REPRODUCTIVE STRATEGY OF THE FRESHWATER PEARL MUSSEL *MARGARITIFERA MARGARITIFERA*

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SUMMARY

(1) The reproductive strategy of the freshwater pearl mussel (*Margaritifera margaritifera* L.) is marked by two components yielding a high fertility maintained under varying densities.

(2) The first component is a combination of a 'high life expectancy during the reproductive period', a 'high fertility which is independent of age' and an 'absence of a postreproductive period' resulting in a single female producing *c.* 200×10^6 glochidia during its reproductive life span of up to 75 years.

(3) The second component reflects the selective values of different modes of reproduction at varying population densities. At high densities most animals are dioecious. At low densities females become hermaphrodites and self-fertilization dominates. But also under these conditions the males probably compensate for some of the deleterious effect of inbreeding.

(4) This strategy offers three advantages: (i) due to the extended reproductive period populations are less vulnerable to fluctuations in reproductive success; (ii) the reproductive costs are evenly dispersed over the reproductive period; (iii) even sparse (founder) populations can persist for a long time and are able to reproduce successfully.

INTRODUCTION

If the geographical range, abundance and age of a species are measures of its fitness, then the freshwater pearl mussel must be considered one of the most successful animal species. The Margaritiferidae are a very ancient family. Their inception is thought to be anywhere between the upper Paleozoic and upper Mesozoic periods (Walker 1910; Smith 1980). The pearl mussel formerly (until man intervened), occurred in high densities. In North Bavaria the river beds were covered with mussels (Meissner 1914). At present, maximum densities are *c.* 400 m^{-2} (Young & Williams 1984a) but we can assume that they formerly exceeded 1000 m^{-2}. The pearl mussel is widely distributed on a global as well as on a local scale. It occurs in the east of North America, in Europe from North Spain to the arctic and in large parts of the U.S.S.R. (V. Hessling 1859; Walker 1910; Smith 1980; Valovirta 1980; Bauer 1986). It was undoubtedly exterminated in a number of places by ice during the Glacial Epoch (Walker 1910), but in post-glacial times it apparently recolonized nearly all suitable habitats. As it produced valuable pearls, there were numerous attempts in Germany to found new populations (Scherf 1980) but only one of them was successful, suggesting that all suitable rivers were already occupied.

This success cannot be explained by our present knowledge of the ecology of pearl mussels. The mechanisms which enabled the mussel to colonize such a large range are particularly puzzling in view of its apparently poor power of dispersal. The mussels are

mostly sedentary and usually move for some metres only if they are washed to unsuitable places (Young & Williams 1983a). The pearl mussel inhabits streams and brooks. Populations easily disperse downstream by means of glochidia. However, new brooks can only be colonized by host fish which carry parasitic glochidia in their gills. In Europe, the hosts are salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) (Utermark 1973; Bauer 1979; Young & Williams 1984a, b). The resident brown trout is the only host in areas where salmon never occurred, such as the Danube system. As the parasitic stage frequently lasts only from August to October (Bauer 1979), the number of infected hosts immigrating into new rivers must be expected to be low. The pearl mussel is extremely specialized to physical and chemical factors (Wells, Pyle & Collins 1983). Its distribution is restricted to waters poor in lime. Thus, suitable breeding areas are often separated by large zones which are unsuitable for colonization and large distances have to be covered to reach new suitable habitats.

According to the literature (Hendelberg 1961; van der Schalie 1966; Smith 1979) the pearl mussel is dioecious. Sperm is released by the males into the water current which is then ingested by the females. This mode of fertilization should be only feasible when the concentration of sperm in the water is sufficiently high, so that females can ingest adequate numbers of spermatozoa. Therefore, one must assume that the number of fertilized eggs will depend on the distances separating individuals and on the population density (Young & Williams 1983b), and that below a critical density, the fertilization of eggs will be very low. Thus, even when some mussels succeed in colonizing a new river, their initial density will be so low that fertilization of eggs should become highly improbable, due to the very reduced source of sperm.

