The effect of substrate on burrowing in freshwater mussels (Unionidae)

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The burrowing behaviour and rates of burrowing on sand, clay, mud, and gravel were determined for three species of freshwater mussels, *Lampsilis radiata* (Barnes), *Anodonta grandis* Say, and *Elliptio complanata* (Solander). Burrowing is achieved by a series of probing and digging movements by the foot, alternating with adduction or closing of the valves, and foot contraction, which cause the valves to be forced downwards into the substratum. Overall burrowing abilities were superior in sand in comparison to gravel in all three species, and *E. complanata* burrowed more rapidly than the other species in clay, sand, and gravel. Righting was not accomplished in soft liquid mud but burrowing was achieved by frequent, rapid adduction of the valves. Although righting by both *E. complanata* and *A. grandis* in a clay substratum was slower than in either sand or gravel, both species burrowed more rapidly in clay. Although there were differences in burrowing abilities between species and in the four substrata tested, the ultimate success in burrowing by all three species suggests that substrate is not the direct causal factor affecting local distribution of freshwater mussels.

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L'étude du comportement fouisseur et de la vitesse d'enfouissement dans le sable, l'argile, la boue et le gravier chez trois espèces de moules d'eau douce, *Lampsilis radiata* (Barnes), *Anodonta grandis* Say et *Elliptio complanata* (Solander) a révélé que l'enfouissement est le résultat d'une série de mouvements de sondage et de creusage avec le pied en alternance avec l'adduction ou fermeture des valves et la contraction du pied, ce qui enfonce les valves dans le substrat. L'enfouissement est plus facile dans le sable que dans le gravier chez les trois espèces et l'enfouissement dans l'argile, le sable ou le gravier est plus rapide chez *E. complanta* que chez les autres moules. Il ne se fait pas de redressement dans la boue molle et liquide et l'enfouissement se fait alors par des adductions répétées et rapides des valves. Chez *E. complanata* et *A. grandis*, le redressement dans un substrat d'argile est plus lent que dans un substrat de sable ou de gravier, mais les deux espèces s'enfouissent plus rapidement dans l'argile. La capacité d'enfouissement est donc variable selon l'espèce et selon le substrat, mais les trois espèces arrivent finalement à s'enfouir partout, ce qui indique que le substrat n'est pas le facteur déterminant direct de la répartition à petite échelle des moules d'eau douce.

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Introduction

Freshwater mussels of the family Unionidae are widely distributed throughout North America. They have been reported from lakes and streams, on substrata varying from mud and clay to sand and coarse gravel, and are often associated with vegetation (Clarke 1973). Substrate type has been reported to influence the abundance and local distribution of a number of unionids (Negus 1966; Johnson 1970; Harman 1972; Clarke 1973; Fisher and Tevesz 1975; Salmon and Green 1983; and others). In general, it is considered that the texture or physical qualities of the sediments are important in providing stability and allowing the mussels to be firmly imbedded in the substratum. For example, Harman (1972) found that three species of unionids needed soft but firm substrata in which to anchor themselves and that there were preferred substrates. On the other hand, Cvancara (1970, 1972) and Cvancara *et al.* (1967) observed that bottom type was of secondary importance to unionids in some habitats. Green (1971, 1972) found no substratum-related differences in local distribution between two common species of unionids among 32 Canadian lakes.

If the physical quality of the substratum is important in determining local distribution, then relative ability to burrow in different sediments may be a factor in establishing and maintaining habitats and for survival, growth, and reproduction (Kat 1982). It is the purpose of this study to document and compare the burrowing abilities of three species of adult unionids on four different substrata and to test the hypothesis that local distribution of adult mussels, with respect to substratum type, can be related to their burrowing ability.

Methods

The three species of unionids in this investigation were *Lampsilis radiata* (Barnes), *Elliptio complanata* (Solander), and *Anodonta grandis* Say. *Lampsilis radiata* was collected from sandy bottom in shallow water (0.5 m) in the Ottawa River at Oka, 50 km west of Montréal, Canada. *Elliptio complanata* and *A. grandis* were collected from depths of 0.5–2 m in Lac Yvan about 60 km north of Montréal on sand, mud, and gravel bottom. Animals were 6 to 11 cm long. They were held in shallow storage tanks at 15°C on a substratum of coarse gravel prior to testing. Although a period of several months elapsed between time of collection and the termination of experiments, all specimens remained in good health during this period and burrowed readily. Ground commercial vegetable fish food was offered at twice-weekly intervals.

