BIOLOGY OF THE UNCOMMON DREISSENID BIVALVE *MYTILOPSIS LEUCOPHAEATA* (CONRAD, 1831) IN CENTRAL CHESAPEAKE BAY

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ABSTRACT

The dark falsemussel *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae) is an uncommon epifaunal bivalve of oligohaline–mesohaline habitats in Chesapeake Bay. It is small and weakly attached to different substrates by its byssi, but is presumably somewhat protected from predators by its habit of living within byssate clumps of hooked mussels *Ischadium recurvum* (Rafinesque, 1820) attached to eastern oysters *Crassostrea virginica* (Gmelin, 1791). It is less active than *I. recurvum* in terms of crawling from under encumbrances or moving and reattaching when detached from a substrate. Its extensible inhalant siphon should enable it to obtain food and oxygen from the water column even when confined within *I. recurvum* clumps or its own single-species clumps. In terms of egg size and the timing of larval development, it shares a number of characteristics with the freshwater dreissenids *Dreissena polymorpha* and *D. rostriformis bugensis* and with *I. recurvum*. Given the limited numbers of *M. leucophaeata* that seem to be the rule in its native habitat, there are questions, so far unanswered, as to how the population persists, how its spawning is coordinated and how successful is fertilization when widely separated individuals do spawn.

INTRODUCTION

The dark falsemussel, *Mytilopsis leucophaeata* (Conrad, 1831), is a small, poorly known dreissenid bivalve that occurs along the western Atlantic and Gulf of Mexico coasts from New England in the USA to lagoons in Mexico (e.g. García-Cubas, 1981; Marelli & Gray, 1983; Smith & Boss, 1996). A review of published data (Kennedy, 2011) reveals it to be generally uncommon in its North American home range, usually occurring in low numbers attached byssally to eastern oysters *Crassostrea virginica* (Gmelin, 1791) in relatively low salinity habitats. It also attaches to hard substrate such as pier pilings, sticks, stones or bottles (personal observation). On oyster shell it is often nestled among individuals of a more abundant and larger mytilid that also attaches byssally, the hooked mussel *Ischadium recurvum* (Rafinesque, 1820).

Nuttall (1990) reported that the genus *Mytilopsis* first appeared in Europe in the Eocene and invaded the tropical Western Hemisphere in the late Oligocene, subsequently dying out in Europe in the Pliocene. *Mytilopsis leucophaeata* has since reappeared in Europe, being first reported from the River Schelde near Antwerp, Belgium, in 1835 (Nyst, 1835). It was subsequently discovered in additional locations including The Netherlands, Germany and France and has recently expanded its range to Britain, Spain, Ukraine and Finland; outside Europe it has arrived in northern Brazil (summarized in Kennedy, 2011).

Given its scarceness in its native habitat, it is surprising to find that introduced *M. leucophaeata* are an industrial pest in some regions. For example, Rajagopal, Van der Velde & Jenner (1997) reported it to be the dominant macrofouling organism of electricity-generating stations in the Noordzeekanaal of The Netherlands. Laine, Mattila & Lehikoinen (2006) reported that a population near a power plant's cooling-water discharge in the Baltic Sea numbered up to 28,000 individuals m^{-2}. However, the species is apparently capable of short-term but rapid population growth in its native habitat, as demonstrated by an irruption that occurred in 2004 in some tributaries of upper Chesapeake Bay, but which had subsided by 2005 or 2006, depending on location (Bergstrom *et al.*, 2009). No other irruption has ever been reported in the literature on Chesapeake Bay.

The purpose of this paper is to present the findings of investigations on aspects of the biology of this under-studied species in its natural habitat in central Chesapeake Bay. In addition to expanding our knowledge of this species in its native estuarine habitat, the new information may be useful to scientists studying irruptions of this species outside its North American range. Unless otherwise noted, most of the experimental animals were collected from sites in the Choptank River near Horn Point Laboratory (38.35°N, 76.08°W). Investigations were performed opportunistically over a number of years as *M. leucophaeata* were collected in the course of other research. For some experiments on the species, I compared the results with results of similar experiments on *Ischadium recurvum*, which co-exists in the same region of Chesapeake Bay. I also made some comparisons with experiments on two other dreissenid species, the freshwater zebra mussel *Dreissena polymorpha* (Pallas, 1771) and the quagga mussel *D. rostriformis bugensis* (Andrusov, 1897) collected from Lake Ontario.

MATERIAL AND METHODS

Abundance in nature

During numerous studies of Maryland's oysters (e.g. Kennedy & Krantz, 1982; Kennedy *et al.*, 1995), I observed that *Mytilopsis leucophaeata* were uncommon on oyster shell, especially in comparison with *Ischadium recurvum*. To determine relationships between numbers of the two species and the shell size of their eastern oyster substrate, oysters were collected from seven oyster bars in central Chesapeake Bay in May and June

2006. In the laboratory, samples of from 10 to 19 oysters from each oyster bar were examined (total of 80 oysters) for *M. leucophaeata* and *I. recurvum*, the numbers of each attached bivalve were counted, then oyster height (distance from umbo to bill) and *M. leucophaeata* and *I. recurvum* length (longest anterior-to-posterior dimension) were measured. These data were used to determine the relationships among fouling bivalve numbers with oyster size and with each other.

Attachment strength and byssal-thread diameters

Ischadium recurvum seemed to be more firmly attached to substrate by their byssal threads than were *M. leucophaeata*. To measure attachment strength (or detachment force) of the byssi of both species, a 250-g spring balance from Ohaus® was used for nearly all measurements on *M. leucophaeata* and some *I. recurvum*, plus a 22-kg spring balance from Rapala® for most *I. recurvum* and a few large *M. leucophaeata*. The 250-g balance was calibrated with a combination of weights from 10 to 50 g and the 22-kg balance with the same weights and a 1 kg weight. The attachment strengths of 58 *M. leucophaeata* of the full range of available sizes and 26 *I. recurvum* in the same size range were measured in August 2009 for animals attached to oyster shell collected from laboratory ponds. Each bivalve used was attached to the substrate by its own byssi and not the byssi of other bivalves. A small alligator clamp held a bivalve as it was pulled away from the substrate in a vertical direction until it came free. The strength of the pull was recorded and converted to Newtons. In a few instances, the oyster shell surface gave way before the byssi ruptured; such measurements were discarded.

In late April 2010 the byssal-thread diameters of 10 each of the two species were measured for animals that had been attached to oyster shell over winter in our ponds. Byssi were cut where they joined the oyster shell and byssal segments protruding from the shell were then cut and examined under the microscope, an ocular micrometer being used to measure the widest diameters of 20 byssal threads from each animal.

Crawl-out experiments

Because *M. leucophaeata* and *I. recurvum* often occur in mixed-species clumps, I examined their ability to crawl from under obstacles, a behaviour previously studied in a variety of mytilid species (Harger, 1968; Tan, 1975; Kennedy, 1984). For an interdreissenid comparison, I also contrasted *M. leucophaeata* crawl-out behaviour with that of the two species of *Dreissena* under similar conditions. For the experiments, glass bowls 12 cm in diameter by 5 cm deep were used along with glass beads (#3,000) measuring 6 mm in diameter. The beads and bowls were sterilized by boiling in deionized water before each use. Ten large (over 16–17 mm) or 10 smaller individuals of the four bivalve species were placed haphazardly in the bottom of a bowl (one species per bowl) and covered with beads. During the 48-h experiments (below), large experimental animals were covered by three or four layers of beads and smaller animals by two or three layers. The depth of the beads was slightly greater (2 cm) for the 7-day experiments (below). The estuarine species were held in ambient salinities (11–14) whereas the freshwater dreissenids were held in artificial fresh water (Sprung, 1987). All experiments were run at room temperature (23–24°C).

In July 1995, 48-h experiments involving the four species were performed, with the two species of *Dreissena* tested three times and the other two species tested twice. In May 2009, the experiments were repeated with just *M. leucophaeata* or *I. recurvum* held under 2 cm of glass beads for the longer period of 7 days. During all experiments I made note of movements of individuals of each species and recorded how many crawled up to or onto the surface of the beads.