Low motility, specialized habitat selection and a narrow host range are ecological features of the pearl mussel which are satisfactorily demonstrated. However, only limited data on the reproductive biology are available. Some aspects of reproduction, e.g. the mechanisms that govern fecundity, are completely unknown. This present investigation therefore attempts to improve our understanding of the survival strategy of the pearl mussel, its life span and its age-specific fecundity in relation to various environmental factors. As outlined above, the relationship between fecundity and population size is of central importance for the survival strategy on the population level. Therefore, a part of this study deals with the question whether there is a density-dependent mechanism compensating for the reduced source of sperm in sparse populations.

METHODS

The work was carried out during the years 1984–86 in two mountain areas (Fichtelgebirge and Bayerischer Wald) of the south-eastern part of West Germany.

Estimation of age and age-specific mortality

Age was estimated by the method of Hendelberg (1961). For each of seventeen populations, a calibration curve for ligament growth was established using shells of dead individuals. Then the ligaments of live mussels were measured in the field and converted to the age. Altogether 2560 mussels were aged. In order to obtain a survivorship curve under natural conditions, the age-specific mortality rates and their relationship to chemical factors had to be investigated. Due to water pollution recruitment has considerably declined in the last decades (Bauer 1983) and mortality cannot be calculated from the age distribution only. Therefore, the following method was chosen: the age specific mortality

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rates were estimated for eleven populations using the age structure of living and dead
mussels and taking the solubility of shells into account (see detailed description by Bauer
1983). To determine the effects of water pollution the correlation was examined between
mortality data and various chemical parameters, e.g. pH, conductivity, BOD_5, NO_3, NH_4,
Ca and Cl and a survivorship curve under unpolluted conditions was calculated.

Fecundity of natural populations

Reproduction is well synchronized within each population. In the study area, eggs are
deposited into the demibranch during mid-July. Shortly after deposition, they are
fertilized (Smith 1979) and kept in the marsupia for 5–7 weeks until the mature glochidia
are released. To test if specific age-classes preferably take part in reproduction, animals of
two populations were sampled at random during July. After ageing them, the valves were
opened to a gap of about 1 cm using a 'tong' which made inspection for developing
glochidia in the gills possible. The age distributions of mussels with and without glochidia
were then compared. The average percentage of mussels containing glochidia was
determined by sampling 1072 animals in seven populations and inspecting them as
described above.

The number of glochidia produced by a single female was determined for seven
populations (the population size ranged from 50 to 10000 animals) in August
approximately 1 week before glochidia were released. Each of 200 gravid mussels was
kept in a small bucket with only little water and the resulting oxygen stress caused the
release of glochidia (method described by Wellmann 1943). The mussels were then
inspected to ensure that all glochidia had been released. The total number of glochidia per
female was calculated by suspending them and making six subsample counts. The
relationships of fecundity with age, population density and chemical factors were tested
by means of regression analyses.

Fecundity of a sparse experimental population

This experiment was started on 10 May 1985, which was approximately 2 months
before recruitment period began. Fifty-five mussels of about the same age were removed
from a large natural population of about 5000 animals and then placed in the same river
upstream from the population with 2 m between each mussel (Fig. 4). No mussels
occurred upstream from this experimental population. The position of gravid mussels was
then recorded in August and the number of glochidia per female was determined as
described above.

Determination of sex

In an hermaphroditic mussel, spermatogenic and oogenic tissue may be located in
different parts of the foot (Heard 1975). The only exact method to sex a mussel is by
dissection. However, this method cannot be applied to an endangered species like the
pearl mussel and an alternative, harmless method was therefore chosen. By puncturing
the foot in May or June, when gametes were nearly fully developed, c. 0·005 ml tissue fluid
was taken and inspected microscopically for spermatozoa and oocytes. A mussel was
typified as hermaphroditic only if, besides oocytes and spermatozoa, sperm morulae were
also found which are associated with spermatogenesis in mussels (Coe & Turner 1938;
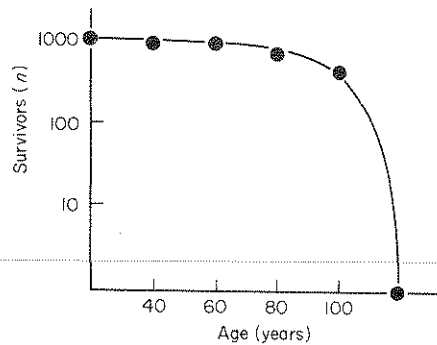Ropes & Stickney 1965; Heard 1975).

