The Distribution of Dragonfly Larvae in a South Carolina Stream: Relationships With Sediment Type, Body Size, and the Presence of Other Larvae

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RESEARCH

The Distribution of Dragonfly Larvae in a South Carolina Stream: Relationships With Sediment Type, Body Size, and the Presence of Other Larvae

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ABSTRACT. Dragonfly larvae were sampled in Little Creek, Greenville, SC. The distributions of five common species were described relative to sediment type, body size, and the presence of other larvae. In total, 337 quadrats (1 m by 0.5 m) were sampled by kick seine. For each quadrat, the substrate was classified as sand, sand-cobble mix, cobble, coarse, or rock, and water depth and distance from bank were measured. Larvae were identified to species, and the lengths of the body, head, and metafemur were measured. Species were distributed differently across sediment types: sanddragons, *Progomphus obscurus* (Rambur) (Odonata: Gomphidae), were common in sand; twin-spotted spiketails, *Cordulegaster maculata* Selys (Odonata: Cordulegastridae), preferred a sand-cobble mix; Maine snaketails, *Ophiogomphus mainensis* Packard (Odonata: Gomphidae), preferred cobble and coarse sediments; fawn darners, *Boyeria vinosa* (Say) (Odonata: Aeshnidae), preferred coarse sediments; and Eastern least clubtails, *Stylogomphus albistylus* (Hagen) (Odonata: Gomphidae), preferred coarse and rock sediments. *P. obscurus* and *C. maculata* co-occurred more frequently than expected by chance, as did *O. mainensis*, *B. vinosa*, and *S. albistylus*. Mean size varied among species, and species preferences contributed to differences in mean size across sediment types. There were significant negative associations among larval size classes: small larvae (<12 mm) occurred less frequently with large larvae (>15 mm) than expected by chance, and large larvae were alone in quadrats more frequently than other size classes. Species may select habitats at a large scale based on sediment type and their functional morphology, but small scale distributions are consistent with competitive displacement or intraguild predation.

Key Words: dragonfly, Odonata, habitat selection, niche partitioning

Competition for resources is an important factor in larval dragonfly communities, causing density-dependent growth and mortality (Crowley et al. 1987, Johnson et al. 1987, McPeek 1998). Interspecific competition among larvae is reduced by species differences in habitat selection. Even within a single pond or stream, larvae of different species exploit microhabitats that differ in physical characteristics like water velocity and sediment type (Eggers 2012), biological characteristics like the cover of emergent, floating, or submerged macrophytes (Remsburg and Turner 2009), the presence of detritus and downed snags (Hawking and New 1999, Burcher and Smock 2002), and chemical characteristics like oxygen availability and the concentration of certain pollutants (Hofmann and Mason 2005). These differences in habitat selection often correlate with pronounced adaptations in larval morphology. Corbet (1999, p. 151–155) categorized larvae as claspers, sprawlers, hiders, and burrowers based on behavior, morphology, and occupancy of different habitats. Indeed, the short, stout legs of gomphid and cordulegastrid larvae—which are so well adapted for burrowing—necessitate dramatic shifts in allometric growth to the adult stage (Leipelt et al. 2010). Some differences in habitat selection are the result of competition and resource partitioning, as species shift habitat or resource use in the presence of other species (Mahato and Johnson 1991, Suhling 1996). As such, some morphological differences may even be the result of "the ghost of competition past" (Connell 1980) and character displacement.

Differences in habitat selection also occur within species, among different larval instars. In burrowing species, small instars typically prefer sediments with smaller particle sizes than larger instars (Worthen et al. 2003, Marczak et al. 2007). These patterns may be a function of physical efficiencies; smaller larvae may burrow better in fine sediments than coarser sediments (Marczak et al. 2007). This partitioning may also result, however, from competitive displacement (Suhling 1996) or predator avoidance (Suutari et al. 2004).

Dragonflies are voracious predators, and they consume one another as both larvae and adults. Intraguild predation (IGP) and cannibalism are important sources of larval mortality (Crumrine and Crowley 2003, Suutari et al. 2004) and can affect everything from individual behavior to habitat selection, community patterns, and evolutionary trajectories. Because smaller species and younger instars are particularly susceptible to predation (Crowley et al. 1987, Hopper et al. 1996, Padeffke and Suhling 2003, Ilmonen and Suhonen 2006, Crumrine 2010a, Suhling and Suhling 2013, Witt et al. 2013), they might be expected to avoid habitats used by larger larvae (Crumrine 2005). Such habitat partitioning, in addition to the variety of indirect effects that can occur among intraguild predators that consume one another and their own species, can reduce both predatory and competitive exclusion and promote coexistence (Crumrine 2010b). The presence of predatory odonate larvae may even cause behavioral and morphological divergence between smaller prey species (McPeek 1995).

