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FACTORS AFFECTING MICRODISTRIBUTION OF TWO SPECIES OF BURROWING DRAGONFLY LARVAE, WITH NOTES ON THEIR BIOLOGY (ANISOPTERA: GOMPHIDAE)

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Progomphus obscurus and *Gomphus externus* larvae were studied in both laboratory and field during July, 1976, regarding their burrowing habits and their association with substrates. They were found to burrow completely beneath bottom substrates by using their front and middle legs, never deeper than 2 cm; small larvae burrowed less deeply. — Field studies revealed that both spp. occurred in the stream in relatively high numbers and were distributed in either a contagious or random manner. Population structure of both spp. was similar and consisted mainly of late instars. Statistical analysis of physical factors measured (substrate particle size, digested organics and detritus) and the occurrence of each sp. demonstrated a correlation between particle size and occurrence of each sp. *P. obscurus* tends to inhabit microhabitats in stream where sand substrate (1-0.625 mm) predominates. Microdistribution of *G. externus* is most strongly correlated with the amount of silt/clay substrate present (less than or equal to 0.0625 mm), but percentage of organics was also significant. Although other environmental factors may have had an effect on the distribution of these 2 spp., the primary factor was substrate particle size.

INTRODUCTION

This investigation attempts to determine some physical factors affecting microdistribution of *Progomphus obscurus* (Rambur) and *Gomphus externus* (Hagen). Burrowing behavior and population structure of these species are also examined.

Most factors affecting distribution of freshwater aquatic organisms which burrow in fine substrates are poorly known (LYMAN, 1943, 1956; ERIKSEN, 1964; GALE, 1971, 1973; MARZOLF, 1965). LYMAN (1943) showed that substrate composition was of great importance in the distribution of burrowing mayfly nymphs of the genus *Hexagenia*. Laboratory substrate preference experiments by GALE (1971) showed that the fingernail clam, *Musculium transversum*, selected mud substrates most frequently and sand least frequently. Adults of another species of fingernail clam (*Sphaerium striatinum*) showed no clear preference for mud, sand, or sandy mud, although small clams exhibited preference for mud over sand or sandy mud (GALE, 1973).

Little is known about the burrowing behavior and factors affecting habitat selection by burrowing larval Odonata. Information about habitat selection by gomphid larvae is mostly restricted to observations which lack quantifiable data (RICH, 1917; HARRISON, 1951; WRIGHT, 1943; MILLER, 1964). CORBET (1963) indicated odonate larvae may select the type of sediment "to which they are adapted" using substrate particle size as a basis, but provides little documentation to support many observations.

Only KEETCH & MORAN's (1966) work with the South African sand-burrowing dragonfly, *Paragomphus cognatus* (Rambur), provided quantitative data on the relationship between substrate particle size and habitat selection. They showed that larvae of *P. cognatus* were able to distinguish substrates of differing particle size. In laboratory experiments they demonstrated that *P. cognatus* generally burrowed in coarse sands (approximately 0.50-0.21 mm) and avoided fine sands (< 0.15 mm), but their findings were unsubstantiated by field data, which showed no significant difference between particle size profiles from stream areas in which larvae were present and those in which they were absent. They suggest that initial choice of habitat is governed by particle size but other factors might lead to a patchy distribution within this habitat.

It has long been suggested that *Progomphus* larvae prefer sandy bottom streams (BYERS, 1930), sandy beds, or sandy reaches within various lotic or lentic habitats (BYERS, 1939; NEEDHAM, 1941; NEEDHAM & WESTFALL, 1955). Needham & Westfall briefly discussed morphological adaptations of *P. obscurus* larvae which allow them to live in shifting sand habitats and account for their great burrowing abilities. No quantitative studies are available on any of the North American species of *Gomphus*, but casual field observations suggest that most species prefer habitats where fine sediments prevail. CORBET (1963) suggested that burrowing dragonfly larvae with dorso-ventrally flattened abdomens typically inhabit finer sediments since the shape of the abdomen helps prevent passive sinking. *G. externus* possess this morphological adaptation and others common to Corbet's "shallow burrowers". Corbet further characterized gomphids, normally living in coarse sediments, as having an elongate abdomen (which is concave ventrally and strongly convex dorsally) and short, robust legs. These larvae, which live in sand, are usually smooth and pale in color. *P. obscurus* possess all characteristics of coarse sediment dwellers.

