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Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair

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Key words: Zebra mussel, *Dreissena*, biology, impact, exotic, Lake St. Clair, shell form, mode of life, reproduction, life cycle, population dynamics, dispersal, distribution, physiology, impact

Abstract

The zebra mussel, *Dreissena polymorpha*, is a new exotic species that was introduced into the Great Lakes as early as the fall of 1985. It differs markedly from native species of bivalves in its: (i) shell form; (ii) mode of life; (iii) reproductive potential; (iv) larval life cycle; (v) population dynamics; (vi) distribution, (vii) dispersal mechanisms; (viii) physiology; (ix) potential impact on the ecosystem; and (x) impact on society and the economy. In body form, it has an anterior umbone, a flat ventral surface with permanent aperture for the byssal apparatus and a shape that together make the animal well adapted for life on a hard surface. The shell has a zebra-stripe pattern, a heteromyarian muscle condition and lacks hinge teeth which make it easily identifiable from native bivalves. The zebra mussel is strongly byssate and has an epifaunal mode of life not seen in native bivalves. The species is dioecious and has external fertilization, the eggs developing into pelagic veligers which remains planktonic for approximately 4 weeks. Gametogenesis begins in late winter to early spring, veligers appear in the water column in late May to early June and disappear in mid to late October in Lake St. Clair. Adults live for about 2 years and have very rapid growth rates. Maximum shell lengths average 2.3 to 2.5 cm. Standing crops as high as $200\,000\text{ m}^{-2}$ are present in the 1-m depths of the Ontario shores. Infestations may be interfering with the normal metabolism of native unionid clams and there is potential of the unionid clam populations being reduced or even eliminated from Lake St. Clair.

1. Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas) was introduced into Lake St. Clair probably in 1985 (Hebert *et al.*, 1989). The species is native to Europe and appears to have been transported to Lake St. Clair in the freshwater ballast of a trans-oceanic ship. Until recently, ships have been discharging some of their ballast water into the Great Lakes and released either veliger larvae or young adults into Lake St. Clair. Adult shells about 2 cm

long were first found in August 1988, near Belle River in Lake St. Clair (Hebert *et al.*, 1989). Assuming it takes the species about 2 years to grow to 2 cm, it is most likely that the species was introduced in either the spring or summer of 1986 as young adults or in the summer or fall of 1985 as veliger larvae. Since adults are benthic and larvae are pelagic, and ships normally take on ballast water from the pelagic zone, the species was probably introduced as veliger larvae in the summer or fall of 1985. The species was not found

in an extensive benthic survey in 1983 (Griffiths, 1987) or in an extensive unionid clam survey in 1986 (Tom Nalepa, U.S. Fish and Wildlife, pers. comm.). However, the numbers and sizes of adults of the pioneering population were probably so small that they could easily have been missed in their surveys.

Dreissena polymorpha differs from native species of bivalves in: (i) shell form; (ii) mode of life; (iii) reproductive potential; (iv) larval life cycle; (v) population dynamics; (vi) distribution; (vii) dispersal mechanisms; (viii) physiology; (ix) potential impact on the ecosystem; and (x) impact on society and the economy. This paper describes the most outstanding features in zebra mussels for each of these eleven attributes. The features are compared to native species of bivalves in the families Sphaeriidae and Unionidae in general, and to the Asian clam, *Corbicula fluminea*. The Asian clam is another exotic bivalve that was introduced to North America in the early 1930's in California (see Britton & Morton (1979) and McMahon (1982) for reviews). It has since spread throughout the United States but has not succeeded in invading the Great Lakes, although it has been found in warm water plumes of hydrogenerating plants or as small, somewhat benign populations in Lake Erie (Clarke, 1981; Scott-Wasilk *et al.*, 1983), Lake Michigan (White *et al.*, 1984) and the St. Clair River (French & Schloesser, 1991). Asiatic clams belong to the family Corbiculidae and are related to the native Sphaeriidae, both being of the superfamily Corbiculacea (Mackie, 1990). The comparisons between zebra mussels and other bivalves clearly demonstrate why the zebra mussel will probably become the dominant bivalve in Lake St. Clair, and in the Great Lakes.

2. Descriptions

2.1. Shell form

The shell of *D. polymorpha* is distinctive (Fig. 1a, b). The common name, zebra mussel, is derived from the pattern of zebra stripes on the

shell and the scientific name, *polymorpha*, refers to the many morphs or forms that occur in the shell's colour pattern, including albino and solid black or brown. In spite of the variability in shell morphs, there are some significant functional, diagnostic features in external and internal shell morphology.

Externally, the umbone of the zebra mussel is acute and lies anterior in position (Fig. 1a). The ventral side of the shell is flattened and has a permanent opening through which the byssal apparatus extends. The shell is medium-sized, averaging 2.3 to 2.5 cm maximum length in Lake St. Clair. The shell shape is perfectly adapted to life on hard substrates: (1) The flat ventral surface allows the animal to be pulled tightly against the substrate by its byssal apparatus, making it difficult for predators to pry the shell from the substrate. (2) The umbone is lateral and adjacent to the substrate, giving the animal maximum upright stability at the surface of the substrate. (3) The shell is tapered dorsally (tent-shaped) making it difficult for predators to get a firm hold to pull the shell from the hard surface.

In other bivalves (see Clarke, 1973 for general reviews), the umbone is rounded and dorsal in position (Fig. 1c-h) and adapted for an infaunal life within sediments. The ventral margin is also rounded and lacks a permanent opening because adults do not have a functional byssal gland. *Corbicula* is medium-size, averaging 3 to 4 cm shell length (Fig. 1c, d) but has yet to be recorded from Lake St. Clair. The shell is glossy and has heavy, evenly-spaced ridges (Fig. 1c). Sphaeriids are small, averaging 5 to 8 mm shell length (Fig. 1e, f), and the shells are thin and fragile. Unionids are large, averaging about 10 cm shell length (Fig. 1g, h) and the shells are typically thick and robust.

Internally, the shell of the zebra mussel lacks cardinal and pseudocardinal teeth (Fig. 1b) but a vestigial lateral tooth may be present (Fig. 1b). The ligament is internal, anterior, and sunk in an elongated pit alongside the vestigial lateral tooth (when present). The umbonal end of the shell bears an apical septum or myophore plate (Fig. 1b) to which attaches the small anterior adductor muscle. The posterior end of the shell

