Reproduction based on local patch size of *Alasmidonta heterodon* and dispersal by its darter host in the Mill River, Massachusetts, USA

David C. McLain[1] and Michael R. Ross[2]

*Department of Natural Resources Conservation, University of Massachusetts,
Amherst, Massachusetts 01003 USA*

Abstract. We studied the reproduction and shell size structure of the endangered dwarf wedge-mussel (*Alasmidonta heterodon*) in the Mill River, Massachusetts, at sites of different mussel abundance, and assessed the dispersal capacity of its host fish, the tessellated darter (*Etheostoma olmstedi*). We quantified 4 phases of reproduction at 5 study sites of contrasting adult mussel abundance (3 low-abundance sites, 1 intermediate, 1 high), including gravidity, glochidial release, host infection rate, and juvenile recruitment. The ratio of gravid to nongravid individuals was higher at the high-abundance site, and comparatively lower at the intermediate- and low-abundance sites. Glochidial release, infection rates on host darters, and juvenile recruitment were directly proportional to mussel abundance. The highest glochidia density (0.12/m³) occurred at the high-abundance site. Mean infection rates during early May to late June ranged from 31% at the high-abundance site to 8% at the intermediate- and 0 to 2% at the 3 low-abundance sites. The high-abundance site showed highest level of juvenile recruitment. Low-abundance sites showed narrow ranges of size classes, probably indicating few year classes. Movement by marked darters was minimal during glochidial release, with 94% of marked darters remaining in locations where they were originally marked. Reproduction by *A. heterodon* in the Mill River depends on mussel patch density, and mussel dispersal by the host fish may be limited to the immediate vicinity of the infection site. Such a low dispersal capacity may lead to a patchy mussel distribution and may hinder colonization and recovery of this species.

Key words: *Alasmidonta heterodon*, *Etheostoma olmstedi*, reproduction, dispersal, patch size, glochidia, infection rate, recruitment, metapopulation, Unionidae.

The dwarf wedgemussel (*Alasmidonta heterodon*) is an endangered freshwater mussel of the Atlantic Slope drainage, occurring from New Brunswick to North Carolina (Master 1986, USFWS 1993). In a range-wide survey, Strayer et al. (1996) reported that all known *A. heterodon* populations were at risk because of low densities and small ranges, with most populations occurring as distinct patches of individuals. The reproductive status of most of these populations is unknown (Strayer et al. 1996).

Although much is known about general mussel reproduction (Watters 1994), comparatively little is known about the level of reproduction needed to sustain viable populations, and only a few studies have addressed reproduction based on mussel population size. Like many animal populations, the ability of freshwater mussels to reproduce successfully may be limited at low density. For example, the reproductive success of eastern elliptio (*Elliptio complanata*) in a Quebec lake was closely tied to the spatial distribution of individuals, with complete reproductive failure at low density occurring because of low fertilization (Downing et al. 1993).

Freshwater mussels may exhibit characteristics of metapopulations (Vaughn 1993, Strayer et al. 1996, Vaughn 1997), consisting of distinct patches of individuals within a regional population that are linked by dispersal (Gotelli 1991). Adult mussels are usually sedentary, so dispersal among patches is largely accomplished during the larval stage (Neves and Widlak 1988, Vaughn 1997). Moreover, floods may displace juveniles and adults downstream (Neves and Widlak 1987, Layzer and Gordon 1993, Tucker 1996); therefore, dispersal by the host fish may be vital to maintaining population structure, especially in upstream reaches. Furthermore, natural recolonization of habitats by declining or extirpated species, and spatial expansion of populations within watersheds, may depend on mobility of host fish (Smith 1985, Lee et al. 1998). Using computer simulations, Lee et al. (1998) suggested that low movement ranges of host fish lead to mussel patchiness or extinction, unless glochidial infection rates are high. If true,

[1] E-mail address: davemclain@aol.com
[2] To whom correspondence should be addressed. E-mail: mrross@forwild.umass.edu

then the dispersal ability of mussels with sedentary host fish may be extremely limited.

