

Locomotion in *Elliptio complanata* (Mollusca: Unionidae): a reproductive function?

JEAN-PIERRE AMYOT* AND JOHN A. DOWNING†

Université de Montréal, Département de Sciences Biologiques, C.P. 6128, Succursale centre-ville, Montréal, Québec, Canada, H3C 3J7

*Author to whom correspondence should be sent

†Present address: Department of Animal Ecology, Iowa State University, 124 Science II, Ames, IA 50011-3221, U.S.A.

SUMMARY

1. Temporal variation in the spatial aggregation of the freshwater bivalve *Elliptio complanata* was studied at a sandy site in an oligotrophic lake over three years.
2. Epibenthic populations varied in aggregation over the season bringing animals closer together during spawning. The complex link between movements of mussels and aggregation dynamics suggested a functional reproductive role for horizontal locomotion of unionid mussels in lentic systems.
3. The rate of locomotion did not differ systematically among males, females or hermaphrodites, and was independent of gravidity, whether compared during spawning, after spawning or throughout the ice-free season.
4. In spite of the high reproductive output of mussels and the energetic cost of locomotion, no relationship was found between the rate of movement of spawning gravid mussels and reproductive output.

Introduction

The ecology of native North American freshwater mussels has recently gained importance due to a growing concern for the loss of species and the decline of many populations (Keller & Zam, 1991; Allan & Flecker, 1993; Williams *et al.*, 1993). This deterioration has been linked to anthropogenic activities such as industrial pollution, agricultural activities and channel modification (Williams *et al.*, 1993), as well as impacts of exotic species [e. g. *Dreissena polymorpha* (Pallas 1771); Ricciardi, Whoriskey & Rasmussen, 1996; Schloesser, Nalepa & Mackie, 1996]. Some species may even reach extinction before we gain a thorough understanding of factors affecting their populations (Bogan, 1993).

The basic life cycles of freshwater bivalves have been well known for nearly a century (Lefevre & Curtis, 1910; Coker *et al.*, 1921; Negus, 1966; Haukioja & Hakala, 1978). The Unionidae of the temperate zone reproduce annually (Ellis, 1978) and most have highly specialised life histories (Jones, Simpson & Humphrey,

1986). Knowledge of reproductive details such as gametogenesis, breeding season, periods of glochidia release, fish hosts and duration of fish parasitism is limited to a few species (Matteson, 1948; Heard, 1975), and much of their ecology is still poorly understood (Kat, 1982; Strayer & Ralley, 1993; Balfour & Smock, 1995; Strayer, Sprague & Claypool, 1996).

Egg formation (Downing *et al.*, 1989) and fertilisation (Matteson, 1948) appear to be the most critical steps in the reproductive cycle. Sperm is generally and synchronously liberated into the water and entrained by the inhalant siphon of females. The sperm fertilises the eggs in the suprabranchial chambers of the female. This mode of fertilisation requires sperm to be sufficiently concentrated in the vicinity of a female. In *Elliptio complanata* (Lightfoot 1786), a common North American lake- and stream-dwelling mussel, although Matteson (1948) suggested that spermatozoa can swim considerable distances, the reproductive success has been associated with spatial aggregation of mussel

populations, so that fertilisation failure is often complete when local density is < 10 mussels m^{-2} (Downing *et al.*, 1993). Male and female mussels must therefore be relatively close in order to achieve successful fertilisation.

Like most native freshwater mussels, *E. complanata* moves both horizontally over the sediment, and vertically in and out of it. The function of mussel locomotion remains unclear, and studies examining locomotion in freshwater mussels have focused on the burrowing mechanism (Trueman, 1968). Horizontal locomotion, in particular, has been studied little. Recent evidence shows, however, that horizontal locomotion in *E. complanata* is minimal in both streams (Balfour & Smock, 1995) and lakes (Amyot & Downing, 1997). Furthermore, locomotion in this mussel, unlike many poikilotherms, is little influenced by water temperature but strongly related to daylength, at least in a lentic environment (Amyot & Downing, 1997). Amyot & Downing (1997) have suggested that this correlation hints at a behavioural rather than a physiological origin for seasonal variations in locomotion. The coincidence of periods of greatest displacement with the breeding season suggests that seasonal locomotion may have a reproductive function.

