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Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*

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Abstract. The reproductive ecology of the freshwater, unionid mussel *Elliptio complanata* was studied by mapping a 6-m × 7-m segment of a population found in a uniform area of the sandy littoral zone of Lac de l'Achigan, Québec. The contents of the marsupia were examined in mussels collected between spawning and larval release. Although unrelated to spatial aggregation, the number of ova carried by mussels varied with body size in a manner that suggests extremely late maturation followed by reproductive senescence in the largest mussels. Egg production was 1–2 orders of magnitude greater than that of other poikilotherms of equivalent mass. Fertilization success was strongly correlated with spatial aggregation, with complete fertilization failure found at local densities of <10 mussels/m^2, >50% successful when local densities were >18 mussels/m^2, and 100% successful only in patches where local densities exceeded 40 mussels/m^2. Fertilization failure is probably frequent at mussel densities found in most lakes. Our data suggest that perturbations altering the density, aggregation, or size distribution of mussel populations may have serious consequences for the maintenance of viable populations.

Key words: aggregation, fecundity, fertilization, body-size, molluscs, mussels, spacing behavior, reproduction, Unionidae, lake.

Reproduction in unionid molluscs is a complex process (Matteson 1948). Broadcast sperm must be entrained in the filtering current of females and eggs are fertilized internally. Fertilized eggs develop into larvae (glochidia) that must be released to parasitize host fish. Glochidia must drop from the host following the parasitic stage and fall into suitable habitat. Reproduction can therefore fail because of incomplete fertilization, unsuccessful parasitization, or misdirected settling. Egg formation and fertilization are critical steps, as many mussels fail to form eggs (e.g., Downing et al. 1989) or achieve complete fertilization (Matteson 1948).

Knowledge of the reproductive ecology of freshwater mussels is particularly important because many populations are endangered. The over-exploitation of mussel populations can severely alter their ability to sustain themselves (Coon et al. 1977). The introduction of exotic species such as the asian clam, *Corbicula fluminea* (Lauritsen and Mozley 1989, Leff et al. 1990), and the zebra mussel, *Dreissena polymorpha* (Hebert et al. 1991), threaten to diminish or eradicate indigenous populations. Several species of freshwater mussels are now endangered (Strayer 1980, DiStephano 1984, Miller et al. 1986). Knowledge of the reproductive ecology of freshwater mussels may, therefore, suggest factors influencing their viability.

Two factors known to have a strong influence on reproduction in animal populations are body size and spatial aggregation. Blueweiss et al. (1978) have shown that reproductive effort in aquatic poikilotherms usually scales as a power-function of body mass. Animal populations are frequently aggregated in space, and this spatial aggregation is thought to permit the finding of mates (Anscombe 1950, Dana 1976, Cowie and Krebs 1979). Spatial aggregation in freshwater mussels could influence reproductive success, either by influencing the rate of egg formation or by improving fertilization rates of individuals, or both. Although improved reproduction is one of the earliest hypothesized reasons for animal aggregation (Anscombe 1950), and assumptions about relationships between aggregation and reproductive success are important to many ecological theories (Bartlett 1960, Arnold and Anderson 1983), tests of such rela-

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One important stumbling block to studies of the relationship between spatial aggregation and reproductive success is that a broad diversity of factors, most notably predation and habitat heterogeneity, have been found to influence the spatial distribution of animals in nature (reviewed by Rasmussen and Downing 1988, Downing 1991), thus confounding relationships between spatial aggregation and reproductive success. Another important technical problem is that most animal populations are spatially dynamic; thus, it is difficult to evaluate the relationship between the spatial heterogeneity of a population during mating and the reproductive success at a later date.