Describing the primary correlates of larval habitat selection is a first step in understanding whether physical characteristics, like sediment type and water flow, or biological factors, such as competition or IGP, are more important determinants of habitat selection and species coexistence in a given system. Most studies on larval habitat selection, however, have examined the effects of physical and biological factors separately. In this study, we described the distribution of odonate larvae in a South Carolina stream as functions of both physical characteristics (sediment type and water depth) and biological factors (the presence of other larvae). In addition, we examined how these patterns varied across species and larval size classes. Although species preferred different sediment types, sediment had little effect on the distribution of different size classes. Rather, the distribution of small larvae was inversely related to the distribution of large larvae, consistent with strong competitive or predatory effects.

Materials and Methods

Odonate larvae were sampled by kick seine in June and July of 2013, in Little Creek on the Furman University campus in Greenville County, SC (34° 55.26' N, 82° 26.07' W, elevation: 330 m). Little Creek is a first order stream originating approximately 2 km upstream on Paris Mountain (elevation: 640 m), a monadnock 10 km N of Greenville, SC. Little Creek runs through a mix of suburban development and woodland before reaching campus, where it runs through a stand of secondary forest dominated by tulip poplar, *Liriodendron tulipifera* L., white oak, *Quercus alba* L., and Virginia pine, *Pinus virginiana* Mill. It is a typical silt-laden, well-scoured suburban stream with highly eroded banks; the sediment is mostly sand, with occasional exposed bedrock, rocky riffle areas, and deeper (1 m) pools. Scouring and erosion eliminate rooted macrophytes, and detritus only accumulate in deeper pools. Over the 2-mo sampling period, 31 plots were sampled on 27 d. Each plot was a 15 m reach of stream. In each plot, three transects were established across the stream at approximately 5 m intervals. Typically, three quadrats (1 m × 0.5 m) were sampled along each transect, at each bank and in the middle of the channel (9 samples per plot). In broad areas, an additional quadrat was sampled in the channel on each transect (12 samples per plot). In total, there were 337 quadrats sampled in 31 plots. For each sample, a quadrat was thoroughly disturbed by kicking the sediment and overturning rocks; larvae, detritus, and sediment floated into the seine. Larvae were gleaned from each sample by hand and identified to species. The body length, head width, and length of a metafemur of all larvae were measured with Vernier calipers (Swiss Precision Instruments, Inc., Los Angeles, CA). After processing, larvae were released downstream from the plot, and transects were sampled in a downstream to upstream sequence, to reduce the possibility of recapture.

For each quadrat, water depth in the center of the quadrat, distance from bank to the center of the quadrat, and sediment type were recorded. Sediment type was qualitatively classified into the following broad categories: sand, sand-cobble mix, cobble, coarse, or rock. Sand was sediment consisting almost entirely of sand. Cobble was sediment consisting of pea-sized gravel. Sand-cobble mix was sediment which was a mixture of sand and cobble. Sediment was classified as coarse if it consisted of large gravel (> pea-sized) to medium-sized rocks (<10 cm diameter). Rock designated quadrats with large rocks (>20 cm diameter) or bedrock.

Analyses were limited to the five most common species: common sanddragons, *Progomphus obscurus* (Rambur) (Odonata: Gomphidae); twin-spotted spiketails, *Cordulegaster maculata* Selys (Odonata: Cordulegastridae); Maine snaketails, *Ophiogomphus mainensis* Packard (Odonata: Gomphidae); fawn darners, *Boyeria vinosa* (Say) (Odonata: Aeshnidae); and Eastern least clubtails, *Stylogomphus albistylus* (Hagen) (Odonata: Gomphidae). These genera are easily identified at all but the earliest instars. In addition, in this region of the South Carolina piedmont, *Progomphus*, *Ophiogomphus*, and *Stylogomphus* are represented by single species, making species identification unambiguous. *Boyeria* and *Cordulegaster* are represented by two and three species, respectively, but *B. vinosa* and *C. maculata* represent over 99.9% and 99.1% of the individuals sampled in the area in previous surveys (Worthen 2002). So, although species identification was done in the field with only a hand lens, there was a high degree of confidence for identifying even small instars of these five species.