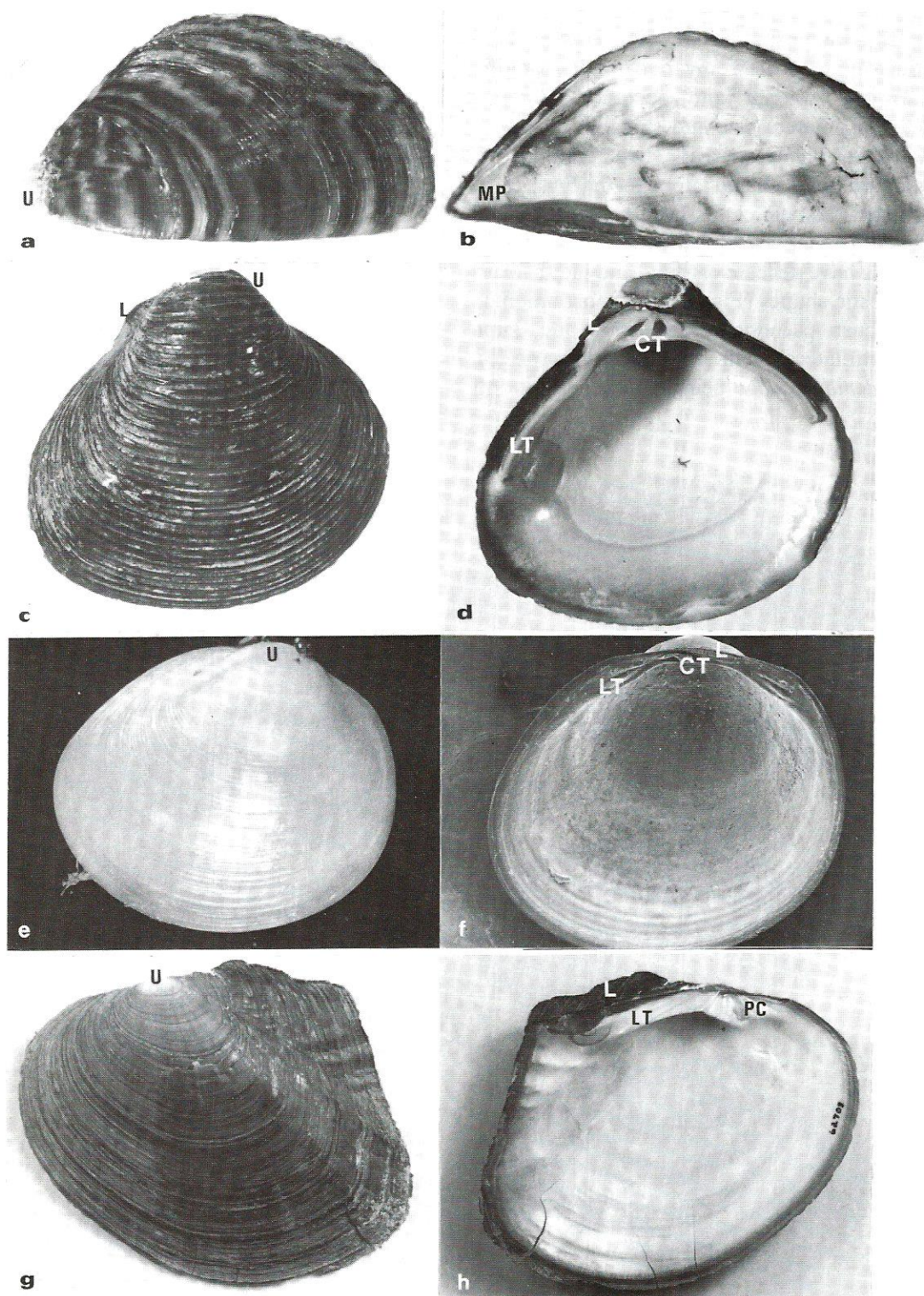


Fig. 1. External (a, c, e, g) and internal (b, d, f, h) features of shells of typical species in four families of bivalves in the Great Lakes. (a, b) Dreissenidae: *Dreissena polymorpha* from Lake St. Clair, shell 2 cm long. (c, d) Corbiculidae: *Corbicula fluminea*, another biofouling bivalve in North America, but not presently in Lake St. Clair, shell 3 cm long. (e, f) Sphaeriidae: *Pisidium lilljeborgi* shown, shell 2 mm long. (g, h) Unionidae: *Lasmigona complanata* shown, shell 9 cm long. CT = cardinal tooth; L = ligament; LT = lateral tooth; MP = myophore plate; PC = pseudocardinal tooth; U = umbone.

bears a large posterior adductor muscle scar, demonstrating the heteromyarian condition of the species (i.e. anterior and posterior adductor muscles of different size and shape).

In other bivalves, distinctive cardinal or pseudocardinal teeth and lateral teeth (Figs. 1f, h) are present; Asiatic clams have heavy triradiate cardinal teeth and serrated lateral teeth (Fig. 1d), sphaeriids have delicate cardinal and lateral teeth of diagnostic shapes (Fig. 1f), and most unionids have robust pseudocardinal teeth and large lamelliform lateral teeth (Fig. 1h) (some species, like *Anodonta grandis*, being an exception). All

native bivalves and *Corbicula* have an external ligament, all lack a myophore plate and all are isomyarian, as indicated in the similar sizes and shapes of the scars for the anterior and posterior adductor muscles.

2.2 Mode of life

Dreissena is epifaunal, living byssally attached to all types of solid substrates, including rocks, floating and sunken logs, breakwalls, and various debris. They also attach to large, living inverte-

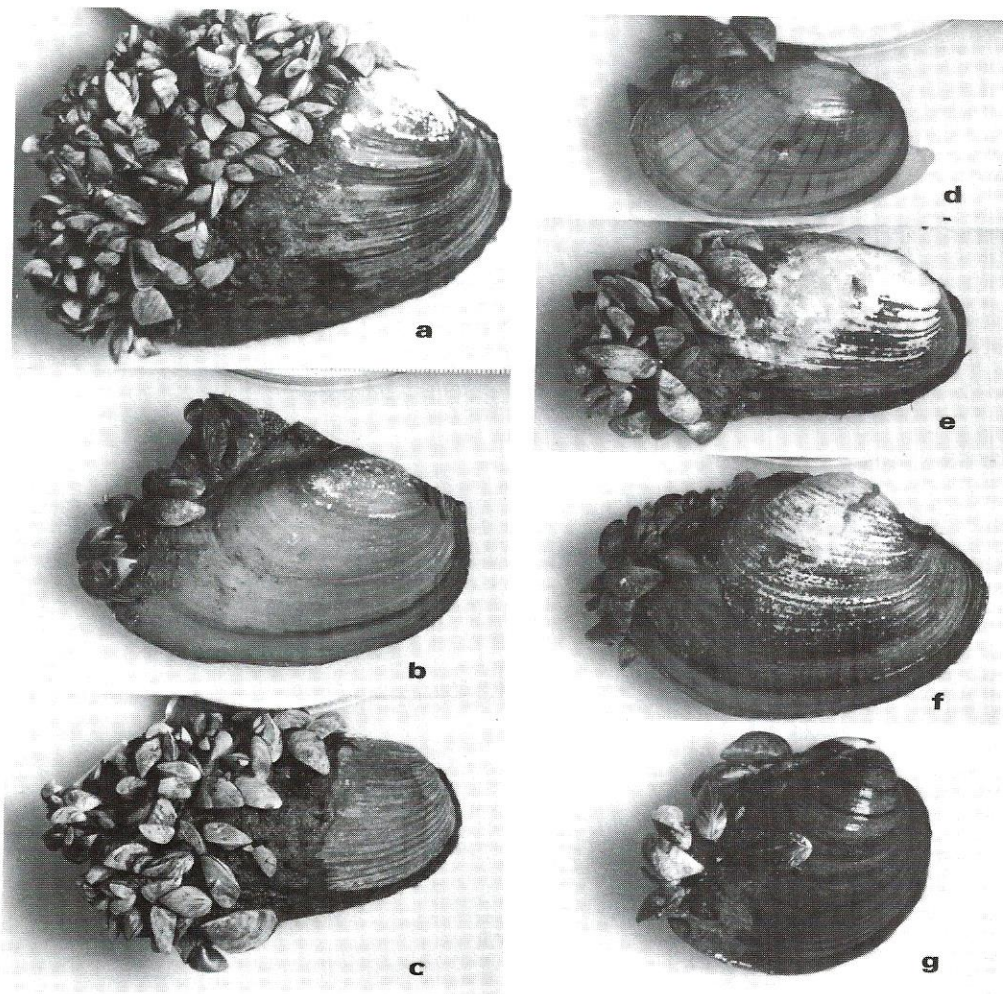


Fig. 2. Species of unionid clams from Lake St. Clair encrusted with zebra mussels. (a) *Proptera alata*; (b) *Lepodea fragilis*; (c) *Elliptio dilatata*; (d) *Lampsilis radiata siliquoidea*; (e) *Actinonais carinata*; (f) *Strophitus undulatus*; (g) *Pleurobema coccineum*.

brates such as unionid shells (Fig. 2) and crayfish. All other bivalves are infaunal, either living buried in the sediments or living at the mud-water interface partially buried in the sediments. Although unionid clams are infaunal and occupy an entirely different niche than zebra mussels, the unionids are ideal substrates for zebra mussels to colonize. Typically, only the posterior third to half of the unionid shell projects above the surface of the substrate while it is siphoning for respiratory and feeding purposes. Hence, only the posterior part of a unionid shell is usually colonized by zebra mussels (Fig. 2). The densities of zebra mussels on unionid shells is highly variable (Fig. 12), but in 1989 averaged nearly 300 per unionid shell throughout Lake St. Clair. This is an order of magnitude higher than first reported in 1988 by Hebert *et al.* (1989). However, densities as high as 10 000 (D.W. Schloesser, U.S. Fish and Wildlife, per. comm.) and 15 000 (P.D.N. Hebert, University of Windsor) have been reported on some unionid shells in Lake St. Clair. All other freshwater bivalves, including *Corbicula*, are infaunal and typically live within the substrate or at the mud-water interface. Some species exhibit substrate preferences (e.g. *Musculium transversum* (Gale, 1969)), but most occur in a variety of substrate types, the particle sizes ranging from mud to coarse gravel. A few species (e.g. *Sphaerium fabale*, *Pisidium fallax*) also prefer to live in rivers and streams with some current. Currents may affect the shell shape of some species of bivalves (Bailey *et al.*, 1983; Mackie & Topping, 1988).