Michaelson and Neves (1995) identified 3 host fish species for *A. heterodon*, the tessellated darter (*Etheostoma olmstedi*), Johnny darter (*E. nigrum*), and mottled sculpin (*Cottus bairdi*), and B. Wicklow (Saint Anselm College, personal communication) documented under laboratory conditions that slimy sculpin (*C. cognatus*) and Atlantic salmon (*Salmo salar*) also served as hosts. In the Mill River, a tributary of the Connecticut River, Massachusetts, USA, the tessellated darter (hereafter "darters") is the only host available for *A. heterodon*. Marking studies have shown that movements of darters during summer may be limited to only a few meters (Reed 1968, May 1969); however, dispersal of darters during their period of infection by *A. heterodon* glochidia (April–mid June, at water temperatures between 10–20°C, B. Wicklow, personal communication) has not been studied.

Knowledge of *A. heterodon's* reproduction associated with local patch size coupled with the dispersal capability of its host fish may have important conservation implications for this species. We quantified the following 4 reproductive parameters for *A. heterodon* in the Mill River, at 5 sites of contrasting adult mussel abundances: 1) proportion of gravid individuals, 2) glochidial density in stream drift, 3) rate of glochidial encystment on darters, and 4) recruitment of juvenile mussels. In addition, we recorded the movement of marked darters during glochidial release by *A. heterodon* to evaluate the dispersal potential of infected darters.

Methods

Study area

We chose 5 study sites in the Mill River (Fig. 1) based on 1998 abundance data for *A. heterodon* from timed snorkel surveys (McLain 2002). Sites 1 to 5 were arranged in order of decreasing adult abundance (as catch per unit effort, CPUE), with catch rates of 25.6, 7.8, 3.3, 2.6, and 1.1 mussels/h, respectively. Sites 1 and 2 were ~500 m apart, and comprised distinctly separate *A. heterodon* patches, whereas other sites were separated from each other by 1.5 to 2.5 km. All sites had similar flow regimes (mean velocity = 0.19–0.23 m/s), mean depth (<1 m), and predominately sand and silt substrate. Other mussel species at the study sites in order of de-

creasing abundance were *Elliptio complanata*, *Lampsilis radiata*, *Ligumia nasuta*, *Pyganodon cataracta*, *Strophitus undulatus*, and *Margaritifera margaritifera* (McLain 2002).

Gravidity

At each site, we visually inspected the marsupial gills of female mussels for gravidity in October 1998. We assumed mussels with swollen and sometimes darkened marsupial demibranchs were brooding glochidia (Michaelson and Neves 1995), and calculated the ratio of gravid to nongravid individuals. We combined mussels from the 3 low-abundance sites (sites 3–5) to minimize bias associated with small sample size.

Glochidial release and infection rates

We quantified glochidial release weekly from 19 April to 21 June 1999 using drift nets (area = 30 cm², 125-μm mesh, see method in Neves and Widlak 1988). We spaced 3 nets evenly across the river at each site. We left nets in place for 10 min while we disturbed the substrate upstream for a distance of 10 m to temporarily suspend glochidia in the water column so that they could be captured by drift nets; this procedure was necessary because *A. heterodon* glochidia sink rapidly after release (Michaelson and Neves 1995). We collected the samples and examined the live glochidia in the laboratory under a dissecting microscope (20×), and counted the number of individuals in a gridded petri dish. Abundance of glochidia in samples was converted to drift density (glochidia/m³).