SPSS software was used for statistical analyses (SPSS 2010). The first set of comparisons examined the effects of sediment type, and the presence of other species, on species distributions. To test the hypothesis that species prefer different sediment types, samples were pooled across plots and transects and the total numbers of individuals of each species found in each sediment type were compared with a χ^2 test of independence. The sediment preference of each species was determined in separate χ^2 goodness of fit tests, by comparing the number of individuals (in a species) in each sediment type to the number expected based on the frequency of quadrats sampled in each sediment type (random placement model). The effect of other species was described with pair-wise χ^2 tests of independence, to determine whether the presence of one species in a sample was independent of the presence of another species in a sample (2 × 2 "presence-absence" contingency tests, with pair-wise expected frequencies computed as the product of the independent frequencies).

The distribution of larvae based on larval size was also examined. Two-way analysis of variance (ANOVA) and Tukey's mean comparison tests were performed to describe how each metric of larval size (body length, head width, and metafemur length) varied across species and sediment types. However, as *C. maculata* was absent from cobble sediments and *P. obscurus* was absent from coarse sediments, the interaction matrix had "empty cells," confounding the interpretation of an interaction effect. As such, only the main effects were analyzed. To describe whether the effect of sediment type on larval size varied among species (the interaction effect), the effect of sediment type on each larval size metric was analyzed in one-way ANOVA for each species, and the results were compared. In addition, Spearman rank correlations were used to describe the relationships between larval size (body length, head width, and metafemur length) and water depth or distance from bank.

Two analyses were conducted to examine patterns of co-occurrence among the four larval size classes (<9 mm, 9–12 mm, 12–15 mm, and >15 mm) and test the hypothesis that small larvae avoid large larvae. First, for each larva, the number of other individuals of each size class, present in the same quadrat, was tallied. For example, in a quadrat that contains three individuals of size class 2, each individual co-occurred with two other members of size class 2, for a total of six co-occurrences of "size class 2 with size class 2." If a single individual of size class 4 was also present, then three incidences of "size class 4 with size class 2" were tallied, as well; even though there was only one individual of size class 4. As such, the total number of co-occurrences by a size class exceeded the total number of larvae in that size class. However, this maintains the independence of each co-occurrence and describes the frequencies at which a single larvae of a given size class co-occurred with individuals in each size class. The observed frequency distribution of co-occurrences by a size class was compared with the expected distribution of co-occurrences based on the relative frequencies of size classes in the data set (random placement model) using a χ^2 goodness-of-fit test. In addition to compare rates of co-occurrence, the frequencies at which each size class was alone in quadrats were compared. A χ^2 goodness-of-fit test was used to compare the number of larvae in each size class that were in samples to expected values based on the relative frequencies of size classes in the data set (random placement model).