2.3. Reproductive potential

Zebra mussels are dioecious. Based on histological examinations of 40 specimens selected at random, the sex ratio of zebra mussels in Lake Erie is about 3 females: 2 males. Gonads are ripe at least by the first week of May (based on specimens first collected on May 2, 1988; Fig. 3a, b), indicating that gametogenesis begins in early spring, or perhaps even late winter. However, veligers do not appear in the water until the end of May to the first week of June (Fig. 3b, c show-

ing partially spent gonads), indicating that gametes are not released immediately. The water temperature was 15 °C when larvae were first seen in Lake St. Clair. The temperature threshold for reproduction in Polish populations of zebra mussels is 15 to 17 °C (Stanczykowska, 1977).

The eggs are 30 to 50 μ dia. According to Stanczykowska (1977), zebra mussels have exceedingly high fecundities, ranging from about 30 000 per female in their first year of sexual maturity to 40 000 in their third and fourth years. Oogenesis and spermiogenesis appear to occur at about the same time. In Lake St. Clair, most zebra mussels are sexually mature by the time they reach 8 to 10 mm shell length; a few mature at even 5.5 mm shell length (Gillis, 1989). Peak reproduction normally occurs in July and August, as indicated by the large proportion with partially spent gonads (Fig. 3e, f). Since most larvae are born in July and August and settle in August and September, most adults do not attain reproductive size until the following year. Only those born in June and July and grow quickly to reproductive size (8 to 10 mm) by August or September can reproduce in the same year of birth. Gametogenesis ceases in September, as indicated by the spent condition of the gonads in all length classes (Fig. 3g, h). Fertilization is external and occurs in the water (Franzen, 1983; Sprung, 1987).

The Corbiculacea are monoecious, the Sphaeriidae being simultaneous hermaphrodites (Mackie, 1990) and *C. fluminea* being dioecious or monoecious in lentic waters (Morton, 1983) and female or monoecious in lotic waters (Morton, 1986). The Unionidae are mostly dioecious, some species capable of developing hermaphroditism in a few individuals (Mackie, 1984).

Internal fertilization is used in all native species of bivalves and in *Corbicula*. However, in *Corbicula* the fertilized eggs are quickly released as trochophores and veligers. In native bivalves, the fertilized eggs are brooded for several months (see larval life cycles below). Since only a small number of larvae can be brooded by any one parent, the number of larvae that are produced is rather small. Hence, external fertilization and

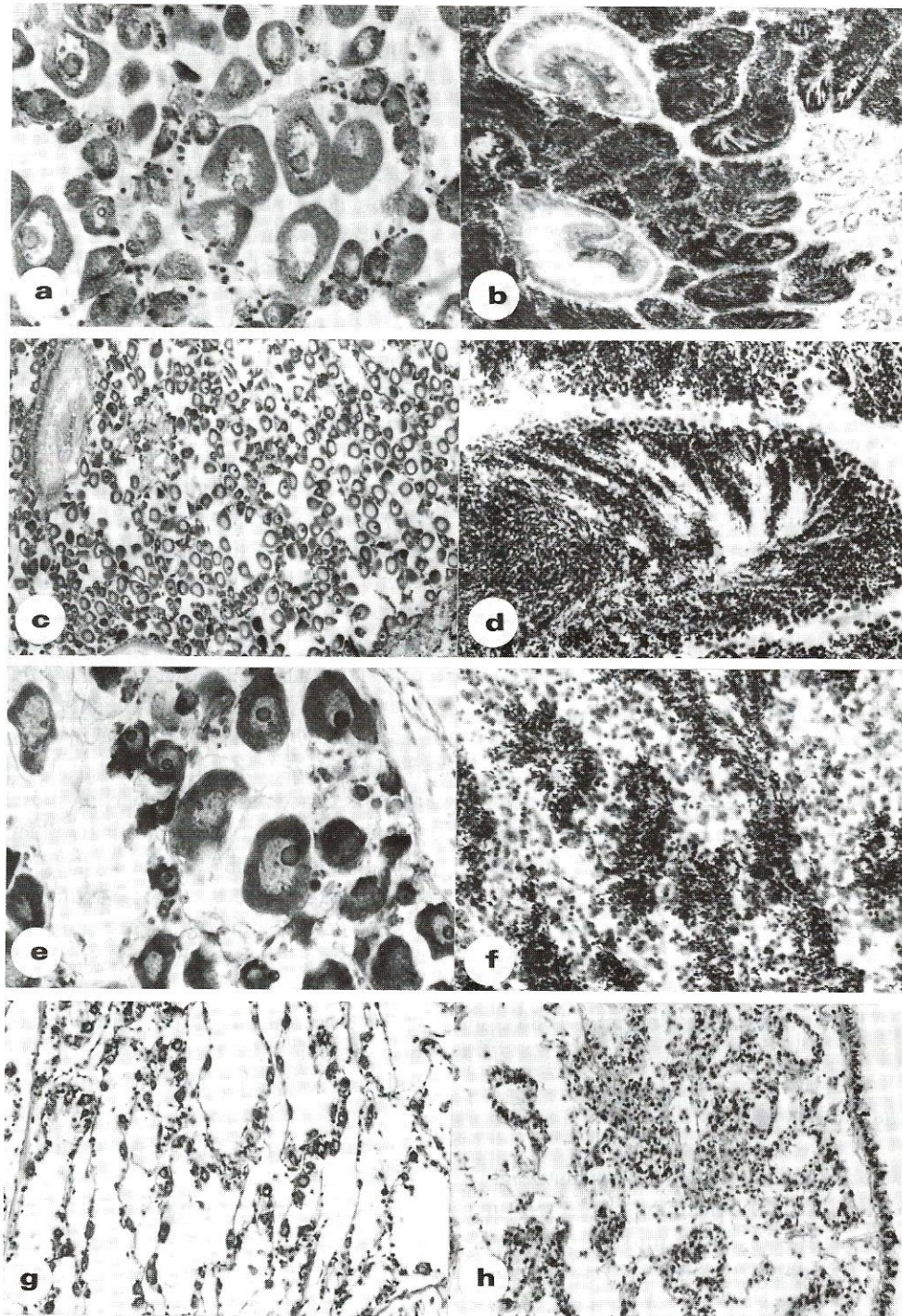


Fig. 3. Gametogenesis in *Dreissena polymorpha*. (a, b) May 2, 1989: (a) ripe female 10.0 mm shell length, 400 \times ; (b) ripe male 12.0 mm shell length, 40 \times . (c, d) May 28, 1989: (c) ripe female 10.8 mm shell length with some spent follicles, 200 \times ; (d) ripe male 10.1 mm shell length, 100 \times . (e, f) August 8, 1989: (e) partially spent female 13.0 mm shell length, 400 \times ; (f) partially spent male 14.7 mm shell length, 200 \times . (g, h) September 22, 1989: (g) spent female 17.8 mm shell length, 400 \times ; (h) spent male 14.4 mm shell length, 100 \times .

development partly explains why *Dreissena* will be much more prolific than native species of bivalves in North American surface waters.

Corbicula displays as great as, or even a greater, fecundity than *Dreissena*, with 25 000 to 75 000 veligers produced in the lifetime of a single clam (Aldridge & McMahon, 1978). Native species of Sphaeriidae, on the other hand, have very low fecundities (e.g. 1–40 eggs adult⁻¹) because they are brooders (Mackie, 1990). Unionidae have exceedingly high fecundities, with up to 2 000 000 glochidia produced by some females (Ellis, 1978), but mortalities are equally as high with only a few glochidia (1 in 10 000) developing and surviving to adulthood. The high reproductive capacities of

the two exotic species also explains in part their success in North American surface waters.

