Larval habitat associations of
Progomphus obscurus at two spatial scales
(Odonata: Gomphidae)

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ABSTRACT

Progomphus obscurus is one of the most abundant dragonflies in South Carolina, USA. We collected dragonfly larvae from 127 sites in the Enoree River and nine of its tributaries, and correlated the abundance of *P. obscurus* larvae with physical and chemical characteristics of these streams. As expected for this burrowing species, larval abundance varied among streams and was significantly correlated with mean silica concentrations and the proportion of sandy-bottom sites in these streams. We also examined habitat associations on a smaller spatial scale. We sampled *P. obscurus* larvae by kick-seine from fine sand, coarse sand, and pebble sediment types in five sites in the Enoree River basin. Larvae were collected, preserved in 75% EtOH, and their body lengths were measured. Sediment samples were collected and Ro-tapped, and mean particle size was calculated. Larvae were present in a greater fraction of the 'fine sand' samples than 'pebble' samples. In addition, abundance was inversely correlated with mean particle size. Mean larvae size was weakly correlated with mean particle size, and inversely correlated with larval abundance. This species is associated with sandy-bottom streams and fine sandy sediments within streams. Changes in sediment characteristics resulting from channelization, increased flooding, and increased stream flow could change sediment composition and impact the abundance of this common dragonfly species.

INTRODUCTION

Identifying the determinants of habitat selection by larval odonates is complicated by the wide array of potentially important physical and biotic factors acting in these dynamic and diverse systems. Odonate larvae are a primary foodstuff of centrarchid fishes and predation by fishes can reduce larval survivorship (Crowder & Cooper 1982; Martin et al. 1991), change community composition (Morin 1984) and alter patterns of behavior and habitat selection. For instance, many odonates will reduce their activity (Steiner et al. 2000) or seek refugia in the presence of predatory fish (Wiseman et al. 1993; Suhling 1999). Competition among dragonfly larvae may also limit distributions and affect habitat selection.

Baumann (2001) found that *Somatochlora alpestris* (Selys), *S. arctica* (Zetterstedt), and *Leucorrhinia dubia* (Vander Linden) would coexist at low densities but were not found together at high densities. Suhling (1996) demonstrated that *Onychogomphus uncatus* (Charpentier) shifted from preferred sandy substrates to gravel and stone in the presence of *Gomphus simillimus* Selys or *Cordulegaster boltonii immaculifrons* Selys.

Abiotic factors are also important determinants of habitat selection, particularly those affecting the structural characteristics of the environment. This often leads to rather discrete assemblages of odonates exploiting microhabitats within the same reach (Burcher & Smock 2002), or exploiting reaches with different vegetational characteristics or flow dynamics (Chwala & Waringer 1997). Substrate characteristics are particularly important to the burrowing odonates of streams and rivers (Keetch & Moran 1966). For example, *Erpetogomphus* sp. prefer coarse substrates with stones and pebbles (Stewart et al. 2003), but *Onychogomphus uncatus* and *Gomphus graslinii* Rambur prefer sandier substrates (Suhling 1999; Leipelt & Suhling 2001). These decisions may have immediate survival value. For example, small *O. uncatus* larvae are more susceptible to fish predation in gravel and pebble sediments than in their preferred sandy substrates (Suhling 1996).

