REVIEW / SYNTHÈSE

A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves

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The ecological and economic impacts of the introduced zebra mussel (*Dreissena polymorpha* (Pallas)) have been due in part to a life history that is conserved with marine bivalves but unique among the indigenous freshwater fauna. There are a number of life history events in *D. polymorpha* that follow external fertilization and embryology. The first is a brief trochophore stage. The development of a velum and secretion of a larval shell lead to a D-shaped veliger, which is the first recognizable planktonic larva. Later a second larval shell is secreted and this veliconcha is the last obligate free-swimming veliger. Conversely, the last larval stage, the pediveliger, can either swim using its velum or crawl using its foot. Pediveligers select substrates on which they "settle" by secreting byssal threads and undergo metamorphosis to become plantigrade mussels. The secretion of the adult shell and change in growth axis lead to the convergent heteromyarian shape. Zebra mussels produce byssal threads as adults, but these attachments may be broken, enabling the mussels to translocate to new areas. The recognition of these life history features will lead to a better understanding of zebra mussel biology. In summary, life history stages of zebra mussels are similar to those of marine bivalves and should be identified morphologically rather than on the basis of size.

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L'impact écologique et économique de l'espèce introduite *Dreissena polymorpha* (Pallas), la Moule zébrée, est attribuable en partie à son type de cycle, commun chez les bivalves marins, mais tout à fait inusité au sein de la faune indigène d'eau douce. Des étapes très distinctives suivent la fécondation externe et l'embryologie de *D. polymorpha*. Un court stade de larve trochophore constitue la première étape. L'apparition d'un voile et la sécrétion d'une coquille larvaire mènent à la formation d'une larve véligère en forme de D, la première larve planctonique bien distinctive. Plus tard, une seconde coquille larvaire est sécrétée et cette véliconque constitue le dernier stade véligère à nage libre obligatoire. Inversement, le dernier stade larvaire, la pédivéligère, peut nager en utilisant son voile, ou alors ramper au moyen de son pied. Les pédivéligères choisissent des substrats sur lesquels elles s'installent en sécrétant les filaments de leur byssus et en se métamorphosant en moules plantigrades. La sécrétion de la coquille de l'adulte et le changement de l'axe de croissance aboutit à la forme convergente hétéromyarienne. Les moules continuent de produire des filaments byssaux à l'âge adulte, mais ces attaches peuvent être brisées, permettant ainsi aux moules de se déplacer vers d'autres endroits. La connaissance de ces caractéristiques permettra de mieux comprendre la biologie de la Moule zébrée. En somme, le cycle de cette moule est semblable à celui des bivalves marins et les divers stades se reconnaissent à leur forme plutôt qu'à leur taille.

[Traduit par la Rédaction]

Introduction

Modern studies of the life history of bivalve veligers began in the last century and were motivated by scientific curiosity and by the recognition of the economic importance of these species (Jackson 1988; Meisenheimer 1899, 1901; Field 1922). Similar interests in the behavioral and physiological aspects of development have continued (Ocklemann 1962; Sastry 1965; Bayne 1964a, 1964b, 1965) and have incor-

porated the need to describe and differentiate among the large number of pelagic larvae for ecological and paleontological purposes (Loosanoff and Davis 1963; Jablonski and Lutz 1983). The consensus from these studies is that larval development, as characterized by Carriker (1961), has been conserved evolutionarily and is relatively consistent among both infaunal and epifaunal species. Therefore, the morphology, physiology, and behavior of bivalve veliger larvae is reasonably well established (see reviews by Bayne 1976; Giese and Pearse 1979; Sastry 1979; Widdows 1991; Lutz and Kennish 1992).

TABLE 1. Developmental times (post fertilization) and sizes (larval height) of *Dreissena polymorpha* larval and postlarval stages

Study	Temp. (°C)	Egg diameter (μm)	Trochophore Height (μm)	Trochophore Time	D-shaped veliger Height (μm)	D-shaped veliger Time (days)	Veliconcha Height (μm)	Veliconcha Time (days)	Pediveliger Height (μm)	Pediveliger Time (days)	Plantigrade Height (μm)	Plantigrade Time (days)
Present study in Lake Erie	Field	—	—	—	80–160, 134[a]	—	120–280, 164[a]	—	>200	—	—	—
Kirpichenko 1964[b]	Field	—	—	—	—	—	—	—	—	—	>191–262	—
Leitch and McLeod 1993	17–24	60–96	95–110	2–4 d	100–110	7–9	—	7–9	—	—	—	—
Lewandowski 1982a, 1982b[b]	>17–19	—	—	—	120	—	214–280	—	—	—	>158; >233	—
Meisenheimer 1901	—	≈65	≈57–80	—	≈70	—	≈162	—	≈170	—	≈224	—
Morton 1969a, 1969b, 1969c	Field	—	—	—	—	—	—	—	—	—	—	90
Nichols[b,c]	20–24	40–89	97–121, 109[a]	2–3 d	115–167, 129[a]	3–5	120–200, 163[a]	8	167–238, 186[a]	10	— –500	35
Skal'skaya 1984[b]	Field	—	—	—	—	—	—	—	—	—	238–262	—
Sprung 1989[b]	20	—	—	6–20 h	111–120	2–4	—	—	—	—	233	18–37
Walz 1973, 1975	Field	110–190[d]	83–95	—	80	—	—	—	<300	—	—	>35
Summary *D. polymorpha*	17–24	40–96	57–121	6–96 h	70–160	2–9	120–280	7–9	>167–<300	10	>158–500	18–90
Summary[e] All bivalves	5–26	40–125	57–150	6–96 h	50–175	<1–9	81–305	2–24	>160–350	6–40	>158–500	6–90
Marine bivalves (i.e., excluding *D. polymorpha*)	5–26	40–125	70–150	8–48 h	50–175	<1–7	81–305	2–24	>160–350	6–40	>160–360	6–47

NOTE: —, unavailable; ≈, approximate or estimated size from photographs.
[a]Mean value.
[b]The larval lengths recorded were transformed into larval heights using the following relationship from Walz (1973): length = 1.06 × height − 27.32; $r^2 = 0.97$, $P < 0.05$, $n = 869$.
[c]Manuscript in preparation.
[d]Observations not included in summary.
[e]Further details pertaining to the 39 species (19 families) of marine bivalves included in the summary data can be found in the Appendix.

