

Running Head: Aggregation and mussel reproduction

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 6m X 7m 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 formation ^{= #eggs?} was 1-2 orders of magnitude greater than other poikilotherms of equivalent mass.

Fertilization success was strongly correlated with spatial aggregation, with complete fertilization failure found at local densities of $<10/m^2$, $>50\%$ 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 with many pitfalls (Matteson 1948). First, 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 when specific host fish are near enough to be parasitized. After the parasitic stage, glochidia must drop from the host and fall into suitable habitat. Reproduction can therefore fail because of incomplete fertilization, unsuccessful parasitization or misdirected settling. The formation of sufficient eggs and their successful fertilization may be the most critical of these steps, as many mussels fail to form eggs (e.g. Downing et al. 1989) or are unable to 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 entire species of freshwater mussels are now endangered (Strayer 1980, DiStephano 1984, Miller et al. 1986). Several authors have suggested that reproduction may be a critical weakness; ~~in freshwater mussels' habits,~~ thus, knowledge of their reproductive ecology may suggest factors influencing the ~~the~~ ^{populations} viability of mussel populations.

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 rarely randomly or

regularly distributed 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 altering the rate of gamete formation or by improving fertilization rates of individuals, or both. Although improved reproduction is one of the earliest perceived reasons for animal aggregation (Anscombe 1959), and assumptions ~~about~~ relationships between aggregation and reproductive success are important to many ecological theories (Bartlett 1960, Arnold and Anderson 1983), tests of such relationships in natural populations are ~~very~~ rare (Hanski 1983, Gilinsky 1984, Vodopich and Cowell 1984).

One important stumbling block to studies of the relationship between spatial aggregation and reproductive success is that a ~~broad diversity~~ ^{array} of factors, most notably predation and substrate heterogeneity, can influence the spatial distribution of organisms in nature (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 at spawning and the reproductive success at a later date.

This research takes advantage of the special characteristics of a population of mussels to assess the relationship between spatial heterogeneity and reproductive success 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 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 day period of the warmest part of mid-summer, only 37% of a population of Elliptio complanata ^{moved} in Lac de l'Achigan, Québec, ~~moved at all~~, and those that did moved randomly at an average rate of only 0.5 mm/h (J.-P. Amyot unpublished data). Many mussels move little throughout their lifetime (ref?). Freshwater mussel populations can thus be sampled accurately and spatial distribution patterns do not change rapidly.

~~This article addresses~~ ^{we} the hypothesis that individual reproductive success in a population of freshwater mussels is influenced by body mass and spatial aggregation. Freshwater mussels are ideal organisms for ~~the~~ study ^{ing} of the effects of aggregation on reproductive success. During spawning, eggs are released into the suprabranchial chamber that acts as a marsupium for developing ^{embryos} gametes (Matteson 1948). Spawning is restricted to a short period of the year, when males release sperm ^{that are} into the water where ~~they are subsequently~~ entrained by the filtering current of the female ^{for} and internal fertilization ~~is achieved~~ (Matteson 1948). Both fertilized and unfertilized ova are retained in the marsupium for a 6 to 8 week period during which the fertilized eggs develop into ~~larval~~ glochidia (Lefevre and Curtis 1910). The rate of production ^{? = redundant} of fertilized ova can therefore be estimated from the contents of the marsupium, if organisms are examined between spawning and the release of glochidia. Unionid mussels are aggregated organisms for which estimates of egg production and fertilization success can be easily obtained.

