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Invasion note

Predator-mediated coexistence of exotic and native crustaceans in a freshwater lake?

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Abstract

The predatory effects of a Dipteran insect, *Chaoborus*, on the competition between exotic cladoceran *Daphnia lumholtzi* and two natives, *D. catawba* and *D. pulex*, were studied for a period of three years in a freshwater reservoir, Lake James, North Carolina (USA). *D. lumholtzi* was first encountered in September 1997 and it was present only between August and October when population densities of native species were low and that of *Chaoborus* sp. was high. The patterns observed in the population dynamics of the exotic *D. lumholtzi* and two natives, *Chaoborus* suggest that a 'predator mediated coexistence' phenomenon might be taking place in Lake James. The strong positive correlation between *Chaoborus* and *D. lumholtzi* and the negative correlation between *Chaoborus*, *D. catawba* and *D. pulex* is supportive of this hypothesis.

Introduction

Competition and predation are often major driving forces structuring many communities. Predators may promote the coexistence of species by lowering the density of certain prey species to a level where competition is reduced, a phenomenon known as predator-mediated coexistence (Paine 1966). In turn, competition is considered to be one of the principal barriers to the colonization of exotic species (Namba and Takahashi 1993). Predators may thus promote invasion by modifying interactions of potential competitors (Shurin 2001).

The invasion into North American lakes in the 1990s of the southern hemisphere cladoceran (water flea) *Daphnia lumholtzi* Sars 1885 (Havel and Hebert 1993), in systems where native *Daphnia* spp. and crustacean predators also occur, provides an opportunity to study the potential of predator-mediated coexistence of exotic and native species in freshwater ecosystems.

Daphnia lumholtzi has a pronounced helmet that can reach lengths nearly equal to the body. The tail spine also reaches extreme proportions, sometimes exceeding the body length; smaller spines are also on the carapace margins (Havel and Hebert 1993; East et al. 1999). The long helmet and post-abdominal spine of *D. lumholtzi* are probably cyclomorphic (seasonal (cyclic) changes in morphology) projections developed to avoid predation. Although temperature, turbulence, and food limitation are thought to contribute to formation of head spines or helmets, experiments have shown that spine formation is an effective defense mechanism against predators (Dodson 1974; Sorensen and Sterner 1991; Havel and Hebert 1993; Swaffar and O'Brien 1996).

The predatory effects of the dipteran phantom midge larvae *Chaoborus* on *Daphnia* have been examined by several workers (Havel and Hebert 1993; Swaffar and O'Brien 1996; Kolar et al. 1997; Shurin 2001). Swaffar and O'Brien (1996) reported that late instar

Chaoborus punctipennis use *D. magna* as prey, but fourth instars were unable to ingest *D. lumholtzi*. The larger spines of *D. lumholtzi* appear to be a selective advantage over other *Daphnia* species against predators.

We examine here the spatial and temporal population dynamics of *D. lumholtzi* and two common native species (*D. catawba*, *D. pulex*) and a potential predator, *Chaoborus* sp., in Lake James, North Carolina.

Methods

Lake James is located at the edge of the Blue Ridge Escarpment 64 km east of Asheville, near the top of the Catawba River drainage system in Burke and McDowell Counties, North Carolina. The lake is a hydropower reservoir formed by the impoundment of headwater streams of the Catawba River. Monthly zooplankton samples were taken from March 1997 to September 1999 at two stations in the Linville and Catawba basins of the lake using a 0.5 meter in diameter, 76 μm of pore size Wisconsin plankton net. A calibrated meter in the net corrected for backflushing during vertical halls from the bottom to surface. Temperature, conductivity, and other data were collected using a Hydrolab DataSonde 4 multiprobe.

Samples were fixed with 10% formalin containing Rose Bengal stain. In the laboratory each sample was concentrated, diluted to 200 ml, thoroughly stirred, and then subsampled with a 1-ml Hensen–Stempel pipette. Subsamples were loaded into a Sedgewick–Rafter counting cell in order to count and identify individual zooplankton. Population densities were determined from counts and volumetric data.

