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Antipredator defences in *Eubosmina* waterfleas

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Dissertation

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Avhandling för filosofie doktorsexamen i ekologisk zoologi, som enligt den biologiska sektionsstyrelsens beslut kommer att offentligt försvaras fredagen den 8:e december 2000 kl 10.00 i föreläsningssalen, Zoologiska institutionen, Medicinaregatan 18, Göteborg. Fakultetsopponent är professor Wilson Kerfoot, Michigan Technological University, Houghton, USA.

Lagergren, O. Ragnar. 2000. Antipredator defences in *Eubosmina* waterfleas

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Key words: zooplankton, predation, swimming, escape efficiency, inducible defences, *Eubosmina coregoni*, *Eubosmina longispina*, *Leptodora kindtii*, Cladocera, hydrodynamics, temperature, *Bosmina*

Abstract

For zooplankton, the ability to avoid predation greatly affects individual fitness. In most lakes, predators include both invertebrates and vertebrates. Invertebrate zooplankton predators that are able to coexist with fish are usually not much larger than their prey. Threfore, differences in prey morphology greatly affect the ability of such predators to catch, handle and ingest the prey. By developing morphological defence traits such as spines, helmets, unwieldy size or shape, zooplankton may reduce their vulnerability to invertebrate predators. This thesis aims to clarify morphological variation in *Eubosmina* (Cladocera) in relation to predation, in particular by the predaceous cladoceran *Leptodora kindtii*.

In laboratory experiments, the antennule length of *Eubosmina* significantly affected the likelihood of escaping *Leptodora* after being caught. Of three species compared, the two possessing very long antennule both had about six times greater escape success than the species with short antennule.

When the subspecies *Eubosmina coregoni gibbera* was cultivated in the presence of chemical cues from *Leptodora*, carapace height and antennule length became significantly larger than in the control groups. As the abundance of *Leptodora* varies seasonally, this may explain why the antennule length and carapace height of *E. gibbera* are larger during periods of high population size of *Leptodora.*

Morphological defences may also incur costs. The swimming speeds of *E. longispina* and *E. gibbera* were compared in a laboratory experiment. *E. longispina* has a low carapace and short antennule and is significantly more vulnerable to predation by *Leptodora*, than is *E. gibbera*, with its high carapace and long antennule. *E. gibbera* had greater drag and swam more slowly than *E. longispina.* As swimming speed most likely influences food intake, this result suggests that morphological defence may entail costs that select against the defence when predator pressure is low.

The hydrodynamic cost is affected by temperature. At low temperature it is more expensive to wear large morphological defences that increase body surface area. This may be one reason why shape and morphological defences of zooplankton are dependent on temperature in most cases.

Another aspect of cost is the extra amount of energy, nutrients or brood chamber space required to produce young. This kind of cost might be reflected in a correlation between investment in predator defence and clutch size. I found such a relationship for antennule length but not for carapace height in *E. gibbera*.

In summary, this thesis suggests that morphological defence traits in *Eubosmina* are the outcome of a trade-off that may be determined by the abundance and species composition of predators as well as environmental conditions as temperature and food abundance. The results help to explain the great morphological variation found in the genus *Eubosmina.*

List of papers

This thesis is a summary based on the following papers, which will be referred to by their roman numerals.

I. Hellsten, M. E., Lagergren R. & Stenson J. (1999) Can extreme morphology in *Eubosmina* reduce the predation risk from *Leptodora*? An experimental test. Oecologia **118:** 23-28.

II. Lagergren R. & Stenson J. A. E. (2000) Chemical cues from the invertebrate predator *Leptodora kindtii* affect the development of cyclomorphic traits in *Eubosmina coregoni gibbera*. J. Plankton Res. **22**: 1213-1219.

III. Lagergren R., Hellsten M. E. & Stenson J. A. E. (1997) Increased drag and thus lower speed, a cost for morphological defence in *Bosmina* (*Eubosmina*) (Crustacea: Cladocera). Funct. Ecol. **11:** 484-488.

IV. Lagergren R., Lord H. & Stenson J. A. E. (2000) Influence of temperature on hydrodynamic costs of morphological defences in zooplankton: experiments on models of *Eubosmina* (Cladocera). Funct. Ecol. **14:** 380-387.

V. Lagergren R. Morphological traits and clutch size variation in a cyclomorphic population of *Bosmina* (*E.*) *coregoni* var. gibbera (Crustacea: Cladocera). Manuscript.

Contents

Introduction

Predation and zooplankton

Predation is one of the most important ecological factors in zooplankton communities (Brooks 1968; Zaret 1980). The predator-prey interactions of the pelagic regions of lakes differ from those in terrestrial environments in at least one crucial respect. Refuges that would stabilise predator-prey cycles (Begon et al. 1990) are few. Predation is intensive 24 hours a day and variation in the risk of being killed significantly contributes to the variation in fitness in the prey populations. Thus, there has been strong selection to evolve adaptations that reduce the risk of being killed.

The pelagic food web has two main kinds of predators with different mechanisms of prey detection, visual and tactile predators. Invertebrates are usually tactile. Tactile predators are further divided into cruising predators, which cruise around to encounter prey that comes in their way, and ambush predators, which wait stock-still for a prey to come into strike distance (Gerritsen & Strickler 1977). Many invertebrate predators have great potential impact on the small sized zooplankton (Nero & Sprules 1986; Vanni 1988; Branstrator & Lehman 1991). While zooplankton can migrate vertically into the dark depth to avoid being eaten by visual predators (Zaret & Zuffern 1976; DeStasio 1993), there is no refuge from predators that hunt with mechanical receptors. To be successful these predators have to detect, grasp, handle and ingest the prey item and during every phase in this sequence there is a chance that the prey is lost. The strike and handling efficiency of invertebrate predators are strongly affected by small differences in prey morphology. Body structures on the prey obstructing predator handling of the prey may thus may be powerful defences against invertebrate predators (Dodson 1974a). A larger body size can also be an efficient defence. This is a consequence of the small size difference between predator and prey as large invertebrate predators rarely manage to coexist with fish in the pelagic zone of lakes. Consequently, invertebrate predators can not select prey sizes exeeding limits set by their grasping appendages (Wong & Sprules 1985; Swift 1992; Branstrator 1994; Manca & Comoli 1995).

Fishes, on the other hand, hunt mostly by sight and select large and visible prey items. The mouth size of a fish is rarely limiting for its ability to engulf a zooplankton. In the case of fish predation, it is seldom beneficial for the zooplankton to evolve morphological defences. An exception seems to be the extremely long-spined *Daphnia lumholtzi* (Kolar and Wahl 1998). Behavioural traits and reduction of the visibility are probably much more important adaptations for reducing mortality caused by fishes (Zaret & Kerfoot 1975; O´Brien et al. 1979). The evolutionary dilemma that comes from the need to be small to reduce risks vs visual predators and the need to become large to reduce risks vs tactile predators is in some species solved by adding transparent structures (O´Brien 1979).

Morphological defences

Different species of invertebrate predators often have preferences for specific prey and certain ways to handle prey (Dodson 1974). For example, the large predaceous copepod, *Heterocope septentrionalis* is effective on young instars of *Daphnia* but the effectiveness is reduced by large tail spines and thickened carapaces in the prey (Dodson 1984). On the other hand, a long tail spine makes the prey easier to grasp and handle for *Chaoborus* larvae (Repka et al. 1995). Given the apparently specialised nature of the predatory feeding apparatus, the best position for a protuberance on the prey depends on the predators preferred grasping and handling ttechnique.

Several studies have documented the effectiveness of morphological defences against invertebrate predators (e. g. O´Brien et al. 1979, Havel & Dodson 1984, Tollrian 1995a). One reason that small alterations in morphology may have great adaptive significance is that invertebrate predators are often abundant but quite ineffective. Zooplanktivorous copepods often drop captured prey when they try to manipulate them (Kerfoot 1977b). In a study by Kerfoot (1975), most *Bosmina longirostris* individuals had been handled by predatory copepods several times. The consequence is that small differences in escape probability per predator encounter have large effect on the probability of prey to survive for a longer time, since the escape probability is multiplied several times if the total predation risk is calculated.

An important aspect of morphological traits that are assumed to function as anti-predator defences is the allometry or rate of growth compared to body growth. The growth of most traits can be approximated to

$$TL = k\,(BL)^{x} \qquad (1)$$

where TL=length of the trait, k=a constant, BL=body length and x=the relative growth rate. Eq. 1 is usually analysed on a double logarithmic scale which gives a strait line with the slope x,

$$\log TL = x \log BL + \log k. \qquad (2)$$

This approach has been fruitful not only in studies of cyclomorphosis but also in a large number of other biological sciences (Gould 1966). Invertebrate zooplankton predators tend to select small sized prey (Kerfoot 1977b; Wong & Sprules 1985) so defences should be most important when prey are small. This reasoning predicts that traits functioning as defence against these predators ought to have negative allometry (i.e. x<1, Fig. 1 A and B) if the main predator prefers small prey. Tollrian (1995) showed that in *Daphnia pulex*, morphological antipredator defence against *Chaoborus* is most developed in the most vulnerable size-classes.

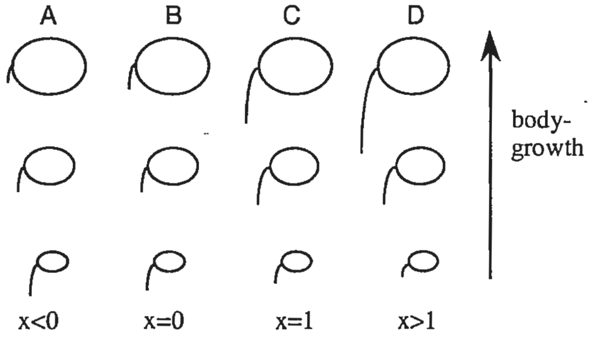

Fig. 1. Development of a fictitious trait at four different relative growth rates (x). If x<0 (A) both absolute and relative size of the trait diminish when the body grows. When x=0 (B) absolute size is constant but relative size of the trait diminishes. In the special case when x=1 (C), relative size is constant but absolute size increases with increased body size. When x>1 (D) both absolute and relative size of a trait increases as the body grows.

Positive allometry (i.e. x>1, Fig. 1D) is not the common case of cyclomorphic traits in cladocerans but occurs in both *Daphnia* and *Bosmina*. Positive allometry is often taken as a sign of an alternative purpose of the trait e.g. protection against fish predation. The only known cladoceran with a morphological defence working against fish is *D. lumholtzi*. Both the tail spine and helmet of this species grow with strong positive allometry (Yurista 2000). One important thing to consider in the case of positive allometry is that the trait takes extreme proportions as the body grows. This circumstance may limit the size of the organism (otherwise large individuals should have absurd proportions) alternatively force the allometry to shift to a lower value as body grows. Consequently, the relationship between the relative size of morphological traits and body length is not linear. This means that fitting the data to eq. 2 may be misleading, for example making it impossible to detect relationships where the relative development of a morphological defence shows a maximum at medium body lengths. Another risk with that analysis is the strong influence of size distribution. In case of positive allometry, animals at the upper end are certainly outliers laying under the regression line (as in figure 2a) as the relationship in reality is concave (Fig. 2b). In that case, if you find a positive or negative allometry may simply depend on the number of large animals measured.

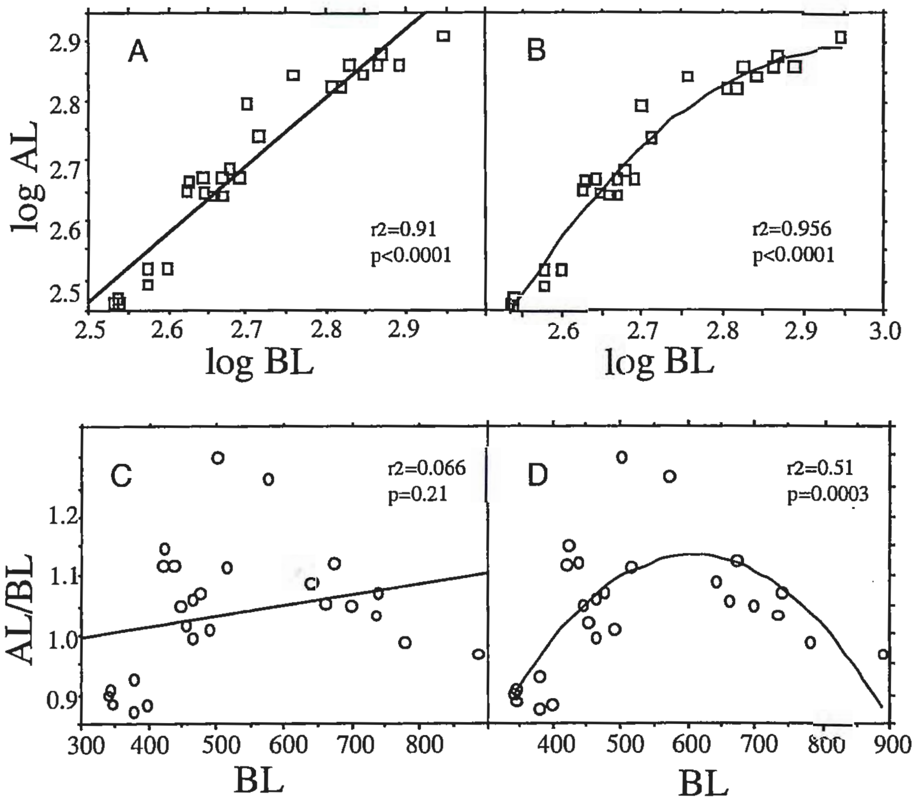

Fig. 2. Four possible ways to analyse the allometric relationship between antennule length (AL) and body length (BL). A) Simple regression on log-transformed data. B) Second degree polynomial regression on log-transformed data. C) Simple regression on AL/BL - BL. D) Second degree polynomial regression on AL/BL - BL. The data is from a population of *Eubosmina coregoni retro-extensa* in Lake Södra Färgen.

An alternative way of viewing the allometric relation of a trait to size is to plot relative size ($RS=TL/BL$) to BL. Positive allometry ($a>1$) refers to a significant positive relationship between RS and BL. Negative allometry ($a<1$) gives a negative slope on the RS-BL plot but should be interpreted with caution because the error in length measurements automatically means that a greater length gives a lower RS. So what is the point of choosing this form instead of the well-established log-log-allometry?

Any form of regression should fulfil at least two purposes: a) interpretability of achieved parameters and b) an adequate description of the relation between the dependent and the independent parameters in the actual interval of x-values. Figure 2a shows an example of positive allometry of antennule length (AL) in a population of *Eubosmina coregoni* var. *retro-extensa*. The fit to the regression line of the log transformed data is good ($R^2=0.91$) and most researchers may be fully content with this result. However, the observant examiner detects the consistent outliers under the regression line in both ends. What does this mean and how can it be examined and interpreted? The choice of a curvilinear regression of the log-log data on the form $y = a + bx + cx^2$, gives a much better fit to the data. However, it is not easy to interpret the coefficients a, b, and c and give them biological meanings. Another alternative would be to plot RS of AL (i.e. AL/BL) against size (BL) as in figure 2c. The regression shows a positive relationship (as it should if the allometry is positive) but the fit is not very good ($R^2=0.066$) and not significant ($p=0.21$). A second degree polynomial regression should do better which is confirmed in figure 2d ($R^2=0.51$, $p=0.0003$). This is better than 2c but worse than both 2a and 2b, but still the plot gives a some new and important information not available in figure 2a. The transition from positive to negative allometry at intermediate sizes becomes obvious. New questions and testable hypothesis not possible to detect from figure 2a also arise.

-What affects the position of the AL/L maximum?

-Is decreasing benefits or increasing costs the reason to the switch from positive to negative allometry?

-Is the position of the maximum within a clone fixed or variable?

-Is the position of the maximum within a population positively or negatively correlated to the height of the maximum?

-How do environmental conditions and kairomones (chemical cues released by predators) affect this?

The first question is of special interest because it stresses the question of adaptation. Both costs and benefits may in many ways be size dependent.

Typically, the benefits of cyclomorphic traits are associated with predation protection. The size of the predator in relation to the size of the prey probably affects whether small or large individuals have most to gain from morphological antipredator defence. Factors that may come into play here are: a) the relationship between size and vulnerability (the effect of morphological defences excluded), b) size dependent efficiency of morphological antipredator defence, c) size distribution of predators, d) size dependent encounter probability between predator and prey. Earlier investigations have mainly dealt wit factor a) and since most invertebrate predators are not significantly larger than their prey they prefer the smaller individuals. This gives a negative relationship between benefit and size and may explain why most antipredator traits show negative allometry (e.g. Black 1980). Fish predation, which is more intensive on larger individuals may be the reason to the occurrence of positive allometry (Yurista 2000). However, alone this can hardly explain why relative size of cyclomorphic traits should peak at intermediate sizes as in *Daphnia cucullata* (Lampert and Wolf 1986) and some species of *Bosmina* (Lagergren unpublished data).

The addition of factor d) has been proposed to be the reason why not the smallest but the next smallest *D. pulex* have the most developed neckspines against *Chaoborus* predation (Tollrian 1995a). Swimming speed usually increases with size (Dodson and Ramcharan 1991). This leads to higher encounter rates for larger individuals than for small ones, but at a certain size, the diminished vulnerability of larger individuals more than compensates for higher encounter rates. Lower benefit of morphological antipredator traits at small size may also be explained by factor b. If the size of grasping apparatus of the predator is much bigger than the size of the prey, the prey have little to gain from antipredator defence (Swift 1992). If this is the case for small but not the for large prey individuals, large individuals should have much to gain from morphological defences whereas small individuals should do better if they instead put recources on growth. This may be the reason why helmet and tail spine lengths of *Daphnia lumholtzi* protecting against fish fry show positive allometry (Yurista 2000) and may also explain why traits of Bosminids and small *Daphnia* in lakes with dense populations of the large predaceous cladoceran *Leptodora kindtii* also show positive allometry.

Another problem to take into account when determining allometry by measuring individuals of different age and size at just one occasion is the overlapping of individuals born during different environmental conditions. In periods when the size of traits are increasing, small individuals are born with long traits whereas large individuals have relatively small trait as large individuals have experienced the conditions leading to long featured morphology for a shorter proportion of their lives than the young. This may lead to an underestimation of relative growth during trait size increase and the other way around when traits are diminishing.

Behavioural defences

Many different behaviours that reduce the predation risk have been recorded in zooplankton. These include everything, from close range attack responses to diel migrations over tens of meters. Alertness to predator attacks can be induced by the presence of predators (Tollrian and Dodson 1999). The direct contact with a predator may result in escape responses enabling the animal to escape. Such escape responses are certainly well developed in copepods, if detecting a disturbance by mechanical sensors, they can achieve very rapid swimming for short distances (Gerritsen 1978). Cladocerans also have such escape responses but they are not as rapid and effective as in copepods (Kerfoot 1978). Another way to confuse a predator is to "play dead" (akinesis) which is a common defence in cladocerans. When contacted by a predator, they passively sink with the antennae protectively folded into the lateral sheaths. Invertebrate predators that just have missed an attack have great difficulties in relocating passively sinking prey (Edmunds 1974).

Swarming is a common response to fish predation in zooplankton (e. g. Jakobsen & Johnsen 1988). The confusion of a predator encountering many prey simultaneously, together with the dilution effect, reduce the predation risk per individual in the swarm. This effect includes both visually hunting and tactile predators. In some cases, prey swarms are induced by predator kairomones (Kvam & Kleiven 1995).

At the largest behavioural scale, zooplankton can show daily patterns of vertical migration. Zooplankton reduces its exposure to visual predators by avoiding the food rich and light upper layers during the day and migrate up to feed in the upper layers during night protected by darkness (Hutchinson 1967; Lampert & Sommer 1997). Diel vertical migration can be regarded as a special case of depth selection behaviour (De Meester et. al 1999). Inverse migration, i.e. deeper position during night than during day, also occurs. This behaviour has been shown to be a response to avoid normally migrating invertebrate predators (Neill 1990; Ohman 1990). The main cost for diel vertical migrations is the missed feeding opportunity when spending time in the cool deep water with low food levels instead of the warm and food rich surface waters.

