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A range-wide assessment of populations of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia:Unionidae)

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Abstract. The purpose of this study was to estimate the densities and sizes of the major remaining populations of *Alasmidonta heterodon*, a unionid mussel listed as endangered by the United States Fish and Wildlife Service. We studied 13 streams from New Hampshire to North Carolina. At 2–9 reaches on each stream, we assessed *A. heterodon* populations using both timed searches and quadrats, and measured the shell lengths of all living *A. heterodon* that we found. All populations of *A. heterodon* that we studied had 3 characteristics: 1) low density, with mean densities typically $<0.01–0.05/m^2$; thus, low or declining density per se may threaten populations of *A. heterodon*; 2) recent reproduction, as shown by the presence of young animals or gravid females; and 3) vulnerability to loss from small ranges, low population densities, linear ranges, or a combination of these 3 factors. Furthermore, several of the populations that we studied included 100s to 10s of 1000s of animals, so these populations probably were too large to be strongly affected by many of the conservation problems of small populations (e.g., inbreeding, demographic stochasticity). These populations were large enough to provide animals for experimental studies, attempts to reestablish historical populations, and the like. Other populations, especially those in the Neuse basin of North Carolina, had exceedingly low densities, and may have contained fewer than 100 adults. The most robust populations of *A. heterodon* probably were those in the Connecticut River (New Hampshire), Ashuelot River (New Hampshire), Neversink River (New York), Po River (Virginia), and Shelton Creek/Tar River (North Carolina)—and perhaps the Little River (North Carolina).

Key words: Unionidae, freshwater mussel, dwarf wedgemussel, endangered species, streams.

Many of North America's endemic freshwater mussel species are endangered or declining (Allan and Flecker 1993, Neves 1993, Williams et al. 1993). To assess the degree of endangerment, decline, or recovery of these rare animals, reliable measures of the health of their populations are needed. Most typically (e.g., US FWS 1993), the status and trends of mussel populations are described in terms like "poor," "good," "declining," "stable," etc., based on the experience of the biologists monitoring the population. Methods and terminology for monitoring and describing mussel populations differ among biologists and across states and provinces, making it difficult to compare populations of mussels in different regions (or at different times).

The primary goal of this study was to provide comparable assessments of the major remaining populations of a rare unionid, *Alasmidonta heterodon*, which was formerly known from about 70 sites in streams between North Carolina, USA, and New Brunswick, Canada (Clarke 1981, US FWS 1993). Although it uses common, widespread fish (*Etheostoma olmstedi* and *Cottus bairdi*) as hosts (Michaelson and Neves 1995), *A. heterodon* apparently never was a common animal (e.g., Ortmann 1919). By 1990, it had declined to the point that it was listed as endangered by the United States Fish and Wildlife Service (US FWS). It is now known from 25–30 streams, most of which are thought to support small populations. Our study assessed the largest existing populations of *A. heterodon* with a standardized, repeatable procedure. In addition to providing specific information about *A. heterodon*, we raise some general issues about assessing and monitoring populations of rare mussels, which we hope will help to develop better designs for future work. In a companion paper (Strayer et al. 1996), we evaluated the cost, precision, and sensitivity of our sampling designs.

Methods

Our study included the 12 streams and rivers thought by US FWS (1993) to support the largest remaining populations of *A. heterodon* (Table 1), as well as the Po River (Virginia), which in 1993 was discovered to contain *A. heterodon*. In each stream, we defined our study area as the known range of *A. heterodon* (except for the Po River, where the range of *A. heterodon* had not

TABLE 1. Qualitative assessment and range size of remaining populations of *Alasmidonta heterodon*, from US FWS (1993). Streams are listed from north to south; the streams we studied are marked with an asterisk. US FWS assessments were "based on information provided by those individuals from each state or region most familiar with their respective populations" (US FWS 1993), rather than on a uniform protocol. Since 1993, several populations have been discovered in New Hampshire, Massachusetts, Virginia, and North Carolina. No assessment of these populations has been published, but except for the Po River, Virginia (see text), most apparently are small.

