Freshwater Biology (2000) **44,** 641–648

Substratum patch selection in the lacustrine mussels *Elliptio complanata* and *Pyganodon grandis grandis*

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SUMMARY

1. Sediment selection was investigated under controlled conditions in two common lake-dwelling species of freshwater mussels (Bivalvia: Unionidae), *Elliptio complanata* and *Pyganodon grandis grandis*.
2. Sediment choice was determined in six independent experiments under controlled conditions by distributing mussels randomly or evenly in tanks containing patches of sand and mud, and following their movement among sediment patches in experiments lasting between 30 and 45 days.
3. In all experiments, both species were found most frequently in muddy sediment patches. Movement toward muddy patches occurred rapidly: an average of nearly 80% of *Pyganodon grandis grandis* were found in mud after 30 days. *Elliptio complanata* moved rapidly to patches of mud at the start of experiments, but occupation of muddy sediments appeared to decrease after about 30 days.
4. Our results contrast with many field studies that suggest populations of lake-dwelling freshwater mussels infrequently inhabit mud and silt. We therefore postulate that large-scale mussel distribution in lakes is influenced most strongly by factors other than sediment composition.

Keywords: freshwater mussels, lakes, mud, preference, sand, substrate, substratum, Unionidae

Introduction

Because many species of freshwater mussels are now endangered (Williams *et al*., 1993), knowledge of their ecological requirements is needed to improve conservation efforts (Huehner, 1987). Sediment quality has long been thought to be one of the most important characteristics limiting mussel distributions. Anthropogenical siltation and sediment modification are, for example, listed among the principal sources of mussel habitat destruction (Bogan, 1993). Therefore, the search for conservation measures would be helped with an understanding of the optimal substratum for mussels.

Observations of the field distribution of mussels in lakes have implied that firm sediments (e.g. sand, gravel) are better for mussels than mud and silt. For example, the discriminant analysis of Green (1971) of mussel abundance in Canadian lakes showed that a higher sediment organic matter content discriminated low mussel density from high-density sites. Harman (1972) examined 650 sites in New York lakes and concluded that mussels live most frequently on firm yet penetrable sediments ranging from clean cobble to gravel. Cvancara (1972) suggested that lake mussels prefer gravel over muddy substrata, while Cvancara & Freeman (1978), Ghent, Singer &

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Johnson-Singer (1978) and Stern (1983) concluded that only a few mussel species (e.g. *Pyganodon* spp.) are even able to survive on soft, muddy substrata in lakes. Strayer *et al*. (1981) found that lake mussels were notably absent from soft sediments in deeper waters. Kat (1982) concluded that muddy substrata have a negative impact on growth of *Elliptio complanata* (Solander), suggesting that mud is a marginal mussel habitat. Hinch, Bailey & Green (1986) suggested that muddy substrata may interfere with the feeding of mussels, and that sand is a preferred habitat for lake mussels, such as *Lampsilis*. The analyses of Huehner (1987) of *Lampsilis* spp., *Elliptio dilatata* (Rafinesque) and *Pyganodon grandis grandis* (Say), suggest a preference for sand over mud or gravel. Bailey (1992) found that habitat structure relevant to mussels was defined by a sand–mud gradient in sediment quality. Observations of lake sediments on which mussels are most abundant have generally led to the conclusion that sand and gravel represent the best habitats for lake mussels, except perhaps for some species of *Pyganodon*.

Anecdotal evidence suggests that river and stream mussels are also more frequently found in firm substrata than silt and mud, while statistical analyses have yielded somewhat more equivocal results. The observations of Coker *et al*. (1922) suggest that mussels prefer sand and gravel to other sediments. Strayer *et al*. (1981) found that stream mussels were more rarely found in mud or muddy sand than in sand or gravel. Salmon & Green (1982) found that river mussels were most abundant in coarse sediments. Holland-Bartels (1990) found that Mississippi River mussels were rarely found in silt but frequently found in fine to medium sand. Detailed analyses have concluded, however, that little of the variation in lotic mussel distribution can be explained by sediment quality. For example, Strayer & Ralley (1993) examined the distribution of six species of unionids in the Neversink River, New York, and concluded that sediment granulometry did not predict the abundance of mussels in a stream. Strayer *et al*. (1994) studied the distribution of five mussel species in the Hudson River prior to the arrival of zebra mussels *Dreissena polymorpha* (Pallas), concluding that substratum quality had little demonstrable impact on mussel abundance. Tevesz & McCall (1979) suggested that the broad substratum tolerance of unionids implied by such field studies may be a real characteristic of their ecology, perhaps evolved due to reduced competition and predation pressure in freshwater compared with marine habitats. A recent review of sediment–mussel associations (Brim Box & Mossa, 1999) has noted considerable debate and uncertainty concerning the response of mussels to sediments, prescribing the need for quantitative work to determine the mechanisms through which sediments impact mussels.