From a bioenergetic point of view, because of the energy cost associated with bivalve displacement (Trueman, 1983), the rate of displacement of females may be less than that of males. Such a strategy during the spawning period would enable females to conserve energy, allowing greater production of embryos, which is much more costly than producing sperm (Russell-Hunter, 1979).

The hypothesis that the spatial dynamics of freshwater mussels might serve to enhance reproduction has not been examined explicitly in the literature. Such a study might greatly improve our knowledge of mechanisms governing the reproduction and viability of unionids. This knowledge is critical to the understanding of the basic life-history strategy of endangered freshwater bivalves.

The goal of our study was to examine the horizontal movement of members of a lentic population of the freshwater mussel *Elliptio complanata* as a process that could generate temporal aggregation dynamics, bringing male and female mussels closer together during spawning, and spacing them further apart during the rest of the year. We postulate (i) that spatial aggregation is seasonally dynamic in an epibenthic

population of *Elliptio complanata*; (ii) that aggregation is most marked during spawning; (iii) that aggregation dynamics are linked with horizontal movements of mussels; (iv) that males move farther than females prior to spawning; (v) that both sexes have similar patterns of locomotion during the nonspawning period and (vi) that extreme movements of gravid mussels leads to decreased reproductive output.

Materials and Methods

Experiments were conducted in the sandy littoral zone of Lac de l'Achigan (45°57' N, 73°58' W), 60 km north of Montréal, Canada. This lake (area, 5.08 km²) has a mean depth of 11.6 m, but the north shore is composed of gently sloping, sand beaches. *Elliptio complanata* is the most abundant mussel in the lake with local densities reaching 70 m^{-2} (Downing *et al.*, 1989). We studied a population of *E. complanata* within a 5 × 8 m area at depths ranging from 1.5 to 2 m. The site appeared homogeneously sandy with no trace of predation on mussels. Each mussel was labelled underwater using SCUBA equipment in order to minimise perturbation. Mussels were marked by attaching a numbered plastic label (Dymo™) to the posterior face of one valve with underwater glue (Devcon Wet Surface Repair Putty™) delivered using a disposable syringe. Disturbance was minimal because animals were only touched gently during labelling.

Measures of mussel positions

The positions of marked individuals were measured over nearly 3 years in the same quadrat. On each sampling date, the relative position of each mussel was measured using rulers attached to stakes marking the corners of 1-m² quadrats. Since only quadrat corners were marked, movement of mussels across the study area was unrestricted. These geometric data were transformed to *x-y* co-ordinates by triangulation. Mussel positions, when compared between weeks, allowed the measurement of spatial aggregation as well as the distances each animal travelled, and the frequency of their movements throughout the ice-free season. The determination and measurement of locomotion are described elsewhere (Amyot & Downing, 1997). In total, 781 individuals of *E. complanata* were marked over the course of the experiment, but since some mussels situated near the edges of the site

left the study area, some endobenthic juveniles became epibenthic and a few others died during the experiment, we limited the sample used in the analysis of locomotion to 527 individuals that were marked at the start and could be followed to the end of the study. Mussels were considered to be epibenthic if they protruded visibly from the sediment surface and endobenthic when completely buried, leaving a small depression at the surface. Disruption of mussels was avoided during position measurement by using a mobile support (5.5×1 m) made from 10-cm diameter ABS-plastic pipes to keep divers at a distance of 40 cm above the sediment surface.

We recorded the position of *E. complanata* individuals weekly during the summer season and twice each month during spring and autumn. No observations were made during winter because of ice cover. Field works were performed during July–November 1988, May–November 1989 and May–June 1990. Field works ended on 25 June 1990, while female mussels still held maturing glochidia. This was ascertained by periodic sampling of adjacent mussels and visual inspection of the marsupial gills to estimate the maturity of larvae. Then, all epibenthic individuals were removed and brought to the laboratory. Each marked mussel was sealed underwater in an individual plastic bag to avoid loss of glochidia by spontaneous abortion (Lefevre & Curtis, 1910; Matteson, 1948). We also sieved the sediment of all quadrats to a depth of 30 cm to collect all marked and unmarked endobenthic mussels. Only ten (1.3%) marked individuals were found buried, leaving 8.9% of the initially marked population that had either died or emigrated.