STUDY AREA AND METHODS

STUDY AREA

Mud Creek is a second-order stream originating 22.5 km north of Lawrence, Kansas in Jefferson County. It flows southward to the Kansas River flood plain where it turns and flows in a southeasterly direction until it enters the Kansas River in northeastern Douglas County, Kansas. Before its lower reaches were channelized, Mud Creek was 32.8 km long with a differential elevation of 121.6 m. It is normally a slow-moving, warm water stream. The amount of flow varies seasonally with the water becoming very turbid during high water stages. HUGGINS & MOSS (1974) described this stream and its basin along with an analysis of the fish population structure and a listing of the more common aquatic macroinvertebrates.

The present study was conducted in a 100 m section of Mud Creek adjacent to the Kaw Valley Fish Farm 1 km north of Lawrence Municipal Airport. This section of Mud Creek is characterized by a single small riffle and a small number of short, deep pools. Over 80 percent of this section consists of long reaches of normally shallow stream runs (characterized by a usually unbroken flow pattern). These runs include areas of erosion and deposition which provide areas of varying velocity and substrate composition. Substrates in stream runs are various mixtures of small gravel, sands and silt/clay with quiescent areas containing various amounts of detritus.

BIOLOGICAL METHODS

Field and laboratory observations were made on burrowing activities and patterns of *P. obscurus* and *G. externus* prior to initiation of quantitative study of their microdistribution. Larvae were collected from one area of the stream and released for observation in an undisturbed area of the stream visually similar to the collection site. Burrowing depth was measured in laboratory and field. Laboratory measurements were made by placing various size groups in 20.5 cm x 8.25 cm specimen dishes (finger bowls) filled with 4 cm of substrate and 7 cm of stream water. Size groups were based on total length and consisted of the following sizes: *G. externus*: medium, 16-18 mm; large, 25-28 mm; and *P. obscurus*: medium, 16-20 mm; large 23-26 mm.

Two groups, consisting of five specimens of each species were introduced into each dish and measurements were made after an hour by probing with a calibrated wooden dowel 2 mm in diameter. Striking a buried larva generally resulted in a detectable movement which was checked by excavating the insect. Field measurements were made with a similar wooden dowel in several shallow sandy reaches of the stream which allowed for observation of trails left in the smooth sand surface by the burrowing activity of *P. obscurus*. No *G. externus* trails were visible.

Gut contents of 17 medium- and large-sized larvae of each species were examined by removing crop, proventriculus, and ventriculus of preserved larvae and identifying their contents using dissecting and compound microscopes.

Quantitative field samples were taken during the first two weeks of July, 1976. Climatic conditions during the study period were stable; characterized by sunny skies, warm days (mean air temperature 27°C) and no precipitation. A stovepipe sampler similar to the collecting cylinder described by CUMMINS (1961), which retained both substrate materials and organisms, was used to obtain all samples. The sampler was constructed from galvanized stovepipe 55 cm long and 22.2 cm in diameter with two handles attached near the top of the pipe. This sampler enclosed 0.039 m^2. The sampler was brought down rapidly at arm's length in front of the collector and forced approximately 10 to 20 cm into the bottom substrates at randomly selected points. A subsample of the top 2.5 cm^2 of substrate was removed from the sampler, placed in a small, white plastic tray, checked for organisms, then returned to the laboratory in a labeled plastic bag and dried in an oven at 30°C for 24 hr. Substrate samples were then sealed and stored for later analysis. The rest of the stovepipe sample was sieved with a strainer (approx. 1 mm mesh). All odonates were collected and placed in vials containing 80 percent ethanol.

The larvae were returned to the laboratory where they were enumerated and identified to species. The two most abundant species, *P. obscurus* and *G. externus*, were classified by instar using head width measurements since this is one of certain body measurements which serve as reliable indicators of age (or instar) in many species. In the present study maximum head width was plotted against frequency of occurrence for both species. Exuviae collections were made in order to identify the final instar stage. Instars were designated numerically in a manner similar to LUTZ (1968): final (F=0), penultimate (F-1=1), antepenultimate (F-2=2), etc. This designation is advantageous in comparing the two species since their total numbers of instars are unknown.