Human impacts can have a dramatic affect on these biotic and abiotic variables, and can influence patterns of habitat selection and local odonate abundance. Richter et al. (1997) list the three leading anthropogenic threats to stream eco-systems as altered sediment loads and nutrient inputs, exotic species, and altered hydrologic regimes associated with impoundment operations. In particular, increased runoff and erosion can change stream velocity and sediment load, and change the type, distribution, heterogeneity, and stability of sediments available to burrowing species. For example, dams may reduce downstream sediment load by 80%, while increasing average baseflow (Williams & Wolman 1984). This increases the 'erosive power' of the discharge, resuspending fine sediments and leaving behind a 'coarsened' substrate of pebbles, cobbles, and rocks (Williams & Wolman 1984). This may explain why some dammed rivers have less diverse communities of burrowing odonates relative to undammed rivers (Donnelly 1993). Human activity can also affect stream chemistry. Although many odonates are broadly tolerant to most chemical parameters (Roback & Westfall 1967; Cannings & Cannings 1987; Wallace et al. 1991; Buss et al. 2002), low dissolved oxygen (Steiner et al. 2000), and solutes such as chloride, nitrite, and zinc may limit the distribution of some species (Watson et al. 1982; Carchini & Rota 1985; Ferreras Romero 1988; Worthen et al. 2001a). Because many chemicals become sequestered in the sediment, burrowing species may be exposed to higher concentrations of chemical pollutants than other species.

Progomphus obscurus Rambur is one of the most abundant dragonfly species in streams and rivers of the piedmont of South Carolina, USA, often comprising between 20-40% of the odonate larvae captured in field collections (Worthen 2002, 2003). Categorized as a "shallow burrower" (Corbet 1999: 620), *P. obscurus* digs to 2 cm into the sediment (Huggins & DuBois 1982). It is a habitat specialist, preferring sandy sites (Byers 1939; Needham 1941; Burcher & Smock 2002) with mean particle sizes between 0.625 and 1 mm (Huggins & DuBois

1982). Because of its dependence on sandy substrates, *P. obscurus* might also be particularly responsive to anthropogenic impacts on stream ecosystems. In 1999 - 2001, the interdisciplinary River Basins Research Initiative of Furman University conducted a survey of water quality in the Enoree River and nine of its tributaries in South Carolina, USA. The watershed includes the cities of Greenville and Spartanburg, Paris Mountain State Park, parts of Sumter National Forest, and a matrix of suburban and agricultural landscapes. In 1995, 53.7% of this watershed was forested, 25.6% was cultivated/grassland, and 10.0% was urbanized (Lahlou et al. 1998). However, over the last 20 years, the human population of the Greenville-Spartanburg area has increased by 50%, impervious surface area has doubled, and the amount of farmland converted to development has increased by 400% (Spartanburg County Planning Commission 2000). The region is one of the most rapidly-developing areas of the country, ranking fifth in the nation in a recent survey of urban sprawl (Ewing et al. 2002). As such, this is an excellent region to study anthropogenic effects on aquatic systems.

The tributaries vary in their chemical and physical attributes, largely as a function of human land-use patterns and differences in underlying geology (Andersen et al. 2001; Worthen et al. 2001a, 2001b). Kings Creek and Indian Creek are notably different than the other streams, with significantly higher concentrations of silica, bicarbonate, calcium, and magnesium (Andersen et al. 2001; Worthen et al. 2001b). In addition, these two drainages have sandy substrates throughout, whereas the other streams have a greater variety of substrate types (Worthen et al. 2001b). The objective of our study was to determine whether the physical and chemical differences among these streams correlated with habitat use by *P. obscurus*. In addition, we conducted a subsequent survey of microhabitat selection at five sites to describe the relationships between particle size, larval abundance, and larval size on a smaller spatial scale.

METHODS

Habitat associations with water chemistry at large and small scales

In 1999 - 2000, our multidisciplinary research team conducted a chemical and biological inventory of the Enoree River and selected tributaries to describe the impact of suburban development on water quality. The Enoree River drains a 1,193 km² sixth-order watershed in the piedmont of South Carolina (USA). Odonates were sampled at 127 sites in the Enoree River and nine of its tributaries in May - July 1999 (63 sites) and May - July 2000 (64 sites). These are the months for the greatest recruitment of *Progomphus obscurus* larvae (Phillips 2001). Sampling sites were located upstream from bridge crossings. Organisms were only sampled once at each site. At each site a reach of 50-100 m was sampled by electrofishing with a Smith-Root Electrofisher® for a standard total shocking period of 8 minutes. The substrate was kicked vigorous during shocking intervals and the stunned organisms were collected downstream with a seine (1.5 m x 3.3 m, mesh size: 3.0 mm) and dip nets. Electrofishing can provide accurate estimates

of population size and diversity (Taylor et al. 2001). Odonate larvae were collected, preserved in 75% EtOH, and identified to species using the taxonomic keys of Huggins & Brigham (1982), Merritt & Cummings (1996), Westfall & May (1996), and Needham et al. (2000).