FIG. 1. Calculated survivorship curve of a population attaining a maximum life span of *c*. 100 years in an unpolluted river (0·5 ppm NO_3-N). Only mussels older than 20 years are considered.

Sex change in males and females

On 6 May 1986 eighty-four mussels from a large population were marked, sexed and replaced upstream. The mussels were punctured again on 23 June 1986 to see if any sex change had occurred and if males and females equally had changed sex.

Mechanisms causing sex change

Fourteen sample sites were selected from eight rivers. At these sites a total of 404 mussels were sampled, aged and sexed. The following variables were also recorded at each sample site: mussel density at the site, density within the next 15 m upstream, size of the whole population upstream, velocity of the water current (m s^{-1}) and the water discharge (1 s^{-1}). Analysis of the data, using multiple regression techniques, were carried out to identify the parameters that relate to hermaphroditism within the mussel samples.

RESULTS

Life span

The pearl mussel exists in many races which differ considerably with respect to shell morphology and longevity (Fig. 3). For seventeen populations analysed, the mean maximum life span is 93 ± 9 years. Water pollution in Central Europe is detrimental to the establishment and survival of young mussels (Bauer 1983) so that these classes are hardly to be found. All mortalities recorded here are therefore restricted to an age of 20 years and older.

Mortality rates (= percentage of animals dying in 10 years) vary considerably between the populations. They are less then 10% in some populations whereas others suffer mortalities of 70–80% in all age-classes. Correlation analysis showed that for every 20 years class there is a positive linear relationship ($P < 0·05$) between mortality and nitrate concentration in the water. This relationship was used to calculate a survivorship curve under natural unpolluted conditions. For convenience I will refer to a mussel population with a maximum life span of 100 years. Unpolluted mussel rivers exhibit very low ($\pm 0·5$ ppm N) nitrate values (Bauer 1986). The corresponding survivorship curve (Fig. 1) suggests that most animals die of 'old age' which is apparently determined by their

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Sexual maturity and proportion o

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FIG. 2. Age distributions of musse distinguished statistically.
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physiological longevity. Accordingly the mean expectation of further life (e_x) is high for young mussels. A 20 years old mussel on the average will live for 73 more years.

Fecundity of natural populations

Sexual maturity and proportion of mussels containing glochidia

Mussels reach sexual maturity at an age of about 20 years (Fig. 2). Unfortunately, as younger age-classes are usually not present in the study area, the exact age at maturity is difficult to determine. Young & Williams (1984a) found that in healthy populations in Scotland the youngest mature mussels were 12–13 years old, a value which is probably also valid for Central Europe.

The age distributions of mussels with and without glochidia cannot be distinguished (Fig. 2). Thus, the percentage of gravid mussels is the same for all age-classes, indicating that all age-classes from 20 years upwards equally take part in reproduction.

According to Bauer (1979) and Young & Williams (1984a) the percentage of mussels containing glochidia is independent of the population density. In the study area between 10% and 70% of a population is gravid. However, a great deal of this large variation might be due to small sample sizes from sparse populations. Pooling all samples (1072 mussels) 32% were found to contain glochidia.