Movement and byssal attachment experiments

To compare the ability of *M. leucophaeata* and *I. recurvum* to move and to reattach byssally to a surface, experiments in April and May 2009 involved 20-cm glass bowls placed on individual sheets of plain paper covered with a grid of 2.5 by 2.5 cm squares. Individuals of a particular species in same-species tests were placed on squares on five rows, with an empty square between individuals. Individuals in mixed-species tests were placed on adjacent squares, alternating the species (e.g. *M. leucophaeata*, then *I. recurvum*, then *M. leucophaeata* etc.). The bowls were examined at irregular intervals over a 3-day period and notes were made about movement by individual bivalves from their starting square and about the presence of byssal threads. Experimental animals were tested at room temperature in ambient river water of a salinity similar to that from which they had been collected.

Larval development

I used three larval broods to provide information on development and metamorphosis of *M. leucophaeata* larvae, and subsequent development of settled juveniles at ambient salinities and room temperature. For Brood 1, a few hundred *M. leucophaeata* were collected from an oyster bar in the Choptank River in February 1992. They were placed, still attached to the oysters, in running Choptank River water in the laboratory. They were held in ambient conditions while temperature and salinity rose gradually and naturally until mid-June (23°C; salinity 12). They were then detached from the oysters and placed in containers in running river water chilled to 20°C. On July 11, about 100 individuals were removed to a large glass dish containing salinity 12 water at room temperature. Spawning occurred within 90 min as evidenced by the presence of eggs in water samples pipetted from the dish (no spawning behaviour was observed).

When the eggs were discovered, samples were placed in a Sedgwick–Rafter cell and the diameter of unfertilized eggs measured under a microscope with a calibrated ocular micrometer. The spawning dish's contents were washed through a 105-μm screen to trap debris and into a 20-l culture vessel containing 1 μm-filtered water adjusted to salinity 15 by use of 5 μm-filtered seawater. Larvae were cultured at room temperature and at salinity 15 until they metamorphosed. After the first 48 h of development the culture water was renewed every second day by retaining the larvae on Nitex® screens, discarding the old culture water and providing new filtered water. Larvae were fed algal food (*Isochrysis* sp. clone CISO) daily. These larvae formed the basis for the report by Conn *et al.* (1993) that dealt solely with external appearance of *M. leucophaeata* as an aid to identification. Here I provide measurements of size over time and report on the development of swimming behaviour and respiration/feeding currents. When embryos and larvae were sampled, the culture water was first agitated vertically with a perforated plastic disk plunger to distribute the organisms randomly within the water column. A few millilitres of culture water (with organisms) were extracted by pipette periodically over the first 24 h and daily thereafter for 11 more days, placed in a Sedgwick–Rafter cell and examined under a microscope. The ocular micrometer was used to measure larvae for shell length (maximum anteroposterior distance, μm) and occasionally for height (maximum dorsoventral distance, μm). After the larvae metamorphosed and attached to the walls of the culture vessel, juveniles were

held in salinity 15 water and fed daily for 26 more days, with length measurements taken on Days 30 and 37.

A second brood of larvae was produced from Choptank River adults in May 1995 in water of salinity 11.5 and treated as above. The juveniles from this brood were observed from Days 15 to 49 while I made notes on their morphological development and behaviour. A third brood was spawned in June 1995 (salinity 12) and used to provide data on larval development during the first 24 h after fertilization to supplement developmental data from Brood 1.

For comparisons with larvae of the two species of *Dreissena* and with *I. recurvum*, I used data from animals spawned in the laboratory by use of techniques similar to those used to spawn *M. leucophaeata*. Some of the data on the dreissenid species were included in Wright *et al.* (1996).

RESULTS

Abundance in nature

Sizes of the 80 eastern oysters taken from seven oyster bars and examined for numbers of attached *Mytilopsis leucophaeata* and *Ischadium recurvum* ranged from 66 to 165 mm (average 102 mm). Every oyster had from four to 166 *I. recurvum* attached, for a total of 2,529 and a mean of 32 *I. recurvum* per oyster. By contrast, 39 of the 80 oysters bore no *M. leucophaeata* (all 10 oysters from Tolly Point bar had none), with only one to 13 *M. leucophaeata* attached to the remaining oysters, for a total of 123 animals. There was thus an average of three *M. leucophaeata* per oyster that had *M. leucophaeata* attached ($n = 41$) or 1.5 individuals per oyster examined ($n = 80$).

For each of the seven oyster bars, when numbers of *M. leucophaeata* or *I. recurvum* were regressed on oyster height, none of the regressions differed from zero. Data for all seven bars were combined and again the regressions of numbers of each species on oyster height were not different from zero (Fig. 1: upper, middle). To explore the relationship between the numbers of the two species occurring together on oysters, I combined the data for all oyster bars. The subsequent statistically significant regression for *M. leucophaeata* number on *I. recurvum* number yielded an R^2 value of 0.57 (Fig. 1: lower).

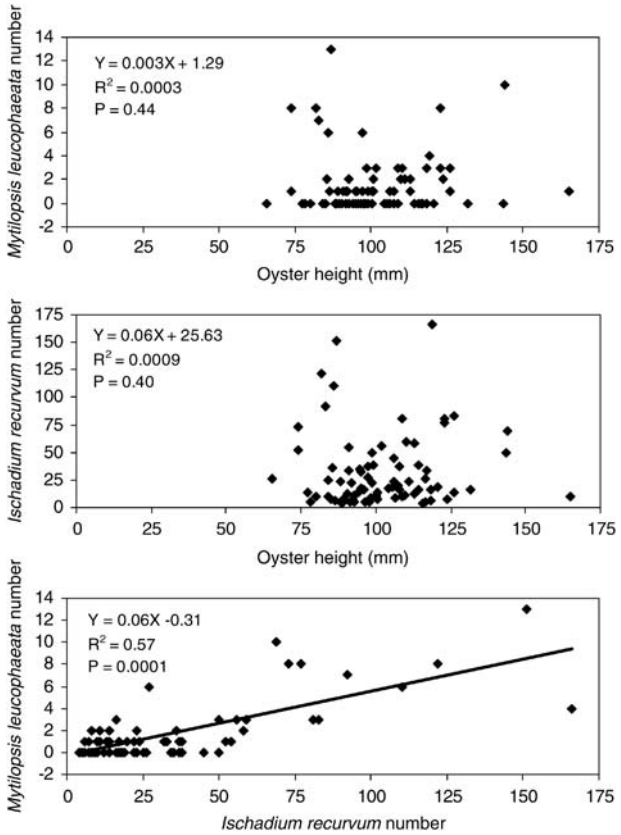

Figure 1. Numbers of *Mytilopsis leucophaeata* or *Ischadium recurvum* in relation to oyster height (upper and middle panels) and the relationship between numbers of *M. leucophaeata* to *I. recurvum* on oysters (lower panel). Numbers developed from 80 oysters collected from seven oyster bars in central Chesapeake Bay.

Attachment strength and byssal-thread diameters

Shell lengths of individuals used in the attachment-strength study ranged from 6.8 to 23.4 mm for the 58 *M. leucophaeata* and 8.1–19.7 mm for the 26 *I. recurvum*. A linear regression of attachment strength (Newtons) upon length (mm) fitted the data best for each species (Fig. 2). Based on the regression equations, the predicted attachment strength was 1.01 N for a 10-mm *M. leucophaeata* and 2.41 N for a 20-mm specimen; these data compare with 1.94 and 8.74 N for 10- and 20-mm *I. recurvum*, respectively (Table 1). Average byssal-thread diameters were positively and significantly correlated with mussel size for both species (Fig. 3), but byssi of *I. recurvum* were about twice the diameters of those of *M. leucophaeata* of a similar size.