We determined glochidial infection rates on darters weekly from 3 May to 28 June 1999 within a 50-m reach at each site by capturing fish with an aquarium dip net while snorkeling, and then examining individuals for glochidial cysts. We examined ~33% of darters with cysts under a dissecting microscope (20×) in the field to verify that glochidia were *A. heterodon* and not *P. cataracta* or *S. undulatus*; the latter 2 species also have hooked glochidia and may occur on darters (Van Snik Gray et al. 2002). We used descriptions from Hoggarth (1993) and Wiles (1975) as well as known specimens to identify glochidia to species. We released all darters after examination for glochidia. We considered infection rates as the proportion of darters infected
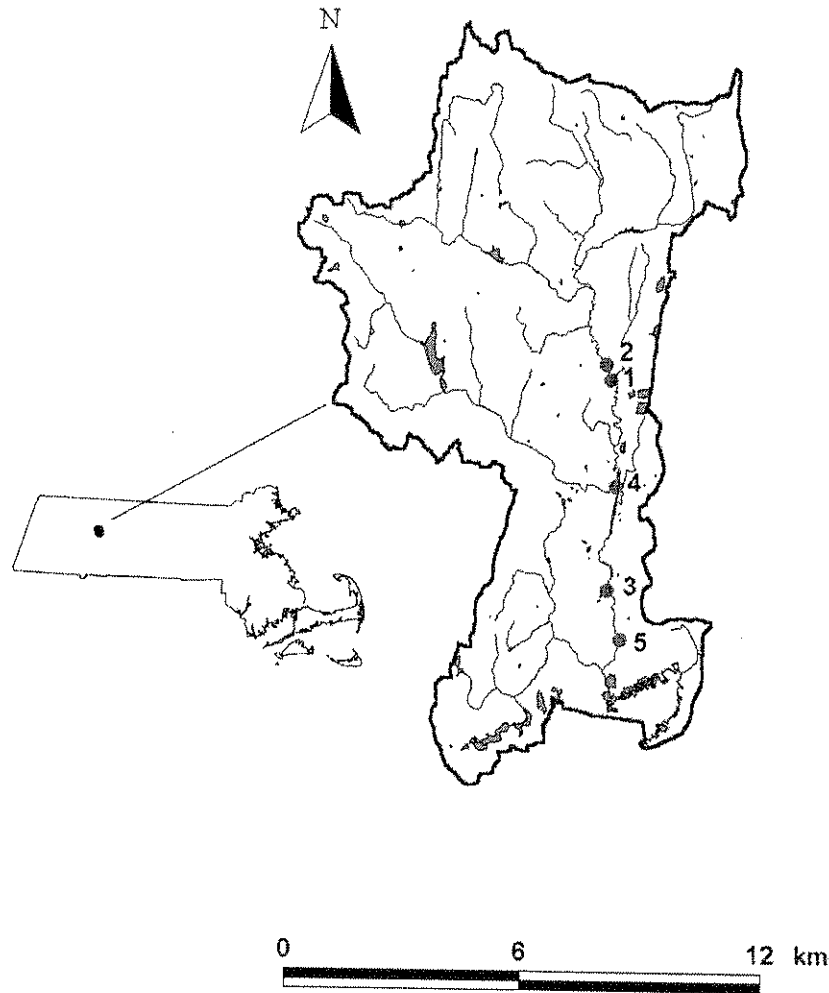
FIG. 1. Study sites on the Mill River, Massachusetts. Sites are numbered from 1 to 5 in order of decreasing abundance of the mussel *Alasmidonta heterodon*.

with glochidia, and incidence of infection as the number of glochidia per fish.

Juvenile recruitment

Substrate excavation and sifting is an effective method for detecting juvenile mussels (Richardson and Yokley 1996, Smith et al. 2000), so we quantified juvenile recruitment by wet-sifting substrate from 40 quadrats (0.25 m², substrate depth range 10–15 cm) through a series of 4-, 2-, and 0.5-mm mesh screens within a 50-m reach at each site. We placed quadrats 1 m apart so we could excavate a full quadrat without obstructions from large woody debris. We recorded the number of juveniles (<8 mm length) in samples from each site.

Shell size

We used mussel shell size structure to indicate temporal patterns of reproduction, including consistency of yearly recruitment (Michaelson and Neves 1995, Strayer et al. 1996). We measured the total shell length (nearest 0.1 mm) from anterior to posterior of all live mussels at each site using dial or vernier calipers. We used age–length data for *A. heterodon* from Michaelson and Neves (1995) to assign size intervals used for length–frequency graphs. We assumed that intervals reflected decreasing growth rates (i.e., by becoming progressively narrower as length increased), and we considered these intervals as size classes.

Host dispersal

We quantified darter dispersal during glochidial release by snorkeling a 50-m reach of river sectioned into five 10-m long blocks and marking darters captured in each block. In October 1998, we captured 44 darters with aquarium dip nets and marked each subcutaneously with red latex dye before releasing them back into the study site; marks on this date were the same regardless of fish position within the 50-m reach. On 10 May 1999, we caught 39 unmarked darters, marking each fish with red latex dye in different locations relative to the dorsal fin, to identify the specific 10-m study block from which fish were captured. All autumn (October)-marked darters that were recaptured in Spring 1999 were marked again to identify the 10-m section where they were subsequently found. We returned each fish to the study block where it was recaptured.

