

Ecological factors limiting the distributions and abundances of Odonata

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Overview

Many ecological processes contribute to regulating the distributions and abundances of odonate species. In local populations, mortality imposed by predators (including cannibalism and predation by other odonates) on larvae appears to be the dominant factor limiting abundances of many odonate species, although lower growth rates due to food limitation and stress responses to the presence of predators also contribute to limiting population sizes in most species that have been studied. Little is known about such processes in the adult stage of the life cycle, but parasites have been shown to limit adult survival and fecundity. Predation also causes many species to segregate among different water bodies with different top predators in eastern North America: different assemblages of odonate species are found at ponds and lakes that support centrarchid fishes than at fishless ponds and lakes. However, this pattern of species segregation between fish and fishless water bodies is not apparent in other parts of the world. Stream-dwelling odonates also show analogous types of segregation to different types of stream (e.g. small creeks compared with large streams and rivers), but the ecological processes that enforce this segregation is not known. Many unanswered questions about the ecological regulation of odonates makes them a continually fascinating group for study.

5.1 Introduction

Every budding amateur odonatologist quickly learns the type of habitats to search if he or she wants to find a particular species. If one is after a *Calopteryx*, then a slow-flowing stream with woody structures is needed. If an *Epithea* is sought, then one goes to a lake with good macrophyte beds. *Gomphus* can be found around sandy-bottomed waters. This predictability in species distributions results from the fact that different species have different ecological requirements to maintain population abundances greater than zero.

Although individuals of species can sometimes be found in places where they cannot sustain a population (e.g. migrant individuals passing through

an area, or a so-called sink population that is only maintained at a site by continual immigration from nearby thriving populations), the distribution of a species in the environment is determined largely by the distribution of suitable habitats to maintain source populations (i.e. populations that can be maintained without continual immigration) (Pulliam 1988). Local abiotic factors such as the temperature and water chemistry as well as biotic factors such as the abundances of various food resources, predators, and parasites all affect the survival, growth, and fecundity individuals at a particular site. At some sites, local ecological conditions will allow a species to have an adequate combination of survival, growth, and fecundity to maintain a source population. However, at other

sites, a subset of these factors will make it impossible for the species to maintain a source population. Thus, the factors that limit local abundances are also those that shape the distribution of a species on the local landscape.

In this chapter, I review recent experimental and observational studies of the environmental features that shape the distribution and abundances of odonates among various water bodies. First, I reiterate the basic life cycle of the typical odonate and explore the various ecological factors that have been identified to influence survival, growth, and fecundity in various life stages. Then I examine how these same factors may limit the distributions of species among various habitat types. The results of this review highlight the importance of the larval phase of the life cycle to local population regulation, but they also highlight the glaring gaps in our knowledge about many aspects of odonate ecology.

5.2 What factors regulate population abundances locally?

Local population abundance is the outcome the demographic processes that impinge on all life stages of a species. The odonate life cycle has three primary stages: eggs, larvae, and adults (Corbet 1999). Eggs are deposited into water bodies, and may either enter a diapause phase to pass through harsh environmental conditions (e.g. many *Lestes* species in temporary ponds have diapausing eggs to pass through periods of pond drying) or begin developing immediately. After hatching, individuals emerge as aquatic or semi-aquatic larvae. Individuals can remain as larvae for weeks (e.g. those occupying vernal ponds) to years (e.g. semi-voltine species in permanent waters) depending on species. At the end of the larval phase, individuals metamorphose into aerial adults that may survive for a few days (e.g. most species) to months (e.g. those species that pass the dry season in tropical climes).

Local population abundances are determined by the component demographic rates of each of these life stages (McPeck and Peckarsky 1998). These component demographic rates are: mortality rates in all three stages, growth and development rates in the egg and larval stages, and fecundity rates as

adults. For the most part, these demographic rates are determined by how the phenotypes of individuals in a stage interact with the ecological environment in which they find themselves, but size and energy reserves at the end of the larval phase may also have some influence on adult fecundity (i.e. carryover effects from larval to adult stage).

