Colony size in *Conochilus hippocrepis*: defensive adaptation to predator size

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Abstract

Conochilus hippocrepis colonies were analysed in relation to the presence and size of the predaceous calanoid copepod *Parabroteas sarsi*. *Conochilus* colonies increase in size throughout the season from May to August and then disappear from the lake. Simultaneously, *Parabroteas* developed from CI to CV and adults. We observed that when the predaceous copepod begins to prey on *Conochilus*, colony size increases in relation to maxilliped length of the predator. Our results show that the increasing size of the colony of *Conochilus* is an effective defense against *Parabroteas* predation.

Introduction

Planktonic rotifers are an important component of the diet of aquatic predators, especially of invertebrate predators, who prefer smaller prey individuals such as rotifers (Williamson, 1983). Since carnivorous planktonic invertebrates are size-dependent predators (Zaret, 1978; Gliwicz & Pijanowska, 1989), changes in the body shape and size of their prey may be effective antipredator responses (Sih, 1987; Dodson, 1989). Among the different defenses of planktonic rotifers against predators, coloniality increases effective size and therefore may protect individuals in the colony from predation (Stemberger & Gilbert, 1987; Wallace, 1987).

All species of the genus *Conochilus* form colonies of different sizes. This feature may provide protection from predation by copepods, *Asplanchna* and *Leptodora* (Gilbert, 1980; Williamson, 1983; Edmondson & Litt, 1987; Wallace, 1987). *Conochilus* colonies often persist in Northern Hemisphere lakes in the presence of copepod predators like *Epischura* and *Diacyclops* (Stemberger & Evans, 1984; Stemberger & Gilbert, 1987). Similarly, in a small fishless pond of the Southern Andes (41° S) *Conochilus hippocrepis* (Schrank) coexists with the large predaceous calanoid copepod *Parabroteas sarsi* Daday. Early studies revealed that total prey length of *Daphnia* is a good predictor of susceptibility to *P. sarsi* (Balseiro & Vega, 1994).

In this study we analysed by indirect evidence the effectiveness of the coloniality of *Conochilus hippocrepis* in permitting the coexistence with the predator *Parabroteas sarsi*.

Methods

The study was carried out in Laguna Fantasma, a small, fishless, temporary pond near Nahuel Huapi lake (41° S, 72° W, Argentina). The hydroperiod of the pond extends from autumn (April) to early summer (December). From mid summer to early autumn, the pond remains dry and often freezes during winter (July). In particular, in 1994 the ice remained only for one week. A maximum depth of 1.3 m was recorded during June and July. Based on our unpublished observations of samples taken in early autumn, we know that *Conochilus hippocrepis* population develops from resting eggs that hatch just after the first autumn rainfalls fill the pond. The pond was sampled for *C. hippocrepis* approximately every 10 days (range = 6–20 days) over a three month interval (May 31, 1994 to August 31, 1994). We both took qualitative and quantitative samples of the zooplankton of Laguna Fantasma to monitor the population dynamics and animals sizes of *C. hippocrepis* and *P. sarsi*. Qualitative
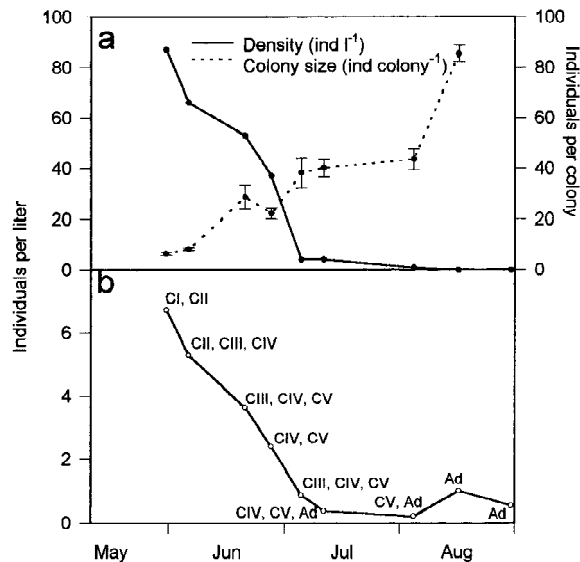
Figure 1. *Conochilus hippocrepis* and *Parebroteas sarsi* densities in Laguna Fantasma during autumn-winter 1994. a: *Conochilus hippocrepis* density (ind l^{-1}) and colony size (ind colony^{-1}). b: *Parabroteas sarsi* density (ind l^{-1}) indicating the developmental stage present in each sampling date.