On 25 June 1999 we snorkeled the original capture site and observed locations of marked darters. On 3 and 21 July we recaptured marked darters with aquarium dip nets to insure the same individuals were not counted twice. On each of the 3 resampling dates, we snorkeled 300 m upstream and 300 m downstream from the marking site to search for marked darters that may have moved outside the original capture area. We measured the distance from marked darters to the center of their original marking block, assigning a movement value of 0 m to darters observed within their original block. We calculated the mean distance traveled in the 650-m reach as a measure of darter dispersal during the glochidial infection period.

Statistical analysis

We compared the observed gravid to non-gravid ratios at the high-, intermediate-, and combined low-abundance sites to an expected ratio of 1:1 using χ^2 goodness-of-fit tests (Conover 1971). We examined the relationship between adult *A. heterodon* abundance and glochidial release, juvenile abundance, and darter infection rates among the 5 sites using simple linear correlation. We tested for significant linear relationships between *A. heterodon* abundance and glochidia release, darter infection, and juvenile recruitment using an inferential *t*-test method (see Berenson et al. 1983). We examined

the range of *A. heterodon* size classes by plotting shell length–frequency graphs and comparing coefficients of variation (= CV) in mussel shell length among sites. We used $\alpha = 0.05$ for all statistical tests.

Results

Gravidity

At the high-abundance site (site 1), the ratio of gravid to nongravid individuals did not differ from 1:1 ($\chi^2 = 0.59$, $p = 0.5$, $n = 108$); a similar ratio was observed at 1 of the 3 low-abundance sites (site 4: $\chi^2 = 0.82$, $p > 0.05$, $n = 11$) despite 7 of 11 (64%) individuals being gravid. In contrast, ratios from the other 2 low-abunance sites were significantly <1:1 (site 3: $\chi^2 = 3.77$, $p = 0.05$, $n = 13$; site 5: $\chi^2 = 5.44$, $p > 0.05$, $n = 9$). The gravid to nongravid ratio at the intermediate site (site 2) was marginally <1:1 ($\chi^2 = 3.60$, $0.05 < p < 0.10$, $n = 47$).

Glochidial release and infection rates

Few *A. heterodon* glochidia were present in drift samples at any site (Table 1), although we observed females releasing glochidia directly into the water column. Most (86%) glochidia in drift samples occurred during April and May. Glochidial density was positively correlated with abundance of *A. heterodon* among sites ($r = 0.99$, $p < 0.05$, $n = 5$). Mean weekly infection (proportion of darters with at least 1 glochial cyst) was positively correlated with *A. heterodon* abundance ($r = 0.99$, $p < 0.05$, $n = 5$; Table 1). Only 1 to 3 cysts were observed per darter, with almost 67% of infected darters having only 1 cyst. Glochidia were attached to the pectoral fins (~90%) or the head (~10%), with only few found on the caudal fin. There was no evidence of glochidia on darters from species other than *A. heterodon*.

Juvenile recruitment

Density of *A. heterodon* juveniles was positively correlated with adult abundance ($r = 0.99$, $p < 0.05$, $n = 5$). Most juveniles occurred at site 1, and no juveniles were found at 2 of the low-abundance sites (sites 4 and 5, Table 1).

TABLE 1. Reproductive output and abundance of *Alasmidonta heterodon* at 5 study sites in the Mill River. CPUE = catch per unit effort. Values in parentheses for *A. heterodon* CPUE, % gravid individuals, and % infected darters are *n*, and values in parentheses for glochidial and juvenile density are *n* and SE, respectively.

	Site				
	1	2	3	4	5
Alasmidonta heterodon CPUE					
(no./h)	25.6 (320)	7.8 (47)	3.3 (13)	2.6 (13)	1.1 (9)
% gravid individuals	46.3 (108)	36.2 (34)	23.1 (13)	63.6 (11)	11.1 (9)
Glochidial density (no./m³)	0.12 (10, 0.24)	0.04 (10, 0.30)	0.01 (10, 0.12)	0.01 (10, 0.07)	0 (10, 0)
% infected darters	30.9 (193)	8.4 (236)	2.1 (224)	0 (80)	0 (184)
Juvenile density (no./m²)	1.7 (40, 0.12)	0.6 (40, 0.07)	0.1 (40, 0.25)	0 (40, 0)	0 (40, 0)

Shell size

Sites 1 and 2 showed a wide range of *A. heterodon* size classes, indicating a somewhat regular cycle of reproduction and recruitment (Fig. 2A, B). In contrast, sites 3 to 5 showed fewer size classes and a high proportion of a single size class (Fig. 2C–E), indicating that most individuals were close in size/age, and reproduction or recruitment was irregular. The low CV at site 4 (7.7%) indicated a uniform size structure (Fig. 2D) relative to other low-abundance sites (Fig. 2 C, E) and high- and intermediate-abundance sites (Fig. 2A and B, respectively).