A direct method of analysing the mechanisms underlying mussel–substratum associations is to perform experiments offering sediment choice. Bailey (1989) surprisingly found that *Lampsilis radiata siliquoidea* (Barnes), taken from both sandy and muddy substrata, moved preferentially to mud when both sand and mud substrata were available. Michaelson & Neves (1995) performed substratum choice experiments on *Alasmidonta heterodon* (Lea) and found that they always moved toward finer sediments. These results contrast with the general results of field observations of distribution. If this behaviour is consistent among species, the natural distribution of freshwater mussels may not be due to substratum preference *per se*, but to factors that alter the growth or survival of freshwater mussels, such as reproduction, predation or the chemical and physical characteristics of muddy and sandy habitats. Unfortunately, controlled analyses have examined sediment choice in only a very few species.

The purpose of this study was to offer mussels a substratum choice and test preferences under controlled laboratory conditions in two important lacustrine unionid mussels, *Elliptio complanata* and *Pyganodon grandis grandis*. Our expectation, based on the observed distributions in nature, was that both species would tend to choose sand/gravel substrata over mud.

Methods

Six experiments offering patches of sand versus muddy sediment were performed for each species. At the start of each, mussels were uniformly or randomly arranged within a basin containing equal surface areas of sand and mud distributed in distinct patches. The animals were allowed to move freely over 30–45 days in each experiment and changes in the number of animals found in each substratum type after different time periods were used to assess choice. Tests were performed independently for *E. complanata* and *P. grandis grandis*.

Experimental conditions

We prepared four experimental basins that were 2.31 m long, 0.61 m wide and 0.3 m deep. Basins were constructed of marine-grade plywood and lined with epoxy. Each basin had a head box at one end for water inflow and an outlet box at the other, resulting in a total bottom area of 1.98 m × 0.61 m. Two sediment types, mud and sand, were placed on the bottom in a pre-determined pattern to an average depth of 8.1 cm. Sand was obtained from Lac de l'Achigan (Amyot & Downing, 1991) and mud was obtained from Lac Croche, a humic lake on the property of the Station de biologie des Laurentides of the Université de Montréal (46°N, 72°W). Both of these lakes contained freshwater mussels. Sediments were arranged in a checkerboard pattern in some of the basins (12 alternating squares of mud and sand, 0.30 m × 0.33 m) and in a striped pattern in others (six alternating stripes of mud or sand 0.61 m × 0.33 m) so that each basin contained an equal surface area of mud and sand. No differences in responses were found in experiments differing in spatial arrangements of sediments, so no distinction was made between these treatments here. The organic matter content of mud (% dry mass) was approximately 23%, the organic matter content of sand was approximately 0.8% and the spatial configuration of sediments and their composition did not change appreciably during the experiments.

The basins were filled to a depth of about 25 cm with natural lakewater and both water and natural suspended food were renewed continuously from Lac Croche using the running lakewater system of the Station de biologie des Laurentides. Water was renewed at approximately 2.5 L min^{-1} to supply suspended food and remove waste products. Thus, the volume of each basin was totally replaced several times each day. Renewal water was passed through a baffle to diffuse currents. Light was supplied by two banks of fluorescent lights operated on a 12 h day/night cycle. The experiments were performed from August to October, and thus the temperature of the lakewater supply decreased gradually from 12.2 to 6.2 °C over the experimental period. Two experiments were performed for each species during each of three experimental series; thus, six replicate experiments were performed for each species over three different time periods.

Experimental animals were obtained from lacustrine populations found throughout the Laurentian region. *Pyganodon* used in these experiments were obtained from a depth of 1–2 m in Lac Brûlé, and *Elliptio* were obtained from the same depth in Lac de l'Achigan, near the Station de biologie des Laurentides. Voucher specimens are deposited at the Illinois Natural History Survey (Champaign, IL, U.S.A.). A random selection of the same individuals was used in each experiment to conserve the small parent populations. As is commonly the case for these species in this and other regions, *Elliptio* was found in sandy sediments while *Pyganodon* was found in sand overlain by a shallow layer of mud. Shell length of *Pyganodon* averaged 10.3 cm (SD = 1.5) and *Elliptio* averaged 7.4 cm (SD = 0.8). Mussel density during experiments (30–33 m^{-2}) was within the range reported for natural populations (0.09–53 m^{-2} m^2; see Downing & Downing, 1993).

