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June 1995

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Waterways Experiment Station

Zebra Mussel Research Program

A Histological Study of the Reproductive Pattern of Zebra Mussels

by Shiao Yu Wang, Dana R. Denson
University of Southern Mississippi

Prepared for Headquarters, U.S. Army Corps of Engineers

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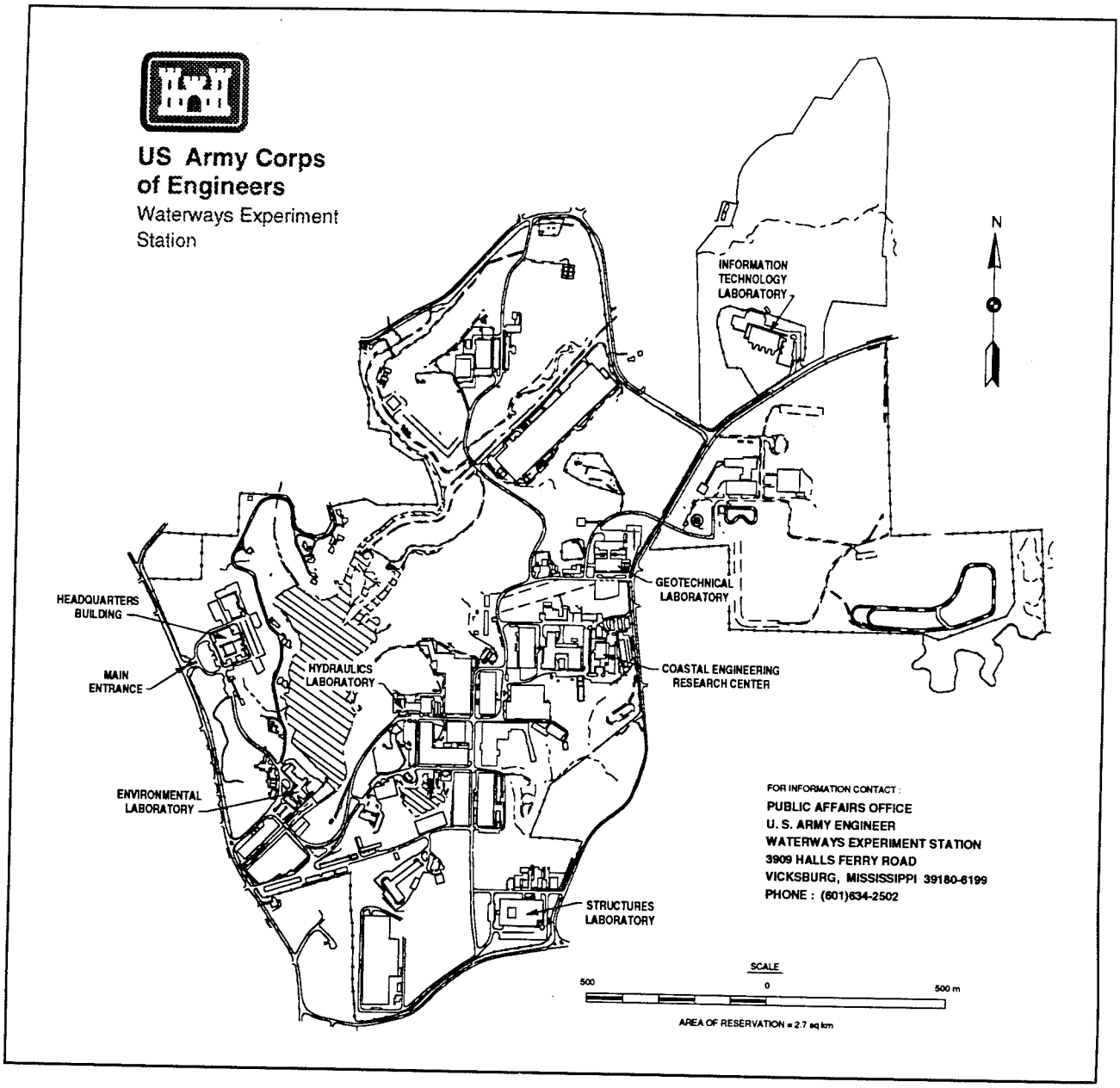

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Preface

The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 specified that the Assistant Secretary of the Army, Civil Works, will develop a program of research and technology development for the environmentally sound control of zebra mussels (*Dreissena polymorpha*). As a result, the U.S. Army Engineer Waterways Experiment Station (WES) initiated a program to develop control strategies for this species.

This report was prepared for WES by Dr. Shiao Wang and Mr. Dana Denson, Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS, under Contract No. DACW39-93-K0002. Drs. Andrew C. Miller and Barry S. Payne, Environmental Laboratory (EL), WES, managed the contract for this work. Dr. Edwin A. Theriot, WES, was Program Manager of the Zebra Mussel Research Program.

During the conduct of this study, Dr. Theriot was Chief, Aquatic Ecology Branch; Dr. Conrad J. Kirby was Chief, Ecological Research Division; and Dr. John W. Keeley was Director, EL.

Dr. Robert W. Whalin was Director of WES at time of publication of this report. COL Bruce K. Howard, EN, was Commander.

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1 Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), is a freshwater bivalve mollusc introduced into North America within the past decade. A native of Eastern Europe, it spread through Western Europe during the last century and became established on this continent after apparently being released as larvae from the ballast water of a trans-Atlantic ship in the vicinity of Lake St. Clair, between Great Lakes Erie and Huron in 1985 or 1986 (Hebert, Muncaster, and Mackie 1989). The mussel has since spread into all of the Great Lakes (Roberts 1990) and has been sighted as far west as Duluth, MN, and Green Bay, WI, as far east as the St. Lawrence River, and as far south as New Orleans, LA.

Dreissena polymorpha is a byssate epifouling bivalve, attaching by means of proteinaceous byssal threads to any hard surface in the water (Kilgour and Mackie 1993). No other purely freshwater bivalve native to North America has this mode of life as an adult. The zebra mussel's reproductive cycle is characterized by a planktonic veliger larvae that requires no host, but floats in the water column for about 1 month before settling to the bottom to assume benthic life (Stanczykowska 1977). All other indigenous freshwater bivalves require either a host fish or the gill chamber of an adult bivalve for larval development (Mackie 1991). Because it possesses these characteristics, the zebra mussel has been able to occupy a unique ecological niche, endowing it with the ability to very rapidly infiltrate the waters into which it has been introduced.

The rapid expansion of zebra mussels in the United States has resulted in serious problems, from both an economic and an ecological standpoint. Natural substrata for settlement of *Dreissena* larvae are wood, stones, and other hard objects in streams and lakes. The firm surfaces of water intakes for power plants and water treatment facilities, boat hulls, navigational buoys, dams, breakwaters, and locks, therefore, provide ideal sites for establishment of colonies of zebra mussels. These and like structures are consequently densely colonized by these bivalves; so densely, in fact, that their function is often impaired, if not completely halted, because of such infestations. The waterworks at Monroe, MI, which serves approximately 45,000 homes, experienced water outages several times between the fall of 1989 and the spring of 1990 because of severe infestations of zebra mussels (LePage 1993). In the same city, densities of zebra mussels in the cooling water intakes of the Detroit

Edison power plant were as high as 800,000/m^2 in 1989 (Kovalak, Longton, and Smithee 1993). Artificial substrata placed in the harbor at Kenosha, WI, to observe colonization rates by *Dreissena polymorpha* showed an increase in density from zero to 28,000 mussels per square meter between 31 July and 11 September 1991 (Kraft 1993). Removal of the encrusting bivalves is expensive in terms of labor, materials, and downtime for the facility. The Monroe water treatment plant noted above spent $300,950 for removal of zebra mussels between 1989 and 1991 (LePage 1993).

Because any firm surface in the water is subject to colonization by zebra mussels, the hard exoskeleton of freshwater macroinvertebrates are also densely encrusted. This type of infestation has most seriously affected the rich unionid mussel fauna in North American fresh waters. The exposed portions of the valves of unionids may be so thickly colonized by *Dreissena polymorpha* that opening and closing of the valves is hampered, resulting in difficulty in ventilation and filter feeding (Mackie 1991). Hunter and Bailey (1992) have shown that a strong negative correlation exists between the biomass of attached zebra mussels and the abundance of native unionid bivalves. Densities of up to 15,000 zebra mussels per unionid have been reported (Mackie 1991). Unionids that are free of zebra mussel infestation have been shown to have twice the lipid reserves of encrusted unionids (Hebert et al. 1991). Aggregations of *Dreissena* on the valves of unionids have resulted in reduced survival, lowered glycogen levels, and reduced cellulase activity in the host bivalves (Haag, Berg, and Garton 1993).

The filter feeding activity of enormous numbers of zebra mussels in some areas may cause ecological complications beyond their competitive effects on unionids and other macroinvertebrates. Removal of suspended materials from the water could cause a movement of the bulk of available energy from the planktonic to the benthic habitat, resulting in an alteration of existing food webs (Hebert et al. 1991).

In 1991, a second species of dreissenid mussel was discovered in the Erie Canal near Palmyra, NY, among clumps of zebra mussels. Initial differences in shell morphology were noted by May and Marsden (1992), who then performed allozyme tests to separate the two into separate species. The new species was given the name "quagga mussel," after an extinct relative of the zebra. Additional differences in the shell morphology of the two species were noted by Pathy and Mackie (1993). The quagga mussel has now been identified as *Dreissena bugensis* Andrusov, which is native to the Black Sea drainage of the Ukraine (Rosenberg and Ludyanskiy, in preparation; Spidle, Marden, and May, in preparation).

In order for timely, cost-effective, and environmentally sound control strategies to be determined, a thorough knowledge of the basic biology of *Dreissena* must be ascertained. The goal of the present research was to determine seasonal patterns and characteristics of reproduction in zebra mussels. The reproductive status of mussels was determined by histological examination of the gonadal tissue. Knowledge concerning the reproductive cycle of zebra mussels

is needed in establishing mussel control programs since periods of gamete release are times when vigilance is especially critical to prevent settlement of new recruits.