Burrowing was observed on four natural substrata: freshly sieved lake sediment (0.7-mm mesh) that produced a liquid mud, a clay lake sediment (2–4 μm) that became firm and compacted on settling, washed sand (0.5–1 mm), and coarse washed gravel (4–10 mm). Solid glass beads (3-mm diameter), which were also used as a substratum, allowed for observation of foot movement below the substratum surface. Records of burrowing activity were obtained by connecting a fine nylon line from the posterior end of one valve to the

TABLE 1. Comparison of mean rates of burrowing of three species of Unionidae in sand, gravel, and clay

	Lampsilis radiata					*Elliptio complanata*					*Anodonta grandis*				
	Sand	Gravel	*t*	df	*P*	Sand	Gravel	*t*	df	*P*	Sand	Gravel	*t*	df	*P*
Righting time (min)	12.0 (5.2)*	28.8 (10.2)	4.40	22	0.001	5.3 (1.3)	5.3 (3.3)	0.96	25	NS	2.9 (1.6)	5.3 (2.7)	3.10	25	0.01
Righting cycles	8.2 (3.6)	13.4 (5.7)	7.46	22	0.001	6.9 (2.1)	6.0 (2.0)	0.97	25	NS	4.5 (1.3)	5.6 (1.9)	0.85	25	NS
Burrowing cycles	17.3 (8.1)	17.5 (9.3)	0.33	22	NS†	19.1 (8.6)	37.5 (11.3)	4.58	25	0.001	13.8 (7.9)	21.6 (9.3)	2.47	25	0.01
Depth burrowed in 30 min (cm)	1.3 (0.3)	0.7 (0.2)	3.07	22	0.01	4.3 (0.6)	4.6 (0.5)	1.25	25	NS	2.6 (0.3)	2.6 (0.4)	0.82	25	NS
						Clay	Gravel	*t*	df	*P*	Clay	Gravel	*t*	df	*P*
Righting time (min)						12.2 (5.6)	5.3	4.83	22	0.001	9.6 (4.9)	5.3	2.83	22	0.01
Righting cycles						10.6 (3.9)	6.0	3.71	22	0.01	7.3 (2.3)	5.6	2.61	22	0.02
Burrowing cycles						22.3 (11.6)	37.5	1.21	22	NS	20.9 (12.3)	21.6	0.44	22	NS
Depth burrowed in 30 min (cm)						6.2 (0.9)	4.6	3.99	22	0.01	4.4 (0.5)	2.6	3.38	22	0.01

*Standard deviation is given in parentheses.
†NS, not significant.

pen of an ink kymograph. From these records the numbers of righting and burrowing cycles, the length of time for righting, and the depth burrowed were determined.

Results

According to Trueman (1968*a*, 1968*b*) and Trueman and Ansell (1969), burrowing in most bivalves consists of two phases. In animals lying on the surface, a series of probing and digging cycles continues until the foot has obtained sufficient purchase to allow the shell to turn and remain upright. This first righting phase is followed by further probing and digging while the shell is forced deeper into the substratum. At the end of the burrowing phase further horizontal movement may continue and this is accomplished by the same sequence of digging cycles. On sand, clay, and gravel, the burrowing behaviour of the three spcies of unionids examined conformed to the above pattern and to that observed in another freshwater mussel, *Anodonta anatina*, by Brand (1972). Typical burrowing traces in clay, sand, mud, and gravel are shown in Fig. 1.

As expected, neither righting nor burrowing by the three species was successful on a freshly sieved mud stratum that had a liquid consistency. Recordings of activity on liquid mud shown in Fig. 1 indicate frequent adduction of the valves of mussels lying flat on the surface without righting being achieved. Foot extension of animals lying on the liquid mud was observed, together with probing movements and pedal dilation, but no purchase was achieved. However, frequent expulsion of water upon adduction, coupled with the weight of the animals, formed a depression beneath the mussels. The animals gradually sank into these depressions and, by continued movement of the valves and foot, became partly buried.

The results of tests of burrowing abilities of the three species on sand and gravel and of two of the species on clay are summarized in Table 1. The righting time includes the period from the onset of probing by the foot until the shell is upright.