Life history shifts

If the life history is adapted to the actual predator regime, the organisms can reduce their lifetime predation risk. By adjusting the resource allocation between growth and reproduction animals can reduce the exposure time of the most vulnerable size classes. Theoretical models predict that adaptive responses to size-selective predation would be to achieve earlier maturation at smaller size by reduced adult survival, e.g. predation from fish, while reduced juvenile survival should select for larger neonates and later age at maturity (Roff 1992). These predictions have been supported by several studies on zooplankton, where kairomones have induced adaptive shifts in life history parameters. For example when exposed to kairomones from the phantom midge larvae *Chaoborus* (a predator preferring small *Daphnia*), *Daphnia pulex* delay the time to maturity and thus achieve an adaptive larger body size (Tollrian 1995b). Fish kairomones on the other hand induce shifts towards more and smaller eggs as well as smaller size at maturity (Spitze 1992).

The family Bosminidae

Distribution and taxonomy

Bosminids are among the most common and widely distributed fresh water zooplankton occurring in all continents and almost all climatic zones. In Scandinavia, almost every lake has one or more population of *Bosmina*. The family Bosminidae comprises two genera, *Bosminopsis* and *Bosmina*. The genus *Bosmina* consists of four subgenera, *Bosmina*, *Neobosmina*, *Sinobosmina* and *Eubosmina*. The taxonomy in the genus *Bosmina* is complicated, confused by the extreme phenotypic variability within species. Since the first description by O. F. Müller (1785), the number of formally described species has ranged from 2 to 56 world-wide (DeMelo & Hebert 1994). The number of subspecies/morphs/forms is even higher (see e.g. Liljeborg 1901).

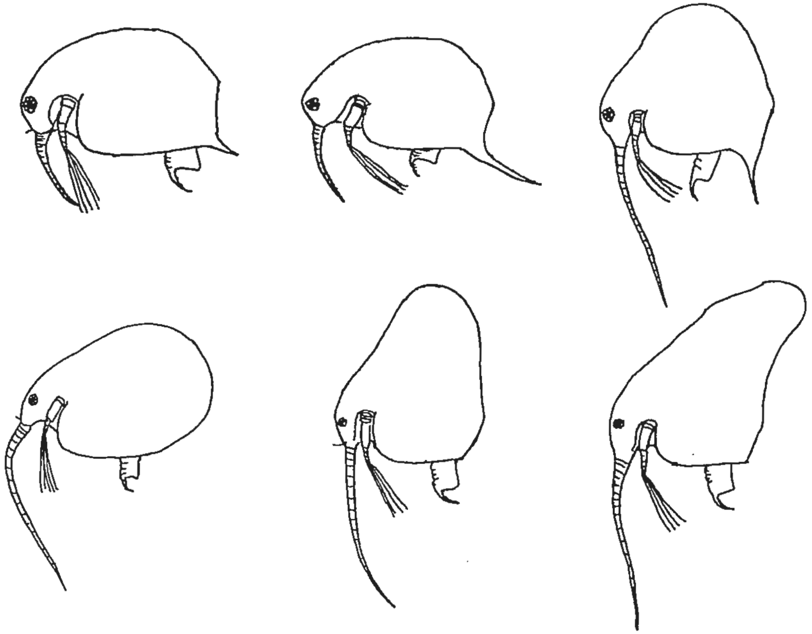

Fig. 3. Examples of morphologic variation within the genus *Eubosmina*.

Morphology

The size of a *Bosmina* is between 0.3 and 1.2 mm. Its soft body tissue is protected by an external bivalve cuticular carapace. In most species the carapace ends in a caudal spine, called mucro. They have two pairs of antennae. The first pair, the antennule, is thought to function as a predatory defence (Kerfoot 1975; Kerfoot & Peterson 1980). The second pair is used for swimming. There is a great morphological variation in *Bosmina*, especially within the subgenus *Eubosmina*. The most varying traits are the length of the antennule and mucro and the shape of the carapace (Fig. 3). Many populations also show seasonal morphological changes, so called cyclomorphosis (Hutchinson 1967, Hellsten & Stenson 1995). The allometry of the antennule and mucro lengths are also very variable. In the same river system relative growth of mucro varied between -0.031 to +1.479 and antennule length between -0.252 and +1.473 in an investigation of 10 lakes of the Nissan river system (all lakes sampled within a week in August, Lagergren unpublished data). However, much less is known about the adaptive significance of these traits in *Eubosmina* compared to morphologic variation and cyclomorphosis in *Daphnia*.

Ecology and Behaviour

Bosminids are herbivorous zooplankton living mainly on phytoplankton, but they can also ingest bacteria (DeMott 1982). A *Bosmina* swims continuously at a relatively high speed

(Zaret & Kerfoot 1980). This way of swimming differs from the swimming behaviour of most other cladoceran zooplankton (e.g. Daphnidae) which have a more jerky swimming pattern with passive sinking between short swimming jerks. The way a Bosmina feeds also differs from other cladocerans and it is possible that its way of feeding is linked to swimming behaviour. Unlike *Daphnia*, *Bosmina* has two ways of feeding. First, they can use pure filtration, which is the common way of food gathering in cladocerans, but they can also feed selectively on high-quality food items by actively capturing and directing them into the food grove (DeMott & Kerfoot 1982). In this way, *Bosmina* can explore food resources more like a hunter than a passive collector which may aid in the competition with other phytoplankton feeders. This feeding behaviour may explain the continuos cruising of *Bosmina*. As suggested by DeMott (1982), the faster they swim, the more food particles come in their way. Therefore, the food intake may be influenced by the swimming speed.

Predators

Some studies have shown that Bosminids can be an important food source to planktivorous fishes (Stenson 1972, 1976; Horppila 1994, Jakobsen & Johnsen 1988). Even in situations when *Bosmina* is not the dominating zooplankton species, the stomach content of Roach (*Rutilus rutilus*) in a eutrophic lake can be composed of more than 90 % *Bosmina* (Lagergren and Nilsson unpublished). It is possible that the continuos swimming and the lack of rapid escape response make them easier to detect and catch by visual predators, than would be expected by size alone. However, one species of *Bosmina*, *B. crassicornis*, is associated with periods of intense fish predation. It is possible that its short and sharply bent antennule in some way reduce the vulnerability to fish predation (Sanford 1993).

Although the predation risk from vertebrate predators may be of great importance, invertebrate predators may be of equal or greater importance in some situations. Phantom midge larvae, copepods and other cladocerans have all been reported to be capable of regulating populations of *Bosmina* (Branstrator & Lehman 1991; Kerfoot 1977b; Luecke & Litt 1987). Morphological defences against these predators may be effective and it is possible that much of the morphological variation among Bosminids reflects adaptations that reduce the predation risk at certain predator regimes. However, few experimental studies on *Bosmina* have addressed these questions.

General methods

The first three studies in my thesis were conducted on animals sampled in the field and studied in the laboratory. We collected *Eubosmina* from two lakes, lake Östersjön (57° 93'N, 12° 70'E) (M.S. 1, 2 and 3) and lake Södra Färgen (56 °55'N, 13 °20'E) (M.S. 1). The experiments were performed in small aquaria or Petri dishes. In the third paper, on the hydrodynamic cost of a morphological trait, a theoretic model is included. In the fourth paper, we used plastic models to further evaluate the importance of hydrodynamic costs and the influence of temperature. The last study is the only field investigation. I examined the cyclomorphosis and relationship between cyclomorphic traits and clutch size in the *Eubosmina coregoni gibbera* population of lake Östersjön on field sampled animals during two seasons 1996 and 1999.

Results and discussion

I. The vulnerability of three morphologically different *Eubosmina* populations to predation by *Leptodora kindtii* (I)

In lake Östersjön (120 km north of Göteborg, Sweden) two morphologically and genetically distinct populations of the genus *Eubosmina* occur (Hellsten & Stenson 1995; Hellsten & Sundberg 2000). *E. coregoni gibbera* has a high protruding carapace and a very long antennule whereas *E. longispina* has a more normal *Bosmina* morphology with a low carapace and shorter antennule. The two populations replace each other during the season. *E. gibbera* is most abundant in the summer, *E. longispina* dominates in the spring and autumn (Hellsten & Stenson 1995). *E. longispina* shows no cyclomorphosis whereas *E. gibbera* is cyclomorphic in both antennule length and the size of the carapace with the most extreme forms appearing in July to August. The replacement of *E. longispina* by *E. gibbera* and the cyclomorphosis in *E. gibbera* is correlated with the population development of the cladoceran predator *Leptodora kindtii*, which is most abundant in the summer (Hellsten & Stenson 1995).

In this study, we investigated if the extreme morphological traits in *E. gibbera* reduce its vulnerability to *Leptodora* predation. In one experiment we investigated the escape efficiency and handling time of *E. longispina*, *E. gibbera* and *Eubosmina coregoni retro-extenca* that has antennule as long as *E. gibbera* but a carapace more like *E. longispina*. The intention was to study *Leptodora* handling these three species to evaluate whether antennule length and/or carapace height might affect escape efficiency.

We found that both *E. gibbera* and *E. retro-extensa*, the two species with very long antennule, had about six times higher escape efficiency than *E. longispina*. This difference is great compared to the anti-predator effect of morphological defences found in other species (e.g. Havel & Dodson 1984; Mort 1986). The results indicate that the length of the antennule, which is the most discriminating trait between *E. longispina* and the other two species, is crucial for the ability of *Eubosmina* to escape this invertebrate predator. Moreover, there was a significant positive correlation between antennule length and handling time.

We also tested the difference in survival between *E. gibbera* and *E. longispina* during 12 h of exposure to *Leptodora*. In this experiment, *E. longispina* was eaten significantly more often than *E. gibbera*. Together the two experiments show that the morphology of the prey can affect the chance to survive during periods of high predation pressure from *Leptodora*. The antennule length seem to have a have great impact on the chance to escape after capture. But what is the function of the high carapace? It is possible that the carapace height affects another step in the chain of events from encounter to successful predation, e.g. the chance to avoid being captured.

How does this difference in escape efficiency affect the ability of these species to survive in the lake? The expected encounter rate, Z, between a prey and any of the predators in the population, can be calculated using

$$Z = \pi r^2 N (v^2 + 3u^2) / 3u \qquad (3)$$

where r is the encounter radius of the predator, N is the population density of the predators [ind/l], v is the swimming speed of the prey and u is the swimming speed of the predator (Gerritsen & Strickler 1977). Inserting $r = 2$ mm (Browman et al. 1989), N=1 ind/l (a typical summer density of *Leptodora* in lake Östersjön), v=2.94 mm/s (Lagergren et al. 1997) and u=13.4 mm/s (Browman et al. 1989) gives 14.8 encounters per 24 hours. Given this high encounter rate, even with such a high chance to escape as 70 % the probability to survive 24 hours should be only $0.7^{14.8} = 0.007$ if they got caught in every encounter. As they obviously can coexist with such high densities of *Leptodora*, the probability to be captured in an encounter situation has to be much less than 1. It is possible that the high carapace affects this probability. Behaviours that decrease the spatial and temporal overlap between *Eubosmina* and *Leptodora* may also be important. These questions should be addressed in future research.

II. Are morphological traits affected by chemical cues?

Inducible defences should be a successful strategy when the abundance of predators is varying and permanent defences imply costs when predation risk is low (review see Harvell 1990; Tollrian & Dodson 1999). The population density of *Leptodora kindtii* in lake Östersjön varies during the season (Hellsten & Stenson 1995). As *Bosmina* can diminish the predation risk from *Leptodora* by morphological defences (Hellsten et al. 1999), which also may imply costs, the *Bosmina* population that can change its morphology in response to the concentration of *Leptodora* kairomones, should have an advantage in this environment.

In this study, we tested if chemical cues from *Leptodora* affects the size of cyclomorphic traits in *E. gibbera*. *E. gibbera* were cultivated individually in small aquaria containing filtered lake water. In half of the aquaria, one *Leptodora* was present behind a net.

We found that both the carapace height and antennule length were significantly larger in the individuals grown in *Leptodora*-treated water. In the juveniles, however, there was no difference in these traits even if antennule length varies seasonally also in the juveniles (Lagergren m.s. V). This difference in response between juveniles and adults may be the proximate reason why relative growth of AL change from negative to positive allometry when *Leptodora* population increases (Lagergren m.s. V). So why should the *Leptodora* treatment affect the juveniles less than the adults? The ultimate reason may be that juvenile *Eubosmina* are easy to catch and handle even if they defend themselves with morphological defences. *Leptodora* catches its prey in a feeding basket formed by the thoratic limbs, the head and the thorax (Herzig & Auer 1990). The size of this feeding basket is strongly correlated with the body length (Manca & Comoli 1995). A juvenile *Eubosmina* is smaller than the size of the feeding basket of even the smallest *Leptodora*. When the size of the prey is much smaller than the predator's maximum prey size, morphological defences are less effective (Swift 1992). However, developing a high carapace and long antennule as an adult may get it out of reach from a great proportion of the *Leptodora* population. An interesting observation is that in Lake Viksjön, a neighbour lake to lake Östersön where the *Leptodora* population is still denser (up to 1.5 individuals per litre), the population of *Eubosmina coregoni gibbera* is even more extreme and the population of *Daphnia cucullata* also has very long tail spine and head crest, traits that increase the total height in the same way as the carapace and antennule in *Eubosmina*.

III. A hydrodynamic cost of morphological defence?

Theoretical models on inducible defences predict that the benefits of a morphological defence have to be balanced by some sort of cost to develop and/or maintain it (Harvell 1990). Most studies on costs of morphological defences in zooplankton have focused on reproductive parameters (e.g. Riessen 1984; Black & Dodson 1990; Riessen & Sprules 1990). However, these early findings of great reproductive costs have now been called in question as direct consequences of the changed morphology (Lüning 1994; Tollrian 1995b). The problem of measuring cost in terms of changes in life history parameters (e.g. age at maturity) on individuals developing morphological defence if exposed to predatory kairomones is that the kairomones also induce adaptive shifts in the life history parameters. How much of the observed changes in the life history parameter that are directly caused by the changed morphology is hard to estimate. In an experimental study where this effect was controlled for, Tollrian (1995b) found no direct cost of the well-known *Chaoborus*-induced neck spines in *Daphnia pulex*. He suggested increased vulnerability to visual predators as being the main cost. However, it remains to be tested if such small structures, like the neckspines of *Daphnia pulex*, significantly increase predation risk from visual predators. Another way to tackle the problem is to estimate the direct consequences of the different morphologies in form of the amount of extra body tissue or volume of young (Kerfoot 1977a) or increased drag. The last point was suggested by Stenson (1987) to be a cost of gelatinous capsules in *Holopedium gibberum* and by Brönmark & Miner (1992) of induced humpbacks in crusian carp, *Carassius carassius*, but has otherwise attracted little attention.

All structures on the surface of an animal affect the drag to some extent. The question is how much and how this may affect the individual fitness. Increased drag may influence the energy consumption for swimming or the swimming speed (Stenson 1987). The swimming speed of most herbivorous zooplankton is higher than what would be expected if swimming was only a way of compensating for the sinking speed (Dodson 1996). As a high swimming speed also increases the encounter rate to ambush predators, such as the phantom midge larvae *Chaoborus,* there must be some benefit of swimming at such a high speed. This benefit may be that swimming speed in some way affects the food intake. The swimming speed may influence the food intake either by a direct relationship between swimming speed and food intake, as suggested by DeMott (1982) and Dodson et al. (1995), or by the time the animals have to spend on moving between food patches (Davis et al. 1991; Tiselius et al. 1994). We examined the relative differences in drag between two morphologically different populations of *Eubosmina*, *E. longispina* and *E. gibbera*, by developing a hydrodynamic model. We also measured swimming speed using three-dimensional video technique.

We found that *E. longispina* swam almost 40% faster than *E. gibbera*. The model predicted that drag should be higher for *E. gibbera* . Assuming they use the same amount of energy for swimming, *E. longispina* should swim about 10 % faster than *E. gibbera*. The difference in observed mean speed was apparantly much higher than the model predicted.

A lower swimming speed may imply a great cost when food has a patchy distribution or when the food concentration is low. Cuddington and McCauley (1994) found that only the fast swimming species were able to locate patches of high food density, in a comparison between a slow and a fast swimming cladoceran. Moreover, Bosminids use the so called dual feeding mode (DeMott 1982) which means that they can use both passive filtering and active capture of food particles. Using the latter mode, the swimming speed probably affects the feeding rate positively, even though the food is uniformly distributed, because the encounter rate with the preferred food items is increased (DeMott 1982). The cost in terms of increased drag may explain replacement cycle of *E. gibbera* and *E. longispina*. In the summer, when the predation risk from *Leptodora* is high, *E. gibbera* outcompetes the non-protected form, *E. longispina*, but in spring and autumn when the predation risk is lower, *E. longispina* outcompetes *E. gibbera* because of better feeding efficiency. The result also suggests that the patchiness and abundance of food should affect the competition between these species. In fact, both *E. gibbera* and the even more spectacular species, *Eubosmina coregoni thersites*, are foremost found in eutrophic lakes (Stenson personal observation; Hofmann 1996).

IV. Does temperature affect hydrodynamic costs?

The idea of a temperature viscosity mediated ultimate explanation was the first and for long time prevailing hypothesis about cyclomorphosis, first presented by Wesenberg-Lund (1900). Cyclomorphic traits were thought to act as sinking speed reducers and as changes in temperature leads to changes in viscosity which affect sinking speed this could explain why these traits vary seasonally and most often positively with temperature. Today, predator defence related hypothesis rule but fact persists, many cyclomorphic traits are correlated to temperature. There are at least three other possible ways temperature may affect cyclomorphic traits, hypotheses that can be incorporated in the antipredator defence theory.

1. If the predation rate is strongly correlated to water temperature, temperature may be used as an alternative or complemental clue (to kairomones) for prey to predict the need for predator defence.
2. Water temperature affects the activity of predators. This means that the predation rate from each predator may be lower at low temperatures and thus decrease the need for defence in their prey.
3. Viscosity changes may affect hydrodynamic costs of antipredator traits.

Of these hypotheses, which not necessarily exclude each other, the second one has attracted most attention. In this study, we tested the potential significance of the third hypotheses. We used plastic and mathematic models to compare the drag resistance of *E. gibbera* to *E. longispina* for a range of Reynolds number. From these measurements we calculated energy expenditure and achieved distance per antennae stroke for different temperatures.

The results show that the long-featured, thin and high body of *E. gibbera* is increasingly maladapted when temperature drops. At 20 °C *E. gibbera* should swim about 15 % slower than *E. longispina* if using the same amount of energy, at 5 °C the difference should be about 19 %. So why should high viscosity affect *E. gibbera* to a larger extent than *E. longispina*?

The drag of an object moving through a fluid is made up of two forces, pressure and viscous drag. The Reynolds number (Re), which is a very important tool in hydrodynamics, is an estimate of the relative importance of these forces. At low Re the viscous forces, which are due to friction, dominate whereas pressure drag dominates at high Re. At a low temperature the viscosity of water increases which lowers the Re of objects moving in it. The viscous forces that dominate at low Re are mostly affected by the external surface area of the object. The more spherical body of *E. longispina* exposes less area, volume kept constant, and that is why the drag of *E. gibbera* rises more steeply than for *E. longispina* when temperature decreases.

The significance of this result can only be speculated about at the moment but it is clear that it should be more important for some sorts of morphological defences than others. One prediction is that helmets or helmet-like structures should be more restricted to warm periods than spines as a helmet increases the surface area much more than a spine. Such a relationship is not predicted by the first two hypotheses about temperature and morphological defence relationships stated above.

V. Clutch size and cyclomorphic traits in *Eubosmina coregoni gibbera*

The cyclomorphosis of *E. gibbera* involves two traits, the length of the antennule and the height and shape of the carapace (Hutchinson 1967, Hellsten and Stenson 1995). This field investigation includes a detailed study on seasonal variation in size and allometry of these traits and clutch size measurements addressing questions of an alternative hypothesis and reproductive costs of these traits which may function as antipredator defences.

