Influence of Current Velocity on Substratum Selection by Naucoridae (Hemiptera): An Experimental Approach Via Stream Simulation

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Environ. Entomol. 22(3): 571–576 (1993)

ABSTRACT Microhabitat preferences of three sympatric naucorids (*Ambrysus circumcinctus* Montandon, *Limnocoris lutzi* La Rivers, and *Cryphocricos hungerfordi* Usinger) from the South Llano River of central Texas were evaluated in laboratory experiments. Each species was individually subjected to all paired contrasts produced from three substratum size classes (coarse gravel, small pebble, and small cobble). Within each contrast, three trials were conducted, each involving a different current velocity (slow, 6.6 ± 0.1 cm/s; intermediate, 9.8 ± 0.1 cm/s; and fast, 13.7 ± 0.5 cm/s). The gravel substratum was never preferred; moreover, preference in the pebble versus cobble contrast, when present, was only shown for the cobble substratum. Overall, *A. circumcinctus* exhibited consistent substratum preferences (cobble > pebble > gravel) independent of current velocity. *C. hungerfordi* preferred cobble over either gravel or pebble substrata; however, a synergistic effect between current velocity and substratum size was detected in the gravel versus pebble contrast. Finally, *L. lutzi* exhibited the highest degree of velocity-dependent substratum selection. Laboratory analyses corroborated field investigations and offered insight into the influence of interacting abiotic variables on the microdistribution of Naucoridae.

KEY WORDS current velocity, substratum size, lotic ecology

THE THEORY OF EROSION and deposition (Moon 1939) suggests that the substratum and current are directly correlated within the physical-stream environment. Therefore, it is difficult to assess their individual effects on a stream fauna under natural conditions (Minshall 1984). Nonetheless, both are important abiotic factors that influence the microdistribution of stream invertebrates in a variety of habitats (Harman 1972, Allan 1975, de March 1976, Minshall & Minshall 1977, Lamberti & Resh 1979, Erman & Erman 1984, Statzner et al. 1988). Because of the close relationship between substratum type and current velocity, any interpretation of the effect of one of these abiotic factors that excludes the other would be unrealistic (Reice 1980). Substratum characteristics and flow attributes should be simultaneously controlled to assess the relative role of each in affecting site selection and population density. Works by Cummins & Lauff (1969), Wiley (1981), and Fuller & Rand (1990) produced lotic environments within laboratory settings to observe the manner in which abiotic variables influence stream biota. These laboratory streams permit the control and manipulation of important abiotic and biotic parameters, while simultaneously reducing confounding effects. Such simulation is ideal for studies of habitat selection.

Creeping water bugs (Hemiptera: Naucoridae) are predacious aquatic insects common in lentic and lotic habitats of the southwestern United States and tropical regions of the world. Although these insects are considered keystone consumers in many aquatic systems (Sites & Willig 1991), little is known of their biologies (Gonsoulin 1973, Constantz 1974, Venkatesan & Cloarec 1988). Most literature concerning naucorids addresses taxonomic (e.g., Usinger 1947; La Rivers 1971, 1974, 1976; Polhemus & Polhemus 1988) or biogeographic questions (e.g., La Rivers 1951, Davis 1986). The United States contains five naucorid genera (*Ambrysus*, *Cryphocricos*, *Limnocoris*, *Pelocoris*, and *Usingerina*), which comprise 21 species. The South Llano River in central Texas harbors eight species (Sites & Willig 1991), the most species rich assemblage of naucorids known to occur in temperate regions.