Surprisingly, this statement can also be extended to ". . . fresh-water bivalves belonging to the family Dreissenidae [that] have a free-swimming larval life and pass through trocophore and veliger stages like most marine forms. The early development of *Dreissena* has been more thoroughly investigated in the laboratory than that of any other bivalve . . . " (Cox 1969, pp. N95–N96). These words, though dated, are noteworthy given the ecological and economic impacts of the recent introduction of freshwater zebra mussels into North America (Hebert et al. 1989, 1991; Roberts 1990; Griffiths et al. 1991; O'Neill and MacNeill 1991; Nalepa and Schloesser 1993). Unfortunately this information and its implications have been slow to enter into most discussions of zebra mussel biology (see Ackerman and Claudi 1991; Claudi and Ackerman 1992; Sprung 1993). Moreover, the terminology and sequence of life history events, especially with respect to larval settlement, have been confused in previous studies (Kirpichenko 1964; Mackie 1991; Hopkins and Leach 1993). Any effort to understand the impact of zebra mussels will require an understanding of this organism's basic life history, and a comparison with marine bivalves is the logical approach.

The purpose of this study is to review the early life history of the freshwater zebra mussel (*Dreissena polymorpha* (Pallas)). It is assumed, and there is evidence (S.J. Nichols, unpublished observation), that this description applies equally well to the second dreissenid (*Dreissena bugensis*) recently identified in the Laurentian Great Lakes (May and Marsden 1992; Ludyanskiy 1993; Domm et al. 1993; Rosenberg and ... 1994). The life history of zebra mussels is des-

cribed chronologically under the ecological categories of (*i*) pelagic larval forms, (*ii*) primary settlement and metamorphosis, and (*iii*) postmetamorphic movements (secondary settlement). A comparison is made throughout to marine bivalves with veliger larvae, since, unlike indigenous freshwater bivalves (Pennak 1989; Mackie 1991), zebra mussels have conserved a free-swimming veliger larval stage.

Bivalve size

The "size," shape, morphological characteristics (e.g., functional foot), and behavior of bivalve larvae can be used to determine developmental state (Loosanoff and Davis 1963; Loosanoff et al. 1966) and can also be used as taxonomic distinguishing characters in a known fauna (Chanley and Andrews 1971; see review in Lutz and Kennish 1992). Size is the least defined characteristic of these features, as it can be described by at least three dimensions: (*i*) length, the distance from the umbone to the posterior margin of the shell perpendicular to the axis of the hinge; (*ii*) height, the distance from the ventral to the dorsal margin of the shell parallel to the axis of the hinge; and (*iii*) depth, the distance between the valves perpendicular to the axis of the hinge. Since larval height is the largest metric, it should be used to describe size. It is not uncommon, however, to find larval size described by larval length, since length becomes the largest metric following metamorphosis. This has been the case in *D. polymorpha*, for which both length and height have been reported. The regression of larval length on height provided by Walz (1973) was used to transform the reported *D. polymorpha* lengths into heights to facilitate comparison among
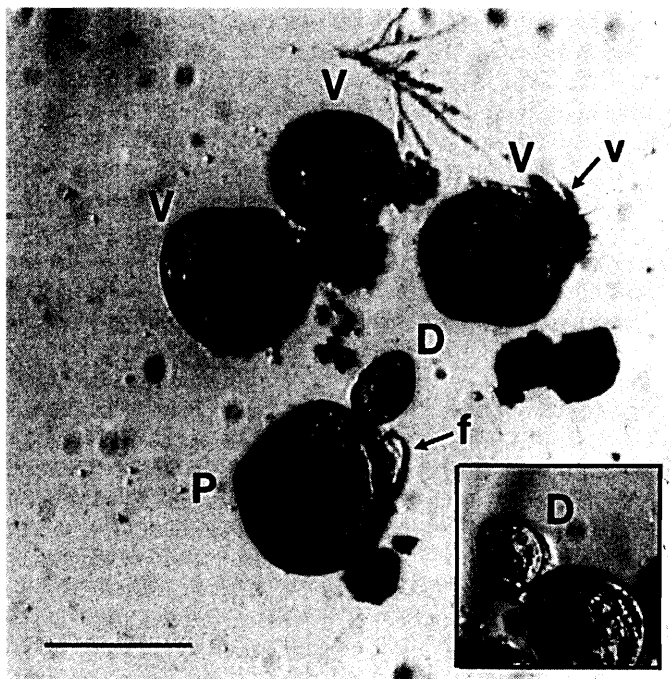
FIG. 1. Photograph of *Dreissena polymorpha* larval stages in a plankton sample taken in August 1992. The inset is a side view of the D-shaped veliger seen in oblique view in the group photograph. D, D-shaped veliger; V, veliconcha; P, pediveliger; *v*, velum; *f*, foot of pediveliger. Scale bar = 200 μm.
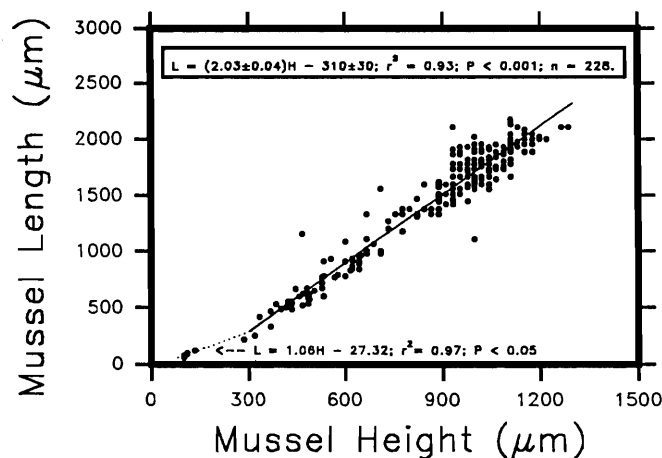