For cladocerans, it has been proposed that brood chamber volume may limit clutch size when food is in excess (Kerfoot 1974). As cyclomorphosis in *E. gibbera* involves the shape of the carapace it might be influenced by seasonally varying clutch or egg sizes. This hypothesis was rejected based on the results from this investigation. When carapace height increased from May to July and August, clutch sizes clearly decreased. The space in the brood chamber probably did not increase as animals also were significantly thinner in the summer.

Whether larger traits are associated with reproductive costs were tested on the clutch size data by regression analysis between clutch size and size of the traits. An association was shown to be present for long antennule but not for the carapace height. Higher carapaces were associated with higher clutch sizes contradicting both the cost hypothesis and the results from the seasonal variation. What does this mean? The reason for the result may be that the variation in the relative body height (i.e. body height through body length) is more of a variation in proportions involving both body length and body height than just a variation in height. Thus an animal that puts much resources height growth may get a slower length growth. A low and a high animal of the same body length (in the analysis, animals of the same length were grouped) may thus be of different ages/instars.

The allometry of antennule length and body height was also investigated. Both these traits show positive allometry (which means that the relative size is larger for large animals) except in the beginning of the season when the allometry of antennule length is negative. Positive allometry has often been proposed to be a sign of another use of the trait than predator protection against invertebrate predators as these use to select small prey (Lampert & Wolf 1986). However, large invertebrate predators may also cause a selection for positive allometry. Even if these predators prefer small individuals in the first hand, juvenile *Eubosmina* may be so small that morphological defences do not make any difference for escape ability. The dominating invertebrate predator in Lake Östersjön, *Leptodora kindtii*, is a large predator which may cause such a relationship. The allometry of the antennule length showed a significant positive relation to the population size of this predator. The possibility that extreme *Bosmina* morphology deters fish predators is not excluded. However, even if the cyclomorphosis and traits of *E. gibbera* are spectacular the only known cladoceran with a morphological defence againt fish, *Daphnia lumholtzi*, is even more extreme and also larger.

Concluding remarks

The studies of this thesis support the hypothesis that invertebrate predation can explain some of the great morphological variation in the genus *Eubosmina*. Extreme traits, e.g. antennule length and carapax height exceeding the length of the body, may have evolved as defences against invertebrate predators, such as *Leptodora kindtii*. Long-featured species have higher survival and better chance to escape in association with *Leptodora* than more short featured forms. We have shown that these extreme traits may be associated with costs, both developmental (reduced clutch size) and maintenance (increased drag). The best strategy for *Eubosmina* in this situation when trait have both benefits and costs would be to change morphology in response to the abundance of *Leptodora*. In concordance with the hypothesis, the presence of chemical cues affected the size of antipredator traits, i.e. antennule length and body height. The hydrodynamic cost of large sized morphological defences, as the high carapace of *E. gibbera*, is affected by water temperature. At low temperature the disadvantage is greater due to increased viscocity of the water. This circumstance may restrict the development of extreme sized morphological defences to periods with high temperatures.

Acknowledgements

First I would like to thank all staff at the section of animal ecology for a very inspiring and nice atmosphere during all years (not at least my former room-mates Carina Härlin, Jonas Pettersson and Johan Höjesjö). Especially, I would like to thank my supervisor, professor Jan Stenson, for inspiration, co-operation and criticism on earlier drafts of this thesis. I am also thankful to Dr Maria Hellsten who introduced me to the *Bosmina* world, both in the field and lab, and was a co-writer of two papers. My discussions with Jan-Erik Svensson have often helped and inspired me with the work and planning of experiments. Torgny Bohlin and Donald Blomqvist have helped me with statistical problems. Professor Malte Andersson, Fredrik Sundström and Jörgen Johnsson have read and greatly improved the thesis. During last years Hans Lord and Nils Lundqvist have been part of the *Bosmina* research group and have contributed much by creativity, discussion and enthusiasm. I would also thank the pike-perch populations of the lakes for attracting valuable field assistance.

The study was financially supported by grants from Adlerbertska, Längmanska cultural, Collianders, Kungl. och Hvitfeldtska, Helge Ax:son Johnson, Wilhelm och Martina Lundgrens scientific funds and from funds administrated by the Royal Swedish Academy of Sciences.

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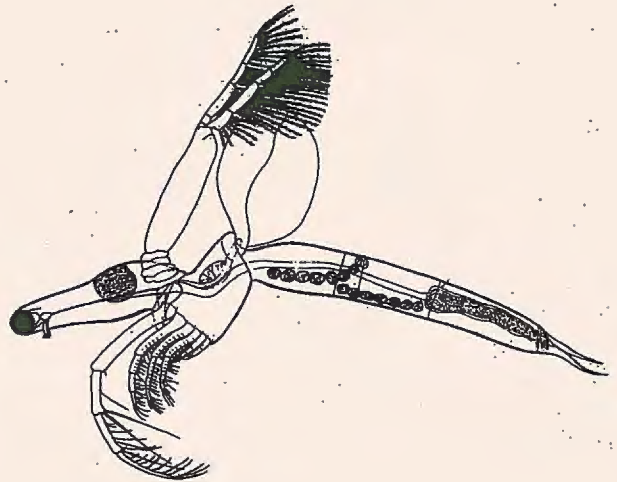

I

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Can extreme morphology in *Bosmina* reduce predation risk from *Leptodora*? An experimental test

Received: 8 June 1998 / Accepted: 5 October 1998

Abstract *Bosmina* (Cladocera) populations, especially within the subgenus *Eubosmina*, show a variety of phenotypes that exhibit large differences in body size and shape and antennule length. In some populations, the morphological traits also vary during the season, with the most extreme forms occurring in periods with high densities of certain invertebrate predators. However, while temporal phenotypic variation in other cladocerans, as in the family *Daphnidae*, has been shown to be an adaptation to reduce the risk of predation by invertebrate predators, the reason for such changes in *Bosmina* is much less clear. We examined whether certain morphological traits in *Bosmina* species could act as a defence against invertebrate predators. We tested three *Bosmina* forms (subgenus *Eubosmina*), differing in morphology from each other, which are found in lakes together with the predator *Leptodora kindtii* (Cladocera). *Bosmina* (*E.*) *longispina* has a relatively low and elongated carapace with a caudal mucro, and short antennule, *B.* (*E.*) *coregoni gibbera* has a higher and more protruding carapace without caudal mucro, and a much longer antennule. Finally, *B.* (*E.*) *coregoni retro extensa* has a carapace like that of *B. longispina* but with no caudal mucro and a much longer antennule. In one experiment, *B. longispina* and *B. gibbera* were exposed for 12 h to *Leptodora* in Petri dishes. In a second experiment, we observed directly the escape efficiency of *B. longispina*, *B. gibbera* and *B. retro extensa*, and the handling time of *Leptodora*. The two *Bosmina* forms with more extreme morphological features had a lower death rate and higher escape efficiency than *B. longispina*. Prey that escaped did so, in most cases, within 5 min. Predator handling time was correlated to predator body length and antennule length of the prey. The results suggests that *Bosmina* species with extreme morphological traits may be less vulnerable to invertebrate predators.

Key words Cladocera · Morphological defences · Predation · *Bosmina* · *Leptodora*

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Introduction

Predation can have a strong impact on zooplankton communities acting as a selective force influencing the evolution of defence strategies in the prey (Zaret 1980; Jeffries and Lawton 1984; Lima and Dill 1990). In aquatic communities, the environment offers few possibilities to avoid predators by hiding in refugia. Instead prey have evolved adaptations that reduce the encounter rate with predators, or hunting success of the predator after encounter (Sih 1987). One way for large and more conspicuous zooplankton to decrease the encounter rate with visually hunting predators (mainly fish) is to migrate to levels of low light intensity where predation pressure is reduced (Zaret 1980; Lampert 1989). Smaller zooplankton, on the other hand, may instead be more vulnerable to invertebrate predators. Many invertebrate predators rely on chemical or hydromechanical cues for localizing prey (Pastorok 1980; Stenson 1987; Herzig and Auer 1990) and independent of their hunting strategy, or how they detect the prey, they have to hold and manipulate the prey item after catch. Therefore, one way to reduce the possibility of being attacked and captured is to develop morphological traits (spines, helmets, unwieldy size or shape) rendering it difficult for the predator to capture and handle the prey. Several such examples are known. For example, in cladocerans, helmets (Mort 1986) and neckspines (Havel and Dodson 1984; Tollrian 1995) in *Daphnia* and gelatinous capsules in *Holopedium* (O'Brien et al. 1979) have been shown to be effective against invertebrate predators. Furthermore, in many cases, the morphological traits developed only in the presence of predators (Hebert and Grewe 1985; Stenson 1987; Dodson 1988; Tollrian 1990, 1994).

Bosmina (Cladocera) show a variety of phenotypes, especially within the subgenus *Eubosmina*, where many of the species exhibit large differences in body size and shape, and antennule length (Lieder 1983). One possible reason for the variation in morphology might be that some traits have evolved as antipredator defences against tactile predators. This could also explain why many of the morphological structures in *Eubosmina* types occur cyclically, i.e. under periods of high predation pressure. Compared to *Daphnia*, the relationship between morphological transformations and predator handling efficiency is less clear and more contradictory for *Bosmina*. Some studies point to predator defence as an important factor (Kerfoot 1978, 1987; Black and Hairston 1983; Sprules et al. 1984; De Stasio et al. 1990), while others have failed to document this (Gerritsen 1983; Johnsen and Raddum 1987). Moreover, these studies are mainly made on *Bosmina longirostris*, a species where the morphological traits are less dramatic, comprising differences in antennule and caudal mucro length. However, within the *Eubosmina* species complex, few studies (Johnsen and Raddum 1987) have been made on the importance of morphological traits in relation to invertebrate predators.

Leptodora kindtii (Cladocera) is an efficient predator which can severely impact zooplankton populations during the summer (Cummins et al 1969; Lane 1978; Edmondson and Litt 1987; Herzig and Koste 1989; Lunte and Luecke 1990; Branstrator and Lehman 1991; Lehman 1991). *Leptodora* has a tactile mode of hunting with setae on the first thoracic limb acting as mechanoreceptors. Together with thorax and head, the other thoracic limbs form a feeding basket into which the prey is pushed (Zaret 1980; Herzig and Auer 1990). Feeding basket size is strongly correlated with predator body length (2–10 mm) (Manca and Comoli 1995), and *Leptodora* prefers smaller prey items (< 1.5 mm) (Herzig and Auer 1990; Branstrator 1994). A detailed description of *Leptodora* feeding behavior is given in Browman et al. (1989). Although the efficiency of *Leptodora* as a predator is well documented, no studies have investigated how different morphological traits in the prey may influence the handling efficiency of the predator.

The aim of this study was to test whether *Bosmina* species with different morphology are equally vulnerable when exposed to *Leptodora*, or if unwieldy size or shape increase the escape possibility of the prey. Three different *Bosmina* forms were tested, all within the subgenus *Eubosmina* (Fig. 1), each differing in morphology from the others. All three forms are found in lakes together with *Leptodora*. *B.* (*E.*) *longispina* (Leydig) has a relatively low and elongated carapace with a caudal mucro (Fig. 1), and short antennule, i.e. a more typical *Bosmina* morphology. *B.* (*E.*) *coregoni gibbera* (Schoedler) has a more extreme body shape than *B. longispina*: the carapace lacks a caudal mucro and the antennule is much longer. *B.* (*E.*) *coregoni retro extensa* (Liljeborg) has a carapace more like *B. longispina* but without a caudal mucro, and with a long antennule like *B. coregoni gibbera*. Further, during the summer *B. coregoni gibbera* increases in size, the carapace becomes more protruding in shape, and the antennule also grows much longer, while *B. longispina* during the same period does not change in morphology (Hellsten and Stenson 1995). In the following we refer to the three *Bosmina* forms as *B. longispina*, *B. gibbera* and *B. retro extensa*.

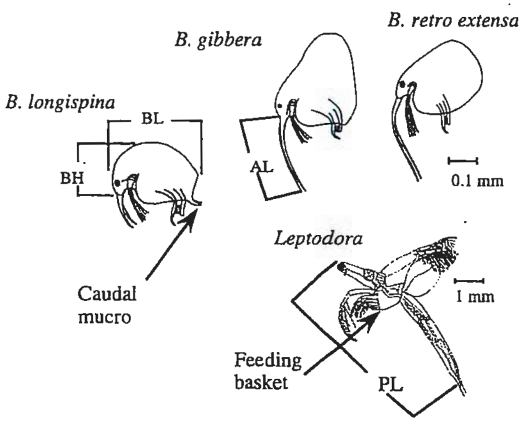

Fig. 1 Lateral view of prey and their predator *Leptodora*. Figures indicate the features that were measured: body length (*BL*), body height (*BH*), antennule length (*AL*), and predator length (*PL*). On *Bosmina longispina*, the *caudal mucro* is also indicated, and on *Leptodora*, the *feeding basket*. Note that *Leptodora* is drawn to a different scale than the three *Bosmina* types

Materials and methods

Animals were collected from two different lakes in southwest Sweden at the beginning of July 1995 and 1996. In Lake Östersjön (57°93′N, 12°70′E), *B. gibbera* and *B. longispina* coexist together with *Leptodora*, and in Lake Södra Färgen (56°55′N, 13°20′E) *B. retro extensa* and *B. longispina* coexist together with *Leptodora*.

In a first experiment, we tested survival of *B. gibbera* and *B. longispina* during a 12-h period (night experiment) when exposed to *Leptodora*. Two days prior to the experiment, animals were collected in Lake Östersjön with a plankton net (100 μm) drawn by vertical hauls from near the bottom to the surface. *Leptodora* were picked out, put in plastic vessels (250 ml) containing filtered lakewater (through 100-μm mesh), and starved for 24 h before the experiment. *B. longispina* (body length 0.55 ± 0.02, mm ± SE) and *B. gibbera* (body length 0.56 ± 0.02, mm ± SE) were picked out and put in Petri dishes. Nineteen replicates, each containing ten *B. gibbera*, ten *B. longispina*, and one *Leptodora* (body length 3.7 ± 0.44, mm ± SE) were then kept in darkness for 12 h at 20°C. Eleven Petri dishes with ten *B. gibbera* and ten *B. longispina* in each, but no predator served as the control group. Each Petri dish (diameter 95 mm, height 20 mm) contained approximately 70 ml of filtered lakewater. The water volume was sufficient for both prey and predator to swim around without any problems.

After 12 h, all living *Bosmina* were counted. We defined as dead prey either those missing or actually seen dead in the dishes. Alive prey caught in the surface tension were also counted. We also noted if the predator was still alive. If not, the Petri dish was excluded from the analysis.

In the second experiment, prey were collected approximately 1 week in advance, placed in 250-ml containers with filtered lakewater, and kept at 20°C. *B. gibbera* and *B. longispina* were collected from Lake Östersjön and *B. retro extensa* from Lake Södra Färgen. *Leptodora* were collected from Lake Östersjön, and Lake Södra Färgen a few days before experimentation, and starved for 20–35 h at 18°C.

Observations were carried out as follows. Approximately 60 individuals from one *Bosmina* population were put in a Petri dish (hunting dish), containing 70 ml of filtered lakewater, together with three or four *Leptodora*. During the experiment, only attacks and captures were recorded, not attacks and escapes. Whenever a *Leptodora* had attacked and captured a *Bosmina* (retaining it in its feeding basket), it was transferred as fast and carefully as possible to an empty dish (eating dish) with a plastic Pasteur pipette. The opening of the pipette was wide enough (diameter 6.5 mm) not to injure or affect the predator in any substantial way. In only a few cases did the predator lose its prey during this transfer and these were excluded from the analysis. All predators with a captured prey were treated similarly and subsequently all prey were also treated equally, so any methodological errors should be the same for all predators and prey. By transferring the predators, we were able to follow each encounter and the handling process from the catch to an eventual escape, or to the final eating of each prey. The observation technique allowed us to estimate each handling event within the time span of at most 10 s. *Bosmina* that succeeded in escaping were controlled for a period of 90 min to see if they had sustained any damage. Animals were then preserved in 70% ethanol. Injuries and parts eaten on a prey were recorded. Transferred predators were replaced by new ones in the hunting dish. All Petri dishes were illuminated from 30 cm above with a swan-neck cool point source (Volpi Intralux 150H) giving a light intensity of about 2300–2800 lux in the hunting dish and 1200–1800 lux in the eating dishes. As the Petri dishes were placed on a white background, both prey and predator were easily seen by watching their shadow image.

In the first experiment, mean survival was estimated and tested with the Wilcoxon signed-rank test. Escape efficiency in the second experiment was defined as the number of prey escapes divided by the total number of prey that were caught and retained by the predator, for each of the three *Bosmina* forms. When captured, handling time was estimated as the time between first contact and final release of the eaten prey. We also measured predator length, and body length, body height and antennule length of the prey (Fig. 1) and tested differences in body measurements among forms as well as correlation among body measurements after log transformation of the variables. Since mutiple tests addressed a common null hypothesis (no difference in body measurements among the *Bosmina* forms), we adjusted α-levels using the sequential Bonferroni method to ensure an overall significance level of 5% (Rice 1989; Chandler 1995).

Predator handling time was tested with one-factor ANOVA after log transformation of the variables and checking the assumptions for analysis of variance. Finally, the importance of prey body measurements, and predator body length in relation to handling time was tested with multiple regression analysis.

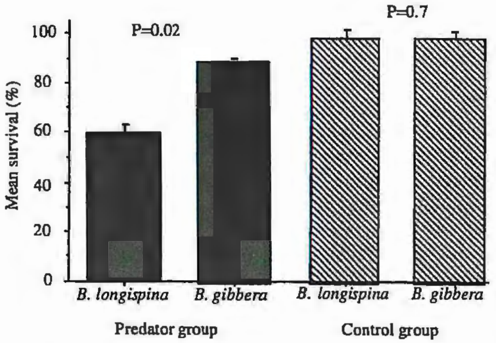

Fig. 2 Percent survival (mean ± SD) for *B. longispina*, and *B. gibbera* exposed to the predator *Leptodora* during a 12-h period (night experiment), and percent survival in the control group. Differences in survival were tested with the Wilcoxon signed-rank test (experimental group $n = 16$, control group $n = 11$)

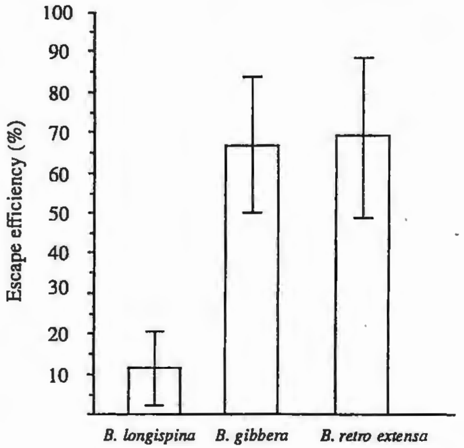

Fig. 3 Escape efficiency (%) with 95% confidence intervals for individuals exposed to *Leptodora* in the attack experiment (*B. longispina* $n = 43$, *B. gibbera* $n = 30$, *B. retro extensa* $n = 20$)

Results

Mean survival was significantly higher for *B. gibbera* than for *B. longispina* when exposed to the predator in the first experiment (Fig. 2). In the control group both species survived equally well (Fig. 2). *Leptodora* was found in good condition in 16 out of 19 replicates. Both prey types were caught in the surface tension although there was a tendency for *B. gibbera* to get caught there more often (*B. gibbera* 53%, *B. longispina* 33%). Therefore, individuals of both *Bosmina* forms, trapped in the surface tension, were excluded from the analysis since they were regarded as non-accessible prey for *Leptodora*. Excluding the floaters is a conservative method and since more *B. gibbera* were caught at the surface, this should underestimate the advantage of the gibbera form.