2 Materials and Methods

Samples of zebra mussels were collected monthly at the Black Rock Lock in Buffalo, NY. Clumps of mussels were scraped from the wall of the lock using a long-handled scraping device, wrapped in damp paper towels, placed into resealable plastic bags, and sent to the laboratory at the University of Southern Mississippi in Hattiesburg via Federal Express overnight service. Mussels were kept cool in transit using containers of gel ice and were processed immediately upon arrival.

From each of 19 monthly samples (May 1992 - November 1993), a subsample of approximately 48 zebra mussels was randomly chosen and divided into four size classes. These classes were as follows: less than 10 mm in shell length, from 10 to 15 mm, from 15 to 20 mm, and greater than 20 mm in shell length. The entire soft body (exclusive of byssus) was dissected from inside the valves and was then stabilized for 18 to 24 hr in Davidson's fixative (Humason 1979), composed of 95-percent ethanol (33 percent by volume), 37-percent formaldehyde (22 percent), glacial acetic acid (11.5 percent), and distilled water (33.5 percent).

When fixing was completed, tissues were washed in flowing tap water overnight. Afterwards, they were dehydrated in a graded series of ethyl alcohol solutions, as follows: 50 percent overnight, 60 percent overnight, 60 percent for 2 hr, and 70 percent overnight. Samples were then placed into a Fisher Model 166a Histomatic Tissue Processor in which they were carried through the following solutions for 1 hr each: 80-percent ethanol, 95-percent ethanol (three times), 100-percent ethanol (three times), toluene (three times), and paraffin (three times). Upon completion of tissue processing, they were imbedded in Paraplast Plus imbedding medium in Lab-Line TiMS base molds with VWR imbedding rings.

When tissue blocks were dry and cooled, they were removed from the base molds, trimmed using single-edged razor blades, and then sectioned at a thickness of 5µm using an American Optical Company model 820 rotary microtome. Serial section ribbons were floated on warm water, then placed on glass microscope slides and allowed to dry on a slide warmer. When dry, coverslips were mounted on the slides using Cytoseal adhesive.

Examination of the slides followed using American Optical Series model 150 binocular light microscopes. For each animal sampled, the gonadal tissue was viewed to determine the sex (if possible) and reproductive state from the appearance, configuration, and density of the products of gametogenesis, which are contained within acini that lie peripheral to and often intermingled with the digestive gland. The index of reproductive state utilized follows. It is basically modeled after Mann (1979).

a. *Inactive.* Those animals showing no evidence of current or previous gametogenic activity (mainly juveniles).

b. *Early active. Males*: Acini containing numerous spermatogonia and spermatocytes, but few or no spermatozoa (which are apparent because of the sharply defined head portion and the presence of eosinophilic tails in the lumen of the acinus).

   Females: Oogonia arising along the wall of the acinus beneath the follicular membrane; lumen appears mainly empty; no free oocytes; occasionally, a few remnant ova from the previous season might remain.

c. *Late active. Males*: Numerous spermatozoa with tails oriented toward, but not filling, the acinus lumen.

   Females: Acinus contains both free and attached oocytes, which partially fill the lumen; nuclei distinct; oocytes retain ovoid shape.

d. *Ripe. Males*: Acinus densely filled with spermatozoa whose tails completely fill the acinus lumen in a coordinated swirling pattern.

   Females: Acinus completely filled free and some attached ova, which often assume cuboidal shape because of packing.

e. *Spent. Males*: Acinus partly or wholly empty of spermatozoa; degradation of any residual gametes is apparent.

   Females: Acinus is partly or wholly empty of oocytes; degradation of residual gametes is often apparent; remaining oocytes resume ovoid shape.

For clarity, the *Early active* and *Late active* categories above have been combined as simply developing in the Results and Discussion sections below.

The sex of inactive mussels (*i.e.*, those that had not yet reached reproductive maturity) was not determinable using these methods, as sexual dimorphism is not seen other than in the gametes. In the case of spent mussels, however, the sex was usually obvious from the appearance of the acinus. In most, some residual gametes remained, allowing sexing. Even in those few individuals in which all gametes had been shed, the characteristic appearance of the acinus often made determination of the sex of the zebra mussel possible.

3 Results

The reproductive status of a total of 900 zebra mussels collected from May 1992 - November 1993 (19 months) were examined histologically. The monthly proportions of zebra mussels in the three different reproductive state categories (developing, ripe, and spent) are shown in Figure 1. Photomicrographs of the different reproductive stages for female *Dreissena polymorpha* are shown in Figures 2a-c. The same stages in gamete development in male zebra mussels are shown in Figures 3a-c.

In May 1992, when the present study was initiated, 100 percent of the mature zebra mussels examined showed signs of gamete development (Figure 1). None of these yet contained mature gametes. By June, however, 54 percent of the mussels were ripe, while 46 percent had not yet reached maturity. July marked the highest proportion of mussels with mature gametes, when 98 percent of adult zebra mussels had ripe gonads. Although spawning appears to have occurred as early as June, the maximum number of spent animals was seen in August. Of the 59 mussels collected on 28 July 1993, none appeared to have released significant amounts of gametes. In less than 1 month, however (August 26), 65 percent of adults from the monthly subsample had already spawned. This proportion increased to 81 percent in September. All of the mussels had spawned by October, and degradation of residual gametes was extensive in many of these.

Reinitiation of gametogenesis occurred in November, with 38 percent of mature mussels contained developing gametes. During December 1992 and January 1993, the proportion of mussels with developing gametes increased, accompanied by a decrease in the relative amount of residual gametes and connective tissue within the acini, indicative of a gradual resorption of these materials. Seventy-one percent of mature mussels showed gamete development by February 1993, with 29 percent of them still in a spent condition. Of those showing gamete development in February, nearly 70 percent were females. Gamete development was apparent in greater than 92 percent of adult mussels in March, with all of those classified as "late active" in development being females. All mature mussels in the April 1993 samples were active in production of gametes. Again, the female mussels appeared to be farther along in development of ova than the males in development of spermatozoa. The first appearance of ripe zebra mussels in 1993 was seen in May, when

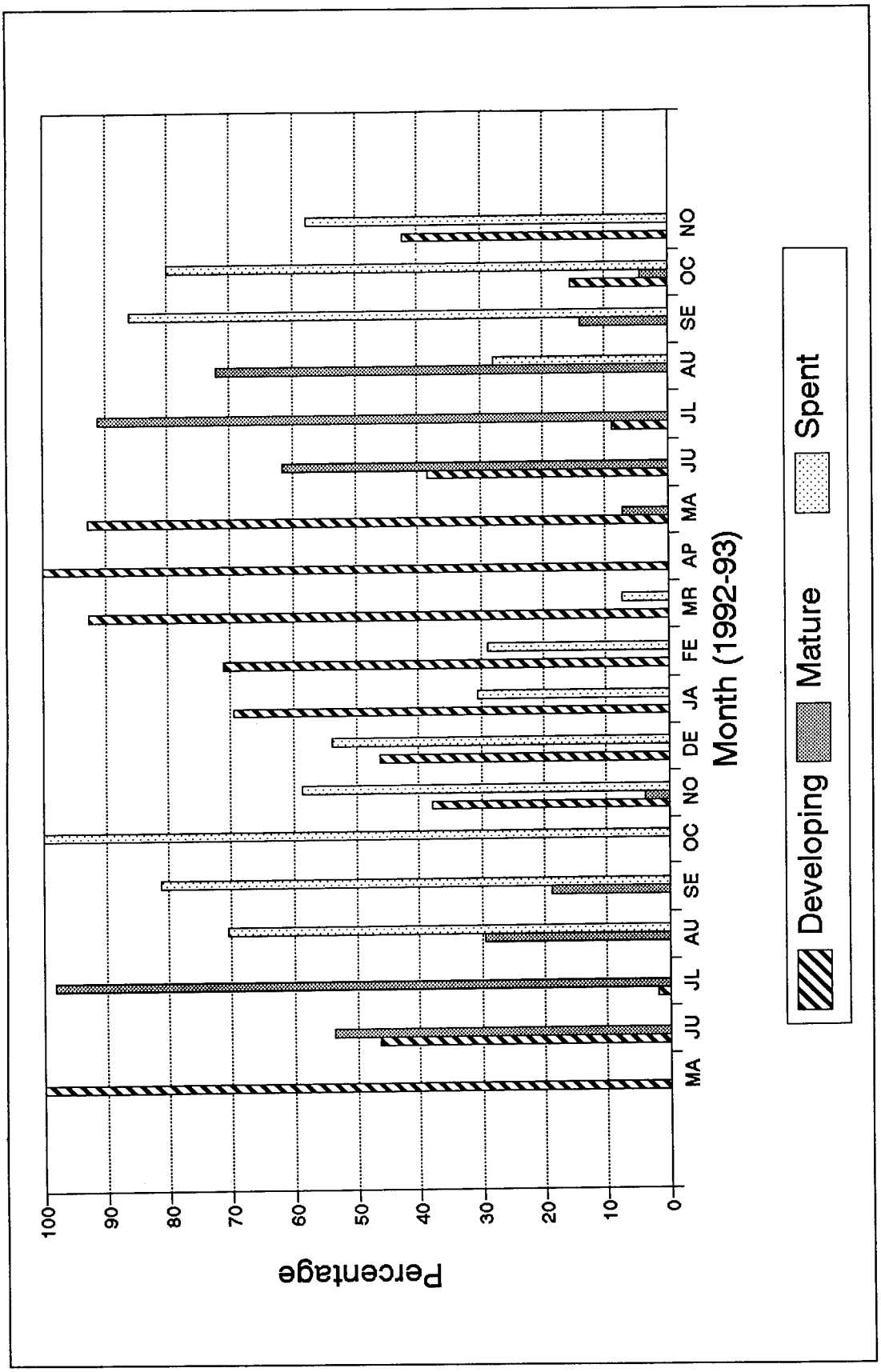


Figure 1. Percentages of adult zebra mussels classified as developing, ripe, and spent over time

