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Competition in natural populations of *Daphnia*

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Abstract  I investigated the competitive relationships between two species of *Daphnia*, *D. galeata* and *D. cucullata*, and their interspecific hybrid. The term hemispecific competition was introduced to describe competition between parental species and hybrids. In eutrophic Tjeukemeer both parental species were found to compete with the hybrid, whereas competition between *D. galeata* and *D. cucullata* seemed limited. Although the effect of competition on life history traits of daphnids may be profound, the influence of the competitors on the seasonal dynamics of the *Daphnia* species seems limited.

Key words  Coexistence · Hybrid · Competition · *Daphnia* · Hemispecific

Introduction

In the debates on competition and coexistence of species two different viewpoints can be distinguished (Bengtsson et al. 1994). The researchers advocating the 'equilibrium' viewpoint (e.g. Tilman 1982) assume that species can coexist through the avoidance of competition by niche segregation, or in 'Lotka-Volterra' terms by higher intraspecific than interspecific competition rates. The other view on coexistence of species emphasises the role of disturbance in the maintenance of the species diversity in a system (e.g. Paine 1966; Levin and Paine 1974). Although some species might be mutually exclusive under stable environmental circumstances, the speed of the process of exclusion may be so slow that the environment changes during the exclusion process, resulting in different competitive relationships and in other superior species. The process of exclusion may also be disturbed by some event, which 'resets' the system to an earlier successional stage, a phenomenon regularly observed in the succession of forest systems (e.g. Doyle 1981; Boersma et al. 1991).

Although competition between species has been the subject of research ever since the publications of the Lotka-Volterra models in the beginning of this century, competitive interactions between species and hybrids have been largely overlooked until now. This gap in our current knowledge is illustrated by the fact that no proper word exists to describe the competition between parentals and hybrids. In this paper, I will use the term hemispecific competition to describe the competition between the hybrids and the parent species, as distinct from intra- and interspecific competition.

Despite the wealth of information on genetic processes of hybridization and on the geographic distributions of hybrid and parental taxa, few experimental data exist on the relative fitness of hybrid offspring among environmental conditions (see Barton and Hewitt 1989; Harrison 1993). The zoological 'hybrid' literature is especially characterized by a lack of ecological data on hybrids. On the one hand this might be caused by the relative difficulties in recognising hybrids using traditional taxonomical methods, and on the other hand by the fact that, in a number of models on hybrid maintenance, endogenous factors, such as incompatibilities of parental genomes and resulting lower fitness of hybrids, are used to explain hybrid zone maintenance (Schwenk and Spaak 1995).

In facultatively parthenogenetic species genomic problems are probably of lesser importance, as parthenogenesis often occurs without meiosis. Therefore, the significance of competition between hybrids and parentals for hybrid maintenance is likely to be higher in animals which reproduce parthenogenetically. A large number of cladoceran zooplankton species have a cyclic parthenogenetic mode of reproduction. Hence, cladoceran zooplankton is well suited to study competitive relationships between hybrids and parental species, especially so since
in a large number of habitats parental species co-occur with their interspecific hybrids (Schwenk and Spaak 1995).

Competition and coexistence between species have been extensively studied in zooplankton communities (Mort and Jacobs 1981; Hebert 1982; Tillmann and Lampert 1984; Kerfoot et al. 1985; Romanovsky and Feniova 1985; Matveev 1986; Vanni 1986; Bengtsson 1987, 1993; Hanazato and Yasuno 1987; DeMott 1989; MacIsaac and Gilbert 1989; Schwartz and Hebert 1989; Rothhaupt 1990; Kirk 1991; Milbring and Bengtsson 1991; Weider 1992). Different workers have, however, expressed different views on the coexistence of species. The equilibrium view, with niche segregation, was advocated by, for example, Hutchinson (1951), Makarevich and Likens (1975) and DeMott and Kerfoot (1982), whereas the importance of changing environments and disturbances has been emphasized by such authors as Hebert and Crease (1980), Bengtsson (1986, 1987, 1993), Sommer et al. (1986), Weider (1992) and Spaak (1994). Although the existence of interspecific hybrids in cladoceran zooplankton has been widely recognized by now, the main body of the studies cited above only considered interactions between species and largely ignored the competitive relationships between species and hybrids.