Host dispersal

Of the 44 darters marked in October 1998, 10 were recaptured in May 1999. Eight of the 10 (80%) were found in the original 50-m capture block, 1 moved 10 m downstream, and 1 moved ~500 m upstream. The long distance traveled by the latter darter probably occurred before glochidial release by *A. heterodon* (April–June). That darter remained in the same pool from 3 May to 21 July.

A total of 39 darters were captured and marked in the 5 study blocks on 10 May 1999, and nearly 80% of marked darters were recaptured on subsequent surveys in June and July (Table 2). A total of 75 of the 80 (94%) recaptured darters occurred in the same 10-m section where they were marked. Only 2 darters moved outside of their original capture block between 10 May and 21 July. One darter moved into the adjacent downstream block when the water depth in the original section decreased to a few cm, whereas the other darter moved from the marking block to an area 19 m downstream.

The mean distance traveled by each darter was ~2 m (*n* = 80, Table 2).

Discussion

Gravidity

Reproductive output of *A. heterodon* was affected by local population abundance (patch size) among the 5 study sites because the site with the highest abundance of adult *A. heterodon* also had the highest proportion of gravid females, glochidial density, host infection, and density of juvenile mussels. In contrast, all measures of reproduction at low-abundance sites were low, although the intermediate-abundance site showed some evidence of successful reproduction, as indicated by intermediate glochidal and juvenile density and % host infection.

Low abundance of adult mussels coupled with a skewed gravid to nongravid ratio may hinder reproduction. At site 2 and sites 3 to 5 (the latter combined because of low sample size), low gravid to nongravid ratios were followed by low rates of reproduction, although it is important to point out that our data encompassed only 1 y. Michaelson and Neves (1995) reported 0 gravidity for *A. heterodon* in 2 North Carolina streams during the 1st year of their 2-y study, and an average of 41% gravidity the 2nd year. It is therefore possible that substantial interannual variation in the proportions of gravid females of *A. heterodon* may occur in the Mill River.

Glochidial release and host infection

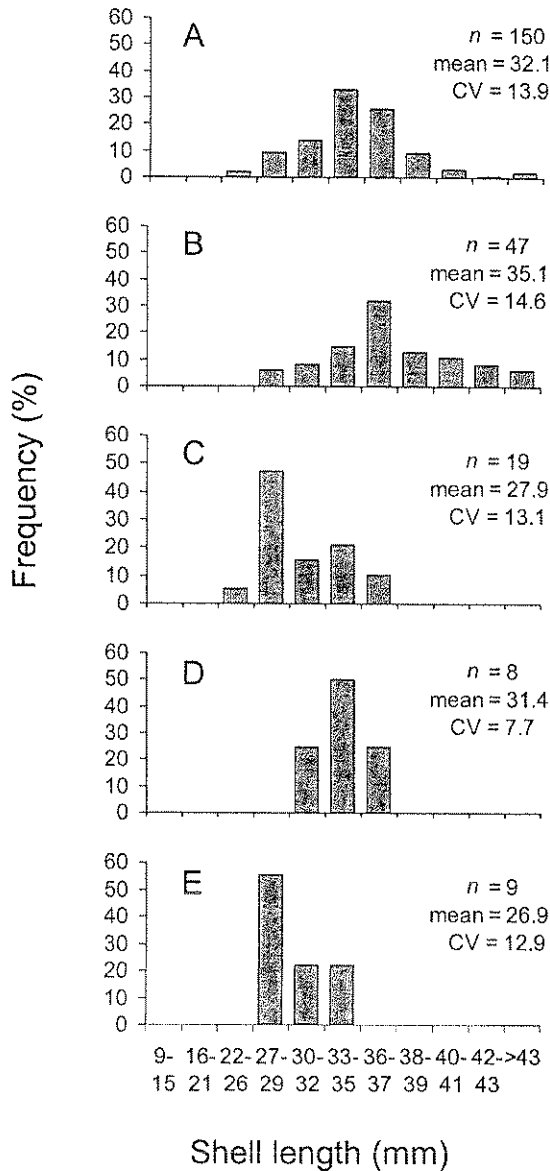Many previous studies have reported low rates of glochidial infection on host fish (4–14%:

FIG. 2. Frequency of shell lengths of *Alasmidonta heterodon* at 5 study sites (A–E = sites 1–5, respectively) in the Mill River. The size-class intervals were derived from age–length data from Michaelson and Neves (1995). *n* = the number of individuals, mean = mean shell length, CV = coefficient of variation.