FIG. 2. Lengths and heights of larval and postlarval *Dreissena polymorpha* valves. Regressions are presented for heights <300 μm (Walz 1973) and >300 μm (regression coefficients ± standard errors).

studies in Table 1 (length = 1.06 × height − 27.32; r^2 = 0.97; P < 0.05; n = 869; for heights ranging between 80 and 305 μm).

Principal life history events

Development: egg to pediveliger

This description pertains to *D. polymorpha* and other bivalves with planktotrophic development. It therefore excludes descriptions of species with direct and lecitrophic development as well as species with larval brood protection (e.g., Corbiculidae and Pisidiidae) and parasitic larval development (e.g., glochidia, haustoria, and lasidia larvae of Unionacea; Cox 1969; Burky 1983; Mackie 1984, 1991). It should be noted that these latter specialized modes of larval development are typical of extant North American freshwater bivalves. The Dreissenidae are thus more conservative, evolutionarily, in possessing planktotrophic larvae like their marine counterparts. It is also important to note the early contributions of Korschelt (1892) and Meisenheimer (1899, 1901) to characterizing the developmental biology of *D. polymorpha*, and bivalves in general.

The life history of *D. polymorpha* begins with the external fertilization of gametes that are released into the water column by dioecious individuals (reported egg diameters range from 40 to 96 μm, although Walz (1973) reported a range of 110–190 μm; range for bivalves excluding *D. polymorpha* = 40–125 μm; Table 1). There are, however, reports that a small portion (e.g., ≤4%) of the mussels in a population can be hermaphroditic (Antheunisse 1963; Nichols and Kollar 1991). After fertilization and protostomic embryology, which includes spiral cleavage, blastulation, and gastrulation, a trochophore larva develops (57–121 μm diameter; 6–96 h post-fertilization, bivalve range = 70–150 μm, 8–48 h;

Table 1). The trochophore, which is free swimming, becomes a veliger with the development of the velum, a larval organ of feeding and locomotion. The possession of a velum thus characterizes all subsequent larval stages as veligers. Within 2–9 days post fertilization (dpf), the developing veliger larvae secrete an unornamented and D-shaped shell from shell glands. Since these first larval shells, or prodissoconch I, are D-shaped in profile, the larvae are referred to as D-shaped or straight-hinged veligers (70–160 μm in height; bivalve range = 50–175 μm, <1–7 dpf; Table 1, Fig. 1; subtle differences in size and shape have been noted between the two dreissenid species at this stage; S.J. Nichols, unpublished observation). Later, but within 7–9 dpf, a second, more ornamented larval shell, or prodissoconch II, is secreted by the mantle tissue. It has the pronounced umbonal region near the hinges and is round or clam-like in profile. This umboned veliger or veliconcha (120–280 μm in height; bivalve range = 81–305 μm, 2–24 dpf; Table 1, Figs. 1 and 2) is the last veliger stage that is free swimming and is typically found in the plankton.

While there is considerable growth in the veliconcha, several new organs systems also develop. One of these is the foot and its development leads to a change in behavior as well as the new name of pediveliger (167 – <300 μm in height; >10 dpf; bivalve range = >160–350 μm, 6–40 dpf; Table 1, Fig. 1). The other changes, which are related to feeding, involve the gill filaments that form in the mantle cavity. The gill filaments do not reach maturity until after metamorphosis, which follows this stage. Conversely, the foot (and associated byssal apparatus) is well developed in the pediveliger and is used for swimming near the bottom as well as crawling on surfaces. These behaviors differentiate the pediveliger from earlier veliger larvae. Upon receiving the proper cues, sometime between 18 and 90 dpf, a pediveliger will "settle" and secrete a byssal thread onto an appropriate surface. Pediveligers have therefore been referred to as settling veligers (Kirpichenko 1964). Once anchored, the pediveliger will undergo metamorphosis to become a postveliger or plantigrade mussel (>158–500 μm in height; bivalve range = >160–360 μm, 6–47 dpf; Table 1). However, without an appropriate surface, usually a filamentous alga (de Blok and Geelen 1958), settlement and metamorphosis may be delayed in the marine mussel *Mytilus edulis* for up to a month before byssal

attachment (Bayne 1965). It has not been established whether a similar delay occurs in *D. polymorpha*, although some data, such as the time until settlement reported above, support such a phenomenon (Table 1).