We take advantage of the special characteristics of a population of mussels to address the hypothesis that individual reproductive success is influenced by body mass and spatial aggregation in a situation where substrate heterogeneity and predation are low. Unionid mussels are often distributed non-randomly (Downing and Downing 1992), exhibiting a high degree of spatial heterogeneity even in habitats that appear to be homogeneous (Kessler and Miller 1978, Sephton et al. 1980, Mitchell and Collins 1984, Downing 1991). There are few important predators of freshwater mussels, and predation pressure can be assessed by the occurrence of onshore shell deposits such as muskrat middens. Unionid mussels live partially buried in sediments (Coker et al. 1922, Ghent et al. 1978, Hinch et al. 1986), and are motile (Matteson 1948, Kat 1982) but move slowly (Long 1983). For example, over a 17-d period of the warmest part of mid-summer, only 37% of a population of *Elliptio complanata* in Lac de l'Achigan, Québec, moved, and then only at an average rate of 0.5 mm/h (J.-P. Amyot, unpublished data). Freshwater mussel populations can thus be sampled accurately and spatial distribution patterns do not change rapidly.

Freshwater mussels are ideal organisms for studying the effects of aggregation on reproductive success. During spawning, eggs are released into the suprabranchial chamber which acts as a marsupium for developing larvae (Matteson 1948). Spawning is usually restricted to a short period of the year, when males release spermatozoa into the water where they are subsequently entrained by the filtering current of the female and internal fertilization is achieved (Matteson 1948). Both fertilized and unfertilized ova are often retained in the marsupium for a 6–8 wk period during which the fertilized eggs develop into larval glochidia (Lefevre and Curtis 1910). The rate of production of fertilized ova can therefore be estimated from the contents of the marsupium, if organisms are examined between spawning and the release of glochidia.

Methods

We studied a monospecific population of *Elliptio complanata*, in an approximately 6-m × 7-m area of the sandy littoral zone of Lac de l'Achigan, Québec (45°57'N, 73°58.4'W) where there was no evidence of predation or substrate heterogeneity. Sampling was performed on 2 and 3 July, a period between spawning and the release of mature glochidia. The synchrony of glochidial release was verified by periodic sampling of an adjacent population throughout June and July. The spatial arrangement of the population was determined geometrically (±0.5 cm) by laying out a 42-m² grid at 1.5-m depth in a portion of the littoral zone that had no apparent spatial variation or gradient in substrate quality (Downing 1991). A grid of 1-m² squares was staked out using polyethylene rope. The position of each mussel within each 1-m² quadrat was determined by SCUBA divers using a 1-m × 1-m wire screen with 0.5-cm² meshes, superimposed over each quadrat. Data were recorded underwater on polyethylene notepads. The relative position of all mussels to each other or to any point in the sampling space could be calculated from the X, Y coordinates. Endobenthic mussels (Amyot and Downing 1991) were not censused. The local density ($D_{0.5}$), or number of other mussels within a 0.5-m radius, was used as an organism-specific measure of aggregation. This sampling scale was chosen on the basis of observations of mussel movements (J.-P. Amyot, Université de Montréal, unpublished data), and our expectation that sperm may not diffuse much farther than 0.5-m while remaining viable (Lefevre and Curtis 1910). Our results are not sensitive to this scale, however, because other measures of local aggregation, such as distance to nearest neighbor were also calculated and examined.

After measurement of position, each of the mussels in the study population was collected for analysis of size, sex, and reproduction. Maximum shell length was measured (±0.01 mm) using an electronic digital caliper. Because of the effect of sexual composition on reproduction, the sex of each mussel was determined by microscopical analysis of sections of gonadal tissue (Downing et al. 1989). The gonad of each mussel was excised immediately after collection and fixed in 95% ethanol. Thin sections of tissue were cut from various parts of the gonad and examined after staining, using the protocol of Heard (1975). Several (2–6) different sections of each gonad were examined microscopically. Since about 80% of this population was hermaphroditic to some degree (Downing et al. 1989), sexuality was quantified by determining the proportion of the gonad area occupied by male and female tissue and sorting the animals into five sexual categories: <10% female, 10–40% female, 40–60% female, 60–90% female, and >90% female (Downing et al. 1989).