Stream	Status	Range length[a] (km)	Range area[a] (ha)
*Connecticut River, New Hampshire	fair to good	27	500
*Ashuelot River, New Hampshire	fair to poor	6	10
Muddy Brook, Connecticut	poor	1.6	na
*Neversink River, New York	very good	9	40
Norwich Creek, Maryland	poor	0.8	na
Long Marsh Ditch, Maryland	poor	4.8	na
*McIntosh Run, Maryland	fair	5	2
Nanjemoy Creek, Maryland	fair	1.6	na
*Aquia Creek, Virginia	fair to good	0.8	0.7
South Anna River, Virginia	poor	0.8	na
Nottoway River, Virginia	poor	0.8	na
*Tar River/Shelton Creek, North Carolina	very good	20	10
Cedar Creek, North Carolina	poor	<1.6	na
*Crooked Creek, North Carolina	good	2.4	1
Stony Creek, North Carolina	poor	<1.6	na
*Little River, North Carolina	fair to good	24	30
*Swift Creek, North Carolina	good	24	30
*Turkey Creek, North Carolina	good	9	6
*Moccasin Creek, North Carolina	good	10	10
Middle Creek, North Carolina	poor to fair	2.4	na

[a] US FWS (1993) gave range size in terms of stream length, which was converted where possible to areas using our measurements of stream widths; na = not applicable

yet been established). In the Po, we studied sites near the place where *A. heterodon* was initially found, and used our results and those of Neves (1995) to define the range of *A. heterodon*. Unless otherwise noted, the assessment of population size or density that we present are areally weighted to apply to the entire study area in each stream. We use the term "population" to refer to all individuals of *A. heterodon* in each stream's study area, without implying any genetic communication among the members of such populations.

We visited the streams between June and August, 1994, establishing 2–9 (Table 2) study reaches per stream. Study reaches typically encompassed the entire width of the stream, and ran for 100 m (wide streams) to 200 m (narrow streams). Study reaches usually were chosen in accessible places (often near bridges) for which we had no specific prior knowledge about the density of *A. heterodon*. In 4 streams (the Ashuelot, Connecticut, Neversink, and Tar rivers), previous studies (e.g., Cutko 1993, Fichtel 1993, Strayer and Ralley 1993, J. Alderman, personal communication) had identified areas of relatively high mussel density. We used a stratified design in these streams, using existing information to circumscribe the high-density areas, then measuring the size of the circumscribed area and estimating the density of mussel populations therein. Data from these high-density areas were folded into our stream-wide estimates using standard formulas for stratified designs (Thompson 1992). The midchannel of the Connecticut River was too deep to examine by our methods, so work on this river was confined to areas within 15 m of the shore. The results we present for the Connecticut (which is 175 m wide) assume that mussel densities in midchannel were equal to those in the 15-m band. Alternatively, one could derive a lower bound on the population size in the Connecticut by as-

TABLE 2. Measures of population density of *Alasmidonta heterodon* in the study streams. Streams are listed from north to south. Values are weighted means for the entire area in each stream known to contain *A. heterodon* (cf. Table 1); 90% confidence limits on the mean density index are shown in parentheses. Density index is a derived estimate of the absolute density of the mussel population, based on catches in both timed searches and quadrats (see text for derivation).

Stream	n[a]	Frequency[b]	CPUE (h^{-1}) (wading)	CPUE (h^{-1}) (snorkeling)	Quadrat density (no/m^2)	Density index (no/m^2)
Connecticut River	9	0.50	0.004	3.7	0.04	0.03 (0.01–0.05)
Ashuelot River	7	1.00	2.3	3.0	0.004	0.04 (0.02–0.06)
Neversink River	6	1.00	1.9	1.9	0.05	0.04 (0.02–0.06)
McIntosh Run	5	0.60	1.0	1.8	0.04	0.03 (0.01–0.05)
Aquia Creek	8	0.38	0	1.3	0	0.007 (0.003–0.01)
Po River	3	0.67	1.2	0.6	0	0.01 (0.003–0.03)
Tar River/Shelton Creek	5	0.80	1.0	2.3	0.03	0.03 (0.01–0.05)
Crooked Creek	2	0.50	0	0	0	0
Little River	3	0.33	1.3	0	0.06	0.03 (0–0.06)
Swift Creek	2	0	0	0	0	0
Turkey Creek	3	0	0	0	0	0
Moccasin Creek	3	0	0	0	0	0

[a] Number of study reaches
[b] Proportion of reaches at which the species was detected by any method

suming that no mussels lived beyond this 15-m band, and thus dividing the results we present by a factor of 5.8.