Particle size analysis of substrate samples was accomplished by wet sieving with a deflocculent (sodium metaphosphate) to allow the separation of silt and clay. Four particle size groups were separated in the sieving process (Tab. 1). In most instances these particle sizes were combinations of the particle size categories suggested by CUMMINS (1962) which were modified from WENTWORTH (1922).

Table I
Substrate particle size terminology and categories for finer particle sizes

This paper	CUMMINS (1962)	WENTWORTH (1922) *Name*	WENTWORTH (1922) *Particle size range (mm)*
			32-64
Pebble	Pebble	Pebble	16-32
			8-16
			4-8
Gravel	Gravel	Granule	2-4
Coarse sand	Very coarse sand	Very coarse sand	1-2
	Coarse sand	Coarse sand	0.5-1
	Medium sand	Medium sand	0.25-0.5
Fine sand	Fine sand	Fine sand	0.125-0.25
	Very fine sand	Very fine sand	0.0625-0.125
Silt/Clay	Silt	Silt	0.0039-0.0625
	Clay	Clay	< 0.0039

A two-gram subsample from the original substrate sample was analysed for digestible organic matter and detritus. Percentage organic matter was determined by peroxide digestion (SOIL CONSERVATION SERVICE, 1972) after removal of detritus larger than 0.5 mm. Detritus was separated from mineral matter with the aid of a dissecting microscope and only its presence or absence was recorded. No effort was made to sort this matter into size classes as RABENI & MINSHALL (1977) did in their study.

STATISTICAL METHODS

Percentages of the following variables were initially used for statistical analysis: silt/clay, fine sand, coarse sand, gravel, and digested organics. Additional variables dealing with presence/absence of detritus, number of *P. obscurus* and that of *G. externus* present per sample were included in statistical analysis. Seventy-four cases (samples) were analyzed with an additional 15 cases (which did not contain dragonflies) analyzed in the principal components analysis.

Preliminary studies using principal components and stepwise regression analyses (BMDP programs) of all variables including the coarse and fine sand categories indicated non-significant differences between these two sand categories. Therefore, the two sand categories were combined (% sand) for all further analyses.

Of the 74 cases undergoing complete analysis, fifteen contained both *P. obscurus* and *G. externus* but only three of these contained both species in equal numbers. In the 59 remaining cases, only one of the two species was present in each sample. One-tailed student's *t* test was used to compare samples which contained larvae with samples which did not. Arcsin transformations were used on those data recorded as percentages (SOKAL & ROHLF, 1969).

The spatial dispersion of each species was calculated using the index of dispersion (I) outlined by ELLIOTT (1977). This test is based on the equality of variance and mean in a Poisson series and can be used to determine if a population is spatially distributed in a random, regular, or contagious (clumped) manner.

The following analyses were made using BMDP (1975 version) programs on a Honeywell 66/60 computer at the University of Kansas Academic Computer Center. Stepwise regressions were computed using BMDP 2R. During separate runs, the number of individuals per sample of either *G. externus* or *P. obscurus* was used as the dependent variable. A principal components analysis of variables was conducted using BMDP 4M. A principal components analysis of cases was also conducted by transposing the data matrix prior to using BMDP 4M. A stepwise discriminant analysis of cases was conducted using BMDP 7M. Finally, an UPGMA cluster analysis was conducted using BMDP 2M.

RESULTS

BIOLOGICAL RESULTS

When *P. obscurus* and *G. externus* larvae were released into the stream both species quickly oriented upstream while being carried along with the current. They utilized anal propulsion to reach the substrate surface where they attempted to stabilize their position with their head directed upstream. *P. obscurus* were stronger "swimmers" and were able to reach and stabilize themselves upon the substrate faster than *G. externus.*

Larvae of *P. obscurus* spread their hind legs downward and outward from their body. This allowed their hind legs to act as braces in the sand and prevented the dragonfly from being swept downstream. They initiated burrowing activity immediately after becoming stable and were able to burrow from sight in two to five seconds. Burrowing was accomplished using the front and middle legs only. This species was never observed to burrow deeper than 2 cm. Most individuals were found from 8-17 mm below the surface (distance measured from dorsal surface of larva to substrate surface). Generally, smaller larvae burrowed less deeply than larger ones.