Metamorphosis: primary or direct settlement, pediveliger to plantigrade

Primary or direct settlement of pediveligers signals the onset of metamorphosis, which transforms the veliger larva into a postveliger or plantigrade mussel. Settlement is an active process in which pediveligers swim or crawl onto and eventually select the site and substrate on which to settle (Jonsson et al. 1991; J.D. Ackerman and B. Sim, unpublished observations). *Dreissena polymorpha* pediveligers have been shown to select preferentially filamentous substrates such as aquatic plants (e.g., Characeae) and the underside of artificial substrates on which to secrete byssal threads (Lewandowski 1982b). Byssal adhesion is a common feature of larval and postmetamorphic bivalves, which evolved to function during metamorphosis (Yonge 1962). *Dreissena polymorpha* and members of a number of other taxa have the ability to produce byssal threads throughout the life cycle. These taxa are, therefore, convergent in the possession of an adult byssal apparatus (Yonge and Campbell 1968; Ackerman et al. 1993; Eckroat and Steel 1993; Morton 1993).

The principal morphological changes that follow primary settlement are the loss of the velum, the development of the gills and mouth, and the secretion of the dissoconch or adult shell. An interdissoconch shell, which forms prior to the dissoconch in a number of marine families (e.g., Mytilidae and Pectiniade; Lutz and Kennish 1992), has not been described in *D. polymorpha*. The filter feeding function of the velum is taken over by the gill filaments. The eulamellibranch gill filaments increase in number, size, and complexity, occupying most of the mantle cavity. There are also associated developments of labial palps around the mouth and an anterior reorientation of the mouth. The foot also increases in size and there is a similar reorientation in the mantle cavity. The increased growth of the foot, gills, and mouth are facilitated by the new growth axis of the dissoconch shell. The clam-like shape of the plantigrade is quickly lost and replaced by a more triangular and familiar heteromyarian or mussel-like shape (Morton 1993; see Fig. 2). The completion of these developments transforms the plantigrade into a juvenile, which with further growth and onset of sexual maturity becomes the adult. Kirpichenko (1964) has characterized this sequence, on the basis of mantle morphology, as the postveliger stage (plantigrade), siphon-forming stage (juvenile), and branchisiphonal stage (adult).

Post-metamorphic behavior: secondary settlement

As in marine bivalves (Sigurdsson et al. 1976), recruitment in *D. polymorpha* appears to occur in two phases, although direct settlement involving a single settlement event probably also occurs (McGrath et al. 1988; see review in Lutz and Kennish 1992). In the two-phase model, the first phase involves the settlement of pediveligers and subsequent metamorphosis, while the second phase involves the translocation of mussels (plantigrades, juveniles, and adults) to new areas. Post-settlement movements in *D. polymorpha* have long been recognized. Juvenile mussels can crawl over substrates at a rate of 7 cm/night (Shevchenko 1949). There have been a number of reports of movements of small mussels from substrates, including aquatic plants (Oldham 1930;

Russel-Hunter, cited in Yonge and Campbell 1968; Morton 1969c; Kachanova 1961; Lewandowski 1982b; Claudi and Ackerman 1992). Lewandowski (1982b) demonstrated that pediveligers recruit preferentially to aquatic plants and later migrate, on floating plant material, to other substrates including adult mussel colonies. A similar argument has been presented to account for the anomalous increase in the frequency of the first year class in subsequent years of a population survey (Morton 1969c). This is consistent with the recent observation that the greatest recruitment occurs at the periphery of mussel beds rather than in the proximity of adults when densities are high (Hebert et al. 1991).

Post-settlement movement of *D. polymorpha* has been observed throughout the year in Lake Erie (Claudi and Ackerman 1992). In the spring, juvenile and adult mussels translocate onto freshly deployed substrates in the field and within industrial plants. Some of the mussels involved in these movements may have originated from those that overwintered under rocks and in crevices. The overwintering population of plantigrades (some on the order of 300 μm in length) and small juveniles may serve as a pool of translocators in the spring (Kirpichenko 1964; Claudi and Ackerman 1992). Translocation onto fresh substrates in the spring is temperature dependent. Juvenile translocators were first found during weekly inspections at the end of April 1992, when water temperature exceeded 8°C (R. Claudi, D. Lowther, and J.D. Ackerman, unpublished observations). Later in the summer, juveniles ≈1 mm in length were found in plankton tows, indicating that mussels could be resuspended in the water column. Post-metamorphic mussels were also found in horizontal nearshore plankton tows and on pot-scrubber collectors deployed in mid water near established *D. polymorpha* populations (Martel 1993). Greater numbers of individuals were found during periods of high wave action, but drifting juveniles were also observed during calm periods (Martel 1993).

Post-metamorphic *D. polymorpha* can readily return to the water column through a number of mechanisms. The most obvious are rafting on macrophytes and other flotsam (Lewandowski 1982b; Martel 1993; J.D. Ackerman, unpublished observation) and crawling on the air–water interface (Oldham 1930; Shevchenko 1949). *Dreissena polymorpha* may also use thin threads, which originate from the siphon or foot, to contact the surface and float from these (Kirpichenko 1971; J.D. Ackerman, personal observation in August 1990). It is also possible for these threads to be used for drifting through the water column. This would account for the presence of post-metamorphic mussels and juveniles ≈1 mm in length in plankton tows and on midwater collectors (Ackerman and Claudi 1991; Claudi and Ackerman 1992; Martel 1993). The summary in Table 2 of settlement in *D. polymorpha* is remarkably similar to what has been described in *Mytilus edulis* and other marine bivalves.

