occurrence of agonistic interactions was also recorded. Each group participated in one trial a day; about 6 h after the daily trial, groups received a second feeding of 25 pellets. If no trials were run on a given day, groups were given their ration of 75 pellets in a single feeding.

After a focal fish was observed three times in a particular treatment, it was assigned to a new treatment in a new tank based on a modified Latin square design (Box et al. 1978). New groups were assembled with new competitors. After the six focal fish were observed under all three treatments, they were returned to holding tanks and totally new groups with new focal fish were assembled. Data were collected on 18 subject crucian carp and their competitors, representing a total of 54 trials of each treatment type.

For analyses, we used the median foraging performance of each focal fish and its identified competitor under each competitive regime; performances were matched across treatment types based on focal fish and compared via Wilcoxon's signed-ranks tests (Sokal & Rohlf 1981). Additional behavior patterns were compared across treatments with *G* tests for goodness of fit and

independence with Williams' correction (Sokal & Rohlf 1981) and Mann-Whitney *U* tests.

2.3. Growth experiments

From 22 June – 26 July 1986 we conducted a longer term (34 d) experiment at the Enonkoski facility that examined effects of body size of competitors on growth and glycogen stores of small crucian carp. Six groups of 10 small crucian carp were measured (60–69 mm TL), weighed (3.0–5.1 g), and individually marked as focal fish by partially clipping combinations of anal, pelvic, and caudal fins. These fish were then introduced to one of two different populations of competitors:

- 1) 29 unmarked small crucian carp (55–75 mm) or
- 2) six large crucian carp (100–109.5 mm).

Each treatment was replicated three times, with all groups having comparable total biomasses (120.8–126.4 g with small competitors, 122.7–126.0 g with large competitors).

The six groups were placed in identical, circular, fiberglass tanks, 22 cm deep and 159 cm in diameter. Tanks were flow-through with a median daily water temperature of 18.3°C during the experiment. Tanks were well-lit with natural and artificial light. Each group was fed a daily ration of Tess Elite Plus 2.0 pellets in two installments (0900 and 1800); daily rations were approximately 3% of a group's biomass (initially 3.7 g of food, increased to 4.1 g as fish grew). Any crucian carp that died during the experiment was replaced the same day with an appropriately-sized individual, however, data presented here are based only on focal fish that survived the experiment.

At 11 to 12-d intervals, all fish were weighed to correct ration size; focal fish were also measured (TL). Here we consider only change in mass of focal fish over the entire experimental period. At the end of the experiment, all focal fish were sacrificed, their livers removed and weighed, and glycogen content per unit mass of liver determined using methods described in Siu et al. (1970). Mann-Whitney *U* tests were used to compare change in mass, relative liver size, and relative hepatic glycogen content of focal fish held with small versus large competitors.

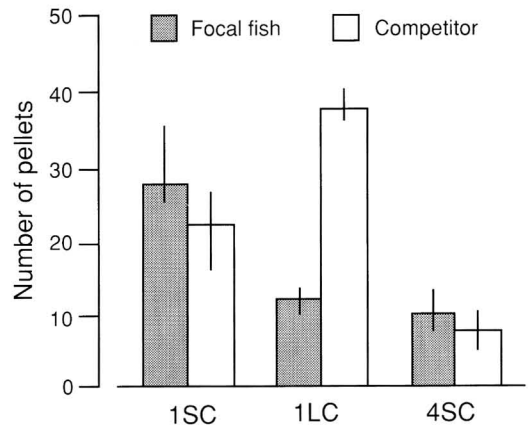


Fig. 1. Medians and 95% confidence intervals for the number of pellets obtained (out of 50 possible) by small (60–69.5 mm) focal crucian carp and by one marked conspecific competitor under three treatments. 1SC = focal fish and one small competitor, 1LC = focal fish and one large competitor (100–109.5 mm), and 4SC = focal fish and four small competitors.

3. Results

3.1. Foraging performances without competitors

In the absence of competitors, small crucian carp took significantly longer to find and process 0.1 g of food (median = 36.5 min, 95% C.I. = 25.7–48.2) than large crucian carp (median = 18.7 min, 95% C.I. = 13.5–25.0; Mann-Whitney *U* test; $P = 0.007$). These rates translated into time investments of 1.1 min/pellet for small crucian carp and 0.6 min/pellet for large crucian carp.

3.2. Foraging performances with competitors

Small focal crucian carp enjoyed significantly greater foraging success when feeding in the company of one small competitor than with one large or four small competitors (Wilcoxon signed-ranks tests; $P < 0.01$ in both cases). Each of the 18 fish ate more pellets in 1SC trials than 1LC or 4SC trials (Fig. 1). Performances did not differ significantly between 1LC and 4SC trials ($P > 0.10$).