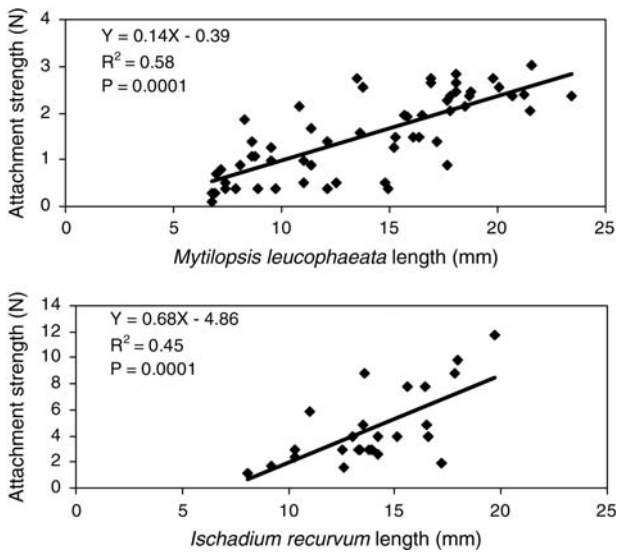

Figure 2. Linear regressions of byssal attachment strength (Newtons, N) on shell length of 58 *Mytilopsis leucophaeata* and 26 *Ischadium recurvum*, measured while attached to oyster shell.

Crawl-out experiments

Mytilopsis leucophaeata were somewhat less active than the other bivalves tested for the ability to crawl from under encumbrances. During the two 48-h experiments just 10% of small and 15% of large *M. leucophaeata*, respectively, reached the surface of the glass beads, compared with 20% of small and 35% of large *I. recurvum* (Table 2). During the three 48-h experiments on the two species of *Dreissena*, 50% of small and 70% of large *D. rostriformis bugensis* reached the surface of the glass beads, as did 50% of small and 40% of large *D. polymorpha*. The average sizes of the small and large bivalves used in these experiments were very similar regardless of whether they reached the bead surface or not. In the 7-day

Table 1. Comparisons of attachment strength in Newtons (N) of byssus-forming dreissenid and mytilid bivalves.

Geographic location	Habitat conditions	Bivalve species	Animal size or shell area	Attachment strength (N)	Additional information	Reference
		Dreissenids				
Chesapeake Bay	Estuarine holding ponds	*Mytilopsis leucophaeata*	10 and 20 mm	10 mm, 1.01* 20 mm, 2.41*	On oyster shell and measured in April	This paper
Mumbai, India	Laboratory	*Mytilopsis adamsi*	Not given	1.1	Attached to slate plates for 10 d	Udhayakumar & Karande (1989)
Poland	Lake Śniardwy	*Dreissena polymorpha*	7–28 mm	10 mm, 0.11† 20 mm, 0.4†	Attached to stones, in summer	Prejs *et al.* (1990)
Ontario, Canada	Laboratory	*Dreissena polymorpha*	10.0 ± 0.08 mm	Range: 0.2–8.8; $\bar{X}$ ± SE: 1.4 ± 0.4	On rocks	Ackerman *et al.* (1995)
		Dreissena rostriformis bugensis	10.4 ± 0.2 mm	Range: 0.12–9.8; $\bar{X}$ ± SE: 1.55 ± 0.07	On rocks	Ackerman *et al.* (1995)
Vistula River, Poland	Laboratory	*Dreissena polymorpha*	<7 to >18 mm	Range: ~0.2 to ~2.1‡	Attached to plastic for 6 d	Kobak (2006)
Milwaukee, Wisconsin	Laboratory	*Dreissena polymorpha*	5–10 mm for 32-h attachment; 'slightly larger' for 2- to 3-month exposure	Averages after (1) 32 h = 0.31; (2) 2 months = 1.13; (3) 3 months = 1.56	Acrylic plates for 32-h experiment; PVC plates for 2- to 3-month experiment	Peyer *et al.* (2009)
	Laboratory	*Dreissena rostriformis bugensis*	5–10 mm for 32-h attachment; 'slightly larger' for 2–3 month exposure	Averages after (1) 32 h = 0.12; (2) 2 months = 0.97; (3) 3 months = 1.69	Acrylic plates for 32-h experiment; PVC plates for 2- to 3- month experiment	Peyer *et al.* (2009)
		Mytilids				
Chesapeake Bay	Estuarine holding ponds	*Ischadium recurvum*	10 and 20 mm	10 mm, 1.94* 20 mm, 8.74*	On oyster shell and measured in April	This paper
Sippewissett Beach, MA, USA	Low (L), mid (M), or high (H) shore	*Mytilus edulis*	Not given	16.7 (L), 9.8 (M), 4.9 (H)		Glaus (1968)
Santa Barbara, CA, USA	Open shore	*Mytilus galloprovincialis*	Shell area (length × height) = 2 cm^2	14.4	Based on regressions for animals <32.7 mm long	Harger (1970)
	Open shore	*Mytilus californianus*	Shell area (length × height) = 2 cm^2	23.2	Based on regressions for animals <32.7 mm long	Harger (1970)
	Open shore	*Septifer bifurcatus*	Shell area (length × height) = 2 cm^2	39.1	Largest mussels were 35–45 mm long	Harger (1970)
South Wales UK	Exposed outcrop	*Mytilus edulis*	Mean size = 31 mm	12.7	Data for April (values higher in September)	Price (1980)
Tatoosh Island, WA, USA	Exposed shore	*Mytilus californianus*	Not given	140.0–241.8	Measured in summer	Witman & Suchanek (1984)
Friday Harbor, WA, USA	Exposed (E) or protected (P) shore	*Mytilus galloprovincialis*	Not given	103.8 (E), 6.1 to 7.1 (P)	Measured in summer	Witman & Suchanek (1984)

Continued

Table 1. *Continued*

Geographic location	Habitat conditions	Bivalve species	Animal size or shell area	Attachment strength (N)	Additional information	Reference
Southwest England	Not given	*Mytilus edulis* ME, *M. galloprovincialis* MG and hybrids H	30 mm	ME, 13.4 MG, 21.6 H, 17.6	Measured in September	Gardner & Skibinski (1991)
Southwest England	High shore (HS) and low shore (LS)	*Mytilus edulis* ME and *M. galloprovincialis* MG	32–34 mm	HS–MG, 19.4 HS–ME, 14.1 LS–MG, 23.0 LS–ME, 15.7	Measured in May	Willis & Skibinski (1992)
Halifax, Canada	Tidepools and emergent rocks	*Mytilus edulis* and *M. trossulus*	~0.1–1.5 cm^2 cross-sectional area	0.5–18 N; increased with size	Measured over the year	Hunt & Scheibling (2001)
Plettenberg Bay, South Africa	Mid-mussel zone	*Mytilus galloprovincialis* MG and *Perna perna* PP	20 mm	MG, 5.4[§] PP, 8.6[§]	Measured in January (summer)	Zardi *et al.* (2006)
Matanzas, Chile	Rock platform RP and rock outcrop RO	*Perumytilus purpuratus* PP and *Semimytilus algosus* SA	15–25 mm	PP–RP, 27[¶] PP–RO, 21[¶] SA–RP, 21[¶] SA–RO, 15[¶]	Centrally located mussels within monolayer beds, measured in December (summer)	Caro *et al.* (2008)

*Estimated from regressions (see text). †Calculated with equation in Preis *et al.* (1990: fig. 4). ‡Estimated from Kobak (2006: fig. 4). §Data on 20 mm individuals derived from regressions developed for solitary mussels over the size range of 23–69 mm. ¶Estimated from Caro *et al.* (2008: fig. 1).

