Hydrobiologia (2005) 543: 113–118
DOI 10.1007/s10750-004-6948-7

Primary Research Paper

Predator density and dissolved oxygen affect body condition of *Stenonema tripunctatum* (Ephemeroptera, Heptageniidae) from intermittent streams

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Received 15 February 2004; in revised form 27 July 2004; accepted 30 November 2004

Key words: hypoxia, mayfly, predation threat, Ouachita Mountains, Arkansas

Abstract

The effects of population density, fish density, and dissolved oxygen on body condition of late-instar nymphs of *Stenonema tripunctatum* (Ephemeroptera, Heptageniidae) were investigated using nymphs sampled from isolated, upland stream pools over summer in central Arkansas, USA. All three factors exhibited high variation among pools. Body condition was negatively related to fish density, and positively related to dissolved oxygen (when included in the model). High fish densities may be related to low body condition because they cause reduced foraging or force earlier emergence at small body sizes. These results emphasize the combined effects of biotic and abiotic factors on body condition in mayflies, and support earlier findings that population density is a less-important factor.

Introduction

Body condition is an indicator of individual growth, and is an important estimator of future reproductive success and survivorship of mayflies (Dahl & Peckarsky, 2003). *Stenonema tripunctatum* (Ephemeroptera, Heptageniidae) is a dominant stream mayfly and principal prey item for fishes occurring in small, Ouachita Mountain headwater streams (central Arkansas, USA). During summer, these intermittent streams dry, and densities of aquatic insects and fishes increase (Williams et al., 2003) as pools become moderately, or completely isolated (Taylor & Warren, 2001). Little is known about how these dynamics affect body condition of aquatic insects.

Results in the literature differed concerning the effects of intraspecific density on insect body condition. Condition values of odonates in some studies were lowest when intraspecific densities were high (Johnston et al., 1984; Pierce et al., 1985), but an experimental study (Baker, 1989) failed to detect an intraspecific density effect. Pool drying in intermittent streams caused insect densities to increase (Williams et al., 2003), which can possibly result in higher levels of intraspecific competition, especially when resources were aggregated (Silver et al., 2000). However, pool drying also caused fish densities to increase which can reduce size at emergence (Dahl & Peckarsky, 2002), or reduce aquatic insect densities (Williams et al., 2003) and relax intraspecific competition.

Dissolved oxygen might also influence body condition of aquatic insects. Although, *S. tripunctatum* has usually been found in streams that were not limited by dissolved oxygen (>6.0 mg l^{-1}; Lewis, 1974), pools in these intermittent streams varied greatly in dissolved oxygen, and some pools with *S. tripunctatum* had low dissolved oxygen during summer dry-down. Hypoxia, or low concentrations of dissolved oxygen (<2 mg l^{-1}), can notably reduce growth of fishes, either directly (Baltz et al., 1998; Secor & Gunderson, 1998; Phelan et al., 2000), or indirectly by inhibiting foraging (Hale, 1999; Buentello et al., 2000). Aquatic organisms may, however, be seasonally acclimatized for living in hypoxic habitats (Love & Rees, 2002). None-the-less, low dissolved oxygen has been shown to influence the distribution and behavioral patterns of mayflies (Wiley & Kohler, 1980), and may also affect body growth or condition.

Intraspecific and predator densities, and dissolved oxygen were hypothesized to affect body condition of field-collected, late-instar *S. tripunctatum*. Specifically, three predictions were made: (a) body condition will be negatively associated with intraspecific density; (b) body condition will be positively associated with fish density; and (c) body condition will be highest under conditions of greater dissolved oxygen concentration.