Neves and Widlak 1988, Holland-Bartels and Kammer 1989, Weiss and Layzer 1995). However, these studies generally focused on community-wide infection rates without considering whether particular fish species could serve as hosts for the mussel species present. In addition, some of the mussel inventories included sampling during times of the year when infection rates would be expected to be low. Such analyses might show higher rates of host infection if focused on glochidial release periods for particular mussel–fish host combinations. For example, peak proportions of rainbow darters (*Etheostoma caeruleum*) infected by glochidia of Pleas' mussels (*Venustaconcha pleasii*) in a Missouri stream was ~64%, with incidence ranging from 1 to 73 (mean = 16) glochidia per darter (Riusech and Barnhart 2000). During the period of peak glochidial release by *A. heterodon* in the Mill River, proportions of infected darters also was high (up to 52% in late May at site 1), although incidence did not exceed 3 glochidia per darter. Such low incidence may indicate this species' reliance on broadcasting glochidia rather than on a host-attracting mechanism (Haag and Warren 1998). *Alasmidonta heterodon* has no elaborate lure to attract its host, although under laboratory conditions this species may undulate its mantle in the presence of a suitable host fish (B. Wicklow, Saint Anselm College, personal communication).

Juvenile fish may serve as suitable hosts for some mussel species (Bauer 1994). In the Mill River, we did not observe juvenile darters in the study sites until the end of the glochidial release period (mid June). Furthermore, Layzer and Reed (1978) reported juvenile tessellated darters remained on their natal territories through summer. Thus, it appears unlikely that juvenile tessellated darters are important hosts for *A. heterodon*.

Host dispersal

Results of the darter mark-recapture study support the hypothesis that darter dispersal is minimal during glochidial release by *A. heterodon*, reinforcing findings reported for other benthic fish (Reed 1968, May 1969, Brown and Downhower 1982, Freeman 1995). Reed (1968) found that 6 species of marked darters generally showed only local movements (riffles to adjacent pools) following fin-clipping. May (1969) reported that variegated darters (*Etheostoma variatum*) were mainly sedentary in local riffles and pools during spring and summer, although fish moved as much as 5 km downstream during autumn and winter. Freeman (1995) recorded movements from 43 to 420 m by 12% of recaptured blackbanded darters (*Percina nigrofasciata*), although only 4% of fish moved >33 m during

TABLE 2. Numbers of recaptures and movements of marked tessellated darters (*Etheostoma olmstedi*) in five 10-m blocks in the Mill River. Recaptures are the number of marked fish caught on a subsequent date. Distance traveled is the distance that fish were caught outside of their original marking block to the center point of their original capture block. Darters caught within their original block were assumed to have moved 0 m. Values in parentheses for mean distance traveled are *n* and SE.

| | Block | | | | | |
	1	2	3	4	5	Total
Marked 10 May 1999	19	3	8	3	6	39
Recaptured 25 June 1999	13	1	3	1	3	21
Recaptured 3 July 1999	18	0	6	3	4	31
Recaptured 21 July 1999	15	1	5	3	4	28
Mean distance traveled (m)	1.1 (46, 0.6)	8.5 (2, 1.5)	0 (14, 0)	0 (7, 0)	0 (11, 0)	0.8 (80, 0.4)
Maximum distance traveled (m)	19	10	0	0	0	

spring. However, *Percina* species may move more than *Etheostoma* species because they possess a smaller swim bladder and frequently swim above the substrate (Page and Burr 1991).

Reliance on the tessellated darter as a host by *A. heterodon* may be advantageous because of high darter abundance (Goodchild 1993), although limited darter dispersal may cause patchy distributions of mussels, leading to metapopulations. Mussel reproduction was minimal in low-abundance sites, so the ability of small patches to increase may depend on propagules emigrating from larger patches (rescue effect, sensu Gotelli 1991). The degree of connection between patches of *A. heterodon* is unknown.