Water samples were collected at each site every week for seven weeks in May - July 1999 or 2000. Although streams were sampled in different years, climatic conditions were very similar. For instance, total rainfall over the 1999 and 2000 sampling periods differed by only 1.5 cm (May - July total rainfall: 1999 = 23.67 cm; 2000 = 22.17 cm; National Weather Service 2003). Cation concentrations – aluminum, calcium, iron, magnesium, manganese, potassium, silicates, sodium, and zinc – were determined with a Varian ICP-AES (Inductively coupled plasma-atomic emission spectrometer). Anion concentrations – phosphate, nitrate, fluoride, bromide, chloride, and nitrate – were measured using a Dionex DX-120 ion chromatograph. Alkalinity, conductivity, pH, temperature, turbidity, total organic carbon, and concentrations of dissolved oxygen and carbonate were also measured. For a complete description of the analytical procedures, see Andersen et al. (2001) or Worthen et al. (2001a).

The relationships between water chemistry and habitat use by P. obscurus were described at two scales. At the stream scale, the mean larval abundance/site of P. obscurus was compared among streams with ANOVA ($n = 127$ sites sampled, distributed across 10 streams). In addition, the stream means for larval abundance/site were correlated with stream means for all chemical parameters and with discriminant functions describing the chemical variability among streams (Worthen et al. 2001b). At the site scale, abundance/site of P. obscurus was correlated with site means for all chemical parameters. Finally, the range of exposure for P. obscurus for each chemical parameter is also reported, and these are compared with those of Roback (1974).

Habitat associations with sediment type at large and small scales

At each sampling site, the substrate was categorized as 'sand' ($n = 91$) or 'pebble' ($n = 36$). The relationship between P. obscurus abundance and variation in sediment types at a large scale (among streams) was described by correlating mean larval abundance and frequency of sites occupied in each stream with the percentage of sites in each stream categorized with 'sand' substrates. The relationship between P. obscurus abundance at a smaller scale (among sites) was described by comparing the frequency of 'sand' and 'pebble' sites used by P. obscurus with a χ^2 contingency test. The mean abundance of P. obscurus larvae ($\log_{10}$ transformed) in the two sediment types were compared with a Student's t-test. Because the number of unoccupied samples (larval abundance = 0) varied significantly across sediment types, we chose to exclude values of zero in the larval abundance comparisons. This makes the abundance comparison completely independent of frequency effects, and explicitly tests for difference in abundance in occupied habitats.

In summer 2002 we conducted a more explicit survey of small-scale habitat use by P. obscurus larvae. Larvae and sediment samples were collected from five sites in the Enoree River Basin in South Carolina that had an abundance of dragonflies

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Table 1. Mean abundance/site of *Progomphus obscurus* larvae ($\log_{10}$ backtransformed) and the percentage of sites used in the Enoree River (ER) and nine of its tributaries, listed from north to south: Upper Enoree (UE), Beaverdam Creek (BD), Mountain Creek (MC), Brushy Creek (BC), Rocky Creek (RC), Gilder Creek (GC), Durbin Creek (DC), Indian Creek (IC), and Kings Creek (KC). Also presented are the means (± 1 s.d.) for chemical variables that were significantly correlated with the first discriminant function (silica, Si^{4+} [mg·l⁻¹], and bicarbonate, HCO_3^- [mg · l⁻¹]) and second discriminant function (dissolved oxygen, DO [mg·l⁻¹]), and the percentage of sites categorized with 'sand' substrates in each stream. Spearman correlations between these variables and *P. obscurus* abundance and frequency are listed; *: $p < 0.05$; **: $p < 0.01$.

