Adv. Odonatol. 6 : 101-111 April, 1994

SPATIAL DISTRIBUTION OF THE LARVAE OF *GOMPHUS PULCHELLUS* SÉLYS (ANISOPTERA : GOMPHIDAE

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The distribution of larval *Gomphus pulchellus* Sélys in a gravel pit pond near Braunschweig (Lower Saxony, Germany) was investigated by sampling different structure types. It could be shown that the larvae live predominantly in detritus habitats. There were only little differences in spatial distribution between the last four instars. In choice chamber experiments the larvae burrowed themselves mostly into detritus-covered substrates as opposed to uncovered substrates. Given the choice between sediments of different particle size, larvae preferred the finer ones, especially fine sand, but they did not clearly differentiate between sediments more similar in particle size. Comparing the field results with experimental data and findings for *G. pulchellus* made in Southern France, it is suggested that spatial distribution is influenced mainly by the existence of coarse detritus and to a smaller extent by sediment particle size.

INTRODUCTION

The substrate is one of the most important ecological factors for aquatic insects (CUMMINS & LAUFF, 1969 ; MINSHALL, 1984). Whereas in some species of Ephemeroptera, Plecoptera, Trichoptera and Diptera the effects of substrate composition on distribution have been shown (eg. RABENI & MINSHALL, 1977 ; TOLKAMP, 1980), little is known about burrowing dragonfly larvae. Most information on habitat selection, especially in gomphids, is restricted to field observations (MÜNCHBERG, 1932 ; LIEFTINCK, 1941 ; WRIGHT, 1943 ; MILLER, 1964).

Investigations on the relationship between substrate particle size and habitat selection in *Paragomphus cognatus* were made by KEETCH & MORAN (1966) in laboratory experiments. HUGGINS & DUBOIS (1982) demonstrated a correlation between the distribution of larvae of two gomphid species, *Progomphus obscurus* and *Gomphus externus*, and grain size, and, in *G. externus*, with organic matter.

This study attempts to determine the relationship between substrate composition and spatial distribution of different instar larvae of *Gomphus pulchellus*. In order to distinguish the larval stages, population structure was examined.

The west Mediterranean dragonfly *G. pulchellus* has increased its distribution in the last 100 years to central Europe (RUDOLPH, 1980). Whereas in Southern France the larvae seem to live predominantly in lotic habitats (AGUESSE, 1958 ; 1960), at its eastern expansion, in east Lower Saxony, they were found mostly in gravel pits and canals (MÜLLER & SUHLING, 1990).

It has long been suggested that *G. pulchellus* larvae prefer sandy sediments without vegetation (eg. BEYER, 1938). The larvae possess a dorso-ventrally flattened abdomen, which is common in "shallow burrowers" (CORBET, 1963). So, according to CORBET, it should inhabit finer sediments. Little is known about population structure and larval development of *G. pulchellus* and RIS (1911) suspected a three year life-cycle.

STUDY AREA AND METHODS

STUDY AREA

This study was carried out in a gravel pit pond 10 km east of Braunschweig (Lower Saxony, FRG). Of the 12 autochthonous dragonfly species present *Gomphus pulchellus* was the most frequent. Since 1987 a great number of emerging *G. pulchellus* have been found every year. The pond is used for bathing and fishing, and fish known to be living in it include *Cyprinus carpio, Gobio gobio, Esox lucius* and *Perca fluviatilis*.

The pond could be divided into three zones of different structure and size with a total surface area of about 8500 m^2 (Fig. 1). The biggest part which has no vegetation consists of a zone with a sandy or gravelly bottom situated next to the shoreline (1970 m^2) and the muddy central part of the pond, which was more than 1 m deep (maximum depth : 3.5 m ; 5540 m^2). The third zone is characterized by the only aquatic plant in the pond, *Potamogeton natans*, which covered a total area of 990 m^2 in dense stands predominantly in the southern area.