In the second experiment, *B. gibbera* and *B. retro extensa* escaped *Leptodora* about six times more often than did *B. longispina* (Fig. 3). The escape efficiency was 67% and 70%, respectively, for the two extreme forms, but only 12% for *B. longispina*. Most *Bosmina* escaped within 5 min (Fig. 4). In some rare cases, individuals escaped unharmed after up to 26 min in the feeding basket. The majority of *Bosmina* that escaped were still alive, and with no visible injuries after 90 min of observation. Further, *Bosmina* also often showed thanatosis up to 10 s after escape, i.e. with antennae protectively folded into lateral sheaths, they passively sink (Kerfoot 1978), and then swim away in a protean way, meaning that the escape behaviour is sufficiently unsystematic for the predator to predict the position in the next moment (Edmunds 1974).

Mean body height was significantly higher in *B. gibbera* and mean antennule length in *B. longispina* was significantly shorter compared with *B. gibbera* and *B. retro extensa* (Table 1, $P<0.05$ Scheffe's *F*-test). Predator body length did not vary among groups (Table 1).

Body measurements in the prey were strongly correlated (log body length and log body height 0.88, log body height and log antennule length 0.73, and log body length and log antennule length 0.47, $n=49$, Pearson correlation coefficient), so we only tested the effect of antennule length, together with predator body length, on handling time. Predator length and prey antennule length explained about 20% of the variation in handling time ($R^2=0.18$, $P=0.004$, $n=49$, multiple regression). Predator handling time of ingested prey was negatively correlated with predator body length ($R^2=-0.79$, $P=0.02$, $n=49$, multiple regression) and positively correlated with antennule length of the prey ($R^2=0.30$, $P=0.003$, $n=49$, multiple regression). Finally, handling time among prey groups of those prey eaten by *Leptodora* was not statistically different although there was a tendency towards longer handling time of *B. gibbera* [*B. longirostris* 1.4 ± 0.05 (log min ± SE), $n=34$; *B. retro etxensa* 1.3 ± 0.1, $n=6$; *B. gibbera* 1.6 ± 0.1, $n=9$; $P=0.07$, one-factor ANOVA].

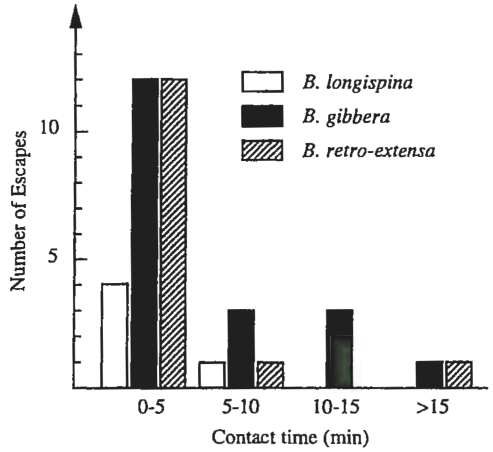

Fig. 4 Number of prey escapes in relation to contact time with the predator ($n=38$)

Discussion

The environment in aquatic communities is such that zooplankton have few possibilities to avoid predators by hiding in refugia. To escape being eaten by visually hunting predators, zooplankton may migrate vertically into the dark depths of lakes. But if they are more exposed to invertebrate predators that hunt with mechanoreceptors, developing morphological defences is a better strategy.

Bosmina is a relatively small zooplankton and cannot outswim the large and faster *Leptodora* – it must instead rely on other defence mechanisms. The higher survival of *B. gibbera*, and the higher escape efficiency of *B. gibbera* and *B. retro extensa* suggest that their morphology can act as a defence against a tactile predator like *Leptodora*. Given the choice, in the first experiment, *Leptodora* preyed more often on *B. longispina*, although *B. gibbera* was also eaten. *B. gibbera* was caught more often in the surface tension, which may have produced a higher density of *B. longispina* in relation to *B. gibbera*. However, when animals caught in the surface tension were excluded, *B. gibbera* still had a higher survival rate. The predator swims much faster than either prey, and due to the limited size of the vials, the encounter rate was probably higher than in nature, where prey can disperse more and other kinds of prey are also available.

The difference in predation on the two *Bosmina* species by *Leptodora* may contribute to the numeric relations between the species observed in the field. In Lake Östersjön, *B. gibbera* is more common during periods with dense *Leptodora* populations, and *B. longispina* in some years disappears almost entirely during these periods (Hellsten and Stenson 1995).

Other studies have shown that morphological traits can make the prey less vulnerable to invertebrate predators (Kerfoot 1978; Havel and Dodson 1984). One example is *B. longirostris*, which under high predation pressure from copepods, demonstrates a larger body

Table 1 Mean body measurements (mm ± SE) of prey caught (escaped or handled) by *Leptodora*, and mean body length of *Leptodora* (mm ± SE). Differences in mean body measurements between prey type were tested with a one-factor ANOVA. *Asterisks* denote $P < 0.05$ with sequential Bonferroni adjustments (probability values from analysis of variance). Statistically different groups are indicated by different superscripts

	B. longispina ($n=43$)	*B. gibbera* ($n=30$)	*B. retro extensa* ($n=20$)	*P*-value
Mean length	0.46 ± 0.01^a	0.47 ± 0.02^a	0.51 ± 0.02^a	n.s.
Mean height	0.34 ± 0.01^a	0.49 ± 0.02^b	0.36 ± 0.01^a	0.0001*
Mean antennule length	0.19 ± 0.005^a	0.53 ± 0.02^b	0.52 ± 0.02^b	0.0001*
Mean length of *Leptodora*	3.8 ± 0.15^a	4.1 ± 0.15^a	4.2 ± 0.33^a	n.s.

size, and longer antennule and caudal mucro (Kerfoot 1987). Although the morphological traits in this species are less conspicuous than those of the *Bosmina* forms in our experiment, the morphological changes were still large enough to reduce mortality rates.

In the second experiment, the two forms with extreme morphology, *B. gibbera* and *B. retro extensa*, escaped more often than *B. longispina*. This result supports our interpretation that extreme morphology in *Bosmina* can reduce predation risk from tactile predators. The most discriminating characters among the three forms are the shape of the carapace and antennule length. *B. gibbera* and *B. retro extensa* escaped equally well, which implies that the length of the antennule is important for escape efficiency. When copepods capture *Bosmina*, they often manipulate the prey to expose the soft underparts, and during this manipulation the antennule may interfere with the handling attempts of the predator (see Zaret 1980). However, the chance of escaping is just a small component in the course of predation from encounter to successful prey ingestion (Lima and Dill 1990), and carapace shape may affect the ability of the predator to capture the prey.

The magnitude of the difference in escape efficiency between *B. longispina* and the more extreme forms is quite large. Compared with *B. longispina*, the other two forms had an almost 6-fold higher chance of escaping. In a study by Havel and Dodson (1984), spined *Daphnia* morphs had an approximately 1.5- to 2-fold higher escape chance than unspined morphs when exposed to *Chaoborus*. Our experiment used predators within a limited size range, and it is possible that the escape chance decreases as the predator becomes larger. Predator body length in relation to prey size is an important determinant of predator success. In *Leptodora*, the size of the feeding basket is strongly correlated to body length (Manca and Comoli 1995), and prey availability is thereby correlated to predator length. Furthermore, according to our regression analysis, handling time decreased with increasing predator length. Although we used prey and predator within a limited size range, clearly the prey were not too large. Herzig and Auer (1990) estimated that *Leptodora* with a body length of about 4 mm would be able to capture prey with a maximum body length of 0.6 mm. The results are in accordance with other studies where prey size and handling time were correlated to the size of *Leptodora* (Browman et al. 1989; Branstrator 1994).

Prey body measurements were strongly correlated, and we tested the effect of antennule length on handling time in the multiple regression analysis, since antennule length was the character significantly discriminating both *B. gibbera* and *B. retro extensa* from *B. longispina*. Both predator length and antennule length affected the handling time, but explained only 20% of the variation. Therefore, we suggest that the total form and size of the prey will also influence the handling time. This is supported by the tendency towards longer handling time of *B. gibbera*. The longer antennule and the shape of the body may make it difficult for the predator to turn the prey into an appropriate position. There are few reports on how *Leptodora* eats its prey. Apparently, it is mainly a fluid feeder, i.e. by piercing the carapace of its prey near the head with sharp protuberances it sucks out the juices (Mordukhai-Boltovskaia 1958), but can also tear a hole in the carapace and then suck out the juices (see Browman et al. 1989). It is also possible that the carapace in *B. gibbera* is more robust, making it more difficult for the predator to either pierce or tear a hole in the carapace. This has been suggested for other species (Kerfoot 1978; Havel and Dodson 1984).

To summarize, we have shown that extreme morphological traits in *Bosmina* enhance the survival rate and escape success when they are attacked by predators such as *Leptodora*. In some cases, this may explain why phenotypically variable forms are so common within this genus. Further studies of phenotypical variation in *Bosmina* and the co-occurrence of invertebrate predators are, however, needed.

Acknowledgements We thank Malte Andersson and Björn Arvidsson for valuable criticism and comments on the manuscript. The study was supported by grants from The Anna Ahrenberg, Colliander, Helge Ax:son Johnson, Kungl Hvitfeldtska, Hierta Retzius, and Wilhelm och Martina Lundgren Foundations for Scientific Purposes.

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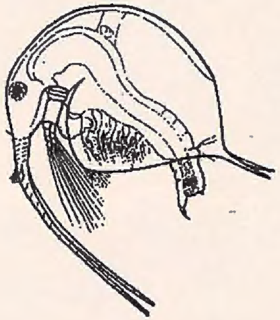

SHORT COMMUNICATION

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

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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'Brien *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 = $k_1 + k_2 \cdot (\mathrm{BL}) + k_3 \cdot (\mathrm{BL})^2$]. 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 $\mathrm{AL}_{\mathrm{rd}}$ as the relative development of antennule length and $\mathrm{CH}_{\mathrm{rd}}$ as the relative development of carapace height. For each aquarium, mean $\mathrm{AL}_{\mathrm{rd}}$ and $\mathrm{CH}_{\mathrm{rd}}$ 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 CH_{rd} and AL_{rd} were calculated, we also conducted the same kind of analysis on simple regressions on log transformed data [log (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 AL_{rd} 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 ($P = 0.076$, marginally significant). When only adults were considered, AL_{rd} 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: $CH = -1178 + 5.77 \cdot BL - 0.00439 \cdot BL^2$ and $AL = -838 + 5.31 \cdot BL - 0.00480 \cdot BL^2$; and for the simple regressions on log-transformed data: $\log CH = -1.31 + 1.514 \cdot \log BL$ and $\log AL = -0.54 + 1.236 \cdot \log BL$.

Compared with the starting condition, CH_{rd} remained the same in the *Leptodora*- treated water but declined in the control, whereas AL_{rd} 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 CH_{rd} and AL_{rd} 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 I. Relative development of carapace height and antennule length of *Eubosmina coregoni gibbera* reared in *Leptodora*-treated water (*L.k.*) or water that was not conditioned with *Leptodora* (no *L.k.*). The sample sizes (n) refer to number of aquaria. For each trait, differences were tested by two-factor ANOVA. The numbers within parantheses represent the analysis on relative measurements calculated from the regression on log-transformed data

Trait	Date	Relative developments				ANOVA					
		L.k.		No *L.k.*		Date		Treatment		Date × treatment	
		Mean	n	Mean	n	F-value	P-value	F-value	P-value	F-value	P-value
Carapace height	July	0.94	4	0.84	14	0.88	0.36	11.74	0.0019	0.42	0.52
	August	0.95	8	0.88	6	(0.21)	(0.65)	(18.19)	(0.0002)	(0.33)	(0.57)
Antennule length (all)	July	0.81	8	0.71	15	3.35	0.076	9.59	0.0038	0.033	0.86
	August	0.86	9	0.77	8	(3.81)	(0.059)	(8.73)	(0.0055)	(0.37)	(0.55)
Antennule length (juvenile)	July	0.84	5	0.84	5	0.99	0.34	0.017	0.90	0.030	0.87
	August	0.80	4	0.79	6	(0.76)	(0.39)	(0.82)	(0.38)	(1.22)	(0.28)
Antennule length (adult)	July	0.76	4	0.69	14	6.46	0.017	6.44	0.017	0.017	0.53
	August	0.87	8	0.76	6	(4.63)	(0.040)	(5.34)	(0.028)	(0.0001)	(0.99)

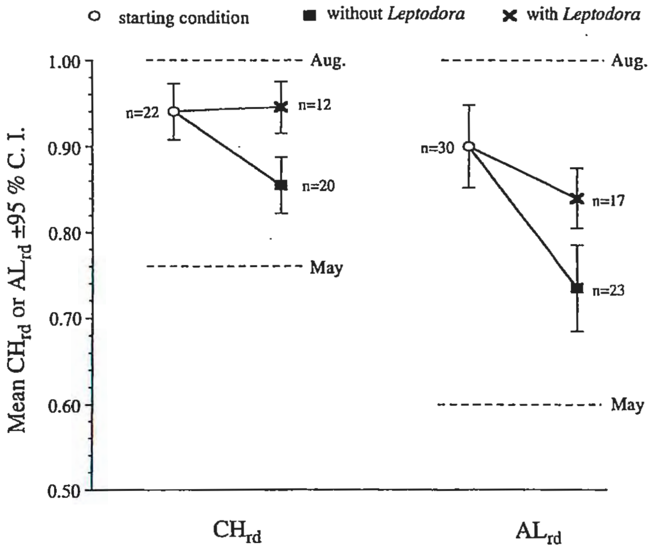

Fig. 1. Mean relative carapace height (CH_{rd}) and antennule length (AL_{rd}) of *Eubosmina* at the beginning of the experiment and after 14 days exposure or no exposure to *Leptodora*. The results from both experiments are pooled. The sample size, *n*, is for individuals measured in the starting condition 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.

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 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 gibbera* 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 gibbera* 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 gibbera*.

Acknowledgements

We thank anonymous referees for valuable criticism and comments on the manuscript. The study was financially supported by grants from The Colliander (R.L.), Regnells zoological R.L.), Hierta Retzius (R.L.), Kungl. Hvitfeldtska (R.L.) and Wilhelm and Martina Lundgren (R.L. and J.A.E.S.) foundations for Scientific purposes, and the Swedish Natural Science Research Council (J.A.E.S.).

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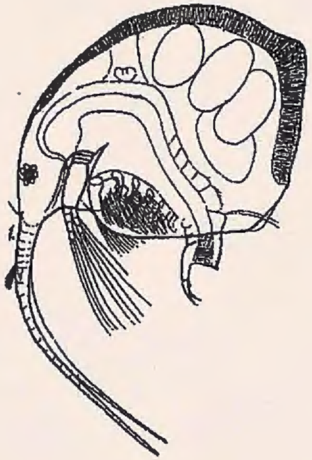

III

Functional Ecology 1997
11, 484–488

Increased drag, and thus lower speed: a cost for morphological defence in *Bosmina (Eubosmina)* (Crustacea: Cladocera)

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Summary

1. The swimming speed of two forms, an extreme and a typical, within the cladoceran subgenus *Eubosmina* were examined using a three-dimensional video-technique. The extreme form has a very high carapax and extremely long antennule, features probably involved in predator defence.
2. It was found that the extreme form swam almost 40% slower than the typical form.
3. Calculations show that the extreme form had to work at least 12% harder to swim at the same speed, or if it used the same amount of energy to swim, the extreme form would swim 6% slower. Increased drag, because of its distinguishing carapax and antennule, is thus the most likely explanation for the slower swimming speed of the extreme form, assuming it selects the same power output.
4. Swimming speed can be correlated to food intake either by the frequency of hits to edible food particles or by the time to swim from a poor food patch to a good one. So the reduced speed is probably a great cost for the extreme form.

Key-words: Modelling, optimal feeding, swimming speed, zooplankton
Functional Ecology (1997) **11,** 484–488

Introduction

Predation is one of the most important evolutionary forces in zooplankton communities. Small planktonic species suffer from the predation of larger carnivorous invertebrates which has led to the evolution of defensive morphological structures such as spines, helmets and gelatinous capsules, thus making it more difficult for the invertebrate predators to handle them (O'Brian, Kettle & Reissen 1979; Havel & Dodson 1984).

Since it is often the case that defended morphs are replaced by undefended morphs when the predation pressure declines (Kerfoot & Peterson 1980), it is reasonable to assume that there should be some cost to develop and maintain a morphological defence (Harvell 1990). Most studies of the costs of morphological defences have focused on measurements of reproductive parameters (e.g. Reissen 1984; Black & Dodson 1990) but an important question is how does the structure of these traits negatively affect fitness? Lüning (1994) proposed that the reproductive costs did not necessarily have to be directly associated with the defences but argued instead that induced life-history shifts may present another explanation to the decreased reproductive rates observed in some experiments. Direct costs might be increased time and resources needed for the body development – which have been proposed to be the major cost of *Daphnia* possessing neck and tailspines (Reissen 1992) and in the long-featured morphs of *Bosmina longirostris* (Kerfoot 1977, 1987). Another cost could be increased drag and a higher energy expenditure for motion or a lower speed. The swimming speed may influence filtering rate and the frequency of hits to edible food particles (Gerritsen & Strickler 1977; DeMott 1982). Costs in this sense have not been investigated to any large extent but have been suggested as a cost for gelatinous capsules in *Holopedium gibberum* (Stenson 1987).

In Östersjön, a lake in southwest Sweden, two forms appear within the cladoceran subgenus *Eubosmina*, one typical *E. longispina longispina* (Leydig) and one extreme *E. coregoni gibbera* (Schoedler), the latter with a very high carapax and long antennule. Hellsten & Stenson (1995) have described a replacement cycle wherein the typical form is replaced by the extreme, from early spring to autumn, coinciding with the hatching of the cladoceran predator *Leptodora kindtii* Focke. In an experimental study, the extreme form survived significantly better than the typical form when exposed to the cladoceran predator *Leptodora kindtii* (M. Hellsten & R. Lagergren, unpublished observations).

These very different forms (Fig. 1) of continuously swimming *Eubosmina* provide suitable material with which to study the costs of morphological defences in terms of increased drag. This study includes a model of how the drag could affect the two forms and an experiment wherein the swimming speed of the two forms was measured with the help of video-technique.

Methods

Specimens were collected from a eutrophic lake (1·5 km^2; max. depth 32 m) in southwestern Sweden (57°93′N, 12°79′E) called Östersjön. The samples were collected in May when both forms are present in the lake. Animals to be used in the experiment were chosen from field samples and kept in aquaria at ≈ 22 °C, until they were filmed.

The animals were filmed in a cubic glass chamber with sides of 2·1 cm, giving a volume of 9·26 cm^3. Illumination was provided by a circular 'cold-light' lamp (Schott) situated ≈ 12 cm above the chamber. The water in the chamber was filtered (25 µm) lake water from Östersjön and was held at the same temperature as that in the aquaria.

Both forms were held in the same aquarium and were chosen in random order. Each specimen was filmed during a 5-min period with the three-dimensional technique described by Ramcharan & Sprules (1989) using one camera and four mirrors. The mirror system gives a figure of the aquarium from two directions on the TV monitor. This makes it possible to see the animals' movements in three dimensions. The first five sequences, in which the animals swam quite straight, were analysed for a period of at least 2 s, the movement was plotted on the screen and the speed was calculated as $(x^2 + y^2 + z^2)^{1/2}\, t^{-1}$. The average speed was then calculated for each animal. After filming, the body length (L) and height (H) of each individual was measured, and the H/L value was used as an estimation of the degree of 'humpbackness' (see Fig. 1).

The side profile area (S_{SP}) for 16 randomly chosen individuals of both forms was estimated by weighing pieces of paper of the animals' shapes. These had been drawn by using a dissecting microscope with a drawing tube attached to it. The S_{SP} were used in the calculations of drag.

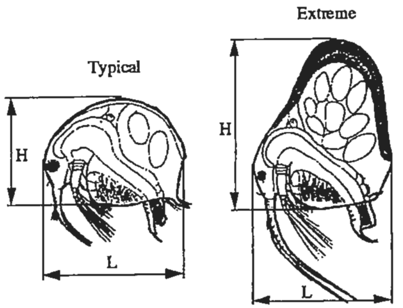

Fig. 1. The two forms of *Bosmina* (E.). Features measured are body length (L) and body height (H).