Results

In total, 241 larvae from the five target species were present in 337 samples, with sediment characterized as: sand ($n = 169$), sand-cobble mix (77), cobble (26), coarse (31), and rock (34). Across the entire community, species were not distributed independently across sediment types (χ^2 test of independence, $\chi^2 = 96.732$, df = 16, $P < 0.0001$; Fig. 1). When analyzed separately, most species exhibited significant, nonrandom distributions across sediment types. Over 50% of *S. albistylus* larvae occurred in rocky and coarse sediments, significantly more frequently than these sediment types occurred in the data set (18%, $\chi^2 = 135.50$, df = 4, $P < 0.0001$; Fig. 1). *B. vinosa* was significantly more common in coarse sediments ($\chi^2 = 87.95$, df = 4, $P < 0.0001$; Fig. 1), and *O. mainensis* was significantly more common in coarse sediments and cobble ($\chi^2 = 71.20$, df = 4, $P < 0.0001$; Fig. 1) than expected by chance. *C. maculata* was more common in the sand-cobble mix than coarser sediment types ($\chi^2 = 9.66$, df = 2, $P < 0.05$), after pooling categories so expected occurrences were > 5 (Sokal and Rohlf 1981). Although more than 60% of *P. obscurus* occurred in sand
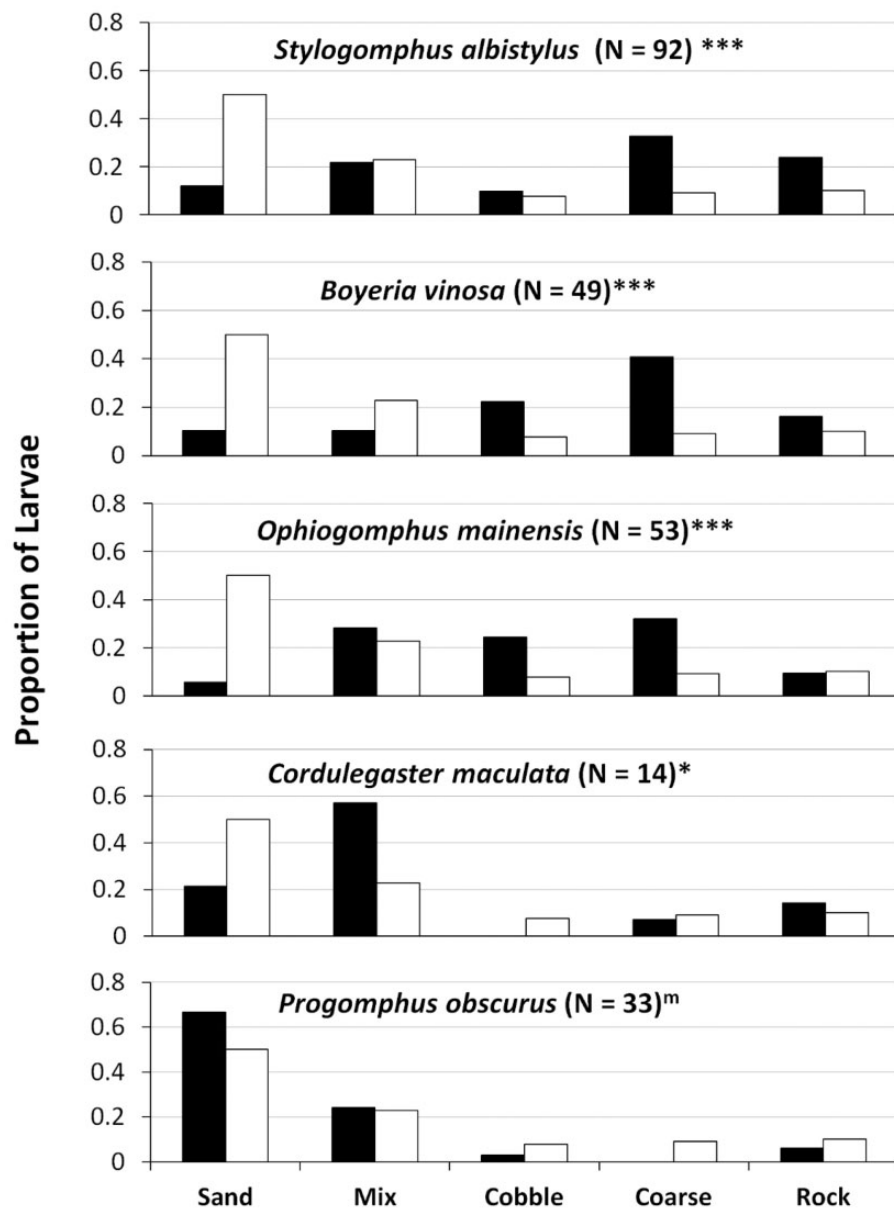
Fig. 1. Proportions of larvae of five odonate species found in five sediment types and comparisons with random placement models. Black bars, observed proportions; open bars, proportions expected based on the frequency of samples in each sediment type ($N = 337$). Significance levels from Chi-square goodness-of-fit tests: ***$P < 0.0001$; *$P < 0.05$; "m," $P = 0.06$.

(Fig. 1), this was only marginally significantly different from expected values because sandy sediments represented nearly 50% of the samples ($\chi^2 = 5.74$, df $= 3$, $P = 0.06$, after pooling categories so expected occurrence were > 5; Sokal and Rohlf 1981).

Species were not distributed independently of one another across quadrats. *P. obscurus* and *C. maculata* co-occurred more frequently than expected by chance ($\chi^2 = 3.85$, df $= 1$, $P = 0.05$), as did the other three species that were most common in coarser sediments (*S. albistylus* vs. *O. mainensis*, $\chi^2 = 30.69$, df $= 1$, $P < 0.0001$; *S. albistylus* vs. *B. vinosa*, $\chi^2 = 32.39$, df $= 1$, $P < 0.0001$; and *B. vinosa* vs. *O. mainensis*, $\chi^2 = 59.9$, df $= 1$, $P < 0.0001$). All other pair-wise comparisons were insignificant. There were no pairwise comparisons where species occurred together less frequently than expected by chance.