Methods

We studied a nearly monospecific population of Elliptio complanata, in an approximately 6m X 7m 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, which was between spawning and the ^{release} ~~ejection~~ of mature glochidia, as verified by ^{how?} periodic sampling of adjacent populations 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. 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 1m X 1m overlay of wire screen with 0.5 cm² meshes, superimposed over each quadrat. Data were recorded on polyethylene notepads. The relative position of all surface-dwelling mussels to each other or to any point in the sampling space could be calculated from the X,Y coordinates. 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, unpublished) and our expectation that sperm could not be expected to diffuse much farther than 0.5m while remaining viable (Lefevre and Curtis 1910). 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 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 method of Downing et al. (1989) was used to determine the sex of each mussel by microscopical analysis of sections of gonadal tissue. 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 and the appropriate proportion of the gonad area occupied by male and female tissue was noted by sorting the animals into five categories: <10% female, 10 to 40% female, 40 to 60% female, 60 to 90% female, and >90% female (Downing et al. 1989).

3 animals were included

The number of eggs produced by each mussel and the proportion of the eggs that were fertilized were determined by microscopical analysis of the contents of the marsupium of all animals found 1 m or more ^{within?} ~~from~~ 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 in the supra-branchial chamber were removed ^{and} ~~quantitatively~~ ^{and} under a dissecting microscope. The eggs and glochidia were preserved in 80% ethanol. Gametes were counted by mixing the samples with glycerol, evaporating most of the alcohol to stabilize the suspension, distributing the gametes randomly in petri dishes of known area, and counting 6-15 replicate fields under 40X magnification. The number of unfertilized eggs and developing glochidia was counted in each sample. Fertilized eggs ^{= embryos} (glochidia) can be differentiated easily from unfertilized eggs by visual inspection (Lefevre and Curtis 1910). The number of eggs and glochidia

produced by each mussel was related to the size and local density of mussels using least squares regression (Draper and Smith 1981) and nonparametric analyses (Conover 1971).

Results and Discussion

Elliptio complanata was very abundant and highly aggregated in Lac de l'Achigan. The mean density calculated from ³⁶⁴ 1 m² quadrats was 26.6 mussels/m² 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 <25 neighbors within 0.5 m, whereas a few (<2%) were found in very dense clumps of >45 organisms (Fig. 1). The distribution of nearest neighbor distances (Fig. 2) shows that some mussels were spaced by as little as 0.5 cm, and others by as much as 35 cm.

Don't see
pattern
Fig. 2

Gamete 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 shows that there was no significant tendency for females (>90% female gonad) bearing ova or glochidia to be found in denser aggregations ($p=0.213$) than those found without gametes in their marsupia. Only about 16% of the mussels with predominantly female gonadal tissue failed to produce or retain ova in their marsupium. Regression analysis shows that in animals bearing 90% female tissue or more, the probability (P) that fertilized or unfertilized ^{eggs} ~~gametes~~ were found in the marsupium varied significantly with body length approximately as:

meaning
what
historically?

unclear
mussels

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

how much better is quadratic vs linear?

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

The production of gametes by animals retaining ova in their marsupia also reflected the same pattern (Fig. 3). Excluding the organisms containing <1000 ova, which may have aborted due to disruption before collection (Matteson 1948), the relationship between body-length (L_{max}) and the number of ova found in the marsupium (O) was:

what was linear value?

$$\log O = -97.773 + 107.35 \log L_{max} - 28.126 (\log L_{max})^2 \quad (2)$$

($R^2=0.5$; $n=57$; $p<0.0001$) where both independent variables had significant partial effects ($p<0.001$). This analysis suggests again that the maximum ovum production occurred at the intermediate size of about 80 mm. Elliptio complanata increased their production of ova 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.

The annual egg production of Elliptio complanata was greater than that of other aquatic poikilotherms of equivalent body-size. The fresh body-mass (W; g) and L_{max} (mm) of an adjacent population of Elliptio complanata were related as:

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

($r^2=0.93$; $n=120$; $p<0.00001$). Blueweiss et al. (1978) found that the fecundity of amphibians and aquatic poikilotherms normally varies approximately as $347 W^{0.47}$. Plotting this general relationship on Fig. 3, employing eq. 3 to convert W to L_{\max} , indicates that Elliptio complanata produced and retained a number of gametes 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 (glochidia are $<4 \mu\text{g}$ fresh mass each; Clarke 1973, cf. predictions of Blueweiss et al. 1978 of 0.7 to 1.2 g), but is possibly necessitated by the uncertainty of successfully infecting host fish with the parasitic larval stage (Lefevre and Curtis 1910, Matteson 1948).

