Impact of fish predation on a small-bodied cladoceran:
limitation or stimulation?

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Abstract

In seven enclosure experiments the short-term effects of exposing Bosmina longirostris, a small bodied cladoceran, to high levels of fish predation were analyzed. The density of Bosmina did not change significantly in the experimental enclosures, suggesting no direct fish impact on Bosmina demography. However, detailed studies revealed strong fish effects on some demographic and life history parameters of Bosmina. While the mean size of individual Bosmina decreased, reproduction enhanced (due to larger clutch sizes and a higher proportion of gravid females) in the enclosures with fishes. There is life history shift towards lower females sizes at a first reproduction in the fish enclosures.

The maintenance of Bosmina density in the fish enclosures may be attributed to: (1) higher reproductive rate due to elevated food level; (2) a life history shift towards smaller size reducing vulnerability to fish predation; (3) release from copepod predation caused by the presence of fish.

Introduction

Planktivorous fish prey selectively on conspicuous zoo- plankton, selecting large, pigmented, actively moving individuals (Hrbacek et al., 1961; Brooks & Dodson, 1965; Zaret, 1980). Elimination of easily visible, egg-carrying females affects the reproductive rate and lowers the probability of prey population recovering (Gliwicz & Pijanowska, 1989). Planktonic populations can be effectively controlled by fish; in extreme situation, fish can lead to the extinction of their prey (Gliwicz, 1985). On the other hand, fish which reduce the abundance of large-bodied individuals, protect small-sized zooplankton from competition for limited food resources (Vanni, 1987). Nutrients released to the water by the fish stimulate phytoplankton growth, thus improving food conditions for filter feeding zooplankton (Lamarra, 1975; Anderson et al., 1978; Schindler, 1993). Fish can reduce the invertebrate predation risk for small-bodied zooplankton by feeding on relatively large sized planktonic predators (Dodson, 1974).

Which effect (either suppression or stimulation) predominates, is highly dependent on prey size: bigger individuals are strongly suppressed by fish, and small bodied animals can benefit from the presence of fish.

The aim of this paper was to analyze short term responses of the small-bodied cladoceran Bosmina longirostris (O. F. Muller) to exposure to fish pressure in a series of in situ enclosure experiments.

The lake, its plankton and fish

Lake Wirbel (surface area 11 ha, mean depth 1.8 m, max depth 4 m) is a highly eutrophic, polimictic lake located in Mazurian Lakeland in north-eastern Poland. The phytoplankton composition changed during the experimental period from early spring (dominated by diatoms, blue-greens and green algae) to the early summer (dominated by blue-greens and diatoms).

The lake zooplankton was numerically dominated by rotifers (mainly Keratella cochlearis (Gosse), Polycarthra spp. and Trichocerca spp.). Cyclopoid copepods (mainly Mesocyclops sp.) were the most abundant group of planktonic crustacea during experiment. Bosmina longirostris was the most abundant cladocer-
Figure 1. Mean ± 1 SD chlorophyll a concentration in seven experiments, in fish-free (empty bars) and fish (filled bars) enclosures.

Figure 2. Mean ± 1 SD density (top) and mean ± 1 SD body length (bottom) of Bosmina at the end of seven experiments in fish-free (empty bars and circles) and fish (filled bars and circles) enclosures.

The lake was inhabited by numerous populations of various fish species that are either obligatory or temporary plankton feeders: Leucaspis delineatus Heckel, Rutilus rutilus L., Blicca björkna L., Perca fluviatilis L., and Scardinius erythrophthalmus L. (Prejs et al., 1994).

Materials and methods

Seven 11-day experiments were performed from the beginning of May to mid-July 1988. In each of the experiments two sets of three enclosures (polyethylene bags of 300 dm³ capacity each) were used. Each bag was filled with lake water containing natural zooplankton. Three enclosures were always left fish free while three roach R. rutilus (1+, 60–100 mm l.t.) were added to each of the remaining enclosures. Dead fish were removed from enclosures but not replaced. Fish survival in the enclosures is shown in the Table 1.

Water samples for chlorophyll determination and zooplankton samples were taken from the lake at the beginning of each experiment and then from each enclosure after 11 days. Chlorophyll a concentration in the fraction of particles <50 μm was determined using a standard method (Golterman & Clymo, 1969). This gave a measure of phytoplankton biomass available for filter-feeding zooplankton. Twenty-five liter zooplankton samples were randomly taken at three different depths: 0, 50, 100 cm with a 1 l Patalas sampler. Samples were filtered through 50 μm mesh and preserved with 4% sugar formalin.

Zooplankton was counted under a dissecting microscope. Seventy individuals of B. longirostris were measured in each sample. Gravid females and number of eggs carried in brood chambers were counted. Six size classes have been distinguished: I – 200–240 μm, II – 241–280 μm, III – 281–320 μm, IV – 321–360 μm, V – 361–400 μm, VI – >400 μm. The size distribution of
gravid females was obtained from additional measurements of 40–70 egg-carrying individuals, if present, in each enclosure.