MODEL

There are two kinds of drag, pressure drag (D_p), which depends on inertial forces, and friction drag (D_v), which depends on viscous forces. The Reynolds number (*Re*) which is of great importance in fluid mechanics is an estimate of the relative importance of these forces. Since the *Re* values for a swimming *Bosmina* range from 0·8 to 5, depending on size and swimming speed, the most important of the two drags will be viscous drag. The other sort of drag, pressure drag, becomes important when $Re \gg 1$ (Vogel 1981; Alexander 1983). Equation 13.1 in Vogel (1981) states that

$$D = C_{DVS} \cdot \mu \cdot S^{1/2} \cdot U, \qquad \text{eqn 1}$$

where D = drag, C_{DVS} is a constant due to the shape of the body, μ is the kinematic viscosity of the fluid, S is the wetted surface area and U is the velocity, is trustworthy up to $Re \approx 1$. With that equation as a basis, the relative changes in speed (with constant power) and power (with constant speed), owing to changes in the H/L ratio, can be calculated as follows:

A regression line between H/L and the 'relative side profile area' (rS_{SP}) was made for the 16 individuals on which the side profile area (S_{SP}) was measured (Fig. 2). The parameters were well correlated. rS_{SP} is independent of the body length, without unit but proportional to S_{SP}. If the S_{SP} is assumed to be proportional to the wetted surface area (S), the relative change in S is possible to calculate from different H/L ratios. The constant C_{DVS} depends upon the shape of the body, but the difference in shape between the morphs leads to very little change in its value (Vogel 1981); thus, C_{DVS} can be regarded as a constant for all H/L ratios. The drag (D) then becomes proportional to $S_{SP}{}^{1/2}U$. Power (P) = DU and the relative change in power needed for locomotion keeping the velocity constant can be calculated for different H/L values as:

$$P \propto D \propto S_{SP}{}^{1/2}. \qquad \text{eqn 2}$$

Similarly the relative change in velocity with constant power output is possible to calculate. The result is:

$$U \propto 1/S_{SP}{}^{1/4}. \qquad \text{eqn 3}$$

These equations can give the predictions shown in Fig. 3.

Results

The mean length of the animals used in the experiment did not differ between the two forms (Table 1). The extreme form swam significantly slower than the typical ($P < 0{\cdot}005$ Mann–Whitney U-test, $n = 14$).

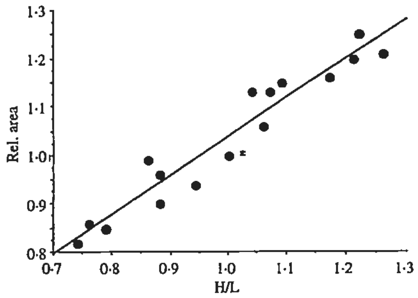

Fig. 2. The regression line ($rS_{SP} = 0{\cdot}805\ H/L + 0{\cdot}234$; $r^2 = 0{\cdot}93$) between H/L (see Fig. 1) and relative side profile area (rS_{SP}) that was used in the calculations of drag (Fig. 3). Each point represents one animal. The individual marked with * is the starting point whose rS_{SP} was set to 1. The S_{SP} for remaining individuals can be calculated as $L_0{}^2A_x/L_x{}^2A_0$, where L_0 = the length of the individual chosen as starting point; L_x = the length of individual x; A_0 = the side profile area of the individual chosen as starting point; and A_x = the side profile area of individual x.

Among the specimens of each form there was no correlation between H/L and speed (F-test, $P > 0{\cdot}05$ in both cases, $n = 14$).

Discussion

The results show that the typical form swims almost 40% faster than the extreme form. Increased drag seems to be the most likely explanation for the extreme form swimming more slowly than the other form. Our model suggests a relation between the H/L value and swimming speed owing to differences in drag (Fig. 3). It is evident that the difference in swimming speed between the mean H/L ratio of the extreme and the typical form would be only about 6% if they use the same amount of energy when swimming. This figure is considerably less than the observed difference of 40%. The speed of a *Bosmina* varies during a single stroke (Zaret & Kerfoot 1980) with the highest speed being around 10 mm s^{-1} in *Bosmina longirostris*. *Eubosmina* swims faster than *Bosmina longirostris* (Stenson 1990) and it may attain an *Re* value of > 10 just after a stroke when the speed is highest. In higher *Re*, where pressure drag becomes the dominating force, the shape of the body becomes more important for the drag (Vogel 1981); thus the difference in drag between the forms is certainly greater than these simplified calculations predict. A relation between H/L and speed (as the model predicts) could not be determined among the specimens of each form. This was probably due to a small variance in H/L and a large variance in speed.

So how could the difference in swimming ability influence the food intake of these animals? DeMott (1982) writes that 'the continuous swimming of *Bosmina* could be a behavioural adaptation to increase the encounter rate with food particles'. As algae are slow-moving particles, increased speed in the predator implies higher encounter rates (Gerritsen & Strickler 1977). This means that swimming speed would be correlated to the efficiency in food gathering; thus the lower the speed, the less the food intake by the filter-feeding zooplankton. Accordingly, this could imply a greater cost for the extreme form than for the typical.

A model on optimal foraging of a *Eubosmina*, if food intake is correlated to swimming speed, may look something like Fig. 4. Without swimming, the movement of the filtering apparatus itself gives some food intake which then rises asymptotically (functional response type 2; Holling 1966) with increased swimming speed. The energy consumption rises linearly from a basal metabolism (linearly because a *Bosmina* regulates its swimming speed mostly by varying the time between strokes; Zaret & Kerfoot 1980) and the slope of the line depends on the drag. The model predicts that the form with increased drag optimizes its net food intake if it reduces its swimming speed.

It has not been proven that the food intake depends on the swimming speed but if the concentration of food particles is uneven, optimal foraging would be to

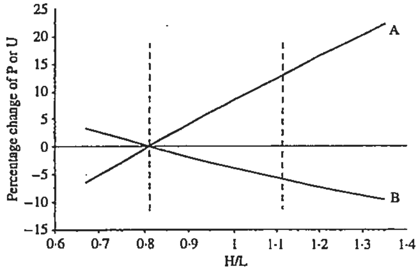

Fig. 3. Curve A demonstrates how much individuals of different H/L (see Fig. 1) have to work, to swim at the same speed, in comparison with an individual of the typical form with an H/L value of the average. Curve B shows how the H/L value affects the speed if individuals use the same power for locomotion. The dotted vertical lines represent the mean H/L values for the typical and extreme form, respectively.

Table 1. Mean swimming speed (mm s^{-1}), mean body length and mean H/L for typical form (T) and extreme form (E) The sample size was $n = 14$ for both forms. The difference in mean speed between forms is significant $P < 0{\cdot}005$, Mann–Whitney U-test

	Speed		Body length (mm)		H/L	
Form	Mean	SD	Mean	SD	Mean	SD
T	4·08	0·92	0·47	0·07	0·81	0·07
E	2·94	0·56	0·47	0·04	1·11	0·09

swim slowly in high food concentration but more quickly if the concentration is low in order to leave the low concentration as fast as possible. In a comparison between slow-swimming *Ceriodaphnia dubia* and fast-swimming *Daphnia pulex*, it was shown that only the faster swimmer was able to locate the good food patches (Cuddington & McCauley 1994). This means that the slower swimming speed may be a cost even if the food intake does not depend on the swimming speed directly, because it takes more time to swim from a poor food patch to a good one.

Another explanation for the extreme form swimming more slowly may be differences in swimming behaviour. Lower speed reduces the risk of encounters with predators (Gerritsen & Strickler 1977). It could be that the extreme form has a behaviourally lower swimming speed regardless of the presence of a predator or not. Contradictory to this hypothesis is the fact that the typical form suffers more from encounters with predators and thus should swim slower than the extreme form.

The relative importance of different ultimate costs remains to be solved in the case of this as well as other species and may be affected by conditions such as the food concentration. At low food concentrations, animals probably suffer more from reduced swimming speed and feeding efficiency because the net energy gain falls faster (with reduced food concentration) for an animal with increased drag (Ware 1975). Interestingly, the extreme form is most often found in eutrophic lakes (J. Stenson, personal observations).

We conclude that drag is probably an important force working against the evolution of certain phenotypical adaptations used as predator defence in zooplankton. Extreme *Eubosmina* forms, which are prevalent under high predation risks, have a morphology that significantly increases drag. When predation risks decline, on the other hand, selection will favour a morphology that is less costly.

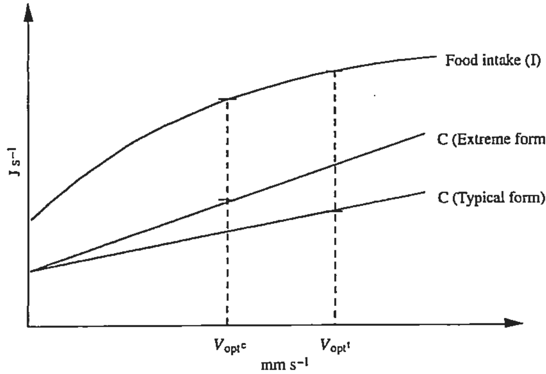

Fig. 4. Hypothetical curves of food intake (*I*) and cost of swimming (*C*) for feeding *Bosmina*, of typical and extreme forms, plotted as a function of swimming speed. A simple model that supposes that the animals try to maximize net energy gain per time unit (E/t), $E/t = I - C$, predicts that the optimal swimming speed, V_{opt}, is lower for the extreme form than for the typical. $V_{opt}e$ = optimal swimming speed for the extreme form, $V_{opt}t$ = optimal swimming speed for typical form.

Acknowledgements

We thank Adrian Thomas and two anonymous referees for valuable criticism and comments on the manuscript. The study was supported by grants from Anna Ahrenbergs fond, Collianders stiftelse, Helge Ax:son Johnsons stiftelse, Wilhelm and Martina Lundgrens fond and Kungl. Hvitfeldtska stipendieinrättningen.

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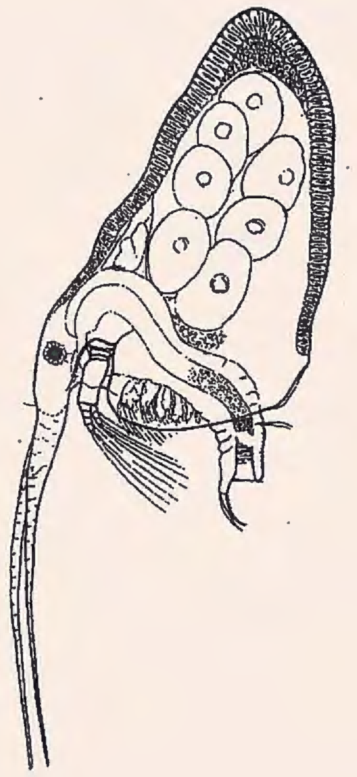
Received 17 April 1996; revised 6 November 1996; accepted 21 November 1996



IV

Functional Ecology 2000
14, 380–387

Influence of temperature on hydrodynamic costs of morphological defences in zooplankton: experiments on models of *Eubosmina* (Cladocera)

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Summary

1. If swimming speed is correlated to fitness (e.g. by affecting food intake or the chance to evade predators) or considerable energy is expended in swimming, zooplankton wearing protruding structures (as predator defence) that significantly increase drag resistance must pay a cost for the better protection against predators that these traits imply.

2. In an experiment with plastic models, the drag and energy consumption of swimming in two species of *Eubosmina* were examined. *Eubosmina longispina* has a typical *Bosmina* morphology with a low carapace and short antennule, whereas *E. coregoni gibbera* has a very high carapax and long antennule.

3. At 5 °C, *E. c. gibbera* had 32–45% higher drag than *E. longispina*. At 20 °C, the difference is 20–45%.

4. A mathematical model of swimming predicts that these differences in drag should result in 18–20 (at 5 °C) or 14–16 (at 20 °C) percentage lower speed for *E. c. gibbera* than for *E. longispina* if they use the same amount of energy in swimming.

5. The relative difference in drag or swimming speed between the two species was highest at low Reynolds number (i.e. low speed or low temperature). These results show that hydrodynamic costs of extreme morphology may increase with decreasing temperature.

6. The increased cost of morphological antipredator defence at low temperatures may be enlightening with regard to the role of temperature in the induction of cyclomorphic traits in zooplankton. This may be one explanation for why extreme forms of *E. c. gibbera* and some *Daphnia* are only found in the summer when water temperature is high.

Key-words: Cyclomorphosis, drag, energy expenditure, swimming, viscocity

Functional Ecology (2000) **14**, 380–387

Introduction

Cyclomorphosis, i.e. temporal, cyclic morphological changes that occur in plankton (Black & Slobodkin 1987), has been a matter of concern to limnologists for some time. Until the 1970s, the dominant hypothesis was that the phenomenon was due to buoyancy or sinking rate regulation. Since varying temperature leads to changed viscosity, which affects sinking speed, animals were thought to alter their morphology to regulate the sinking speed to a proper level. With Dodson (1974), the opinion changed towards invertebrate predation as the ultimate cause. Morphological structures such as spines and helmets in prey make it more difficult for an invertebrate predator to grab and handle its prey (Dodson 1974). Thus, when the densities of invertebrate predators increase, there is a selection for prey clones with well-developed defensive structures (Brock 1980; Kerfoot & Peterson 1980) or plastic clones with inducible antipredator traits (Gilbert 1966; Kreuger & Dodson 1981; Harvell 1990). The benefit of reduced predation is balanced by the costs of developing or maintaining the structure (Kerfoot 1977; Riessen 1984; Havel & Dodson 1987; Stenson 1987). When predator density declines, the benefits no longer compensate for the costs and the selection is for a more short-featured morphology. Although much evidence points towards predation being the ultimate cause (e.g. Hebert & Grewe 1985; Dodson 1989), in many studies invertebrate predators have not, by themselves, been a sufficient factor to induce morphological defences. Temperature has been shown to be an additional positive factor (Grant & Bayly 1981; Havel 1985) needed as a complementary (Hanazato 1991a) or the only influencing factor (Havel & Dodson 1985) in the induction of cyclomorphic

traits in some *Daphnia* species. The question is whether temperature is an alternative clue, indicating that the density of an invertebrate predator is going to change or if it directly influences the costs or benefits affecting the optimal size of a morphological defence.

The energy cost of swimming has been investigated for some zooplankton, mostly copepods. Most theoretically achieved results suggest that the swimming cost for small crustaceans is small (Vlymen 1970; Klyashtorin & Yarzhombek 1973). However, many of the simplifications in the models lead to underestimates of energy expenditure. Most models have not considered the effect of the propulsive non-steady velocity mode of swimming, which is probably of great importance. In a detailed study, Morris, Gust & Torres (1985) found the active to standard metabolism ratio of the marine copepod *Pleuromammia xipias* to range from 1·2 to 3 when swimming velocity ranged from 18 to 32 mm s^{-1} (or 2·9–5·2 body lengths s^{-1}).

The swimming speed of most herbivorous zooplankton is higher than should be expected if swimming was only a way of compensating for the sinking speed (Dodson 1996). As a high swimming speed also increases the encounter rate to ambush predators, such as the phantom midge larvae *Chaoborus*, there must be some benefit of swimming at such a high speed. This benefit may be that swimming speed in some way affects the food intake. The swimming speed may influence the food intake either by a direct relationship between swimming speed and food intake, as proposed by DeMott (1982) and Dodson, Hanazato & Gorski (1995), or by the time the animals have to spend on moving between food patches (Davis *et al.* 1991; Tiselius, Nielsen & Nielsen 1994). The ability to avoid predators in behavioural ways may also be affected by swimming speed (Jakobsen & Johnsen 1988).

All objects protruding from the surface of an animal affect the drag in some way; they may thus entail a hydrodynamic cost leading to lower food intake or greater energy cost for swimming for the animal. If these assumptions are correct, temperature may affect cyclomorphosis in another way. The swimming speed of small animals is reduced at low temperatures since water is more viscous (Podolsky & Emlet 1993). Hydrodynamic costs should thus be more pronounced when water temperature is low and morphological antipredator responses should not be possible to the same extent.

Bosminids have, in comparison with *Daphnia*, a steady, continuous mode of swimming that is quite fast, up to 9 mm s^{-1} (or 18 body lengths s^{-1}) (R. Lagergren, unpublished data). In the subgenus *Eubosmina*, there is great morphological variation and many morphs/species show cyclomorphosis (Hutchinson 1967; Hellsten & Stenson 1995). Much less is known about the adaptive significance of the varying traits in these species than in *Daphnia*. However, in Lake Östersjön, Sweden, *Eubosmina coregoni gibbera* (Schoedler) (hereafter called *gibbera*) has been shown to show cyclomorphosis in carapax height and antennule length (Fig. 1), with the most extreme form appearing when the cladoceran predator *Leptodora kindtii* Focke has its maximum density in the summer (Hellsten & Stenson 1995). The related species *E. longispina* (Leydig) (hereafter called *longispina*) is most abundant in spring and autumn. *Gibbera* has a better chance of survival in association with *Leptodora* owing to a higher escape ability than *longispina* (Hellsten, Lagergren & Stenson 1999), but *gibbera* swims slower than *longispina*, which can be explained by increased drag due to the high carapace and long antennule (Lagergren, Hellsten & Stenson 1997).

The aim of this study was to investigate the effect of temperature on hydrodynamic costs associated with morphological traits, using *longispina* and an extreme form of *gibbera* as models. The study is based on observations of balanced plastic models sinking in glycerine.

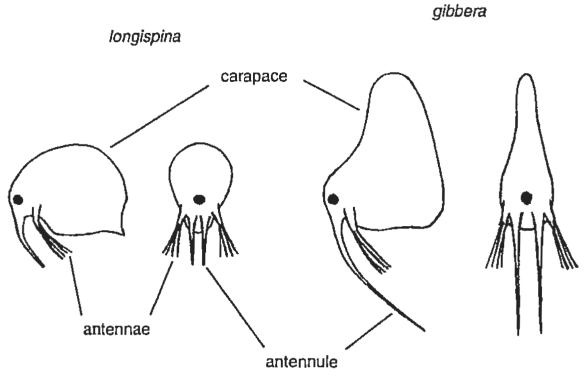

Fig. 1. The two species of *Bosmina*. The models used in the experiments were larger copies of these animals except the exclusion of the thrust producing antennae.

Materials and methods

There are two kinds of drag: pressure drag, which depends on inertial forces, and friction drag, which depends on viscous forces. The Reynolds number (*Re*), which is of major importance in fluid mechanics, is an estimate of the relative importance of these forces. The same *Re* guarantees that the flow patterns around the bodies are the same (Vogel 1994). However, the pushing of water by the antennae, which makes the animal move, leads to a somewhat different flow pattern around the real animal compared to the model, which has no moving appendages and 'swims' by gravity. This difference may influence quantitative analysis of drag but should probably not influence the models of the two *Eubosmina* species differently. Relative comparisons, of the kind in this study, are not likely to be affected significantly. The

Re is proportional to the length and speed of the object and inversely proportional to the kinematic viscosity. If the size of an object is scaled up, the *Re* can be held constant either by increasing the kinematic viscosity of the fluid or decreasing the speed. The intention of this experiment was to test enlarged models of these *Eubosmina* species in a more viscous fluid than their natural habitat, thus exposing the models to the same range of *Re* under which the animals normally live.

Eubosmina coregoni gibbera and *Eubosmina longispina* (Fig. 1) from Lake Östersjön (S. W. Sweden) collected in May (*longispina*) and August (*gibbera*) were chosen as model organisms for this study.