Local population abundances can be quite constant from generation to generation, suggesting strong population regulation (Crowley and Johnson 1992). Population regulation occurs when the component demographic rates change in a negative density-dependent fashion. Negative density dependence means that a per-capita demographic rate changes in a way that will slow the rate of overall population increase—less positive or more negative—as population size increases. Thus, negative density dependence implies that mortality rate increases or fecundity decreases with population size.

5.2.1 Eggs

Little is known about demographic rates in the egg stage. Eggs certainly may die or fail to develop because they are unfertilized, or development may be arrested. However, we know nearly nothing about causes or rates of egg mortality in the field. One study found that 22.6% of the eggs of *Lestes disjunctus*, a species that oviposits endophytically in plants above the water, failed to hatch (Duffy 1994). Eggs of the stream-dwelling *Calopteryx splendens* developed faster and had lower mortality when oviposited into faster-flowing water than those placed in slow-flowing water, because encrusting algae was less likely to overgrow the eggs in faster water (Siva-Jothy *et al.* 1995). Although egg parasites and predators are certainly prevalent in many insect groups, these sources of egg mortality seem to be rare among odonates (Fursov and Kostyukov 1987). In addition, the degree to which demographic processes acting in the egg stage are density dependent is also unknown.

5.2.2 Larvae

Because many species spend the majority of their life as larvae, the larval stage is a demographically

critical phase of the life cycle for determining both distributions and abundances in water bodies in a local area. Moreover, larval mortality due to predation is the overriding demographic force shaping abundances for most species. The predominant larval predators are fish (Morin 1984; McPeck 1990b, 1998; Johnson *et al.* 1995, 1996; Johansson and Brodin 2003; Stoks and McPeck 2003b), other odonates, including intraguild predation and cannibalism (McPeck and Crowley 1987; Van Buskirk 1989; Wissinger 1992; Wissinger and McGrady 1993; Anholt 1994; Hopper *et al.* 1996; ClausWalker *et al.* 1997; Ryazanova and Mazokhin-Porshnyakov 1998; Crumrine 2005; Imonen and Suhonen 2006), and other aquatic insects (Della Bella *et al.* 2005; Magnusson and Williams 2006; Wissinger *et al.* 2006). The identities of the dominant predators depend on the types of water body inhabited by a species (see below). Field experimental results indicate that up to 80% of larval mortality is due to the dominant predator with which a species lives (McPeck 1990b, 1998; Johnson *et al.* 1995, 1996; Stoks and McPeck 2003b), and that larval mortality rate due to predation increases with increasing larval odonate density (McPeck 1998). Also, the intensity of predation will depend on the structural complexity of the physical environment (e.g. the type of macrophyte species present) in which this interaction takes place (Crowder and Cooper 1982; Dionne and Folt 1991; Rantala *et al.* 2004; Warfe and Barmuta 2004). Thus, predation on larvae is probably the primary factor regulating local abundances of many odonate species (McPeck and Peckarsky 1998).

Parasites are prevalent in odonates, and are possibly significant sources of larval mortality and hindrances to growth, although the demographic effects of parasites have been much better studied in the adult stage (see below). Some of the major parasites that infect odonates as larvae are nematodes (Moravec and Skorikova 1998) and microsporidians (Kalavati and Narasimhamurti 1978), among others.

Larval growth rates are also very sensitive to environmental conditions and often change in a negatively density-dependent manner. Odonate larvae are often food-limited (Johnson *et al.* 1987; McPeck 1998), meaning that food levels are less than those that could sustain maximal growth

rates. This limitation can be due to lower productivity of the habitat overall, or because of resource competition with other groups in the food web (Johnson *et al.* 1987, 1995, 1996; Baker 1989; Martin *et al.* 1991). Although limited food availability often slows growth, food levels are rarely low enough for starvation to be a significant source of mortality.