Ambrysus is the most speciose naucorid genus within the United States. *Ambrysus circumcinctus* Montandon is the most abundant naucorid in the South Llano River, where it easily can be

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0046-225X/93/0571–0576$02.00/0

found under large rocks in swift waters (Sites & Willig 1991). *Cryphocricos* is represented in the United States only by *C. hungerfordi* Usinger (Polhemus & Polhemus 1988); the South Llano River demarks the northeasternmost known boundary (Sites 1990). Cuticular evidence suggests plastral respiration within this genus (Parsons & Hewson 1974). This species is morphologically hydrodynamic and exploits swift, deep, benthic habitats that contain large stones (Parsons & Hewson 1974, Sites & Willig 1991). In the United States, *Limnocoris* is represented by only one species, *L. lutzi* La Rivers. The species is considered a substratum generalist (Sites & Willig 1991) and occurs in riffle habitats. Although little is known of the ecology of this species, its abundance is correlated with stream depth (Sites & Willig 1991). *L. lutzi* is the smallest (adult size) naucorid inhabiting the South Llano River. The basic microhabitat associations of each of these three species were described by Sites & Willig (1991), who stressed the importance of substratum size and current velocity; however, they could not uncouple the two. The purpose of this study was to evaluate the influence of current velocity on substratum selectivity for each of the three naucorid species.

Materials and Methods

An artificial stream (Fig. 1), described in detail elsewhere (Herrmann et al. 1992), was used to evaluate substratum preferences of the three most common riffle-dwelling naucorids (*A. circumcinctus, C. hungerfordi,* and *L. lutzi*) of the South Llano River (Sites & Willig 1991). Each species (n = 18) was offered all paired contrasts of three substratum size classes: (1) coarse gravel (8–16 mm), (2) small pebbles (16–32 mm), and (3) small cobbles (64–128 mm) (Wentworth [1922] classification scheme after Minshall [1984]). Each contrast was replicated under three current velocities (mean ± SD): (1) slow (6.6 ± 0.1 cm/s), (2) intermediate (9.8 ± 0.1 cm/s), and (3) fast (13.7 ± 0.5 cm/s), which each represent different trials. These velocities include commonly encountered flow attributes of riffles within the South Llano River, although slower than the mean ± SD current (33.80 ± 23.02 cm/s) of riffles examined by Sites & Willig (1991). In all cases, water depth was held constant with a 5.1-cm lower weir. Four identically designed streams were used, and each trial was conducted in a randomly assigned stream.

Each stream contained eight quadrats that were dusted with a fine layer of washed sand (≈1 mm deep) before each trial. The left upstream-most quadrat was packed loosely with the larger rock class and the smaller rock class placed in the right upstream-most quadrat. Thereafter, the two substratum size classes alternated in a checkerboard pattern. This arrangement reduced the potential of biased selection related to complex hydraulic features (see Statzner et al. 1988).

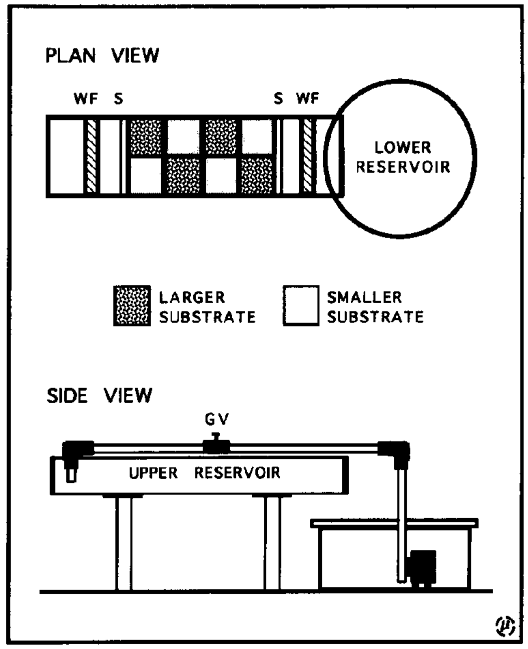

Fig. 1. Diagramatic representation of artificial streams used in substratum selection experiments (see Herrmann et al. 1992). Design consists of a simple water-fall system that can obtain current velocities of 0–45.5 cm/sec. Four paired quadrats (30.5 by 30.5 cm) occur within each stream. Stream depth was controlled with a lower weir. GV, Gate valve; WF, weir frame; S, screen; P, pump.