Materials and methods

Fourteen stream sites were sampled across the Alum Fork of the Saline River drainage (Arkansas) in June and July (2002; Fig. 1). Streams ranged from first to third order and are intermittent during summer when flows lessen (Taylor & Warren, 2001). Habitats ranged from being completely modified by humans (box-culverts) to natural with little human influence. Substrates were generally the same across sites and mainly included small and large boulders. During midday (1000–1400), dissolved oxygen was measured in milligrams per liter (mg l^{-1}) using a Yellow Springs Instrument Model 85 (YSI-85) and averaged across months. Pool volume was calculated as the product of pool length, mean pool width ($n = 4$), and mean pool depth ($n = 16$). Each month, pool width was measured along the same 4 transects. Depth was measured at four equidistant points along each transect. Volume was averaged across months.

Macroinvertebrates were collected in July using D-frame sweep nets and Hester–Dendy samplers (Hester & Dendy, 1962). Six, 10 s passes of the sweep net were made and covered all available microhabitats. Samplers (approximately 1 trap per 10 m^3 of pool volume) were installed in deeper parts of a pool by securing them to metal stakes (0.95 cm diameter, 61 cm long) anchored in the stream bed. The bottom plate of each sampler was flush with the substrate. Samplers were set in June and left for 1 month to allow macroinvertebrate colonization (Crowe, 1974). Insects were preserved in 70% ethanol mixed with Rose Bengal dye to stain living tissue, and identified in the laboratory using Merritt and Cummins (1984) and Lewis (1974). Density of *S. tripunctatum* was calculated

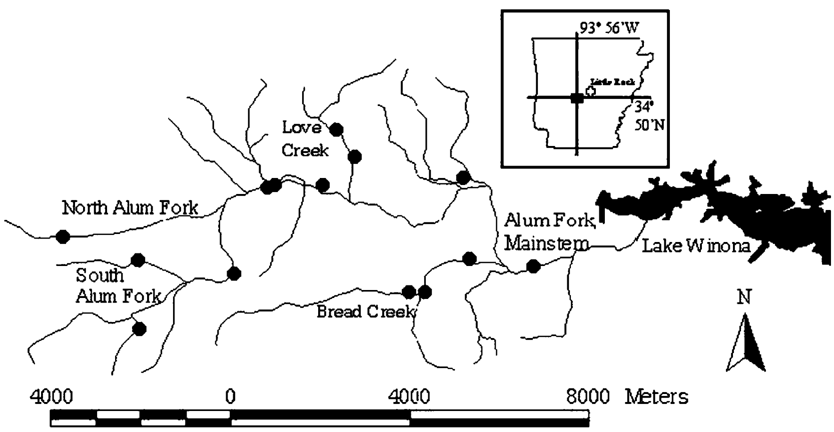

Figure 1. Study sites in the Alum Fork of the Saline River in the Ouachita Uplands of Central Arkansas. All sites were sampled for fishes and insects in the summer of 2002. *Stenonema tripunctatum* were not found in the South Alum Fork, the most upstream site in Love Creek, and one site in Bread Creek.

as the total number of individuals from sweep-nets and Hester-Dendy traps per unit of pool volume.

Fishes were sampled in each pool with Gee minnow traps (approximately 1 trap per 10 m^3 of pool volume) for 48 h in June and in July. Traps were checked and rotated within each pool after 24 h, and reset for another 24 h. The funnel diameter of the traps (~3 cm) allowed the collection of juvenile sunfish and other small bodied fishes. Fishes were identified and released to the pool of capture during each sampling period. Prior to the first release, fins were clipped to exclude recaptures the subsequent day from the data set. Density was calculated as the number of fish collected per unit of pool volume, and averaged for each site across months.

Air-dried mass of late-instar *S. tripunctatum* was estimated by weighing individuals on a Sartorius analytic balance (± 0.0001 SD). Because mass may be reduced by ethanol-preservation, true mass was underestimated for all specimens equally, which did not affect the scope of this study, but likely resulted in an underestimate of true body condition. Individuals were blotted on a paper towel and allowed to dry until excess moisture was removed. Legs were usually missing from specimens, and all legs were removed prior to weighing. Because head width may be proportionally different among instars (Benke et al., 1999), late instars were defined as those with a head width >0.33 mm and fully developed hind pads that extended along the thorax. Greatest head width was measured with an ocular micrometer. Body condition was estimated as residuals from the regression of mass on head width. Head width and body mass were log-transformed prior to regression to normalize variance. Head width was correlated positively with body mass ($r^2 = 0.78$; $p < 0.0001$; Fig. 2) allowing for statistical removal of body size influence from body mass.