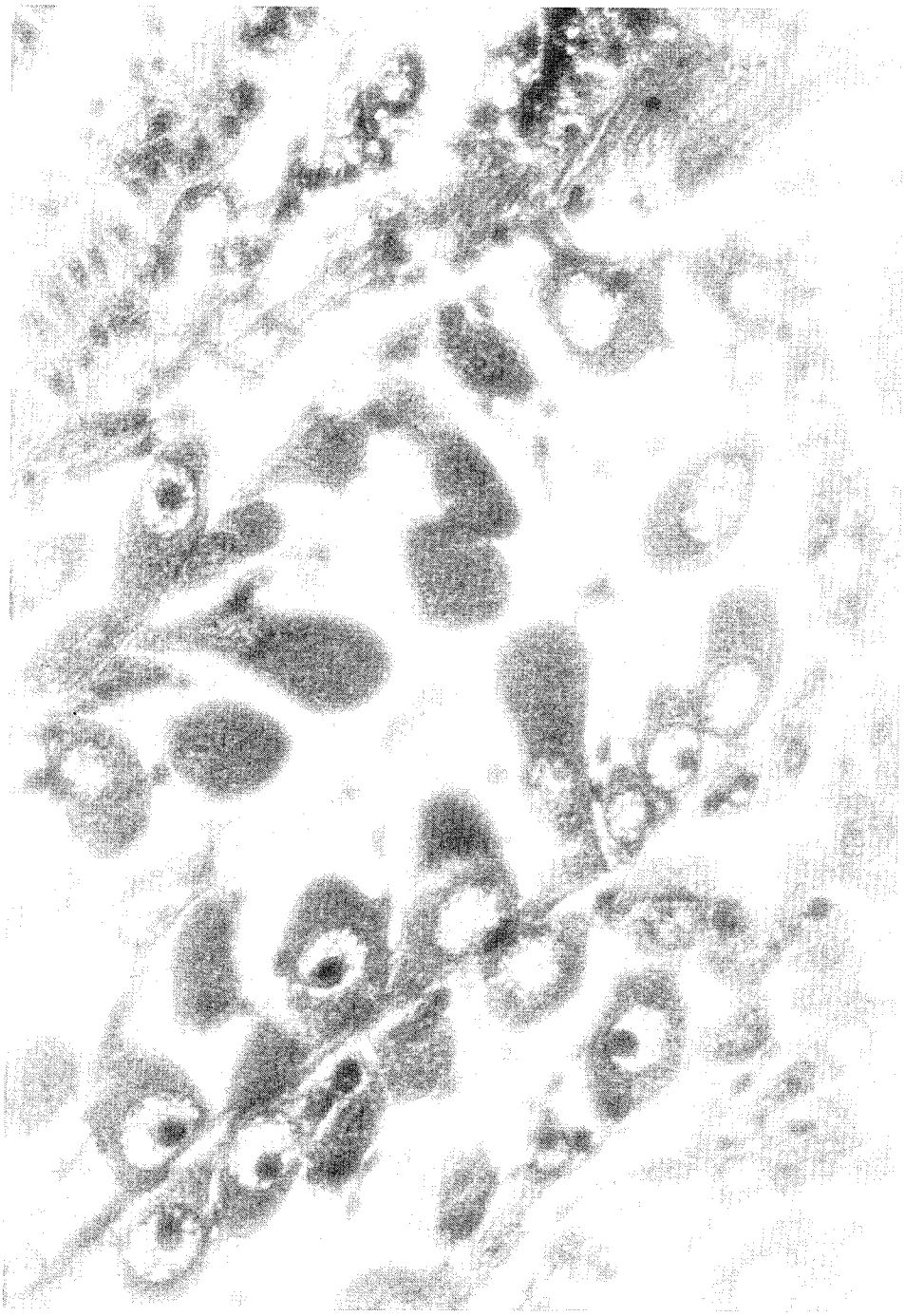
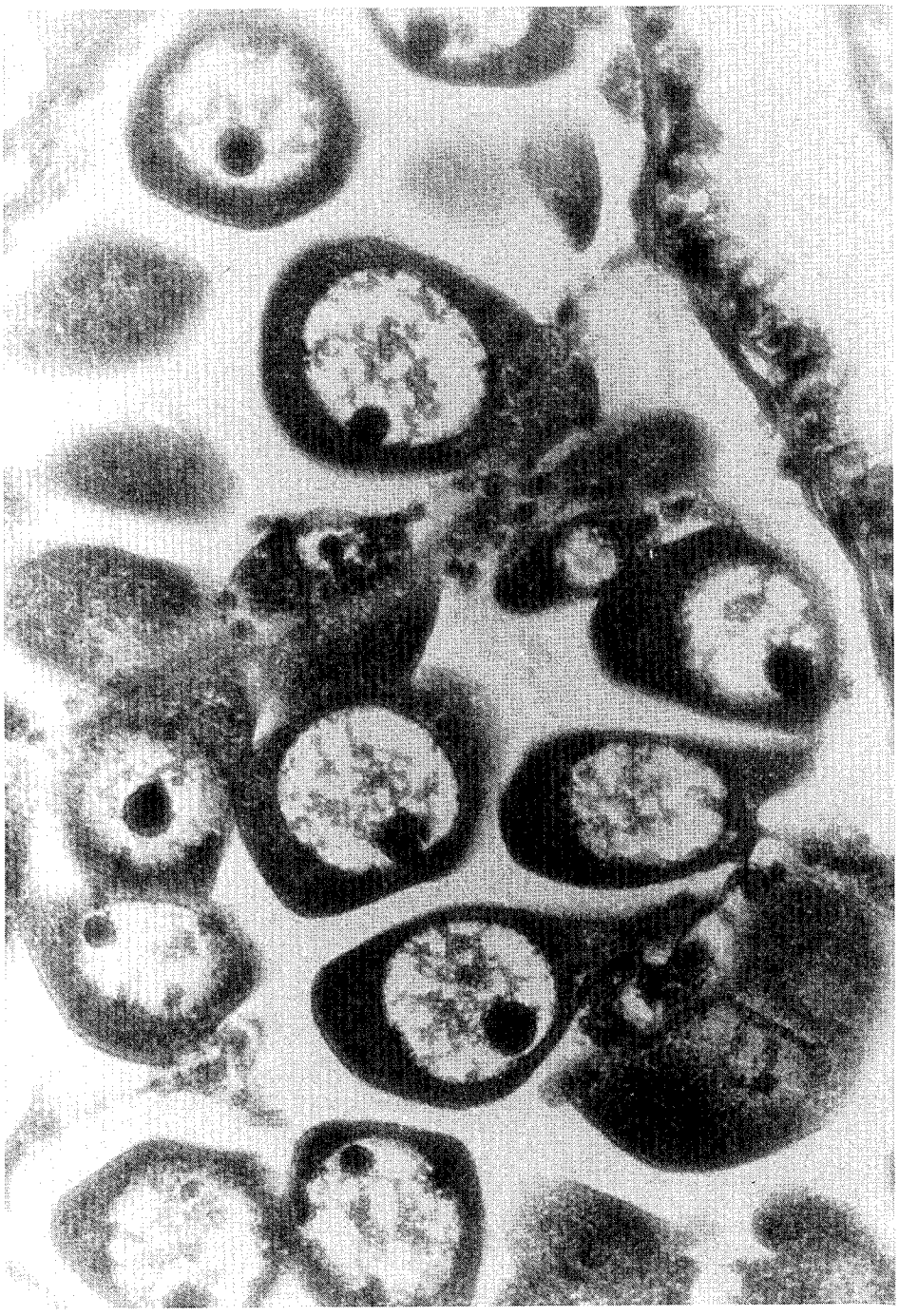


Figure 2. Light photomicrographs of gonadal tissue of female zebra mussels at different stages of development: a. developing; b. mature; c. spent (Sheet 1 of 3)



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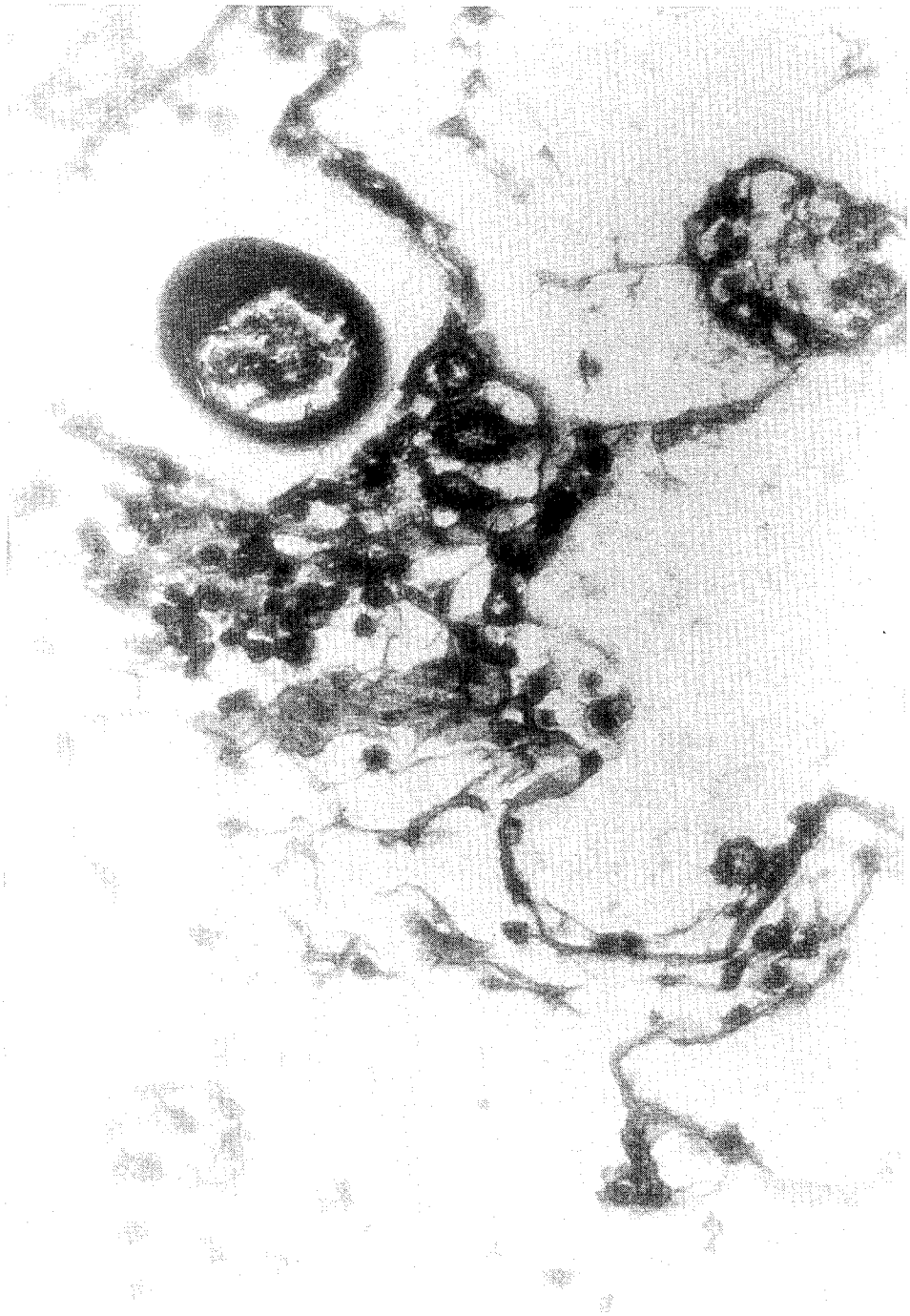