FIELD METHODS

In June 1990, 12 regular sampling stations (Fig. 1) were established at sites representing six structural types of benthic habitat in the pond (Tab. I). To determine the structural types, particle size analyses of four substrate samples at each station were made by dry sieving. Additionally the presence or absence of detritus at the station was noted. The terms for sediments are used according to WENTWORTH (1922). A total of 189 samples was obtained by sampling the 12 stations in four-week periods from June to September, 1990. Samples were taken to a depth of 0.5 m with a modified surber-sampler, with a mesh width of 1.0 mm and a base of 0.25 m^2. In the deeper

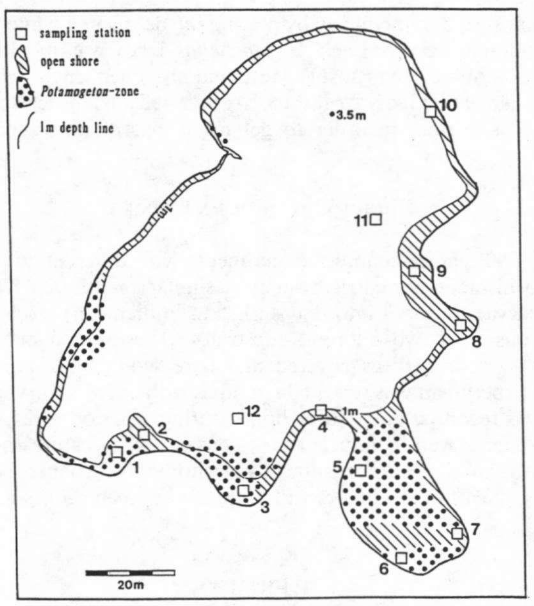

Fig. 1. Map of the investigated gravel pit pond showing the location of the pond zones, the sampling stations, and the 1 m depth line.

Table I

Benthal structures in the different water areas of the pond and number of samples taken in these structures in 1990

pond aerea	depth	structures	sampling station	number of samples
Potamogeton natans — zone	< lm	coarse detritus on sand (cd/s)	1,3,5	39
		boulder with detritus	6	19
		boulder	2	19
open shore-	> lm	sand	4, 9, 10	40
		gravel	7, 8	39
central parts	> lm	mude	11, 12	32

regions samples were made by drawing a dredge (width : 0.4 m) along the bottom for a distance of 1 m.

Samples were sorted immediately by placing the debris in a white pan and manually searching for odonate larvae. Each *G. pulchellus* larva was measured alive using a calliper rule to determine head capsule width and abdomen length. Head capsule width was used to assign individuals to instars. Additionally hand-net samples were made in each four week period, in order to get more information about the population structure of *G. pulchellus.*

Choice Chamber Experiments

In August 1990, choice-chamber experiments with different substrates and larvae of the last two instars were carried out in a similar manner as Keetch & Moran (1966). Single larvae were put into bowls (0.25 m in diameter), each bowl was divided into four sections with two different substrates. These could be substrates of two different grain sizes or detritus covered and bare sediment of equal grain size (see Tab. III). Each experiment was repeated ten times with different larvae. The distribution of the larvae was recorded every three hours during a period of 24 hours. The choice chamber experiments were conducted in a constant-temperature room at 20.0°C. In order to locate the larval positions in the bowls without disturbance, larvae were marked with little floats, fixed to their bodies with a thread between thorax and abdomen.

RESULTS

Observations in the Field

From June to September, 1990, a total of 192 larvae of *G. pulchellus* were caught at the study site, 94 of these at the regular sampling stations and the rest by hand-net sampling in the *P. natans* zone. The larvae could be clearly separated into instars by using measures of head capsule width (Fig. 2). Only larvae of the last five instars were found. Final instar larvae appeared at the end of July and simultanously F-4 and F-3 larvae became rare.

Larvae of *G. pulchellus* were the most abundant in the samples. Less than 10 of each of the following species were also caught : *Platycnemis pennipes. Erythromma najas, Anax imperator, Aeshna grandis, Somatochlora metallica* and *Orthetrum cancellatum*. All of these, except *O. cancellatum*, were found in the *P. natans* zone, too.