Figure 2. Colony size (ind colony^{-1}) and colony diameter (mm) of *Conochilus hippocrepis* in Laguna Fantasma, autumn–winter 1994.

samples were obtained by horizontal trawls with a 35 μm mesh net from the surface to near the bottom. To obtain quantitative samples 30 litres of pond water were collected using a Schindler-Patalas trap and filtered through a 35 μm mesh net.

On each sampling date, living colonies of *Conochilus* were counted and measured, and the number of individuals per colony was determined. Colony diameter was estimated as the greater axial diameter. The density of each copepodid instar of the predator was estimated, and body size and length of the maxilliped were measured. For the analysis of the data, a weighted mean of the maxilliped length for each sampling date was obtained as the sum of the products of the density of the instar and the maxilliped length divided by copepod density. This estimation was called weighted maxilliped length (WML).

$$WML = \frac{\sum_{i=1}^{6} d_i \cdot m_i}{\sum_{i=1}^{6} d_i},$$

where i is the copepodid instar from CI to CVI (adults), d_i the instar density and m_i the maxilliped length of the instar.
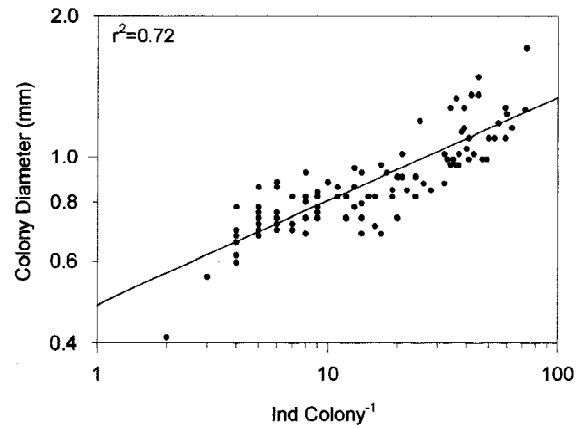
Results

During the winter period the temperature of Laguna Fantasma remained very low, with values below 7 °C. *Conochilus hippocrepis* started the season with high densities of more than 80 individuals l^{-1}. *Conochilus* density declined to 4 ind l^{-1} in July and remained low until early August. The rotifer was not detected in the quantitative samples in late August (Figure 1a). On the other hand, colony size (individual per colony) increased throughout the population cycle from 8 up to 80 ind colony^{-1} (Figure 1a). As a consequence, colony diameter showed a similar trend. However, this increment is not linear with the number of individuals per colony. Recruitment of the first 10 individuals to the colony results in a two-fold increment in diameter, and another two-fold increase is reached with a ten-fold increase in colony size, fitting a power model ($R^2 = 0.72$, $P < 0.05$) (Figure 2).

