



Hypoxia and lost gills: Respiratory ecology of a temperate larval damselfly

Timothy M. Sesterhenn^{a,*}, Erin E. Reardon^{b,1}, Lauren J. Chapman^{b,c}

^a Department of Biology, University of Kentucky, 101 Morgan Building, Lexington, KY 40506-0225, USA

^b Department of Biology, McGill University, 1205 Dr. Penfield Ave., Montreal, Quebec, Canada H3A 1B1

^c Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460, USA

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ABSTRACT

Damselfly larvae, important predators and prey in many freshwater communities, may be particularly sensitive to hypoxia because their caudal lamellae (external gills) are frequently lost. In this study, we address how lost lamellae interact with low oxygen to affect respiration and behavior of the widespread North American damselfly *Ischnura posita*. Results showed no effect of lost lamellae on resting metabolic rate or critical oxygen tension. Ventilation behaviors increased only when dissolved oxygen (DO) was at or below 25% saturation and these behaviors were not affected by the number of lamellae. Use of the oxygen-rich surface layer occurred almost exclusively at the lowest dissolved oxygen level tested (10% saturation, 2.0 kPa). Damselflies that were missing lamellae spent more time at the surface than individuals with intact lamellae. The negative relationship between body size and time at the surface, and the negative relationship between body mass and critical oxygen tension suggest that larger *I. posita* may be more hypoxia tolerant than smaller individuals. Overall, *I. posita* was minimally affected by missing lamellae and seems well-adapted to low DO habitats. Average critical oxygen tension was very low (0.48 kPa, 2.4% saturation), suggesting that individuals can maintain their metabolic rate across a broad range of DO, and behaviors changed only at DO levels below the hypoxia tolerance thresholds of many other aquatic organisms.

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1. Introduction

Compared with air-breathers, water-breathing organisms face a much greater respiratory challenge given the reduced oxygen availability and diffusion rate even in fully-saturated water (Graham, 1990). Hypoxia, or low dissolved oxygen (DO), compounds this challenge to breathing underwater. Hypoxia occurs naturally and is rapidly increasing worldwide in both coastal and inland waters due in part to eutrophication caused by anthropogenic nutrient additions (Diaz, 2001; Diaz and Breitburg, 2009). Much work is still to be done to fully understand the impacts of hypoxia on aquatic organisms. The bulk of our current understanding comes from the fish literature; effects of hypoxia on aquatic insects are less well understood, despite the tremendous diversity of this group (reviewed in Hoback and Stanley, 2001). Existing studies do suggest that insects react similarly to fish when faced with hypoxia, both by changing behavior and reducing growth (reviewed in Hoback and Stanley, 2001; Harrison et al., 2006); however, many

of these studies have been conducted on terrestrial insects. Understanding the respiratory ecology of aquatic insects is an essential step toward predicting the population and community level responses to the growing frequency and intensity of hypoxia in freshwaters, which may be exacerbated by climate change (Ficke et al., 2007).

Larval Odonata (dragonflies and damselflies) are a particularly useful group for examining responses to hypoxia because they play key roles in many freshwater communities as predators and/or prey and often occupy the role of top predator in fishless systems (Corbet, 1999). The respiratory ecology of damselfly larvae is particularly interesting and potentially complex because of their caudal lamellae, three structures extending from the distal end of the abdomen, which contribute to oxygen uptake in some species (Eriksen, 1986, Apodaca and Chapman, 2004) but can also serve a variety of other functions including ion regulation (Wichard and Komnick, 1974), locomotion (Burnside and Robinson, 1995), intra-specific signaling (Rowe, 1985), and weaponry (Rowe, 1992). Lamellae that appear especially well-adapted for gas exchange are extensively tracheated and connected to internal hemolymph circulation (Corbet, 1999), but even these lamellae are considered accessory respiratory organs that augment the respiratory role of rectal epithelial pads (Wichard and Komnick, 1974). Lamellae are frequently lost through autotomy – at any given time in a given population up to 90% of individuals may be missing at least one la-

* Corresponding author. Present address: Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907-2061, USA. Tel.: +1 765 494 8086; fax: +1 765 494 9461.

E-mail addresses: tsesterh@purdue.edu (T.M. Sesterhenn), E.E.Reardon@exeter.ac.uk (E.E. Reardon), lauren.chapman@mcgill.ca (L.J. Chapman).

¹ Present address: Biosciences, University of Exeter, Stocker Road, Exeter, Devon EX4 4QD, UK.

mella (Stoks, 1998). If lamellae do play an important role in gas exchange, their absence may strongly influence damselfly respiratory ecology.

Damselflies also vary in their respiratory response to hypoxic stress. Some damselflies maintain a relatively constant metabolic rate across a range of oxygen partial pressures before a sharp decrease at the critical oxygen tension (Lawton, 1971; Apodaca and Chapman, 2004), similar to some other aquatic insects (e.g. Kölsch and Krause, 2011). The critical oxygen tension is defined as the oxygen partial pressure below which a further reduction in DO causes a shift from a regulated, relatively DO-independent, metabolic rate to a strongly DO-dependent metabolic rate (Beamish, 1964; Ultsch et al., 1978, Fig. 1). High physiological tolerance to hypoxia has been linked to a low critical tension, and thus critical tension is often used as a proxy for hypoxia tolerance (Chapman and McKenzie, 2009). One potential mechanism that may allow damselflies to regulate their metabolic rate over a range of oxygen partial pressures is their use of behaviors that increase the efficiency of oxygen uptake, similar to aquatic caddisfly larvae (Fox and Sidney, 1953; van der Geest, 2007), hellgrammites (Kinnamon et al., 1984), and several terrestrial insects (Harrison et al., 2006). For example, ventilation rate generally increases as DO decreases in damselfly larvae, but the type of ventilation behavior varies among species. Some species seem to specialize in “pull-downs” (lowering then raising the entire body, Eriksen, 1984), abdomen waves (Lawton, 1971; Miller, 1994), spreading of wing pads (Apodaca and Chapman, 2004), or rectal pumping (drawing water into the abdomen to bathe rectal epithelial pads then expelling it after extracting the oxygen, Miller, 1993). Yet, to our knowledge, the relationships between these behaviors and lamella morphology has not been investigated. Several damselfly species share the response of moving toward the water’s surface in hypoxic conditions (Robinson et al., 1991; Miller, 1994; Apodaca and Chapman, 2004) to access the oxygen-rich surface layer of water, a phenomenon often described (in fishes) as aquatic surface respiration (or ASR, Kramer and McClure, 1982).