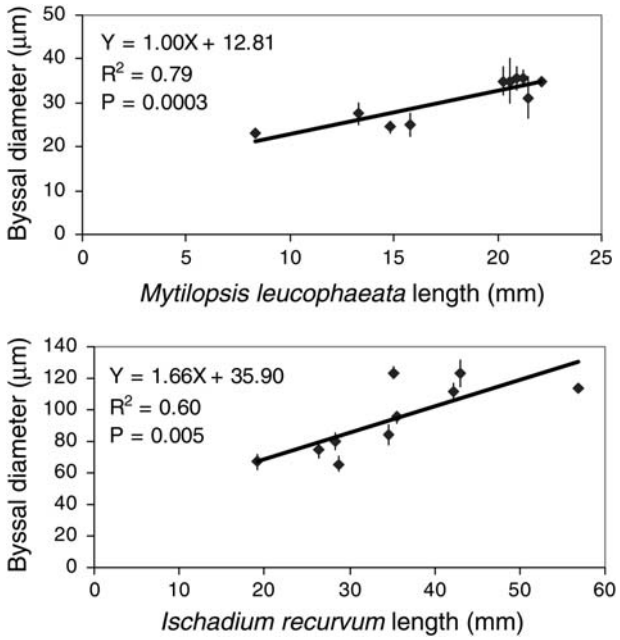

Figure 3. Linear regressions of average byssal diameters ($n = 20$ byssi per bivalve; bars are SE) *vs* bivalve length for 10 *Mytilopsis leucophaeata* and 10 *Ischadium recurvum*.

experiment, 50% of small and 20% of large *M. leucophaeata* reached the surface of the glass beads, compared with 50% of small and 60% of large *I. recurvum*.

Movement and byssal attachment experiments

Ischadium recurvum were much more active than *M. leucophaeata* in these experiments. During the April 2009 experiment, no *M. leucophaeata* (size range: 15.3–22.4 mm) in their single-species bowl moved from their starting square over the 3-day experiment and only two were attached by byssi after 3 days. By comparison, *I. recurvum* (21.1–28.0 mm) in their single-species bowl were more active, with movement seen as early as Hour 3. By Hour 20, one four-animal clump and one two-animal clump of *I. recurvum* had formed, with the mussels remaining in those clumps throughout the 3-day experiment. Also, by Hour 20, eight of 10 *I. recurvum* were attached by byssi, with nine byssally attached at the end of 3 days. In the mixed-species bowl (*M. leucophaeata*: 13.5–22.0 mm; *I. recurvum*: 20.6–29.5 mm), some *I. recurvum* had moved slightly after 3 h. After 20 h, all *I. recurvum* had formed clumps with each other and with some *M. leucophaeata*, but five of the 10 *M. leucophaeata* had not moved. After 3 days, there were five clumps of two to six animals that were of mixed species; three *M. leucophaeata* had still not moved.

During the May 2009 experiment, no *M. leucophaeata* (13.7–21.3 mm) had moved after 3 h. One had moved slightly after 7 h, and more so by Hour 23. Another had moved by 48 h, and two more had moved by the end of the experiment on Day 3. By Hour 3, two had formed a byssus, with three attached byssally by Hour 28; no others had formed a byssus by the end of the experiment. As in the April experiment, *I. recurvum* (16.9–22.5 mm) were more active; one had moved after 1 h, two pairs had formed after 2 h, there were three pairs after 3 h and only one mussel had not moved by Hour 3, although it had formed a byssus. After 7 h there were two clumps of four *I. recurvum* and all had moved, with nine anchored by byssi. All *I. recurvum* had byssi after 22 h. This

Table 2. Comparisons of results of experiments on bivalves covered by small glass beads or gravel and left to reach the surface within 48 h.

Species	Size range (mm)	Number used	Percent on surface after 48 h	Mean size on surface (mm) ± SD	Mean size on bottom (mm) ± SD	Reference
Mytilopsis leucophaeata (2 experiments)	S 10.0–15.4	20	10	14.4 ± 1.34	13.0 ± 1.64	This paper
	L 17.4–23.7	20	15	18.9 ± 1.24	19.8 ± 1.42	
Ischadium recurvum (2 experiments)	S 9.5–14.2	20	20	12.2 ± 0.77	11.7 ± 1.38	This paper
	L 16.4–20.8	20	35	18.7 ± 1.48	18.1 ± 1.16	
Dreissena polymorpha (3 experiments)	S 9.1–16.0	30	50	13.1 ± 2.10	12.5 ± 1.52	This paper
	L 17.6–23.7	30	40	20.1 ± 2.00	18.2 ± 1.49	
Dreissena rostriformis bugensis (3 experiments)	S 9.6–16.7	30	50	13.8 ± 1.35	12.4 ± 2.01	This paper
	L 16.5–23.0	30	70	19.0 ± 1.58	18.6 ± 1.21	
Mytilus edulis from US East Coast	10–20	75	~89	ND	ND	Harger (1968)*
Mytilus galloprovincialis from US West Coast	10–20	75, 200	~53, 72	ND	ND	Harger (1968)*
Mytilus californianus from US West Coast	10–20	200	~13	ND	ND	Harger (1968)*
Perna viridis in Singapore	7.5–27.5	100	~76	ND	ND	Tan (1975)†
Perna canaliculus in New Zealand	10–20	40–50	~45	ND	ND	Kennedy (1984)‡
Mytilus galloprovincialis in New Zealand	10–20	50	~5	ND	ND	Kennedy (1984)‡
Aulacomya maoriana in New Zealand	10–20	25–40	~2	ND	ND	Kennedy (1984)‡

L, larger animals; S, smaller animals; ND, no data. *Placed 5 cm of 5- to 7.5-mm pea gravel over the mussels at 12–18°C; used 75 West Coast *M. galloprovincialis* in comparisons with 75 East Coast *M. edulis* (three experiments) and 200 *M. galloprovincialis* in comparisons with 200 *M. californianus* (two experiments). †In two experiments, placed 5 cm of ~7-mm gravel over five size classes of mussels (10 per size class) at an unstated temperature (presumably tropical) and in marine salinities. Each experiment ran for just 1 day. ‡Placed 3 cm of 3- to 8-mm gravel over the mussels held at 12–17°C and salinity 32–36 in three experiments.

situation persisted until the experiment ended after 3 days with one clump of four, one of three and three singles.

These differences in activity between the two species persisted in the mixed-species bowl (*M. leucophaeata*: 14.7–22.6 mm; *Ischadium recurvum*: 15.5–21.6 mm). Within 1 h one *I. recurvum* had moved from the floor of the bowl to attach to the wall and three had clumped with one *M. leucophaeata*. By Hour 3, nine *I. recurvum* had moved, with eight in clumps and one by itself. In comparison six *M. leucophaeata* had not moved and were still by themselves at Hour 3; the other four had *I. recurvum* attached to them. By Hour 5, five *M. leucophaeata* remained in their original square, with the other five living in three mixed clumps with *I. recurvum*; there was one additional single-species clump of *I. recurvum*. Only one *I. recurvum* had no byssus. By Hour 23 two *M. leucophaeata* had still not moved from their squares, one had done so but was alone and the remaining seven were clumped with *I. recurvum*; all *I. recurvum* had moved and formed byssi. This situation continued until Day 3, except that one of the two lone *M. leucophaeata* had formed a byssus.

Larval development

Unfertilized eggs of *M. leucophaeata* averaged 61 μm in diameter (Table 3). About 4 h after fertilization, ciliated rotating balls of cells were present, followed within another 8 h by trochophores with apical flagella. Straight-hinge larvae were seen by 21 h, with some trochophores still present. By Day 4, rounded umbos were seen on many animals, with one side of some larvae elongating by Day 5. An apical flagellum was still seen in 8-day larvae but there was no sign of an eyespot or an active foot. By Day 9, most larvae were lying on their side without swimming in the Sedgwick–Rafter cell, presumably because metamorphosis had occurred. On that day, nonswimming animals that extended their foot ranged from 145 to 180 μm whereas animals still in possession of their velum measured from 140 to 168 μm; a 151-μm larva had both a well-developed foot and a velum. The umbo was prominent in many 9-day-old larvae. Two larvae (170 and 179 μm) seen at Day 10 had both a velum and an active foot. After 10 days, there were still no eyespots so it appears that larval *M. leucophaeata* and early juveniles do not develop this structure.