A Pearson correlation coefficients test was used to determine the statistical correlations between the population densities of *Chaoborus* and *Daphnia* sp., water temperature, and conductivity, using SAS statistical software.

Results

We first found *D. lumholtzi* in Lake James in September 1997. It has established stable late summer and fall (August–October) populations in Lake James. It appears when water temperatures reach an annual maxima (about 30 °C) and persists until the temperature drops to about 15 °C (Figures 1A–C). In late summer and fall, conductivity ranges from 40 to 70 mV (Figures 1A–C).

In September 1997 *D. lumholtzi* had a population density of 2 individuals/M3 in the Catawba and 3 individuals/M3 in the Linville basin. In October 1997 populations reached 4 individuals/M3 in the Catawba and 3 individuals/M3 in the Linville basin. During these months *D. catawba* and *D. Pulex* had their lowest population densities, whereas *Chaoborus* had its highest density. Population densities of *D. catawba* and *D. pulex* oscillated around 40 individuals/M3 in spring then dropped to about 5 individuals/M3 in the fall.

In 1998 *D. lumholtzi* had a population density of 8 individuals/M3 in October and 1 individual/M3 in September in the Catawba basin. In the Linville basin only 2 individuals/M3 were collected in October. Population densities of *D. catawba* and *D. pulex* fluctuated between 10 and 45 individuals/M3 during spring, but was relatively low in the summer and fall in both basins.

In 1999 *D. lumholtzi* had a population density of 5 individuals/M3 in August and 15 individuals/M3 in September in the Catawba basin. In the Linville basin the densities were 2 individuals/M3 in August and 14 individuals/M3 in September. *D. catawba* and *D. pulex* densities fluctuated between 40 and 75 individuals/M3 in the spring then drop back to about 20 individuals/M3 in the summer.

There is a strong positive correlation ($R = 0.789$ and $P = 0.0001$) between the population densities of *Chaoborus* and *D. lumholtzi*, whereas the densities of *Chaoborus* and *D. catawba*, and *D. pulex* are inversely correlated ($R = -0.061$ and -0.087, respectively). The densities of *D. lumholtzi* was also negatively correlated with *D. catawba* and *D. pulex* ($R = -0.049$ and -0.183, respectively).

Discussion

As the density of *Chaoborus* goes up in Lake James, that of the natives *D. catawba* and *D. pulex* goes down and *D. lumholtzi* in turn goes up. This pattern reoccurs over the 3-year study period. The emergence of *D. lumholtzi* in the late summer and fall when the density of *D. catawba* and *D. pulex* are the lowest suggests that there may be competition between the native species and *D. lumholtzi* in the early summer. We suggest that this pattern may be a result of predator-mediated coexistence.

In enclosure experiments, Mumm (1996) found that *Chaoborus* effected the structure and size distribution