Fertility

The number of glochidia produced by a single female is very high (Fig. 3). It varies considerably between the individuals and is apparently not dependent on age except for two populations in Fig. 3 (the second ones from below) which suggest an increase of fertility up to 50 years and thereafter a decrease. Because of the large variation and
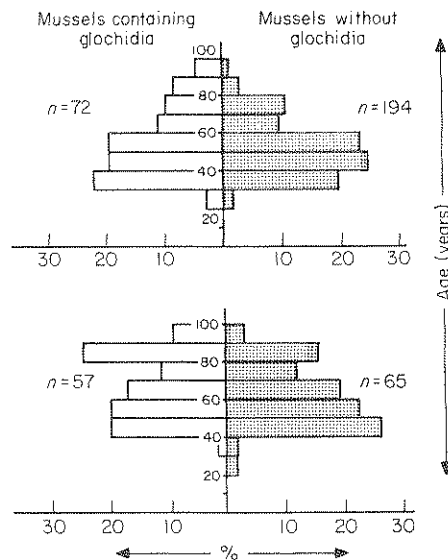

Fig. 2. Age distributions of mussels with and without glochidia. The distributions cannot be distinguished statistically.
Upper population: chi-square = 7·5, d.f. = 5, $P = 0·18$
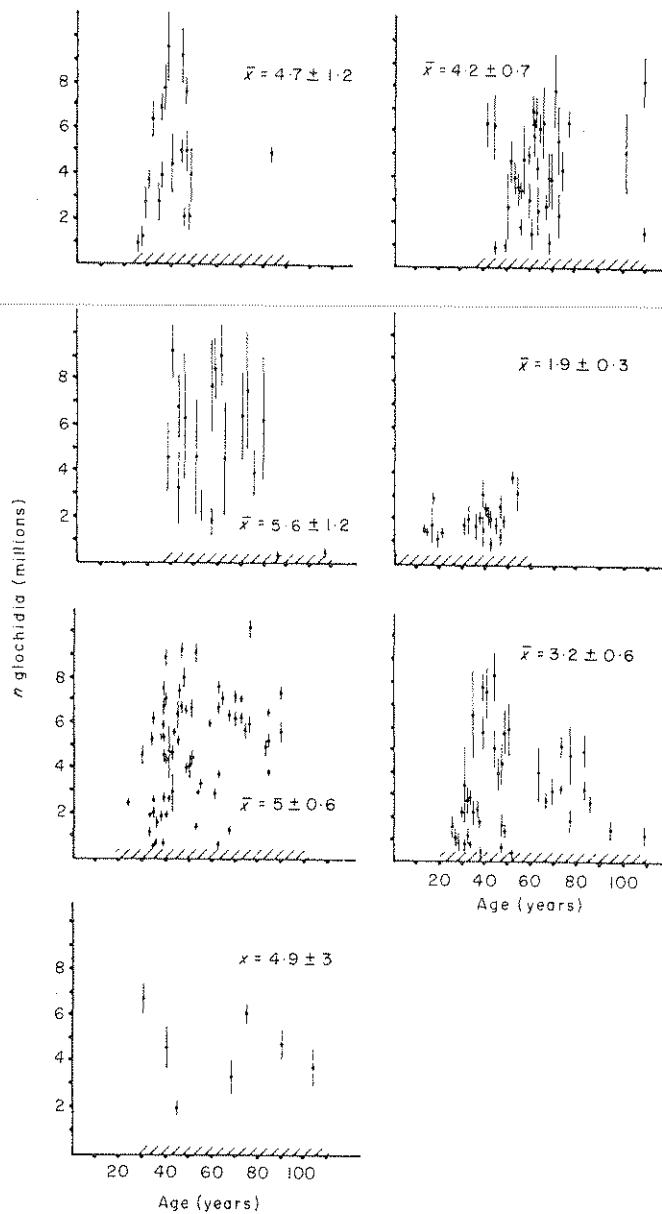Lower population: chi-square = 2·95, d.f. = 4, $P = 0·56$

FIG. 3. Fertility of seven pearl mussel populations. For every female the mean number of glochidia ($\pm$c.i.) of six subsample counts is given. The hatched part of the abscissa gives the age-classes present in the population.