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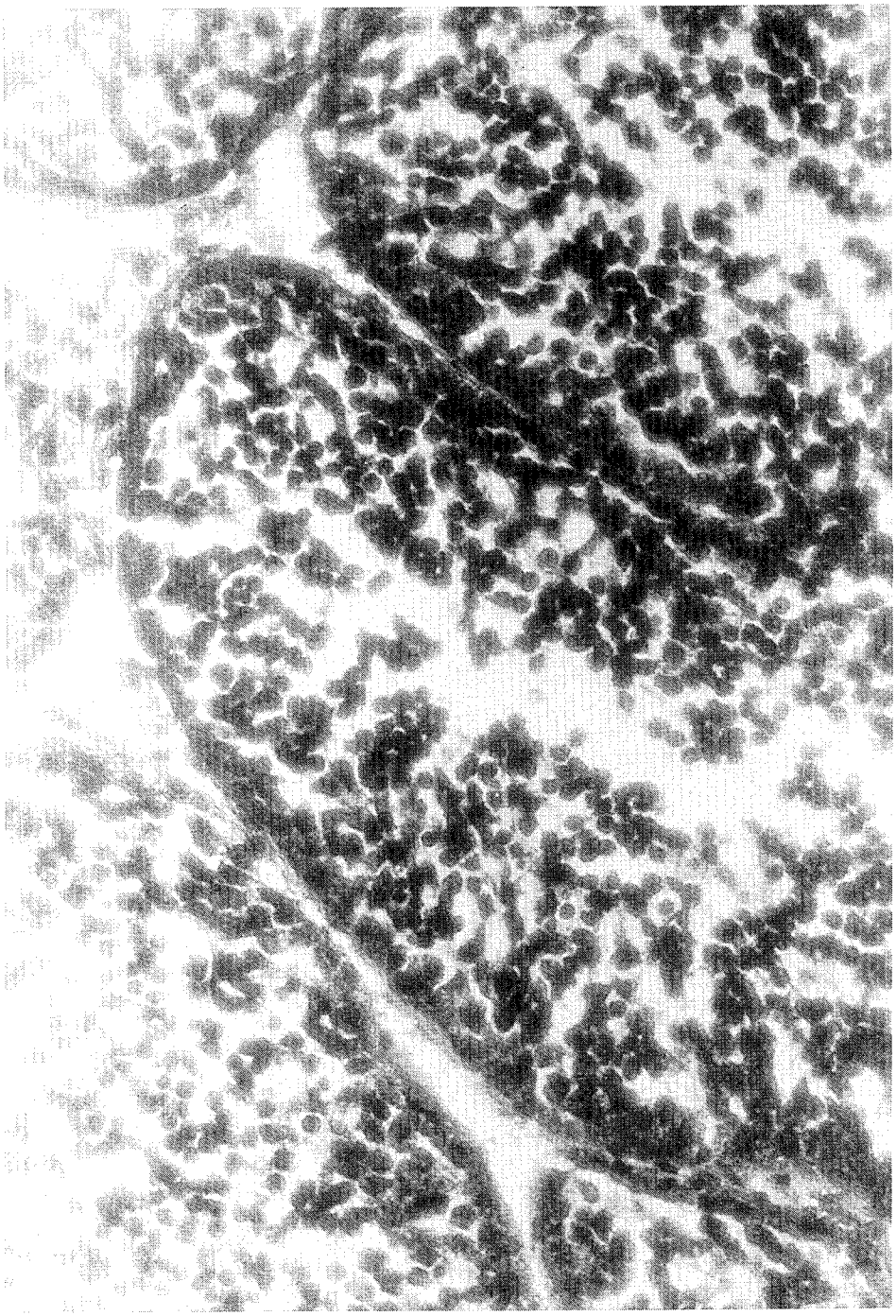
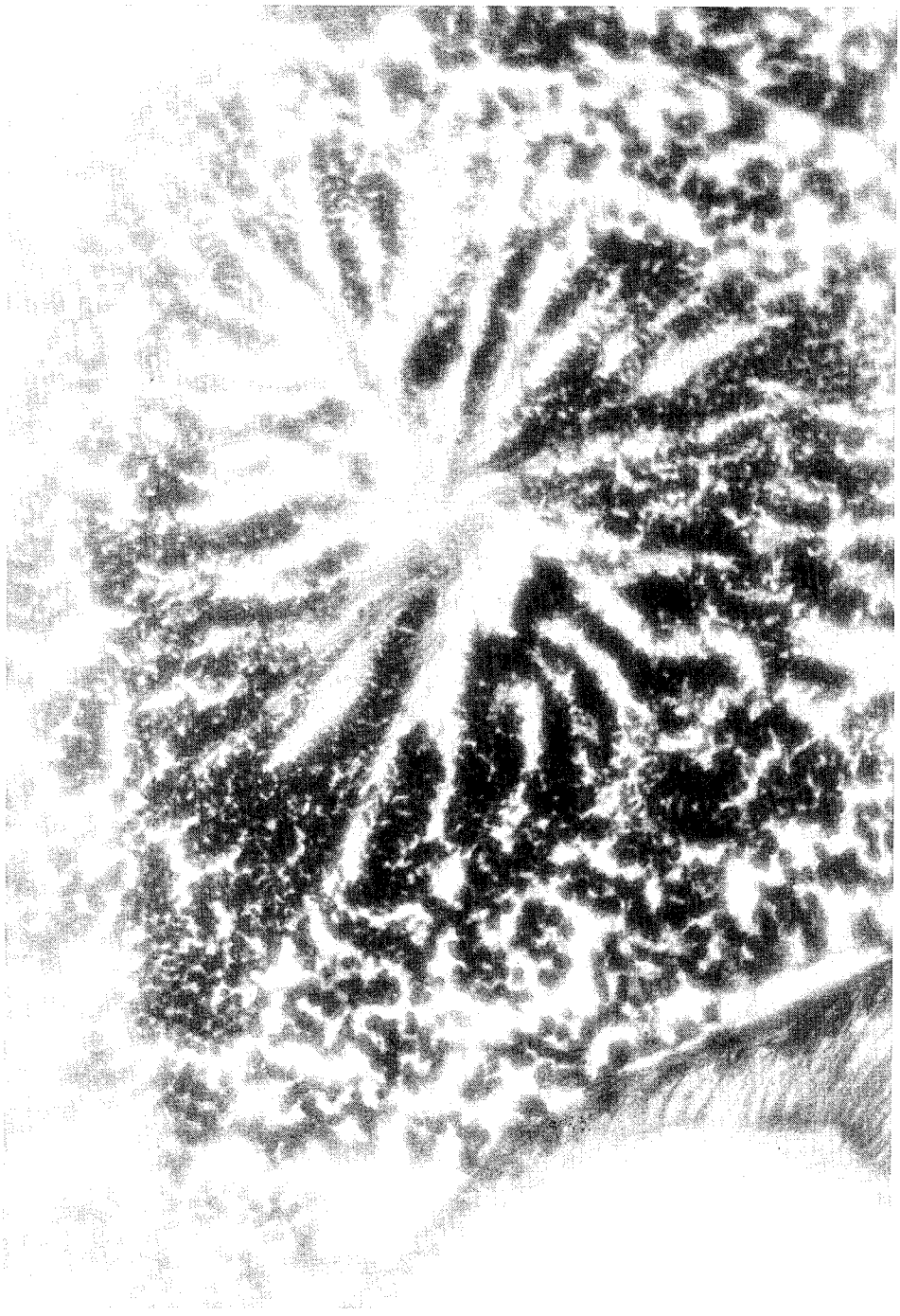


Figure 3. Light photomicrographs of gonadal tissue of male zebra mussels at different stages of development: a. developing; b. mature; c. spent (Sheet 1 of 3)