ANOVA were used to describe how three size metrics (body length, head width, and metafemur length) varied between species and sediment types. Again, as two species were absent from two sediment categories, only the main effects were evaluated (using Type III Sum of Squares which evaluates each effect after accounting for other effects in

the model; SPSS 2010). Species differed significantly in all three size metrics ("SPECIES" effects, ANOVA, Table 1a). Larvae of *S. albistylus* were smaller than the other species in each metric (Table 1b). *P. obscurus* and *C. maculata* were significantly longer than larvae of the other species, but *C. maculata* larvae had wider heads and longer metafemora than *P. obscurus* (Table 1b). There were also significant differences in larvae size across the five sediment types ("SEDIMENT TYPE" effects, ANOVA, Table 1a). In general, larvae in rock substrates were shorter and had narrower heads and shorter metafemora than larvae in sand and sand-cobble mix (Table 1c). These differences in size across sediment classes, however, might be a function of species distributions, as the larger *P. obscurus* and *C. maculata* preferred sand and sand-cobble mix, whereas the smaller *Stylogomphus* preferred rocky sediments. One-way ANOVA were performed on each size metric, for each species, to determine whether the pattern of size-class variation across sediment types varied among species. There were no significant effects of sediment type on any size metric for *P. obscurus*, *C. maculata*, *B. vinosa*, or *S. albistylus* ($P > 0.05$). For *O. mainensis*,

sediment type had a significant effect on body length (df = 4, 48, F = 3.464, P = 0.014) and head width (df = 4, 48, F = 4.301, P = 0.005) but not on metafemur length (df = 4, 48, F = 2.126, P = 0.092). For all measurements, larger *O. mainensis* larvae were in rock and sand sediments, and smaller larvae were in sand-cobble mix.

When all larvae were included in the analysis, all three larval size metrics were significantly inversely correlated with water depth; body length and metafemur length were significantly inversely correlated with distance from the bank (Spearman rank correlations, Table 2). These relationships were largely driven by strong patterns in *P. obscurus* and *C. maculata*; relationships were very weak in the other species (Table 2). There was only a weak, insignificant relationship between water depth and distance from the bank (Pearson r = 0.100, df = 339, P = 0.07), so partial correlations were not performed.

Larvae were subdivided into four size classes with roughly equal frequencies: "<9 mm" (n = 56), "9–12" mm (71), "12–15 mm" (54), and "> 15 mm" (60) to examine their patterns of co-occurrence. Larvae in the smallest size class co-occurred more frequently with other small larvae, and less frequently with large larvae (size 4), than expected by their relative abundances ($\chi^2 = 18.51$, df = 3, $P < 0.001$; Fig. 2). The

same pattern was seen in the second size class, with significantly fewer co-occurrences with large larvae than expected ($\chi^2 = 26.23$, df = 3, $P < 0.0001$; Fig. 2). Larvae in size class 3 were also found with large larvae less frequently than expected but not to a statistically significant degree ($\chi^2 = 6.47$, df = 3, $P > 0.05$; Fig. 2). Although large larvae were similar in relative abundance to the other size classes, they co-occurred with other larvae much less frequently than smaller size classes (77 co-occurrences vs. 135, 206, and 115, respectively). Indeed, large larvae were found alone in quadrats at a significantly higher rate (25/60 = 41.6%) than larvae in the other size classes (small = 21.4%, class 2 = 15.5%, class 3 = 25.9%; $\chi^2 = 9.22$, df = 3, $P < 0.05$). As large larvae were avoided by all other size classes to similar degrees, the distribution of co-occurrences with other size classes mirrored their relative abundances in the data set ($\chi^2 = 1.76$, df = 3, $P > 0.05$; Fig. 2).

Discussion

The goal of this survey was to describe how the larval distribution of common dragonfly species related to sediment characteristics, the distribution of other dragonfly species, and the presence of other dragonfly larvae from different size classes. Interestingly, the five most common species showed significant differences in sediment type preferences. Different species preferred each of the five sediment types to different degrees, creating a pattern of habitat partitioning. These patterns of habitat selection based on sediment characteristics were consistent with previous reports.