Although egg production was not related to spatial aggregation, fertilization success was significantly correlated with spatial aggregation in this population (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%. The fertilization ^{success} rate was strongly correlated with the number of other mussels found within a 0.5m radius of each animal ($D_{0.5}$). Both non-parametric Kruskal-Wallis analysis ($p=0.0034$) and regression analysis ($r^2=0.17$; $n=65$; $p<0.0001$) show that the fraction of ova fertilized varied with local density of mussels. Fig. 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), it 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 1900's (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} ~~organisms~~ far from dense aggregations. *

Elliptio complanata must solve at least two reproductive problems. First, gamete production occurs late in life in females, increasing to a maximum near 80 mm length, but decreasing in very large (probably old) individuals. The analysis of Blueweiss et al. (1978) suggests that a mussel of average length ($L_{max}=75\text{mm}$ or fresh body mass of 8 g; eq. 3) should become sexually mature at 93 days. 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. in press) 8-10 years (Downing et al. 1989). Both the probability of ovum production 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. ^{ref.?}

The second problem that Elliptio must solve is that eggs, once produced, must be fertilized, and fertilization success is strongly linked to the ^{density} ~~spatial disposition~~ 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/m². At mean densities of 1.5 mussels/m², 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/m² are surpassed. Even at average densities of 10/m², aggregated distributions mean that nearly 60% of the mussels will be at local densities insufficient to ensure full fertilization. Solitary mussels have little chance of fertilization and those found with large numbers of mussels close to them will achieve almost complete fertilization.

Looking at these two problems in concert illustrates the precarious nature of the perpetuation of mussel populations. The general trend in the production of fertilized ova can be approximated by multiplying the probability that ova will be produced by a given mussel (eq. 1) by the number of ova produced by mussels producing ova (eq. 2), and multiplying this result by the most probable fertilization success read from the LOWESS trend in Fig. 4. Solutions 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 will 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. Further increase in density above 20-40 mussels/m² appears to have little influence on reproductive success. Second, populations composed of small individuals will have reduced reproductive success due to the prevalence of immature mussels, while populations composed of very large mussels will also have

Product
of 3
factors

reduced reproductive success probably due to the high frequency of *evidence?*
senescence. Finally, the optimal size and density zone for reproduction is
fairly narrow with very steep sides (Fig. 5). Therefore, successful
reproduction in Elliptio complanata seems to be strongly influenced by the
size distribution of the population, its overall density, and the degree of
aggregation achieved during spawning. The conservation of freshwater mussel
species will therefore require close attention to factors altering the size
composition, density, or spatial distribution of mussel populations.

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FIGURE LEGENDS

Fig. 1. Frequency distribution of local density or 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).

