Cannibalism and early instar survival in a larval damselfly

Abstract Cannibalism by larval damselflies late in larval development on larvae a few instars smaller has been widely documented. I examine here the survival of eggs oviposited near the end of the flight season of adult Enallagma boreale in the presence and absence of potential cannibals, individuals that hatched from eggs earlier in the season, over an extended part of the life-cycle. The role of competition as a modifier of cannibalism was examined by manipulating egg density, environmental productivity, and habitat complexity. Survival in the absence of potential cannibals ranged from 5% to nearly 50% but was only 0–3% in the presence of cannibals. Survival of small larvae was related to manipulations of habitat complexity but not initial density or resources. There were no significant interactions of the presence of large larvae with other experimental treatments on the survival of small larvae. The mean size of small larvae was greater in the presence of cannibals. This may be because the cannibalism treatment reduced the density of small larvae and reduced competition for resources, or that the cannibals preferentially fed on small larvae and only relatively large individuals remained. Fertilization of the habitat or manipulating the initial density of small larvae did not affect mass of small larvae at the end of the experiment, which would be expected if small larvae were affected by competition for resources. Potential cannibals, however, emerged at higher mass when small larvae were present at low density and when productivity of the habitat was increased. This suggests that the negative effect of competition by small larvae outweighs the positive effect of being potential prey for large larvae.

Key words Cannibalism · Competition · Exploitation Enallagma boreale · Interference

Introduction

When a population of generalist predators includes both large and small individuals, the potential exists for cannibalism to have strong effects on mortality rates and hence population dynamics (Polis et al. 1989). Coenagrionid damselfly larvae are generalist predators that interact aggressively when they encounter each other (Rowe 1980; Baker 1981, 1983), and large larvae will kill and eat small larvae (Lawton 1970; Baker and Clifford 1981; Johnson 1991). Thus the fate of a clutch of eggs will depend in part on the number and size of larvae already present. Previous studies of larval odonates (Van Buskirk 1989; Wissinger 1989) have shown that cannibalism and intra-guild predation markedly affect survival, but these experiments have examined cannibalism by larvae near the end of their development on larvae only a few instars smaller. The significance of cannibalism on early life history stages is unknown.

Competition, both within and among size classes of larvae, can have important effects on mortality by reducing growth rates and thereby extending the vulnerable period (Werner and Gilliam 1984). Conversely, low larval density, and high productivity of the habitat could ameliorate mortality rates by permitting rapid growth to relatively invulnerable size classes. Increasing per capita resources could also reduce cannibalism by providing older instars with alternative prey (Johansson 1992).

Cannibalism can be viewed as an extreme form of interference competition (Fox 1975; Polis 1981). Within size classes, interactions among individuals may not result in mortality or injury but may still be costly in terms of energy expended and time not spent foraging (Schoener 1973). In a previous experiment, I manipulated habitat complexity to test whether density dependence of growth and development rates was due to resources of interactions among individuals (Anholt 1990). Those experiments showed that interference was at most a tiny component of the observed density dependence within size classes. However, because there was little size variation, cannibalism was almost absent from those experi-
ments. The effect of interference competition generally, and cannibalism specifically, appears to increase as size classes diverge (Wissinger 1988; Van Buskirk 1989; McIsaac and Gilbert 1991).

This experiment measures the effect of cannibalism by middle instar larvae of the coenagrionid damselfly *Enallagma boreale* Selys on earliest instar larvae hatching from eggs oviposited late in the season. I also investigated whether competition among early instar larvae altered the rate of cannibalism by manipulating initial egg density, environmental productivity, and habitat complexity.

**Methods**

Sixteen 1.1-m-diameter inflatable wading pools were housed in an unheated cinder block building with a glass roof on the University of British Columbia (UBC) campus in Vancouver, British Columbia. Pools were filled with 100 l of tap water (depth 0.1 m) and allowed to stand for 72 h. All substrate and biota used in the experiment were collected from Placid Lake in the UBC Malcolm Knapp Research Forest near Haney, British Columbia. Mud was sieved through a 425-μm-opening sieve bucket, and added to a depth of 3 cm. Zooplankton were collected on 30 July 1987 with a 125-μm-mesh plankton net and density of adult copepods and cladocera estimated. Zooplankton were then added by volume so that each pool received an inoculum of approximately 3000 (30 l–1) adult zooplankton and associated juveniles. Predominant species were *Daphnia rosea* Sars and *Diaptomus kenai* Wilson. Damselfly larvae are generalist predators feeding on the most abundant available prey (Akre and Johnson 1979). Late instar larvae of *E. boreale* and other coenagrionid damselflies are capable of growing and completing development at a per capita prey density of 10 l–1 (Lawton et al. 1980; Anholt 1990). The densities used are well within the natural range of densities; maximum densities recorded from Placid Lake for all crustacean zooplankters is 50 l–1 (Neill 1978). The experimental pools were self-sustaining; no additional animals were added during the experiment, and every pool continued to support a population of damselflies and zooplankton at the end of the experiment.

A completely crossed four-way factorial design was used with two levels for each treatment. The four treatments were: (1) presence or absence of older instars, (2) initial egg density, (3) habitat complexity, and (4) nutrient addition. With the exception of nutrient addition the experiment was a completely crossed four-way factorial analysis of variance design. Only the main effects and the two-way interactions that incorporated the presence of large larvae were tested.

**Nutrient addition**

Eight pools received additional nutrients to stimulate algal growth and secondary productivity. Nitrogen and Phosphorus were added as dissolved NaNO₃ and K₂PO₄ in the atomic ratio 40:1 N:P. Ratios lower than this tends to encourage the growth of inedible cyanobacteria (Neill 1984). Fertilized pools received 0.33 μg l–1 of P three times per week until the experiment was terminated. The zooplankton community of Placid Lake has been demonstrated to respond to this level of nutrient addition by increasing population growth rates and biomass (Neill 1984). Because some pools received more sunlight than others I decided to add nutrients to the sunlit pools rather than randomize across pools. This arbitrary decision potentially confounds treatment with position but space limitations prohibited randomizing within space blocks. Manipulated pools were greener and appeared to have higher concentrations of zooplankton; there was no effect on water temperature. Densities were not estimated to reduce disturbance levels.

**Census**

Adults began emerging on 13 April 1988: As many as possible were collected and weighed as they emerged. Some escaped, and others were eaten by spiders. I counted the exuviae of final instar larvae to determine the number that emerged. No adults emerged from pools where large larvae were absent, suggesting that all emerging adults began the experiment as late instar larvae.

All larvae surviving to December 1988 were collected from the pools and preserved in 70% ethyl alcohol. Head capsule width, fore wing pad length, and total length (excluding lamella) were measured with an ocular micrometer under a dissecting microscope. Individuals were then dried in an oven at 40°C and weighed on an analytical balance to 0.1 mg.

**Analysis**

The experiment was a completely crossed four-way factorial analysis of variance design. Only the main effects and the two-way interactions that incorporated the presence of large larvae were test-