SHORT COMMUNICATION

Chemical cues from the invertebrate predator Leptodora kindtii affect the development of cyclomorphic traits in Eubosmina coregoni gibbera

Ragnar Lagergren and Jan A.E. Stenson
Göteborg University, Department of Zoology, Section of Animal Ecology, Box 463, SE 405, 30 Göteborg, Sweden

Abstract. The induction of two cyclomorphic traits, antennule length and carapace height, in Eubosmina coregoni gibbera by the cladoceran predator Leptodora kindtii was investigated in an experimental study. It was found that both carapace height and antennule length were significantly larger when the predator cues were present. However, antennule length only differed in adults, while juveniles showed no difference in antennule length between the treatments. Our results indicate that morphological anti-predator traits can reduce the vulnerability of adults, whereas the small size of juveniles may prevent the anti-predator traits from being effective.

Predation is a key factor in the evolution of aquatic communities. By size-selective predation, fish can effectively eliminate large and conspicuous species of zooplankton (Brooks, 1968; Zaret, 1980). Small species, on the other hand, may be more susceptible to invertebrate predators, whose ability to handle and ingest the prey often depends on body size and shape of the prey (Dodson, 1974; Kerfoot, 1977; Swift, 1992). In addition to direct effects on prey numbers, the mere ‘smell’ of predators in the water can induce shifts in behaviour, life history and morphology of prey populations (Larsson and Dodson, 1993).

In zooplankton, the induction of morphological anti-predator traits by chemical cues (kairomones) released by invertebrate predators is a well known phenomenon (Tollrian and Harvell, 1998). Individuals possessing such morphological defences elude a higher proportion of predator encounters than non-induced ones because they are more difficult to grasp and handle by the predators (O’Brian et al., 1979; Havel and Dodson, 1984; Tollrian, 1995a). An inducible defence may evolve when the abundance of predators is unpredictable and the defence is associated with some sort of cost (Harvell, 1990). As the abundances of most invertebrate predators vary seasonally, inducibility of defences may explain why many traits in zooplankton, especially in cladocerans and rotifers, show cyclic morphological changes (Dodson, 1974).

Although the morphological variation in the genus Bosmina, especially the subgenus Eubosmina, is as great as in Daphnia, much less is known about the adaptive significance of varying traits in these species. In Eubosmina coregoni gibbera (Shoedler), both the length of the antennule and the height of the carapace vary considerably during the season (Hutchinson, 1967; Hellsten and Stenson, 1995). In Lake Östersjön in southwest Sweden, the presence of the most extreme forms coincides with the population maximum of the cladoceran predator Leptodora kindtii (Focke) (Hellsten and Stenson, 1995). Furthermore, the
extreme morphology of *E. coregoni* gibbera has been shown to be effective as protection against *Leptodora* predation (Hellsten et al., 1999). However, it has not yet been determined whether cyclomorphic traits in *E. coregoni* gibbera are induced by predators, and it has not been shown whether chemical cues from *Leptodora* induce morphological changes in any zooplankton.

The aim of the present study was to test whether the presence of *L. kindtii* influences the size of two anti-predator structures, antennule length and carapace height, in *E. coregoni* gibbera.

Animals were collected from lake Östersjön (57°93′N, 12°70′E) on two occasions in 1998, 12 July and 12 August. One day after being collected, juveniles of *E. coregoni* gibbera were picked out and placed (one individual in each) in 36 triangular aquaria with a bottom area of 95 × 22 mm and a top surface area of 22 × 22 mm. To obtain the starting conditions of the traits, 15 individuals were preserved in 70% ethanol. Each aquarium was divided into two halves by a net (mesh size 200 µm). The aquaria were filled with 80 ml filtered lake water (50 µm). In 18 of the aquaria, one *Leptodora* (body length 3–8 mm) was placed in one of the compartments in chemical, but not physical, contact with the *Eubosmina*; the remaining 18 aquaria served as controls. The *Leptodora* were kept in plastic cans together with a mixture of other zooplankton, including *Bosmina*, before they were used in the experiment. The aquaria were held in natural light conditions at 21 ± 1°C. Water was not changed during the experiment but we have kept clones of *Bosmina* for several weeks without adding any food under these conditions; algal growth is sufficient to maintain populations of about 100 ind. l⁻¹. The vitality of the *Leptodora* was monitored once daily during the experimental run, and dead and weak individuals were replaced with new ones. After 14 days (i.e. one to two parthenogenetic generations), all live *Eubosmina* were picked out and preserved in 70% ethanol. Body length (BL), carapace height (CH) and antennule length (AL) were measured on all *Eubosmina*, to the precision of ±4 µm, according to Hellsten and Stenson (Hellsten and Stenson, 1995).