Tracking observations with *P. obscurus* revealed that, once below the substrate surface, their burrowing activities appeared to be of a random course since their trails ran in all directions: upstream, downstream, and across the stream. These trails meandered and would cross themselves at times.

G. externus larvae were released in areas with less current and did not use their hind legs as braces. Instead, all their legs were used to maintain stability on the substrate surface. Burrowing responses in this species were slower and more deliberate (generally requiring 40-70 sec to bury themselves). The larvae often waited two minutes or more before beginning burrowing activity. Like *P. obscurus*, they used only their front and middle legs for burrowing, but were found to be shallower burrowers than *P. obscurus*, with medium to large individuals normally burrowing only 3-5 mm deep. Smaller larvae burrowed shallower than larger ones. No trails were ever observed.

Over 90% of all recognizable food items recovered from gut contents of both species were midge larvae (Chironomidae); those of the genera *Lenziella*, *Polypedilum*, *Saetheria* and *Stictochironomus* were the predominate food items recovered from *P. obscurus*. *Gomphus externus* utilized *Lenziella*, as well as larvae of *Chironomus* and Tanypodinae. Also found in the gut contents of *G. externus* were one larva of the riffle beetle, *Stenelmis*, fragments of aquatic earthworms (Oligochaeta) and partial remains of the mayfly nymph *Caenis*.

One hundred twenty-nine random stovepipe samples were taken during the study period. Over one-half of these (74 samples) contained odonate larvae. All but three of these were either *P. obscurus* or *G. externus*. Two *Plathemis lydia* (Drury) and one *Libellula luctuosa* (Burmeister) were collected in samples that also contained *G. externus* larvae. Although gomphid standing crop estimates generated for each individual sample varied from 256.4 larvae/m^2 to 0/m^2, the mean standing crop calculated from all samples was 42.5 larvae/m^2. Based on all samples, *P. obscurus* averaged 30.0 larvae/m^2 while *G. externus* averaged 12.5 larvae m^2.

Histograms (Figs. 1, 2) show relative frequencies of head width for both species taken during the study period. Although the histogram peaks appear to be distinct, their interpretation should be tempered with the knowledge that individuals were collected over a two week period and some growth probably occurred. In both species, larvae in the F-1, F-2 and F-3 stages accounted for over 80% of the population. Collections of exuviae for both species helped identify the final instar stage and indicated that both species were on wing during this study. Additional flight period information and emergence data from this area support the premise that these species are not

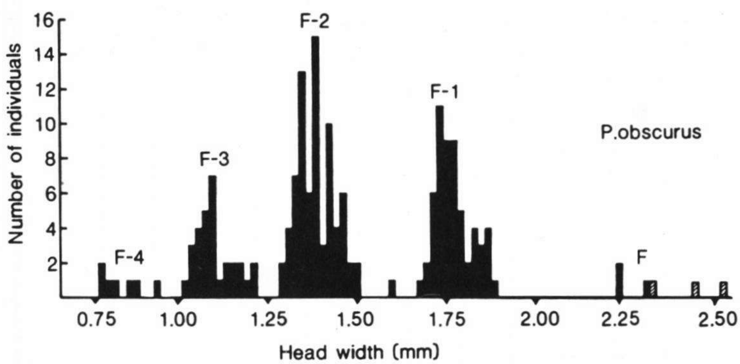

Fig. 1. Size frequency histogram for *Progomphus obscurus* larvae (solid bars) and exuviae (line bars), collected July 1-14, 1976. — (F = final instar, — F-1 = penultimate instar, — F-2 = antepenultimate instar, etc.).

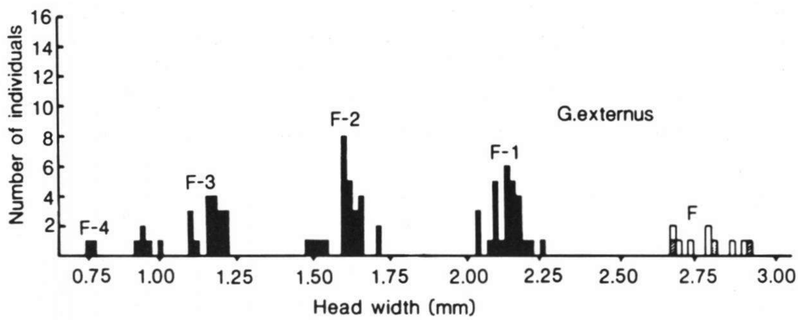

Fig. 2. Size frequency histogram for *Gomphus externus* larvae (solid bars) and exuviae (line bars), collected July 1-14, 1976. — (F = final instar, — F-1 = penultimate instar, — F-2 = antepenultimate instar, etc.)

temporally separate in the final larval stages or as adults.