Measure of aggregation

The local population density at the sediment surface fluctuated in response to seasonal vertical migration cycles (Amyot & Downing, 1991, 1997). Therefore, the distance to the nearest neighbour (Clark & Evans, 1954) was chosen as an efficient (Pielou, 1977) descriptor of spatial patterns of mussel populations. The distance to nearest neighbour yields a coefficient of randomness (R). The x - y position of all epibenthic mussels was used to calculate the mean distance to nearest neighbours for each sampling date. The mean distance to nearest neighbours that would be expected if the individuals of that population were randomly distributed was also calculated. The ratio of observed mean distance

to expected mean distance yielded the coefficient R , measuring the degree to which the observed distribution departs from random expectation:

$$R = \frac{\bar{r}}{E(r)} = \frac{\frac{\sum r}{n}}{1/2\sqrt{\rho}} \quad (1)$$

where \bar{r} represents the mean distance to nearest neighbours in the observed population, and $E(r)$, a derivation of Poisson's exponential function (see Clark & Evans, 1954), represents the mean distance to nearest neighbour of a randomly distributed population; ρ is the density of the observed distribution expressed as the number of individuals per unit area.

A population can be considered aggregated when the index R is significantly less than 1. Clark & Evans (1954) provide a formula for estimating the error associated with R :

$$C = \frac{\bar{r} - E(r)}{\sigma_{E(r)}} = \frac{\bar{r} - E(r)}{0.26136/\sqrt{n\rho}} \quad (2)$$

where C is the standard variate of the normal curve and $\sigma_{E(r)}$ an integration of the product of the probability distribution function r by r^2 (see Clark & Evans, 1954), represents the standard error of the mean distance to nearest neighbour in a randomly distributed population of the same density as the observed population. Significant differences from randomness of each R -value obtained were ascertained using this method.

As R is sensitive to sampling boundary effects, mussels living in a narrow strip along the edge of the sampling area were only used as 'neighbours' in the analysis to avoid systematic overestimates of R . The width of the strip was proportional to the observed mean distance to nearest neighbour (Pielou, 1977).

Time of spawning

According to Matteson (1948), the breeding time of *E. complanata* in Ocqueoc Lake in Michigan extends from the end of April to mid-June, reaching a maximum around mid-May. The spawning maximum coincides with the period when water temperatures reach 20 °C. The maturation of larvae takes roughly four weeks after spawning. In Lac de l'Achigan, ice melts and water temperature reaches 20 °C approximately 2 weeks later than in Ocqueoc Lake. Environmental conditions may vary from year to year, but based on our examination of maturing glochidia,

spawning of *E. complanata* must have begun in early May in Lac de l'Achigan, reaching a peak at the end of May but continuing to the end of June.

Mussel characteristics

Shell size, sex and reproductive output of all epibenthic individuals followed throughout this study were determined at the end of the field study. Shell length was measured using a digital caliper (± 0.01 mm). As *Elliptio complanata* is not sexually dimorphic, sex determination required removal and histological examination of the gonads. The gonadal mass of each mussel was preserved in 80% ethanol. Transverse sections of gonadal tissues were stained and observed under a microscope following the protocol of Heard (1975). Because some individuals can be hermaphroditic (Heard, 1975), sex was separated into five categories: < 10%, 10–40%, 40–60%, 60–90% and > 90% male tissue, following Downing *et al.* (1989).

Reproductive output was estimated as the number of glochidia or eggs present in the outer gills of each gravid female. This was determined by sectioning and putting the gills of each gravid mussel in a 1-L glass container. The 100 μ m filtered contents of the sampling bag were added to collect any eggs or glochidia that may have been released by spontaneous abortion during transportation, and the glass container was filled to 800 mL with 80% ethanol. This solution was mixed briefly at moderate speed using a domestic electric beater to break gill structures and liberate the larvae. Reproductive output was estimated by counting the larvae in four 1-mL subsamples at 40 \times magnification.