Two experiments were performed over each time period with each species. Each experiment began with 50% of the experimental animals positioned in each substratum type, with animals being able to move freely throughout the experiments. Other details of experimental conditions differed slightly among the three series of experiments.

Experiment series one (1 August–14 September)

Forty mussels were introduced at positions determined using a random number generator in each of the four basins. Two of the basins (one with checkerboard sediments and one striped) were used for each species. The number of mussels found in each sediment square or rectangle was noted at least once each week until the end of the experiment.

Experiment series two (14 September–21 October)

Thirty-six mussels were used in each basin. Equal numbers of mussels were placed at positions within each square or stripe. In this way, three mussels were put randomly within each sediment square, and six mussels were placed randomly within each stripe. The number of mussels in each square or stripe was counted three times each week until the end of the experiment.

Experiment series three (21 October–18 November)

Thirty-six mussels were again used in each basin. Mussels were distributed evenly among sediment patches and their numbers counted as in experiment series two.

Because analyses of temporal trends can be complicated by the lack of independence of sequential data, we chose to analyse the six independent experiments as replicate samples of the selection of sediments by mussel species after different discrete time intervals. We therefore calculated the mean and 95% confidence interval of the fraction of mussels found in muddy sediment patches at different time intervals since the beginning of each experiment. For example, sediment selectivity after 10 days was calculated as the average fraction of mussels in mud, averaging across all independent experiments, where measurements were made 10 days after the start of experiments. Angular transforms of data were not performed because averages were seldom greater than 70% or less than 30%, the ranges of proportional data for which such transformation is beneficial (Steel & Torrie, 1960). Sediment selectivity would be indicated if the confidence intervals around the fraction of mussels found in a substratum type did not overlap 50%.

Results

Mussel distributions changed systematically toward patches of mud in both species in all experiments (Figs 1 & 2). The most dramatic shift toward muddy substratum was shown in *Pyganodon*, where the fraction of mussels found in mud departed significantly from 50% only a few days following the beginning of experiments (Fig. 1). Habitation of muddy patches climbed steadily throughout the experiments until an average of nearly 80% of the mussels were found in patches of mud after about 35 days. Use of muddy substratum by *Pyganodon* reached an asymptotic distribution with about 75% in mud and 25% in sand, but all experiments were terminated after about 45 days.

Elliptio also moved into patches of mud (Fig. 2). The behaviour of *Elliptio* was somewhat different, however, in that movements to mud patches after the start of experiments were not as strong, nor were they as persistent as the response of *Pyganodon*. In five out of six experiments using *Elliptio*, animals initially moved toward mud immediately after the beginning of experiments, but tended toward a more random distribution after experiments had run for

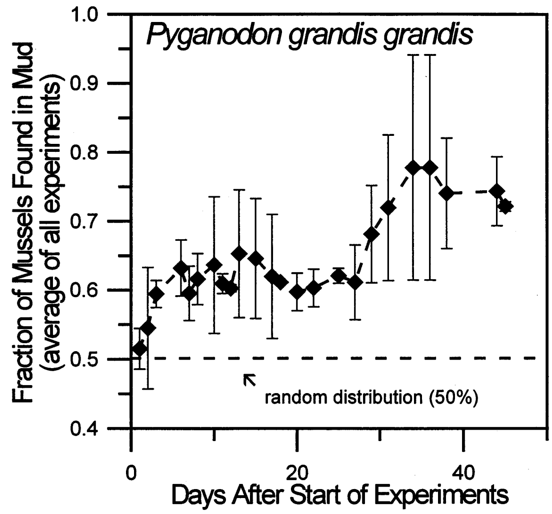

Fig. 1 Changes in the proportion of *P. grandis grandis* found in patches of mud over the duration of six laboratory experiments. Bars indicate 95% confidence intervals calculated for each period after the start of experiments across all replicate experiments. Samples sizes varied between two and six, depending upon the number of observations made after each time interval.