Substrate composition varied greatly among samples. Most samples were mixtures of sand containing little silt/clay or silt/clay containing little sand. Only two samples contained significant amounts of gravel (24.1 and 53.1% gravel) while the mean gravel percentage for samples with gomphids was only 4.7%. Percentage of silt/clay varied from a low of two percent to a high of 82.9% with a mean of 25.7%. Percentage sands, like silt/clay and gravel, was highly variable among samples with fine sand ranging from 2.6 to 91.5% while the mean for all samples was 51.5%. The mean percentage for coarse sand was much less (18.1) but also varied considerably (0.0 to 57.1).

Fifty-nine percent of the subsamples contained detectable amounts of digestible organics. The amount of organics varied from undetectable to a high of 6.49% while the mean percent for all subsamples was 0.76. Detritus was collected from 57% of all subsamples. Detrital material consisted mostly of leaf fragments with few twig and stick fragments.

STATISTICAL RESULTS

Student's *t* tests (significance level = 0.05, one-tailed) were performed between those samples containing a predominance of either species and those samples without odonates. The *t* test involving *P. obscurus* and the samples without odonates revealed that there was no significant difference (0.814) between samples when compared to the appropriate critical value for the student's *t* distribution (1.671). The student's *t* value for the *G. externus* versus the samples without odonates was 0.234 which was well below the critical *t* value for this test (1.684). These results demonstrate that samples were from statistically similar substrates independent of the presence of gomphids. A departure from a Poisson series was found in the *P. obscurus* samples (D = 2.26). This value was greater than expected ($P < 0.05$) and therefore a contagious distribution is suspected. The *G. externus* value (D = 1.96) was the same as the expected (P = 0.05) and its distribution could be random or contagious. Results of the principal components analysis of all samples (including the 15 cases without odonates) showed that variables measuring percent sand and presence of *P. obscurus* were closely related. Similarly, variables measuring percentage silt/clay and presence of *G. externus* were closely related.

A principal components analysis of the variables found that the first four variables (% silt/clay, % sand, % gravel, and % digested organics) explained a cumulative proportion of 0.884 of the total variance with the percent silt/clay variable explaining the first 0.543 units of this total. The variable dealing with the presence or absence of detri-

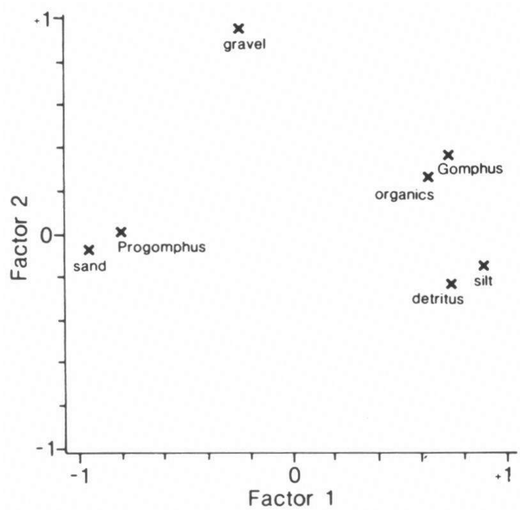

Fig. 3. Unrotated factor plot from principal components analysis on first two factors explaining 70.1% of the total variance.

tus raised this proportion to 0.951 with the variable measuring *P. obscurus* explaining the rest.

The principal components plot (Fig. 3) revealed the presence of three very distinct groups. The first group contained only variables dealing with *P. obscurus* and percent sand. The second group contained variables dealing with *G. externus*, percent digested organics, percentage silt/clay, and presence/absence of detritus. The percent gravel variable made up the third group. Stepwise regression analysis verified the results obtained through the principal components analysis of variables.