Similarly, small competitors in 1SC trials, matched for analysis by the focal fish with which they competed, ate significantly more pellets than the marked competitors followed in 4SC trials (Wilcoxon signed-ranks test; $P < 0.01$; Fig. 1). Large fish in 1LC trials ate significantly more pellets than small fish followed as competitors in either 1SC or 4SC trials ($P < 0.01$ in both cases; Fig. 1). It should be noted that one small or one large crucian carp was capable of eating all 50 pellets during a trial and all five fish typically fed in 4SC trials (C. Paszkowski & W. Tonn, personal observations).

Foraging activity was more intense under some competitive regimes than others. Groups in 1SC trials took significantly longer to collect all 50 pellets (median = 23 min, 95% C.I. = 19–27) than in either 1LC trials (median = 11 min, 95% C.I. = 8.5–14) or 4SC trials (median = 8.5 min, 95% C.I. = 5.5–12; Wilcoxon signed-ranks test with pairing based on focal fish; $P < 0.01$); differences between 4SC and 1LC trials were not quite significant ($0.10 > P > 0.05$).

We analyzed records in more detail to examine how behavioral interactions between competitors may have contributed to feeding patterns of groups and individuals. For example, one reason for differences in trial lengths across treatments might be that bigger groups of small crucian carp or groups containing large fish discovered the presence of food earlier in a trial and/or began feeding more readily (i.e., were less timid). This did not appear to be the case as focal fish and/or the marked competitor began feeding in the first minute of a similar proportion of trials across treatments, i.e., feeding was recorded in the first minute after food introduction in 78% of 1SC trials ($n = 54$), 87% of 1LC trials ($n = 54$), and 74% of 4SC trials ($n = 53$; G test of independence, $G = 3.19$; $P > 0.05$).

It is also possible that differences in performance of focal fish among treatments reflected their responsiveness versus that of their competitors. Examination of individual trials revealed that focal fish began feeding before or within the same minute interval as marked competitors in 90% of 1SC trials ($n = 52$), 77% of 1LC trials ($n = 52$), and 78% of 4SC trials ($n = 50$). Focal fish did not differ significantly across trial types in readiness to initiate feeding, regardless of the

identity of their foraging mates (G test of independence, $G = 4.14$; $P > 0.05$).

We calculated the amount of foraging time invested per pellet consumed by the focal fish and its marked competitor by dividing the total time that food was available (i.e., the amount of time required for all 50 pellets to be consumed by the group) by the number of pellets obtained by the individual fish. Median values for small focal fish were 0.8 (95% C.I. = 0.7–0.9), 0.9 (0.7–1.3), and 0.8 (0.6–1.5) min/pellet for 1SC, 1LC, and 4SC trials, respectively. These time investments did not differ significantly from each other, neither did any of these performances differ significantly from time invested per pellet by solitary small fish (Mann-Whitney U tests; $P > 0.10$ in all cases). In contrast, large crucian carp displayed greater flexibility in feeding, investing significantly less time per pellet in the presence of competitors (0.3 min/pellet, 95% C.I. = 0.2–0.4) than in their absence (Mann-Whitney U test; $P = 0.001$).

Crucian carp moved and fed in loose shoals. Agonistic interactions between shoal members were observed under all three treatments. During these interactions, one individual would follow a second, repeatedly nudging or nipping the eyes, opercular flaps, caudal fin, caudal peduncle, pectoral fins, or anal region; the second fish simply tried to avoid the first. This behavior was only observed after food was introduced into the tank but sometimes continued after all pellets had been taken up. The aggressor often appeared to be attempting to induce regurgitation in the recipient and sometimes succeeded, whereupon aggressor (and recipient) ate the regurgitated food. The 25 trials that involved one or more agonistic interaction were not evenly distributed across treatments (G goodness of fit test, $G = 12.66$; $P < 0.01$). Agonistic behavior occurred in only three 1SC trials (6% of 1SC trials, 12% of observed cases of aggression), five 1LC trials (9% of 1LC trials, 20% of observed cases), but 17 4SC trials (32% of 4SC trials, 68% of observed cases). During all interactions in 1LC trials, the large competitor was the aggressor. If the likelihood of interaction within a treatment type is assumed to be proportional to the number of crucian carp present during trials, the observed occurrence of agonistic behavior across treatments does not differ significantly from the expected distribution (G goodness of fit test, $G = 2.07$; $P > 0.10$).