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because of the absence of a clear relationship between age and fecundity for each population the mean number of glochidia per female was calculated. The mean fertility is remarkably independent of environmental factors. No significant correlation ($P > 0.05$) could be found with the population size, the water discharge, the number of mussels per water discharge or chemical factors.
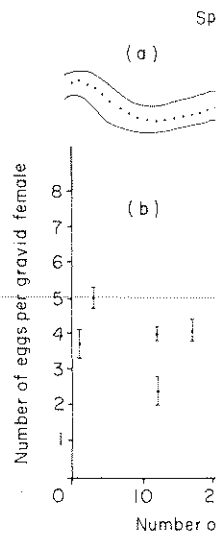
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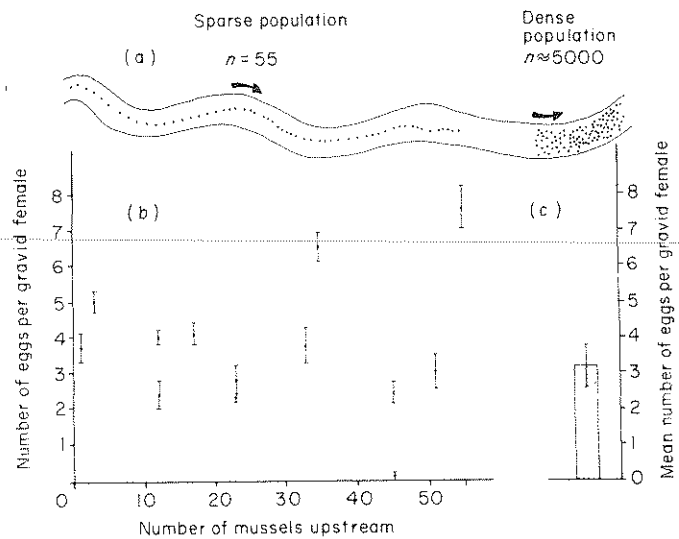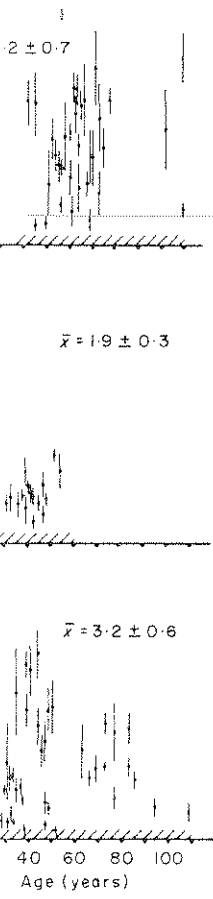significant correlation $(P > 0.05)$
harge, the number of mussels per

Fig. 4. Fertility of a sparse population (ordinate = number of eggs in millions). (a) Experimental arrangement. (b) Mean number of developing eggs ($\pm$c.i.) for every gravid female in the sparse population. (c) Mean number of developing eggs produced by 66 females of the dense population.

Fecundity of a sparse experimental population

This experiment also revealed that fecundity is independent of population density. The mean fecundity of the sparse and the dense population is of the same magnitude (Fig. 4).

Within the sparse population there is no relationship between fecundity and the accumulative number of mussels (males) upstream. Even the last but one mussel upstream did not show any decrease in the number of developing eggs. The successful fertilization of this female is puzzling and suggests occurrence of hermaphroditism in pearl mussels.

Sex change in males and females

If the pearl mussel is gonochoric and the mode of fertilization is as described in the introduction, then one would expect a decrease of fertilized eggs with decreasing mussel density upstream. However, this was not the case. Subsequently, the sex of eighty-four mussels was determined and it was found that, in contrast to the published data a considerable percentage of hermaphrodites occurred (Fig. 5). These hermaphrodites consisted mostly of the type 'female hermaphrodite' (Coe 1943), i.e. the gonad fluid showed a clear preponderance for female tissue.

Two and a half months after replacing these mussels somewhat upstream from the collecting site some had changed their sex. Many females switched to hermaphrodites (Fig. 5). Some of the hermaphrodites on the other hand switched to females, but only three of the males had changed their sex. The possibility cannot be excluded that these males were sexed incorrectly; i.e. that they were hermaphrodites, but the female tissue had not been recorded with the method applied here.