Larval growth rates also decrease with increasing larval density, which is the hallmark of competition (Johnson *et al.* 1985; Pierce *et al.* 1985; Crowley *et al.* 1987; Anholt 1990; McPeck 1990b, 1998; Fincke 1992b; Van Buskirk 1992; Stoks and McPeck 2003b; Suutari *et al.* 2004). These decreases may be caused by resource limitation. The other major factor limiting larval growth is in fact the presence of mortality threats such as predators and cannibals. Many studies have shown that odonate larvae grow more slowly in the presence of conspecific cannibals and other predators (Crowley *et al.* 1988; Martin *et al.* 1991; Johansson 1996; Schaffner and Anholt 1998; Stoks and Johansson 2000; Johansson *et al.* 2001; McPeck *et al.* 2001; Stoks and McPeck 2003a, 2006; Brodin and Johansson 2004; McPeck 2004; Dmitriew and Rowe 2005; Stoks *et al.* 2005a, 2006b). Larvae generally respond behaviourally to the presence of mortality threats by reducing activity, which may then alter their short-term rate of food intake (Dixon and Baker 1988; McPeck 1990a; Johansson 1992, 1993; Ryazanova and Mazokhin-Porshnyakov 1993; Wiseman *et al.* 1993; Shaffer and Robinson 1996; ClausWalker *et al.* 1997; Koperski 1997; Elkin and Baker 2000; Hopper 2001; Suhling 2001; Trembath and Anholt 2001; Stoks *et al.* 2003; Brodin and Johansson 2004; Brodin *et al.* 2006; Crumrine 2006; Stoks and McPeck 2006; Wohlfahrt *et al.* 2006).

These non-lethal effects of mortality threats are usually thought to be causally related: reduced short-term feeding rates cause reduced growth. However, recent studies have shown that this relationship may be only fortuitous. A number of odonate species show strong stress responses to the presence of mortality threats that can account for most or all of these decreases in growth rate (McPeck *et al.* 2001; Stoks and McPeck 2003a, 2006; McPeck 2004; Stoks *et al.* 2005a). Larvae feed at slower rates in the presence of predators, but continue to eat for longer so that over the course

of a day they consume the same total amount of food. However, they are physiologically less able to convert ingested food into their own biomass in the presence of mortality threats. These stress responses can reduce larval growth rates by more than 50% in some species, and the interspecific variation in growth rates in natural populations can be explained by interspecific differences in the levels of these responses (McPeck 2004). At present, the physiological basis for this stress response is unknown.

One must also remember that processes influencing growth rate will also indirectly affect the total mortality that a particular cohort experiences by altering the length of the larval period (McPeck and Peckarsky 1998). Processes that slow growth and development rates will expose larvae for longer to potential mortality sources: larvae will spend longer time in smaller size classes and will thus be more susceptible to both cannibals and predators (McPeck and Crowley 1987; Dixon and Baker 1988; Van Buskirk 1992; Wissinger 1992; ClausWalker *et al.* 1997; Crowley 2000; Peckarsky *et al.* 2001; Crumrine 2005). In fact at both intraspecific and interspecific levels, larval growth and survival differ among groups in ways that suggest strong trade-offs between these two fitness components (Anholt and Werner 1995; Johansson 1996; McPeck 1998; Elkin and Baker 2000; McPeck *et al.* 2001; Stoks and McPeck 2003b; McPeck 2004; Brodin and Johansson 2004; Stoks *et al.* 2005a, 2005b).

Ecological factors that decrease larval growth rates may be most critical for species that live in water bodies that may potentially dry completely during the larval period. The effects of pond drying have been studied extensively in amphibians (e.g. Semlitsch and Wilbur 1988; Leips *et al.* 2000), but much less is known about odonate responses to drying. Many odonate species inhabit water bodies that dry periodically. For example, larvae of the giant helicopter damselfly, *Megaloprepus coerulatus*, inhabit water-filled treeholes and must develop rapidly to metamorphose before the water dries (Fincke 1994). Also, many species have life-history adaptations to occupy temporary ponds that may dry (Stoks and McPeck 2003b). In such habitats, rapid growth is crucial.