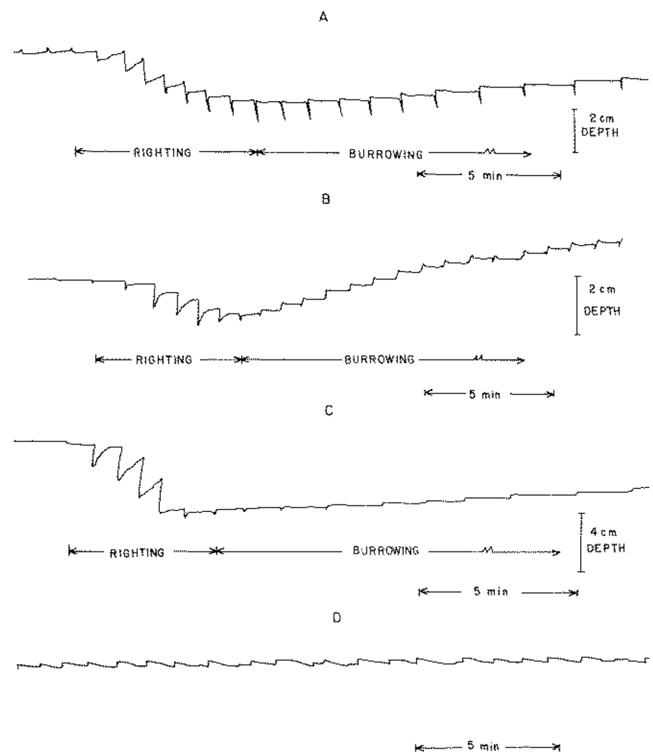

FIG. 1. Typical burrowing and righting traces of Unionidae. (A) *Anodonta grandis* in sand. (B) *Elliptio complanata* in gravel. (C) *Anodonta grandis* in clay. (C) *Lampsilis radiata* in liquid mud.

Burrowing cycles begin upon the completion of righting.

From Table 1 it may be seen that *Lampsilis radiata* is able to right more quickly and has fewer righting cycles on sand than on gravel. The depth burrowed in 30 min was also greater in sand than in gravel but the number of burrowing cycles was the same on the two substrata.

In *Elliptio complanata*, the time of righting, the number of righting cycles, and the depth burrowed in 30 min were the same on both sand and gravel substrata. However, more burrowing cycles were required in the gravel to reach the same depth as in sand. Righting time was considerably longer in clay than in gravel and the number of righting cycles was greatest in clay. Although there was no statistically significant difference between the mean numbers of burrowing cycles in clay and gravel, the total depth burrowed in clay was significantly greater.

Anodonta grandis took longer to right in gravel than in sand but there was no significant difference in the number of righting cycles. The depth burrowed was the same in sand and gravel but the number of cycles was greater in gravel. Righting time was longer in clay than in gravel or sand but the depth penetration in 30 min was greatest in clay.

Discussion

Our observations indicate that substratum particle size has an influence on the ability and speed of righting and burrowing by unionid mussels. *Lampsilis radiata* and *Anodonta grandis* righted more rapidly in sand than in gravel but there was no difference in rates of *Elliptio complanata* on the two substrata. *Lampsilis radiata* was also able to burrow more deeply in 30 min in sand than in gravel, whereas *E. complanata* required more burrowing cycles in gravel than in sand to penetrate to the same depth. Thus, although righting and burrowing abilities were not superior in sand in all respects, overall efficiency was greater. It appeared that the instability of coarse gravel inhibited rapid righting and burrowing.

While righting did not occur in liquid mud in any of the species, burial was achieved by a combination of water expulsion from the shells, shell and foot movement, and as a consequence of the weight of the animals on a soft surface. Trueman *et al.* (1966) have shown that jets of water forced out beneath the shells in marine bivalves facilitated penetration. Furthermore, in a natural habitat, flowing water probably assists in coverage by mud and helps to account for the presence of unionids in such habitats. Salmon and Green (1983) noted that *Anodonta grandis* can occur in a semiliquid substratum.

A clay substrate proved more difficult for both *Elliptio complanata* and *Anodonta grandis* to right on than either sand or gravel but both species burrowed more deeply in clay in 30 min than in sand or gravel. It appeared that clay, a softer substrate, did not provide the purchase necessary for rapid righting but once burrowing began, clay was more suitable for digging and anchoring.

While substratum particle size does have an influence on righting and burrowing ability by unionid mussels, it is apparent that both phases can be accomplished on a variety of substrata. It may, therefore, be questioned whether substratum has a direct cause and effect relationship to distribution, or whether the factors that determine substratum distribution (erosional or depositional) are responsible for local mussel distribution. Local distribution of juveniles will also be influenced by the location of release of glochidia from fish hosts as well as by current velocity. Furthermore, adult unionids are known to have a high degree of mobility (Negus 1966; Kat 1982) and must encounter a variety of substrata during their lives. Ability to burrow in different substrata is not consistent with the notion of substratum selected for physical qualities and, indeed, as Kat (1982) has pointed out, occurrence on a particular substratum is not evidence of selectivity. We conclude that burrowing ability has not been shown to be strongly related to substratum selection and, hence, local distribution.

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