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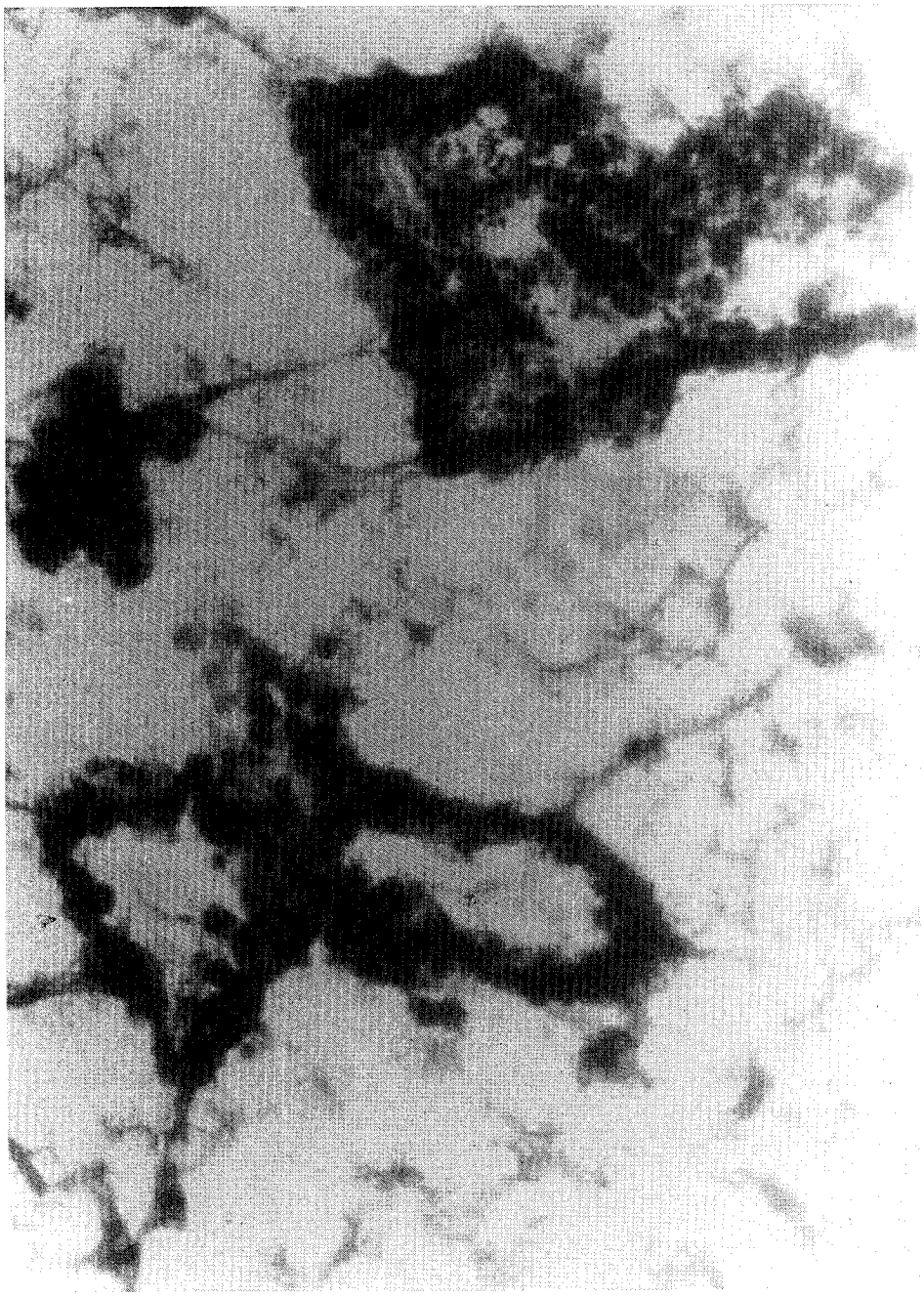

Figure 3. (Sheet 3 of 3)

7 percent contained ripe gonads. Most of the other 93 percent were in the "late active" developmental stage. In the month of June, the percentage of ripe mussels increased to 61 percent. Spawning was not yet apparent in any of the mussels sampled this month.

Ninety-one percent of adult mussels contained mature gametes by July 1993, and limited spawning had taken place in some mussels, especially the larger individuals. By August, 28 percent of mature mussels had spawned, while 72 percent had ripe gonads containing mature gametes. Only 14 percent remained unspent by the 26 September samples, 86 percent of the zebra mussels having already released most of their gametes. Virtually all mussels were spent in the October 1993 samples. Unlike the same month in 1992, however, initial gametogenesis was apparent in more than 15 percent of the zebra mussels comprising this monthly sample set. By November 1993, gamete development was seen in 42 percent of zebra mussels, the remainder still characterized as being in a spent state.

A slight female bias was present in the ratio of the sexes of zebra mussels from the Black Rock Lock. Of 743 mussels whose sex was determinable histologically, 55 percent were females. Monthly ratios of female to male zebra mussels (Figure 4) show that the largest difference in numbers of the sexes was seen in samples collected in August and September 1992, when females accounted for 61 and 69 percent of the total number of mature mussels sampled, respectively. A bias toward females was seen in 13 of the 19 sample months. A greater occurrence of females was especially true in the very large zebra mussels. Data for mussels greater than 20 mm in shell length show that nearly 70 percent in this size range are females. There was no indication of hermaphroditism among any of the 900 zebra mussels examined.

The results of this study indicate that the mean size of female zebra mussels is generally greater than that of male zebra mussels. Monthly mean shell lengths of female and male zebra mussels are given in Figure 5. The mean length of females was greater than the mean length of males in 14 of the 19 months of the study. Overall, the mean length of female zebra mussels was 17.6 mm, while the mean length of male zebra mussels was 16.6 mm.

Zebra mussels apparently begin reproducing at a very small size. The smallest mussel examined that contained developing gonads was a female of 4.58-mm shell length. The smallest male was 6.80 mm in shell length. During the course of the investigation, mature zebra mussels within the 7.5- to 10-mm size range were not uncommonly encountered. Although most were much smaller, the largest zebra mussel examined was a spent male measuring 36.05 mm in shell length.

The development of gametes begins earlier in larger zebra mussels than in smaller ones. When gamete development was first seen in November 1992, the mean shell length of mussels with developing gametes was 18.9 mm (Figure 6). By December, the mean length was 21.2 mm. The mean size gradually decreased over the ensuing months, to a minimum of 12.6 mm in May

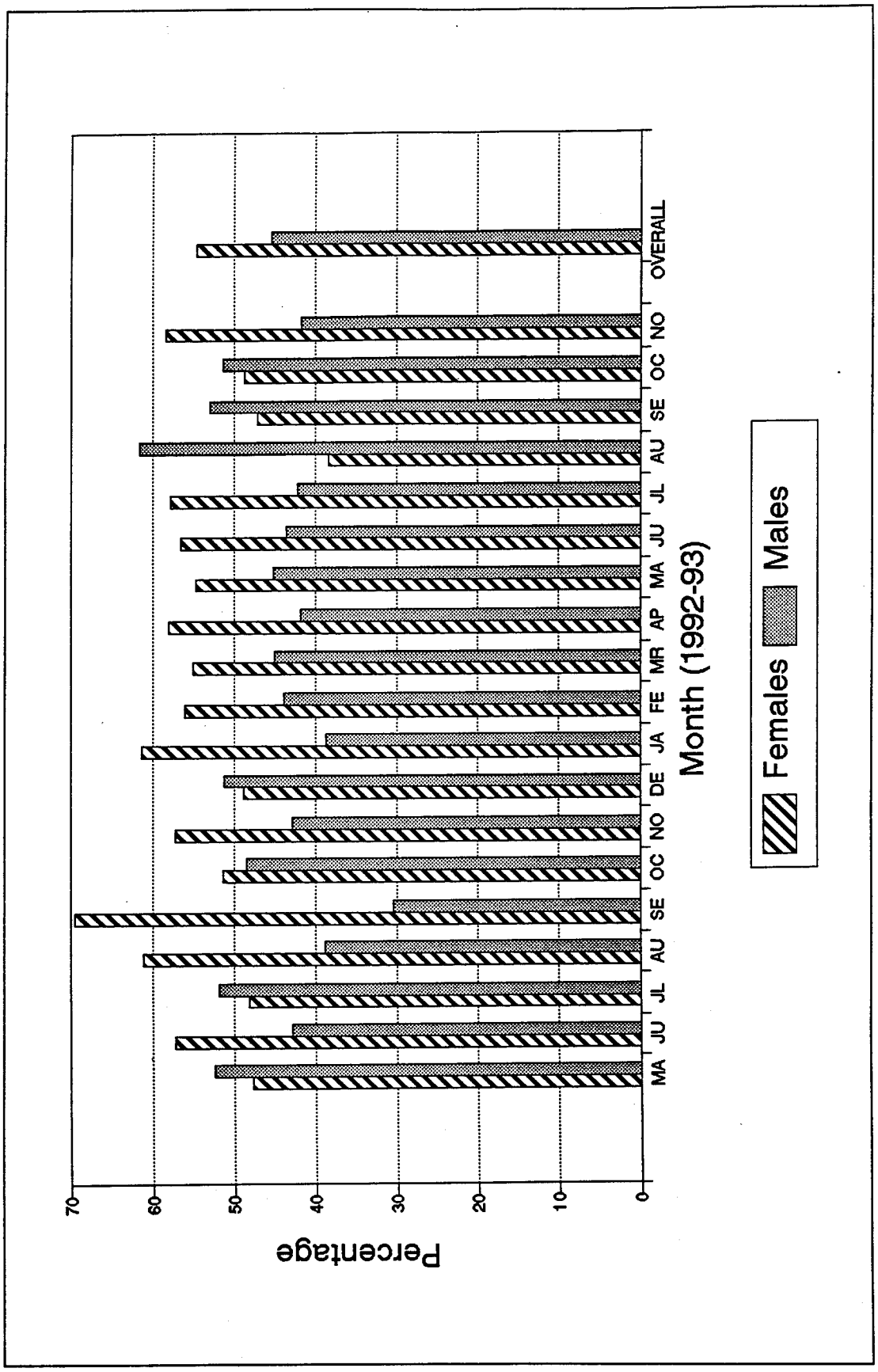

Figure 4. Relative proportion of female and male zebra mussels in monthly samples