The number of eggs produced and the proportion of the eggs that were fertilized were determined by careful microscopical analysis of the contents of the marsupium and adjacent tissues of all mussels found 1 m or more within the perimeter of the study area. Underwater, each mussel was sealed immediately in an individual plastic bag (Whirl-pak®) to avoid the loss of eggs and glochidia due to spontaneous abortion on disruption (Lefevre and Curtis 1910, Matteson 1948). The contents of the plastic bag were filtered and retained, the gills were removed from each mussel, and the eggs, embryos, and glochidia found among the gills and adjacent tissues were removed quantitatively under a dissecting microscope. Fertilized eggs (glochidia) can be differentiated easily from unfertilized eggs by visual inspection (Lefevre and Curtis 1910). Because glochidial release was found to be quite synchronous in this population, and mussels were sampled just before glochidial release, successfully fertilized eggs were taken to be those that showed perceptible development at sampling. The eggs and glochidia were preserved in 80% ethanol and counted by mixing the samples with glycerol, evaporating most of the alcohol to stabilize the suspension, distributing the eggs and glochidia randomly in petri dishes of known area, and counting 6–15 replicate fields under 40× magnification. The numbers of unfertilized eggs and developing glochidia were counted in each sample and were related to the size and local density of mussels using least squares regression (Draper and Smith 1981) and nonparametric analyses (Conover 1971).

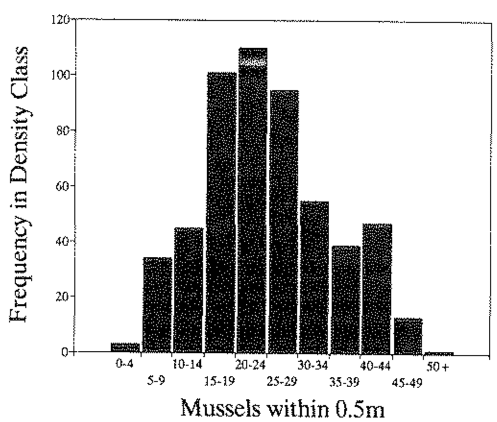


FIG. 1. Frequency distribution of the number of other mussels located within a 0.5-m radius of each mussel (see Downing et al. 1989 for a map of the spatial distribution of this population).

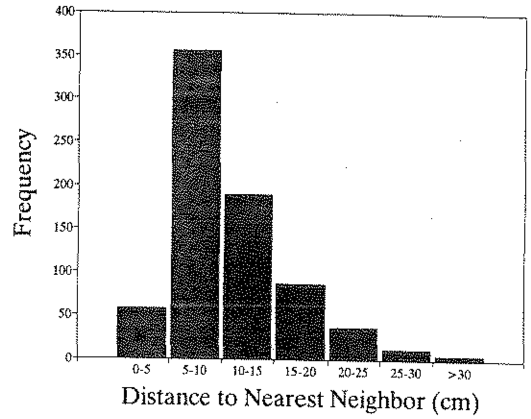
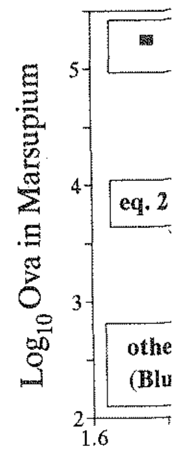


FIG. 2. Frequency distribution of the distance from each mussel to its nearest neighbor.

Results

Elliptio complanata was very abundant and highly aggregated in Lac de l'Achigan. The mean density calculated on the basis of regularly spaced 1-m^2 sections of the population was 26.6 mussels/m^2 and the $(n - 1)$ weighted variance (s^2) was 150.2. The population was significantly aggregated ($\chi^2 = 198$; $p < 0.001$; Elliott 1979). More than 50% of the organisms had fewer than



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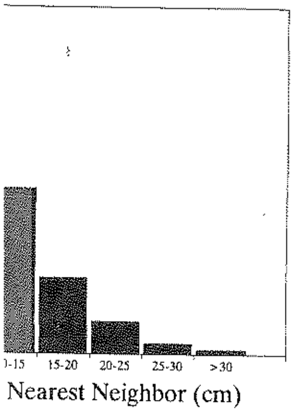