Fifteen-day-old juveniles were seen travelling over the container bottom on their foot, which was heavily ciliated at its tip. Suspended particles entered the mantle cavity behind the foot so presumably the mantle folds had not fused. After Day 15, particulate matter only entered the mantle cavity via the inhalant siphon, although particles were drawn towards the shell along the ciliary tracts of the foot. The mantle in specimens examined on Day 16 and measuring >194 μm was fused and there were two siphonal openings, the outer edge of the infaunal siphon being surrounded by papillae. Two papillae had formed between the siphons and each had a pigment spot at its base. The inhalant siphon had a flexible trumpet-shaped opening bearing actively beating cilia, whereas the exhalent siphon had a pursed, nipple-shaped end. There were no tentacles at the end of either siphon, but papillae occurred on or near the base of both siphons, as well as extending back along the dorsal edge of the mantle. The flared opening of the extended exhalent siphon of a 19-day juvenile was estimated to be about three times greater in diameter than the opening of the extended inhalant siphon.

The juvenile shell bore dark markings on animals as small as 0.8 mm. After 30 days, juveniles in Brood 1 ranged up to 2.6 mm long, with one animal 3.3 mm long after 37 days (Brood 2 animals grew more slowly). Some juveniles attached to the container walls with byssal threads.

DISCUSSION

As in the newly settled juvenile stage, the extensible siphons of larger *Mytilopsis leucophaeata* are separate, with the mantle fused between. The trumpet-shaped inhalant siphon can be extended a number of millimetres from the shell opening. On oyster shell, *M. leucophaeata* is often nestled among the usually more abundant *Ischadium recurvum* and may not even be visible (personal observation). Its extensible siphons should therefore be useful for accessing the water column near the outer surfaces of

Table 3. Comparison of developmental details and dimensions of eggs, larvae, and juveniles of *Mytilopsis leucophaeata* with data for two species of freshwater dreissenids (*Dreissena polymorpha* and *D. rostriformis bugensis*) and of *Ischadium recurvum* that co-exists with *M. leucophaeata*.

Developmental data	*Mytilopsis leucophaeata*	*Dreissena polymorpha*	*Dreissena rostriformis bugensis*	*Ischadium recurvum*
Rearing conditions	~23°C; salinity ~12–15	~24°C; freshwater	~23.5–24°C; freshwater	~23°C; salinity 6.2–6.7
Egg diameter	58–65; 61.1 ± 1.72; 25	70–86; 77.3 ± 4.08; 90	64–82; 72.7 ± 3.67; 55	66–76; 70.9 ± 2.28; 20
Developmental stage 1 h after fertilization	2–8 cells	1–4+ cells	1–4+ cells	2–4 cells
2 h	8+ cells	1–4+ cells	1–4+ cells	8+ cells
4 h	Spherical ball of cells, 23% rotating; $n = 93$	89% spherical ball of cells, 17% rotating; $n = 95$	46% spherical ball of cells; $n = 117$	Spherical ball of cells
6 h	62% rotating; $n = 50$	53% rotating; $n = 70$		40% spherical, 60% rotating
8 h	84% swimming in circles; 8% in directed swimming; 8% immobile; $n = 50$	80% rotating; $n = 24$	32% rotating; $n = 117$	100% rotating; 10–20% had apical flagellae by 8–9 h; $n = 20$
10 h				85% trochophores with apical flagellum; $n = 20$
12 h	20% trochophores with an apical flagellum (perhaps paired); $n = 30$	75% rotating; $n = 36$	80% rotating; $n = 40$	Fast-swimming trochophores with paired apical flagellae; $n = 20$
16 h	45% trochophores; $n = 20$			
20 h		A few trochophores with an apical flagellum present	A few trochophores with an apical flagellum present	35% D-hinge; $n = 20$
21 h	Some D-hinge larvae present			
24 h	Predominantly D-hinge; $L = 71–83$; 78.8 ± 3.5; 25	Predominantly D-hinge; $L = 73–92$; 83.2 ± 4.8; 10	D-hinge seen at 29 h; $L = 70–81$; 74.1 ± 3.5; 10 $H = 62–70$; 65.6 ± 3.0; 10	70% D-hinge; $n = 20$
2 days	$L = 73–93$; 84.8 ± 5.3; 45 $H = 62–76$; 69.5 ± 3.7; 20		$L = 71–86$; 79.3 ± 4.4; 10 $H = 63–72$; 68.6 ± 3.2; 10	100% D-hinge; $n = 20$
3 days	$L = 76–104$; 88.5 ± 7.8; 41 $H = 60–92$; 73.7 ± 7.6; 16		$L = 70–91$; 83.2 ± 5.9; 10 $H = 70–80$; 74.7 ± 4.1; 10	
4 days	Umbos in many larvae; $L = 82–112$; 98.4 ± 8.5; 20			
5 days	$L = 90–140$; 117.8 ± 13.5; 20			
6 days	$L = 104–156$; 135.3 ± 13.2; 20			
8 days	$L = 104–189$; 155.6 ± 22.7; 20			
9 days	Metamorphosed animals present; $L = 81–197$; 157.3 ± 24.3; 20			
10 days	$L = 111–209$; 154.7 ± 26.8; 20			
11 days	$L = 129–248$; 161.6 ± 26.2; 20			
16 days*	$L = 194–347$; 283 ± 42.0; 20			
19 days*	$L = 194–377$; 277 ± 42.9; 20			
21 days*	$L = 245–449$; 335 ± 62.6; 20			
28 days*	$L = 265–413$; 328 ± 34.9; 20			
30 days	$L = 1.1–2.6^{\dagger}$; 1.8 ± 0.4†; 25			
37 days	$L = 0.8–3.3^{\dagger}$; 2.1 ± 0.7†; 25			
37 days*	$L = 377–775$; 530 ± 108.9; 20			
42 days*	$L = 0.5–1.3^{\dagger}$; 816 ± 198.6; 20			
49 days*	$L = 0.7–1.2^{\dagger}$; 864 ± 133.3; 20			

Measurements (μm, except where noted) of eggs are diameters and of shelled larvae are length (*L*, maximum anteroposterior distance) and height (*H*, maximum dorsoventral distance). Egg diameter, length and height data are presented as range; mean ± 1 SD; sample size (*n*). Some of the data on the two species of *Dreissena* were used in Wright *et al.* (1996). *Data are from Brood 2. †Values are millimetres.

clumps of *I. recurvum*. This should also be true for individuals within any large clumps of *M. leucophaeata* that might form.

Abundance in nature

Clearly, while *I. recurvum* was very common on the oysters sampled, *M. leucophaeata* was not. Neither species displayed any relationship between their abundances and the size of oyster shells on which they occurred (Fig. 1). Perhaps no relationship should be expected for bivalves that can form three-dimensional clumps of individuals byssally attached one on top of another. The positive relationship between numbers of *M. leucophaeata* and *I. recurvum* may indicate an attraction of one species to the other, perhaps

during larval settlement, but this hypothesis needs to be tested.

Attachment strength and byssal-thread diameters

Mytilopsis leucophaeata were more weakly attached to oyster shell than were *I. recurvum* of a similar size (Table 1). Similar differences in attachment strength also occur between other dreissenids and mytilids for which there are published data (Table 1). Note that these data are for animals tested in spring or summer in their relevant hemisphere using variations of the spring-balance equipment used here, except for Ackerman *et al.* (1995) who used a wall jet and Peyer, McCarthy & Lee (2009) who used two commercial instruments to measure byssal-thread strength.

Prejs, Lewandowski & Stańczykowska-Piotrowska (1990) and Kobak (2006) reported that attachment strength in *Dreissena polymorpha* was positively correlated with shell length, as were the values presented here for *M. leucophaeata* (Fig. 2). For the most part the data for dreissenids in Table 1 are for animals of comparable sizes, facilitating comparisons. The data show that, over a range of geographical locations, attachment strengths of dreissenids are low.

Pathy and Mackie (1993) compared the mytiliform shell morphology of *M. leucophaeata* with the shells of *D. polymorpha* and *D. rostriformis bugensis* in North America. *Mytilopsis leucophaeata* is distinguished from the latter two species by an apophysis that extends from the narrow myophore plate and that is the attachment surface for the anterior byssal retractor muscle. Pathy and Mackie (1993) predicted that the resultant muscle attachment configuration would allow *M. leucophaeata* to attach more strongly to substrates by its byssi than could the other two dreissenids. The available data provide mixed support for this prediction (Table 1).