3.3. Growth experiment

Most focal crucian carp survived the entire growth experiment (28 of 30 in each treatment) and most individuals increased in length (23 of 28 with small competitors, 27 of 28 with large competitors). Preliminary analysis (Kruskal-Wallis tests; Sokal & Rohlf 1981) showed no difference in changes in mass, final liver size, or final liver glycogen content among tanks within a treatment, therefore, data from individual focal fish were combined across replicate tanks for analyses ($n = 28$ for each treatment).

Small crucian carp held with large fish tended to gain more mass (median = 1.0 g, 95% C.I. = 0.8–1.2) than those held with an equivalent biomass of small fish (median = 0.7 g, 95% C.I. = 0.5–0.9); these differences, however, were not significant (Mann-Whitney U test; $P = 0.06$). Livers of a group of small crucian carp sacrificed at the beginning of the experiment ($n = 9$) equalled 2.0% (95% C.I. = 1.6–2.4) of total body mass and contained 5.6 μg glycogen/mg (95% C.I. = 3.0–10.8). Although experiments were halted in July, when crucian carp are still typically investing in general somatic growth rather than building glycogen stores for use over winter (e.g., Hyvärinen et al. 1985, Tonn et al. 1989), focal fish in both treatments displayed marked increases in liver size and glycogen content. However, focal crucian carp held with large competitors had significantly larger livers (median = 10.5% of body mass, 95% C.I. = 9.4–11.4) than those held with small competitors (median = 9.1%, 95% C.I. = 8.2–10.0; Mann-Whitney U test; $P = 0.04$). Focal fish held with large conspecifics did not, however, have higher concentrations of glycogen within their livers (median = 260.8 $\mu\text{g}/\text{mg}$, 95% C.I. = 241.8–272.8) than those held with small fish (median = 242.2 $\mu\text{g}/\text{mg}$, 95% C.I. = 222.1–255.8; Mann-Whitney U test; $P = 0.08$).

4. Discussion

Our experiments demonstrated that conspecific competitors can have negative impacts on food intake, growth, and glycogen accumulation of small crucian carp. Impacts were increased by either an increased density of competitors or an

increase in their body size. As a result, total biomass of competitors was a better overall predictor of the intensity of competition than either number or size of competitors alone.

What factors contributed to reduced food intake by small crucian carp when faced with an increased biomass of competitors? Initiation of feeding was not inhibited (nor facilitated) by the presence of one large or four small competitors, nor was the effectiveness of search behavior. Although these results generally run contrary to expectations (Pitcher et al. 1982, Magurran & Pitcher 1983, Morgan 1988a), this may have been due to the simplicity of the foraging environment, the uniform distribution of food, or the limited range of group sizes in our experiments.

The greater feeding intensity in 1LC and 4SC trials could simply have been related to increased hunger levels among these fish, compared to fish in 1SC trials, because a given amount of food had to be shared among a greater biomass of consumers (Morgan 1988a). However, comparisons of foraging rates (time invested per pellet consumed) of individual small fish in the presence and absence of competitors suggested that small fish may have been searching for and processing food at near-maximal rates in both situations. In contrast, large crucian carp were able to increase their foraging rates significantly in the presence of competitors.

We suggest that exploitation competition can largely explain the greater impact that a large competitor had compared to a small competitor. In our experiments without competitors, large crucian carp had a foraging rate nearly twice that of small individuals. This is consistent with a more intensive study of body size/food size relations for crucian carp that was conducted with a larger size range of fish and food items but measured only handling (processing) time (Paszkowski et al. 1989). As one would predict from these foraging results, our competition experiments demonstrated that increasing the body size of the competitor had a negative impact on the food intake of small crucian carp. Experimental studies with other fish species have also generally found that larger individuals enjoy exploitative advantages (Werner 1974, Mittelbach 1981, Galis & de Jong 1988, but see Persson 1987). The superior exploitative ability of larger fish can often be

attributed to increased encounter rates and handling efficiencies, due to increased swimming capacities (Yates 1983), better vision (Fernald 1988), and larger mouth size (Wankowski 1979).

In crucian carp, this exploitative advantage may also be related to the way in which food is processed within the pharyngeal apparatus (Paszkowski et al. 1989, see also Street et al. 1984, Sibbing 1988). Use of the pharyngeal teeth for extended processing allows for multiple prey processing, i.e., crucian carp take several prey items into the oral and pharyngeal cavities before mechanically breaking them down together and passing them further along the gut. In our competition trials, fish took in a relatively large number of pellets in a short time, thereby making them unavailable to competitors, before pausing to process the food. Large fish were capable of taking in large "mouthfuls", e.g., a median of 23 pellets in the first 2 min of 1LC trials (maximum = 39). Small crucian carp had much more limited capabilities, taking in medians of 7, 7.5, and 10 pellets in the first 2 min of 1LC, 4SC, and 1SC trials, respectively (maximum = 24). Under natural conditions, the ability of larger fish to quickly monopolize many food items could be particularly advantageous in exploiting patchily distributed food sources.