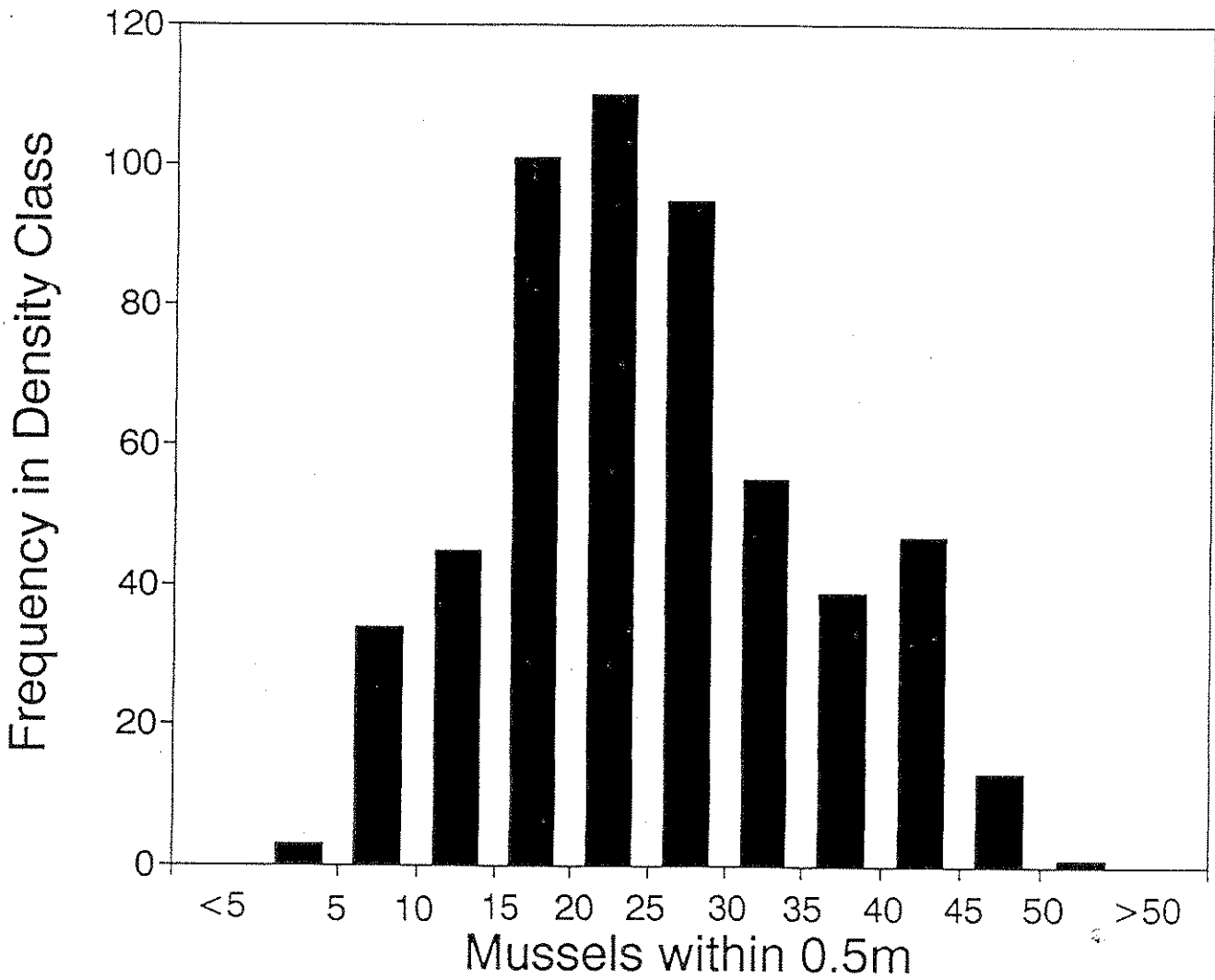
Fig. 2. Frequency distribution of the distance from each mussel to its nearest neighbor.

Fig. 3. The relationship between of the number of ova (fertilized and unfertilized) found in the supra-branchial 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. Logarithms are to the base 10.

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 0.5m radius). The curved line is an unbiased, locally weighted, sequentially smoothed trend line (LOWESS; Cleveland 1979).

Fig. 5. General trend in the relationship between reproductive success (annual production of fertilized ova) and body size and local spatial density. Predicted values were obtained as the products of the predictions of equations 1 and 2 multiplied by the fertilization probability read from the LOWESS trend in Fig. 4. Local mussel densities are the average density of mussels within a 0.5m radius.