5.2.3 Adults

Although previous work has elucidated much about the factors that influence mating success, we know comparatively little about the population processes that operate in the adult stage to affect population growth rates. Mortality rates of adults are quite high for most species, with most individuals living on average only a few days or weeks after they metamorphose into adults (Fincke 1982, 1986, 1994; Anholt 1991, 1997; Córdoba-Aguilar 1994; Bennett and Mill 1995b; Cordero 1995; Marden and Rowan 2000; Beukema 2002; Thompson and Fincke 2002). Also, because of the differences in breeding tactics of males and females, females sometimes have higher mortality rates than males (Bennett and Mill 1995b; Anholt 1997; Marden and Rowan 2000; Beukema 2002; Kery and Juillerat 2004; Córdoba-Aguilar *et al.* 2006). Females of most species spend considerable time away from water bodies to forage and presumably to reduce harassment by males, but at the expense of greater mortality (Anholt 1997; Marden and Rowan 2000; Anholt *et al.* 2001). In fact, the primary determinant of female lifetime fecundity is the number of times a female is able to return to the pond to oviposit (Fincke 1982, 1986; Bennett and Mill 1995a; Cordero *et al.* 1998).

Food limitation on females may play a substantial role in limiting population abundances. At emergence, odonate adults have substantially depleted stores of fat and tend to lose weight over the first few days of the adult period (Anholt *et al.* 1991; Anholt 1997; Marden and Rowan 2000). The gonadal tissue of odonates does not mature until they are adults, so the number of eggs a female has to lay depends primarily on the amount of food she eats as an adult (Richardson and Baker 1997). However, we know almost nothing about the degree to which female fecundity is limited by resource availability or by competition over those resources.

One interaction about which we do know a great deal is how various parasites influence adult survival and reproduction. Odonates are hosts for many parasites, both internal and external, and these parasites can be substantially detrimental to the adults they infect. For example, adults infected with gregarines have lower fat content, are poorer flyers, and sometimes are shown to survive more

poorly (Åbro 1996; Siva-Jothy and Plaistow 1999; Siva-Jothy *et al.* 2001; Marden and Cobb 2004; Canales-Lazcano *et al.* 2005; Córdoba-Aguilar *et al.* 2006). Likewise, ectoparasitic mites (Acari) frequently also reduce survival and fecundity of adults (Åbro 1982; Forbes and Baker 1991; Leonard *et al.* 1999; Rolff 1999; Rolff *et al.* 2001).

These findings about mortality and fecundity in adults strongly suggest great opportunities for adult demographic processes to operate in a density-dependent manner. In particular, competition for resources and parasitism can be strongly density dependent in other species, and so may make similar contributions to population regulation in odonate populations. This should be a fruitful area for research into population regulation in the future.

5.3 What factors set the distributions of species among water bodies?

Odonates can be found associated with just about every type of freshwater habitat in nature. Most odonate species are relatively strong flyers, and all species as adults have at least the capacity to travel in the order of one to a few kilometres to move between water bodies. However, each type of water body has a characteristic species assemblage that can typically be found there. Surprisingly, we know very little about the ecological factors that limit species distributions to particular habitats. Although adult choice may play a proximate role in setting limits, species distributions are probably ultimately set by processes acting on the aquatic larval phase. Some ecological limits are probably set by physical requirements, some by structural features of the habitat, and some by species interactions.

Although most species are restricted to fully aquatic environments, a few species around the world can be found as larvae in upland habitats (e.g. a few *Megalagrion* species are found in wet leaf litter) where relative humidity is always high (Polhemus and Asquith 1996). The larvae of a number of species develop in small water-collection sites scattered throughout forests (e.g. water that collects in epiphytes and bromeliads, discarded fruit husks, or treeholes; Polhemus 1993; Fincke 1994; Polhemus and Asquith 1996; Englund 1999).

A number of the most threatened and endangered species in North America, including the only odonate species on the US Endangered Species List (*Somatochlora hineana*; http://ecos.fws.gov/tess_public/SpeciesReport.do?groups=I&listingType=L), are often associated with bogs and wetlands that tend to be more extreme in terms of some physical factor. For example, *S. hineana* is restricted to intermittent carbonate-rich wetlands that overlay dolomite bedrock (Zercher and Team 2001). *Williamsonia lintneri*, a species that is listed as threatened or endangered in a number of US states, is restricted to low-pH fens and bogs (Westfall and May 1999). The rarity of these physically extreme habitats contributes to the rarity of species occupying these types of habitats, and habitat destruction only exacerbates their difficulties.