As the name "common sanddragon" implies, *P. obscurus* is known to prefer sandy sediments (Byers 1939, Huggins and DuBois 1982, Burcher and Smock 2002, Worthen et al. 2003), specifically preferring sands with mean particle sizes between 0.5 and 1.0 mm (Huggins and DuBois 1982, Worthen et al. 2003). In our study, *P. obscurus* showed only a marginally significant preference for sandy sediments. Given the strong preferences demonstrated in the literature, however, we believe the weakness of our pattern is simply a statistical artifact. Although 66% of *P. obscurus* larvae were found in sandy sediments, it was difficult to resolve this preference statistically because over 50% of the samples were from this sediment type. There were also significant inverse relationships between the size of *P. obscurus* larvae and distance from bank. This may be a consequence of smaller *P. obscurus* larvae preferring silt with smaller particle sizes (Worthen et al. 2003) where they have increased burrowing efficiency (Marczak et al. 2007). Silts tend to accumulate in deeper pools in the channel, and sands dominate on the bank—particularly at point bars. However, the relationship between water depth and distance from the bank is weak, probably because deeper water can be found in both the center of the stream channel and in pools that form along cut banks or beneath undercut stumps along the bank. As such, these relationships between body size, water depth, and distance from the bank may not reflect patterns with particle size but could simply be the result of late instars moving close to the bank to emerge.

Like *Progomphus*, *Cordulegaster* species are shallow burrowers (Corbet 1999, p. 157). However, they typically prefer slightly coarser sediments and a broader range of habitats. For example, *Cordulegaster*

Table 1. (a) Summary of ANOVA (type III sum of squares) describing the variation in mean larval body size as functions of species and sediment type, and comparisons of body size metric means (b) across species and (c) across sediment types (means followed by the same letter are not significantly different, Tukey's test, P = 0.05)

(a) ANOVA summary		Body length		Head width		Metafemur length (mm)	
	df	F	P	F	P	F	P
Species	4	32.77	0.0001	17.73	0.0001	1.05	0.0001
Sediment type	4	3.84	0.005	5.39	0.0001	5.12	0.001
Error	232						

(b) Species Means (± 1 SD)	N	Body length (mm)	Head width (mm)	Metafemur length (mm)
S. albistylus	92	9.7 ± 2.7 a	2.5 ± 0.7 a	2.1 ± 0.7 a
B. vinosa	49	11.8 ± 5.1 ab	3.5 ± 1.2 b	2.3 ± 0.9 a
O. mainensis	53	13.8 ± 3.1 b	3.6 ± 1.1 bc	3.0 ± 0.9 b
C. maculata	14	17.5 ± 2.7 c	4.1 ± 0.7 c	3.6 ± 0.6 c
P. obscurus	33	18.2 ± 4.4 c	3.5 ± 0.6 bc	2.9 ± 0.6 b

(c) Sediment Means (± 1 SD)	N	Body length (mm)	Head width (mm)	Metafemur length (mm)
Rock	39	9.8 ± 3.7 a	2.6 ± 0.9 a	2.1 ± 0.7 a
Coarse	68	11.3 ± 3.0 ab	3.0 ± 0.7 ab	2.4 ± 0.7 ab
Cobble	34	13.3 ± 5.3 bc	3.6 ± 1.3 c	2.8 ± 1.0 c
Sand-cobble mix	56	14.1 ± 4.7 c	3.6 ± 1.3 c	2.9 ± 1.1 c
Sand	44	14.9 ± 5.6 c	3.2 ± 0.8 bc	2.5 ± 0.7 bc

Table 2. Spearman rank correlations between three metrics of larval size (body length, head-width, and metafemur length) and the depth of water and distance from bank of the quadrat where larvae were found

Species	N	Correlations with distance from bank			Correlations with depth		
		Body length	Head width	Metafemur length	Body length	Head width	Metafemur length
All larvae	241	**−0.163***	−0.113	**−0.145***	**−0.228****	**−0.206****	**−0.198****
S. albistylus	92	−0.168	**−0.206***	**−0.261***	−0.096	−0.087	0.039
B. vinosa	49	0.195	0.167	0.100	−0.171	−0.123	−0.018
O. mainensis	53	−0.003	0.143	0.129	−0.126	0.016	−0.028
C. maculata	14	−0.258	−0.302	**−0.588***	−0.397	−0.464	−0.518
P. obscurus	33	**−0.508****	**−0.474****	**−0.438***	−0.302	−0.300	−0.291