Drawings of individuals of the two species were made from different directions (top, side, under and back) by using a dissecting microscope to which a drawing tube was attached. This provided a good image of the three-dimensional structure of the animals. Models of each species were then sculpted in gypsum. Both models were given the same length (~27 mm) and volume (~5 ml). The lower body height of *longispina* was compensated by a greater thickness, a trait that differs significantly between the two species (R. Lagergren, unpublished data). These models were used to make silicone moulds. The experimental models were then cast in acrylate plastic in these moulds. For antennules, pieces of salmon ribs were used. The experimental models lacked antennae, since these are used for propulsion. To give the models the correct density and centre of gravity, they were weighed down with different amounts of lead. The models were loaded so they fell vertically, head first, towards the bottom under their own weight. During the fall, the body was oriented in the same way as in natural swimming with a maximum divergence of 30° in the medial plane.

The experiments were performed in an aquarium with a symmetrical octagonal bottom surface with a least radius of 20 cm and a height of 37 cm. The aquarium was large enough to avoid 'edge effects' (Vogel 1994) down to $Re = 0{\cdot}5$ according to the method of Schlichting (1979). It was filled with 48 dm^3 98·5% glycerine. The temperature was held constant at $21{\cdot}0 \pm 0{\cdot}1$ °C. At this concentration and temperature, the glycerine had a dynamic viscosity of 0·967 Pa s and a density of 1258 $\mathrm{kg\ m}^{-3}$. The viscosity was determined with a rotatory viscosimeter (Rheomat 15, Contraves AG, Zürich, Switzerland).

To compensate for the refractional problems arising when an object in an aquarium is observed from outside, the following procedure was performed. A ruler was held in the centre of the aquarium so as to be observed by a video camera. The graduation of the ruler was then transformed to the wall of the aquarium by marking the points that coincided with the graduation of the ruler when observed through the video camera.

A model was held just below the surface in the centre of the aquarium. It was dropped and allowed to fall towards the bottom. This was recorded by a Panasonic video camera that took 25 frames s^{-1}. The speed was measured in the interval from 20 to 30 cm from the surface, where there was neither acceleration nor retardation. This indicated that the terminal sinking velocity had been reached and that the gravitational force was exactly balanced by drag forces. Nine different masses, resulting in *Re* from about 0·5–10, were tested for each species. The mass of the models was estimated to the nearest 0·01 g and the volume to ±0·2 ml. To estimate the wetted surface area of the models, they were carefully covered with a non-elastic woven tape. The surface area of the model was determined by weighing the removed tape. The number of recorded drops per model mass was between 10 and 18. The highest numbers were for the heaviest models. As the camera only took 25 frames s^{-1}, it was difficult to measure the exact time at high fall speeds.

MODEL

The body drag as a function of speed for a *Eubosmina* of natural size, swimming in water, can be calculated as follows using the results of the experiment. When the terminal sinking velocity is reached, the gravitational force,

$$F_g = V(\rho_{ob} - \rho_{me})g, \qquad \text{eqn 1}$$

where F_g is the gravitational force, V is the volume of the object, ρ_{ob} is the density of the object, ρ_{me} is the density of the medium and g is the gravitational acceleration, is exactly balanced by the drag force:

$$D = 2^{-1}\rho_{me} S_{wa} U^2 C_{dwa} \qquad \text{eqn 2}$$

(Vogel 1994, page 89) where D is drag, S_{wa} is the wetted surface area of the object, U is speed, C_{dwa} is the so-called drag coefficient. C_{dwa} is dimensionless and a function only of the Reynolds number (*Re*). Definition of C_d according to wetted surface area is preferable because, at low *Re*, this area becomes most important for drag (Vogel 1994). If eqn 1 and eqn 2 are combined, C_{dwa} can be calculated. The Reynolds number is calculated by the equation

$$Re = \rho_{me} l U \eta^{-1}, \qquad \text{eqn 3}$$

where l is the greatest length of the object in the direction of flow, U is the velocity of the object and η is the dynamic viscosity of the fluid (Pa s). Knowing the *Re*, the speed that gives rise to the same *Re*, if a *Bosmina* at natural size moves in water, can be calculated using eqn 3. Then the drag of the *Bosmina* moving at that speed can be calculated by inserting the achieved C_{dwa} and U-values together with the other known parameters in eqn 2. As the shape is unaltered, the area is proportional to body length squared and the S_{wa} at natural size is:

$$S_{ns} = S_{mod} l_{ns}^2 / l_{mod}. \qquad \text{eqn 4}$$

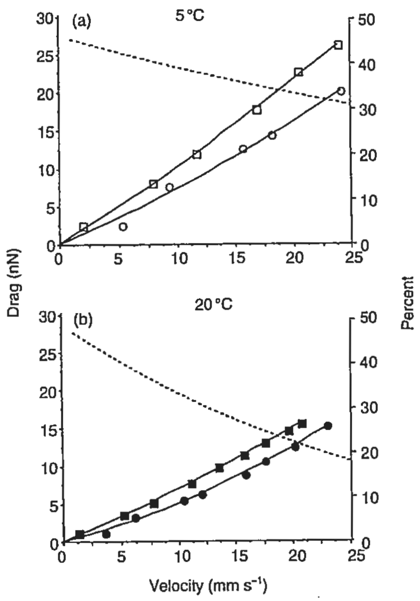

Fig. 2. Left *Y*-axis is drag against velocity at 5 °C (a) and 20 °C (b) calculated for *Bosmina* at natural size (□, ■ *gibbera* and ○, ● *longispina*). An expression of the form $D = k_1U + k_2U^2$ has been calculated by the least square method for each temperature and species. (As Reynolds numbers over 8, at 5 °C, imply speeds over 25 mm s^{-1}, which is unrealistic, the three highest measurements for each species have been excluded from panel a and in the analysis of the expressions at 5 °C.) The equations are: *longispina* 5 °C – $D = 6{\cdot}58 \times 10^{-6}U + 0{\cdot}074 \times 10^{-3}U^2$; *gibbera* 5 °C – $D = 9{\cdot}63 \times 10^{-6}U + 0{\cdot}057 \times 10^{-3}U^2$; *longispina* 20 °C – $D = 4{\cdot}29 \times 10^{-6}U + 0{\cdot}091 \times 10^{-3}U^2$; *gibbera* 20 °C – $D = 6{\cdot}40 \times 10^{-6}U + 0{\cdot}054 \times 10^{-3}U^2$. On the right *Y*-axis (the dotted line) is the percentage extra drag, experienced by *gibbera* compared with *longispina*, as a function of velocity.

The subscripts refer to natural size (ns) and model (mod). The body length at natural size (l_{ns}) has been set to 0·5 mm which is close to the population mean of the two *Bosmina* populations in Lake Östersjön (Hellsten & Stenson 1995). As some parameters vary with the temperature (η in eqn 3 and ρ_{me} in eqns 2 and 3), different temperatures yield different values of U and D. Calculations were done for 5 and 20 °C; the result is shown in Fig. 2. A curve of the form

$$D = k_1U + k_2U^2, \qquad \text{eqn 5}$$

where k_1 and k_2 are constants, was fitted to the relationship between velocity and body drag for each species and temperature. This equation gave good fit to the data ($r^2 > 0{\cdot}99$).

The equations for drag *vs* swimming speed can then be used to determine speed *vs* time, the net energy cost and the distance travelled during a single antennae stroke performed by these *Eubosmina* species. However, eqn 5 is valid only in a steady flow. When a body accelerates, an additional force, the so-called added mass or unsteady force, arises because of the reaction of fluids to acceleration. This unsteady force, G, can be calculated using:

$$G = \alpha\rho_{me}V\,\mathrm{d}U/\mathrm{d}t, \qquad \text{eqn 6}$$

where α is the added-mass coefficient, a shape-dependent factor that is close to 1·0 (Daniel 1984). A *Bosmina* uses its antennae for swimming and an antennae beat resembles a human breaststroke (Zaret & Kerfoot 1980). The forward directed force (F_f) during an antennae stroke is thus supposed to be proportional to the sine of the angle between the antennae and the direction of swimming. To simplify, we assume that the force developed is constant throughout the power stroke. F_f, during the antennae stroke, thus varies as

$$F_f = F_{max}\sin\{[180° - (\alpha_s + \alpha_e)]d^{-1}t + \alpha_s\}, \qquad \text{eqn 7}$$

where F_{max} is the maximal force (when the antennae pass at 90° from the body), t is time, α_s and α_e are the angles between the antennae and the direction of swimming at the beginning and end of the sequence, respectively, and d is the duration of the stroke (Fig. 3). From eqn 5, eqn 6 and eqn 7, together with the following physical relationships:

$$F = ma, \qquad \text{eqn 8}$$

$$a = \mathrm{d}U/\mathrm{d}t, \qquad \text{eqn 9}$$

$$F = F_f - D - G, \qquad \text{eqn 10}$$

the following differential equation is acquired:

$$\frac{\mathrm{d}U_1}{\mathrm{d}t} = \frac{F_{max}\sin\{[180° - (a_s + a_e)]d^{-1}t + a_s\} - k_1U - k_2U^2}{m + \rho_{me}V}$$

$$U_1(0) = 0. \qquad \text{eqn 11}$$

Expression 11 is Newton's second law of motion, eqn 8, with the right side of the equation being the forward force available (force developed minus drag forces) divided by body mass, m, plus added mass, $\rho_{me}V$. If eqn 11 is solved in the time interval from 0 to d, the curve of velocity as a function of time $U_1(t)$ for the acceleration phase is obtained (Fig. 4). For the recovery part of the cycle ($F_f = 0$) the differential equation is

$$\frac{\mathrm{d}U_2}{\mathrm{d}t} = \frac{-k_1U - k_2U^2}{m + \rho_{me}V} \quad U_2(0) = U_1(d), \qquad \text{eqn 12}$$

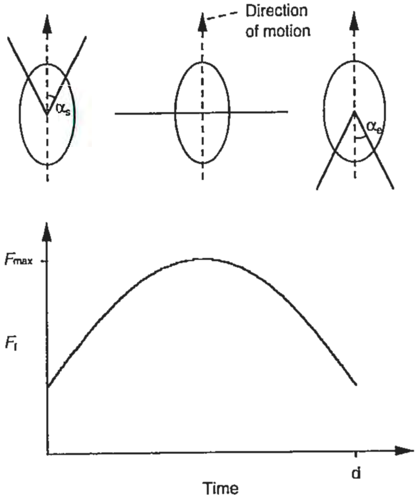

Fig. 3. Antennae positions and resulting forward directed force (F_f) during an antennae stroke. If F_f is supposed to be proportional to sin α, the expression becomes $F_f = F_{max}\sin\{[180° - (\alpha_s + \alpha_e)]d^{-1}t + \alpha_s\}$ where F_{max} is the maximum force (when $\alpha = 90°$), α_s is the angle at the beginning of the stroke, α_e is the angle when the stroke is completed and d is the duration of the stroke. α_s and α_e have been estimated to 20° from Zaret & Kerfoot (1980) based on observations on *Bosmina longirostris*. The graph is valid only if the stroke velocity and the forward velocity of the animal are constant throughout the entire power stroke. Neither stroke nor forward velocity is constant, but even if this is a simplification, the function considers the propulsive non-steady mode of swimming of a *Bosmina* reasonably well.

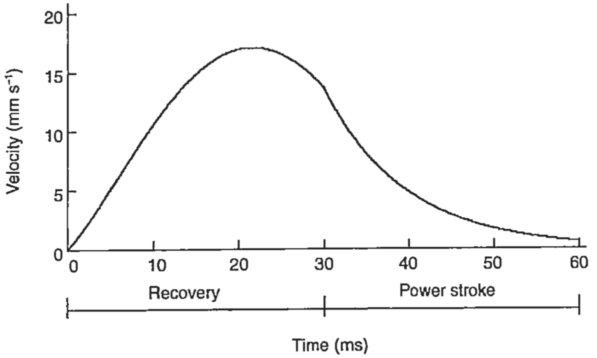

Fig. 4. Model prediction of velocity of the animal during power stroke and recovery. The example is for *longispina* at 5 °C and the net energy cost of this sequence, due to body drag and acceleration, is 46·5 pJ.

where $U_1(d)$ is the body speed reached after the antennae stroke. When eqn 12 is solved, the second part of Fig. 4 is obtained. The distance reached in one stroke (L) is

$$L = \int_0^d U_1(t)\mathrm{d}t + \int_d^{d+r} U_2(t)\mathrm{d}t, \qquad \text{eqn 13}$$

where r is the time of the recovery part. The amount of energy needed (E) is

$$E = \int_0^d U_1(t)F_f(t)\mathrm{d}t. \qquad \text{eqn 14}$$

The model is then used to calculate distance travelled (L) and energy expenditure (E) for the two species at 5 and 20 °C by varying the value of F_{max}. The duration of the power stroke ($d = 30$ ms), recovery stroke ($r = 30$ ms) and the angles of antennae at the end and beginning of the stroke ($\alpha_s = \alpha_e = 20°$) have been taken from Zaret & Kerfoot (1980) based on observations on *Bosmina longirostris*. The body mass was estimated to 33 µg by

$$m = \rho l_{ns}^3 l_{mod}^{-3} V_{mod} \qquad \text{eqn 15}$$

($\rho = 1050$ kg m^{-3}, $l_{ns} = 0{\cdot}5$ mm, $l_{mod} = 27$ mm and $V_{mod} = 5 \times 10^{-6}$ m^3). Differential equations and integrals were calculated with Mathcad plus 6·0 professional.

Results

The standard errors of the terminal sinking speed measurements were, in all cases, less than 0·5% of the sinking speed. In the C_{dwa} *vs* Re plot (Fig. 5), the curve-fit equation

$$C_{dwa} = \frac{1}{4}\left(\frac{24}{Re} + \frac{6}{1 + Re^{1/2}} + 0{\cdot}4\right), \qquad (16)$$

for a sphere, given by White (1974), is included. (The original equation was divided by a factor four, because the C_d was given for frontal area which is one-quarter of the surface area of a sphere.) Our data show that this equation gives a good prediction of the C_d-values for Re from 4 to 12. For lower Re, the achieved C_d values are somewhat higher.

The calculated values of body drag as a function of speed at natural size for the two species at water temperatures of 5 and 20 °C are shown in Fig. 2. The drag is clearly higher for *gibbera* than for *longispina* at any speed and temperature in the range measured. The second degree term is higher for *longispina* than for *gibbera*, which means that the relative difference in drag between the two species decreases with increased speed as indicated in Fig. 2. The drag is greater at 5 °C than at 20 °C at all speeds, owing to the higher viscosity. Lowering the temperature from 20 to 5 °C leads to an increase in drag of 32–50% for *longispina* and 44–50% for *gibbera*.

The solutions of the differential equations (eqns 13 and 14) give the speed as a function of time during an antennae stroke (Fig. 4). The agreement with the observed speed *vs* time graph in the closely related species *B. longirostris* (Zaret & Kerfoot 1980) is quite satisfactory.

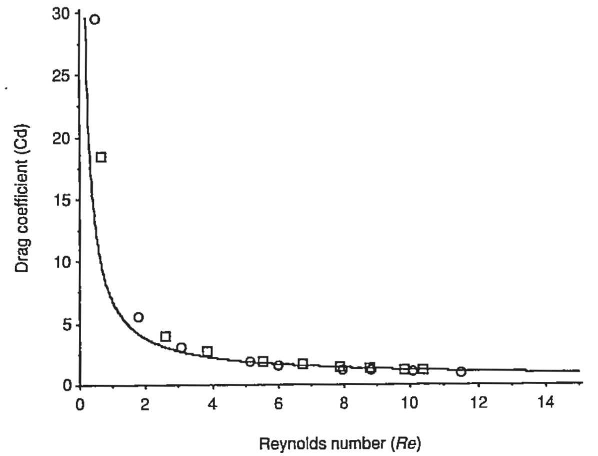

Fig. 5. Drag coefficients (based on wetted area) and Reynolds numbers calculated from the model experiment. The squares represent *gibbera* and the circles *longispina*. The solid line is the curve-fit equation (eqn 16) given by White (1974).

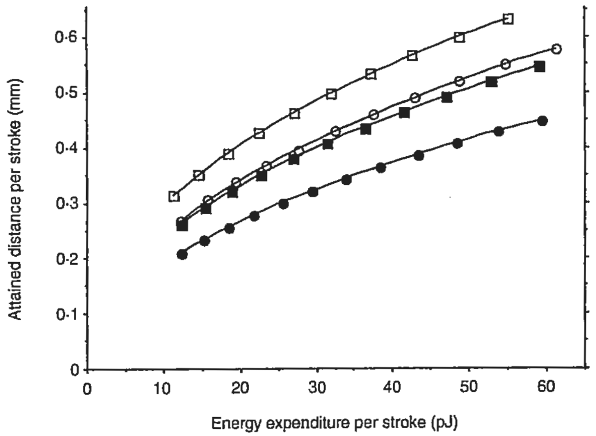

Fig. 6. Model prediction of distance travelled per antennae stroke as a function of work done (due to body drag and acceleration) for *gibbera* (circles) and *longispina* (squares) at 5 °C (closed symbols) and 20 °C (open symbols).

The distance travelled as a function of net energy expended on each swimming stroke, as simulated by the model, is shown in Fig. 6. The figure shows that *longispina* swimming at 5 °C and *gibbera* at 20 °C are quite close to each other, whereas *gibbera* at 5 °C reaches 20–23% shorter and *longispina* at 20 °C reaches 17–20% longer on each stroke using the same amount of energy on each stroke. The temperature affected *gibbera* to a greater extent than *longispina*, the lowering of temperature from 20 °C to 5 °C should reduce the distance travelled per antennae stroke by 20–22% for *gibbera* but only 16–19% for *longispina*.

Discussion

Drag calculations of the swimming of small crustaceans are fraught with difficulties. Since their Reynolds number (*Re*) is in the transitional range from viscous to pressure drag and the speed varies all the time, no equations are reliable for this purpose. At *Re* below 1, viscous drag due to the exposure of body surface is of greatest significance for the total body drag (Purcell 1977; Vogel 1994). The spheroid shape is the one that minimizes drag in this situation. The cost of protuberances such as spines is low at low *Re* because they have a very small surface area in comparison to the animal itself. On the other hand, traits such as enlarged helmets and carapaces increase the body surface to a greater extent and may thus significantly affect the drag. At higher *Re*, a streamlined body becomes more efficient and the advantage of a small surface area diminishes.

The results of this study show that the difference in drag between *longispina* and *gibbera* decreases as *Re* increases (greater speed and/or higher temperature). This can be explained by *gibbera*, in spite of its extreme morphology, being more streamlined than *longispina*. The advantage of the small surface area, associated with the more spherical shape of *longispina*, decreases as *Re* increases (Fig. 2), a result that is in concordance with hydrodynamic theory. The difference in drag between the two species is thus dependent on which *Re* you choose to examine. Only to look at the *Re* given by the mean speed may thus be misleading. This indicates the importance of calculating the drag for varying *Re* to enable integration of the drag over the entire stroke cycle. Although some simplifications occur in our analysis, e.g. the motion of the antennae during the recovery phase and the force function (Fig. 3), it considers the nature of the propulsive non-steady mode of swimming and integrates the drag over all *Re* to which the animal is exposed during swimming. The difference observed in mean swimming speed between *gibbera* and *longispina* at 21°C was about 40% (Lagergren *et al.* 1997). According to our model, the difference in mean speed attained (i.e. distance achieved per stroke times beat frequency), if the same amount of energy and the same beat frequency are used, is about 18–20% at 5 °C and 15–17% at 20 °C.