Table II
Correlation matrix derived from principal components analysis of variables
(Italicized numbers indicate strong positive or negative correlations)

	Silt/Clay	Sand	Gravel	Organics	Detritus	*Progomphus*	*Gomphus*
Silt	1.000						
Sand	- *0.960*	1.000					
Gravel	- 0.310	+0.031	1.000				
Organics	+0.450	- 0.463	- 0.035	1.000			
Detritus	+*0.591*	- *0.549*	- 0.244	+0.456	1.000		
Progomphus	- *0.622*	+*0.613*	+0.137	- 0.337	- 0.435	1.000	
Gomphus	+*0.567*	- *0.605*	+0.030	+*0.548*	+0.417	- *0.560*	1.000

The correlation matrix generated from the principal components analysis) (Tab. II) revealed strong correlations between *P. obscurus* and percentage sand (0.613) and *G. externus* and percentage silt/clay (0.567). The variable dealing with the occurrence of *G. externus* also correlated with the percent of digested organics found in the substrate (0.548) and to a lesser degree with the presence of discernible detritus (0.417). This same analysis found de-

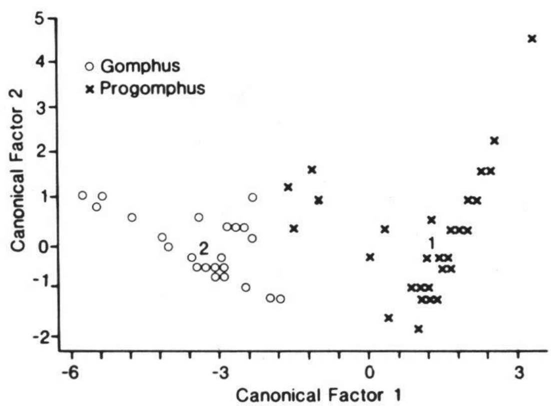

Fig. 4. Scatter plot from stepwise discriminant analysis of cases made to detect outliers which may have affected analysis. Group means (1 and 2) and cases (circles and crosses) are plotted.

tritus to be correlated with percentage silt/clay and organics found in the substrate. Several strong negative correlations were also observed: between occurrence of *P. obscurus* and percentage silt/clay (-0.622), and presence of *G. externus* and percentage sand in the substrate (-0.605). The variables dealing with these two species were negatively correlated with each other (-0.560).

A classification matrix was produced through the stepwise discriminant analysis that correctly classified 93.6% of the *P. obscurus* into one distinct group based on all variables (Fig. 4). Three cases (samples) which were incorrectly placed with *G. externus* contained both species, with the number of *P. obscurus* individuals being more numerous. One hundred percent of *G. externus* cases were correctly classified by this analysis.

An UPGMA cluster analysis of cases also revealed the presence of two groups (one contains *P. obscurus* and the other *G. externus*). Three cases (which contained equal numbers of both species) occurred near the center of the *P. obscurus* cluster. This analysis was conducted since it is not dependent on any of the underlying assumptions (e.g. multi-variate normal distribution) necessary in the other analyses.

DISCUSSION

Statistical analyses of the physical factors measured and the occurrence of *P. obscurus* and *G. externus* clearly demonstrate a correlation between substrate particle size and distribution of these organisms. Larvae of *P. obscurus* tended to inhabit those microhabitat areas of a stream in which sand substrate (1-0.625 mm) predominated. The microdistribution of *G. externus* was most strongly correlated with the amount of silt/clay substrate (less than or equal to 0.0625 mm) present, but the percentage of organics was also significant. Gravel substrates were not inhabited by either species. All of these substrate conditions probably result from current velocities associated with these microhabitat areas. In general, current velocity is the primary factor which accounts for substrate particle sizes composing the stream bed (LEOPOLD et al., 1964).