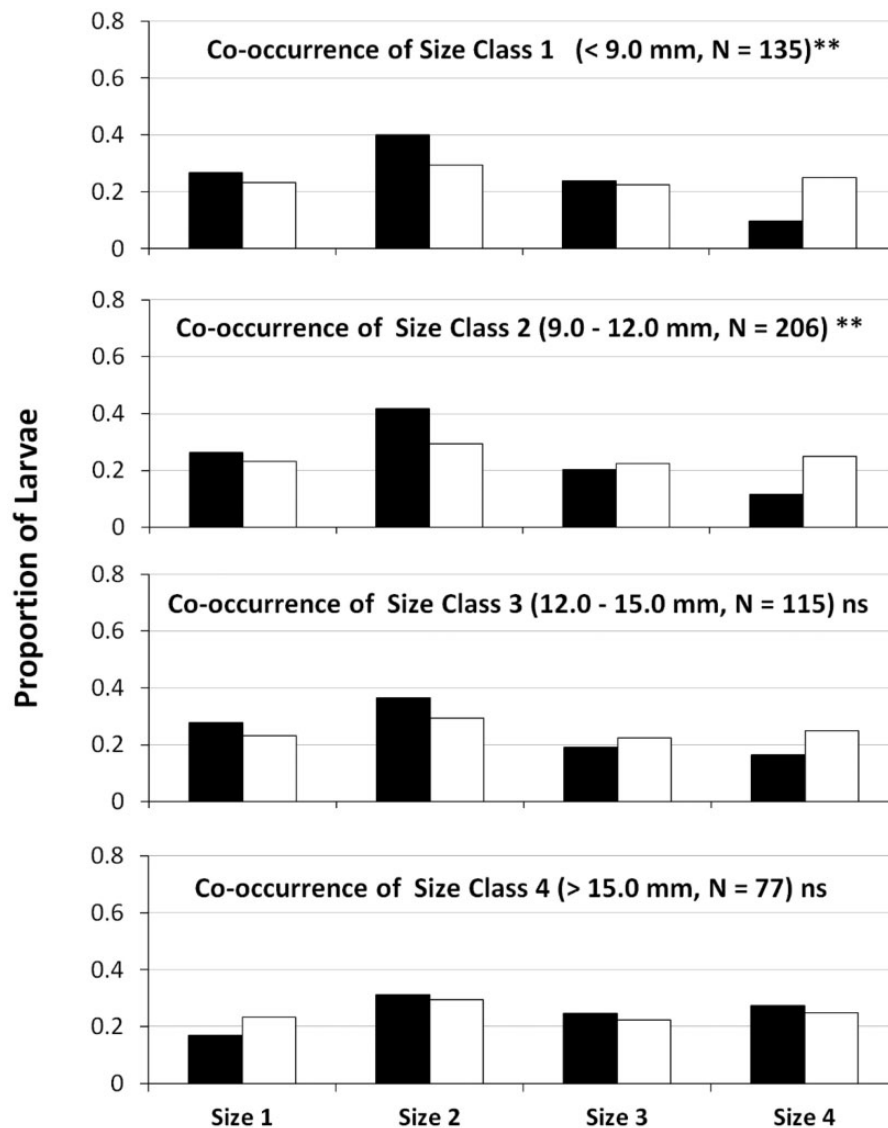Significant relationships are in bold (*$P < 0.05$; **$P < 0.01$).

Fig. 2. Proportion of larvae of four size classes co-occurring with other larvae in each size class and comparisons with random placement models. Black bars, observed proportions; open bars, proportions expected based on the frequency of each size class. Significance levels from Chi-square goodness-of-fit tests (df = 3): **$P < 0.001$; NS, $P > 0.05$.

boltonii can bury themselves effectively in sediments with mean particle sizes of 1.0–2.0 mm (Corbet 1999, p. 158–159), and Burcher and Smock (2002) found that *C. maculata* was found in equal abundance in sand, silt, and debris dams (though not on snags). Although our sample of *C. maculata* is small ($N = 14$), our results are consistent with these findings. Most of the individuals (57%) were found in sediments with a sand-cobble mix, but others were found in sandy (21%) to rocky habitats (14%).