In support of the prediction, attachment strengths calculated for small *D. polymorpha* (10 and 20 mm) from the equation in Prejs *et al.* (1990) are weak (Table 1). Kobak's (2006) *D. polymorpha* <11 mm long were also comparatively weakly attached (mean values 0.3–0.7 N, estimated from his Fig. 4), individuals between 11 and 13 mm were of intermediate attachment strength (1–1.4 N) and animals from 14 to 18+ mm were most strongly attached (1.4–1.8 N). In contrast, average values for *M. leucophaeata* were 0.82 N for 6.8–11 mm animals ($n = 21$), 1.46 N for 11.4–13.8 mm animals ($n = 8$) and 2.04 N for 14.8–23.4 mm animals ($n = 29$). Thus, the values for *M. leucophaeata* are higher than for *D. polymorpha*. However, because Kobak (2006) measured attachment strengths just 6 days after *D. polymorpha* were allowed to attach to a substrate, and because Peyer *et al.* (2009) observed that attachment strength of the two species of *Dreissena* increased with length of attachment, Kobak's (2006) values may be anomalously low. My data are for *M. leucophaeata* that had lived for many months in an estuarine pond, so presumably they had attained their maximum attachment strength.

Contradicting the prediction of Pathy and Mackie (1993), the remaining data for dreissenids in Table 1 show that *D. polymorpha* and *D. rostriformis bugensis* from Wisconsin and Ontario had attachment strengths similar to or greater than those presented here for *M. leucophaeata*. Indeed, the upper end of the range for Ontario animals is much higher than the highest value I measured (compare Table 1 with Fig. 2).

For the mytilids in Table 1, size data were not always reported, or the experimenters reported a dimension other than length, so comparisons among experiments on attachment strength are hindered. However, the values for mytilids of a size range similar to that of my *M. leucophaeata* (e.g. Zardi *et al.*, 2006; Caro *et al.*, 2008) are much higher than for *M. leucophaeata*. My values for *I. recurvum* are also lower than those reported for Chilean mytilids, but are similar to that of *Perna perna* in South Africa. However, in addition to size, another factor hindering comparisons of attachment strength is that of wave exposure. The data for mytilids in Table 1 refer mostly to animals that live on marine rocky shores. Byssal strength would be expected to be higher for wave-exposed animals than for animals in quieter habitats; this is demonstrated by the data on *Mytilus galloprovincialis* in Friday Harbor. My *I. recurvum* were collected from small estuarine ponds that do not experience waves or currents, so their byssal attachment values may be lower than they might be had they been taken from a region of the Bay that experiences fast currents.

The byssal threads of *M. leucophaeata* were much thinner than those of *I. recurvum* (Fig. 3), with the byssus of a 20-mm *M. leucophaeata* calculated from the relevant regression to be 33 μm in diameter compared with 69 μm for a 20-mm *I. recurvum*. Such differences may be a partial explanation for the lower attachment strength of *M. leucophaeata* in comparison with that of *I. recurvum*. This hypothesis is supported by the fact that Pearce and LaBarbera (2009) report that the breaking force for byssi of *Geukensia demissa* and *Modiolus modiolus*, species with small byssal diameters, was much less than that for byssi of *Mytilus edulis* and *M. californianus*, species with much larger byssal diameters (see below).

There are few data in the literature on byssal-thread diameters of bivalves. From regression equations that Zardi *et al.* (2006) developed for two species of rocky-shore mussels in South Africa in summer, estimated byssal diameters for 20-mm mussels are as follows: solitary (living outside a mussel bed) *Perna perna* and *Mytilus galloprovincialis*, 78 μm; aggregated (living within a monolayered mussel bed) *P. perna*, 78 μm and *M. galloprovincialis*, 64 μm. Thus, byssal diameters for Chesapeake Bay *Ischadium recurvum* in these size classes are similar to those of the shore-dwelling mussels. A study by Pearce and LaBarbera (2009) of four mytilid species provided mixed results. The average byssal diameter for semi-infaunal *Geukensia demissa* and *Modiolus modiolus* held in aquaria was 38 and 46 μm, somewhat less than for my bivalves. By contrast, *Mytilus edulis* and *M. californianus* held in aquaria and epifaunal *Perna canaliculus* collected from the field had average diameters of 150, 130 and 132 μm, exceeding my values.

Care must be taken in drawing conclusions from these disparate studies that used organisms subjected to different habitat or experimental conditions. Nevertheless, the available data indicate that dreissenids are more weakly attached than are mytilids. Also, bivalves living on wave-beaten shores had greater byssal-thread diameters than did semi-infaunal species that were partially buried in sediment that might provide additional support. However, it remains difficult to see clear patterns when comparing my data with published information. *Mytilopsis leucophaeata* resembles the semi-infaunal species *Geukensia demissa* and *Modiolus modiolus*, which may reflect the fact that its habit of nestling within clumps of *I. recurvum* provides some structural support. *Ischadium recurvum* resembles the mussels from wave-exposed shores, although it is continuously submerged in Chesapeake Bay and not subject to the surge of breaking waves.

Crawl-out experiments

In terms of ability to crawl out from under obstacles, *M. leucophaeata* was more passive than were *I. recurvum* and the even more active species of *Dreissena* (Table 2). Comparable data for other bivalves are few (Harger, 1968; Tan, 1975; Kennedy, 1984; Table 2). Harger (1968) reported that small *Mytilus edulis* crawled out more rapidly from under 5 cm of gravel

(0.5–0.75 cm diameter) within 48 h than did *Mytilus californianus* of the same size, with proportionately more East Coast *M. edulis* reaching the gravel surface than West Coast specimens within 48 h. Tan (1975) observed that *Perna viridis* measuring from 2.5 to 27.5 mm were also very active, with an average of 76% reaching the gravel surface within 24 h. Kennedy (1984) studied 10- to 20-mm animals in New Zealand and reported that 45% of *Perna canaliculus* reached the gravel surface within 48 h, with *Mytilus galloprovincialis* and *Aulacomya maoriana* being much less likely to crawl to the surface in that time interval. Based on these crawl-out experiments, *M. leucophaeata* is among the least active of the bivalves studied, although more active than *M. galloprovincialis* and *A. maoriana* from New Zealand.

Kennedy (1984) noted that individual *Aulacomya maoriana* (a relatively inactive species) in mixed-species mussel clumps in New Zealand usually occur next to the rock face, with the slightly more active *Mytilus galloprovincialis* and much more active *Perna canaliculus* growing over them. A similar pattern of hugging the settlement surface and living under mixed-species clumps (of *Mytilus galloprovincialis* and *M. californianus*) occurs in *Septifer bifurcatus*, a small mytilid that Harger (1968) noted did not crawl out when placed under gravel. I conclude that *M. leucophaeata* may be predisposed to remain under *Ischadium recurvum* if co-mingled. Indeed, Hinkley (1907) reported on them nestling among *I. recurvum* "as if seeking protection". In this position, individuals may find refuge from potential predators impeded by the greater attachment strength of *I. recurvum*. Among those predators are two species of mud crabs that live on eastern oyster reefs and eat *M. leucophaeata* (Milke & Kennedy, 2001). In addition, the blue crab *Callinectes sapidus*, which is a common resident of the same Bay environment, will eat *M. leucophaeata* (personal observation). However, although *M. leucophaeata* may be more easily detached than *I. recurvum* from a substrate, Blundon & Kennedy (1982) reported that its shell was more resistant to crushing forces in the laboratory than was the shell of *I. recurvum*.

Movement and byssal attachment experiments

In the single-species bowls used in experiments on movement and byssal attachment, no *M. leucophaeata* had moved and only two had produced byssi by the end of the April experiment, and only four had moved and only three were attached by the end of the May experiment. In contrast, *I. recurvum* began moving and forming clumps early in both experiments in their single-species bowls. In the mixed-species bowls, the clumps that formed incorporated *M. leucophaeata*, presumably the result of *I. recurvum* activity. These findings add to the impression that *M. leucophaeata* is a relatively passive organism in nature.