Temperature affects the drag to a greater extent in *gibbera* than in *longispina*. The great disadvantage of the extreme morphology of *gibbbera* at low temperature may at least partly explain why it is not present in early spring and disappears in late autumn when the water has a low temperature and high viscosity (Hellsten & Stenson 1995). Water temperature as a good predictor of the degree of expression of morphological antipredator defences has been recorded by Luecke & Litt (1987). They proposed low activity of the predator, *Chaoborus*, at low temperatures as being the cause of a better prediction of neck teeth

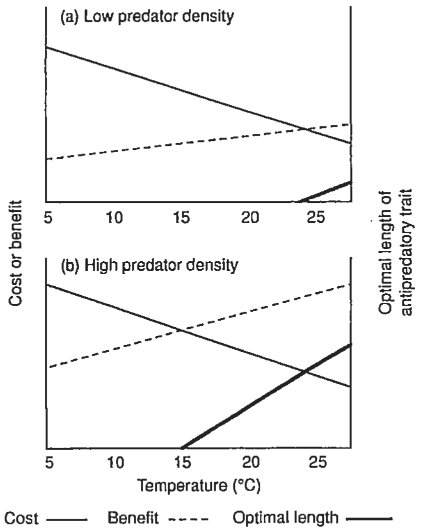

Fig. 7. Model of the optimal size of a hydrodynamically costly antipredator defence. The benefit of the defence increases with increasing temperature since the activity of predators increases with increasing temperature. The cost decreases with increasing temperature since the drag decreases with increasing temperature. Optimal size of the antipredator trait is supposed to be proportional to the difference between benefit and cost.

production in *Daphnia pulicaria*, taking into account both *Chaoborus* density and temperature. This may influence the benefit of a morphological defence but more research is needed before the relative importance of these two mechanisms can be assessed. A hypothetical cost–benefit model of the influence of temperature on the optimal expression of a hydrodynamically costly antipredator defence, in which both of these mechanisms are considered, is shown in Fig. 7. The model predicts a temperature where the morphological defence begins to be beneficial and a gradual increase in the degree of development with increase in temperature. At higher predator density, the defence is beneficial at lower temperature.

The development of morphological antipredator traits may also be affected by food density (i.e. density of phytoplankton particles). The model by Riessen (1992), assuming a cost in the form of increased time to maturity, predicts that the threshold value of predator density where morphologically defended morphs of *Daphnia pulex* have a greater rate of increase than undefended morphs should be lower at low food concentrations. The prediction based on this model is thus a negative correlation between food density and the degree of development of morphological antipredator traits. However, this kind of cost has been questioned as a direct cost and may instead be due to induced life-history shifts (Tollrian 1995). On the other hand, if a morphological antipredator trait has a hydrodynamic cost, which affects food intake, the cost should be most pronounced at low food concentrations since the lower the food concentration, the greater the velocity needed to catch food or to swim between food patches, resulting in greater cost. This predicts a positive relationship between food density and defences, particularly in species where the size of morphological defences are large relative to the size of the body. In *Daphnia carinata*, a species that develops large head crests in response to notonectid predators, food concentration strongly affected crest size (Benzie 1991). In other *Daphnia* species with smaller relative size of antipredator traits, food concentration had only a minor effect (Hanazato 1991b) or no effect (Tollrian 1995) on crest or spine development. The extreme *Eubosmina* morphs, *thersites* and *gibbera*, are primarily found in eutrophic lakes (Hofmann 1996; J. A. E. Stenson, personal observation), a circumstance that may depend on the fact that the cost of a hydrodynamic handicap is too great in lakes with low food availability.

In conclusion, this study has shown that the degree of morphological difference that exists between these *Eubosmina* species leads to significant differences in drag resistance and swimming speed. Temperature had a significant effect on the relative difference in drag between the two species. The extreme morphology of *gibbera* is most unprofitable in cold water of high viscosity where the need for food is accentuated. We suggest that water temperature may in this way affect the trade-off between the costs and benefits associated with morphological antipredator defence.

Acknowledgements

We thank Åke Norberg, Jens-Uwe Friemann and anonymous referees for valuable criticism and comments on the manuscript. The study was financially supported by grants from Collianders stiftelse (RL), Hierta Retzius (RL), Kungl. Hvitfeldtska (RL), Wilhelm, Martina Lundgrens fond (RL, JAES) and the Swedish Natural Science Research Council (JAES).

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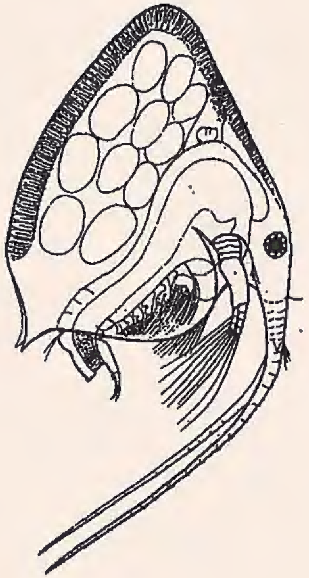
Received 28 April 1999; revised 15 December 1999; accepted 16 December 1999



V

Clutch size variation and morphology in a cyclomorphic *Bosmina* population

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Abstract: Clutch size, cyclomorphosis and allomometric growth were analysed in a population of the humpbacked *Bosmina (E.) coregoni* var. *gibbera*. This species shows cyclomorphosis in two traits, antennule length, a likely defence against invertebrate predators, and body height. As the size of the brood chamber can be affected by the height cyclomorphosis, the variation in height might lead to seasonally varying clutch sizes. Individuals with long antennule and extreme body height may pay a cost in terms of decreased reproductive capacity. I tested this hypothesis by comparing the seasonal variation in clutch size with that in body size and shape.

Relative growth rate and size of antennule and body height increased from mid May to August. Body height and, at times, antennule length showed positive allometry being relatively larger in large individuals which means . The of positive allometry in antennule length coincides with high population densities of the predatory cladoceran *Leptodora kindtii*. Clutch size shows a decreases from spring to late summer, whivh contradicts the hypothesis that the cyclomorphosis in height is caused by a seasonal variation in reproductive demand. However, within dates antennule length was negatively related and body height positively related to clutch size. I conclude that the long antennule imposes a cost which reduces the reproductive capacity. The hypothesis that carapace cyclomorphosis is driven by seasonally varying clutch sizes is rejected.

Key words: Zooplankton, cyclomorphosis, clutch size, cost

Introduction

A great number of explanations for cyclomorphosis (the yearly cyclic changes in zooplankton morphology) have been suggested in the last decades (see Jacobs, 1987 for a review). Today most evidence points to predation as the ultimate cause (Dodson, 1974; Dodson, 1989b; De Stasio *et al.*, 1990). Because the strike and handling efficiencies of some invertebrate predators are strongly affected by small differences in prey morphology, enlargements of certain morphological traits are selected for when these predators become abundant (Dodson, 1974). When predation pressure declines, costs, associated with the defensive structure select for a reduction of the size of the trait (Kerfoot, 1977; Harvell, 1984; Reissen, 1984).

Some of the most spectacular examples of cyclomorphosis are found among subspecies (or forms) of the cladoceran *Bosmina (E.) coregoni*. Whereas foremost antennule and mucro show cyclomorphosis in *Bosmina longirostris* (Hutchinson, 1967; Kerfoot, 1975b; Black, 1980; Hanazato, 1992) and *Bosmina (E.) longispina* (Black and Hairston, 1983; De Stasio *et al.*, 1990), also the entire body profile varies seasonally in some forms of *Bosmina coregoni*, e.g. *gibbera* and *thersites* (Hutchinson, 1967; Hellsten and Stenson, 1995). It has been shown in experiments that the high carapace of these animals implies a cost in terms of increased drag (Lagergren *et al.*, 1997), but the benefit of the trait is not clear.

The form *B. (E.) coregoni gibbera* (hereafter referred to as *gibbera*) has experimentally been found to survive significantly better than *B. (E.) longispina*, which have normal low carapace, when exposed to the cladoceran predator *Leptodora kindtii* (Hellsten *et al.*, 1999). However, another discriminating trait, the long antennule, may have a greater impact on prey vulnerability. This can be concluded since *B. (E.) c. retro-extensa*, a morph with equally long antennule but no hump, survived equally well as *gibbera* during *Leptodora* predation

(Hellsten *et al.*, 1999). Lagergren and Stenson (2000) showed that the smell from *Leptodora* induces the development of longer antennule as well as higher carapace but if the high carapace also protects against invertebrate predators has not been shown.

Another possible benefit of a higher carapace is that the space of the brood chamber may be enlarged. In cladocerans, brood chamber space can restrict clutch size, especially during high food conditions (Kerfoot, 1974). Increased brood chamber volume might be a response to good food conditions when clutch sizes are large or to high densities of invertebrate predators when neonates are born big (Stibor, 1992) or with large morphological defences (Kreuger and Dodson, 1981). For helmeted *Daphnia* species a reduced maximum clutch size due to a reduced brood chamber volume has been proposed (Jacobs, 1967) and supported by field data on *D. retrocurva* (Reissen 1984). However, no such cost could be found in *D. cucullata* (Tollrian, 1991). If food conditions or the size of the neonates vary seasonally and increased carapace height incurs costs, this might favour evolution of plastic variation in carapace height. This alternative hypotheses has not been tested.

On the other hand, costs for body height and antennule length may reduce reproductive capacity. In *B. longirostris*, individuals with longer antennule has been shown to lay fewer eggs (Kerfoot, 1977). If this is the case also for individuals with high carapace and long antennule in *gibbera* has not been shown.

The aim of this study is to test if the seasonal variation in height of *gibbera* is correlated with changes in clutch size, as predicted from the hypothesis that cyclomorphosis in carapace height should be caused by varying demands of space in the brood chamber. This was done by comparing the seasonal patterns of clutch size and morphology in field sampled animals. The alternative hypothesis that great height and long antennule lead to reduced reproductive capability was tested by regressions with brood size within each date and length class. I also describe the cyclomorphosis in height and antennule length by analysis of allometries.

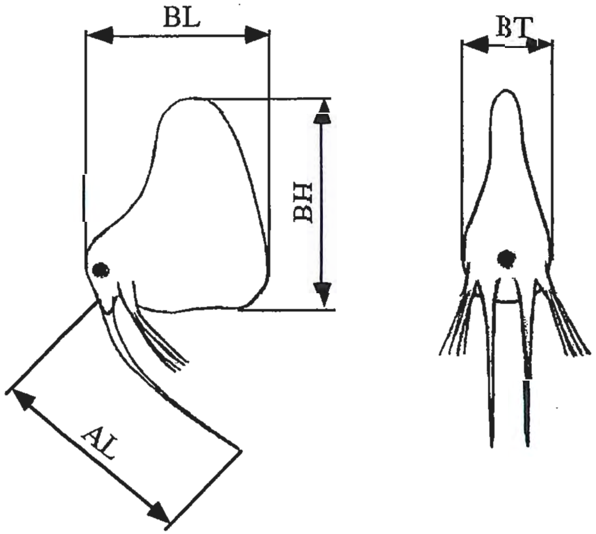

Fig. 1. The summer form of *E. c. gibbera* showing measured features, body length (BL), body height (BH), body thickness (BT) and antennule length (AL).

Methods

The *Bosmina* population of Lake Östersjön, SW Sweden (57° 93' N, 12° 79' E) was investigated during two seasons, 1996 and 1999. The lake is described in more detail in Hellsten and Stenson (1995). Samples were taken at four occasions in 1996 (13/5, 29/5, 10/6 and 25/6) and 1999 (10/5, 2/6, 18/7 and 20/8). Animals were collected by vertical hauls from bottom to surface with a plankton net (diameter 40 cm, mesh size 200 µm) and were kept alive in 20 litre tanks. After two hours of transportation to the laboratory, the animals were kept at 10 °C. Single individuals were picked out randomly and fixed in a droplet of 70 % ethanol. This procedure was used to exclude the risk of egg dropping when animals were conserved. Measurements of morphological traits, egg number and egg length and diameter (of one randomly chosen egg in each clutch) were done in a binocular microscope on 20-52 pregnant females per date. The measured traits were body length (BL) body height (BH) and antennule length (AL) (Figure 1). The precision in measurements was ±3 µm for body traits and ±1.5 µm for egg length and egg diameter. Eggs were divided in four developmental stages. Stages one to four corresponds to stages 1, 2-4, 5-6 and 7-8 respectively according to Green (1956). All eggs were counted within 36 hours after the animals were sampled from the lake.

In 1999, five samples at each date were also taken with a small net (diameter 15 cm, mesh 100 µm) for quantitative analysis of population sizes of Bosminid species and potential invertebrate predators. These samples were concerved in Lugol's solution. From these samples the traits BL, AL, BH and body thickness (BT) were measured on about 50 randomly selected individuals of *gibbera* to supplement the data set for allometric analysis. In May, too few individuals of *gibbera* were found in these samples so allometric analysis were carried out only on animals picked from the tanks aimed for clutch size analysis.

Animals were divided into size classes before statistical analysis. Cyclomorphic patterns were analyses with animals divided into 25 µm intervals from 250 µm and clutch size analyses were done with pregnant animals divided into 25 µm intervals from 375 µm.

Allometry between BL and AL and BL and BH was calculated by regression on log transformed data. In order not to bias the result because of the size distributions, which were quite different at different dates, the means of body length, body height and antennule length of each size class were used as points in the analysis. The regression had the form $Y = k X^b$ where the exponent b is the relative growth of trait Y and X is body length.

As collinearity, i.e. strong correlation between x-varables (James and McCulloch 1990), was a great problem with the data set, the test for costs in terms of lower clutch sizes associated with the antipredator traits AL and BH was made in a somewhat unconventional way. Animals were divided in 25 µm BL size class intervals and for each date and size class the regression between AL/BL (or BH/BL) and clutch size was calculated. The null hypothesis, that only chance decides if these regressions happen to be positive or negative, was then tested by comparing the number of positive and negative slopes of the regression lines by sign test. Some investigations have found indications that food conditions may affect the extent of cost (Kerfoot, 1977). The data was therefore analysed for two periods 10/5-2/6 and 10/6-20/8 as well as the whole period. This separates the data after high and low clutch sizes as well as negative and positive allometry of AL in the first and second groups respectively.

Results

Cyclomorphosis

The seasonal variation in the traits AL and BH are shown in Fig. 2. Both traits vary seasonally in all size classes ($p<0.05$, ANOVA, Bonferroni adjusted p-values (Sokal and Rohlf 1995)). Generally, AL is shorter in May-June and longer in July-August while the differences are small between May and June and between July and August. The BH is lowest in August for the 300-350 and 350-400 size classes, but for larger size classes August BH is significantly higher than in May to June and of the same height or higher than in July. The difference between dates in the smallest size class was much greater and consistent for AL than for BH.

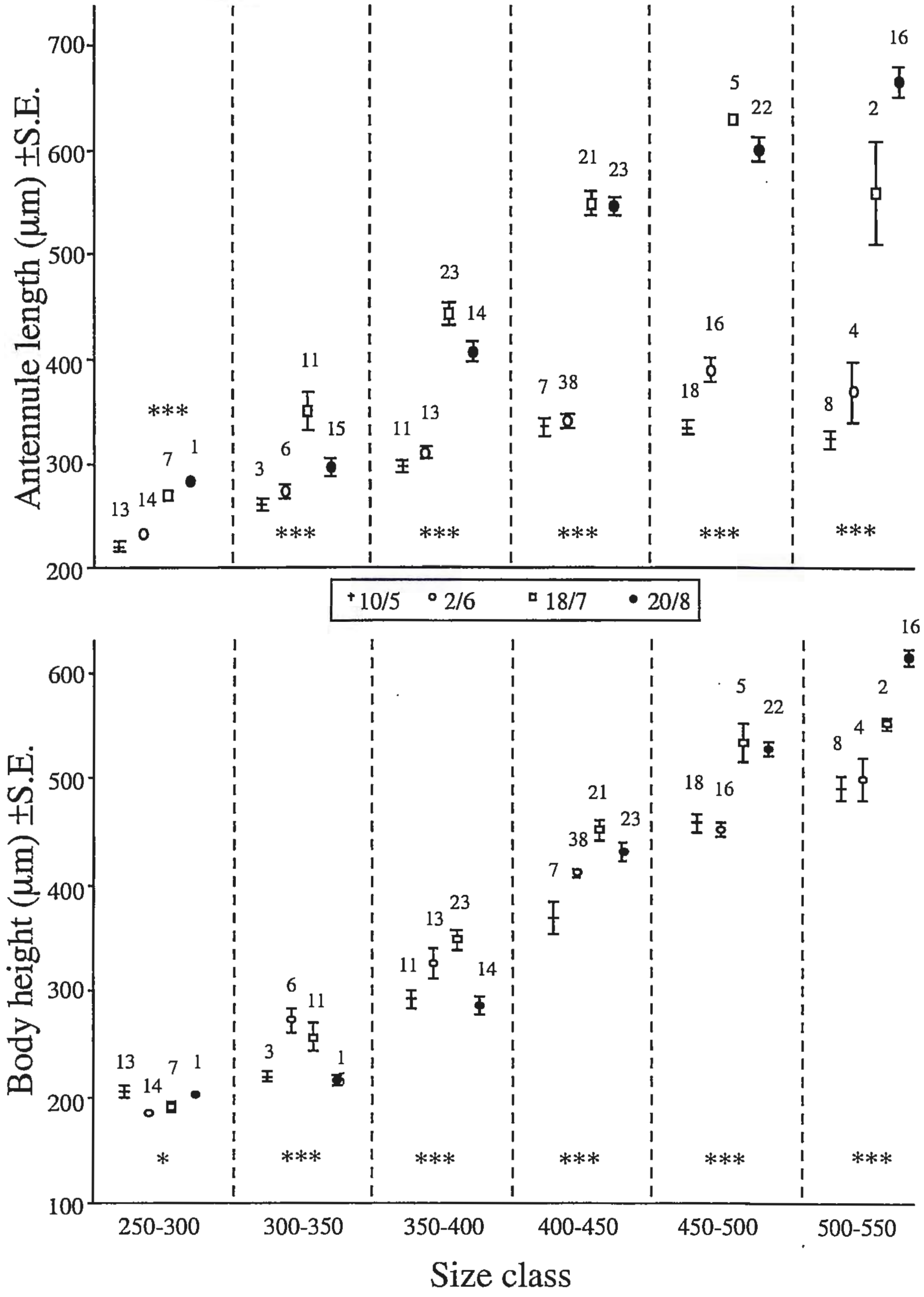

Fig. 2. Seasonal variation of antennule length and body height in Lake Östersjön 1999. Data was divided in 50 µm intervals and differences between dates were tested with one way ANOVA for each size class. Sample sizes and the significance of the ANOVA tests (*=$p<0.05$; ***=$p<0.001$) are noted.

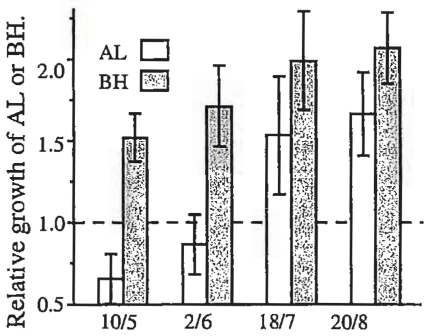

Fig. 3. Seasonal changes in relative growth of AL and BH in Lake Östersjön in 1999. The error bars represents ±95 % confidence intervals.

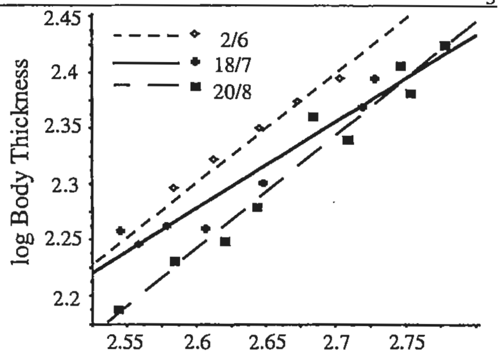

Fig. 4. Seasonal changes of body thickness. Each point represents the mean of BL and BT for one size class. The difference between regression lines is significant ($p<0.0001$, ANCOVA).

Allometry

The allometry of AL is negative in the spring and beginning of June but then changes to strong positive allometry (Fig. 3). The positive allometries show that carapace always grows faster in height than in length, but the relative growth increases from 1.5 in May to about 2.0 in July and August. The third trait, body thickness, also varies between dates, the animals being significantly thinner in July and August than in the beginning of June ($p<0.0001$, ANCOVA) (in May to few animals were measured to be included) (Fig. 4).

Seasonal variation in clutch size

Clutch sizes did not follow the seasonal pattern of BH variation, which should be expected if carapace height cyclomorphosis was caused by seasonally varying demand of brood chamber volume. In fact, the two variables show a clear inverse relationship for all size classes (Fig. 5). Egg sizes did not vary in concert with clutch sizes or cyclomorphic changes. Eggs were smallest in the summer and larger in both spring and late summer (Fig. 6).