In *Mytilus edulis*, primary settlement occurs preferentially on filamentous substrates such as algae and hydroids (de Blok and Geelen 1958), and pediveligers rarely settle on adult mussel beds (Bayne 1964b; see review in Lutz and Kennish 1992). Following metamorphosis, plantigrades and juveniles (≈1100 μm in length) may cut their byssal connections (possibly by closing their valves while the byssal threads are in tension; Board 1983) and translocate on the bottom and in the water column. Nelson (1928) identified two

TABLE 2. Primary and secondary settlement mechanisms in *Dreissena polymorpha*

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Primary settlement	Pediveligers
Secondary settlement	Plantigrades
	Juveniles
	Adults
Translocation mechanisms	Crawling on substrates
	Crawling on surface films via siphons or foot
	Thread drifting
	Bubble flotation
	Rafting on macrophytes and flotsam

FIG. 3. Relative frequency distribution of the sizes of *Dreissena polymorpha* larvae observed in Lake Erie during the summer of 1992. Arrow indicates size at which the foot of the pediveliger was first visible. The mean values ± standard deviation and the sample sizes are shown in the upper right corner of the figure.

mechanisms of pelagic translocation for *Mytilus edulis*: (1) buoyancy on secreted air bubbles; and (2) attachment on the air–water interface (surface film) by (*i*) the tentacles of the siphon, (*ii*) the cilia of the foot, and (*iii*) the holdfast (attachment plaque) of a byssal thread. Some researchers consider bubble formation to be an artifact of increasing water temperature (9 to 20°C; Sigurdsson et al. 1976). More recently, a third mechanism of "thread drifting" has been characterized in a large number of bivalves (incorrectly referred to as byssus drifting or bysso-pelagic migration, since drifting threads have different morphologies; see Lane et al. 1985).

Although drifting threads in *Mytilus edulis* are produced by the foot, they are unlike byssal threads in a number of ways. Drifting threads are hyaline, have a high mucous content, and do not contain collagen. They are simple in structure, lack attachment plaques (adhesive disks), and have a different glandular origin than byssal threads (Lane et al. 1985). Thread drifting is similar to the gossamer flight of spiders, where filamentous threads serve to increase the viscous drag, decrease terminal velocities, and promote entrainment in faster moving eddies (Sigurdsson et al. 1976; Lane et al. 1985; Beukema and de Vlas 1989; similarities have been seen in the filamentous pollen of seagrasses; Ackerman 1989). Thread-drifting plantigrades have been found in plankton, and in some cases it may take up to 30 days for secondary recruitment to take place in existing mussel beds (Bayne 1964*b*). This spatial and temporal separation of plantigrades and adults is considered to have adaptive value in reducing competition and limiting carnivory by adults (Bayne 1964*b*). Thread drifting is potentially an important mechanism of dispersal (Sigurdsson et al. 1976; Lutz and Kennish 1992).

Discussion

The similarities of morphology, size, and behavior between freshwater zebra mussels and marine bivalves are strong. Unlike the life histories of most freshwater bivalves, that of *D. polymorpha* includes a free-swimming veliger larval stage, primary recruitment of pediveligers, and translocation of post-metamorphic individuals undertaking secondary recruitment. These patterns in larval morphology and behavior indicate interesting evolutionary relationships, which are shared with many marine taxa. Given these patterns it is reasonable to adopt and apply a similar nomenclature to the life history stages of *D. polymorpha* and to expect similarities in other aspects of zebra mussel biology.

The distinctions among veliger stages are important and should be considered in limnological and other ecological research. From a scientific perspective, a simple measure of
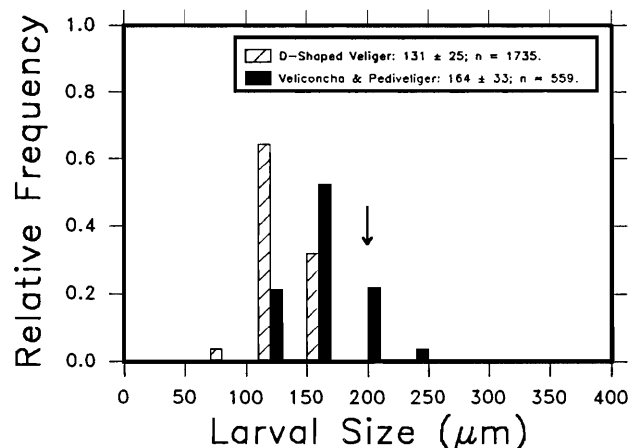
size alone cannot be used to discriminate among *D. polymorpha* veliger stages, owing to the overlap in size among larval stages (Fig. 3, Table 1). This is not unique to zebra mussels, as similar patterns are present within the 39 species (19 different families) of marine bivalves examined (Table 1; cf. Lutz and Kennish 1992). It should be noted that while a single measurement (or mean) has been reported in most marine bivalves, a range of values has been emphasized for the size of *D. polymorpha*. When a similar comparison is made with marine bivalves, for which numerous data sets are available (e.g., *Mytilus edulis*, *Argopecten irradians*, *Mulinia lateralis*, and *Mercenaria mercenaria*), it is evident that the size range within zebra mussel larval stages is reasonable (Table 1). This variation may be explained by the observation that veliger size and development are affected by food concentration (Strathmann et al. 1993).

The identification of the different larval stages of *D. polymorpha* has been largely ignored (Marsden 1992). Unfortunately, there are practical reasons why the identification of larval stages is important, specifically whether and what portion of the larval population are competent to recruit. A simple measure of larval abundance (e.g., veligers per cubic metre) cannot be used to address this issue, since it does not discriminate between incompetent (D-shaped and veliconcha) and competent (pediveliger) larvae, in terms of their ability to settle.

The current model of the life history of *D. polymorpha* is a simplified life history cycle, which has unfortunately been misleading (Mackie 1991; also presented in Hopkins and Leach 1993). This brief depiction of a complex larval biology (cf. Sprung 1993) is in error in both the identification and sequence of life history events. A more complete model of the life history of *D. polymorpha*, as discussed above, is presented in Fig. 4. The major life history stages recognized include, in sequence: (1) fertilization and embryology, i.e., (*i*) cleavage, (*ii*) blastulation, and (*iii*) gastrulation; (2) larvae, i.e., (*i*) trochophore, (*ii*) veliconcha, and (*iii*) pediveliger; and (3) mussels, i.e., (*i*) plantigrade, (*ii*) juvenile, and (*iii*) adult. A synonymy of these stages is presented in Table 3.