Larvae of *G. pulchellus* were found in four out of six investigated substrates (Tab. II). In two similar substrates, boulder and boulder with detritus, the larval densities were similar. (U-test, $U = 182.0$, $n_1 = 19$, $n_2 = 19$, $p > 0.05$), and the two substrates were therefore put together in one category : boulder (Tab. II). The distributions within the five remaining substrate types were significantly different from each other ($p < 0.001$, one-way analysis of variance ; see Tab. II). The majority of all sampled larvae (76.6%) were caught in sand covered with detritus of leaves of *P. natans* (cd/s). The average number of larvae/m^2 (Tab. II) in this substrate was significantly higher ($p = 0.0046$,

Table II

The influence of different substrate types on the distribution of the last four instars of *Gomphus pulchellus* : total number, average number/m² ($\bar{x}$), standard deviation (sd) and level of significance for equal distribution (based on one-way analysis of variance) are given

instar number		number of larvae in :					number of samples (¹)	p =
		cd/sand	boulder	gravel	sand	mud		
all stages :	$\bar{x}$/sample	**8.73**	**2.13**	**0.49**	**0.0**	**0.0**		
	sd	11.75	3.85	1.45			189	0.0000
	total	72	18	4	-	-		
F-3 :	$\bar{x}$/sample	**3.15**	**0.59**	**0.0**	**0.0**	**0.0**		
	sd	4.25	1.62				71	0.0005
	total	10	2	-	-	-		
F-2 :	$\bar{x}$/sample	**6.62**	**0.59**	**0.0**	**0.0**	**0.0**		
	sd	8.71	1.62				71	0.0001
	total	21	2	-	-	-		
F-1 :	$\bar{x}$/sample	**4.81**	**1.18**	**0.0**	**0.0**	**0.0**		
	sd	5.18	2.51				111	0.0000
	total	23	6	-	-	-		
F :	$\bar{x}$/sample	**1.58**	**1.23**	**0.62**	**0.0**	**0.0**		
	sd	3.60	3.26	1.63			118	0.0595
	total	8	6	2	-	-		

(¹) Only samples from a month when more than 2 larvae/instar were found were used to calcuate the average number/m² cd = coarse detritus

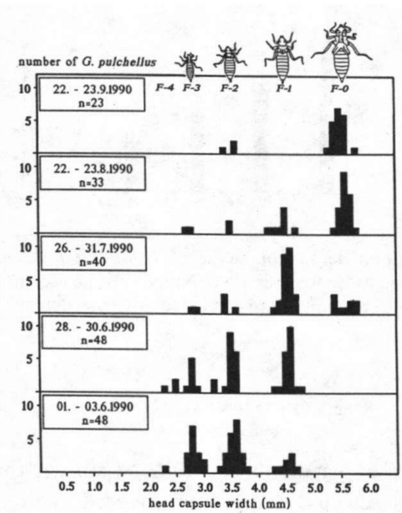

Fig. 2. Head capsule width of *Gomphus pulchellus* larvae, caught monthly from June to September 1990 by surber — sampler or hand net at the study site. Head width was used to determine the larval instars. Instar numbers (F-4, F-3, ...) are given F-0 = final instar larvae.

U-test) than in boulder and very different (p = 0.0001, U-test) from that in any other substrate type.

To get correct results about the distribution of single stages it had to be remembered that not all instars were present in great numbers in the pond at one time (Fig. 2). The use of data from months when an instar was rare or absent could falsify the results. So only distributional data from months with 2 or more larvae of a single stage were used to calculate the average number. The F-3, F-2 and F-1 instars showed a similar distribution (Tab. II) and they were caught only in three substrates. Their densities were highest in cd/s (Tab. II). The density of final instar larvae was highest in this substrate, too, but the difference was not significant (p = 0.0595, one-way analysis of variance). Only F-O and one single F-1 larvae were caught in the gravelly parts of the pond.

Within the period of investigation population density in cd/s decreased from a value of 17.3 individuals per m² in a nearly linear way (Fig. 3), whereas in the boulder substrate it fluctuated at a lower level. However, in September it was approximately on the same level as in cd/s. In gravelly substrates larvae were caught only in August and September.

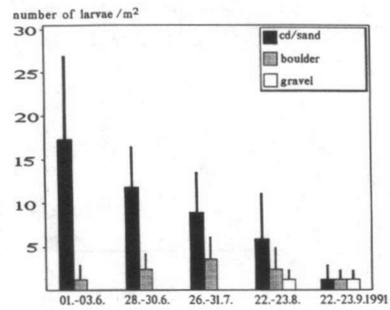

Fig. 3. Changes in population density of larvae of *Gomphus pulchellus* in different substrate types of the pond from June to September 1990. Number of larvae/m² calculated from numbers of larvae caught in samples every month are given. (cd = coarse detritus).