2.4. Larval life cycle

The larval life cycle of *Dreissena* usually takes about four weeks to complete (Stanczykowska, 1964, 1977; Morton, 1969; Wiktor, 1969; Mackie *et al.*, 1989; Hopkins, 1990). Three stages are recognized (Fig. 4a) – a veliger stage; a post-veliger stage; and a settling stage. Each stage can be identified by certain forms. Veligers are identifiable by the presence of tuft of cilia, called the apical tuft. A 'D'-shaped, bivalved shell is

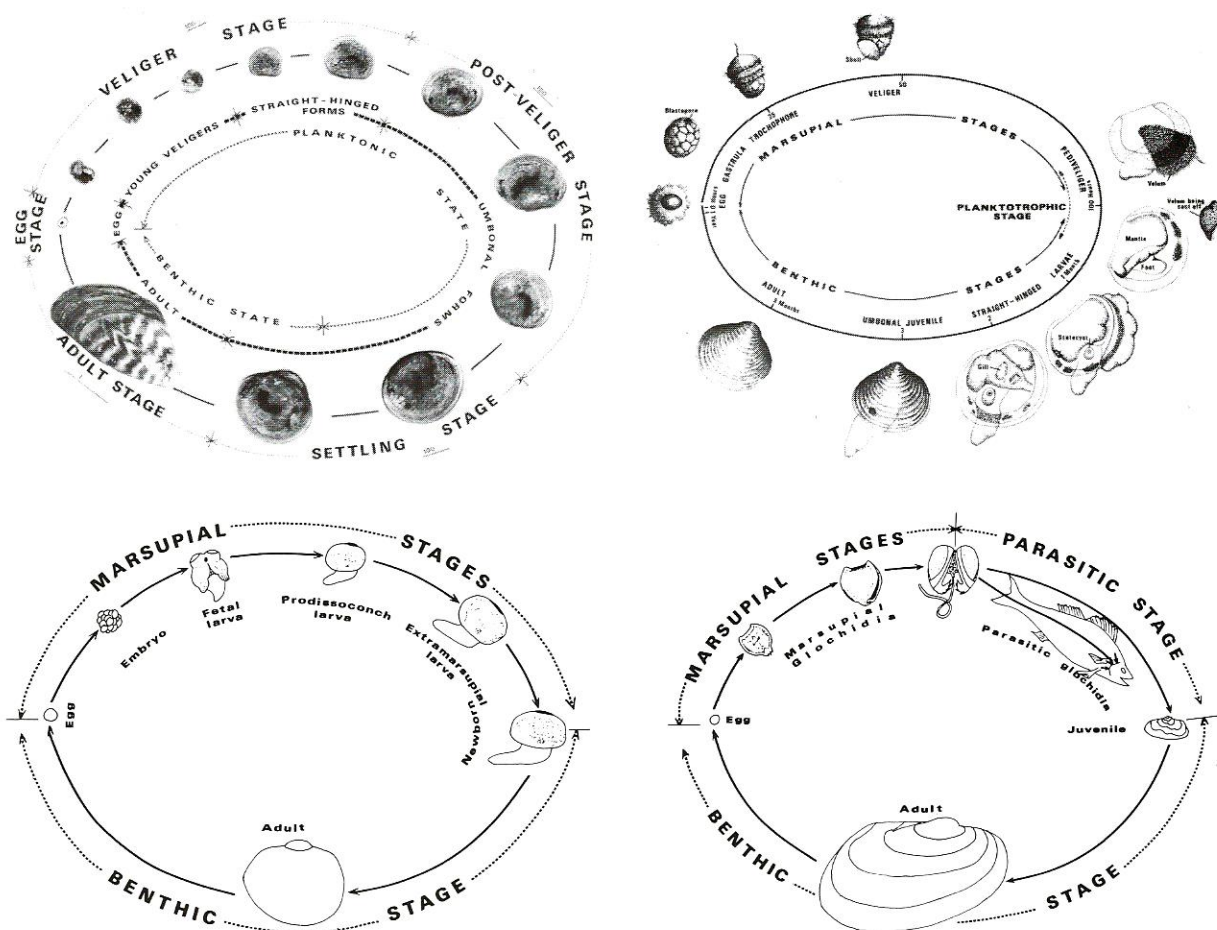


Fig. 4. Life cycles of four groups of bivalves in Lake St. Clair: (a) *Dreissena polymorpha*, times of development for each stage are unknown at present; (b) *Corbicula fluminea*; (c) Sphaeriidae; (d) Unionidae.

formed as soon as the egg hatches. The veliger takes on a sphaerical shape as the shell develops (Fig. 4a). Straight-hinged forms are also part of the veliger stage because the velum is well developed and is not reduced in size or function until an umbone starts to form. The umbonal forms mark the beginning of several anatomical changes. Most notable are the reduction of the velum which becomes the siphons, lengthening of the foot and development of blood and some organ systems. With the loss of the velum the post-veliger larvae enter the settling stage. By the time the umbonal forms settle the byssal gland is completely functional and the young mussel attaches itself immediately to a firm substratum. All three stages occur in the *planktonic state*. Once the young mussel attaches itself to the substrate it becomes an adult and enters the *benthic state*.

The life cycle of *C. fluminea* (Fig. 4b) is similar to that of *D. polymorpha*, but the larval stages are planktonic for only a few days. After about 100 hrs, pediveligers lose the velum, the larvae begin to settle out as straight-hinged forms and take up a benthic existence (Kraemer & Galloway, 1986). A single byssal thread is secreted during the umbonal stage but is soon lost. The byssal gland becomes non-functional by the time the clam is a young adult.

The Sphaeriidae clams are ovoviviparous (Mackie, 1978) and brood their young in brood sacs on the inner gill of the parent (Fig. 4c). Four marsupial stages are recognized (Figs. 4c, 5): (i) Embryos first appear as gastrula in single-walled primary sacs; (ii) the embryos develop most of the organ systems and mature through the fetal larvae stage to the shelled prodissococonch stage within brood sacs. (iii) The prodissococonch larvae grow in size to become extramarsupial larvae which are so large they outgrow their brood sacs, tear the sac wall and eventually come to lie free in the inner gill space. The extramarsupial larvae are born through the excurrent siphon and begin a benthic existence as newborn. Complete larval development requires 1 to 3 months, depending on species. Details on larval development in both *Corbicula* and the Sphaeriidae can be found in Mackie (1990)

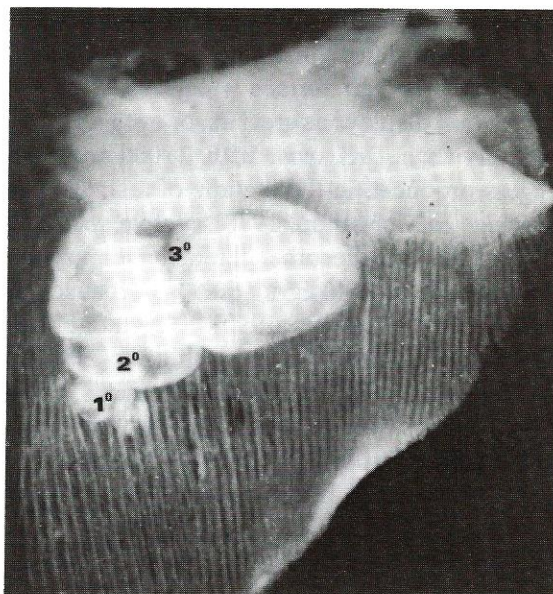


Fig. 5. Brood sac development on the inner gill of a typical sphaeriid, *Musculium securis*. Three stages are shown; the small primary sac (1°) contains embryos; the middle secondary sac (2°) contains fetal larvae; the large tertiary sac (3°) contains prodissococonch larvae. A fourth stage, the extramarsupial larvae which tear themselves free of tertiary brood sacs, is not shown.

The Unionidae clams have still another type of life cycle (Fig. 4d). They are the only freshwater bivalves that have a parasitic larval stage, called a glochidium. The glochidia develop in the gill marsupia for about 9 to 10 months, with 1 000 000 to 2 000 000 glochidia brooded (Ellis, 1978). The glochidia are released through the excurrent siphon in the spring or summer, depending on the species, to enter their parasitic stage. Clouds of glochidia are released when an appropriate fish species passes by. Opercular respiratory movements of the fish draw most of the glochidia into their gill cavity. The glochidia enter the gill tissue, live as parasites on fish blood, develop all the essential organ systems in about one month, enzymatically break free of the gill filaments and then drop to the bottom to begin a benthic existence.

The ovoviviparous and brooding habits of native sphaeriids is clearly less productive than the oviparous habit of zebra mussels. Although

unionids produce millions of glochidia, the larval life cycle is not as efficient as that of the zebra mussel. The enormously high productivity of zebra mussels also partly explains why zebra mussels will become the dominant bivalve in Lake St. Clair.