For completeness, in Fig. 4 the key morphological attribute that distinguishes among the various stages is indicated by a line through the connecting arrow. For example, the
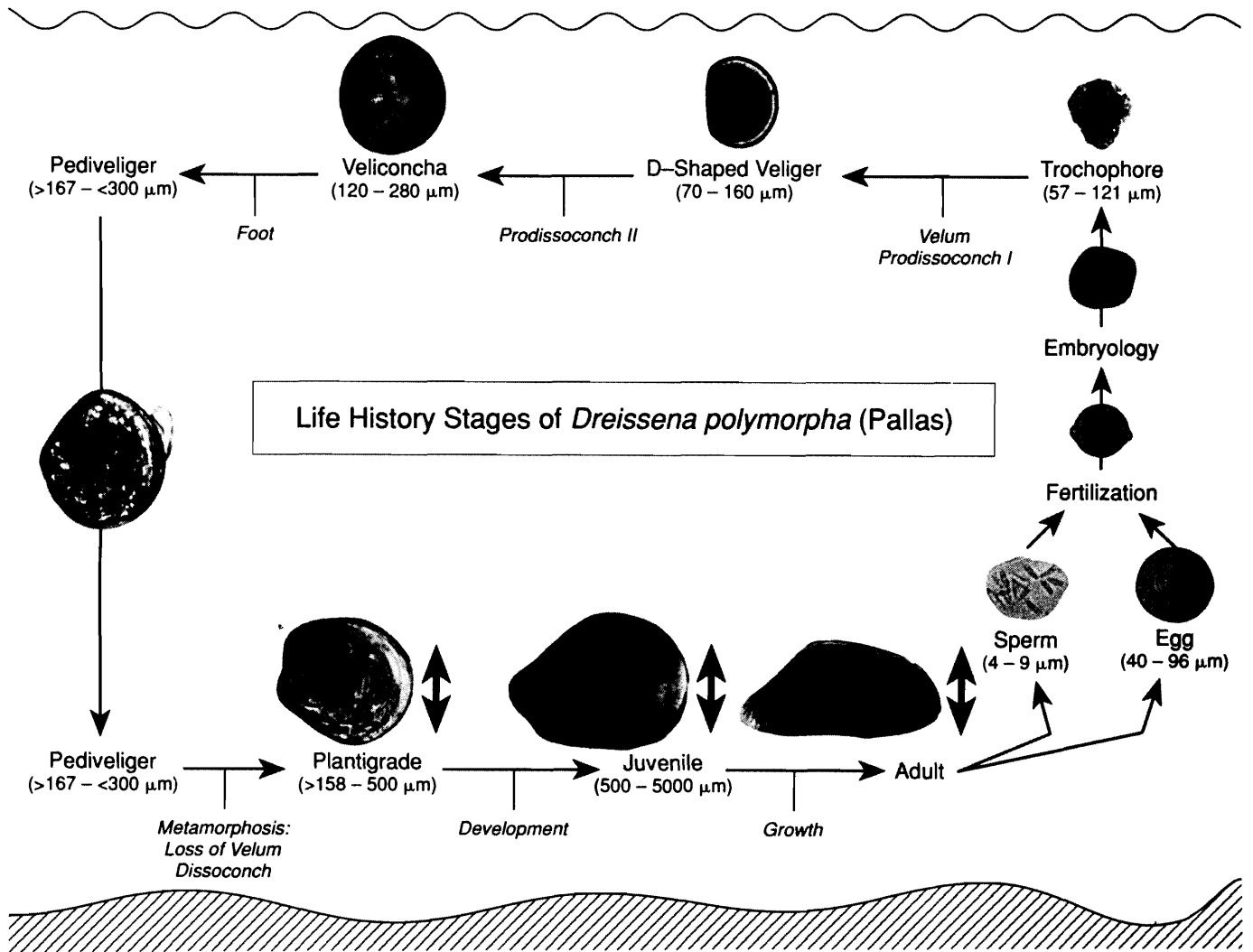
FIG. 4. The life history stages of *Dreissena polymorpha*, with key events indicated below single-headed arrows (see text for details). Double-headed arrows indicate that benthic stages can translocate in the water column. Sizes are as in Table 1 except the following: juvenile from S.J. Nichols (manuscript in preparation); head of sperm from Sprung (1993) and S.J. Nichols (manuscript in preparation).

TABLE 3. Synonymy of nomenclature for *Dreissena polymorpha* life history stages

Larval forms	Trochophore
	Veliger
	D-shaped veliger (straight-hinged)
	Veliconcha (umboned)
	Pediveliger (settling)
Postlarval forms	Plantigrade (postveliger, spat)
	Juvenile (siphon-forming)
	Adult (branchisiphonal)

acquisition of a functional foot notes the transition of a veliconcha to a pediveliger (Fig. 4). The double-headed arrow indicates that benthic forms can be reentrained into the water column. This representation is a reasonable model of the life history of *D. polymorpha*, which should provide the basis for the identification of future research efforts.