Relative measurements of the development of carapace height and antennule length, which are not dependent on body size, enabling a comparison of animals of different size, were calculated as follows. BL, CH and AL were measured on 54 individuals (body length 265–600 µm) that were randomly picked from field samples from lake Östersjön in August 1996. The relationships between the traits and body length were fitted to second degree polynoms [length of trait = \( k_1 + k_2 \cdot (BL) + k_3 \cdot (BL)^2 \)]. For the regression of carapace height, juveniles (body length shorter than 345 µm) were excluded, as these show no cyclomorphosis in this trait. By inserting the body length of each individual in the experiment into the equations, expected lengths of the traits, CH and AL, could be calculated. The measured value was then divided by the expected value to get a measure of the relative development of these traits, compared with the August 1996 population. We hereafter refer to ALrd as the relative development of antennule length and CHrd as the relative development of carapace height. For each aquarium, mean ALrd and CHrd of all individuals was calculated. Differences between the treatments were tested with two-factor ANOVA. To test whether the result
was sensitive to the kind of regression from which CHrd and ALrd were calculated, we also conducted the same kind of analysis on simple regressions on log transformed data \[\log(\text{length of trait}) = k_1 + k_2 \cdot \log BL\].

In some aquaria, all individuals died or were caught by the surface tension. As a result, the number of replicates was reduced to 15 in the control and eight in the Leptodora-reared group in July, and eight in the control and nine in the Leptodora-exposed group in August. There were no differences in mean number of individuals per aquarium between the groups after the experimental run (two-factor ANOVA \(P = 0.40\)). The mean was 2.0 individuals in the Leptodora groups and 2.4 in the control groups.

Both relative carapace height and relative antennule length were significantly larger in Leptodora treatments than in the control groups (Table I). Although ALrd did not differ in the juveniles \((P = 0.9)\), there was a clear difference \((P = 0.017)\) in the adults. Carapace height did not vary between the experiments performed in July and August, whereas relative antennule length showed a tendency to be longer in August than in July when all individuals were included \((P = 0.076, \text{marginally significant})\). When only adults were considered, ALrd was significantly higher in August than in July \((P = 0.017)\). The choice of regression equation did not affect the outcome of the statistical analysis appreciably; all significant \(P\)-values were significant in both analyses (Table I). The equations of the polynomial regressions were: \(\text{CH} = -1178 + 5.77 \cdot BL - 0.00439 \cdot BL^2\) and \(\text{AL} = -838 + 5.31 \cdot BL - 0.00480 \cdot BL^2\); and for the simple regressions on log-transformed data: \(\log \text{CH} = -1.31 + 1.514 \cdot \log BL\) and \(\log \text{AL} = -0.54 + 1.236 \cdot \log BL\).

Compared with the starting condition, CHrd remained the same in the Leptodora-treated water but declined in the control, whereas ALrd was somewhat lower in the Leptodora group and clearly lower in the controls (Figure 1). The reason why the starting conditions of the traits differed from the ‘August values’ (Figure 1) may be that the development of cyclomorphic traits varies between years (the experiment was performed in 1998 and ‘August values’ are from 1996).

The significant difference between control and Leptodora groups shows, however, that the presence of Leptodora is needed to maintain well developed anti-predator traits, CH and AL, in this population of E.coregoni gibbera. The decline observed in CHrd and ALrd when not exposed to the risk of predation by Leptodora suggests that these traits are associated with some costs. A direct cost of induced morphological defence observed in the present study may be an increased vulnerability to fish predation. A higher carapace and longer antennules may increase the visibility of Eubosmina to fish, and this may select against these traits when the risk of fish predation is higher than the risk of being eaten by Leptodora. This kind of cost has also been suggested as important in morphological defences in Daphnia (Tollrian, 1995b). With regard to large morphological changes that significantly increase the surface area of the animal, such as the development of high carapace, a cost in terms of increased drag may also be important (Lagergren et al., 1997).