Stream	Sites	Abundance	% sites used	Si^{4+}	HCO_3^-	DO	% `sand´ sites
UE	13	5.5	70.1	7.3±0.9	13.9±4.5	7.8±0.3	53.8
BD	10	5.9	60.0	4.8±1.0	9.4±2.4	8.3±0.3	60.0
MC	14	3.4	57.1	4.8±0.7	11.4±4.3	7.8±0.5	21.4
BC	14	5.3	64.9	5.9±0.9	17.8±2.5	7.0±0.7	78.6
RC	12	3.2	66.7	5.0±0.8	14.7±2.0	7.4±0.5	58.3
GC	14	14.1	71.4	5.8±1.5	16.7±5.8	8.0±0.5	57.1
DC	15	23.4	86.7	8.9±1.5	22.7±7.9	6.2±0.4	100.0
IC	10	7.4	80.0	16.1±2.3	65.3±11.6	6.1±0.6	100.0
KC	8	15.1	87.5	19.2±2.5	49.9±7.4	6.4±0.7	100.0
ER	17	7.2	76.5	6.4±0.7	21.9±6.5	6.4±0.7	94.1
Correlations							
w / abundance				0.685*	0.418 n.s.	-0.648*	0.669*
w / % sites used				0.903**	0.867**	-0.721*	0.767**

in previous years. At each site, larvae were collected from three different sediment types using a kick seine (1 m x 1 m, mesh size 3 mm). The sediment types were categorized as: 'fine sand', 'coarse sand', and 'pebble'. Although some gomphids also select habitats based on the presence of detritus (Leipelt & Suhling 2001), the abundance of larval *P. obscurus* does not correlate with detritus or the organic content of the sediment (Huggins & DuBois 1982). The fine sand was generally located in pools of slow-moving water, the coarse sand was located along sand bars, and pebbles were found in riffle areas in fast-moving water. Sampling was standardized by sampling a constant area in front of the seine; ca 1 m x 0.25 m. In each sediment type, three samples of invertebrates and sediment were collected, totaling nine habitats sampled per site. Each of the five sites was sampled on two different days for a total of 90 samples (5 streams x 2 days x 9 habitats = 90 samples). *P. obscurus* larvae were identified, preserved in 75% ethanol, counted, and measured for length. Sediment samples were also collected at each sampling location. They were dried at 60°C for one week, weighed, and Ro-tapped through a sieve series using 14 VWR Scientific USA Standard Testing Sieves. Mean particle size for each sample was calculated as: $\Sigma[ps_i \times p_i]$; where 'ps_i' = particle size for sieve 'i' and p_i = percentage of the total sample weight in sieve 'i' (weight of

sediment in sieve 'i' / total weight of sediment in the series of 14 sieves). ANOVA were used to describe differences in mean particle size among sediment type categories. The frequency of sediment type use by *P. obscurus* larvae was compared with a χ^2 contingency test. The effects of 'stream' and 'sediment type' on mean larval abundance ($\log_{10}$ transformed) in occupied sites (no zeroes included, $n = 44$) were described with ANOVA.

The designations of 'fine', 'coarse', and 'pebble' were relative terms applying to sediments within a site. However, there was overlap between these categories. For instance, three samples characterized as 'pebble' had mean particle sizes below the mean value for 'coarse sand'. Given the fairly continuous range of sediment sizes across samples, we also conducted correlation analyses among mean particle size, *P. obscurus* abundance, and the mean length of *P. obscurus* larvae. These analyses were limited to samples containing larvae ($n = 44$), and all variables were $\log_{10}$ transformed prior to analysis.