However, the slowness of this species to produce byssi in my experiments is surprising given data in Rajagopal *et al.* (2005). These authors acclimated *M. leucophaeata* in three size classes (2, 10 and 20 mm) to 20°C and salinity 5.6–5.8, then examined the number of byssal threads produced per animal over 24 h. Based on their Figure 1, at 24°C the 10- to 20-mm sized animals produced an estimated 18–30 threads/animal/day. Similarly, Udhayakumar & Karande (1986) observed that within 24 h of being placed on glass in the laboratory, individual *Mytilopsis adamsi* had spun an average of from 31 byssi (25-mm animals) to 48 byssi (10-mm animals). [Udhayakumar and Karande (1986) refer to this species as *Mytilopsis sallei*, a western Atlantic taxon, but Marielli & Gray (1985) proposed that it was the sister species *M. adamsi* from the eastern Pacific; see also Wangkulangkul & Lheknim (2008).] Udhayakumar and Karande (1989) also observed that 5-mm *M. adamsi* could detach from a surface and reattach up to nine times over 120 h; 15-mm animals could do so up to eight times and 20-mm animals could do so up to three times (although most just attached once). The differences between byssal production and reattachment of my experimental animals and the data reported by Rajagopal *et al.* (2005) for *M. leucophaeata* and by Udhayakumar & Karande (1986, 1989) for a sister species have no obvious explanation.

Larval development

Ackerman *et al.* (1994) reviewed the literature on early life history of marine bivalves to make comparisons with *Dreissena polymorpha* and reported that egg diameters for 28 species ranged between 40 and 125 μm. However, of these *Pandora inaequivalvis* has much larger eggs (105–125 μm) than do the other species. Removing the value for *P. inaequivalvis* yields an egg-diameter range of 40–96 μm for the remaining 27 species. My measurements for four bivalve species in Table 3 fall within that range. The egg-diameter range and average egg diameter for *M. leucophaeata* were smaller than for the two species of *Dreissena* and *I. recurvum* (Table 3). However, differences in egg diameters may reflect geography, food availability or genetic makeup, so the developmental significance of the smaller egg sizes of the two species of *Dreissena* and *M. leucophaeata* is unknown.

Staver & Strathmann (2002) spawned three bivalve species and gave data on egg size, cell cycle duration and time to first swimming at 10 and 14°C (note that these temperatures are much lower than my room temperatures). For their bivalves, the time to develop from the 2-cell to the 4-cell stage ranged from 1.2 to 2.2 h at 10°C and 0.8 to 1.5 h at 14°C. By comparison, all four of my species developed slightly faster (perhaps due to the higher temperatures), reaching at least the 4-cell stage by 1 h after fertilization; indeed, *Mytilopsis leucophaeata* had attained the 8-cell stage by 1 h (Table 3).

The time to first swimming by Staver & Strathmann's (2002) embryos (blastulae or gastrulae) ranged from 11.3 to 40.6 h at 10°C and from 7.0 to 25.2 h at 14°C. In comparison, some spherical balls of *M. leucophaeata* and *D. polymorpha* held at room temperature were moving at 4 h, with *I. recurvum* embryos rotating by 6 h and *D. rostriformis bugensis* embryos moving by 8 h (Table 3).

Trochophores occurred in cultures of *I. recurvum* by 10 h, in cultures of *M. leucophaeata* by 12 h and in cultures of *D. polymorpha* and *D. rostriformis bugensis* by 20 h. These are comparatively rapid development times (see Ackerman *et al.*, 1994). Straight-hinge (D-hinge) larval development was also rapid, occurring by 20 h for *I. recurvum*, by 21 h for *M. leucophaeata* and by 24 h for the two species of *Dreissena* (see also Wright *et al.*, 1996, for data on *D. polymorpha*). Development of *M. leucophaeata* continued to be rapid compared with data in Ackerman *et al.* (1994), with umbos appearing by Day 4 and juveniles settling by Day 9.

Siddall (1980) stimulated adult *M. leucophaeata* to spawn in water of salinity 10 at 35°C and reared larvae to metamorphosis at salinities of 10, 24 and 32, with no apparent effects of salinity on size at or timing of metamorphosis. Larval dimensions at 26°C were 74 μm 2 days after fertilization (similar to my data, Table 3) and 180 μm 6 days after fertilization (slightly larger than my larvae). Siddall's (1980) larvae metamorphosed 6–8 days after fertilization at a mean shell length of 210 μm (slightly faster development than for my larvae) and juveniles measured 270 μm maximum after 12 days, 375 μm maximum after 18 days and 500 μm maximum after 28 days. These data are near the upper ends of the ranges of my data for similar time periods, probably as a result of my rearing temperatures being a few degrees lower than the temperature of 26°C used by Siddall (1980).

Concluding remarks

In conclusion, *Mytilopsis leucophaeata* is an uncommon bivalve on oyster bars in mesohaline habitats in Maryland's Chesapeake Bay, although it is sometimes encountered in large clumps on a variety of substrates. It is small and weakly attached by its byssi, but is presumably somewhat protected from crab (and fish?) predators by its habit of living within clumps of *Ischadium recurvum*. Its morphology, particularly its extensible inhalant siphon, should enable it to obtain food and oxygen from the water column even when confined within clumps of *I. recurvum* or its own species. In terms of egg size and the timing of larval development, it shares a number of characteristics with other dreissenids and with *I. recurvum* from the same estuarine environment.

The role of *M. leucophaeata* in estuarine food webs must be limited, given its general scarcity and its small size. By comparison, the larger *I. recurvum* may play an important role because they can become abundant enough on oyster beds to be pests, forcing harvesters to remove them from captured oysters before selling the oysters to seafood processors. For example, Gutsell (1922) reported that, on some Maryland oyster beds, *I. recurvum* in a bushel of captured bivalves would be double the bulk of oysters. Also, Engle & Chapman (1953) noted that oysters covered with *I. recurvum* were in poorer condition (measured by percent solids and glycogen) than mussel-free oysters. In neither of these reports on high abundances of *I. recurvum* were *M. leucophaeata* mentioned, although there is no way of knowing if this was because the investigators did not notice *M. leucophaeata* or if they were indeed absent.

Mytilopsis leucophaeata may be an interesting animal to investigate in relation to its apparent scarceness in nature and its fertilization success. Given the limited numbers of *M. leucophaeata* that seem to be the rule, how is its spawning coordinated and how successful is fertilization when widely separated individuals do spawn?

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REFERENCES

ACKERMAN, J.D., COTTRELL, C.M., ETHIER, C.R., ALLEN, D.G. & SPELT, J.K. 1995. A wall jet to measure the attachment strength of zebra mussels. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**: 126–135.

ACKERMAN, J.D., SIM, B., NICHOLS, S.J. & CLAUDI, R. 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves. *Canadian Journal of Zoology*, **72**: 1169–1179.

BERGSTROM, P., CAREY, R., HORNOR, S. & JUDY, C. 2009. Poster presentation. Available at http://longislandsoundstudy.net/wp-content/uploads/2010/02/Bergstrom_DFMPOSTER120309FINAL.pdf (accessed 1 December 2010).

BLUNDON, J.A. & KENNEDY, V.S. 1982. Mechanical and behavioral aspects of blue crab (*Callinectes sapidus* Rathbun) predation on Chesapeake Bay bivalves. *Journal of Experimental Marine Biology and Ecology*, **65**: 47–65.

CARO, A.U., ESCOBAR, J., BOZINOVIC, F., NAVARRETE, S.A. & CASTILLA, J.C. 2008. Phenotypic variability in byssus thread production of intertidal mussels induced by predators with different feeding strategies. *Marine Ecology Progress Series*, **372**: 127–134.

CONN, D.B., LUTZ, R.A., HU, Y.-P. & KENNEDY, V.S. 1993. *Guide to the identification of larval and postlarval stages of zebra mussels Dreissena spp. and the dark false mussel, Mytilopsis leucophaeata*. New York Sea Grant Institute, Stony Brook NY. 22 pages.