2.5. Population dynamics

Adults of shell lengths exceeding 8 to 9 mm are reproductively mature by early May and contribute to the newly settled populations in June (Fig. 6, June 27). Larvae that were born late the

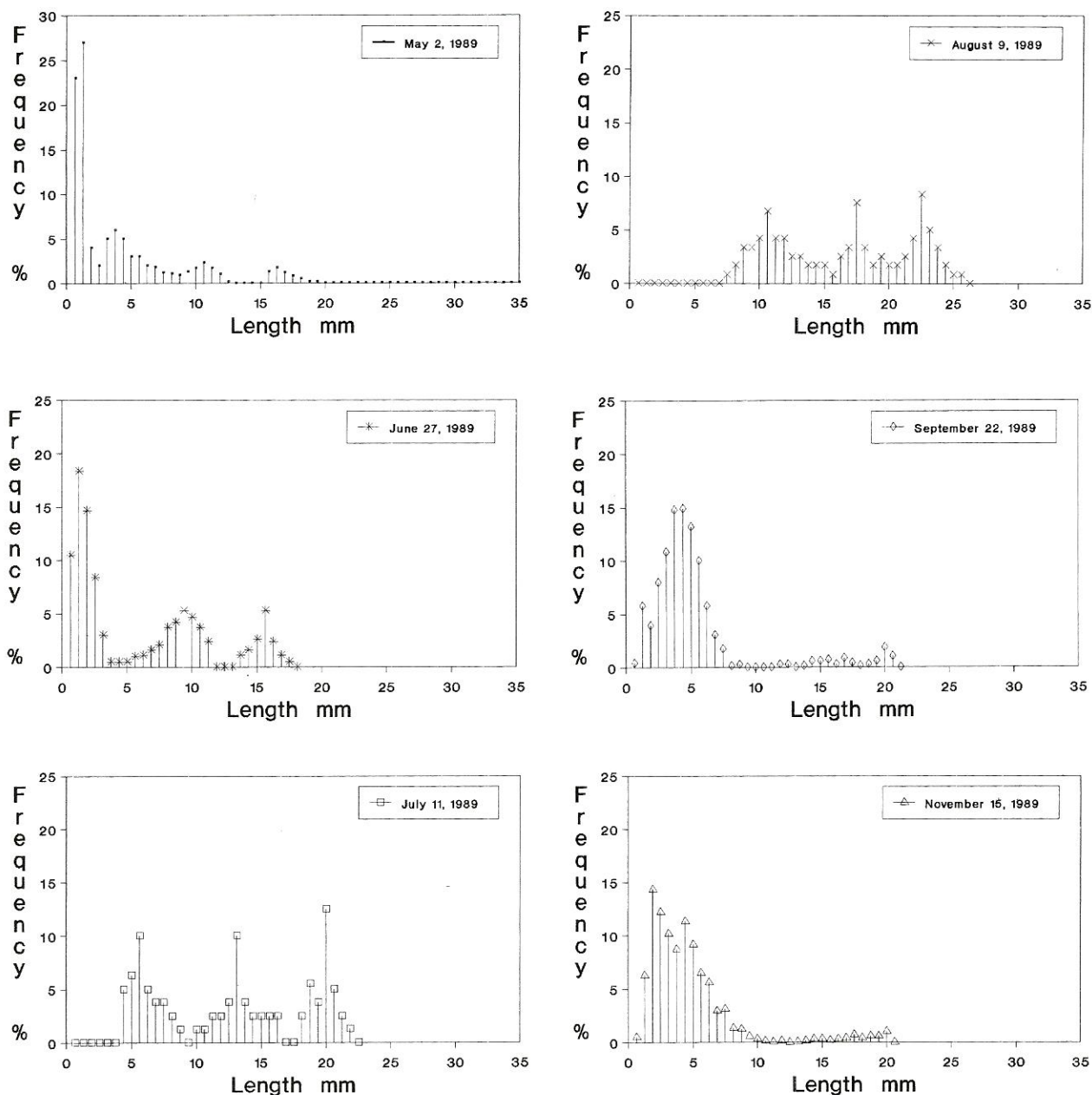


Fig. 6. Length frequency histograms depicting the length class distribution of *Dreissena polymorpha* in Lake St. Clair at Puce, Ontario in spring, summer and fall of 1989.

previous year (e.g. 1988) overwinter as young adults and vary in size between 1 and 4 mm (Fig. 6, May 2). These adults, and those born in late May to June (Fig. 6, June 27), attain a shell length of 15 to 20 mm by the end of the year, as shown by following the growth of mussels on cement blocks and by plotting mean sizes of each cohort (Fig. 7). By the summer or fall after their year of birth (e.g. 1989), all adults are reproductively active and contribute to the veliger population. Some adults that are born in late spring or early summer appear to grow and mature quickly during increasingly warm temperatures and contribute to the veliger population along with those adults born in the late fall of the previous year (Fig. 6, November 15). Hence, there are two periods of reproduction each year, as shown in the length-frequency distributions, once in the spring between May 2 and June 27 and again in the fall between September 22 and November 15 (Fig. 6). The growth rate of adults can be exceedingly fast, as much as 0.5 mm d^{-1} , as measure-

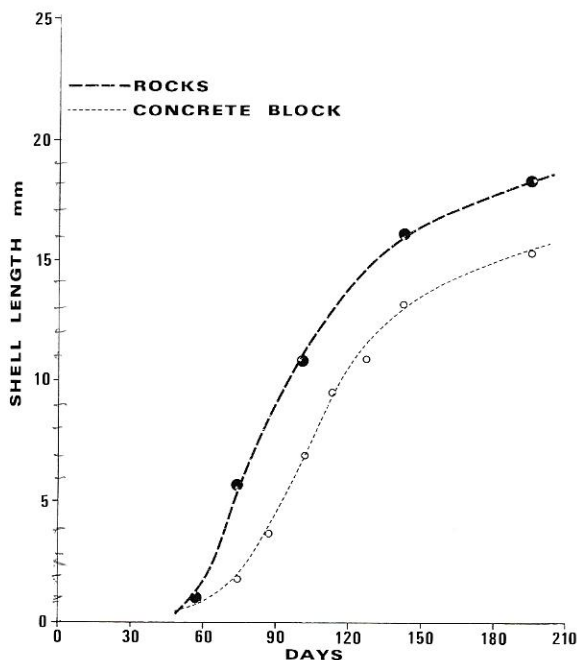


Fig. 7. Growth rates of *Dreissena polymorpha* as determined from plots of mean lengths of cohorts from Fig. 6 and from measurement of adults collected from cement blocks placed in Lake St. Clair in early May, 1989.

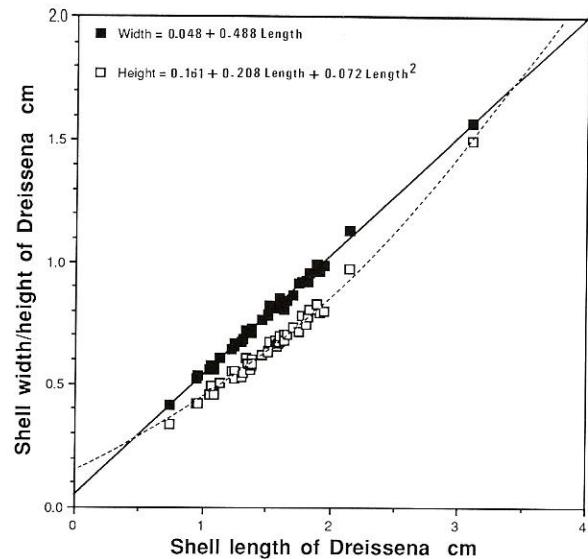


Fig. 8. Allometry of shell growth in *Dreissena polymorpha* in Lake St. Clair.

ments of adults on artificial substrates (cement blocks) in Lake St. Clair have shown. Typically, however, adults grow 1.5 to 2.0 cm y^{-1} . Most adults attain 1.5 cm shell length by the fall (Fig. 6). In the second year a few grow to exceed 3 cm in shell length. Most adults appear to die after 2 years of age (Fig. 6, September 22).

The allometric relationships between length, width and height of the shell of the zebra mussel in Lake St. Clair are shown in Fig. 8. The relationships between shell length and tissue dry weight and total dry weight are shown in Fig. 9. Allometry of shell growth and the length-weight relationships are similar to those reported for British (Morton, 1969) and Polish (Stanczykowska, 1977) populations of *D. polymorpha*.