RESULTS

Habitat associations with water chemistry at large and small scales

The mean abundance/site of *Progomphus obscurus* larvae differed significantly among streams ($\log_{10}$ transformed data, ANOVA $F = 2.08$, $df = 9, 117$, $p = 0.04$, Table 1), and was significantly correlated with differences in water chemistry. Mean *P. obscurus* abundance correlated with stream centroid scores along the first discriminant function (DFA1; $r_s = 0.673$, $p = 0.03$ $n = 10$), and with concentrations of bicarbonate, and silica (Table 1). The mean abundance of *P. obscurus* did not correlate with either the second discriminant function (DFA2; $r_s = -0.042$, n.s.) nor dissolved oxygen (Table 1). The percentage of sites used by *P. obscurus* larvae in each stream also correlated with DFA1 ($r_s = 0.915$, $p = 0.001$) and concentrations of silica and bicarbonate (Table 1). And, although the percentage of sites used did not correlate with DFA2 ($r_s = -0.188$, n.s.) it was inversely correlated with dissolved oxygen concentration (Table 1).

At the site scale, the abundance of *P. obscurus* larvae correlated with several variables, including pH, conductivity, and concentrations of sodium, calcium, magnesium, bicarbonate, and silica (Table 2). In addition, larvae were found at sites with more extreme chemical properties than previously reported for this species (Table 2).

Habitat associations with sediment type at large and small scales

Streams differed in the percentage of sites with 'sand' substrates ($\chi^2 = 38.235$, $p = 0.0001$; Table 1), ranging from 21.4% in Mountain Creek to 100% in Kings and Indian Creeks. The mean abundance of *P. obscurus* larvae and the percentage of sites occupied in each stream were both significantly correlated with the percentage of 'sand' sites in each stream (Table 1).

These patterns were also evident at the site scale. When all sites were pooled across streams, *P. obscurus* occupied a significantly greater percentage of the 'sand'

Table 2. Spearman rank correlations (*r*) between the abundance of *Progomphus obscurus* larvae and chemical parameters (*n* = 127 for all correlations). Ranges for sites containing *P. obscurus* are also presented, and extensions (*) from Roback (1974) and variables previously unreported (+) are noted.

Variable	*r*	*p*	Range
pH	0.309	0.001	6.22-7.70*
Cond. ($\downarrow S \cdot l^{-1}$)	0.197	0.03	18.83-401.06+
DO [$mg \cdot l^{-1}$]	-0.092	n.s.	5.26-8.79*
Turbidity	0.104	n.s.	2.69-55.22*
Na^+ [$mg \cdot l^{-1}$]	0.216	0.02	1.66-62.22+
K^+ [$mg \cdot l^{-1}$]	0.140	n.s.	0.72-6.53+
Ca^{2+} [$mg \cdot l^{-1}$]	0.215	0.02	0.88-18.69*
Mg^{2+} [$mg \cdot l^{-1}$]	0.227	0.01	0.51-7.25*
Cl^- [$mg \cdot l^{-1}$]	0.093	n.s.	1.46-77.70*
SO_4^{2-} [$mg \cdot l^{-1}$]	0.107	n.s.	0.59-16.26*
HCO_3^- [$mg \cdot l^{-1}$]	0.382	0.001	7.03-91.82+
NO_3^- [$mg \cdot l^{-1}$]	-0.029	n.s.	0.43-30.86*
PO_4^{3-} [$mg \cdot l^{-1}$]	0.150	n.s.	0.00-2.50+
NO_2 [$mg \cdot l^{-1}$]	0.147	n.s.	0.00-0.99+
Br [$mg \cdot l^{-1}$]	0.040	n.s.	0.00-3.00+
F [$mg \cdot l^{-1}$]	0.181	n.s.	0.04-1.21+
Si^{4+} [$mg \cdot l^{-1}$]	0.233	0.01	2.78-23.30+
Zn^{2+} [$mg \cdot l^{-1}$]	-0.150	n.s.	0.00-0.96+
Mn^{2+} [$mg \cdot l^{-1}$]	0.181	n.s.	0.01-1.35+
Al^{2+} [$mg \cdot l^{-1}$]	0.028	n.s.	0.00-0.28+
Fe^{2+} [$mg \cdot l^{-1}$]	0.142	n.s.	0.05-1.43+