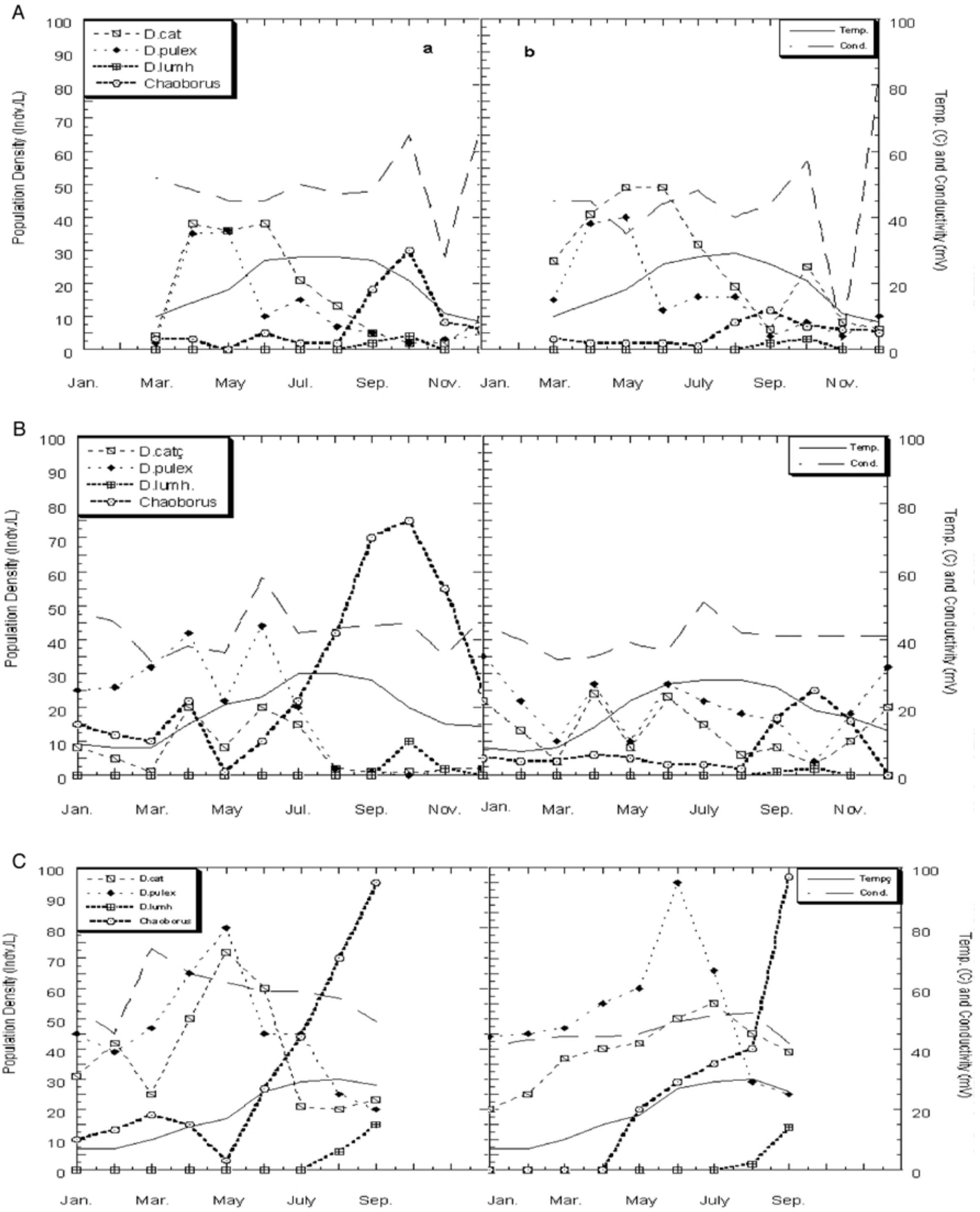

Figure 1. Monthly data on the population density of *D. catawba*, *D. pulex*, *D. lumholtzi, Chaoborus*, epilimnetic water temperature and specific conductance in (a) the Catawba Basin and (b) the Linville Basin, in (A) 1997, (B) 1998, and (C) 1999, respectively.

of zooplankton. *Chaoborus* reduced the density of small cladocerans (such as *Daphniasoma* and *Ceriodaphnia)* significantly, while the largest naturally occurring daphnid, *D. longispina,* was least influenced.

Kolar et al. (1997) found that *D. lumholtzi* increased in abundance only in late summer when water temperature was high in a subtropical Florida lake. Our data also show a correlation between summer temperature maxima and population densities of *D. lumholtzi.*

Temperature may trigger the reproduction of *D. lumholtzi,* but its abundance (and eventually distribution) may be primarily controlled by other factors, such as predation and competition. Experimental studies to further elucidate these relationships will be important.

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