The population of the predator *Parabroteas sarsi* (first instar copepodid) was also high at the beginning of the study period, with a density of 7 ind l^{-1} (Figure 1b). *P. sarsi* has a single cohort in each hydroperiod and, as this cohort develops, copepodid instars grow from CI in autumn to adults in late winter and spring (Figure 1b). This implies that the predator changes its size from 1.5 mm total length for CI to 4.5 mm for adults. The development of the cohort is rather synchronised, so in each date only two or three instars were found together (Figure 1b). Maxilliped length also showed a monotonical increase through the sampling period, from 0.6 mm in CI to 1.6 mm in CV and adults ($R^2 = 0.95$, $P < 0.05$) (Figure 3). From CI to the beginning of adulthood the copepod
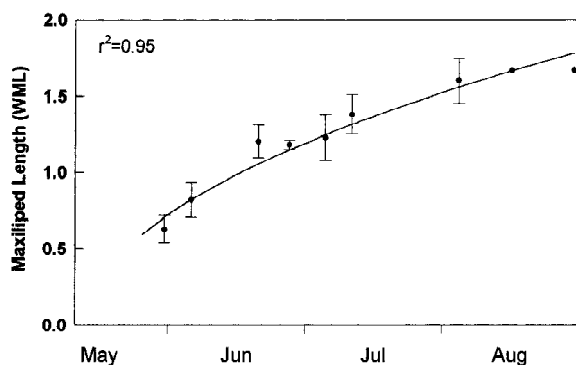
Figure 3. Change of weighted maxilliped length (WML) of the predaceous calanoid copepod *Parabroteas sarsi* in Laguna Fantasma, autumn–winter 1994.
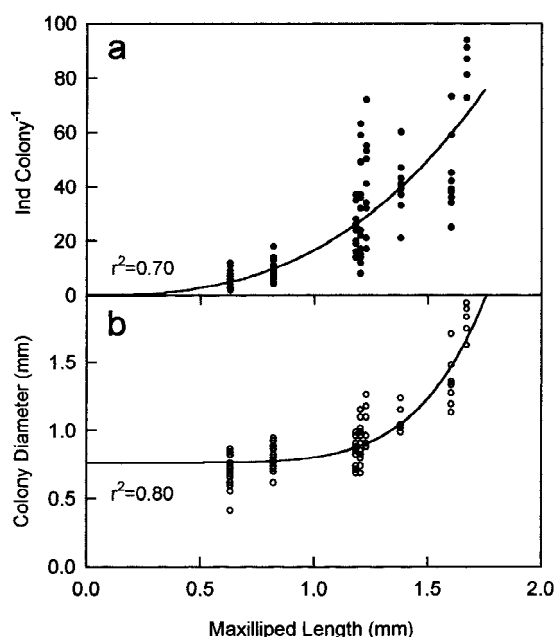

Figure 4. Relationship between colony size and predator size (weighted maxilliped length). a: Colony size expressed as ind per colony. b: colony size expressed as diameter.

coexists with *Conochilus* and after the rotifer disappearance the large *Daphnia middendorifiana* starts its population cycle during spring.

Positive relationships were found between the length of the maxilliped and both individuals per colony ($R^2 = 0.70$, $P < 0.05$) and colony diameter ($R^2 = 0.80$, $P < 0.05$) (Figure 4a, b). In both cases the relationships were of the form $y = a + bx^c$, where y is either colony diameter or individuals per colony and x the maxilliped length (WML). This function relates colony diameter and WML, and it indicates
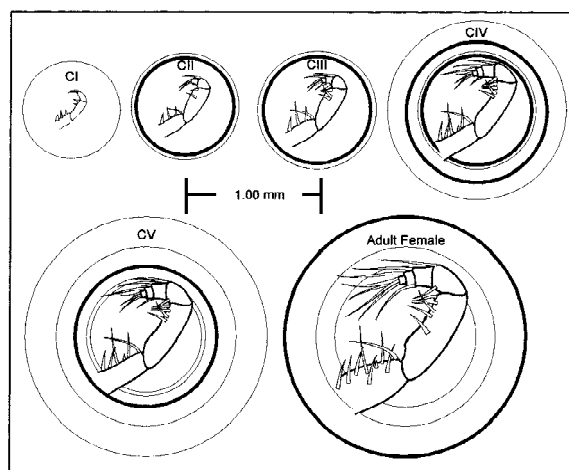

Figure 5. Schematic representation of coexisting relative sizes of maxilliped of *P. sarsi* and colonies of *Conochilus hippocrepis* (circles). Thick circles represent mean colony size when the particular stage of the predator was dominant. Thinner circles represent also the mean colony size when the particular stage of the predator was present but not as dominant.

that there is no colony of a predictable diameter less than 0.7 mm, which is the size of a colony with two individuals (Figure 4b). Colonies of this size coexist with the copepodid I (CI) stage, which apparently can not ingest *Conochilus* (Vega, 1995). Colonies begin to increase in size when larger copepodids, with larger maxillipeds (Figure 5), appear in the lake. It is remarkable that the maxilliped size of the dominant copepodid stage (measured unextended) was always less than the mean colony diameter (Figure 5).