FIG. 1



This is somewhat redundant with
Fig 6. in Downing et al. 1989

FIG. 2

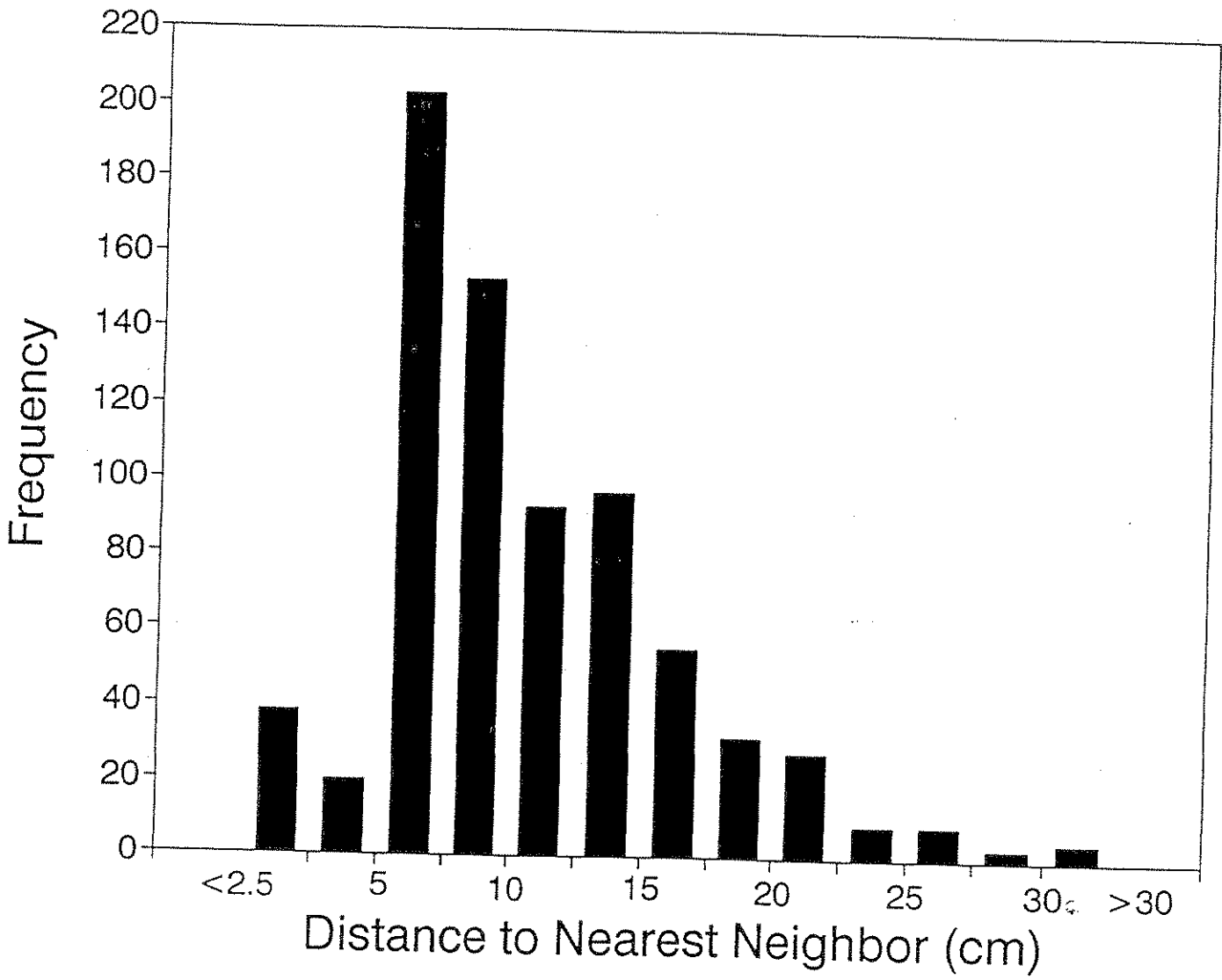