Within each study reach, we evaluated the mussel population by 3 methods: 2 timed searches and quadrat sampling. Timed searches are widely used in studies of mussels (e.g., Cvancara et al. 1976, Hoeh and Trdan 1985, Strayer and Ralley 1991) and other organisms (fish, birds). Results are presented as catch-per-unit-effort (CPUE). Each timed search usually took about 1 h, and included both visual and tactile searches, as appropriate. All live mussels encountered were counted, regardless of species, and immediately replaced in the substratum. The length of all living individuals of *A. heterodon* was measured to the nearest 0.1 mm, using vernier calipers. Timed searches do not locate all mussels in a study area, but in our study, catch rates were correlated with mussel density (Strayer et al. 1996).

First, one of us (DLS) carried out a timed search for mussels while wading. At a few reaches, this search was omitted because of time limitations or because we felt that we would stir up so much sediment that our 2nd timed search would be impossible. Following the timed search while wading, one of us (DLS) put on a mask and snorkel and repeated a timed search of the study reach. Timed searches while snorkeling were not done at some reaches because of poor visibility.

Along with the timed searches, we estimated mussel density by searching 0.25-m^2 quadrats by sight and, where necessary, by feel. We deployed the quadrats in an adaptive cluster sampling design (Thompson 1992). In this design, an investigator places initial sampling units in a traditional design (e.g., random, stratified, regular) and searches them. If the data from any of the initial sampling units satisfy a preset condition (in our case, the presence of an individual of *A. heterodon* or large numbers of other mussels), additional samples are taken in areas adjacent to the initial units. This sampling strategy allows an investigator to concentrate sampling effort in areas of high population density and thereby improve the precision of population estimates (Thompson 1992). Typically, we searched 30–100 (mean = 61) initial quadrats, then searched a variable number (mean = 15) of additional quadrats according to the requirements of adaptive cluster sampling. Other than in North Carolina, we set out the initial quadrats in a random design. Because it appeared that mussels were clustered along the streambanks in the North Carolina streams, we used stratified adaptive cluster sampling (Thompson

1992), placing half of the initial quadrats within 1 m of either bank. Values for the condition dictating the need for further sampling varied among study reaches, and were set following an initial reconnaissance of each reach. The estimator $\hat{\mu}_2$ was used for the mean (Thompson 1992).

Quadrat sampling is insensitive to sparse populations, and all 3 of our indices of population density have large errors (Strayer et al. 1996). To develop a more robust estimate of mean population density for each stream, we combined the 3 estimates into a composite index of density, as follows. The CPUE from the timed search while wading was normalized by dividing by the mean CPUE over all streams, then converted into units of density (D_{CPUEW}) by multiplying by the mean density observed in quadrats over all streams. Thus

$$D_{CPUEW} = \left(CPUEW_i \middle/ \sum_{i=1}^{12} (CPUEW_i/n)\right) \times \left(\sum_{i=1}^{12} D_i/n\right) \quad (1)$$

where $CPUEW_i$ and D_i are the areally weighted mean CPUE (from searches while wading) and quadrat density, respectively, for each stream i, and n is the number of streams studied (12). This procedure was repeated for CPUE from snorkeling searches. The estimated "density index" for each stream was simply the mean of the 3 estimates of density (1 from the quadrats and 1 from each of the timed searches). This index is expressed in terms of actual density (unlike the CPUE), is much more sensitive than the quadrat data to sparse populations, and should have a smaller error than any of the 3 individual indices from which it is derived. Our procedure implicitly assumes that density is a linear function of CPUE. The actual relationship between CPUE and density is unknown for low-density populations. For dense populations of *Elliptio complanata,* density is a power function of CPUE with an exponent between 0.7 and 1 (Strayer, unpublished). Confidence limits around our estimates of the density index were calculated by resampling statistics (Bruce 1993), using 250 runs.