Statistical analysis

Correlation analysis (Pearson's r) was used to test the relationship between (i) the level of aggregation and time; (ii) aggregation dynamics and the rate of horizontal locomotion of mussels (estimated as the daily average distance travelled by epibenthic mussels) and (iii) the movement of gravid females and their reproductive output. Comparison of locomotion among sexes considered two aspects: (i) total number of movements of each epibenthic mussel during a given period and (ii) the cumulative distance travelled (cm) by each epibenthic mussel. We compared the level of aggregation inside and outside the spawning period

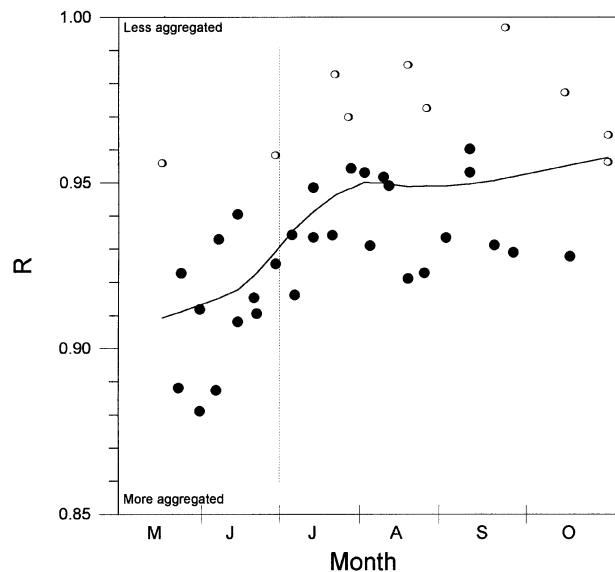


Fig. 1 Seasonal variation of the aggregation (R : coefficient of randomness) for an epibenthic population of *Elliptio complanata*. Open circles (\circ) represent the values of R that were not significantly different from randomness. The trend line was determined using locally weighted sequential smoothing (LOWESS: Cleveland, 1979). The vertical broken line indicates the time at which spawning probably ceased.

using one-way anova. Error distributions of variables were satisfactorily close to normal (Wilk–Shapiro normality statistic > 0.93), except for sex categories (Wilk–Shapiro = 0.66) for which a Kruskal–Wallis one-way ANOVA was used to test for differences in locomotion.

Results

Seasonal aggregation dynamics

The analysis of nearest neighbour distances revealed that epibenthic mussels were frequently spatially aggregated in Lac de l'Achigan (Fig. 1). More than 75% of the estimates of R showed a distribution significantly different from random ($P < 0.05$, C-test). Populations became very aggregated around the end of May, the expected time of maximum spawning in this lake. Following spawning (vertical line in Fig. 1), aggregation declined and R increased systematically with time ($r = 0.529$, $P = 0.0005$), indicating clear seasonal dynamics in distribution. Moreover, comparison of the level of aggregation during spawning (mean $R = 0.9184$, $SD = 0.0246$) with that post-spawning (mean $R = 0.9497$, $SD = 0.0219$) showed that mussels were significantly more aggregated during spawning ($P = 0.0003$, one-way ANOVA). Because *E. complanata*

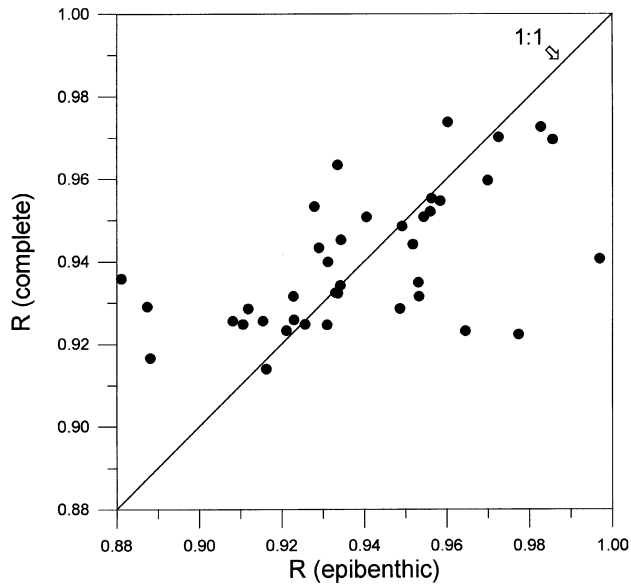


Fig. 2 Comparison of the level of aggregation (R : coefficient of randomness) between the complete population (i.e. epibenthic + endobenthic) and the epibenthic population of *E. complanata*.