Water from the South Llano River was used in all experiments, changed biweekly, and replenished periodically to compensate for evaporation. Before each trial, naucorids were collected from a riffle in the South Llano River and placed in holding containers for no more than 1 h before use. Stream flow was initiated at least 30 min before each trial to stabilize water temperature. Eighteen individuals of a given species were released into each stream and left undisturbed for 32 h, after which the pumps were turned off and the lower weir was removed. This allowed water drainage and minimized naucorid movement. All insects were removed and their locations were recorded. On average, 4.1% of all individuals were found on the upper- or lower-retaining screens, but were not included in any subsequent analyses (Lauff & Cummins 1964).

A replicated goodness-of-fit test based upon G statistics (Sokal & Rohlf 1981) was used to evaluate the hypothesis that each species would occupy the two presented substrata equally in each trial. For each paired contrast of substratum size, the three different velocities constituted the replicates. A significant pooled effect in the absence

Table 1. Separate replicated goodness-of-fit tests at each of three current velocities for the three possible pairs substratum size offered to *A. circumcinctus*, *C. hungerfordi*, and *L. lutzi*.

Tests	df	*A. circumcinctus*		*C. hungerfordi*		*L. lutzi*	
		G^a	%	G^a	%	G^a	%
		Coarse gravel versus small pebble					
Pooled	1	32.10***	—	6.83**	—	17.14***	—
Heterogeneity	2	4.77	—	23.31***	—	15.53***	—
Total	3	36.87***	86.8	30.14***	68.6	32.66***	79.6
Slow velocity	1	15.96***	94.1	3.48	27.8	20.38***	100.0
Intermediate velocity	1	17.23***	94.4	20.38***	100.0	0.06	47.1
Fast velocity	1	3.68	72.2	6.28*	81.3	12.22***	93.3
		Coarse gravel versus small cobble					
Pooled	1	16.77***	—	29.90***	—	1.05	—
Heterogeneity	2	2.40	—	4.99	—	0.28	—
Total	3	19.15***	77.4	34.90***	86.3	1.33	57.4
Slow velocity	1	5.88*	77.8	17.23***	94.4	0.25	53.6
Intermediate velocity	1	2.04	66.7	14.70***	93.8	1.01	62.5
Fast velocity	1	11.25***	88.2	2.97	70.6	0.07	53.3
		Small pebble versus small cobble					
Pooled	1	9.23**	—	11.05***	—	2.01	—
Heterogeneity	2	5.39	—	3.79	—	7.32*	—
Total	3	14.62**	70.4	14.84**	72.2	9.33*	60.0
Slow velocity	1	8.73**	83.3	0.22	55.6	8.73**	83.3
Intermediate velocity	1	0.00	50.0	5.88*	77.8	0.07	53.3
Fast velocity	1	5.88*	77.8	8.73**	83.3	0.53	41.2

Percentage of individuals that selected the larger substratum is indicated (%) for each species.
[a] Significance of G: *, $0.05 \geq P > 0.01$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.

of significant heterogeneity indicated consistent selection of one substratum size, regardless of current velocity. Significant heterogeneity indicated substratum selection that was velocity dependent. Examination of the significance of selection at each velocity revealed whether the interaction involved only differences in the magnitude of selection or changes in the direction of selection (e.g., preference for the large substratum at the slow velocity, no preference at the intermediate velocity, and preference for the smaller substratum at the fast velocity). The absence of both significant heterogeneity and a pooled effect indicated no substratum preference at any current velocity.

Results

A. circumcinctus. The larger substratum was consistently preferred, regardless of current velocity in all paired contrasts (Table 1) involving *A. circumcinctus*. In particular, 86.8% of individuals preferred pebble to gravel, 77.4% preferred cobble to gravel, and 70.4% of individuals preferred cobble over pebble. Current velocity did not affect the magnitude or direction of substratum selection in any case.