Experimental Results

In choice chamber experiments it could be shown that larvae of *G. pulchellus* in most cases selected sediments covered with coarse detritus with a high significance (see Tab. III). Only in the experiment with fine sand was the difference in selection frequency between both substrates not significant (p = 0.0551, t-test for dependent sample surveys).

In all of the experiments with exposed sediments the larvae were found in the highest numbers in the finer ones (Tab. III). The difference between the selection frequencies for the two sediments was significant (see Tab. III), when the difference between the grain size of the tested sediments was large. This was found in the experiments using fine sand against gravel and sand against gravel. There was no or only little significance in the difference of larval selection frequencies in experiments with similar particle size fractions.

Table III

Substrate selection in larvae (F-1, F-0) of *Gomphus pulchellus* in 24 h choice chamber experiments with different substrates (10 larvae at each experiment). Position of each larvae was controlled 8 times. Average number of registrations of larvae in both tested sediments, standard deviation, level of significance (based on t-test for dependent sampling surveys) and number of larvae found predominantly in both substrates are given

tested substrates		average number of registrations (sd)		t-test	number of larve found predominantly ([1]) in :	
A	B	A	B	P =	A	B
detritus on fine sand	: fine sand	6.3 (3.3)	1.7 (3.3)	0.055	8	2
detritus on sand	: sand	7.1 (2.5)	0.9 (2.5)	0.004	9	1
detritus on coarse sand	: coarse sand	7.0 (2.2)	0.8 (2.2)	0.002	9	1
detritus on gravel	: gravel	7.9 (0.3)	0.0	0.000	10	0
fine sand	: sand	5.6 (3.0)	1.9 (2.9)	0.073	7	3
fine sand	: coarse sand	6.1 (3.0)	1.6 (2.4)	0.025	7	1
fine sand	: gravel	6.5 (2.5)	0.7 (1.6)	0.001	8	0
sand	: coarse sand	4.6 (2.6)	2.1 (1.6)	0.160	4	1
sand	: gravel	6.4 (0.8)	2.5 (2.7)	0.002	8	0
coarse sand	: gravel	5.7 (3.2)	1.5 (2.8)	0.049	7	1

([1]) Larvae found in more than 5 of 8 registrations in substrate A (or B)

In all of the experiments two types of larval selection behaviour were observed. Most of the larvae could be found predominantly in one substrate type, but not always at the same place (tab. III). Not all of these larvae selected the same substrate in a tested pair of two substrates. Some other larvae changed the place and the substrate within the controls. Both, unequal choosing behaviour and substrate changing were found mostly in experiments with similar sediment types and in the experiment using fine sand or fine sand with coarse detritus.

Sometimes larvae were found not buried in the substrate but sitting on the surface. This behaviour was shown mostly at night, when larvae were more active. The frequency of sitting on the surface was different in the two experimental series. Whereas in only 1% of all controls in the experiments with detritus larvae were found on the surface, they were found there in 10% of the controls in the bare sediment series.

DISCUSSION

In the investigated pond the larvae of *G. pulchellus* live predominantly in sandy sediments covered with detritus, but they also use stony habitats to a smaller extent. This result corresponds to findings made in an irrigation canal in Southern France (SCHRIDDE & SUHLING, 1992). There the larvae were found in allochthonous detritus habitats with a slow current velocity. Similar habitats are used by some other species of the genus *Gomphus*, such as *G. externus* (HUGGINS & DUBOIS, 1982) and *G. simillimus* (SCHRIDDE & SUHLING, in prep.), and also by *Dromogomphus spinosus* (MAHATO & JOHNSON, 1991). Knowing that the larvae live in the lentic parts of streams and can be found in ponds remaining from dried up rivers in Spain (FERERRAS-ROMERO, pers. com.), it is not surprising to find the species in gravel pit ponds in its northern distribution, which are similar to river backwaters (WILDERMUTH, 1981).