The population dynamics of *C. fluminea* is highly variable and will not be elaborated upon here because the species is not (yet) present in Lake St. Clair proper. Excellent overviews are provided in the proceedings of two *Corbicula* symposia, one edited by Britton (1979), and other appearing in the American Malacological Bulletin, Special Edition No. 2 (1986). The population dynamics of native species of bivalves in North American surface waters have been well studied and reported (see Mackie, 1990 for

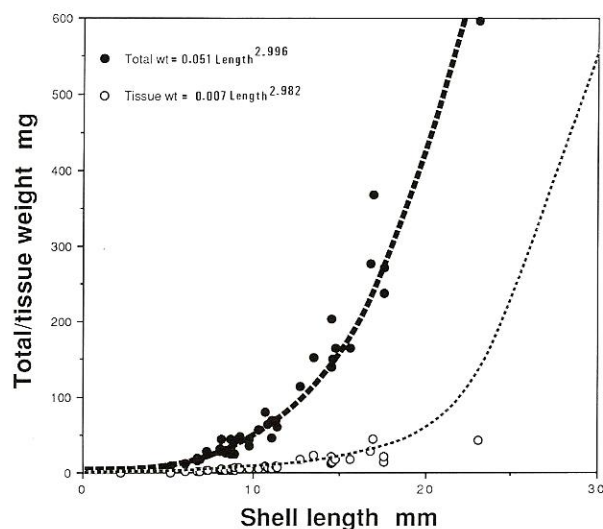


Fig. 9. Relationships between shell length and (a) tissue dry weight and (b) total dry weight of *Dreissena polymorpha* in Lake St. Clair.

Sphaeriidae and Clarke, 1973, for Unionidae). Nothing is known about the population dynamics of either sphaeriid or unionid species in Lake St. Clair. Knowledge of the natural variability in population dynamics of native species of bivalves is needed for a thorough understanding of the potential impact of zebra mussels on native bivalves, especially rare and endangered species. The exceedingly high reproductive capacity and rapid growth rate of the zebra mussel are two other features that will probably result in the dominance of zebra mussels over native bivalves in Lake St. Clair.

2.6. Distribution

In May, 1989, cement blocks (10.16 × 20.32 × 40.64 cm) were placed at Brights Grove in Lake Huron; at Corunna and Port Lambton in the St. Clair River; at Stoney Point, Belle River and Puce in Lake St. Clair; at Amherstburg in the Detroit River; at Wheatley, Port Stanley, Port Dover and Long Beach in Lake Erie; and at Niagara-on-the-Lake in Lake Ontario to determine the rate of spread throughout the Great Lakes. The blocks were examined every two weeks until September

and monthly in October, November, and December. Three vertical plankton hauls were taken with a 60 µ mesh student plankton sampler immediately before the blocks were examined. Only the presence of veliger larvae in the plankton samples were recorded for this part of the study.

In 1988 the zebra mussel was present at only a few isolated localities in the south-east end of Lake St. Clair and as far as Port Stanley in Lake Erie. Zebra mussels did not appear on the cement blocks or in plankton samples at Port Dover and Long Beach until September 1989. Living specimens of zebra mussels were also found at Port Colbourne in September, 1989 (Pers. Comm., Ron Dermott, Fisheries and Oceans, Canada Centre for Inland Waters) and at Port Weller in Lake Ontario in October 1989 (Pers. Comm., Larry King, Ontario Hydro). Based on these analyses, the zebra mussel has extended its range along the Ontario shorelines of Lake St. Clair and Lake Erie at a rate of approximately 250 km y⁻¹. As of December 1989, zebra mussels had not yet appeared on any of the cement blocks, nor in plankton samples taken at the two sites in the St. Clair River or at Brights Grove in Lake Huron.

Zebra mussels occur at all depths in the Ontario

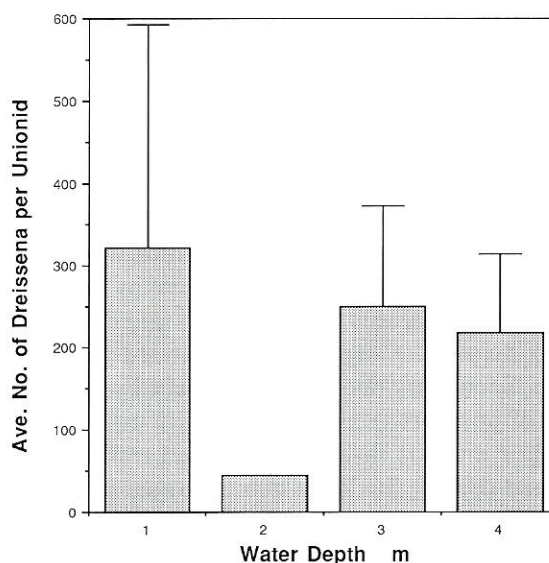


Fig. 10. Average number of *Dreissena polymorpha* per unionid shell in relation to depth in Lake St. Clair.

side of Lake St. Clair. The species occurs wherever there is suitable substrate present. Since the shells of unionid clams are the main suitable substrates in the 3 to 4 m depths, the distribution of zebra mussels in these depths (Fig. 10) is probably closely related to the distribution of unionid clams.

Unlike the zebra mussels, native species of bivalves are usually more common in soft sediments. They are present at all depths in Lake St. Clair but standing crops are relatively small, sphaeriids rarely exceeding 100 m^{-2} (Griffiths, 1987) and unionids rarely exceeding 10 m^{-2} , as determined from SCUBA diving surveys of ten, 1 m^2 quadrats in each of the 1, 2, 3, and 4 m depths near Puce, Ontario; in the summer of 1989, densities of zebra mussels as high as $200\,000 \text{ m}^{-2}$ were recorded in the shallow waters of Lake St. Clair (Mackie, unpublished data). This exceeds the maximum standing crops of sphaeriids and unionids by three and four orders of magnitude, respectively.

2.7. Dispersal mechanisms

The zebra mussel employs passive methods for dispersal during both the larval pelagic state and the adult benthic state. Primary dispersal occurs through the pelagic state by transport of the veligers and post-veligers by lake currents. As a result, the distribution of zebra mussels was initially concentrated toward the south-east end of Lake St. Clair. With the general eastward flow of water in the Great Lakes, the zebra mussel is distributed further eastward or northward than westward or southward. Attachment by means of its byssal apparatus to floating logs and debris has also helped to augment its eastward dispersal rate. Secondary dispersal may occur by the drifting of post-larvae and young adults using byssal and/or mucous threads. Enhanced transport by thread drifting has been demonstrated in several marine bivalve species (Sigurdson *et al.*, 1976; Blok & Tan-Maas, 1977; Lane *et al.*, 1982, 1985; Beukema & de Vlas, 1989) and in the freshwater *C. fluminea* (Prezant & Chalermwat, 1984).

Although similar behaviour has been observed in *D. polymorpha* held in laboratory aquaria (Ron Griffiths, pers. comm.), 'byssal-pelagic' (Lane *et al.*, 1982) transport in zebra mussels in nature has yet to be verified. In such transport, the byssal or mucous threads are monofilaments, distinct in form and function from the attachment byssus threads (Lane *et al.*, 1985). The threads are many times the length of the animal and increase the hydrodynamic drag to enable the young mussels to be transported in the water column by turbulence or currents. In *Corbicula*, small adults (7–14 mm shell length) secrete long mucous threads through their exhalant siphons and act as draglines to buoy the clam into the water column (Prezant & Chalermwat, 1984).

Currents exceeding 1 m s^{-1} have prevented the veligers from invading the St. Clair River in the upstream direction. The dispersal of zebra mussels westward and northward will be accomplished by adults byssally attaching themselves to ships and by veligers in the ballast water of ships that travel from Lake Erie and release them in more northern lakes such as Lake Huron and Lake Superior. Commercial fishing boats and pleasure craft will be among the more common dispersal agents. Some veligers will probably be dispersed in bait buckets or in wet wells of some boats. In fact, the hull of a fishing vessel that had travelled from Lake Erie to Lake Michigan was observed to have been infested with zebra mussels when it was dry-docked at Green Bay, Lake Michigan in September 1989 (Pers. Comm., D.W. Schloesser, U.S. Fish and Wildlife, Ann Arbor, Michigan). Currents will now expedite the dispersal of zebra mussels in the connecting channels and lakes north of Lake St. Clair, including Lake Michigan, Lake Huron and the St. Clair River. Sphaeriids are dispersed mainly by passive mechanisms, such as by attaching to birds and insects (Mackie, 1990). Unionids rely mainly on their host fish species for dispersal during the parasitic glochidial stage. The rate of dispersal by such mechanisms is unknown but is probably relatively slow.