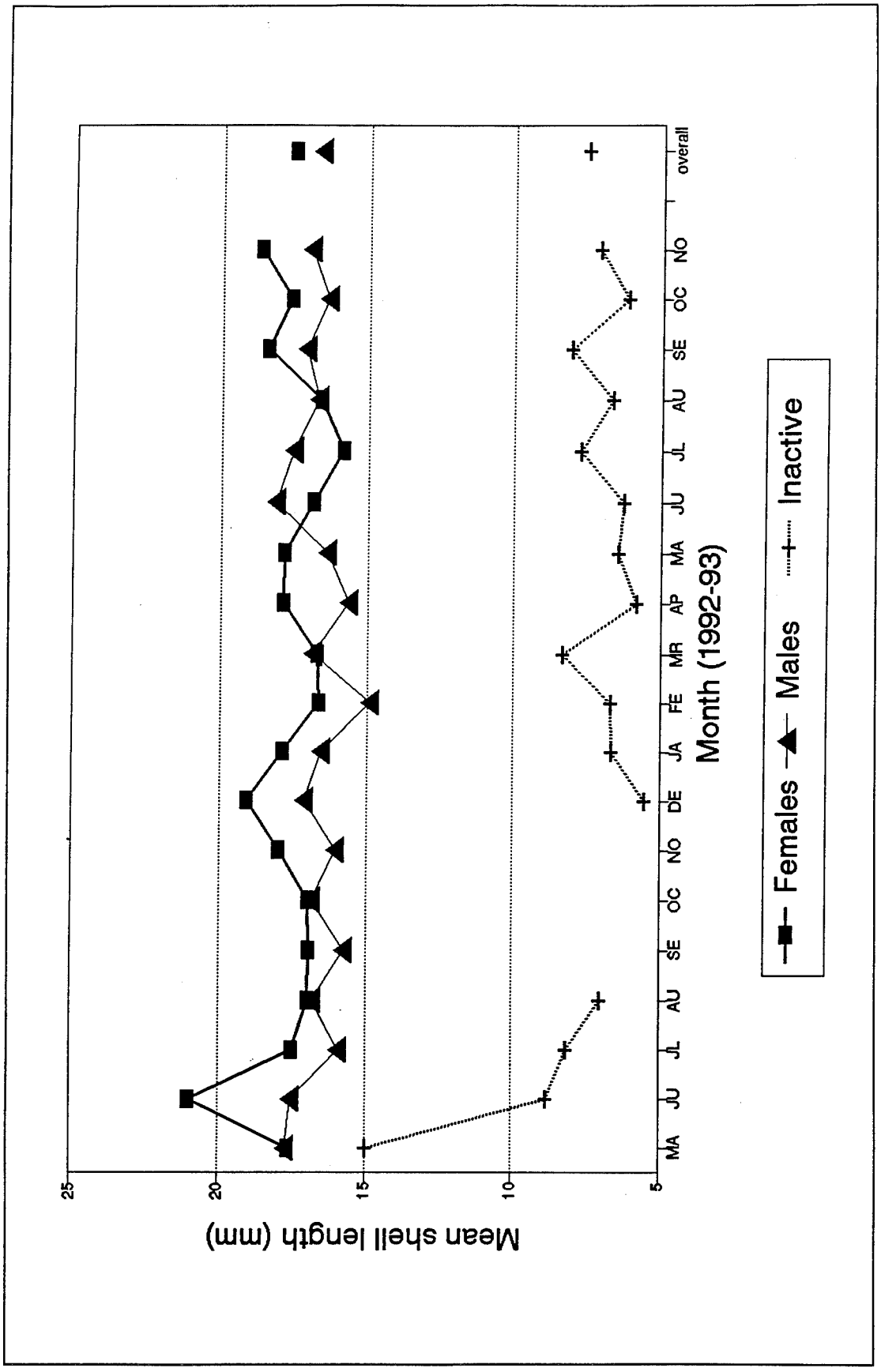

Figure 5. Monthly mean shell lengths of female, male, and inactive (juvenile) zebra mussels

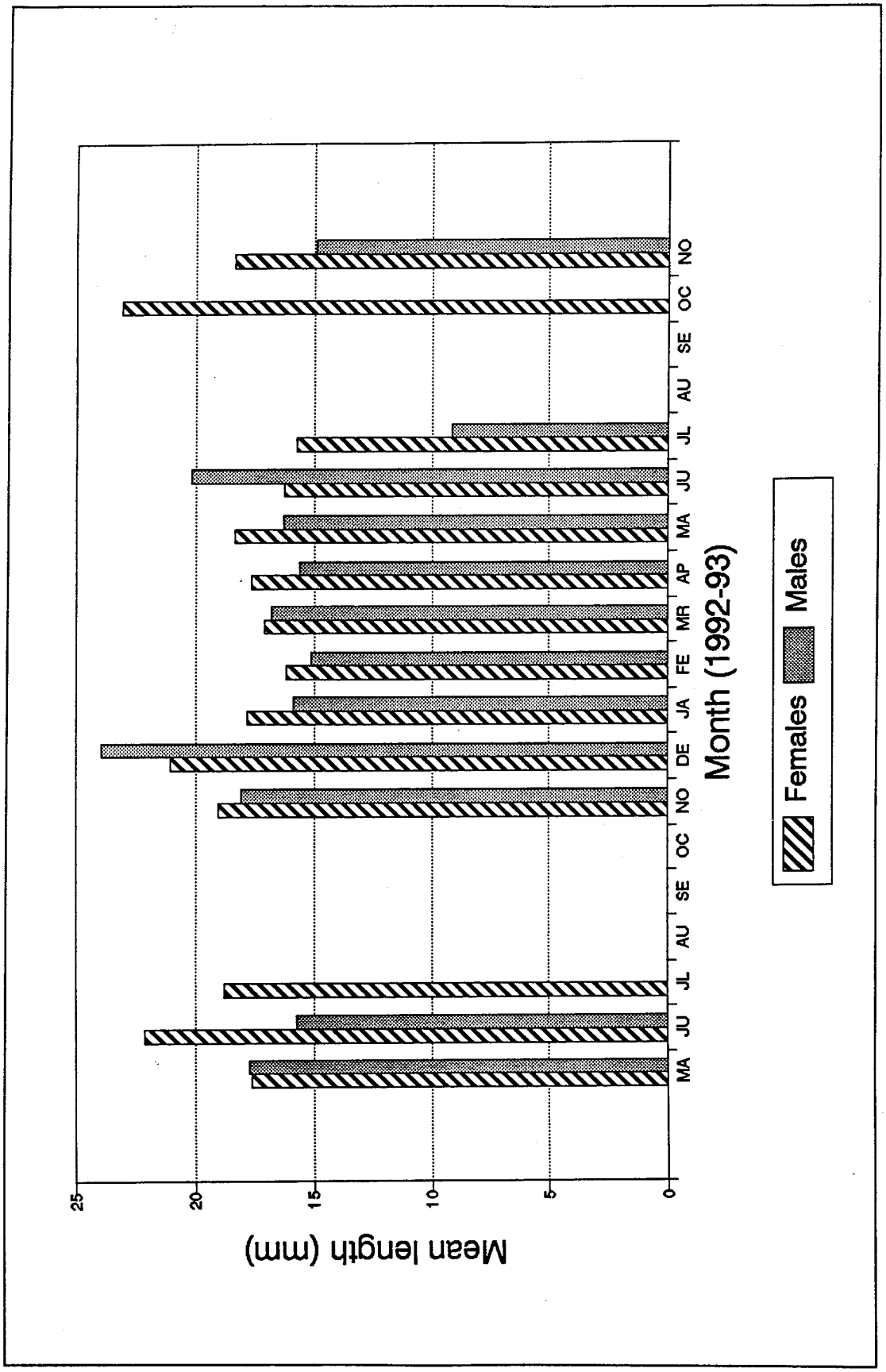

Figure 6. Monthly mean shell lengths of female and male zebra mussels with developing gametes

1993, followed by a mean length of 16.4 mm in June. When visible gametogenesis was reinitiated in October of 1993, the mean shell length of mussels with developing gametes had again increased, this time to a value of 23.1 mm. By November, this figure had decreased to 18.2 mm.

Differential timing of gametogenesis also occurred between the two sexes. Seventy-nine percent of the female mussels sampled in November 1992 showed evidence of development of ova, whereas only 22 percent of males show spermatozoal development (Figure 7). In December, 75 percent of females showed gamete development, while this was seen in only 19 percent of the males. Development of ova was seen in all females in January 1993, but spermatogenesis was apparent in only 47 percent of the males. This disproportionate pattern continued until April 1993, when the ratio of female to male zebra mussels showing gonadal development leveled off at approximately 1:1. At the onset of gametogenesis in the fall of 1993, the developmental difference between the two sexes of zebra mussels was even more pronounced. In October, 17 percent of female acini contained developing ova, while development of spermatozoa was entirely absent in males. By November, nearly 86 percent of females showed evidence of gametogenesis, as opposed to only 7 percent of males. It is obvious that gamete development occurs substantially earlier in females, beginning in the winter, while spermatogenesis generally does not occur until the spring.