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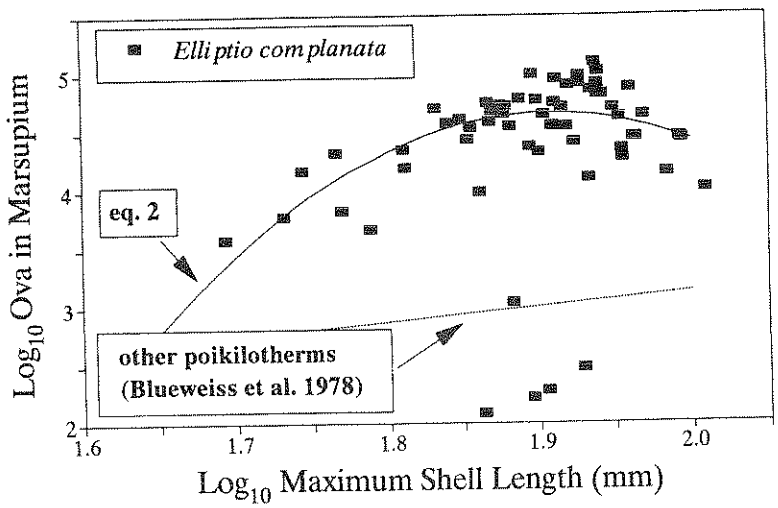

FIG. 3. The relationship between the number of ova (fertilized and unfertilized) found in the suprabranchial chamber of *Elliptio complanata* and the total shell length (mm). The straight line indicates the relationship predicted for aquatic poikilotherms and amphibians by Blueweiss et al. (1978). The curved line is eq. 2. The five animals retaining less than 1000 eggs ($\log_{10}$ova = 3) were excluded from eq. 3. All logarithms are to the base 10.

25 neighbors within 0.5-m, whereas a few (<2%) were found in very dense clumps of >45 organisms (Fig. 1). According to nearest-neighbor distances, some mussels were spaced by as little as 0.5 cm, and others by as much as 30 cm (Fig. 2).

Egg production was more strongly influenced by body size and sex than by spatial aggregation. In the 318 mussels that had <40% female tissue, the probability of finding ova in the marsupium was only 0.012. The corresponding probability for the 225 organisms with >40% female tissue was 0.81. A Kruskal-Wallis one-way analysis showed that there was no significant tendency for females (>90% female gonad) bearing unfertilized eggs or glochidia to be found in denser aggregations ($p = 0.213$) than those found with empty marsupia. Only about 16% of the mussels with predominantly female gonadal tissue failed to produce or retain ova in their marsupium. Regression analysis showed that, in animals bearing 90% female tissue or more, the probability (P) that fertilized or unfertilized eggs were found in the marsupium varied with body length in a significantly curvilinear fashion, approximately as:

$$P = -41.075 + 44.715 \log_{10}L_{max} - 11.902(\log_{10}L_{max})^2 \quad (1)$$

($R^2 = 0.18$; $n = 131$; $p < 0.001$). L_{max} is the maximum linear dimension of the valve (mm) and varied from 15 to 105 mm. Spatial density and nearest neighbor distances had no significant ($p > 0.05$) effect on the residuals of eq. 1, and L_{max} and local density were uncorrelated ($p > 0.05$). This analysis suggests that the highest probability of egg production and retention is found at about 76 mm length and corresponds to an egg production probability of >90%. Corresponding egg production probabilities for smaller and larger individuals were significantly lower, falling to 30% for 45-mm mussels, and about 75% for 100-mm mussels.