sites (78% of 91 'sand' sites) than sites categorized as 'pebble' (50% of the 36 'pebble' sites; χ^2 = 9.66, *df* = 1, *p* = 0.002). Also, when the mean larval abundance in occupied sites was compared across these two sediment types, 'sand' sites had more larvae ($\log_{10}$ backtransformed mean = 20.0 larvae/site, *n* = 71) than 'pebble' sites ($\log_{10}$ backtransformed mean = 10.7 larvae/site, *n* = 18), to a marginally significant degree (*t* = 1.82, *df* = 87, *p* = 0.07).

The effect of sediment type at a small scale was also addressed in summer 2001 by sampling *P. obscurus* from three substrates described as 'fine sand', 'coarse sand', and 'pebble' from sites in Gilder Creek, Mountain Creek, Beaverdam Creek, and two sites in the Upper Enoree. Sediment type categories were significantly different from one another in mean particle size (ANOVA, *F* = 72.92, *df* = 2,87, *p* = 0.0001; Table 3). The percentage of samples occupied by *P. obscurus* larvae varied among these sediment types (χ^2 = 5.96, *df* = 2, *p* = 0.05; Table 1); larvae occupied more of the 'fine sand' samples than the 'pebble' samples (χ^2 = 5.41, *df* = 1, *p* = 0.02; Table 1). Although mean abundances decline from 'fine sand' to 'coarse sand' to 'pebble' (Table 1), they are not significantly different (ANOVA, *F* = 0.418, *df* = 2, 33, *p* = 0.66).

Table 3. Mean comparisons for mean particle size (± 1 s.d.), percentage of samples used by *Progomphus obscurus* larvae, and the mean abundance (± 1 s.d.) of *P. obscurus* larvae in occupied samples (*n*) for sediments categorized as 'fine sand', 'coarse sand' and 'pebble' collected at five sites in the Enoree River watershed. Values in a column followed by the same letter are not significantly different (Tukey's mean comparison tests, $p < 0.05$, for 'mean particle size' and 'mean abundance'; pairwise χ^2 tests for 'frequency', $p < 0.05$).

Sediment type (*n*)	Mean particle size (mm)	% samples used	Mean abundance (*n*)
Fine sand (30)	0.678 ± 0.388 a	66.6 a	5.1 ± 5.2 (20) a
Coarse sand (30)	1.150 ± 0.296 b	43.3 a b	3.5 ± 2.1 (13) a
Pebble (30)	2.130 ± 0.665 c	36.6 b	2.8 ± 2.5 (11) a

We also conducted correlation analyses between mean particle size, *P. obscurus* abundance, and the mean length of *P. obscurus* larvae. Again, these analyses were limited to samples containing larvae (*n* = 44), and all variables were $\log_{10}$ transformed prior to analysis. Larval abundance was inversely correlated with mean particle size ($r = -0.325$, $p = 0.03$; Fig. 1), and marginally inversely correlated with mean larval length ($r = -0.272$, $p = 0.07$). Likewise, there was a weak relationship between mean larval length and mean particle size ($r = 0.289$, $p = 0.057$).

DISCUSSION

The purpose of this investigation was to describe some of the chemical and physical niche parameters for larvae of *Progomphus obscurus*, and to suggest how anthropogenic change might impact this burrowing species. The Enoree River and its nine tributaries differ in their water chemistry. In a previously published discriminant function analysis describing these differences (Worthen et al. 2001b), we found that the first two discriminant functions (DFA1 and DFA2) explained 72.4% and 10.9% of the variance among streams, respectively ($p < 0.0001$). The concentrations of silica and bicarbonate were the only chemical parameters significantly correlated with DFA1 ($r_s = 0.570$, $p < 0.05$; $r_s = 0.451$, $p < 0.05$, respectively), and dissolved oxygen was the only chemical parameter correlated with DFA2 ($r_s = 0.451$, $p < 0.05$; Worthen et al. 2001b).