migrated vertically, depending on season and temperature (Amyot & Downing, 1991), between 4 and 76% of the population remains completely buried beneath sediment surface. When endo- and epibenthic mussels were considered together (as if sediments were transparent) no correlation ($P = 0.127$) was found between aggregation and season. This can also be seen in Fig. 2 by the small range of variation of R -values for the complete population compared with the epibenthic population. Thus, members of the population that can reproduce, (i.e. epibenthic mussels), were significantly closer to each other than they were throughout the rest of the year.

Aggregation dynamics and horizontal movement

A strong positive relationship was found between the rate of locomotion and day length (see Amyot & Downing, 1997). *Elliptio complanata* moves more frequently and further during periods of longest daylight. Fig. 3 shows the degree of spatial aggregation (black circles) and the average distance travelled daily by epibenthic mussels (open circles) in all three years. Aggregation and horizontal locomotion were significantly, negatively correlated ($r = -0.43$, $P = 0.007$). In spring, the epibenthic population began moving in mid-May and accelerated until July. Then, even though

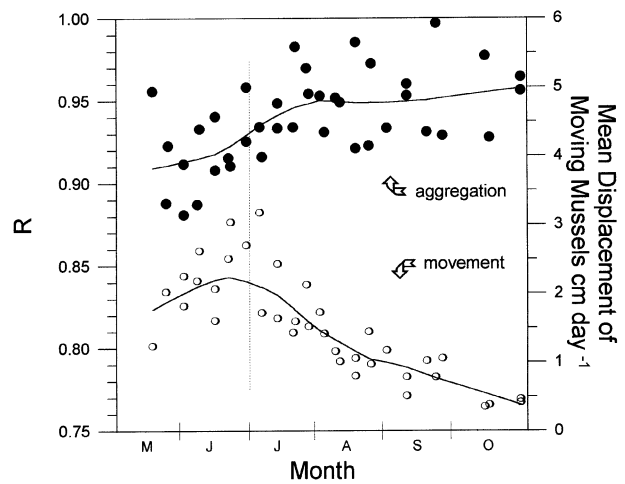


Fig. 3 Comparison of seasonal patterns of aggregation (●) and mean daily distance travelled by epibenthic mussels (○). The solid curves represent LOWESS (Cleveland, 1979) fits to the data of each category.

there was no corresponding change in water temperature, the rate of movement decreased rapidly. During the period when locomotion declined, the spatial distribution of the epibenthic mussels changed from highly significantly aggregated to a spatial distribution approaching randomness. Movement then continued to decrease throughout the ice-free season.

Sex, reproduction and locomotion

Other studies have shown that the Lac de l'Achigan population shows a significant degree of hermaphroditism (Downing *et al.*, 1989). The population was biased towards males, having an overall male–female ratio around 1.5:1 (Table 1). Males, females and hermaphrodites had similar rates of locomotion during spawning, after spawning and over the entire ice-free period (Kruskal–Wallis one-way ANOVA; $P > 0.05$) (Table 2). Simple correlation analysis showed no significant relationship between the number of glochidia found in each gravid mussel and locomotion from their last spawning period (May–June 1990) (Fig. 4).