In this paper I set out to investigate the competitive relationships between two species of the *Daphnia longispina* complex, *D. galeata* (Sars) and *D. cucullata* (Sars), and their interspecific hybrid in Tjeukemeer, a shallow eutrophic lake in the Netherlands. Although there is evidence that hybridization is an ongoing process (Schwenk 1993), I will treat this hybrid as a distinct taxonomical unit here. The emergence of animals from resting eggs, and hence the introduction of new hybrids, is an ongoing process here. The emergence of animals from there is evidence that hybridization is an ongoing process. The equilibrium view, with niche segregation, was advocated by, for example, Hutchinson (1951), Makarevich and Likens (1975) and DeMott and Kerfoot (1982), whereas the importance of changing environments and disturbances has been emphasized by such authors as Hebert and Crease (1980), Bengtsson (1986, 1987, 1993), Sommer et al. (1986), Weider (1992) and Spaak (1994). Although the existence of interspecific hybrids in cladoceran zooplankton has been widely recognized by now, the main body of the studies cited above only considered interactions between species and largely ignored the competitive relationships between species and hybrids.

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In short, in this paper I addressed the following questions: do the three *Daphnia* taxa compete for resources, and is competition important in the seasonal succession?

**Materials and methods**

Comparison between laboratory and field data

*Daphnia galeata*, *D. cucullata*, and *D. galeata × cucullata* were collected from Tjeukemeer, using a 350 μm tow net. The animals were placed individually into 100 ml test tubes, and fed with lake seston which was filtered over a 35 μm filter to exclude other crustacean zooplankton. Three different temperatures of 12.5°C, 17.5°C and 22.5°C were used in the experiments. The medium was changed every other day in the cultures at 17.5°C and 22.5°C, and every 3 days in the 12.5°C cultures. The grandchildren of the animals collected from the field were used for the experiments. The animals were kept at a light-dark rhythm of 16:8 h. Once the animals reached maturity the number of eggs and the length were recorded for every adult instar. The animals were measured from the upper edge of the eye to the base of the tail spine to the nearest 0.01 mm. The number of neonates produced were recorded, and these neonates were removed from the tubes. Judging from the length frequency distributions in field samples, animals rarely survive beyond the fourth adult instar stage. Therefore, the daphnids in the cultures were discarded when they reached this instar.

To test for seasonal differences in growth conditions for *Daphnia* species the experiment was carried out three times, that is: in spring (18 April–31 May), summer (18 July–31 August) and in the autumn (9 October–25 November) of 1990. A number of clones (seasonal clones) were taken randomly from the field for every seasonal period. These were then evenly distributed over the different culture temperatures. In addition, one standard clone was cultured for each taxon in each seasonal period in order to evaluate the importance of temporal differences in clonal composition as a factor influencing the growth rates in the different periods. This standard clone was randomly selected from the spring populations of *D. galeata* and *D. galeata × cucullata*. As *D. cucullata* was not present in high enough numbers at the time the spring cultures were started, this species was cultured only in the summer and autumn periods of 1990. The standard clone of *D. cucullata* was also collected in the summer period. Growth conditions were established using two traits of the animals, which are known to vary greatly as a result of differences in food conditions, namely: size at maturity (SAM), and fecundity.

In the years 1989–1991 quantitative samples were taken weekly in the growing season (April–October) and fortnightly in the rest of the year, using a 5-l Friedinger sampler on five different stations in the lake, at two different depths. These samples were pooled, concentrated by filtration through a 120 μm filter and preserved in 4% formaldehyde solution. The total number of animals were counted, and length-frequency distributions were established in a one-tenth subsample. An additional sample, which was preserved in 95% ethanol, was taken to establish length-fecundity relationships. Using the smallest gravid female found in the field as an estimate of size at maturity would lead to an underestimation of the average value of SAM in the field. Therefore, I used a logit regression technique with length as the independent variable and the presence/absence of eggs as the dependent variable. The length at which 50% of the females had eggs was taken as the average size at maturity in the field (see also Stibor and Lampert 1993).

In order to compare the fecundity of the animals in the field with the laboratory populations it was necessary to correct for length differences between the animals in the laboratory and in the field. The most straightforward way of doing this would be to perform an analysis of covariance with the length of the animals as a covariable. However, as the slope of the regression lines between