Only three samples containing *P. obscurus* were incorrectly placed with *G. externus* (Group 2) in the classification matrix. A scatter plot of all cases along the first two canonical variables displays this incorrect placement (Fig. 4). Observations of *P. obscurus* larvae showed them to be more mobile than *G. externus*, thus their presence in the *G. externus* grouping may have been due to chance alone or through accidental displacement by exposure to stream current. *P. obscurus* did not favor fine over coarse sands as did *Paragomphus cognatus* (KEETCH & MORAN, 1966), but inhabited a fairly broad range of sand particle sizes. Results of the student's *t* tests on samples with and without odonates revealed no significant differences in the physical composition of the two groups of samples. Indices of dispersion for *P. obscurus* and *G. externus* indicated that these species occur in their respective microhabitats in a contagious and a contagious or random distribution, respectively. The spatial dispersion of an ecological population is seldom random or regular, but is frequently contagious (ELLIOTT, 1977). This is not surprising since many environmental factors are unevenly distributed. Also some species tend to aggregate, thus producing a contagious distribution regardless of environmental factors. It appears that absence of larvae in a particular sample may be due to various factors including sample size in relation to population density, dispersion within a microhabitat and/or chance (sampling error).

The occurrence of these two gomphids in two discrete and different microhabitats in Mud Creek is interesting in the light of several other facts. Population structure information derived from the size frequency histograms strongly suggests that their larvae were not temporally separated since similar instars occurred in the same relative abundance. Adult flight data indicated that both species emerge and are on the wing during the same period. It appears that their predominant food is midge larvae. Because so few odonate larvae were examined, little can be said about specific feeding habits, but based on species composition, there seems to be little overlap. The co-existence of these two opportunistic predators in the same aquatic environment at relatively high densities is no doubt facilitated by the strong niche segregation between larvae. Although not temporally separated, spatial separation may help relieve competition pressures between *P. obscurus* and *G. externus* if, in fact, competition occurs between them.

Although our study indicates an extremely strong correlation between substrate particle size and distribution of the two species, other associated factors may influence their distribution within the stream or their stream microhabitat. Laboratory studies by MARZOLF (1965) indicated particle size preference on the part of the burrowing amphipod, *Pontoporeia affinis* Lindstrom, but more important was the presence of bacteria and organic matter in the sediments. This information combined with later investigations (MARZOLF, 1966) led him to conclude that the relationship of the amphipod to the sediment was one of feeding. CUMMINS & LAUFF (1969) concluded that the burrowing mayfly, *Ephemera simulans* Walker, favored sand and gravel substrates but the exact limits of microdistribution were set by other parameters. They suggested that the nature and abundance of detrital food substances is an important factor in setting the limit of this detritivore's microhabitat. Our study showed a positive correlation existed between digestible organics and *G. externus* but their relationship is probably an indirect one.

KEETCH & MORAN (1966) suggested that current speed might be one of the factors affecting the distribution of *P. cognatus* although they did not measure current velocities. This might be a contributing factor since *P. cognatus* does not completely bury itself in the bottom substrates, but this remains to be proven. While current directly affects substrate distribution, its effect on *P. obscurus* and *G. externus* is probably minimal since these dragonflies are seldom exposed to it. Our observations on their burrowing habits indicate that both bury themselves completely and, when experimentally exposed to moderate to low current velocities, can maintain themselves and reburrow in the general downstream area where they were dislodged.

ERIKSEN (1961, 1963) found a general trend of decreasing oxygen concentration with decreasing particle size in stream sediments and suggested the particle size affects water flow through the substrate. BRAEFIELD (1964) suggested that beach porosity (drainage), and thus oxygen levels, will be low regardless of the range of grain sizes as long as greater than 10 percent fine sand ($<$ 0.25 mm) is present. This hypothesis was later supported by ERIKSEN (1966) from stream soil data. It is tempting to suggest that oxygen concentration in the substrate may affect the microdistribution of *P. obscurus* and *G. externus*. We presently lack the data to confirm the suggestion, but would point out that *G. externus* occupy silty microhabitats where there is an obvious reduction in current and a build-up of organic material. Both of these factors could lead to decreased oxygen levels within the substrate. *G. externus* burrowed at shallower depth than *P. obscurus*, a habit that helps the former to remain in closer contact with the overlying oxygenated water column. Future research will be directed towards the investigation of oxygen levels in these microhabitats and the oxygen needs of the larvae.

Although other environmental factors may have an effect on the distribution of the two species studied, the primary influence on the microdistribution is substrate particle size. CUMMINS & LAUFF (1969) concluded that whereas current, temperature or other physical-chemical parameters may limit the general ranges of habitat tolerance (macrodistribution) for certain lotic macrobenthos, particle size or food supply probably exerts primary microdistributional influences.

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