One of the primary environmental features that demarcate habitat distributions is the difference between flowing and standing waters. Characteristic assemblages of species can be found all along the river continuum, from the seeps and springs at the head of first-order creeks up to large rivers (Dijkstra and Lempert 2003; Hofmann and Mason 2005; Salmah *et al.* 2006). Many of these taxa appear to require specific habitat features found only in a particular range along this continuum; for example, *Hetaerina* damselflies in low-order, fast-flowing, rocky-bottomed creeks; *Calopteryx* damselflies clinging to woody roots and stems; burrowing gomphids in sand and mud substrates; and climbing coenagrionids and libellulids in slower-moving waters with macrophytes and emergent vegetation. One of the major physical factors that may limit species distributions along the river continuum is oxygen availability, with species requiring more oxygen being limited to faster-flowing waters in lower-order streams, and those that can tolerate lower oxygen concentrations found in larger-order, slow-flowing areas (Buss *et al.* 2002; Apodaca and Chapman 2004; McCormick *et al.* 2004; Hofmann and Mason 2005). Many other physical and biological factors also change along the continuum (Vannote *et al.* 1980; Power 2006), which may all contribute to limiting the distributions of species. Although we have substantial observational evidence for the impacts of these factors on odonate distributions, almost

no experimental tests have been conducted (e.g. Leipelt 2005).

We best understand the factors setting species distributions among standing water bodies along the gradient of pond permanence, from vernal ponds that dry each year to large lakes that contain water essentially permanently. A major demarcation along this gradient is the frequency with which a pond may dry: if a pond dries at sometime during the year, any larvae present at that time will die. Some groups possess life-history features that permit them to inhabit these temporary waters (e.g. the desiccation-resistant, diapausing eggs of many *Lestes* species; Sawchyn and Church 1973). As a result, species compositions are very different at ponds that do and do not routinely dry during a year (Stoks and McPeck 2003b; Della Bella *et al.* 2005; Magnusson and Williams 2006).

Predators play a significant role in limiting the distributions of species to particular parts of both the stream and pond gradients. Fish play a substantial role in limiting some species to smaller streams (Power 1992; Wiseman *et al.* 1993; Dijkstra and Lempert 2003). However, the clearest experimental demonstrations of habitat limitation by various predators come from work done along the pond permanence gradient in eastern North America. In eastern North America, sunfishes (primarily *Lepomis* species) exclude large, active dragonflies (e.g. *Anax*, *Aeshna*, and *Tramea* species) from ponds and lakes where these fish are found. These large, active dragonflies are relegated to ponds and lakes where fish cannot colonize (Crowder and Cooper 1982; Werner and McPeck 1994), and a set of smaller, less active dragonflies (e.g. *Basiaeschna*, *Celithemis*, *Epitheca*) that are less effective predators co-exist with these fishes (Crowley and Johnson 1982; Blois-Heulin *et al.* 1990; Johnson *et al.* 1995, 1996; McPeck 1998; Johansson *et al.* 2006). In areas of the world where fish taxa besides centrarchids dominate (e.g. western North America, Eurasia) this pattern of segregation between fish and dragonfly waters is much less clear (Johansson and Brodin 2003; Johansson and Suhling 2004; Johansson *et al.* 2006; R. Stoks and D.R. Paulson, personal communication; M.A. McPeck, personal observation).

Species in a number of other genera (e.g. *Enallagma*, *Lestes*) are forced to segregate between ponds and

lakes with fish or with large dragonflies based on their susceptibilities to these two predators (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990; McPeck 1990a, 1990b, 1998; Stoks and McPeck 2003a, 2006). In these segregating taxa, species that are found only with fish typically are moderately active and do not swim away from attacking predators, which are effective phenotypes against fish predators but ineffective against dragonfly predators. In contrast, species that are found only with large dragonflies in fishless waters are more active and swim away from attacking predators, which are effective tactics against dragonflies but not against fish (Pierce *et al.* 1985; McPeck 1990a; Stoks and McPeck 2003a).