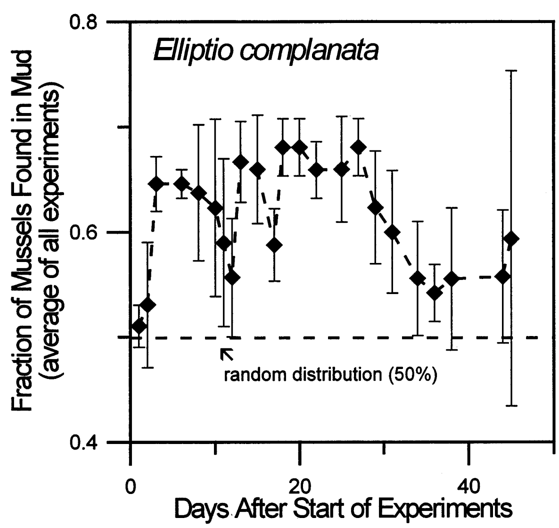

Fig. 2 Changes in the proportion of *E. complanata* found in patches of mud over the duration of six replicate laboratory experiments. Data are as in Fig. 1.

30 days or more. The spatial distribution of *Elliptio* averaged more than 65% in mud from a few days after the start of experiments to about 30 days after redistribution. After 30 days, however, the more frequent habitation of muddy patches was weakened.

Discussion

Our results confirm experimental analyses of sediment selection (Bailey, 1989; Michaelson & Neves, 1995) but contrast with field observations that have suggested that freshwater mussels prefer sand and gravel over muddy sediments. *P. grandis grandis* and *E. complanata* moved toward muddy patches in all of our trials. In *Elliptio*, this selection of muddy patches seemed more ephemeral but, since our experiment lasted only 45 days, we cannot distinguish between weakening preference and natural variability of responses. The decline in habitation of mud by *Elliptio* may also represent a month-long response to perturbation at the start of experiments. It is significant, however, that in none of our trials did freshwater mussels accumulate preferentially in sandy substratum, a finding that runs counter to many field observations of mussel–sediment associations.

The selection of patches of mud in these controlled experiments is a repeatable behaviour and mussels are not simply 'stalled' in patches of mud or move out of them slowly. Mussels in our experiments frequently crossed through patches of mud on rapid traverses, which occurred over short periods. Unpublished observations of individual mussel movements in these chambers show that mussels could cross two sediment patches in 24 h and as many as five patches in 48 h before stopping for long periods in muddy patches. Some mussels were even seen to make forays into patches of sand and return to patches of mud. Our data suggest that, all other things equal, these mussels move toward patches of mud.

Analysis of the transitory dynamics of mussel movement supports the concept that mussels choose organic sediments rather than simply accumulating passively in them. If mussels end up in mud because they move slowly in it or cannot escape it, then one would expect that mussels found in mud at the end of experiments would have traversed fewer sediment patches over the duration of trials. Table 1 shows that mussels ending experiments in mud moved through as many patches or more than mussels ending in sand. Only one of the trials showed that there was any significant difference ($P < 0.05$) in the amount of locomotion exhibited by mussels in different substrates, and this trial showed that mussels ending in mud moved through significantly more patches than those ending in sand. A global Kruskal–Wallace analysis of all species and all experiments also showed that mussels ending in mud moved through more

Table 1 Transitory dynamics of mussels in sediment choice experiments

		Mean patches visited		
Species	Experiment	Ending in sand	Ending in mud	*P*
E. complanata	1a	0.87	1.22	>0.05
	1b	0.91	0.67	>0.05
	2a	1.06	1.37	>0.05
	2b	1.29	1.32	>0.05
	3a	0.79	0.92	>0.05
	3b	0.08	0.64	0.013
P. grandis	1a	0.89	0.76	>0.05
	1b	0.18	0.62	>0.05
	2a	0.89	1.13	>0.05
	2b	0.18	0.76	>0.05
	3a	0.77	1.22	>0.05
	3b	0.46	1.00	>0.05

Data are the average number of sediment patches visited during experimental trials of mussels found in mud versus sand substratum at the end of experiments. *P* is the probability (Kruskal–Wallace test; Conover, 1971) that mussels found in sand and mud traversed the same number of patches during the experiments.

sediment patches than those ending in sand ($P = 0.024$).

Published field observations of mussel abundance have led many authors to believe that freshwater mussels prefer sand and gravel whereas, curiously, the *Elliptio* and *Pyganodon* that we studied and the *Lampsilis* studied by Bailey (1989) moved toward patches of mud. This suggests that, in nature, factors other than substratum selectivity may determine broad-scale patterns in mussel abundance. Some factors that may influence mussel abundance, and may therefore lead to mussel populations being found predominantly in sand and gravel, may be linked to reproduction, predation, food abundance and physical and chemical factors.