The minimal size of mature individual was arbitrarily taken as the length of the smallest egg-bearing female found in each experiment. The proportion of gravid females in a population (number of egg-bearing females divided by number of adult females) and fecundity (number of eggs per gravid females – clutch size, and number of eggs per adult females) was calculated. The clutch size to body length ratio was calculated to eliminate effect of different females body size on their fecundity in the enclosures. The proportion of gravid females was additionally separately determined for each size class of females in the third experiment (where large quantity of gravid females enabled more detailed determination).

Results

Algal biomass was higher in the fish enclosures than in the fish-free ones (ANOVA, \( F = 16.5, p = 0.0005 \)) at the end of all the experiments (Figure 1).

In the fish-free enclosures, the final density of species that were rare or absent in fish enclosures (\( D. \) brachyurum, \( C. \) quadrangula, \( P. \) pediculus, \( L. \) kindti) usually increased. In fish enclosures, large bodied cladocerans (\( L. \) kindti, \( P. \) pediculus) were exterminated while the density of rotifers was on average 5.5 times higher then in fish-free enclosures. The total density of \( Cylclopoidea \) did not differ significantly between the two sets of experimental enclosures (ANOVA, \( F = 2.14, p = 0.85 \)).

In the fish enclosures, \( Bosmina \) density was not clearly affected; in three experiments the final densities of \( Bosmina \) was higher in the fish as compared to the fish-free enclosures while in four others it was lower (Figure 2); all those values did not significantly differ (ANOVA, \( F = 2.22, \ p = 0.14 \)). However, the effect of fish presence on \( Bosmina \) body length was clear cut. The average size of \( Bosmina \) in the fish-free enclosures was significantly larger than in the fish ones (Figure 2) (\( p < 0.0001 \), Mann-Whitney test). The increase in the size of \( Bosmina \) in the fish-free enclosures resulted both from the increased number of large-bodied and decreased number of small-sized individuals (Figure 3).

Size structure of egg bearing females differed between fish and fish-free enclosures (Figure 3); large egg-carrying females were absent in the presence of fish, and females started reproduction at a smaller size (the minimum size of gravid females was significantly lower in the fish enclosures (\( p < 0.0001 \), Mann-Whitney test)).

The clutch size to body length ratio, the mean number of eggs per adult female, and the proportion of egg bearing females within adults were significantly lower in the fish-free enclosures (Table 2) while the mean number of eggs per gravid females did not differ significantly.

In the third experiment (where more detailed analysis was performed), the mean clutch size in the fish-free enclosures was lower (than in the fish presence) when female size was incorporated into the model (Figure 4) (ANOVA, \( F = 172, p < 0.0001 \)) but did not differ significantly when size was not considered (ANOVA, \( F = 1.5, p = 0.22 \)). The proportion of egg-bearing females in separate size classes was lower in the fish-free enclosures (Figure 5).

A significant linear regression (positive slope) between chlorophyll a concentration and number of eggs per adult \( Bosmina \) was found (\( r^2 = 0.33, \ p = 0.01 \) and \( r^2 = 0.26, \ p = 0.05 \) in fish-free and fish enclosures, respectively; data from all experiments pooled).

A significant linear regression (negative slope) between density of Cyclopoidea and average clutch size of adult females was found in fish-free enclosures (\( r^2 = 0.38, \ p = 0.006 \)), but not in the fish ones (\( r^2 = 0.14, \ p = 0.13 \)).
Figure 3. Size distributions of all individuals (on the left hand side) and of egg-bearing females (on the right) of *Bosmina* in fish-free (empty bars) and fish (filled bars) enclosures at the end of seven (I–VII) experiments.
Table 2. Fecundity of *Bosmina* expressed as average clutch size per body length, average clutch size and mean number of eggs per adults, respectively and proportion of gravid females within adults, in fish and fish-free enclosures, at the end of each experiment. Marked with asterix are statistically significant differences between fish and fish enclosures (ANOVA, p<0.05).

<table>
<thead>
<tr>
<th>Exp.</th>
<th>Average clutch size per body length mm⁻¹ *</th>
<th>Average clutch size</th>
<th>Average number of eggs in broad chambers of adults *</th>
<th>Average proportion of gravid females within adults *</th>
</tr>
</thead>
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<tr>
<td></td>
<td>no fish</td>
<td>fish</td>
<td>no fish</td>
<td>fish</td>
</tr>
<tr>
<td>I</td>
<td>14.7</td>
<td>19.7</td>
<td>2.94</td>
<td>2.61</td>
</tr>
<tr>
<td>II</td>
<td>16.2</td>
<td>19.3</td>
<td>2.63</td>
<td>1.95</td>
</tr>
<tr>
<td>III</td>
<td>14.0</td>
<td>26.6</td>
<td>2.69</td>
<td>2.47</td>
</tr>
<tr>
<td>IV</td>
<td>6.8</td>
<td>19.7</td>
<td>1.44</td>
<td>1.35</td>
</tr>
<tr>
<td>V</td>
<td>14.7</td>
<td>23.9</td>
<td>1.53</td>
<td>2.05</td>
</tr>
<tr>
<td>VI</td>
<td>10.5</td>
<td>17.6</td>
<td>1.56</td>
<td>1.67</td>
</tr>
<tr>
<td>VII</td>
<td>12.8</td>
<td>22.3</td>
<td>2.13</td>
<td>1.65</td>
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</table>