This review of the life history of *D. polymorpha* has revealed a number of factors for consideration. There are

important morphological, ecological, and behavioral differences among larval stages, which ultimately bear on issues such as their competency to settle. Larval size alone cannot be used to discriminate among these larval stages; instead, morphological criteria including shell shape and presence of a foot must also be incorporated. The larval stages of *D. polymorpha* are similar to those of marine bivalves because of a common ancestry, which is older than the Miocene (Nuttall 1990). Conversely, similarities among adult *D. polymorpha* and marine bivalves, especially mussels (e.g., byssal adhesion, heteromyarian condition), represent parallel and convergent paths as the result of similar selection pressures (Yonge 1962; Yonge and Campbell 1968; Ackerman et al. 1993; Morton 1993). It is evident that many insights into the biology of freshwater zebra mussels can be derived from a comparison with marine bivalves. Studies of the recruitment, dispersal, and control of *D. polymorpha* should reflect the biology of the larvae and adults, about which a great deal remains to be learned.

Appendix

TABLE A1. Developmental times (post fertilization) and sizes (larval height) of bivalve larval and postlarval stages

	Temp. (°C)	Egg Diameter (µm)	Trochophore Height (µm)	Trochophore Time (h)	D-shaped veliger Height (µm)	D-shaped veliger Time (days)	Veliconcha Height (µm)	Veliconcha Time (days)	Pediveliger Height (µm)	Pediveliger Time (days)	Plantigrade Height (µm)	Plantigrade Time (days)	References
Arcidae													
Arca transversa (= Anadara)	20	52	—	—	70	—	110–130	—	—, 310[a]	—	245–260	—	Loosanoff and Davis 1963; Loosanoff et al. 1966
Noetiidae (= Arcidae)													
Arca transversa	—	—	—	—	70–140	—	130–170	—	—	—	215–320	—	Chanley and Andrews 1971
Noetia ponderosa	19–26	65	—	—	80–160	>1	145	≈23	—	—	185–210	28–42	Chanley 1966; Chanley and Andrews 1971
Mytilidae													
Mytilus edulis[d]	15	70	70	20–24	92	2–2.5	240	22–24	260–265	26–29, 60[c]	>260	—	Bayne 1964b
Mytilus edulis	16–21.5	67[b]	—	—	95	—	140–150	—	215–240	—	—	—	de Schweinitz and Lutz 1976
Mytilus edulis	19	—	70	—	94	—	≈180	—	185–235, 300[a]	—	>215	—	Loosanoff and Davis 1963; Loosanoff et al. 1966
Mytilus edulis	—	≈65	—	—	90–175	1–2	≈150	≈9	—	—	215–305	90[c]	Chanley and Andrews 1971
Mytilus edulis	17	50	—	20	120	<2	—	—	≈280	30	—	8–12	Tortell 1980
Mytilus viridis	23–25	≈55	—	—	80	<1	—	—	240[a]	8	—	30[c]	Tan 1975
Aulacomya maoriana	17	66.3[b]	73[b]	33	80	2.5	>200	>8–15	>300	—	—	—	Tortell 1980
Brachidontes granulata	12–16	70–81	≈100	20	117[b] (5.3)	3	150	12	190–200	30–40, 73[c]	200–240	>18	Campos and Ramorino 1979
Modiolus capax	20±2	—	—	19	108–160	1	165–195	12	230	12–18	>270	12–14	Orduña Rojas and Farfán 1991
Modiolus demissus (= Geukensia) (= Arcuatula demissa)	22	—	—	—	110–115	—	≈170–200	—	200, 295[a]	43[c]	220–275	19	Loosanoff and Davis 1963; Loosanoff et al. 1966
Modiolus modiolus	16–21.5	85[b]	—	—	105	<2	150–160	8	245–295, 340[a]	13–18	—	—	de Schweinitz and Lutz 1976
Pectinidae													
Argopecten irradians (= Aequipecten)	24±1	62[b]	82	20	101	2	122	5	184–190	12–15	200–230	≈19	Sastry 1965
Argopecten irradians	20–23	55–65	—	—	>80	—	145	—	200	—	>175	14	Loosanoff and Davis 1963; Loosanoff et al. 1966
Argopecten irradians	—	—	—	—	85–140	1	≈155	≈5	—	—	175–200	30–47	Chanley and Andrews 1971
Patinopecten yessoensis	8–9	—	—	—	≈150	5–7	200	20	280	40	280–320	—	Ventilla 1983
Anomiidae													
Anomia simplex	Lab.	42–45	≈90	48	>58	—	≈116–127	—	—	—	180–210	12–33	Loosanoff and Davis 1963; Loosanoff et al. 1966
Placunidae													
Placuna placenta	27	45	—	—	50–105	<1	100–200	2–8	180–220	8–10	220–230	10–11	Young 1980
Ostreidae													
Crassostrea virginica	17–33	45–62	—	—	68–75	1	85–90	—	—, 355[a]	—	275–315	12	Loosanoff and Davis 1963; Loosanoff et al. 1966
Crassostrea virginica	—	—	—	—	65–100	—	≈95	≈10	—	—	310–350	—	Chanley and Andrews 1971
Crassostrea gigas	—	—	—	—	70	1.5–2	>95	—	—	—	300	—	Loosanoff et al. 1966
Crassostrea glomerata	17±1	40	—	12–18	50–60	1–4	110	—	320–350	—	350–360	—	Dinamani 1973
Crassostrea iredalei	5–10	48	—	8	64–84	—	81–305	5–22	240–305	16–22	>328	20	Ver 1986
Cardiidae													
Cardium edule	10–15	50	—	—	112	3–5	135–160	>10	250	20	250–350	25	Creek 1960
Laevicardium mortoni	20	60–65	—	—	85	—	≈120–140	—	205, 250[a]	—	<220	8–10	Loosanoff and Davis 1963; Loosanoff et al. 1966
Laevicardium mortoni	—	—	—	—	80–130	≈7	≈120–140	≈7	—	—	205–245	—	Chanley and Andrews 1971
Mactridae													
Mulinia lateralis	—	—	—	—	55–60	—	105	—	—	—	190–230	6	Loosanoff and Davis 1963; Loosanoff et al. 1966
Mulinia lateralis	20–25	≈50	—	9	60–100	0.5	≈120	—	150–200	≈6	185–240	—	Chanley and Andrews 1971
Mulinia lateralis	—	—	—	—	70–75	—	≈150	—	—	—	200–245	6–8	Loosanoff et al. 1966
Rangia cuneata	—	—	—	—	75–135	—	150–170	—	215–240	—	160–175	—	Rhodes et al. 1975
Spisula solidissima (= Mactra)	22	56.5[b]	—	12–16	80.	—	—	—	—	—	220–250	19	Chanley and Andrews 1971
Spisula solidissima	—	—	—	—	80–130	—	≈140	≈10–19	—	—	220–275	—	Loosanoff et al. 1966
Solenidae													
Ensis directus	24	64–73	—	—	80–92	—	115–135	—	—, 270[a]	—	>210	10	Loosanoff and Davis 1963; Loosanoff et al. 1966