The production of eggs by animals retaining ova in their marsupia also increased then decreased with increasing shell length (Fig. 3). Excluding a few organisms containing <1000 ova, which may have aborted as a result of disruption before collection (Matteson 1948), the relationship between body-length (L_{max}) and the number of eggs (E) found in each mussel was:

$$\log_{10}E = -97.773 + 107.35 \log_{10}L_{max} - 28.126(\log_{10}L_{max})^2 \quad (2)$$

($R^2 = 0.5$; $n = 57$; $p < 0.0001$). The significant curvilinearity of this relationship is indicated by the significant partial effects ($p < 0.001$) of both independent variables. This analysis was performed mainly for animals larger than 50 mm in length because smaller animals usually

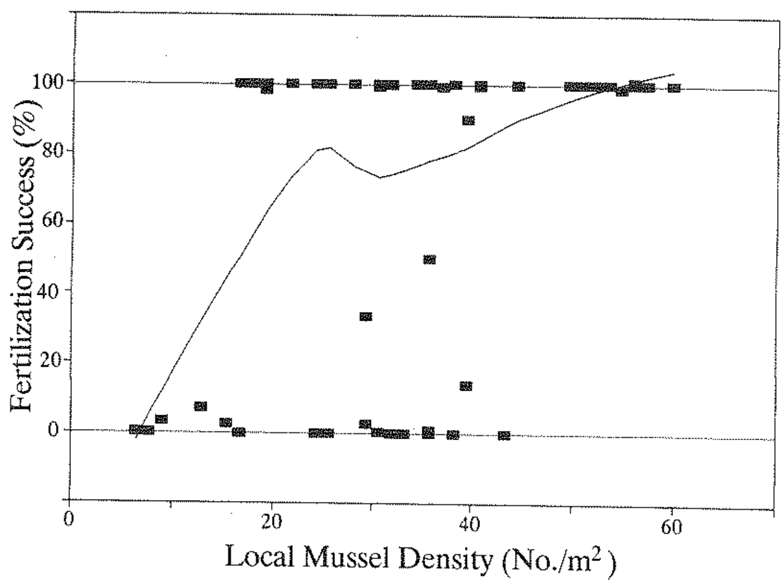

FIG. 4. Relationship between the fraction of ova fertilized and the degree of spatial aggregation experienced by the mussels. Spatial aggregation is measured as the local density (number of other mussels within a 0.5-m radius). The curved line is an unbiased, locally weighted, sequentially smoothed trend line (LOWESS; Cleveland 1979).

did not produce any ova at all (eq. 1). Equation 2 suggests again that the maximum ovum production occurred at the intermediate size of about 80 mm. *Elliptio complanata* increased their production of eggs up to about 75% of their maximum size (Downing et al. 1989), beyond which reproduction decreased. The residuals of eq. 2 were uncorrelated ($p > 0.01$) with all measures of spatial aggregation including the local density ($D_{0.5}$), the distance to nearest neighbor, and the distance to nearest male neighbor.

Although egg production was not related to spatial aggregation in this population, fertilization success was (Fig. 4). The average fraction of ova that developed into parasitic glochidia in mussels with >10% female tissue in the gonad was 72% ($n = 68$; $s = 44$; median = 100%). More than 25% of the organisms found with ova and glochidia in their marsupium had apparent fertilization rates of less than 50%. Fertilization success was strongly correlated with the number of other mussels found within a 0.5-m radius of each animal ($D_{0.5}$). Both nonparametric Kruskal-Wallis analysis ($p = 0.0034$) and regression analysis ($r^2 = 0.17$; $n = 65$; $p < 0.0001$) show that the fraction of eggs fertilized varied with local density of mussels. Although large mussels might be expected to filter more water and thus collect more spermatozoa, there was no significant relationship ($p = 0.33$) between shell length and fertilization rate, nor was there a demonstrable ($p < 0.10$) influence of sexual composition of near neighbors on fertilization success.