Discussion

Coloniality is not a common feature within planktonic rotifers (Wallace, 1987). There are two main hypotheses that may explain the possible advantage of building colonies. An energetic advantage may be achieved if the clearance rate per individual is higher in colonies than in solitary individuals or, if there is an increase in filtering efficiency (Wallace, 1987). However, Wallace (1987) concluded that no increase in clearance rate was associated with colony size in different colonial rotifers. Coloniality can involve an antipredator defense as bigger colonies would be more difficult to manipulate by invertebrate predators such as cyclopoid copepods and *Asplanchna* (Stemberger & Gilbert, 1987). *Parabroteas sarsi* is a very large and voracious calanoid copepod that, as an adult, can

easily capture and ingest prey up to 1.6 mm long (Balseiro & Vega, 1994). In Laguna Fantasma, *Conochilus* coexists with each developmental stage of *P. sarsi*. In the beginning of the season, *P. sarsi* is in the naupliar stage, but soon reaches the first copepodid instar. Although *P. sarsi* has a marked tendency for macrophagy during this time, it only consumes large diatoms and thecamoebae (Vega, 1995). From copepodid II to adulthood, *P. sarsi* is able to ingest rotifers including *Conochilus* (Diéguez, unpublished laboratory observations).

An increase in prey size decreases vulnerability to an invertebrate predator (Gliwicz & Pijanowska, 1989), but there may be a bottleneck, as the prey's offspring can be much smaller than adults. Balseiro & Vega (1994) showed that *Daphnia middendorffiana* solves this bottleneck by the production of a long tail spine in the juveniles. This spine diminishes the predation rate of *P. sarsi*. *Conochilus*, which in Laguna Fantasma coexists with this same predator, has an individual adult size within the size range vulnerable to *P. sarsi*, so not only are the offspring vulnerable but the adults too.

Development of colonies has been observed to protect *Conochilus unicornis* from the effect of interference competition with *Daphnia pulex* (Gilbert, 1988). The advantage of creating a colony is that rotifers may increase their effective size without increasing individual size. Besides, offspring are immediately included in the colony and thus, protected against predators in spite of their smaller size. An increase in predator size may induce an increase in colony size maintaining a similar level of protection. The size of the colony would be determined by the ability of the predator to capture and ingest it. However, it is not necessary to assume that *Parabroteas* chemically induces larger colonies in *Conochilus*. Such an increase in colony size may be a consequence of selective removal of smaller colonies by the predator. As is shown in Figure 5, *Conochilus* colonies are always larger than the mouthpiece of its predator, perhaps indirect evidence that smaller colonies have been removed by predation. Indeed, Vega (1995) found *Conochilus* trophi in CIII CIV and CV gut contents of *P. sarsi*.

The capability of an invertebrate predator to capture and ingest a given prey size should be directly related to the size of the mouthparts of the predator. Obviously, the predator's mouthparts will increase in size during postembryonic development. In a predator with a synchronous cohort development, as observed for *P. sarsi* in Laguna Fantasma, the vulnerable size of prey will change monotonically with time as the predator develops. Thus, if the prey population is affected by the change in the predator size, it would be expected to show a monotonic change in its size. Indeed we observed that the colony size, and the number of individuals per colony, increase with time during the season. The size of *Conochilus* colonies at the beginning is about 700 μm and then increases rapidly. This increase starts when *Parabroteas* maxillipeds reach the size that allow it to capture colonies with two or three individuals. Then the colony size goes on increasing according to the increase in maxilliped size of the predator (Figure 4b).

In natural populations of *C. hippocrepis* we did not observe colonies larger than 1.8 mm in diameter, about 80 ind. colony^{-1}. Colonies of this size were only observed coexisting with adults of *Parabroteas* in late winter and then disappeared from the lake. This disappearance may be related to some negative effect of increasing colony size. For example, when colonies are large, the filtering efficiency of individuals may decrease. This would imply that increasing size would enhance antipredation defense, but simultaneously would decrease energy uptake by the individuals. Thus, one can think that there is a critical size. Colonies larger than this one would not survive in a food limiting environment, but smaller ones would be preyed on by *Parabroteas* adults. However, if increasing colony size reduces filtering efficiency, the upper limit may be influenced by lake productivity, with larger colonies being found in less food-limiting environments, as observed in Lake Washington by Edmondson & Litt (1987).

Acknowledgements

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