Discussion

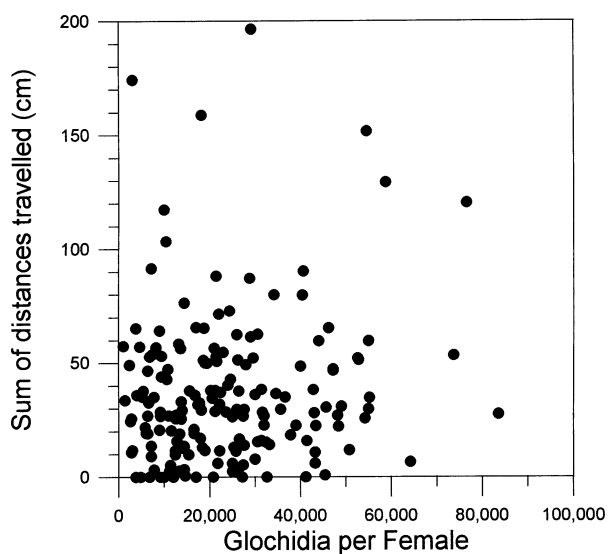
Reproduction in unionid molluscs is complex. The life cycle of freshwater mussels includes a glochidia larva, parasitic on fish, which is highly vulnerable since only a very small proportion of the glochidia are capable of attaching themselves to the fish (Jokela, Valtonen

Table 1 Proportion of epibenthic population, size of shell and reproductive output of each sexual category of mussels. Sexual classes were based on the percentage of male tissue found in sectioned gonads; $n = 701$

Sex (% male)	% of Epibenthic Population	Shell Length (mm) mean (SD)	% with Eggs or Glochidia	Eggs or glochidia/gravid mussel mean (SD)
0–10	38.4	67.9 (11.64)	25.2	24 450 (16 180)
10–40	1.8	69.3 (15.99)	1.3	17 030 (10 130)
40–60	1.8	66.5 (17.58)	1.1	16 410 (16 010)
60–90	0.8	52.6 (6.66)	–	–
90–100	57.2	64.9 (14.94)	–	–

Table 2 Comparison of the rate of movement of each sexual category of mussels for the mean total displacement during 1988, 1989, 1990 combined and the mean total distances travelled (cm) by epibenthic mussels; $n = 527$

	Sex category (% male tissue)					Kruskal–Wallis Statistic	P
	0–10	10–40	40–60	60–90	90–100		
Mean displacement (fraction of population that moved in 1 week)							
Spawning period	0.1028	0.1161	0.0922	0.0685	0.0997	4.785	0.310
Post-spawning	0.0652	0.0697	0.0638	0.0534	0.0645	3.663	0.453
Mean distance travelled (cm)							
Spawning period	1.37	1.55	1.13	0.83	1.22	6.342	0.175
Post-spawning	0.45	0.32	0.50	0.56	0.50	5.999	0.199

**Fig. 4** Relationship between the number of glochidia found in the marsupia of mussels and the sum of distances travelled by each female mussel during their previous spawning time (May–June 1990) ($r = 0.119$; $P = 0.115$).

& Lappalainen, 1991), and because many juvenile mussels do not find a suitable substratum for continued growth (Negus, 1966). Another factor reducing recruitment success is the spatial distribution of mature

individuals. For example, Downing *et al.* (1993) clearly demonstrated that fertilization success was strongly linked to the spatial aggregation of a population of *E. complanata* and pointed out that the spatial dynamics of mussel populations makes perception of this phenomenon difficult.

Elliptio complanata moves horizontally and vertically in both lotic (Balfour & Smock, 1995) and lentic habitats (Amyot & Downing, 1997) following a seasonal cycle. Downward movements may be useful against predation (Negus, 1966), displacement during high flow (Hinch, Kelly & Green, 1989) and wave action during storms, or they may provide shelter during adverse conditions such as periodic pond dryness (Mackie, White & Zdeba, 1980). The utility of downward migration during mid-summer remains obscure. Although some have suggested that horizontal displacement may offset possible downstream displacement in lotic populations (Balfour & Smock, 1995), or aid in locating suitable conditions after being dislodged (Trueman, 1968). Until now, other possible functions of horizontal movement have been little studied.

We know of no other study that has suggested a possible reproductive role for locomotion and spatial dynamics in freshwater mussels. Although some have

Table 3 Level of spatial aggregation represented by R (coefficient of randomness) for epibenthic mussels, male, female, and the entire epibenthic population during the spawning time.