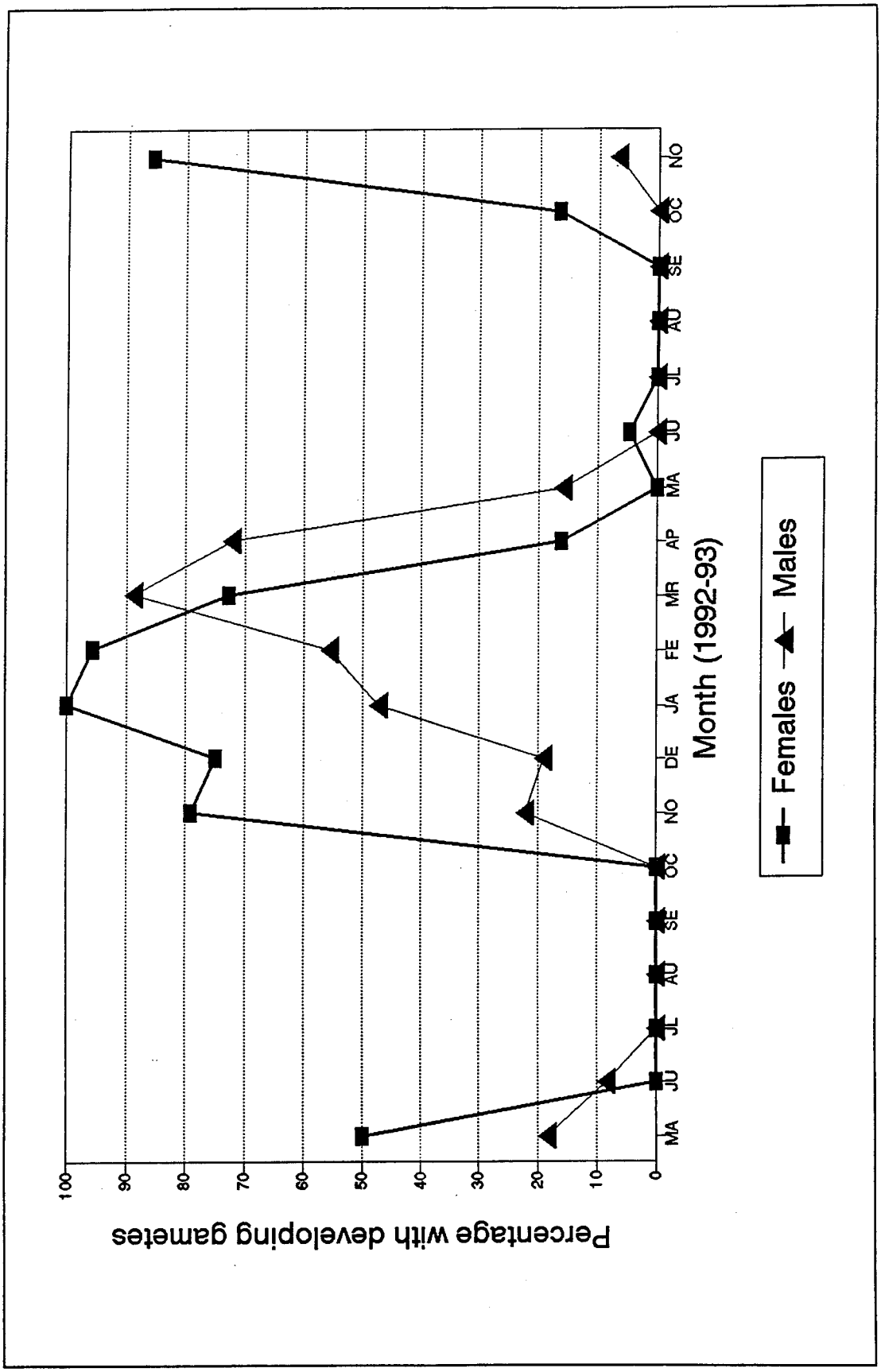

Figure 7. Relative proportion of female and male zebra mussels showing early gamete development over time

4 Discussion

The reproductive cycle of zebra mussels occurs practically year-round. As shown by these results, the reproductive season ends by October, but is reinitiated almost immediately. Early gamete development coincides so closely with the completion of the prior spawning season that acini containing both relict gametes from the previous year and newly synthesized ones for the new season are not uncommonly encountered. Year-round spermatogenesis and oogenesis have also been observed in *Anodonta imbecilis* (Heard 1975) and six species of *Elliptio* (Heard and Guckert 1970).

Spawning of zebra mussels from the Black Rock Lock does not occur in one coordinated event, but takes place intermittently over a period of approximately 2 months. Although a study by Haag and Garton (1992) found that spawning of a western Lake Erie population was a brief and highly synchronous occurrence, results from the present study and those of a number of others (Walz 1978; Mackie 1991; Neumann, Borcherding, and Jantz 1993; Sprung and Borcherding 1991) indicate that the more common pattern is for spawning to take place sporadically over a number of weeks. This type of pattern is probably advantageous to the zebra mussel population because intermittent spawning would greatly reduce the chance of catastrophic mortality because of some perturbation of the environment, as could more easily occur if there was only a single larval class. Further substantiation of sporadic spawning among zebra mussels is shown by the fact that the development of gametes within a given mussel is asynchronous. In a male, for instance, spermatocytes occur at the periphery of the acinus lumen, while spermatogonia are found farther toward the middle of the acinus, with mature spermatozoa ultimately occupying the very center of the acinus lumen. This shows that not all gametes within a zebra mussel reach maturity in unison, suggesting that release of gametes does not occur only once, but perhaps several times over the spawning season, which generally includes the months of August and September (Figure 1).

The timing of gamete development and spawning in zebra mussels has been shown to be influenced by ambient water temperatures (Neumann, Borcherding, and Jantz 1993; Nichols 1993; Sprung 1993). Water temperature readings taken at the time of collection of monthly samples show an inverse relationship with the percentage of zebra mussels from those samples containing developing gametes (Figure 8). During the coldest months of the year, development

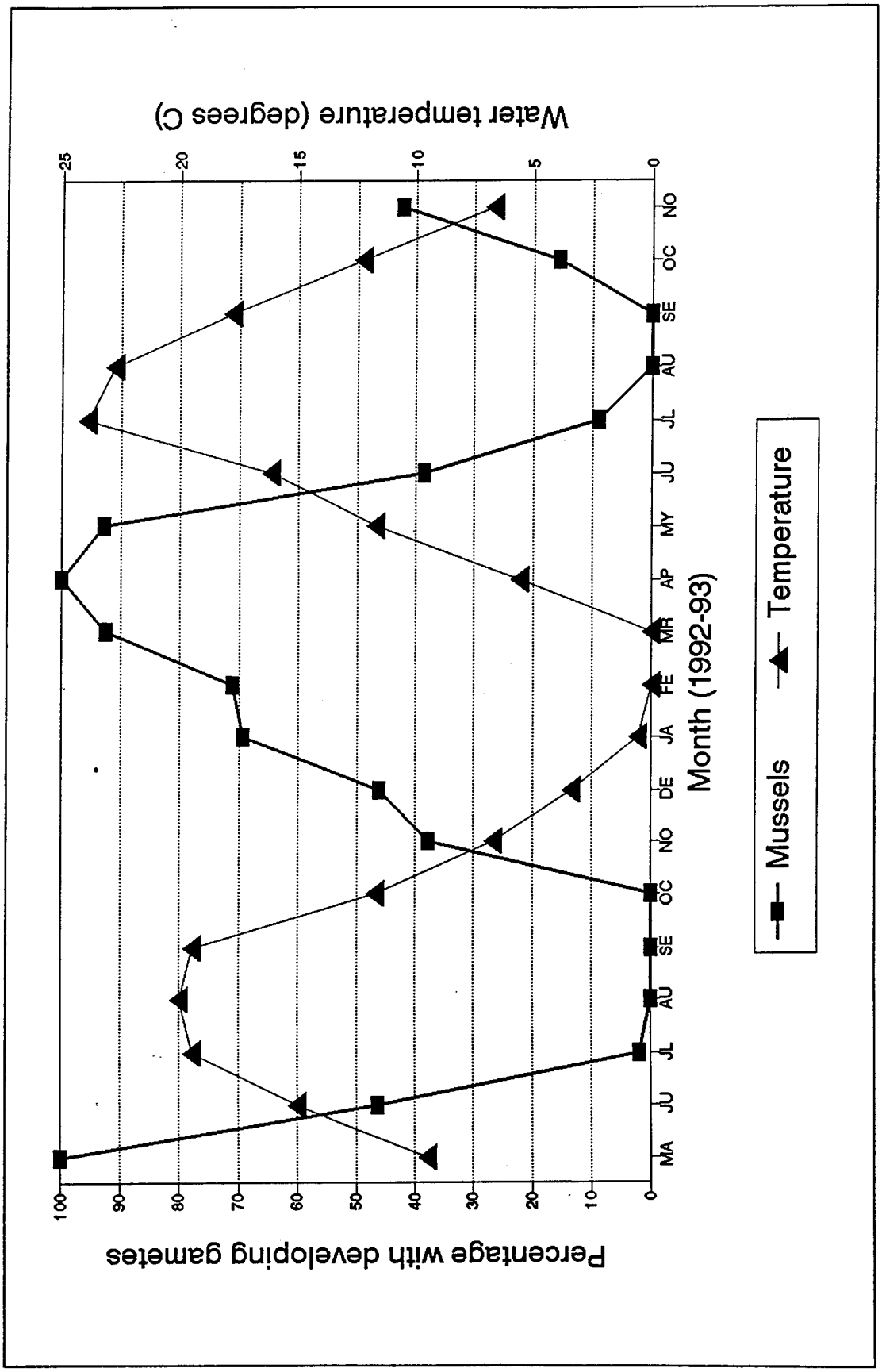

Figure 8. Percentages of zebra mussels sampled monthly showing gamete development in relation to ambient water temperature

of gametes takes place, with the reproductive cells reaching maturity as the water temperature increases in the spring. The cold-weather development of sex cells is probably necessary to allow the synthesis of the large portion of the soft body of zebra mussels, which is eventually comprised of gametes. Stored energy accumulated during the warmer months is probably utilized during the approximately 9 months of gamete development that occurs prior to spawning. The very large portion of the biomass of zebra mussels that is often made up of gametes suggests that such an extended period of development is necessary for maximum production of spermatozoa and, particularly, ova. It is likely that the maturation of gametes and the resulting spawning and development of embryos is timed to allow for growth and development of veligers during the warmer months when phytoplankton is abundant. Neumann, Borcherding, and Jantz (1993) found a similar pattern among zebra mussels from the Rhine River. Spawning of zebra mussels is also closely correlated with increasing water temperatures, as is shown in Figure 9. Threshold spawning temperatures of 12 °C (Sprung 1991; Neumann, Borcherding, and Jantz 1993; Sprung 1993) and 15 °C (Stanczykowska 1977; Mackie 1991) have been documented. Stanczykowska (1977) stated that the optimum spawning temperature based on numbers of ova released is 22 °C. The results of the present study agree with these findings. Spawning occurred in zebra mussels from the Black Rock Lock after temperatures reached approximately 12 °C. Peak numbers of spent zebra mussels were seen after water temperatures had reached the 20 to 22 °C range.