Costs

As shown in Table I, no sign of cost of longer AL could be detected in any of the three groups in this analysis. High carapace, contrary to the cost hypothesis and the BH- clutch size seasonal patterns, showed a significant positive relationship with clutch sizes (Table II). The relationship was clearest in the late period ($p=0.004$) and only marginally significant in May to early June ($p=0.066$). This positive relationship between BH and clutch sizes within dates and size class, may reflect that brood chamber volume really is larger for a higher animal, if compared to an individual with a lower carapace but of the same length. However, it is not sure that these animals are of the same age or instar. If animals had to reduce their speed of length growth if they grow high this pattern should be expected. The cyclomorphosis and variation in BH/BL may rather be a change in proportions changing both BH and BL than just variation in the height of the carapace, thus BL*BH (or if dimensions should be conserved $(BL*BH)^{1/2}$) may be a better measure of size than BL. If the AL/BL-clutch size examination is reanalysed using animals divided in $(BL*BH)^{1/2}$ size classes a significantly higher proportion of regressions are negative than positive in the early period ($p=0.040$) indicating a cost of long antennule (Table III). In the late period no such relationship existed.

Predators

Quantitative sampling of predators were performed only in 1999. The dominating invertebrate predator was the large cladoceran, *Leptodora kindtii* which showed a strong population increase from May to July-August (Table IV). Both the abundance of *Leptodora* ($p=0.047$) and temperature ($p=0.029$) significantly contributed to the variation in relative growth of AL ($R^2=0.99$, $p=0.024$, $n=4$, multiple regression).

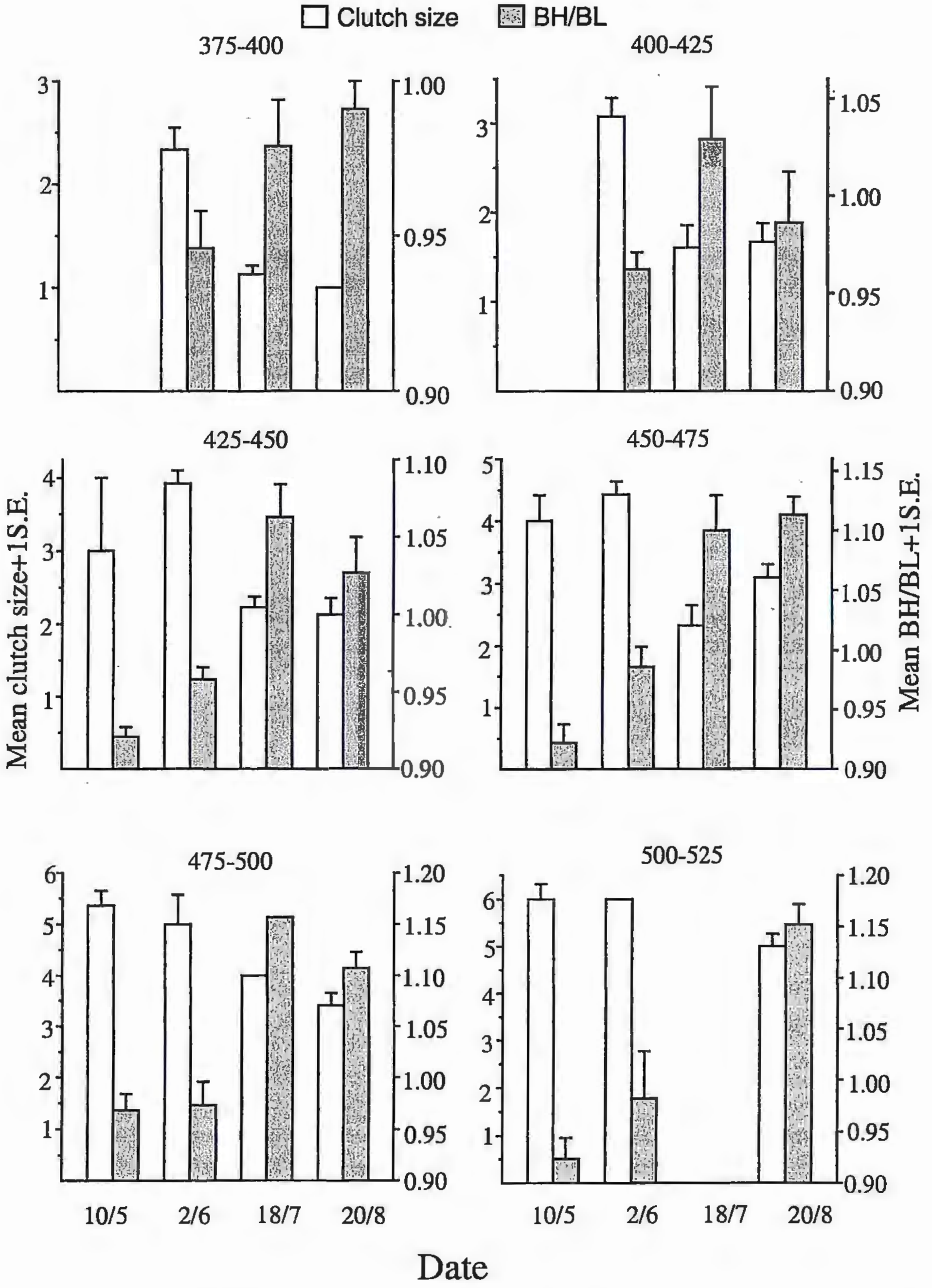

Fig. 5. The seasonal patterns of clutch size and relative carapace height for six size classes 1999. For all size intervals, clutch sizes are decreasing when carapace height increases.

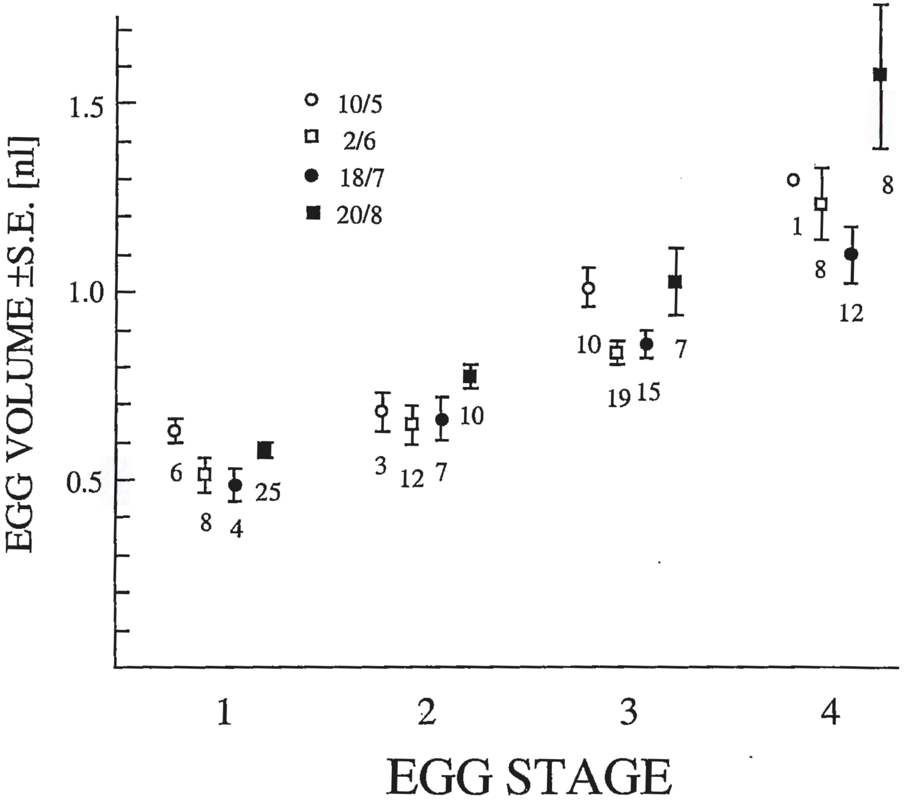

Fig. 6. Seasonal variation in egg volume for developmental stages 1 to 4. Egg volume was approximated to the volume of a spheroid (π EL ED^2/6).

Table I. Regressions of clutch size as a function of AL/BL separately calculated for each BL-size class and date. (Regressions with lower p-value than 0.5 have been excluded.) The H_0-hypothesis no relationship, equal probability of a negative as positive slopes of regression lines, has been tested with two-tailed sign test. A significant p-value means that the number of positive and negative regressions are more unevenly distributed than expected by chance.

Regression slopes	Number of regressions		
	all dates	early period (10/5-2/6)	late period (10/6-20/8)
neg	12	8	4
pos	10	4	6
	p>0.5	p=0.39	p>0.5

Table II. Same as Table I but for regressions of clutch size against BH/BL instead of AL/BL.

Regression slopes	Number of regressions all dates	early period (10/5-2/6)	late period (10/6-20/8)
neg	3	2	1
pos	21	9	12
	p<0.001	p=0.066	p=0.004

Table III. Same as Table I but with size classes divided in $(BL*BH)^{1/2}$ intervals.

Regression slopes	Number of regressions all dates	early period (10/5-2/6)	late period (10/6-20/8)
neg	12	8	4
pos	6	1	5
	p=0.24	p=0.040	p>0.5

Table IV. Surface water temperature and densities of potential invertebrate predators in Lake Östersjön 1999.

Datum	Temp. (°C)	*Leptodora kindtii* (ind/m^3)	*Chaoborus* sp. (ind/m^3)	Cycl. cop. >1.5 mm (ind/m^3)	Cal. cop. >1.5 mm (ind/m^3)
10/5	9	2.4	0	7.9	9.5
2/6	13.5	1.1	0	0	0
18/7	22	11.0	0	0	0
20/8	19	28.3	5.0	1.4	9.9

Discussion

Cyclomorphosis and clutch size

The seasonal patterns of BH and clutch size clearly reject the hypothesis that cyclomorphosis in carapace height is caused by a demand for larger volume of the brood chamber. The increase in BH from late spring to summer was not associated with larger clutches (Figure 5). In fact, in most size classes mean egg numbers were fewer in the summer. However, when the regressions of clutch size as a function of relative body height were analysed for each date and size class separately, significantly more correlations were positive (Table III). This result could be taken to indicate a reproductive benefit of wearing a higher carapace. However, an alternative explanation is that the alteration in proportions of the carapace leads to a shorter BL at a given age or instar, for an individual with a high carapace. Thus "higher" animals may also be older than "lower" animals of the same BL with which they are compared. The decline in clutch sizes during summer may be due to poorer food conditions caused by competition and/or selection from visually feeding fish. Fishes select against females with large clutches which increase the pigmented area and thus the visual size of the female (Svensson 1995). Egg sizes also showed seasonal variation (Fig. 6). Similar cyclic changes in egg size have been observed in *Bosmina longirostris* and may be an adaptation to fish predation as neonates of small size have an advantage during periods of intensive fish predation (Kerfoot, 1974).

Longer antennule were associated with significantly smaller clutch sizes in spring but not in the summer (Table III). Individuals that invest much in predator defence may therefore pay a cost in form of reduced reproduction. Higher costs at richer food conditions was suggested in a theoretical model by Reissen (1992) but was not supported by laboratory studies (Tollrian, 1995). The reason for costs to be more pronounced in the early period may be that optimal clutch sizes are reduced during periods of high risk of fish predation. If animals voluntarily reproduce below their maximum reproductive capacity costs should not be so accentuated. During spring when the population increase is very quick, individuals reproduce at their maximum and reproductive rate may be crucial for fitness. It has been shown also in *Bosmina longirostris* that individuals with long-featured morphology may be at a disadvantage in a low-predation environment, since they have fewer eggs than individuals having a short featured morphology (Kerfoot, 1977). This cost may lead to the observed decline in the trait when predator pressure declines (Kerfoot and Peterson, 1980; Kerfoot, 1987; Hellsten and Stenson, 1995).

The effects of morphological defence on reproductive costs have also been observed in laboratory experiments: *Daphnia* that were exposed to predator smell develop defensive neck spines and reproduce at a lower rate (Reissen and Sprules, 1990; Black and Dodson, 1990). However, the results can also be explained by life history changes induced directly by the predator smell (Lüning, 1994) and investigations that considered this effect failed to detect any reproductive costs (Tollrian, 1995). In my field study clutch sizes were compared between animals of the same length and exposed to the same environment, so the result can not be confounded with induced life history changes. Therefore, it seems likely that clutch size to some extent was directly affected by how much the individuals invested in predator protection, i. e. the antennule.

Why should long antennules be costly? The reason may be that long-featured individuals also lay eggs giving raise to neonates with long AL which may affect the size or nutrient contents of the eggs (Kerfoot, 1977). Long antennule may also have maintenance costs, e.g. a handicap in some way when gathering food.

Allometry

In this population of *gibbera*, both the BH and at times also AL show positive allometry (Fig 3), which also has been shown in earlier studies of this species (Hutchinson, 1967). However, this is not usually the case of most traits that have been explained as antipredator defences in other cladoceran species, e.g. the mucro in *B. longirostris* (Hanazato, 1992) and other *Eubosmina* species (De Stasio *et al.*, 1990). Antennule length in *B. longirostris* (Kerfoot, 1975a; Hanazato, 1992) and *Eubosmina longispina* (Lagergren, unpublished data), neck teeth and tail spines in *Daphnia pulex* (e.g. Havel, 1985) show negative allometry. Negative allometry may exist when a trait protects against small invertebrate predators and the need for a defence is most pronounced in young instars. Positive allometry has often been taken to indicate another function of the trait than anti-predator defence, as invertebrate predators prefer small prey (Lampert and Wolf, 1986).

Examples of other potential functions is reproductive use and protection against fish predation. It is possible that BH and AL in *gibbera* may be a defence against fish predation, but this does not seem likely. The main objection is the small size of *Eubosmina*. The only known species with a morphological defence working against fish predation, *Daphnia lumholtzi*, is larger (body length 0.35 to 1.2 mm) than *Eubosmina* (BL 0.25 to 0.7 mm). Extreme spine lengths are necessary and work only against the smallest fish fry (<50 mm) (Kolar and Wahl, 1998).

A large cladoceran predator, *Leptodora kindtii*, was the most common invertebrate predator in Lake Östersjön during the season 1999 (Table IV). Temperature and abundance of *Leptodora* mainly explain the variation in relative growth of AL. This result is in concordance with earlier results. In *Daphnia retrocurva*, allometric growth of the helmet was positively correlated to lake temperature (Brooks, 1946), and in *D. pulicaria*, temperature together with *Chaoborus* densities better predicted neck teeth development than did predator density alone (Leucke and Litt, 1987). With its large size and large "feeding basket", a *Leptodora* is potentially effective on the smallest *Eubosmina* irrespective of their morphological defence structures. Larger individuals, on the other hand, are closer to the maximum prey size of *Leptodora* where morphological defences usually are more effective against invertebrate predators (Swift, 1992). In a laboratory experiment, *Leptodora* kairomones has been shown to affect AL of *gibbera* only in adult individuals (Lagergren and Stenson, 2000). The relative size versus body length relationship of both AL and BH also speaks in favour of this theory. Relative sizes increase in the beginning, in concordance with both the fish and large invertebrate predation protection hypothesis, but then decrease after a maximum at about 575 µm for BH/BL and 450 µm for AL/BL (Fig 7). This maximum relative size of defence structures correlated to intermediate body size seems to be adaptive as morphological defence against an invertebrate predator, like *Leptodora*, but probably not for a fish defence. A relationship similar to this one is also found for relative helmet size in *D. cucullata*, which shows a clear maximum at intermediate body sizes (Lampert and Wolf, 1986).

If analysed in detail, several differences between the cyclomorphosis in AL and BH and adults vs. juveniles appear in this population of *gibbera*. The relatively high carapace on June 2 for the old juveniles (300-350 μm) and small adults (350-400 μm) size classes (Figure 2) may be caused by a life history shift towards lower size at maturity, as this is the period with most intensive fish predation (Dodson 1989a). If high carapace is an adult character (which seems likely as the brood chamber is a part of the high body), this result means that these animals achieve high carapace earlier in life than others. The low BH for these two size classes in August may also be explained by this hypothesis. Fish predation is probably lower, which is indicated by the higher mean body size (Table V), and *Eubosmina* should mature earlier. Alternatively, August may be a period when the size of the trait is diminishing, and the population consists of adult individuals with fully developed traits and young with low BH.

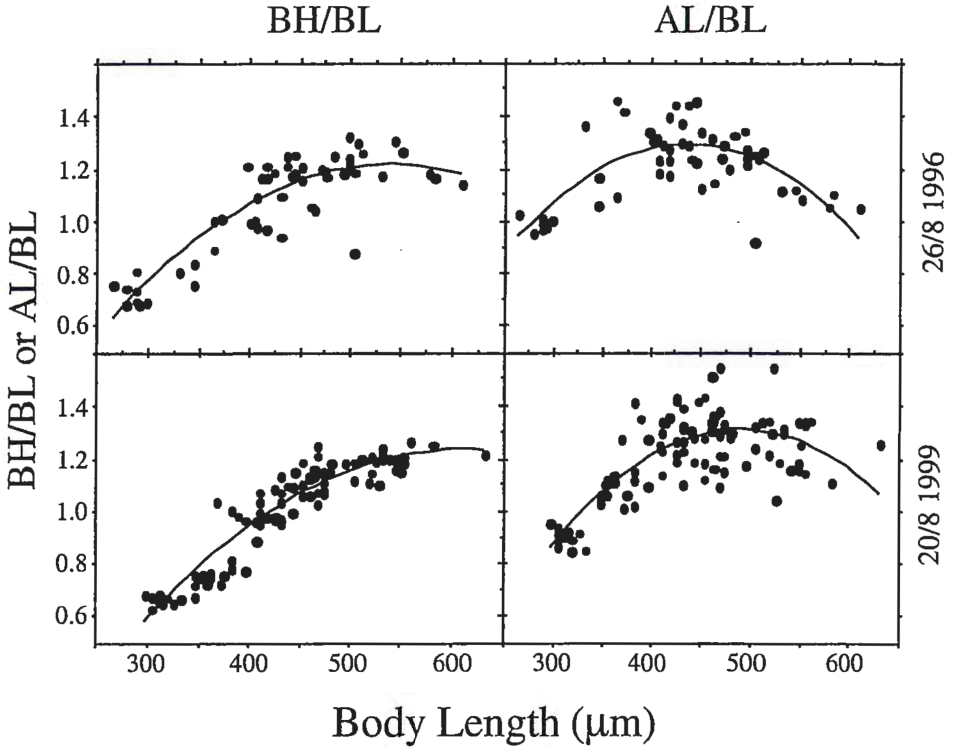

Fig. 7. Relative size of carapace height (BH) and antennule length (AL) in relation to body length (BL). Second degree polynomial regressions are fitted to each data set.

Table V. Population densities of the *Bosmina* populations and mean size of *gibbera* in Lake Östersjön 1999.

Datum	*gibbera* (ind/m^3)	*Eub. longispina* (ind/m^3)	*B. longirostris* (ind/m^3)	mean BL *gibbera* (µm)
10/5	1.9	1.9	1.6	381
2/6	17.3	54.8	25	369
18/7	1306	916	16.5	362
20/8	169	1314	2.1	390

Conclusion

In summary, this analysis of allometry and clutch sizes in *E. gibbera* shows that costs and benefits may differ between different cyclomorphic traits within a population. Carapace height cyclomorphosis did not incur reproductive costs in this study and was not driven by changing brood chamber volume. Longer antennule, however, which are an effective defence against *Leptodora* predation (Hellsten *et al.*, 1999), was associated with fewer eggs, indicating a cost of antipredator defence for long antennule.

Acknowledgements

I am grateful to Malte Andersson, Jan-Erik Svensson and Jan Stenson for critically reading the manuscript. The study was financially supported by grants from the Colliander foundation, Hierta Retzius foundation, Helge Ax:son Johnsons foundation, Kungl. och Hvitfeldtska stipendieinrättningen and Wilhelm och Martina Lundgrens science foundation.

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