C. hungerfordi. Substratum selection was complex for *C. hungerfordi*. In the gravel-versus-pebble contrast, significant heterogeneity occurred in the presence of a significant pooled effect (Table 1). This suggested that substratum selection depended upon current velocity. Moreover, the direction of preference differed depending on current velocity. In particular, the smaller substratum (gravel) was preferred at the slow velocity, whereas the larger substratum (pebble) was preferred at the intermediate and fast velocities. In the gravel-versus-cobble contrast (Table 1), *C. hungerfordi* exhibited a consistent preference for the larger substratum (86.3% of all individuals occurred in the cobble) over the smaller (gravel). Finally, *C. hungerfordi* selected cobble over pebble (72.2% of individuals) regardless of current velocity (Table 1). Current affected the direction of substratum selection for *C. hungerfordi*, but only in the gravel-versus-pebble contrast. In the other contrasts, neither the direction nor magnitude of substratum selection was affected by current. Preference in these last two experiments was consistently in the direction of the larger available substratum.

L. lutzi. Substratum selection varied with current velocity for *L. lutzi* in the gravel-versus-pebble contrast (Table 1). The larger substratum (pebble) was preferred at the slow and fast velocities; whereas no significant selection was apparent at the intermediate current velocity. The significant pooled effect was attributable to strong selection for the pebble substratum only during two (slow and fast) of the three current trials (>90%), which overwhelmed the even distribution of individuals at the intermediate velocity. The absence of significance for any test in the gravel-versus-cobble contrast indicated no substratum selection at any velocity. Current velocity influenced the direction of substratum selection in the pebble and cobble contrast (Table 1). No selectivity could be detected at fast or intermediate velocities; however, in the slow velocity, cobble was preferred over pebble.

Discussion

Laboratory experiments concerning lotic organisms can clarify and complement research conducted in field settings (Cummins 1962). Sites & Willig (1991) presented quantitative analyses of microhabitat associations of each of these three naucorid species; however, they did not uncouple the effects of the substratum and current velocity on microhabitat associations. Because our study regulated both parameters independently, it refined our understanding of specific substratum associations as potentially modified by current speed. We must emphasize here that our experiments addressed the manner in which current velocity could alter substratum selection. Velocity preferences were not evaluated per se.

In each experiment involving *A. circumcinctus,* selection was in the direction of the larger available rock class. This resulted in a hierarchical arrangement of substratum selectivity (cobble > pebble > gravel), which was unaltered by current velocity. In comparison, Sites & Willig (1991) found that mean rock size as well as current speed were significant variables influencing the microdistribution of *A. circumcinctus* (mean rock size and mean current velocity in the quadrats containing this species were found to be 184.7 mm and 37.8 cm/s, respectively). Rock size and current velocity in their field situations exceeded those of our largest rock category (small cobble, upper range of 128 mm) and the fastest current (13.7 cm/s). Apparently current speeds up to 13.7 cm/s do not alter substratum selectivity.

C. hungerfordi often inhabits swift, deep waters in which frequent surface visits to replenish a compressible air store would cause downstream displacement. It has been shown that adult *C. hungerfordi* and *C. barozzii* Signoret have cuticular modifications necessary for plastral respiration (Parsons & Hewson 1974), thereby eliminating the need for frequent surfacing and enabling them to exploit habitats such as large rocks in swift currents. Similarly, nymphs of *C. hungerfordi* use cutaneous respiration and do not need to surface to obtain oxygen (Sites & Nichols 1993). These habitats are generally unavailable to species that utilize compressible air bubbles. As a consequence, *C. hungerfordi* may be associated with larger rocks and swifter currents because it experiences ecological release from interspecific competition with other naucorids. A significant pooled effect existed in all three experiments involving *C. hungerfordi;* however, a current–substratum interaction was observed between pebble and gravel in which the direction of selection was affected by current. Strong association with the larger of the available substrata occurs at fast (81.3%) and intermediate (100%) velocities; however, this relationship is vitiated by slow velocities at which no substratum preference was shown. Similarly, Sites & Willig (1991) found that rock size and current velocity were important variables in determining the microdistributions of *C. hungerfordi* in field situations. Mean rock size in the quadrats containing this species was 189.0 mm, with an average current velocity of 37.2 cm/s. This rock size and current velocity exceeded those tested herein. In our experiments, preference only for the small cobble could be delineated over the other substrata. At faster current velocities, substratum–current interactions may become more prevalent and might confound field interpretations.