Although a single large crucian carp had a greater exploitative impact on food resources than a single small fish, increasing the number of small competitors from one to four also translated into increased levels of exploitation of food resources, but with a more equitable distribution of food among group members than seen in 1LC trials. In 4SC trials, however, interference competition also appeared as a potentially important factor influencing the foraging success of focal fish. Increased density alone may have contributed to the greater observed frequency of interaction, nevertheless, the duration and intensity of agonistic behavior in 4SC trials, and its exclusive association with feeding, were impressive. We saw no evidence for the existence of dominance hierarchies in any of the foraging groups, although the few interactions observed in 1LC trials were initiated by the large fish. Attacks appeared spontaneous and opportunistic, and seemed to increase access to pellets either by displacing a feeding fish or by triggering regurgitation. Agonistic behavior

outside of reproductive activities have been reported for other cyprinids (e.g., Pitcher et al. 1986, Morgan 1988b). Jobling (1985) reported similar behavior patterns in arctic charr (*Salvelinus alpinus*) where linear hierarchies were lacking but short-term episodes of aggression during feeding periods reduced food intake by some individuals and ultimately contributed to growth suppression. Aggression may play an important role in high-density populations where opportunities for contact among small crucian carp are common and food quantity and quality are limited (e.g., Holopainen & Pitkänen 1985, see also Boisclair & Leggett 1989).

The trends we saw in our small scale, short-term foraging performances generally foretold the results of our larger-scale, longer-term growth experiments. Small crucian carp held with low densities of large competitors displayed increases in body mass and final hepatic glycogen content comparable to those held with an equivalent biomass of competitors composed of many small fish. The focal fish in the former treatment did have relatively larger livers than those in the latter, which in nature could translate into a greater probability of surviving periods of winter hypoxia (Holopainen & Hyvärinen 1985). The fact that small crucian carp did slightly worse in growth experiments with more but smaller conspecific competitors might not have been due directly to differences in food intake, but might have reflected greater energetic costs of living in a high-density population (Boisclair & Leggett 1989). Qualitative observations suggested that these dense groups of small crucian carp were more active than groups with large fish. Based on our foraging experiments, direct and often vigorous interactions between individuals might also have been more common in the tanks containing many small fish. Because our short-term experiments indicated comparable foraging performances between treatments with many small versus few large competitors, we suggest that increased energy expenditures by fish living at higher densities, rather than lowered levels of food consumption, contributed to poorer performances in the longer-term growth experiment. The costs of social interactions, in terms of increased metabolic rate, increased physiological stress and decreased growth rate, have been well documented for blen-

noid (Wirtz 1974, 1975) and salmonid fishes (Jobling & Reinsnes 1986 and references therein).

Although our laboratory experiments on intraspecific competition were, by design, a simplification of natural conditions, it is not unrealistic to apply these results to nature, where crucian carp are often the only fish species present in small forest lakes and ponds (Tonn et al. 1990). It is apparent that the older and larger individuals, which are rare but inevitably present in dense populations inhabiting monospecific ponds (Holopainen & Pitkänen 1985, Piironen & Holopainen 1988), can have strong negative effects on the numerically dominant younger and smaller crucian carp and likely contribute to their stunting and winter mortality.

Another factor that can intensify intraspecific competition in these systems is the elevated ecological densities that result from nonrandom patterns of habitat use. Both large and small crucian carp concentrate their activities inshore, but small fish significantly more so than large (Holopainen et al. 1988, in press; Tonn et al. 1989). Small crucian carp foraging inshore would face not only large numbers of similarly-sized fish exploiting available food, but our experiments would suggest interference, in the form of agonistic interactions from other shoal members, could also be significant. Even in lakes where predators are present and overall densities of crucian carp are much lower, intraspecific competition may still be important, as small fish (<80 mm) become highly concentrated inshore (Tonn et al. 1989, Holopainen et al. in press), keeping ecological densities elevated. In turn, reduced growth rates due to competition for food could prolong the vulnerability of small fish to size-limited predation (Tonn et al. 1989, Holopainen et al. in press).

Our study was not designed to address completely the question "Are larger animals competitively superior?" (Persson 1985). Rather, we concentrated on only half of the interaction, comparing the relative effects of large and small competitors on small crucian carp. Like Persson, however, our results suggest that fish ecologists studying competition should give attention to both exploitative and nonexploitative interactions. Effects of intraspecific competition on the behavior and growth of larger crucian carp awaits investigation.

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