Sustainability of Alasmidonta heterodon

Population sustainability of *A. heterodon* in low-abundance sites may depend on periodic strong year classes. The high frequency of a single size class at the low-abundance sites may indicate a high reproductive year locally or perhaps an event that flushed individuals from upstream, higher-abundance sites. The absence of larger/older individuals capable of producing the observed cohort suggests that mussels originated from another source, unless all large individuals died. Conversely, relatively fewer individuals in the smaller size classes in the high- and intermediate-abundance sites could indicate a storm event transported mussels downstream. Downstream dispersal of glochidia, juveniles, adult mussels, and even infected darters, can occur during spates. For example, Tucker (1996) observed adult mussels, especially small-bodied

species, being flushed into stream floodplain during floods. In addition, Layzer and Gordon (1993) recovered adult marked mussels 600 m downstream after several spates. In the Mill River, distributions of small patches of *A. heterodon* with small uniform shell lengths occurring downstream from larger patches of more variable-sized mussel populations is consistent with the hypothesis of storm-assisted dispersal, which for this species could be a more important dispersal mechanism than its host fish.

Low reproduction and dispersal may inhibit the ability of mussels to recover from population depletion caused by natural or anthropogenic disturbance to habitat. Under the conditions of low reproduction and limited dispersal we observed in the Mill River, *A. heterodon* populations may need augmentation for recovery, although more long-term research is needed to investigate mussel dispersal patterns, especially with respect to populations in low-density patches.

Acknowledgements

Literature Cited

BAUER, G. 1994. The adaptive value of offspring size among freshwater mussels (Bivalvia; Unionoidea). Journal of Animal Ecology 63:933–944.

BERENSON, M. L., D. M. LEVINE, AND M. GOLDSTEIN. 1983. Intermediate statistical methods and applications. Prentice–Hall, Inc., Englewood Cliffs, New Jersey.

BROWN, L., AND J. F. DOWNHOWER. 1982. Summer movements of mottled sculpins, *Cottus bairdi* (Pisces: Cottidae). Copeia 1982:450–453.

CONOVER, W. J. 1971. Practical non-parametric statistics. John Wiley and Sons, Inc., New York.

DOWNING, J. A., Y. ROCHON, AND M. PÈRUSSE. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*. Journal of the North American Benthological Society 12:148–156.

FREEMAN, M. C. 1995. Movements by two small fishes in a large stream. Copeia 1995:361–367.

GOODCHILD, C. D. 1993. Status of the tessellated darter, *Etheostoma olmstedi*, in Canada. Canadian Field Naturalist 107:423–430.

GOTELLI, N. J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core–satellite hypothesis. American Midland Naturalist 138:768–776.

HAAG, W. R., AND M. L. WARREN. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. Canadian Journal of Fisheries and Aquatic Sciences 55:297–306.

HOGGARTH, M. A. 1993. Glochidial functional morphology and rarity in the Unionidae. Pages 76–80 *in* K. S. Cummings, A. C. Buchanan, and L. M. Koch (editors). Conservation and management of freshwater mussels: proceedings of a UMRCC Symposium, 12–14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

HOLLAND-BARTELS, L. E., AND T. W. KAMMER. 1989. Seasonal reproductive development in *Lampsilis ventricosa*, *Amblema plicata*, and *Potamilus alatus* (Pelecypoda:Unionidae). Journal of Freshwater Ecology 5:87–92.

LAYZER, J. P., AND M. E. GORDON. 1993. Reintroduction of mussels into the upper Duck River, Tennessee. Pages 89–92 *in* K. S. Cummings, A. C. Buchanan, and L. M. Koch (editors). Conservation and management of freshwater mussels: proceedings of a UMRCC Symposium, 12–14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

LAYZER, J. P., AND R. J. REED. 1978. Food, age and growth of the tessellated darter, *Etheostoma olmstedi*, in Massachusetts. American Midland Naturalist 100:459–462.

LEE, H. L., D. DEANGELIS, AND H. L KOH. 1998. Modeling spatial distribution of the unionid mussels and the core-satellite hypothesis. Water Science and Technology 38:73–79.