According to the above observations the change to hermaphrodites is mainly, if not exclusively restricted to the females.

TABLE 1. Correlation matrix of sexual characteristics, density parameters, the average age of a sample and physical factors

	Hermaphrodites (%)	Males (%)	Log $(n \times m^{-2})$ sample site	Log $[(n+1) \times m^{-2}]$ 15-m upstream	Log (n) population size upstream	$\bar{x}$ age (years)	v (m s^{-1})	Q (l s^{-1})
Males (%)	0·1							
Log $(n \times m^{-2})$ sample site	−0·33	0·28						
Log $[(n+1) \times m^{-2}]$ 15 m upstream	−0·62*	0·11	0·51					
log (n)	−0·73**	−0·01	0·24	0·65*				
$\bar{x}$ age	0·26	0·13	−0·18	−0·25	−0·21			
v	0·17	−0·08	−0·43	−0·35	−0·24	−0·15		
Q	−0·23	−0·17	−0·52	0·04	0·21	0·03	0·11	
log $(n \times Q^{-1})$	−0·7**	0·02	0·38	0·66**	0·97***	−0·22	−0·32	0·00

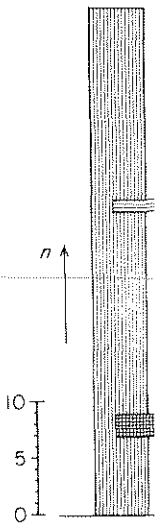* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

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* $P \leq 0.05$.
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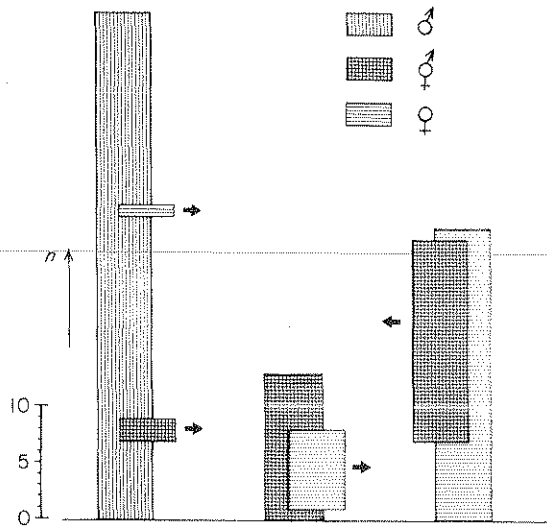
FIG. 5. Sex change of 86 pearl mussels: columns = sex distribution on 6 May; displaced columns with arrows (height above 0 arbitrarily) = mussels having changed their sex by 25 June.

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$P < 0.01$
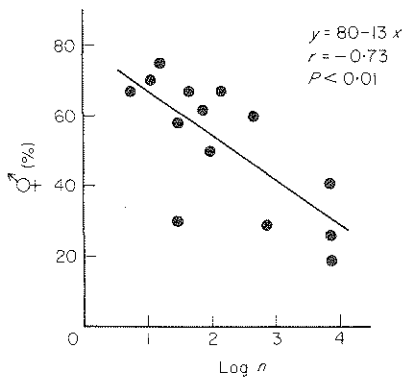
FIG. 6. Relationship between the percentage of females having swtiched to hermaphrodites and the total number of mussels upstream.

Mechanisms causing sex change

The sex ratio (males:(females + hermaphrodites)) of 404 pearl mussels was 1:1 (192 males, 84 hermaphrodites, 128 females). In sparse populations the portion of males frequently deviates from 50% because of small sample sizes. Therefore, in the following analysis the percentage of hermaphrodites is related not to the total number of mussels but to the number of females present in the sample.