A 55 to 45 ratio of females to males, as seen in this investigation, is consistent with the results of other studies of zebra mussel reproduction (Walz 1978; Mackie 1991). It also agrees with various similar studies of other molluscs (Mackie 1984; Webber 1977). Both higher (Mackie 1993) and lower (Stanczykowska 1977) ratios of female zebra mussels to male zebra mussels have been found, however. The greater number of females than males in the zebra mussel population could be a reproductive advantage for these bivalves. A male zebra mussel contains several orders of magnitude more spermatozoa than the number of ova in a female. Despite the fact that the large majority of sperms are lost during spawning, only one spermatozoan is required for fertilization of each ovum. Research has shown that spawning in zebra mussels may be triggered by the release of gametes by nearby mussels (Nichols 1993). Since zebra mussels occur in dense aggregations, the availability of extruded sperm when spawning occurs among these colonies should not be a limiting factor. Consequently, greater natality might be possible in a population composed of more females than males than in one in which the ratio of sexes is 1:1.

One possible reason for the success zebra mussels have had as an invasive species in the United States is the early age of reproduction. Because they are able to reproduce at a small size, it is possible to have two spawning cycles in 1 year. Many mussels in the 5- to 10-mm size range were sexually mature in the present study. Those collected during the fall were likely to be offsprings of spawning that took place earlier that year (Mackie 1991; Smit et al. 1993).

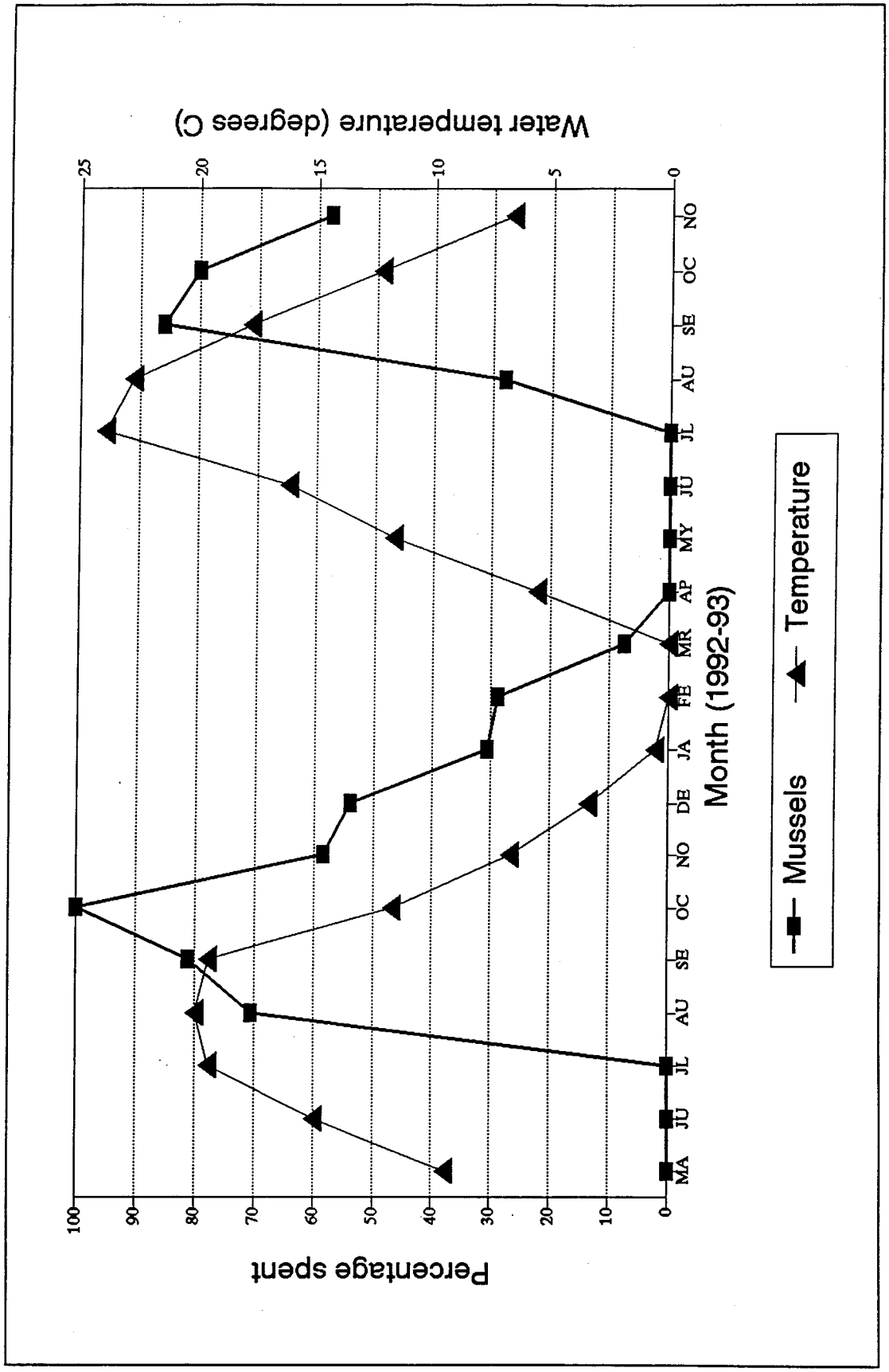

Figure 9. Percentages of zebra mussels sampled monthly in spent condition in relation to ambient water temperature

Many native unionid bivalves (e.g., *Tritogonia, Cyclonaias, Megalonaias,* and *Elliptio*), however, require 4 to 8 years of growth before sexual maturity is reached (Pennak 1978; Jirka and Neves 1992; Woody and Holland-Bartels 1993). This gives zebra mussels an obvious numerical advantage over their indigenous fellow bivalves. A zebra mussel might spawn several times before a native bivalve that was born during the same season reaches sexual maturity. This is likely one reason for the exponential population growth observed among zebra mussels in North America and their resulting strong negative impact on native unionids.

It was noted above that the seasonal initiation of gametogenesis occurred first in larger zebra mussels. It was also noted that, during times of the year when mature gametes were present, gonadal tissue usually made up a larger portion of the biomass of the larger mussels than the smaller ones. Although this study did not include a quantification of gamete production in individual *Dreissena polymorpha*, a strong positive correlation between shell length and relative gamete volume was readily apparent. The ability of large zebra mussels to quickly synthesize large quantities of reproductive cells could be due to greater stored energy reserves that are probably present in the larger mussels. Figure 6 shows that the mean shell length of zebra mussels showing early gamete development was greater in the early winter months of 1992 than in the months that followed. In January 1993, there was a decrease in the mean size of those showing signs of gametogenesis, but an increase in the number of mussels showing such signs. This corresponds to the initiation of gamete production in the more numerous smaller zebra mussels. In October and November of 1993, a similar pattern was observed. That is, signs of gametogenic activity were first discernible among larger mussels. Sastry (1975) found utilization of energy stored in the adductor muscles for the synthesis of gametes in *Aequipecten irradians* and that gametogenesis occurred earlier in larger scallops. In *Mytilus edulis*, lipid and glycogen stored in connective tissue were found to provide energy for gamete development (Chipperfield 1953).

Even more pronounced than the difference between large and small zebra mussels in regard to the initiation of gamete production is the difference between males and females. Ovogenesis consistently preceded spermatogenesis. The same kind of pattern has been noted by Haag and Garton (1992) and Garton and Haag (1993): immature ova became apparent during the winter, but development of spermatogonia was not seen until late spring. It is likely that the development of the larger, more complex ova takes longer than the development of the much smaller spermatozoa. Consequently, earlier initiation of ovogenesis must be an adaptation that allows for coincidental maturation of the two types of gametes.

The reproductive characteristics elucidated from the present study demonstrate a unified theme: enhancement of the reproductive output of zebra mussels. The most striking feature is the year-round nature of the effort. Gamete synthesis begins as soon as spawning has taken place during the fall. Another notable feature is the early age of reproduction. Some mussels as small as 5 mm in shell length are already reproductive. Since so much effort is

devoted towards reproduction, it is perhaps not surprising that zebra mussels are relatively small in comparison to other freshwater bivalves. Available energy is channeled toward reproduction with little devoted to somatic growth.

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13. ABSTRACT *(Maximum 200 words)*

Since its introduction into North America in the mid-1980s, the zebra mussel, *Dreissena polymorpha*, has caused serious economic and ecological problems, particularly in the Great Lakes region, because of its encrustation of both man-made structures and the exoskeleton of macroinvertebrates, most notably unionid bivalves. The present study seeks to thoroughly summarize the seasonal reproductive pattern of zebra mussels, as well as to delineate those aspects of reproduction that likely contribute to the considerable success of the zebra mussel as an epifouler and competitor with native bivalves. The reproductive status of approximately 48 individuals per month was determined by histological examination of the visceral mass from May 1992 through November 1993. Initiation of gamete development occurred in the early winter months (November in 1992 and October in 1993) and continued throughout the winter and into the following spring. Maturation of gametes took place in the late spring/early summer. Spawning began as early as May and continued until September. By October, any residual gametes were extensively degraded. Gametogenesis was resumed almost immediately. Female zebra mussels outnumbered males by a 55:45 ratio. No hermaphrodites were found. Zebra mussels as small as 4.58 mm in shell length showed evidence of gamete synthesis. Gamete development was apparent earlier in larger and/or female mussels.

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Development and spawning were closely correlated with seasonal changes in water temperatures. Results suggest that year-round reproduction, successive spawning episodes, and early reproductive age are important factors in the success of *D. polymorpha*. Consequently, interruption or alteration of factors related to reproductive efforts should prove to be important in future mitigation efforts.