MASTER, L. L. 1986. *Alasmidonta heterodon*, dwarf wedgemussel: results of a global status survey and proposal to list as an endangered species. Report to the US Fish and Wildlife Service, Newton Corner, Massachusetts. (Available from: US Fish and Wildlife Service, 1 Gateway Center, Suite 700, Newton Corner, Massachussetts 02158.)

MAY, B. 1969. Observations on the biology of the variegated darter, *Etheostoma variatum* (Kirtland). Ohio Journal of Science 69:85–92.

McLAIN, D. C. 2002. The freshwater mussels of the Mill River in Hatfield and Whately, Massachusetts. MSc Thesis. University of Massachusetts, Amherst, Massachusetts.

MICHAELSON, D. L., AND R. J. NEVES. 1995. Life history and habitat of the endangered dwarf wedgemussel *Alasmidonta heterodon* (Bivalvia:Unionidae). Journal of the North American Benthological Society 14:324–340.

NEVES, R. J., AND J. C. WIDLAK. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. American Malacological Bulletin 5:1–7.

NEVES, R. J., AND J. C. WIDLAK. 1988. Occurrence of glochidia in stream drift and on fishes of the upper North Fork Holston River, Virginia. American Midland Naturalist 119:111–120.

PAGE, L. M., AND B. M. BURR. 1991. A field guide to freshwater fishes. Houghton-Mifflin, New York.

REED, R. J. 1968. Mark and recapture studies of eight species of darters (Pisces: Percidae) in three streams of northwestern Pennsylvania. Copeia 1968:172–175.

RICHARDSON, T. D., AND P. YOKLEY. 1996. A note on sampling technique and evidence of recruitment in freshwater mussels (Unionidae). Archiv für Hydrobiologie 137:135–140.

RIUSECH, F. A., AND M. C. BARNHART. 2000. Host suitability and utilization in *Venustaconcha ellipsiformis* and *Venustaconcha pleasii* (Bivalvia: Unionidae) from the Ozark Plateaus. Pages 83–91 *in* R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler (editors). Freshwater mollusk symposia proceedings. Ohio

Biological Survey Special Publication, Columbus, Ohio.

SMITH, D. G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. Freshwater Invertebrate Biology 4:105–108.

SMITH, D. R., R. F. VILLELLA, D. P. LEMARIE, AND S. VON OETTINGEN. 2000. How much excavation is needed to monitor freshwater mussels? Pages 203–218 *in* R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler (editors). Freshwater mollusk symposia proceedings. Ohio Biological Survey Special Publication, Columbus, Ohio.

STRAYER, D. L., S. J. SPRAGUE, AND S. CLAYPOOL. 1996. A range-wide assessment of populations of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia:Unionidae). Journal of the North American Benthological Society 15:308–317.

TUCKER, J. K. 1996. Post-flood strandings of unionid mussels. Journal of Freshwater Ecology 11:433–438.

USFWS (US FISH AND WILDLIFE SERVICE). 1993. Dwarf wedge mussel (*Alasmidonta heterodon*) recovery plan. US Fish and Wildlife Service, Hadley, Massachusetts. (Available from: Northeast Regional Office, US Fish and Wildlife Service, 300 Westgate Center Drive, Hadley, MA 01035-9589.)

VAN SNIK GRAY, E., W. A. LELLIS, J. C. COLE, AND C. S. JOHNSON. 2002. Host identification for *Strophitus undulatus* (Bivalvia: Unionidae) the creeper, in the upper Susquehanna River basin, Pennsylvania. American Midland Naturalist 147:153–161.

VAUGHN, C. C. 1993. Can biogeographic models be used to predict the persistence of mussel populations in rivers? Pages 117–122 *in* K. S. Cummings, A. C. Buchanan, and L. M. Koch (editors). Conservation and management of freshwater mussels: proceedings of a UMRCC Symposium, 12–14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

VAUGHN, C. C. 1997. Regional patterns of mussel species distributions in North American rivers. Ecography 20:107–115.

WATTERS, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea. Ohio Biological Survey Miscellaneous Contributions No. 1. Ohio Biological Survey, The Ohio State University, Columbus, Ohio.

WEISS, J. L., AND J. B. LAYZER. 1995. Infestations of glochidia on fishes in the Barren River, Kentucky. American Malacological Bulletin 11:153–159.

WILES, M. 1975. The glochidia of certain Unionidae (Mollusca) in Nova Scotia and their fish hosts. Canadian Journal of Zoology 53:33–41.