The percentage of females having switched to hermaphrodites varied considerably between the sample sites (19–75%, Fig. 6). There was no statistically significant

relationship with age, the flow velocity, the water discharge or the density at the sample site (Table 1). There were, however, correlations with the total number of mussels upstream of the sample site, the number of mussels per water flow (however, these parameters are not independent) and the density within 15 m upstream. If a multiple regression is conducted with the percentage of hermaphrodites as dependent variable, then none of the parameters—except the total number of mussels (log n)—yields a significant explanation of variance. Thus, out of these selected parameters the population size upstream must be considered as the most important one for determining the degree of hermaphroditism within a population (Fig. 6).

DISCUSSION

Longevity and reproductive period

According to Comfort (1957) and Hutchinson (1979) the freshwater pearl mussel is the longest lived invertebrate known. Its average maximum life span in the study area is 93 ± 9 years and contrasts sharply with that attained by other mussels such as *Anodonta* or *Unio* (10–15 years) (Brander 1956; Comfort 1957; Heard 1975; Negus 1966). As far as we know there is no impact of natural enemies on mature mussels (older than 20 years) and mortality rates are low in natural unpolluted rivers.

The survivorship curve is therefore of a type very uncommon for animals under natural conditions. It is convex suggesting that not only the life span is long but most animals also live out their allotted life span and die of old age. The mean expectation of further life for a mussel having reached maturity (at an age of 20 years) amounts to 73 years. As there is no postreproductive period (Figs 2, 3) this value is coincident with the average reproductive life span.

Proportion of females containing glochidia

Thirty-two per cent of the inspected mussels contained glochidia. This value agrees with a recent study and with findings from Northern Germany (Dettmer 1983). As the sex ratio is 1:1 it means that every year 64% of all females take part in reproduction and 36% are pausing. (It seems that in Scottish populations the females reproduce more often as Young & Williams (1984a) found on the average 44% of all mussels being gravid).

Sexual characteristics

Most authors (also those having performed dissections) regard the pearl mussel as strictly dioecious. This discrepancy with the present study is presumably due to the fact that these workers took their samples from large populations where the percentage of hermaphrodites indeed is low and so failed to detect hermaphroditism.

Sex change occurs almost exclusively among females (Fig. 5). If females and hermaphrodites are pooled then the sex ratio is nearly 1:1. This is in accordance with findings of Hendelberg (1961) in Sweden and is an indication that the sex of pearl mussels is presumably determined genetically.

Hermaphroditism may occur in two forms being functionally different in their mating systems. Sequential hermaphrodites rely on a mate (if they do not have possibilities to store sperm) whereas simultaneous hermaphrodites may fertilize their own eggs. As there is no correlation of the percentage of hermaphrodites with the average age of a sample nor with the percentage of males (Table 1), hermaphroditism of the pearl mussel must be

considered as simultaneous. Most The preponderance of female over on male than on female functions a spermatozoa are not released into self-fertilization (Charnov 1979; G strongly suggested by the indepen but especially by the high fertility of the related species *Anodonta cygn*

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considered as simultaneous. Most hermaphroditic pearl mussels are of the female type. The preponderance of female over male tissues indicates that hermaphrodites spend less on male than on female functions and it furthermore indicates that it is likely that the 'few' spermatozoa are not released into the water but that they are used more effectively for self-fertilization (Charnov 1979; Ghiselin 1974; Kat 1983; Williams 1975). Selfing is also strongly suggested by the independence of fecundity with density of natural populations but especially by the high fertility of a sparse population (Fig. 4). Self-fertilization among the related species *Anodonta cygnea* was pointed out by Bloomer (1940, 1943).

Evolution of hermaphroditism in the pearl mussel

Ghiselin (1969) lists three possible explanations of the origin of hermaphroditism. One of these models, i.e. the 'size advantage model', cannot be applied to the pearl mussel as it accounts only for sequential hermaphroditism. The 'gene dispersal model' holds if the flow of genes within a population (or between populations) is limited and the 'low density model' predicts hermaphroditism as an adaptation ensuring reproduction at low population densities. It seems that these last two models explain the evolution of hermaphroditism in the Unionoidea.