The two other gomphid species, *O. mainensis* and *S. albistylus*, preferred cobble and coarse and coarse and rock sediments, respectively. Although they both have the general aspect of Corbet's (1999) "burrower" category, little is known of the habitat preferences of these particular species. The fore and middle tibiae of all *Ophiogomphus* species bear strong spines, suggesting a burrowing habit (Needham et al. 2014, p. 244). Although some species like *Ophiogomphus howei* are found in sand and gravel (Tennessen 1993), others like *Ophiogomphus susbehcha* are found in substrates with cobbles and boulders (Vogt and Smith 1993). Gibbs et al. (2004) report that *O. mainensis* is found more in headwater streams than downstream sites and allude to possible effects

of sediment preference but also list other habitat characteristics that could be responsible for this distribution. Needham et al. (2014, p. 296) state that *Stylogomphus* larvae are found in sand and gravel in rocky streams, but this is a rather general description of habitat preference. Our study certainly confirms these generalities but more specifically defines the sediment type preferences of these species.

Like all aeshnids, *B. vinosa* is characterized as a "clasper" by Corbet (1999, p. 150–151). Needham et al. (2014) report that larvae are typically found under rocks and in heavier debris. In the upstate of South Carolina, *B. vinosa* abundance correlates with the percentage of sandy sites in tributaries (Worthen et al. 2001) and so seems like a habitat generalist. Our results confirm these descriptions; although *B. vinosa* exhibited a preference for coarse sediments, it was found in reasonable numbers in all sediment types.

Curiously, although species tended to use different sediment types, there were strong positive associations between certain species pairs at the quadrat scale. The two species that used sand and sand-cobble mix the most. Indeed, *P. obscurus* and *C. maculata* were found in the same quadrat more often than expected by chance. Likewise, the other three

species that used coarser sediments were also found in the same quadrats more often than expected. And even though some pairs of species had very different sediment type preferences, like *P. obscurus* and *B. vinosa*, there were no species pairs that occurred significantly less frequently than expected by chance. So, it seems unlikely that habitat partitioning based on sediment type is being maintained by interspecific competition, which would create negative associations among species (particularly at small scales).

Although certain species tended to co-occur, there were strong negative associations among larvae of different size classes. Larvae in the two smallest size classes (<9.0 mm and 9.0–12.0 mm) co-occurred with large larvae (>15 mm) significantly less frequently than expected by chance. This could be due to developmental changes in habitat preference, competition, or intraguild predation. If larvae move to different sediments as they grow, then small and large larvae would rarely be found together. Developmental shifts can be largely excluded, however, because for four of the five species, there were no significant differences in larval size across sediment types. Although there were significant "sediment" effects on body size in the two-way ANOVA, those patterns were likely a consequence of species preferences. *P. obscurus* and *C. maculata* were the largest species, significantly larger than the smallest species, *S. albistylus*. These two large species preferred sand and sand-cobble mix, respectively, whereas *S. albistylus* was the most abundant species in rock and coarse sediments (representing 51 of the 107 larvae collected in these sediment types). As such, the significant "sediment" effect on larval size in the two-way ANOVA and the fact that larvae in coarse and rock sediments were significantly smaller than larvae in sand and sand-cobble mix (Tukey's mean comparison) are probably not the result of developmental shifts but are the spurious consequences of large and small species selecting different habitats.

The negative association between small and large larvae is most consistent with the effects of competition and predation. Most odonate larvae are gape-limited generalists that can feed on progressively larger prey as they grow (Corbet 1999, p. 106–107). By avoiding large larvae, small larvae escape competition with large larvae for the small preys they depend upon. In addition, by avoiding large larvae, small larvae avoid intraguild predation (Crumrine 2005), which is known to be a significant agent of mortality in this community (Crumrine and Crowley 2003). Large larvae were generally avoided by other larvae in this survey. They were alone in quadrats significantly more frequently than their relative abundance would predict. Habitat partitioning by size class can reduce both predatory and competitive exclusion and promote coexistence (Crumrine 2010b).

In conclusion, these five common odonate species tended to prefer different sediment types, correlating with differences in their functional morphology. However, pairs of species with similar sediment preferences often co-occurred and no pair of species showed significant negative associations that would indicate competitive or predatory effects at the species level. Rather, negative associations occurred between different size classes. Small larvae co-occurred with other small larvae, avoiding large larvae that were, as a consequence, often alone. These relationships among size classes are not caused by developmental shifts in habitat selection but are consistent with strong competitive or predatory interactions between larvae of different sizes.

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