Figure 4. Clutch size vs body length in fish-free (empty circles) and fish (filled circles) enclosures at the end of the third experiment. (Both regression lines are plotted on the basis of about 180 points which overlap on the graph. Different size of circles was used to demonstrate overlapping filled and empty circles).

Figure 5. Proportion of gravid females in separate size classes of *Bosmina* in fish-free (empty bars) and fish (filled bars) enclosures at the end of the third experiment.

Discussion

The isolation of zooplankton in fish-free enclosures caused an increase in relative density of large-bodied species (*L. kindti, P. pediculus, D. brachyurum, C. quadrangularis*) which were highly suppressed in the lake and in the fish enclosures due to their susceptibility to fish predation. No significant difference in *Bosmina* density between fish-free and fish inhabited enclosures was observed, which might indicate that *Bosmina* was not affected by fish. However, a comparison of size distributions of *Bosmina* from different treatments showed a strong effect of size-selective predation. The number of large-bodied females, usually bearing a large number of eggs was dramatically reduced in the presence of fish. However, the reproductive potential was not higher in fish-free enclosures. There are at least three plausible explanations of the observed phenomena:

1. Despite strong selective predation, survivors could have benefited from the fish presence (e.g. by increased reproduction) to an extent which compensated for losses of large and fecund females. Indeed, the higher proportion of gravid females and larger clutch sizes accounted for an increased reproductive potential of *Bosmina* in the fish enclosures. This could be
caused by an increase in food availability for herbivorous zooplankton due to the indirect effect of fish on phytoplankton growth and enhanced resuspension rate of seston particles. Phytoplankton biomass was always higher and the fecundity of *Bosmina* was positively correlated with chlorophyll *a* concentration when fish were present.

The increased production of eggs in the fish enclosures was probably offset by the absence of large individuals, potentially carrying more eggs, which were selectively removed by fish. Thus the average clutch size did not significantly differ between the two treatments when female size was not considered. Mean number of eggs per body length might be more reliable measure of reproductive effort when comparing females which differ strongly in size.

However, this hypothesis cannot explain the dramatic increase in the minimum size of gravid females in the fish-free enclosures, since the size of primiparous females in cladocerans tends to decrease with a decrease in food concentration (Węgleńska, 1971; Taylor, 1985).

(2) The observed contrasting patterns of population size structures between fish and fish-free enclosures could not have been caused merely by the selective effects of fish predation. It is likely that the different life history traits of *Bosmina* in fish and fish-free enclosures caused size structure difference. Planktonic animals grow often slower in the presence of visual predators (e.g. fish) which select for large prey. They allocate less energy to somatic growth and more to reproduction, which enables them to mature earlier at smaller size, and produce more eggs per body unit than individuals not endangered by fish (Macháček, 1991; Stibor, 1992; Weider & Pijanowska, 1993). In the present experiments a rapid shift in *Bosmina* life history was observed. Soon after the isolation of *Bosmina* from fish in the enclosures, the resource allocation pattern switched to faster growth at the expense of reproduction. Maturation was delayed, size at first reproduction increased and fecundity per unit of body length decreased. Thus animals could achieve high reproductive ratio in further instars once they grew larger.

(3) The observed differences in *Bosmina* size structures could have been influenced by the impact of fish on invertebrate predators. The pressure of invertebrate predation increased in the fish-free enclosures, mostly on either smaller, or slower (e.g. carrying eggs) individuals. Invertebrate predation could enhance differences of *Bosmina* size structures between fish and fish-free enclosures and thus affect *Bosmina* fecundity. Among invertebrate predators, only Cyclopoida were abundant during all the experiments. Though the density of cyclopoid copepods was not lower in the fish enclosures, it is possible that the mere presence of fish could stress them and ‘focus’ their attention on defence against predators (Boolens & Stearns, 1992) and thus release the pressure on the smaller filter feeders. The negative correlation between fecundity of *Bosmina* and Cyclopoida density in fish-free enclosures and the lack of correlation in the enclosure with fish supports this hypothesis. Selective elimination of gravid females (due to their possible reduced ability to escape) or the removal of eggs from brood pouches of gravid females (Gliwicz & Stibor, 1995) could explain these relationships.

It’s likely that all three effects took place in my experiment, but it is hard to judge their relative impact.

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**References**