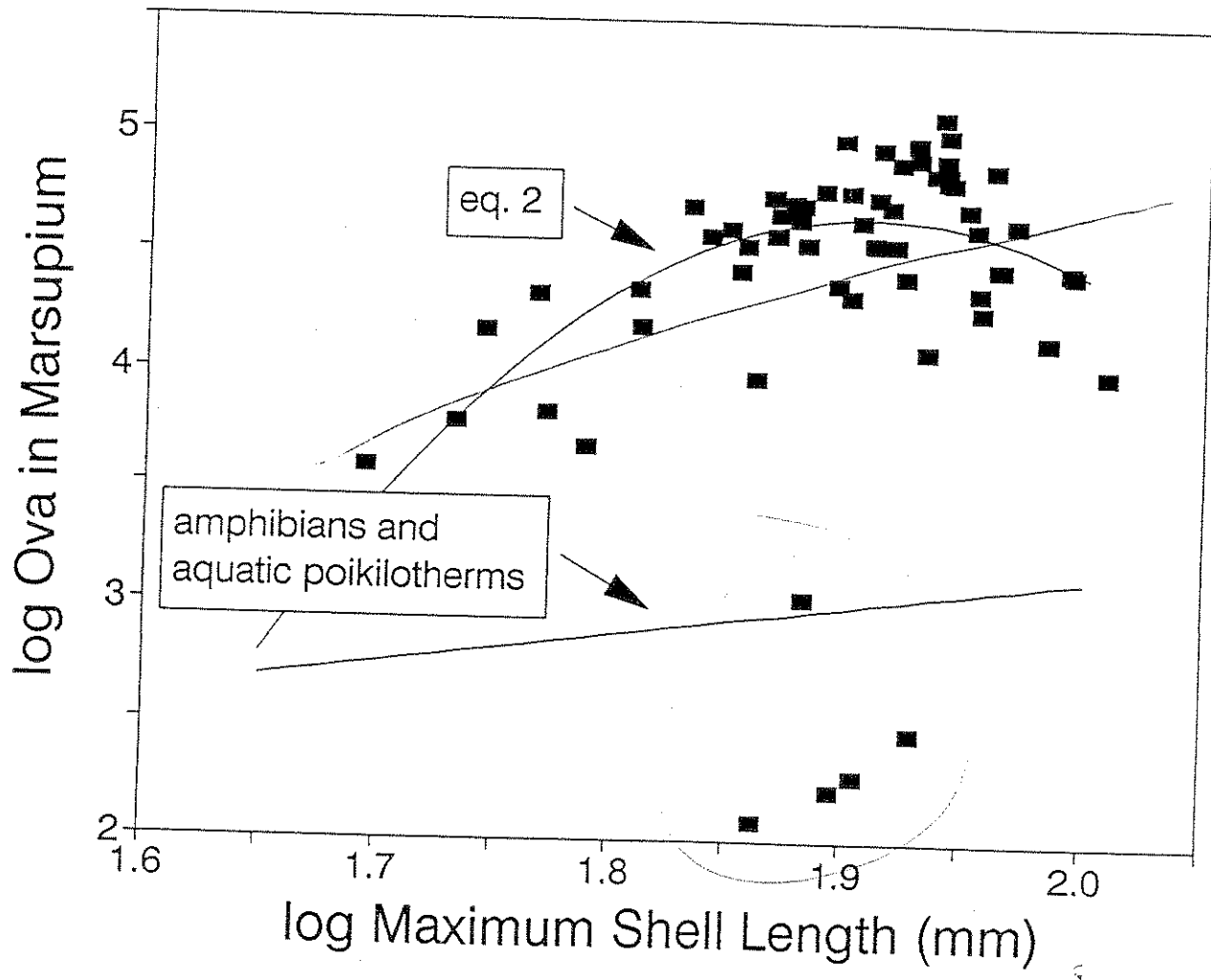
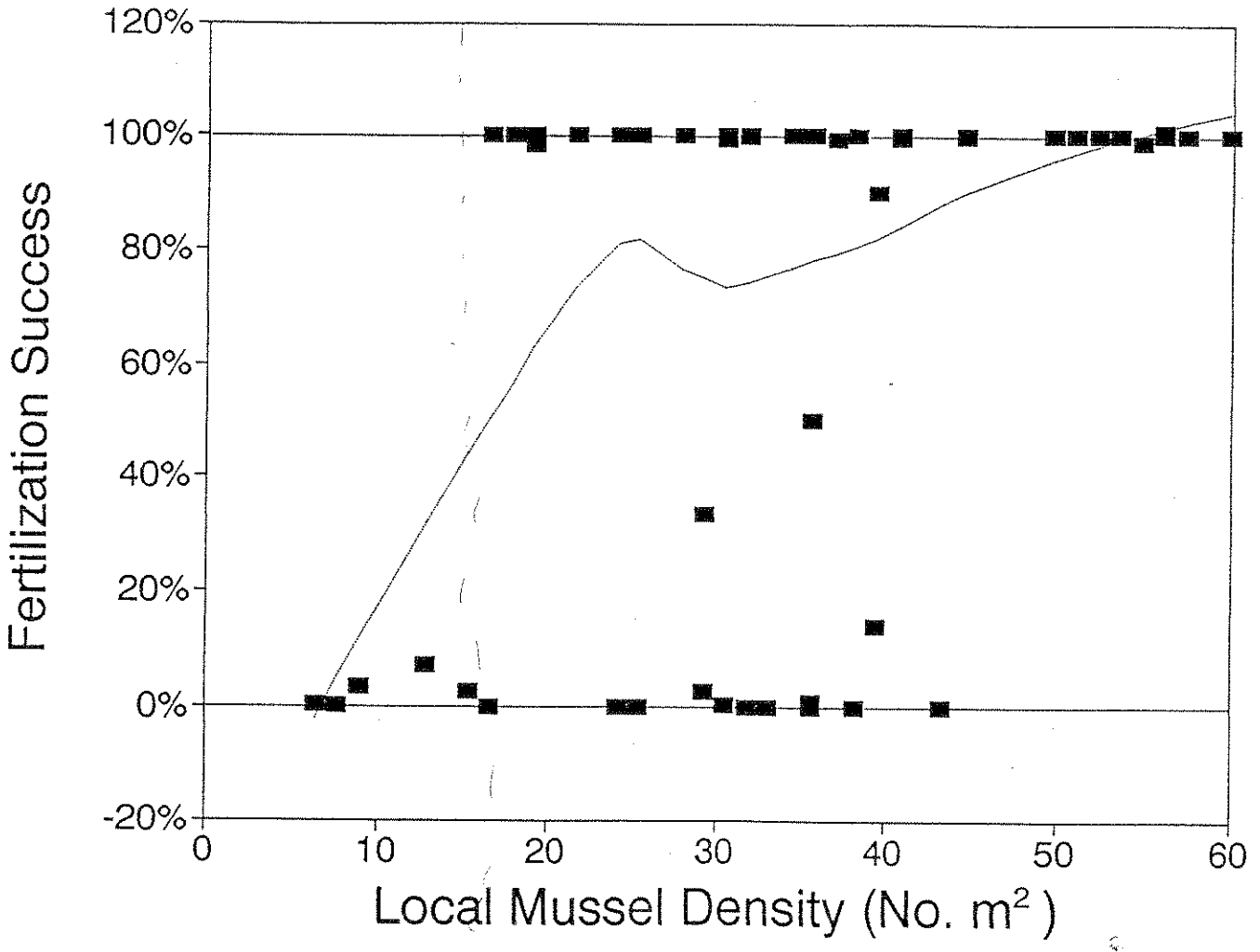