The rapid rate at which zebra mussels have been dispersed throughout Lake Erie and most of

Lake St. Clair is attributable to the planktonic veliger larvae, which are dispersed mainly by water currents, and the byssate feature of adults, which allows them to be transported upstream by attaching to hulls of boats. Clearly, these two features explain why the zebra mussel is becoming the dominant bivalve throughout the Great Lakes.

2.8. Physiology

The threshold temperatures for growth and reproduction apparently vary considerably among populations of zebra mussels. Preliminary analyses of data from Lake St. Clair populations suggest threshold temperatures of at least 10 °C for gametogenesis, 10 to 12 °C for growth and 14 to 16 °C for appearance of veligers. These temperatures are based on samples first taken on May 2 when the water temperature was 10 °C. These are similar to threshold temperatures of 11 to 12 °C for growth (Walz, 1978) and 15 to 17 °C for reproduction (appearance of veligers) reported by

Stanczykowska (1977) and Lewandowski and Ejsmont-Karabin (1983) for Polish populations and by Morton (1969) for British populations. Bij de Vaate (1989) reported threshold temperatures of 6 °C for growth and 12 °C for reproduction for populations in The Netherlands. Studies have yet to be made on specimens collected before May 2 and at temperatures less than 10 °C in Lake St. Clair. Nevertheless, the threshold temperatures for gametogenesis, growth, and larval release are well within the ranges of temperate species and suggest that the zebra mussel will not only succeed in the Great Lakes but many other lakes in North America.

The threshold temperatures for growth and reproduction of *Corbicula* are 16 °C and 22 °C, respectively. The threshold temperature for reproduction is rarely reached in most parts of Lake St. Clair and explains in part why the Asiatic clam will probably not succeed in colonizing the lake.

Collectively, zebra mussels are unrivaled in their capacity to clarify water. This was demonstrated by maintaining 50 mussels (shell length ranging from 2 mm to 15 mm in 10 l of 0, 1.5, 3.0,

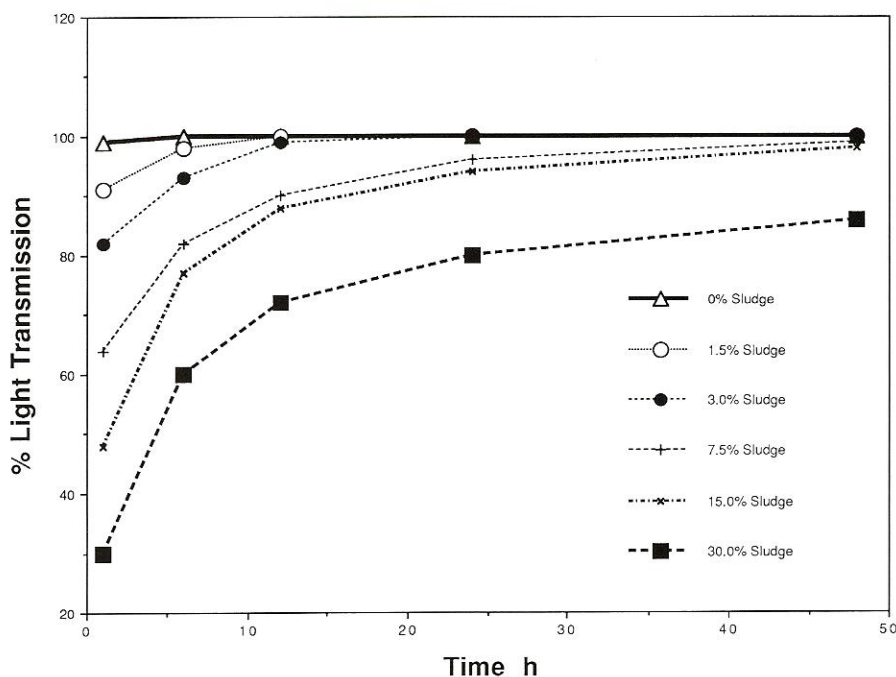


Fig. 11. Ability of *Dreissena polymorpha* to clarify different concentrations of activated sewage sludge.

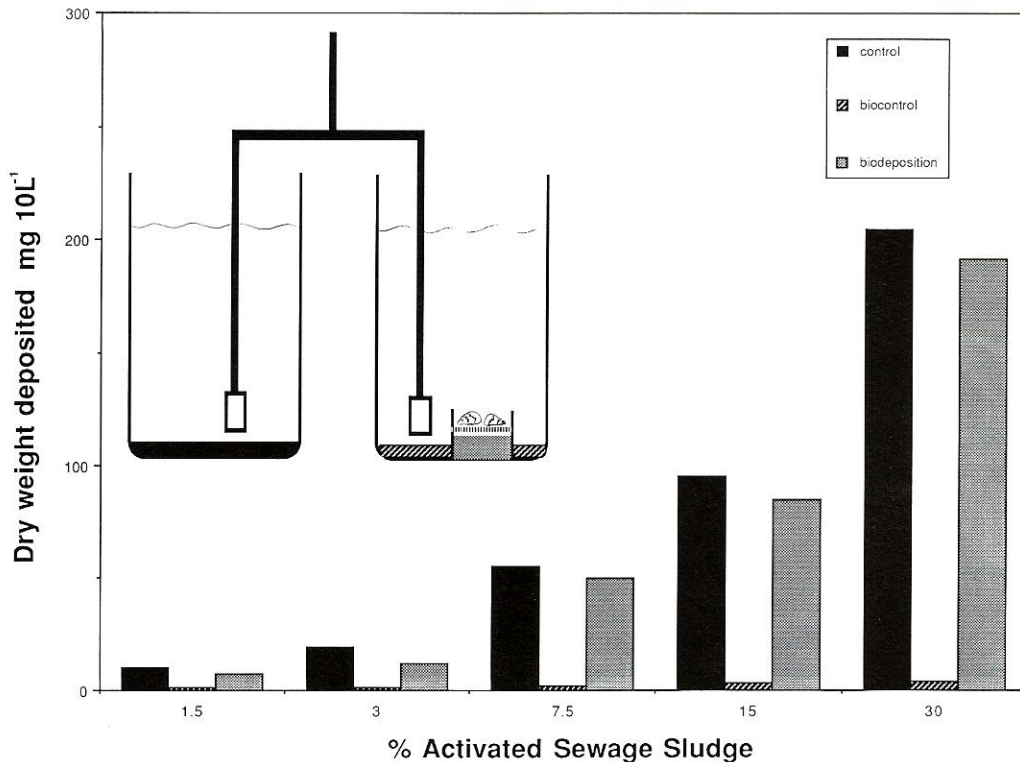


Fig. 12. Biodeposition of different concentrations of activated sewage sludge as pseudofaeces by *Dreissena polymorpha*.

7.5, 15 and 30 percent activated sewage sludge, with continuous aeration for 96 h. The mussels were suspended 5 cm above the bottom of the bucket in 100 mm dia × 50 mm high acrylic tubes with a nylon mesh (1 mm openings) glued to the bottom of the tubes. Water clarity was restored to control levels (0 percent sludge) within 6 h for 1.5 percent sludge, 12 h for 3.0 percent sludge, 24 h for 7.5 percent sludge, 48 h for 15 percent sludge and 96 h for 30 percent sludge (Fig. 11). Nearly all of the suspended organic material was deposited on the bottom as pseudofaeces (Fig. 12). As freshwater bivalves, the zebra mussel's filtration rate (10 to 100 ml individual⁻¹ h⁻¹) is intermediate between Sphaeriidae (0.6 to 8.3 ml individual⁻¹ h⁻¹) and Unionidae (60 to 490 ml individual⁻¹ h⁻¹) (Stanczykowska *et al.*, 1976). *Corbicula* has a filtration rate that far exceeds these on an individual basis (60 to 800 ml h⁻¹). However, the well known ability of *Dreissena* to clarify lakes and watercourses (Morton, 1971; Stanczykowska, 1975; Piesik, 1983; Reiders

et al., 1989) is a consequence of the enormous standing crops that usually prevail in aquatic systems.