	R		
	Male	Female	Population
Minimum	0.8871	0.8926	0.8811
Maximum	0.9934	1.0156	0.9584
Mean	0.9280	0.9300	0.9184

shown a coincidence of mussel activity with water temperature (Matteson, 1948; Jørgensen, Larsen & Riisgård, 1990), or photoperiod (Imlay, 1968), our data indicate that locomotion and spatial dynamics may be behaviourally related to reproduction, bringing mussels closer together during the spawning season. Further, because epibenthic males or females, taken separately, were always less aggregated during the breeding period than the population as a whole (males and females combined), it is likely that spring locomotion brings opposite sexes closer together (Table 3). To our knowledge, this is the first evidence of a functional role for horizontal locomotion in lentic unionids.

We can only speculate about how mussels aggregate during the spawning season. According to Nelson & Allison (1940), spermatozoa of some marine bivalves carry a hormone which, when present in the inhalant water stream of a female, induces an increased rate of pumping of water by the ctenidia, after which ovulation commences. The presence of such biochemical reproduction mediators in freshwater bivalve proximity might explain how mussels locate mates. In marine environments, photosensory structures of varying degrees of complexity have been reported in bivalves, some capable of perceiving movement (Wilbur & Yonge, 1966).

According to Russell-Hunter (1979), egg production may require > 50% of the energy available per year for growth whereas production of sperm may amount to only about 1% of the bioenergetic (as turnover of carbon and nitrogen in growth and reproduction) of males. The fact that locomotion has no perceptible impact on reproduction is therefore puzzling. In theory, energy allocation to locomotion should differ between males and gravid female mussels during the spawning season. Thus, in an evolutionary perspective, gravid female mussels should spend less energy on locomotion compared to males unless reproduction or locomotion are not energetically costly.

Acknowledgments

We are grateful to D. Breton, H. Harvey, S. Lalonde, V. Lapointe, J.-L. Lanctôt, G. Roberge, C. Ménard, J. Shostak, B. Mousseau, and S. Forget for field work, and L. Pelletier for microscopic help. This is a publication of the Groupe d'Écologie des Eaux Douces, Université de Montréal. Financial support for this research was provided by the Natural Science and Engineering Research Council of Canada, a team grant from le ministère de l'éducation du Québec (FCAR), graduate scholarships from FCAR and NSERC to JPA and funding from the College of Agriculture of Iowa State University. We also thank the staff of the Station de Biologie des Laurentides de l'Université de Montréal for their support.

References

- Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.
- Amyot, J.-P. & Downing, J.A. (1991) Endo- and epibenthic distribution of the unionid mollusc *Elliptio complanata*. *Journal of the North American Benthological Society*, **10**, 280–285.
- Amyot, J.-P. & Downing, J.A. (1997) Seasonal variation in vertical and horizontal movement of the freshwater bivalve *Elliptio complanata* (Mollusca: Unionidae). *Freshwater Biology*, **37**, 345–354.
- Balfour, D.L. & Smock, L.A. (1995) Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. *Journal of Freshwater Ecology*, **10**, 255–268.
- Bogan, A.E. (1993) Freshwater bivalve extinctions (Mollusca: Unionidae): a search for causes. *American Zoologist*, **33**, 599–609.
- Clark, P.J. & Evans, F.C. (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.
- Cleveland, W.S. (1979) Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*, **74**, 829–836.
- Coker, R.E., Shira, A.F., Clark, H.W. & Howard, A.D. (1921) Natural history and propagation of freshwater mussels. *Bulletin of the United Bureau of Fisheries*, **37**, 77–181.
- Downing, J.A., Amyot, J.-P., Pérusse, M. & Rochon, Y. (1989) Visceral sex, hermaphroditism, and protandry in a population of freshwater bivalve *Elliptio complanata*. *Journal of the North American Benthological Society*, **8**, 92–99.