Our observation that Leptodora induces morphological changes in both traits measured primarily in adult Eubosmina may lead to the conclusion that this predator shows a preference for large individuals of Eubosmina. However,
<table>
<thead>
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<th>Trait</th>
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<td></td>
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<td>Mean</td>
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<td>Carapace height</td>
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<td>0.94</td>
<td>4</td>
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<td></td>
<td>August</td>
<td>0.95</td>
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<tr>
<td>Antennule length (all)</td>
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<td>0.81</td>
<td>8</td>
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<td></td>
<td>August</td>
<td>0.86</td>
<td>9</td>
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<tr>
<td>Antennule length (adult)</td>
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<td>0.76</td>
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<td></td>
<td>August</td>
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Branstrator (Branstrator, 1998) showed that *Leptodora* effectively handles and consumes bosminids of small size. In *Daphnia pulex*, it has been shown that the most vulnerable size classes have the strongest developed neckspines against Chaoborus predation (Tollrian, 1995a). As the swimming speed of the prey affects the encounter rate with an ambush predator positively, and small *Daphnia* swim more slowly than large, the smallest individuals are not the most vulnerable. However, as *Leptodora* is a cruising predator that swims much faster than *Eubosmina*, the swimming speed in the prey does not affect the encounter rate significantly (Gerritsen and Strickler, 1977). An alternative explanation may be that juvenile *Eubosmina* are easy to handle even if they defend themselves with long antennules, whereas larger individuals have a greater potential to protect themselves by developing morphological defences. It has been shown in Chaoborus that when the size of the prey is much less than the gap diameter of the predator, morphological traits are not effective as anti-predator defence (Swift, 1992). *Leptodora* catches its prey in a feeding basket formed by the thoracic limbs, the head and the thorax (Herzig and Auer, 1990). The size of this feeding basket is strongly correlated with the predator’s body length (Manca and Comoli, 1995). A juvenile *Eubosmina* (~300 μm) is smaller than the size of the feeding basket of even the smallest *Leptodora*. Thus, it is improbable that longer antennules or a higher carapace would significantly decrease the probability of being caught and ingested by *Leptodora*. A better strategy for juvenile individuals.

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**Fig. 1.** Mean relative carapace height (CH$_{rd}$) and antennule length (AL$_{rd}$) of *Eubosmina* at the beginning of the experiment and after 14 days exposure or no exposure to *Leptodora*. The results from both experiments are pooled. The sample size, n, is for individuals measured in the starting condition and number of aquaria (from which the mean for 1-10 measured individuals was estimated) in the other cases. To show the natural range of these traits in the population of lake Östersjön, the mean values in May and August 1996 are marked with dotted lines.
in the presence of predation risk by *Leptodora* is to put as many resources as possible into growth.

For adult *Eubosmina*, the high carapace and long antennules may be an efficient defence against small *Leptodora*. The total height (from the top of the carapace to the tip of the antennule) of an extreme individual of *E. coregoni giber* of 0.5 mm body length is about 1.0 mm. According to Manca and Comoli, only *Leptodora* greater than 6 mm have such a large feeding basket (Manca and Comoli, 1995). The total height of a spring individual of *E. coregoni giber* of 0.5 mm is ~0.75 mm, and *Leptodora* >4.2 mm have feeding baskets that are large enough to feed on these prey. If the total height of the prey is crucial for the strike efficiency of *Leptodora*, *Eubosmina* may become out of reach for a much higher proportion of the *Leptodora* population if they develop long antennules and a high carapace. In addition, longer antennules increase the chance of *Eubosmina* escaping from *Leptodora* after capture (Hellsten et al., 1999).

In both traits, the difference between the *Leptodora*-exposed and control treatments is less dramatic than the natural range of these traits in the population in lake Östersjön (Figure 1). Similar results have also been found in other cladocerans [e.g. (Tollrian, 1990; Hanazato and Ooi, 1992)]. It is therefore likely that additional organic or inorganic factors also affect the induction of morphological traits. Temperature, which has been shown to influence the induction of morphological changes in some studies [e.g. (Grant and Bayly, 1981; Hanazato, 1991)] was quite high and did not vary in our study. As high temperature is most often associated with high densities of *Leptodora* (Hellsten and Stenson, 1995; Manca and Comoli, 1995), temperature and *Leptodora* kairomone may have additive effects on the induction of morphological defences in *Eubosmina*.

We conclude that chemical cues from the predator *L. kindtii* are required to maintain the anti-predator traits well developed in the population of *Eubosmina* studied. Seasonal variation in the abundance of *Leptodora* may thus explain the amazing cyclomorphosis in *E. coregoni giber*.

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**References**