3. Impacts

3.1. Ecosystem

One of the most obvious early impacts of zebra mussels is on native species of unionid clams. Zebra mussels are not selective and are colonizing all species of unionids in Lake St. Clair, including *Lampsilis radiata siliquoidea*, *L. ventricosa*, *Pleurobema coccineum*, *Proptera alata*, *Lasmigona complanata*, *L. compressa*, *Elliptio dilatata*, *Quadrula quadrula*, *Alasmidonta viridis*, *Anodonta grandis grandis*, *Obovaria subrotunda*, *Leptodea fragilis* and *Villosa iris*. There is an exponential increase in the numbers of zebra mussels on unionid shells in relation to the length and surface area of the host unionid shell (Fig. 13a, b). The infestations are

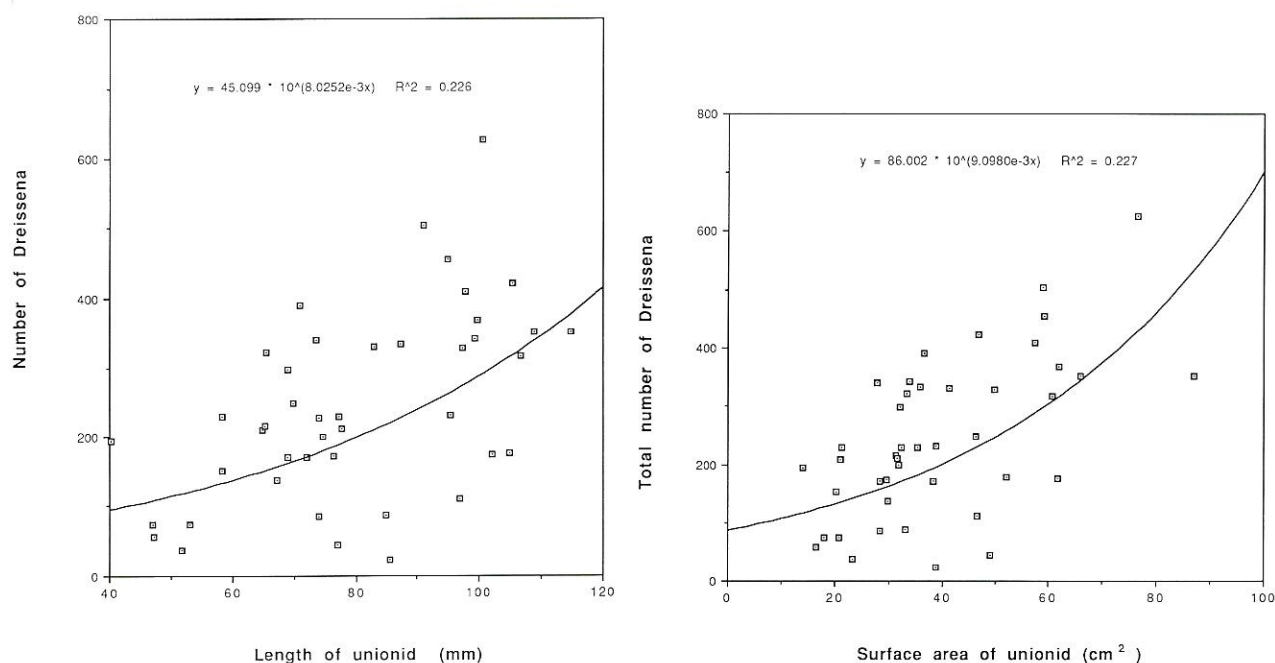


Fig. 13. Relationship between number of zebra mussels and (a) length and (b) surface area of unionid shells in Lake St. Clair.

so great that the unionids are not able to fully open their valves (Fig. 14a), or so invasive that the

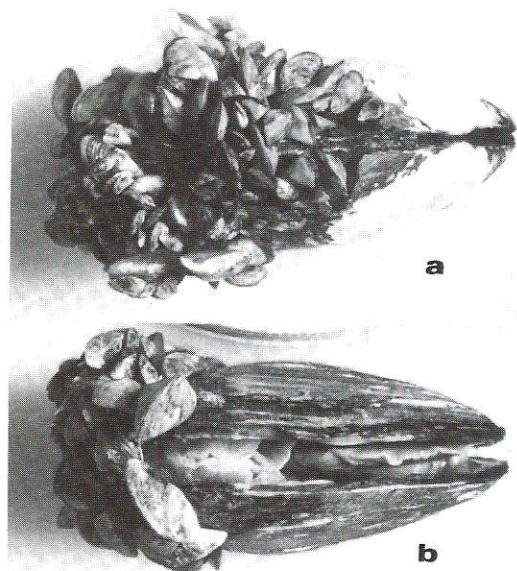


Fig. 14. Encrustations of *Dreissena polymorpha* so intense that the unionid is not able to fully open (a) or fully close (b) their valves.

valves cannot be closed (Fig. 14b). The massive infestations are hypothesized to have one or more of the following effects on unionid clams: (i) The biomass of zebra mussels is so great that normal locomotion and burrowing activities of the unionids are impaired. For most infestations, the biomass of zebra mussels is estimated to be as great as that of the unionid. For example, using the relationship, total dry weight = $0.051 \text{ shell length}^{2.996}$, for *D. polymorpha* in Lake St. Clair (Fig. 9) and total dry weight = $0.058 \text{ shell length}^{2.93}$ for *Lampsilis radiata* (Mackie & Flippance, 1983), a common unionid in Lake St. Clair, and assuming 1000 individuals at an average length of 10 mm for *D. polymorpha* on a single 100 mm long shell of *L. radiata*, the total biomass of zebra mussels (50 g) slightly exceeds that of the unionid (42 g). Unionids with 15 000 zebra mussels probably carry at least five times their own weight (i.e. 231 g of zebra mussels on a 42 g unionid), assuming an average length of 7 mm for zebra mussels. (ii) The concentration of zebra mussels at the posterior end of the unionid affects its balance and/or equilibrium during locomotion.

(iii) Invasive growth of zebra mussels between the valves of a unionid clam limits or even prevents valve closure and will expose the unionid to predators, parasites, disease, and noxious water quality. (iv) Invasive growth at the posterior end also interferes with the normal functioning of the siphons and processes associated with them, especially respiration and feeding. (v) Extensive infestations of zebra mussels limits or prevents valve opening which will impair normal metabolic functions for feeding, growth, reproduction, respiration and excretion. (vi) Enormous numbers of zebra mussels will strip the water of food and nutrients making little or none available to the unionid host which soon starves, loses weight, and dies. (vii) Infestations at the mantle margin of the shell will cause shell deformities, especially at the posterior end. (viii) Complete occlusion of the gape at the posterior end and perhaps of siphons which may cause death by smothering the unionid.

Large populations of zebra mussels have an enormous capacity to remove seston and clarify water. As shown above, they are able to remove suspended materials and nutrients from the water and biodeposit them on the bottom as pseudo-faeces. The following scenario can be hypothesized. The increase in water clarity will result in an increase in the size of the euphotic zone, but primary production can be expected to decline because most of the nutrients will have been biodeposited on the bottom and made available to the benthic community. Reductions in production and biomass of pelagic autotrophs, heterotrophs, herbivorous zooplankton and planktivores, including fish, can be expected to follow. Eventually, this single exotic bivalve species can potentially alter the entire pelagic-benthic energy balance of Lake St. Clair. An ecosystem that once was driven by energy derived from the pelagic zone will be driven by energy derived from the benthic zone. This may have severe socio-economic impacts, especially for commercial and sport fisheries.

3.2. *Socio-economic*

Impacts will not only be felt through changes in the energy balance of pelagic and benthic systems but socially and economically as well. The strongly byssate feature makes the zebra mussel one of the most tenacious and potent biofoulers of any exotic species ever introduced to North America. Navigational aids, such as fishing buoys and markers, have such heavy infestations that they sink below the surface (pers. comm., Joe Leach, Ontario Ministry of Natural Resources); commercial fishing gear, such as trap nets and gill nets, have accumulations of zebra mussels so large that the nets are rendered useless and are difficult to retrieve; hulls of boats and ships are so laden with zebra mussels that their sailing efficiency is impaired; beaches have accumulations of dead shells that are cutting the feet of swimmers; industrial and domestic intakes and pipelines drawing water from Lake St. Clair have such heavy infestations that flow rates have been reduced by as much of 50 percent (pers. comms., Joe Leach, Ontario Ministry of Natural Resources, Wheatley, Ontario and Ron Griffiths, Ontario Ministry of Environment, London, Ontario).

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