- Downing, J.A., Rochon, Y., Pérusse, M. & Harvey, H. (1993) Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*. *Journal of the North American Benthological Society*, **12**, 148–156.
- Ellis, A.E. (1978) *British Freshwater Bivalve Mollusca*. Academic Press, London.
- Haukioja, E. & Hakala, T. (1978) Life history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia*, **35**, 253–266.
- Heard, W.H. (1975) Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia*, **15**, 81–103.
- Hinch, S.G., Kelly, L.J. & Green, R.H. (1989) Morphological variation in *Elliptio complanata* (Bivalvia: Unionidae) in differing sediments of soft-water lakes exposed to acidic deposition. *Canadian Journal of Zoology*, **67**, 855–863.
- Imlay, M.J. (1968) Environmental factors in activity rhythms of the freshwater clam *Elliptio complanatus catawbensis* (Lea). *American Midland Naturalist*, **80**, 508–528.
- Jokela, J., Valtonen, E.T. & Lappalainen, M. (1991) Development of glochidia of *Anodonta piscinalis* and their infection of fish in a small lake in northern Finland. *Archiv für Hydrobiologie*, **120**, 345–355.
- Jones, H.A., Simpson, R.D. & Humphrey, C.L. (1986) The reproductive cycles and glochidia of fresh-water mussels (Bivalvia: Hyriidae) of the Macleay River, Northern New South Wales, Australia. *Malacologia*, **27**, 185–202.
- Jørgensen, C.B., Larsen, P.S. & Riisgård, H.U. (1990) Effects of temperature on the mussel pump. *Marine Ecology Progress Series*, **64**, 89–97.
- Kat, P.W. (1982) Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). *Malacological Review*, **15**, 119–127.
- Keller, A.E. & Zam, S.G. (1991) The acute toxicity of selected metals to the freshwater mussel, *Anodonta imbecilis*. *Environmental Toxicology and Chemistry*, **10**, 539–546.
- Lefevre, G. & Curtis, W.C. (1910) Reproduction and parasitism in the Unionidae. *Journal of Experimental Zoology*, **9**, 79–115.
- Mackie, G.L., White, D.S. & Zdeba, T.W. (1980) *A Guide to Freshwater Mollusks of the Laurentian Great Lakes with Special Emphasis on the Genus Pisidium*. US Environmental Protection Agency, Environmental Research Laboratory, Duluth, Minnesota, 144 pp.
- Matteson, M.R. (1948) Life history of *Elliptio complanatus* (Dillwyn, 1817). *American Midland Naturalist*, **40**, 690–723.
- Negus, C.L. (1966) A quantitative study of growth and production of unionid mussels in the River Thames at Reading. *Journal of Animal Ecology*, **35**, 513–532.
- Nelson, T.C. & Allison, J.B. (1940) On the nature and action of diantlin; a new hormone-like substance carried by the spermatozoa of the oyster. *Journal of Experimental Zoology*, **85**, 299–338.
- Pielou, E.C. (1977) *Mathematical Ecology*, 2nd edn. Wiley, New York, 385 pp.
- Ricciardi, A., Whoriskey, F.G. & Rasmussen, J.B. (1996) Impact of the *Dreissena* invasion on native unionid bivalves in the upper St-Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1434–1444.
- Russell-Hunter, W.D. (1979) *A life of Invertebrates*. Macmillan Publishing Co., Inc., New York, pp. 421–433.
- Schloesser, D.W., Nalepa, T.F. & Mackie, G.L. (1996) Zebra mussel infestation of unionid bivalves (Unionidae) in North America. *American Zoologist*, **36**, 300–310.
- Strayer, D.L. & Ralley, J. (1993) Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society*, **12**, 247–258.
- Strayer, D.L., Sprague, S.J. & Claypool, S. (1996) A range-wide assessment of population of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, **15**, 308–317.
- Trueman, E.R. (1968) The locomotion of the freshwater clam *Margaritifera margaritifera* (Unionacea: Margaritanidae). *Malacologia*, **6**, 401–410.
- Trueman, E.R. (1983) Locomotion in molluscs. *The Mollusca* (ed. W. D. Russell-Hunter), Vol. 4, pp. 155–194. Academic Press, New York.
- Wilbur, K.M. & Yonge, C.M. (1966) *Physiology of Mollusca*, Vol. 2. Academic Press, New York, 645 pp.
- Williams, J.D., Warren, M.L., Cummings, K.S., Harris, J.L. & Neves, J. (1993) Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, **18**, 6–22.

(Manuscript accepted 18 October 1997)