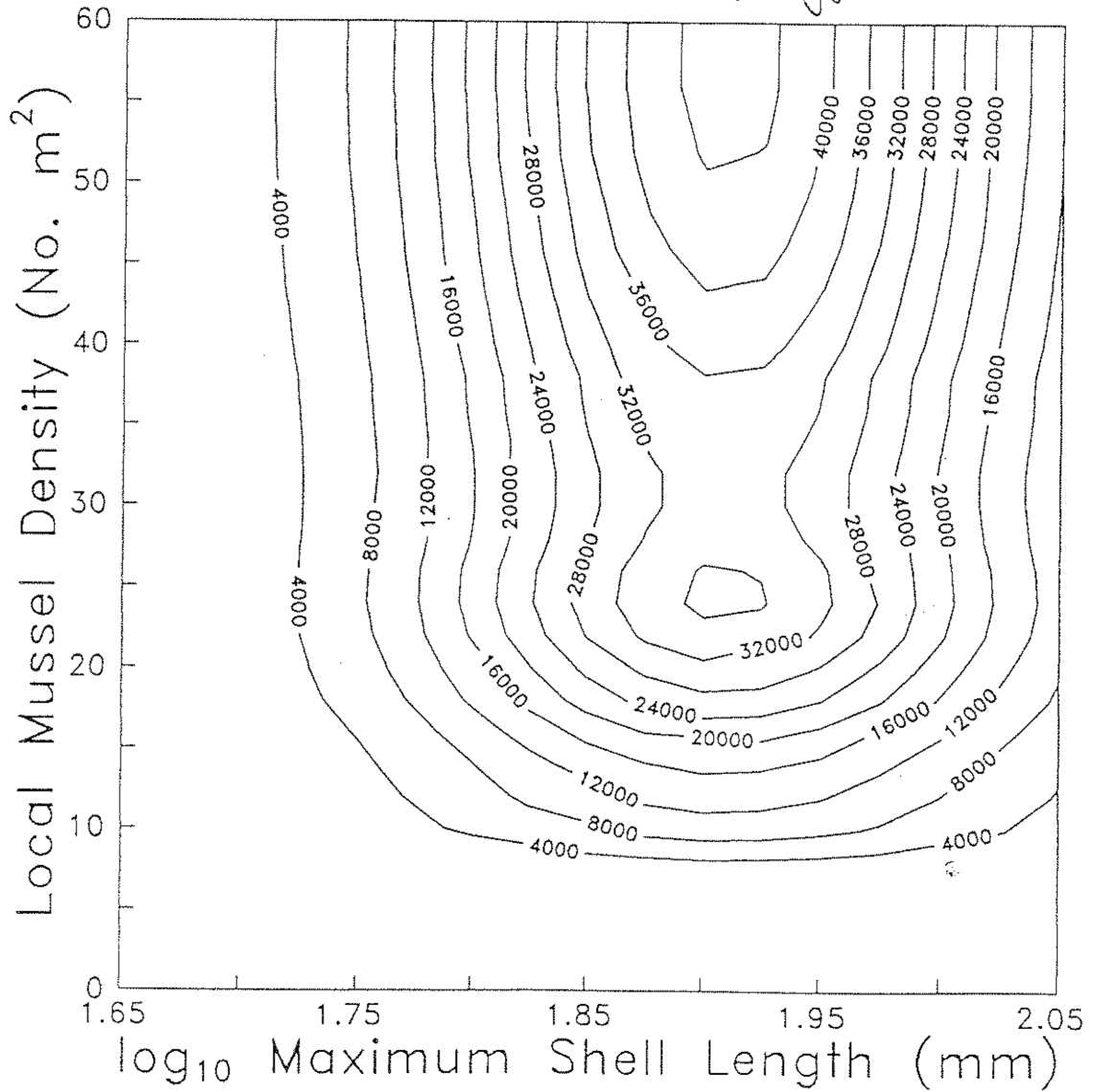
FIG. 3





plot of size of mussel vs fertilization success
why no self-fertilization?

status means of
presenting a product of
3 equations with inherent
variability rampant.



80 mm