Mussels may not, for example, be able to recruit effectively in muddy habitats. Although in patchy sediments, mussels may move frequently to patches of mud, they may not be able to maintain viable populations in uniformly muddy areas. This would be true if recruitment into mud was very low, for example. The obligate, parasitic, glochidial stage of most mussel species must be released from fish in such a way that juveniles settle successfully after release. If fish hosts cannot be infected successfully by populations in mud, if fish do not frequent muddy areas during an appropriate time period after infection to allow glochidial settling, or if glochidia settling into muddy substrata cannot survive, then freshwater mussel populations might not recruit to muddy patches and be found predominantly in patches of sand and gravel.

Mussel survival may be low in areas where mud is the dominant substratum. In lakes, mud accumulates in deeper waters or where turbulence is low. Colder waters at depth in lakes may interfere with mussel physiology or their ability to move rapidly or efficiently enough to remain at the sediment surface. Water turbulence, such as that seen along beaches, may also be necessary to renew suspended food resources. Because of the high rate of decomposition near mud surfaces, pH may be too low, redox potential too low, oxygen too low or decomposition products (e.g. unionized ammonia, H_2S) too abundant to allow mussels to function efficiently, grow and reproduce in mud.

The results of our experiments and those of Bailey (1989) pose an interesting puzzle. It is intriguing that the three most common species of freshwater mussels in North American lakes behave in a way that would draw them into patches of substratum different from those in which they are most frequently found in nature. It is curious that mussels have evolved such a behaviour. If mussels move toward mud yet fail to establish populations there, mussel populations would be unlikely to persist. Therefore, mussels must be able to sense adverse gradients other than mechanical differences in sediments, e.g. chemical or physical variations in the water or substratum. It is puzzling that mussels may have evolved locomotor behaviour that leads them to muddy substrata where populations do not persist. This behaviour may, however, be advantageous when expressed on a local scale, bringing them into richer, softer patches of sediment within areas where sediments are patchy, but other chemical and physical gradients are less marked. For example, in the absence of an oxygen or temperature gradient, by moving toward patches of mud, mussels might be brought to areas that are richer in food or more easily penetrated when mussels become endobenthic in winter (Amyot & Downing, 1991). Further, moving into softer patches of mud may be a predator avoidance behaviour because mud is easier to penetrate and mussels that move deep within it may be less susceptible to predators, such as fish (Cummings & Mayer, 1992) using visual cues. Alternatively, the selection of muddy patches by lacustrine mussels may be a relict behaviour from the supposed primarily riverine evolution of freshwater mussels. Because mud only occurs in areas of low current, the selection of muddy patches may serve to bring mussels indirectly into areas where currents remain low enough to avoid being swept away.

There is some empirical evidence that mussels select patches of substratum that are rich in organic matter. For example, Downing (1991) mapped a population of *E. complanata* living across a depth/sediment gradient and another population living at almost perfectly uniform water depth in sandy substrata in Lac de l'Achigan. The population examined across a depth gradient showed a strong negative correlation between mussel density and the organic matter content of the sediments, reflecting the expected distribution of lacustrine mussels. When examined within the relatively uniform sand at 2 m depth, however, there was a significant ($P < 0.05$) positive correlation between the abundance of mussels and the organic matter content of sediment patches. Thus, whereas analyses across a range of depths in a given lake may give the impression that mussels select sandy substrata, individuals within areas suitable for mussel colonization may actively seek out patches that are richest in organic matter.

Our experiments and those of Bailey (1989) are among the rare analyses of the preference of freshwater mussels for organic versus inorganic substrata under controlled conditions. Experiments by Huehner (1987) and Michaelson & Neves (1995) only used inorganic sediments but found that mussels consistently chose fine sediments over coarse ones. In contrast, field analyses in lakes frequently suggest that mussels are least frequently found in fine sediments like mud and silt. These experimental results indicate that field correlations of mussel abundance and habitat characteristics are unreliable indicators of substratum selection in freshwater mussels. Although substratum quality clearly plays a role, the abundance, and thus the persistence, of this important faunal group must be strongly regulated by a suite of factors. Increased understanding of the interplay of substratum selection and other aspects of mussel ecology could greatly promote effective conservation.

Acknowledgments

The authors thank J.-P. Amyot for interesting discussions of mussel locomotion, David Strayer, James Anthony, Kelly Arbuckle and an anonymous reviewer for helpful comments on an early version of the manuscript, and the staff of the Station de biologie des Laurentides for help in executing this research. Supported by an operating grant to JAD from the Natural Sciences and Engineering Research Council of Canada.

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(*Manuscript accepted 18 January 2000*)