The abundance of *P. obscurus* larvae and the percentage of sites used varied among streams and correlated with DFA1 and concentrations of silica and bicarbonate; the percentage of sites used was also inversely correlated with dissolved oxygen concentration. Larval abundance also correlated with a variety of chemical parameters at the site scale. In general, it seems that *P. obscurus* has a broad ecological tolerance to a variety of chemicals, including those such as nitrates, phosphates, and metals that are signatures of anthropogenic inputs. For instance, there is anecdotal evidence that *P. obscurus* tolerates concentrations of zinc that may be toxic to other species. In 1985, 75,700 l of spent galvanizing solution (HCl, zinc, aluminum, and other chemicals) spilled into the groundwater above the head-

waters of the Upper Enoree River. In 1999, this spill was still affecting the chemistry and biota of the river (Worthen et al. 2001a). *P. obscurus* was found 1.8 km downstream from the spill site, where Zn^{2+} concentrations were 0.94 ppm. Other species such as *Gomphus cavillaris* Needham, *Stylurus scudderi* (Selys), and *Hagenius brevistylus* Selys, that were present on neighboring, uncontaminated tributaries that feed into the Upper Enoree, were only found at sites 6.0 km or more below the spill; where Zn^{2+} concentrations had dropped to 0.33 ppm (unpubl. data). Perhaps exposure to toxins in the sediment has selected for greater chemical tolerances in burrowing species. Only *Cordulegaster maculata* Selys, another burrowing species, was found closer to the spill site (0.7 km) than *P. obscurus*. Wallace et al. (1991) have shown that *C. maculata* is also tolerant of organic pesticides. In any case, *P. obscurus* larvae are tolerant to a wide range of chemical pollutants.

Substrate characteristics seem to be the primary niche determinants for *P. obscurus* larvae; they prefer sandy sites at all scales. At the largest scale, larvae are more abundant and were found in a greater percentage of sites in sandy-bottomed streams. We were surprised to see this pattern at such a large scale, because the designations of 'sand' and 'pebble' were such crude characterizations describing reaches 50-100 m in length. These sites often had a mixture of sediment types, yet our low-resolution descriptor was able to account for a significant fraction of the variation in the distribution of *P. obscurus* larvae.

The chemical patterns and the effects of substrate type are probably related to one another and dependent on the hydrogeological differences between these streams. Kings Creek and Indian Creek have a different underlying geology than
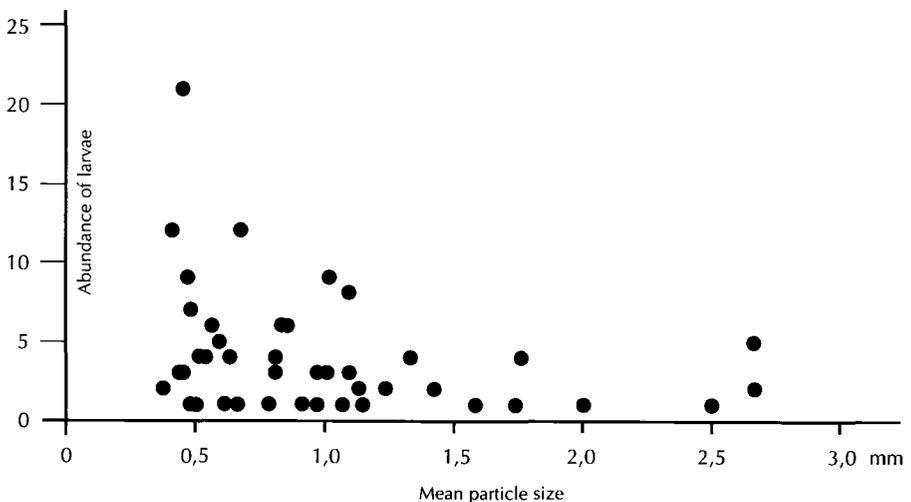
Figure 1: Relationship between the mean abundance/site of *Progomphus obscurus* larvae (in occupied sites) and the mean particle size [mm] of associated sediment. The relationship is statistically significant ($\log_{10}$ transformed values, Pearson correlation, $r = -0.325$, $df = 44$, $p = 0.03$).

the other drainages, which account for differences in stream chemistry and higher silica concentrations (Andersen et al. 2001). In addition, these streams are larger, deeper, and have a lower gradient than those in the upper watershed. This probably contributes to the higher frequency of sandy sites and the lower dissolved oxygen concentrations.