Gene flow will be limited for mussels living in standing water, because motility of spermatozoa is low and their viability is limited (Galtsoff 1964). Thus, at low densities the spermatozoa released by a male may not reach a female within their life time. Under such conditions selection should favour hermaphrodites capable of selfing. As there is no chance of preventing inbreeding, pure males cannot contribute anything to reproduction; all their gametes are wasted. Therefore, the most effective mode of reproduction for a population would be by means of hermaphrodites. These considerations agree with Weisensee (1916) who found populations of *Andonta gygnea* in lakes being entirely hermaphroditic whereas in rivers they were gonochoric. The situation is quite different for mussels living in running water like the pearl mussel. Gene flow is not limited as sperm is distributed quickly over long distances in the water current. However, the number of fertilized eggs will depend on the concentration of spermatozoa per unit of water, which may depend on the water flow, the population size, the distances separating individuals and the position of individuals (Kat 1983). The above analysis shows that the degree of hermaphroditism within a pearl mussel population depends mainly on the population size (Table 1) and this suggests that the 'low density model' is responsible for the development of hermaphroditism. In contrast to *Anodonta* only female pearl mussels are capable of switching to hermaphrodites. This seems to be a waste of male gametes. However, even limited cross-fertilization will increase the gene flow, prevent inbreeding and will thus assure variability in the population. This was shown by Allard (1965) where population variability was drastically increased at the fifth or sixth generation when only 5% or less outcrossings occurred. The males, therefore, might be an important factor in keeping predominantly selfing pearl mussel populations from becoming highly uniform.

Reproductive strategy

The mode of reproduction of the pearl mussel is marked by two components: the first one yielding high fertility and the second one maintaining it under various conditions. The first component is a combination of a 'high life expectancy during the reproductive period' (Fig. 7), a 'high fecundity which is independent of age' and an 'absence of a postreproductive period' (Figs 2, 3). Mussels reach maturity at an age of about 20 years and then continue to reproduce until they die. Every year 64% of the females become

gravid; thus, an average female with a reproductive life span of 73 years reproduces forty-seven times. If one considers an average fertility of 4.2×10^6 glochidia per gravid female (the mean of all populations in Fig. 3) then an average female will produce 197×10^6 glochidia during its life.

The second component reflects the selective value of different modes of reproduction in varying population densities. At high densities the mussels are mainly gonochoric and cross-fertilizing is the predominant mode of reproduction. At low densities females switch to selfing hermaphrodites. In such populations selection for outbreeding is still evident in the presence of pure males still releasing their sperm into the water.

Concluding remarks

According to literature, mortality and fecundity changes are defined by the ageing process (Hamilton 1966; Murdock 1966; Emlen 1970). Emlen (1970) points out that age-specific mortality during the reproductive period should rise with age, while age-specific fertility should first rise to a peak (which in species with indefinite growth may occur very late in life) and then fall. This pattern is evident in most animal species. However, the pearl mussel apparently behaves differently and its reproductive strategy resembles a woody plant more than that of an animal. For unknown reasons it was able to extend its reproductive period considerably and to avoid enemies, resulting in a low and constant mortality during this period. There is, therefore, no selective basis for a peak in reproduction at an age preceding high mortalities or for a postreproductive period at an age which suffers high mortalities.

The advantages gained by such a strategy may be summarized as follows.

(a) Because of the extended reproductive period, populations are less vulnerable to fluctuations in the reproductive success caused by unpredictable environmental factors.

(b) A peak in reproduction means that a maximum number of offspring is produced within a short time. It thus requires a considerable reproductive effort which again may decrease survivorship after the peak (Loschiavo 1968; Tinkle 1969). If, on the other hand, each age-class equally contributes to reproduction, the costs are also evenly dispersed throughout the whole reproductive period. In this way many offspring can be produced without allocating all available resources to reproduction. Accordingly, the pearl mussel belongs to those animal species with a very high output of larvae during its life time.

(c) The above features, combined with the subtle mechanisms governing hermaphroditism, enable even sparse founder populations to persist for 90–100 years and also to reproduce in such a way to allow maximum number of offspring and genetic variability of succeeding generations.

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