Functional and evolutionary studies have shown that these behavioural differences among taxa found co-existing with different predators are the result of adaptive evolutionary responses to living with those predators (McPeck and Brown 2000; Stoks *et al.* 2003; Stoks and McPeck 2006). Moreover, lineages of *Enallagma* are also adapted to live with dragonflies in fishless waters by evolving morphological and biochemical features that make them faster swimmers (McPeck 1995, 1997, 1999, 2000; McPeck *et al.* 1996). Some dragonfly species that co-exist with fish have also evolved the ability to inducibly grow long spines to deter fish predation (Johansson and Samuelsson 1994; Westman *et al.* 2000; Johansson 2002; Johansson and Wahlstrom 2002; Hovmoller and Johansson 2004; Mikolajewski and Johansson 2004; Mikolajewski *et al.* 2006). Thus, predators have been powerful agents of natural selection in the evolutionary histories of odonates and remain significant sources of mortality enforcing habitat distributions today.

5.4 Future directions

As this review attests, odonates have been a prime taxon for study of the ecological and evolutionary regulation of distribution and abundance. Ecologists and evolutionary biologists around the world have made tremendous progress in demonstrating how various ecological factors influence the mortality, growth, and fecundity of specific odonate taxa. However, the gaps in our knowledge of these processes remain vast. In this final section, I would like to highlight what I see as critical gaps to be filled.

To me, our largest gap in understanding is the role that demographic factors operating in the adult stage of the life cycle play in determining local population abundances. As the above review demonstrates, we fairly well understand the forces shaping mortality and growth rates of larvae in many species of dragonflies and damselflies. In addition, although a number of factors (e.g. parasites, predators) influencing adult survival and fecundity have been identified, the quantitative impacts that these factors have on population growth and regulation are largely unmeasured. The main reason for this gap is logistical. Larvae are relatively easy to work with, but anyone who has ever tried to follow a female odonate away from a pond to watch where she spends her time will attest to the difficulty of quantifying the factors that influence adult demography. However, manipulative experiments that quantify the effects of factors shaping adult survival and fecundity are sorely needed to close the loop on population regulation through the full odonate life cycle.

Another glaring hole in our understanding are the processes that regulate the distributions of species across stream orders and habitats. Experiments over the past 20 years have clearly identified predators and hydroperiod as the main ecological factors limiting species distributions among ponds and lakes (see above). Whereas these same factors may play a substantial role across stream orders as well, almost no experimental studies have been done to isolate and identify the factors that shape odonate distributions among streams of various sizes and with various habitat structures.

A personal desire is to understand the differences between lake assemblages dominated by centrarchid fishes and those dominated by other taxa of fish predators. As mentioned above, the checkerboard pattern of species distributions that are found for many odonate taxa between centrarchid dominated and fishless waters in eastern North America is much less evident in areas outside the historical range of centrarchids. Mechanistically, all fish seem to forage on odonates in the same way, but the intensity of that predation appears to differ. The lack of a clear fish/fishless pattern of prey distributions in lakes dominated by non-centrarchid fishes suggests that the reduced predation intensity

from fish in these lakes results in a substantially altered community structure. Experimental comparisons of lakes in areas dominated by centrarchids with lakes in areas dominated by other fish taxa may provide great insights about the overall patterning of the lake food webs.

Finally, as with most taxa, we know much less about taxa in the tropics than their non-tropical counterparts. Tantalizing work by a few have shown the potential richness of ecological interactions that abound in the tropical odonate fauna (Fincke 1992a, 1992b, 1994; Suhling *et al.* 2004, 2005). The periodicity of a long wet and dry seasons may have profound effects on the types of life histories and ecologies that develop in the tropics and may have forced taxa to evolve very different ecological solutions to such problems that are unknown to many temperate taxa.

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