Analysis of variance was used to compare mean insect condition among sites. Multiple regression analysis was used to examine the simultaneous effects of intraspecific density, predator density, and dissolved oxygen on insect condition. All statistical analyses were conducted with SYSTAT (Version 0, SPSS Inc., Chicago, IL, 2000).

Results

Stenonema tripunctatum was collected from 8 of the 14 pools. These pools ranged in size from 12 to 132 m^3, and averaged 42.3 m^3 ± 38.6 SD. Pool densities of *S. tripunctatum* (mean: 1.51 ± 1.26 SD; range: 0.14–3.78) were higher than the those of fishes (mean: 0.26 ± 0.14 SD; range: 0.06–0.42). Dissolved oxygen ranged from 3.54 to 8.23 mg l^{-1} among pools, and averaged 5.61 mg l^{-1} ± 1.37 SD. Thus, pools differed greatly in mayfly and fish densities, and dissolved oxygen concentration.

Body mass of *S. tripunctatum* ranged from 1 to 30 mg ($n = 162$; mean: 6 mg ± 5 SD) and body

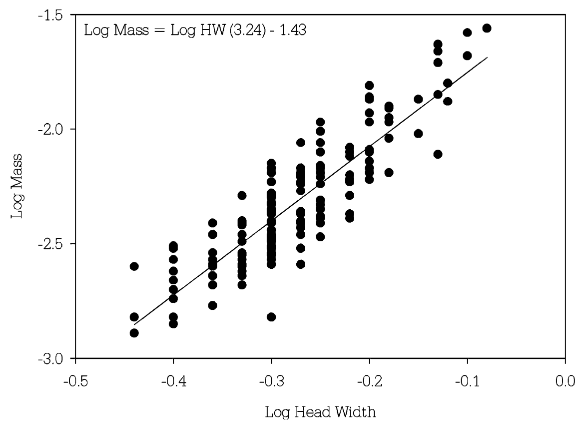

Figure 2. Relationship of mass and head width for *S. tripunctatum* collected in the Alum Fork of the Saline River ($n = 162$; Summer, 2002). Both variables were log-transformed prior to analysis. There was a significant, positive relationship between the two variables (regression equation in figure).

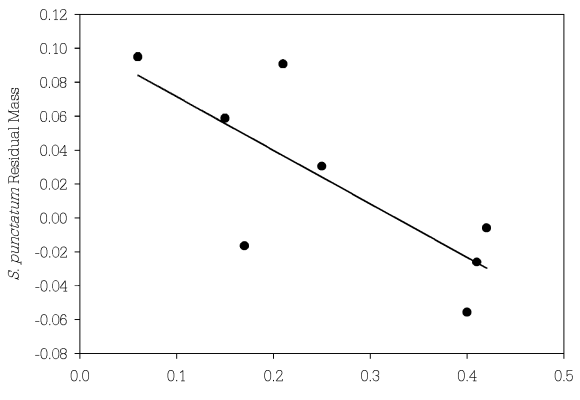

Figure 3. Linear regression of fish density and body condition of *S. tripunctatum* from isolated pools in the Alum Fork of the Saline River (Summer, 2002). Fish density was averaged across months (June and July).

condition differed among sites ($F_{8,153} = 4.35$; $p < 0.0001$). About 88% of variation in body condition was explained when accounting for effects of both fish density and dissolved oxygen. Body condition was correlated negatively with fish density ($\beta = -0.92$; $p = 0.002$) and positively with dissolved oxygen ($\beta = 0.56$; $p = 0.02$), but not with intraspecific density ($\beta = -0.07$; $p = 0.78$). Separate regression analyses using either fish density ($r^2 = 0.59$; $p = 0.02$; Fig. 3) or dissolved oxygen ($r^2 = 0.10$; $p = 0.44$; Fig. 4) as predictors were less informative. Overall, body condition differed among sites and was associated with fish density and dissolved oxygen, but not intraspecific density.