Discussion

Elliptio complanata must solve at least two reproductive problems. First, egg production occurs late in life, decreasing in very large (probably old) individuals. The fresh body-mass (W; g) and L_{max} (mm) of an adjacent population of *Elliptio complanata* were related as:

$$\log_{10}W = -3.998 + 2.615 \log_{10}L_{max} \quad (3)$$

($r^2 = 0.93$; $n = 120$; $p < 0.00001$). The analysis of Blueweiss et al. (1978) suggests that a mussel of average length ($L_{max} = 75$ mm or fresh body mass of 8 g; eq. 3) should become sexually mature at 93 d. Paradoxically, eq. 1 shows that ovum production is highly improbable until body-length is >50 mm, a body size that corresponds to an age of at least (Downing et al. 1992) 8–10 yr (Downing et al. 1989). Only one

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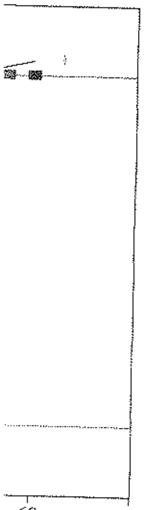

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of the 33 mussels smaller than 50-mm in length contained eggs. Both the probability of producing eggs and the number of ova produced increase with body size up to a shell length of 80 mm (eqs. 1 and 2; Fig. 3) beyond which they fall rapidly. Consequently, reproduction is restricted to a short period of life which may take many years to attain.

Although reproduction begins late in the life cycle, annual egg production of *Elliptio complanata* is greater than that of other aquatic poikilotherms of equivalent body-size. Blueweiss et al. (1978) found that the fecundity of aquatic poikilotherms such as crustaceans, fish, and frogs normally varies approximately as $347W^{0.47}$. Plotting this general relationship on Figure 3, again employing eq. 3 to convert W to L_{max}, indicates that *Elliptio complanata* produced and retained a number of eggs that was 1–2 orders of magnitude greater than other poikilotherms of equivalent organic body mass. This is probably permitted by the small size of hatchlings. Mussel glochidia are less than 4 μg fresh mass each (Clarke 1973) while the analyses of Blueweiss et al. (1978) predict a normal hatchling body mass of 0.7 to 1.2 g for aquatic poikilotherms of this size. The large number of eggs produced is possibly necessitated by the late maturation and uncertainty of successive stages in the parasitic life history (Lefevre and Curtis 1910, Matteson 1948).

The second problem that *Elliptio* must solve is that eggs, once produced, must be fertilized, and fertilization success is strongly linked to the spatial disposition of the population. Figure 4 indicates that most mussels either had very low or nearly complete fertilization success. A LOWESS sequential smoothing (Cleveland 1979) of the data (Fig. 4) suggests that average fertilization success is >50% when local densities are >18 animals/m^2. Although not an "unusual" or extreme population density for unionids (sensu Coker et al. 1922), a density of 18 animals/m^2 is in the upper 70th percentile of average population densities reviewed by Downing and Downing (1992). These findings suggest that fertilization success of ova in sparser populations must be extremely low. The commonness of incomplete fertilization in unionid molluscs has been known since the early 1900s (Lefevre and Curtis 1910), and has been attributed to a "lack of sufficient spermatozoa" (Matteson 1948). It thus seems plausible that sperm production, survival, and dispersal is not sufficient to fully fertilize eggs of mussels not found in dense aggregations.

Fertilization success of *Elliptio complanata* should vary not only with population density, but with the level of spatial aggregation of the population. Given the level of spatial aggregation normally seen in mussel populations (Downing and Downing 1992), and assuming that the frequency distributions of local densities experienced by mussels follow negative binomial distributions (Elliott 1979), one can calculate the probability that mussels will find themselves at local densities >10 mussels/m^2. At mean densities of 1.5 mussels/m^2, local densities of >10/m^2 will be experienced by only one of every 40,000 individuals. The chances do not improve beyond 1 chance in 10 until mean densities of 5/m^2 are surpassed. Even at average densities of 10/m^2, the aggregated spatial distribution of mussel populations means that nearly 60% of the mussels will be at local densities insufficient to ensure full fertilization in this population of *Elliptio complanata*. That mussel populations continue to reproduce even at low *average* densities is explained by the fact that a few individuals will usually be found in aggregations at *local* densities great enough to permit fertilization. Solitary mussels have little chance of fertilization, unless they self fertilize, whereas those found with large numbers of mussels close to them will achieve almost complete fertilization. These observations give rise to the prediction that recruits in sparse populations may be quite homozygous compared with recruits in denser ones.