There are only small distributional differences between larval stages of *G. pulchellus*, but only the final instar larvae crawl into gravelly substrates. This may be because of their greater mobility. In other dragonfly species, e.g. *Epiophlebia superstes* (TABARU, 1984), and some stoneflies (HILDREW *et al.*, 1980) young instar larvae prefer different substrates from the older ones. In June to September 1990 only the last five of probably 10 instars (SUHLING, 1991) of *G. pulchellus* were present in the gravel pit pond. Statements about distribution of early instar larvae in the pond cannot therefore be made, but single findings of third and fourth instar larvae in Southern France (SCHRIDDE, SCHÜTTE & SUHLING, unpublished data) suggest that there are no distributional differences over the lifetime of the larvae. The lack of young larve can possibly by explained by the very low flying and ovipositing activity of adult *G. pulchellus* in 1990 (SUHLING, 1991).

In some species distinct preferences for specific sediments are shown in the laboratory, but the distributional patterns in the field are often different (CUMMINS & LAUFF, 1969 ; MARZOLF, 1966). In these cases the choice of sediment particle size is influenced by other ecological factors, e.g. the presence of food. In *G. pulchellus* the results of the laboratory experiments corroborate the field work results. Except for the fine sand experiment larvae prefer the sediments covered with detritus. In contrast to *Paragomphus cognatus* (KEETCH & MORAN, 1966). *G. pulchellus* prefers finer particle sizes when given a choice between two bare sediments. According to KEETCH & MORAN (1966) larvae of *P. cognatus* distinguish the particle size in a tactile manner by using their tarsal hairs. This is probably similar in *G. pulchellus.*

Comparing the field and laboratory results it can be assumed that the presence of detritus is the primary influence in the spatial distribution of the larvae. The particle size of the sediment has an influence too, but in the field the larvae use middle to coarse sand covered with detritus in preference comparison to bare fine sand. The preference for a distinct particle size is eclipsed by the greater preference for detritus.

What are the reasons for living in detritus habitats ? There are two possible hypotheses : — **1.** The habitat choice is affected by the distribution of food. This is a common reason in a lot of detritivorous benthic macroinvertebrates (EGGLISHAW, 1964 ; PECKARSKY, 1980). However some predators also live in detritus habitats, so as *Plectrocnemia conspersa* (Trichoptera) and *Sialis fuliginosa* (Megaloptera), probably because of the distribution of their detritivorous food animals (HILDREW & TOWNSEND, 1976). In contrast to this, PECKARSKY & DODSON (1980) show that the colonization of artificial substrates by predaceous stoneflies is not influenced by the presence or absence of their food animals. The role of food distribution in habitat selection of predators seems to be species specific. A more or less unspecific predator such as *G. pulchellus* may be little influenced by this factor too. — **2.** Fish predation is one of the most important ecological factors in the distribution of dragonfly larvae (JOHNSON, 1991). In farm ponds, which contain fish, larvae of many of dragonfly species survive only in fish exclosures (MORIN, 1984 ; NEMJO, 1990). In *G. pulchellus* larval distribution may similarly be affected by fish predation. In fish free lakes larvae can be found in zones of bare sand (RUDOLPH, pers. com.). Can the covering with coarse detritus help the larvae to resist fish predation? According to BRUSVEN & ROSE (1981) predation by *Cottus rhoteus* on *Hesperoperla pacifica* (Plecoptera), *Ephemerella grandis* (Ephemeroptera) and *Rhyacophila vaccua* (Trichoptera) is substrate specific. When different combinations of cobbles and pebbles are added to bare sand, predation is reduced. Two of the successfully reproducing species in a North Carolina farm pond are gomphids (MORIN, 1984). Perhaps burrowing under a detritus layer is a good strategy for larvae of *G. pulchellus* to avoid predation. Stony substrates, in which larvae also can be found, may have a similar effect for reducing fish predation.

Some other ecological factors, such as oxygen content, may have their effects on distribution of *G. pulchellus* larvae, but I think fish predation and food are the most probable ones.

ACKNOWLEDGEMENTS

Much of the research reported here was conducted in partial fulfillment of the requirements for a Master of Science degree in Biological Sciences at the Technische Univeristät Braunschweig. It was kindly supported by Prof. Dr. Georg RÜPPELL. I thank Peter SCHRIDDE and Dr. Andreas MARTENS for critical comments. My special thanks to Dr. Peter MILLER for kindly reading the manuscript and giving helpful comments. The work was supported by the Deutsche Forschungsgemeinschaft (DFG).

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