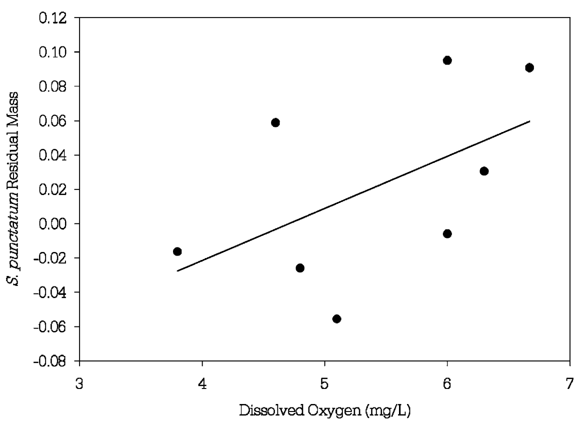

Figure 4. Linear regression between dissolved oxygen and body condition of *S. tripunctatum* from isolated pools in the Alum Fork of the Saline River (Summer, 2002). Measurements of dissolved oxygen were averaged across months (June and July).

Discussion

Body condition for *S. tripunctatum* was affected by predator density and dissolved oxygen, but not intraspecific density, as Baker (1989) found for damselfly nymphs. Although resource availability was not measured, nutrients for *S. tripunctatum* (e.g. detritus, Richardson & Tarter, 1976; diatoms in epilithic algae, Peterson et al., 1998) were likely to have been more abundant and similar across sites, probably resulting in low intraspecific competition for food. Food was not likely to have been more limiting in this system than others because growth, as indicated by the slope of the head width–mass relationship, was similar to that found for other Ephemeroptera (Benke et al., 1999).

Predator density did not influence condition as predicted. Instead, condition was lowest in pools with high predator density, which can be explained in three ways. Firstly, mayflies (*Ephemerella invaria*) emerge earlier at smaller body sizes from fish-dense pools (Dahl & Peckarsky, 2003), suggesting a phenotypically plastic response of development to predator density. Such a response may be an adaptation to live in a habitat with temporal fluctuations in fish and invertebrate predator densities (Barata et al., 2001). Secondly, high fish densities may have inhibited the foraging behavior of mayflies by reducing foraging time (Dixon & Baker, 1987; Kohler & McPeek, 1989; Muotka et al., 1999), space (Holomuzki & Messier, 1993), or efficiency (Peckarsky et al., 1993). Hiding behavior may be important for the co-existence of mayflies and predators (Muotka et al., 1999) and is known for other aquatic insects (Gerridae: Hemiptera; Englund et al., 1992; Krupa & Sih, 1998). Finally, mayfly nymphs in higher condition may be selectively preyed upon by fishes or invertebrates. Invertebrates such as crayfish (*Procambrus*) and odonates are influential predators (Wooster, 1994), but were not quantified in this study.

The most meaningful conclusion from this study was that the combined influence of predator density and dissolved oxygen reduced body condition of *S. tripunctatum*. Condition was lowest in habitats with relatively low dissolved oxygen, but only when variation relating to predator density was accounted for.

Larval body size may be indicative of future reproductive success for some mayflies (Peckarsky et al., 1993; Taylor et al., 1998; Dahl & Peckarsky, 2003). The present study suggested emergence of *S. tripunctatum* within 3 weeks of our July sampling. The effect of reduced larval condition on future survival and reproductive success of adult *Stenonema* remains largely unknown.

Acknowledgements

Financial support for this work was provided by the USDA Forest Service, Southern Research Station, Ouachita Mountains Ecosystem Management Research Project, and the Department of Biological Sciences at Mississippi State University. We thank Brook Herman for helpful comments on the manuscript.

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