Although little is known about factors influencing reproduction in other unionid species, looking at the problems of size and local density in concert may lend insight into the precarious nature of the perpetuation of mussel populations. The general trend in the production of fertilized ova for this population of *Elliptio* can be approximated by multiplying the probability that ova will be produced by a mussel of a given size (eq. 1) by the expected number of ova produced (eq. 2), and multiplying this result by the predicted fertilization success read from the LOWESS trend in Figure 4. Such a procedure, of course, ignores the large amount of variation in egg production and fertilization success

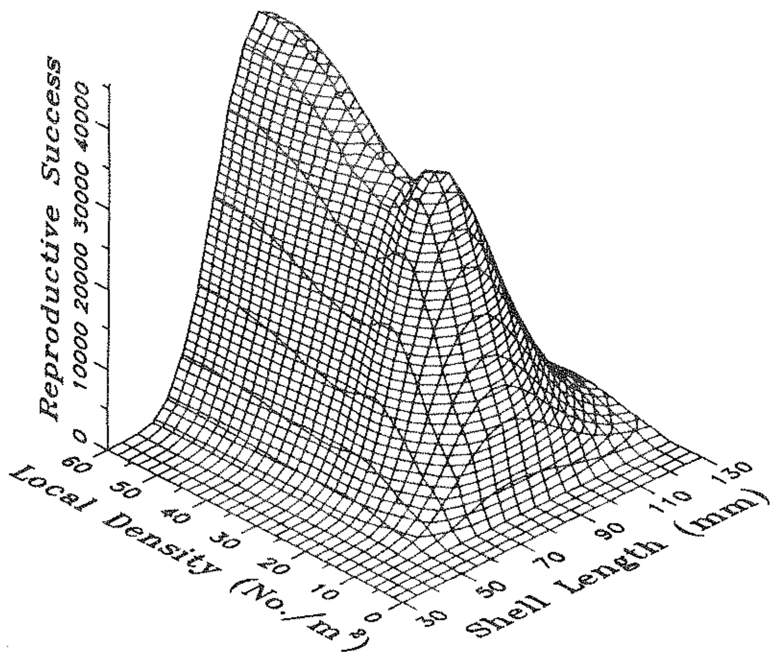

FIG. 5. General trend in the relationship between reproductive success (annual production of fertilized ova) and body size and local spatial density. The response surface was constructed from average predicted values obtained as the products of the predictions of eqs. 1 and 2 multiplied by the fertilization probability read from the LOWESS trend in Figure 4. Local mussel densities are the average density of mussels within a 0.5-m radius.

among individuals of the same size and local density, but gives a general idea of how reproduction varies, on average, for the population. Such calculations over a range of body sizes, at several levels of local density (Fig. 5), illustrate in general how the production of fertilized ova (glochidia) probably varies with size and spatial aggregation (Fig. 5).

First, sparse populations, or those in which dense aggregations cannot be attained, may have very low reproductive rates. If local densities are always $<10/m^2$, then reproductive failure is usually complete. This could occur either in over-exploited populations, those near the limit of their ecological or geographical range, or those in which physical obstacles prevent their forming aggregations. Increase in density above 20–40 mussels/m^2 appears to have little influence on reproductive success. Second, populations composed of small individuals will have low reproductive success because the population is protandric (Downing et al. 1989) and the few small mussels bearing female reproductive tissue are sexually immature. Populations composed of very large mussels will also have reduced reproductive success probably as a result of senescence. Finally, the size and density zone in which significant reproduction is achieved is fairly narrow with very steep sides (Fig. 5). Therefore, successful reproduction in *Elliptio complanata* seems to be strongly influenced by the population's size distribution, overall density, and degree of aggregation achieved during spawning. If other species behave like this population of *Elliptio complanata*, the conservation of freshwater mussel species will require close attention to factors altering the size composition, density, or spatial distribution of mussel populations.

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**Algal periphyton
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Abstract. We examin
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substrata in relation to w
within the communities
Species composition
and alkalinity, and rela
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