Within a reach (at the site scale), we expected *P. obscurus* larvae to prefer 'fine sand' sediments; it is morphologically adapted to a burrowing lifestyle (Needham et al. 2000), and Huggins & DuBois (1982) found that larvae prefer sediments with mean particle sizes of 0.6-1.0 mm. Indeed, *P. obscurus* larvae were found in 'fine sand' sediments nearly twice as often as in 'pebble' sediments. And, although there was not a significant difference in mean larval abundance among our crude sediment-type categories, the relationship between mean particle size and larval abundance was significant in the more precise correlation analysis. Although our results are broadly consistent with Huggins & Dubois (1982), it seems that larvae preferred smaller sediments (down to 0.5 mm) in our study.

There are also marginally significant relationships between sediment particle size and mean larval length ($r = 0.289$, $p = 0.057$) and larval abundance and length ($r = -0.272$, $p = 0.07$). Although these relationships are suggestive of density dependent effects, they can also be caused by a variety of other factors. For instance, all larvae can burrow in fine sediments, but only large larvae can burrow effectively in coarse sediments. So, as a function of habitat selection alone, we might expect to find more larvae of various sizes in fine sediments, and fewer, larger larvae in coarse sediments. This could account for the positive relationship between particle size and larval length, the negative relationship between larval abundance and length, and the negative relationship between particle size and abundance. It is also possible that small larvae are more susceptible to predators (even larger conspecifics) in coarse sediments (Suhling 1999). Removal of small larvae from coarse sediments by predators could also account for these correlations. As such, more research is required to determine whether density-dependent factors are important in this species.

So, although *P. obscurus* is tolerant of most chemical variation in the Enoree Basin, it is strongly associated with sandy substrates at several spatial scales. As Richter et al. (1997) suggest, the leading threats to stream communities may not be the input of toxins, but rather the habitat disturbance, conversion, and homogenization that occurs by anthropogenic changes in sediment loads. Teasing apart the effects of anthropogenic impacts from natural variation is often difficult. In the Enoree River basin, for instance, Indian and Kings Creeks are significantly different in chemical composition from the other streams in the watershed; but this is largely a function of underlying differences in geology (Andersen et al. 2001). These streams are also uniformly sandy, and different from the other streams that have a mixture of substrate types. This may be a function of the geology, or may be affected by siltation from logging in the Sumter National Forest. As such, the relative contribution of natural and anthropogenic factors contributing to the prevalence of sandy sites and the dominance of *P. obscurus* in these streams is unknown. In the other drainages, however, there is some suggestion that substrates might be changing in response to anthropogenic changes in sediment load. The most

pronounced area of development in the watershed is on the east side of Greenville; the area drained by Brushy, Rocky, and Gilder Creeks. Brushy Creek has an unusually high percentage of sandy sites for these northern streams, indicating that increased sediment loading might be affecting this tributary. Although the mean abundance of *P. obscurus* is not unusually high, it represents nearly 60% of the odonate fauna in this stream (Worthen 2002). Although the percentage of sandy sites in Gilder Creek are not as high, *P. obscurus* also dominates in this steam, both in terms of mean abundance and as a fraction of the odonate community (over 50%, Worthen 2002). It seems likely that anthropogenic increases in sediment load may be decreasing the diversity and complexity of odonate communities and reducing them to a subset of burrowing species like *P. obscurus* that thrive in sandy sediments.

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