TABLE A1 (concluded)

Species	Temp. (°C)	Egg diameter (µm)	Trochophore Height (µm)	Trochophore Time (h)	D-shaped veliger Height (µm)	D-shaped veliger Time (days)	Veliconcha Height (µm)	Veliconcha Time (days)	Pediveliger Height (µm)	Pediveliger Time (days)	Plantigrade Height (µm)	Plantigrade Time (days)	References
Ensis directus	—	—	—	—	85–155	—	≈145	≈12	—	—	220–270	—	Chanley and Andrews 1971
Tellinidae													
Tellina agilis	—	—[b]	—	—	75–105	—	≈130	≈7	—	—	200–250	—	Chanley and Andrews 1971
Macoma mitchelli	23	59[b]	—	—	70–80	<1	95–150	>4	>160	7	160–205	6–7	Kennedy et al. 1989
Donacidae													
Donax variabilis	20–25	—	—	—	70–120	—	≈130	≈12	—	—	275–340	—	Chanley 1969; Chanley and Andrews 1971
Dressenidae													
Dreissena polymorpha	17–24	40–96	57–121	6–96	70–160	2–9	120–180	7–9	>167–<300	10	>158–500	18–90	See Table 1
Mytilopsis leucophaeata	26	—	—	—	≈74	≈2	≈180	≈6	210[b]	—	>270	6–8	Siddal 1979
Veneridae													
Mercenaria mercenaria (= *Venus*)	21–30	60–85	85	12	90–140	1–3	140–220	3–20	170–220	6–20	200–230	>6–20	Carriker 1961
Mercenaria mercenaria	15–33	70–73	—	—	≈86–105	—	125–130	—	—	—	170–240	6–8	Loosanoff and Davis 1963; Loosanoff et al. 1966
Mercenaria mercenaria	—	—	—	—	100–155	—	150	≈6–11	—	—	175–235	—	Chanley and Andrews 1971
Mercenaria campechiensis	—	—	—	—	100–110	—	≈142–152	—	—	—	175–215	—	Loosanoff et al. 1966
Venus striatula	Lab.	—	—	—	90–110	2	—	—	—	—	220–240	—	Ansell 1962
Pitar morrhuana (= *Pitar morrhuanas*)	21	49–60	—	—	78–80	—	95–125	—	—, 192[a]	—	160–180	—	Loosanoff and Davis 1963; Loosanoff et al. 1966
Tapes semidecussata (= *Venerupis philippinarum*)	Lab.	60–75	—	—	95	—	120–140	—	—	—	175–220	14	Loosanoff and Davis 1963; Loosanoff et al. 1966
Petricolidae													
Petricola pholadiformis (= *Petricolaria*)	20–25	51–55	—	—	65–75	—	≈130–147	—	—, 193[a]	—	185	13	Loosanoff and Davis 1963; Loosanoff et al. 1966
Petricola pholadiformis	—	—	—	—	70–125	—	≈120	≈10	—	—	165–185	—	Chanley and Andrews 1971
Myidae													
Mya arenaria	20	68–73	—	—	86–90	—	≈123–155	—	165	—	170–228	28	Loosanoff and Davis 1963; Loosanoff et al. 1966
Pholadidae													
Barnea truncata	19–26	—	—	—	55–100	—	≈140	≈19–22	—	—	250–315	35	Chanley 1965a; Chanley and Andrews 1971
Cyrtopleura costata	—	—	—	—	60–95	—	≈120	≈17	—	—	≈300	—	Chanley and Andrews 1971
Teredinidae													
Teredo navalis	—	—	—	—	70–105	—	105	—	—	—	190–200	—	Chanley and Andrews 1971
Bankia indica	20	45[b]	80	—	75–90	<1–3	>90–250	9–15	273[b]	—	300	17–26	Nair and Saraswathy 1971
Pandoridae													
Pandora inaequivalvis	18±1	105–125	150	17.5	≈167	<1	≈200	>2	≈200	3.5	≈200	<4	Allen 1961
Summary													
All bivalves	5–26	40–125	57–150	6–96	50–175	<1–9	81–305	2–24	>160–350	6–40	>158–500	6–90	
Marine bivalves (i.e., excluding *D. polymorpha*)	5–26	40–125	70–150	8–48	50–175	<1–7	81–305	2–24	>160–350	6–40	>160–360	6–47	

NOTE: Whenever possible, a range of values is given. Values in parentheses are standard deviations. —, unavailable; ≈, approximate or estimated size from photographs.

[a] Maximal larval size.

[b] Mean value.

[c] Maximal duration.

[d] There is some confusion over *Mytilus edulis*, which may actually be *M. trossulus* or *M. galloprovincialis* in some regions (e.g., west coast of North America).

Acknowledgements

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