The number of caudal lamellae (and their morphology) should affect the efficiency of lamella ventilation and, therefore, the need for other behavioral and physiological mechanisms to persist under hypoxia. Although there is some evidence for a metabolic cost of lost lamellae (Eriksen, 1986; Apodaca and Chapman, 2004) that has been attributed to reduced respiratory surface area, the links between hypoxic stress and the importance of the lamellae are

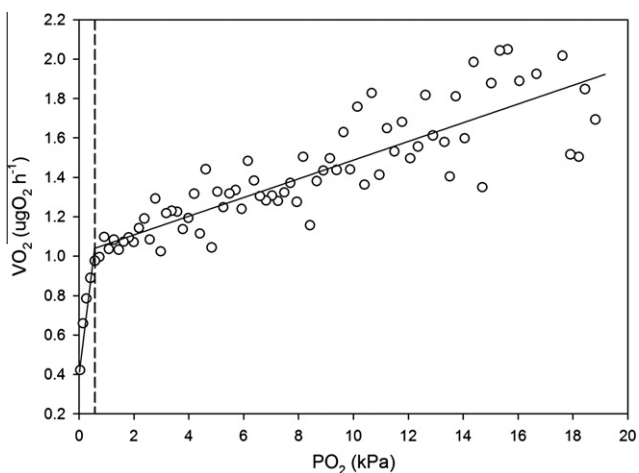


Fig. 1. An example measurement trace output from the respirometry analysis program (Reardon and Chapman, 2010). The solid lines are best-fit linear regression lines that intersect to determine the critical oxygen tension (shown by the dashed line).

not well understood. We hypothesize that the number of caudal lamellae influences damselfly respiratory ecology, and that the role of lamellae may change at different levels of DO.

We selected a widespread, ecologically important, lentic damselfly (*Ischnura posita*) with a distribution from southern Canada to northern Mexico, covering the eastern half of North America (Abbot, 2007). *I. posita* regularly occurs in hypoxic ponds with DO levels notably below the DO minima at collection sites for 65 other odonate species (Roback and Westfall, 1967; Roback, 1974). We measured individual larval damselfly metabolic rates over a DO range from saturation to below the critical oxygen tension, and behaviors at four levels of DO of damselflies that had all three lamellae or were missing two of their three caudal lamellae. We predicted that missing lamellae would reduce metabolic rates without influencing the critical oxygen tension because compensatory mechanisms appear to maintain critical oxygen tension in the face of lamella loss in another hypoxia-adapted damselfly *Proischnura subfurcatus* (Apodaca and Chapman, 2004). We also predicted that ventilation behaviors would increase at lower DO levels to maintain a constant metabolic rate and that the increase would be greater in individuals missing lamellae to compensate for decreased respiratory surface area.

2. Materials and methods

2.1. Animal collection and general care

Damselflies for both experiments were collected with dipnets from fishless ponds at the University of Kentucky’s Ecological Research Facility in Lexington, Kentucky, USA (38° 4.83N, 84° 28.34W). These shallow (<1 m) ponds regularly reach water temperatures over 25 °C and DO levels below 10% saturation (~3 kPa) in the summer months, and they ice over completely in the winter. The only damselfly present is *I. posita*, along with several predatory dragonfly species. The ponds are densely vegetated with *Elodea* sp. and *Lemna* sp. Upon capture, damselflies were examined, and those already missing caudal lamellae or with evidence of regenerated lamellae were returned to the ponds. Only animals with all three lamellae intact were collected and used for experiments.

Resting metabolic rates (rate of oxygen consumption in a resting animal) were determined for damselflies collected in May 2009. Upon collection, damselflies were placed into individual 125 ml polyethylene bottles filled with pre-aerated, de-chlorinated tap water and a small wooden dowel for the animal to grip. The next day, the bottles were capped and packed into a padded box for air transport to the Respiratory Ecology Lab in the Department of Biology at McGill University in Montreal, Canada. There was no mortality during travel. Upon arrival at McGill, the bottles were uncapped and held at room temperature (21 °C). Metabolic trials were performed over the next 4 weeks. During that time, damselfly larvae not involved in trials were fed *ad libitum* daily with hatching *Artemia*; unconsumed *Artemia* died within 24 h and were removed with a pipette. Bottles were bubbled with an airstone so that DO levels remained near saturation, and pre-aerated, charcoal-filtered tap water was added as needed to keep the bottles full.

Animals for behavioral trials were collected from the same location in July 2009. In the laboratory, each damselfly was held individually in a 25 × 95 mm polypropylene vial filled with pre-aerated, de-chlorinated tap water at room temperature (23 °C) for behavioral trials at the University of Kentucky. This different set of animals was fed daily in late afternoon *ad libitum* with hatching *Artemia*; dead *Artemia* were removed the next morning and water changed as needed.

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