Although *L. lutzi* has been viewed as a substratum generalist with sensitivity to current velocity (Sites & Willig 1991), it did exhibit some preferential substratum selection in our study. In fact, current velocity influenced substratum selection in the gravel versus pebble contrast and in the pebble versus cobble contrast. Clearly, current velocity plays an important role in modifying substratum selection for this species, a view which did not emerge from a field study in which their separate effects could not be evaluated.

Field observations suggest that niche partitioning is based primarily on flow characteristics which separate the three naucorid species tested herein from the other five that occur in the South Llano River (see Sites & Willig 1991). The former three naucorid species occur in association with rapidly flowing water, whereas the other five species generally occur in shoreline and backwater situations, frequently among algae and aquatic macrophytes. Shoreline algae often grow among moderate to large alluvium, as well as in silt. Consequently, substratum size exploited by those five species is variable.

Our findings strongly paralleled those of Sites & Willig (1991) even though our simulated riffle velocities were not as fast as some potentially encountered in field situations. Nonetheless, important differences were observed between field and laboratory studies. For example, substratum size was relatively unimportant for *L. lutzi* in field situations, whereas laboratory analyses suggested that at least some consistent substratum bias existed. Similarly, field analyses suggested an important role of current velocity on the microdistribution of *C. hungerfordi.* We expected this, considering the respiratory adaptations of the species for swift waters. Contrary to expectation, current velocity only minimally influenced substratum selectivity in the laboratory. Ironically, this occurred at rock sizes (gravel and pebble) that do not occur in common habitat for *C. hungerfordi*. In reality, a trade-off may exist between substratum size and current velocity. At small rock sizes the importance of substratum size is dependent upon current. Conversely, at larger rock sizes, current does not alter the preference for larger substrata.

Historically, stream ecologists have suggested that substratum characteristics are primarily responsible for determining microspatial arrangements of stream invertebrates (see Minshall [1984] and citations therein). However, more recent work (e.g., Statzner et al. 1988) has redirected attention to flow attributes as primary factors affecting lotic community structure. Strong evidence here suggests that substratum selection by macrobenthic predators varies interspecifically with respect to rock size and can be altered by current velocity. The inability to uncouple the effects of current velocity on substratum selection in natural environments, where the two may be correlated, could give rise to erroneous conclusions concerning the relative importance of hydraulic or substratum attributes. Even in situations when current velocity may not appear to affect the presence or absence of species directly, it may have an indirect effect by modifying substratum selection. Thus, the uncoupling of abiotic factors when determining microhabitat selection of benthic organisms is imperative.

Acknowledgments

We thank C. Len Ainsworth for support from the State of Texas Special Line Item: Texas Tech University Center at Junction. We also thank J. Back, L. Baker, C. Langner, R. Stevens, and J. York for their laboratory assistance; B. Nichols and S. Cox for technical assistance; and G. Camilo, T. Elkner, D. Moorhead, and H. Thorvilson for critical reviews of an earlier version of this manuscript. This project was supported by the State of Texas Higher Education Coordinating Board Advanced Research Program grant #003644-081. This is contribution T-4-344, College of Agricultural Sciences, TTU; and Missouri Agricultural Experiment Station journal series paper No. 11,527.

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Received for publication 15 June 1992; accepted 28 December 1992.