ENGLE, J.B. & CHAPMAN, C.R. 1953. Oyster condition affected by attached mussels. *Proceedings of the National Shellfisheries Association*, **1951**: 70–78.

GARCÍA-CUBAS, A. 1981. Moluscos de un sistema lagunar tropical en el sur del Golfo de México (Laguna de Términos, Campeche). *Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Publicaciones Especiales*, **5**: 1–182.

GARDNER, J.P.A. & SKIBINSKI, D.O.F. 1991. Biological and physical factors influencing genotype-dependent mortality in hybrid mussel populations. *Marine Ecology Progress Series*, **71**: 235–243.

GLAUS, K.J. 1968. Factors influencing the production of byssus threads in *Mytilus edulis*. *Biological Bulletin*, **135**: 420.

GUTSELL, J.S. 1922. A review of the mussel situation of Maryland Chesapeake waters. *Sixth Annual Report of the Conservation Commission of Maryland*. Baltimore, MD, pp. 39–44.

HARGER, J.R.E. 1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. *Veliger*, **11**: 45–49.

HARGER, J.R.E. 1970. The effect of wave impact on some aspects of the biology of sea mussels. *Veliger*, **12**: 401–414.

HINKLEY, A.A. 1907. Shells collected in northeastern Mexico. *Nautilus*, **21**: 68–72.

HUNT, H.L. & SCHEIBLING, R.E. 2001. Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season. *Marine Ecology Progress Series*, **213**: 157–164.

KENNEDY, V.S. 1984. Crawling and clustering behavior of three species of intertidal mussels in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **18**: 417–423.

KENNEDY, V.S. 2011. The invasive dark falsemussel *Mytilopsis leucophaeata* (Bivalvia: Dreissenidae): a literature review. *Aquatic Ecology*, **45**; doi:10.1007/s10452-010-9344-6.

KENNEDY, V.S. & KRANTZ, L.B. 1982. Comparative gametogenic and spawning patterns of the oyster *Crassostrea virginica* (Gmelin) in central Chesapeake Bay. *Journal of Shellfish Research*, **2**: 133–140.

KENNEDY, V.S., NEWELL, R.I.E., KRANTZ, G. & OTTO, S. 1995. Reproductive capacity of the eastern oyster *Crassostrea virginica* infected with the parasite *Perkinsus marinus*. *Diseases of Aquatic Organisms*, **23**: 135–144.

KOBAK, J. 2006. Factors influencing the attachment strength of *Dreissena polymorpha* (Bivalvia). *Biofouling*, **22**: 141–150.

LAINE, A.O., MATTILA, J. & LEHIKOINEN, A. 2006. First record of the brackish water dreissenid bivalve *Mytilopsis leucophaeata* in the northern Baltic Sea. *Aquatic Invasions*, **1**: 38–41.

MARELLI, D.C. & GRAY, S. 1983. Conchological redescriptions of *Mytilopsis sallei* and *Mytilopsis leucophaeta* of the brackish Western Atlantic (Bivalvia: Dreissenidae). *Veliger*, **25**: 185–193.

MARELLI, D.C. & GRAY, S. 1985. Comments on the status of recent members of the genus *Mytilopsis* (Bivalvia: Dreissenidae). *Malacological Revue*, **18**: 117–122.

MILKE, L.M. & KENNEDY, V.S. 2001. Mud crabs (*Xanthidae*) in Chesapeake Bay: claw characteristics and predation on epifaunal bivalves. *Invertebrate Biology*, **120**: 67–77.

NUTTALL, C.P. 1990. Review of the Caenozoic heterodont bivalve superfamily Dreissenacea. *Paleontology*, **33**: 707–737.

NYST, P.-H. 1835. Mollusques. *Bulletin de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*, **2**: 235–236 + 1 Figure.

PATHY, D.A. & MACKIE, G.L. 1993. Comparative shell morphology of *Dreissena polymorpha*, *Mytilopsis leucophaeata*, and the 'quagga' mussel (Bivalvia: Dreissenidae) in North America. *Canadian Journal of Zoology*, **71**: 1012–1023.

PEARCE, T. & LABARBERA, M. 2009. A comparative study of the mechanical properties of mytilid byssal threads. *Journal of Experimental Biology*, **212**: 1442–1448.

PEYER, S.M., McCARTHY, A.J. & LEE, C.E. 2009. Zebra mussels anchor byssal threads faster and tighter than quagga mussels in flow. *Journal of Experimental Biology*, **212**: 2027–2036.

PREJS, A., LEWANDOWSKI, K. & STAŃCZYKOWSKA-PIOTROWSKA, A. 1990. Size-selective predation by roach

(*Rutilus rutilus*) on zebra mussel (*Dreissena polymorpha*): field studies. *Oecologia*, **83**: 378–384.

PRICE, H.A. 1980. Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis* L. *Journal of the Marine Biological Association of the United Kingdom*, **60**: 1035–1037.

RAJAGOPAL, S., VAN DER GAAG, M., VAN DER VELDE, G. & JENNER, H.A. 2005. Upper temperature tolerances of exotic brackish-water mussel, *Mytilopsis leucophaeata* (Conrad): an experimental study. *Marine Environmental Research*, **60**: 512–530.

RAJAGOPAL, S., VAN DER VELDE, G. & JENNER, H.A. 1997. Shell valve movement response of dark false mussel, *Mytilopsis leucophaeta*, to chlorination. *Water Research*, **31**: 3187–3190.

SIDDALL, S.E. 1980. Early development of *Mytilopsis leucophaeata* (Bivalvia: Dreissenacea). *Veliger*, **22**: 378–379.

SMITH, D.G. & BOSS, K.J. 1996. The occurrence of *Mytilopsis leucophaeata* (Conrad, 1831) (Veneroida: Dreissenidae) in southern New England. *Veliger*, **39**: 359–360.

SPRUNG, M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. *Archiv für Hydrobiologie (Supplement 79)*, **1**: 69–86.

STAVER, J.M. & STRATHMANN, R.R. 2002. Evolution of fast development of planktonic embryos to early swimming. *Biological Bulletin*, **203**: 58–69.

TAN, W.H. 1975. The effects of exposure and crawling behavior on the survival of recently settled green mussels (*Mytilus viridis* L.). *Aquaculture*, **6**: 357–368.

UDHAYAKUMAR, M. & KARANDE, A.A. 1986. Adhesive strengths of some biofouling organisms. *Current Science*, **55**: 656–658.

UDHAYAKUMAR, M. & KARANDE, A.A. 1989. Byssal threads of *Mytilopsis sallei* (Recluz) and their adhesive strength. *Proceedings of the Indian Academy of Sciences (Animal Sciences)*, **98**: 65–75.

WANGKULANGKUL, K. & LHEKNIM, V. 2008. The occurrence of an invasive alien mussel *Mytilopsis adamsi* Morrison, 1946 (Bivalvia: Dreissenidae) in estuaries and lagoons of the lower south of the Gulf of Thailand with comments on their establishment. *Aquatic Invasions*, **3**: 325–330.

WILLIS, G.L. & SKIBINISKI, D.O.F. 1992. Variation in strength of attachment to the substrate explains differential mortality in hybrid mussel (*Mytilus galloprovincialis* and *M. edulis*) populations. *Marine Biology*, **112**: 403–408.

WITMAN, J.D. & SUCHANEK, T.H. 1984. Mussels in flow: drag and dislodgment by epizoans. *Marine Ecology Progress Series*, **16**: 259–268.

WRIGHT, D.A., SETZLER-HAMILTON, E.M., MAGEE, J.A., KENNEDY, V.S. & MCININCH, S.P. 1996. Effect of salinity and temperature on survival and development of young zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels. *Estuaries*, **19**: 619–628.

ZARDI, G.I., NICASTRO, K.R., MCQUAID, C.D., RIUS, M. & PORRI, F. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. *Marine Biology*, **150**: 79–88.