Alasmidonta heterodon occurs in or near all of our study reaches. Nevertheless, populations were too sparse at many reaches to be detected by our sampling program. It is important to consider how large a population could have been overlooked, given the sampling effort. We (Strayer et al. 1996) extended the approach of Green and Young (1993) to estimate the densest population likely to be overlooked in streams where population densities were below our detection limits. Our goal was to solve for the population density that would have given us a 50% chance of detection. The probability of detection of *A. heterodon* by any of k independent sampling methods is

$$p(\text{detection}) = 1 - \prod_{i=1}^{k} p(\text{no detection})_i \quad (2)$$

According to Green and Young (1993), the probability of not detecting a species in n quadrats is

$$p(\text{no detection}) = e^{-mn} \quad (3)$$

where m is the mean density per quadrat. For timed searches, we assumed that catches of rare species follow a Poisson distribution, so

$$p(\text{no detection}) = e^{-M} \quad (4)$$

where M is the mean number of individuals seen during the search. Because we collected data on both actual densities and catch rates over a large number of reaches, we can predict M as a function of population density (Strayer et al. 1996). Note, however, that M can be estimated from population density only with considerable error, so resampling methods are needed to derive an unbiased estimate of M. We used 1000 runs with Resampling Stats® (Bruce 1993) to estimate M from population density, assuming that mean catch rates of *A. heterodon* were 1/3 of those of *Elliptio complanata* (Strayer et al. 1996) and had the same variance. To estimate the largest population likely to have been overlooked, we then assumed the population was restricted to 1 reach (the reach of least sampling effort) per stream, and combined and solved equations 2–4.

All estimates and statements in this report refer to individuals of *A. heterodon* that are visible at the sediment surface. Young *A. heterodon* (i.e., < 25 mm and < 3 y old) were rarely seen and presumably were buried out of sight beneath the sediment surface. Moreover, in at least some unionid populations, substantial numbers of adults are buried beneath the sediment surface

TABLE 3. Measures of population density of unionid species other than *Alasmidonta heterodon* in the study streams. Figures are areally weighted means over the range occupied by *A. heterodon* in each stream. Species are listed in alphabetical order and streams are listed from north to south.

	CPUE (h^{-1}) (wading)	CPUE (h^{-1}) (snorkeling)	Quadrat density (no/m^2)
Alasmidonta undulata			
Connecticut River	na	0.2	0.00007
Ashuelot River	1.9	4.8	0.04
Neversink River	0.2	0.3	0.03
Crooked Creek	1.2	3.6	0.1
Little River	0	0.7	0.03
Swift Creek	0	1.0	0
Turkey Creek	0	1.0	0
Moccasin Creek	0	0	0.07
Alasmidonta varicosa			
Neversink River	3.9	8.1	0.02
Anodonta implicata			
Neversink River	0.8	0.2	0.03
Elliptio complanata[a]			
Connecticut River	na	18	0.1
Ashuelot River	728	1603	25.6
Neversink River	84	214	5.9
McIntosh Run	101	112	2.5
Aquia Creek	254	155	0.6
Po River	248	327	5.5
Tar River/Shelton Creek	166	158	1.6
Crooked Creek	134	132	6.0
Little River	279	570	21.4
Swift Creek	181	366	10.5
Turkey Creek	107	202	3.6
Moccasin Creek	76	123	3.1
Elliptio "lanceolata"[a]			
Po River	0	1.5	0
Little River	1.3	0	0.2
Swift Creek	0.6	2.6	0
Turkey Creek	1.1	2.0	0
Moccasin Creek	1.8	7.2	0.2
Fusconaia masoni			
Little River	0.7	0	0
Swift Creek	0.6	1.6	0
Moccasin Creek	0	0.3	0
Lampsilis cariosa			
Tar River/Shelton Creek	0	0.4	0
Lampsilis radiata			
Connecticut River	na	3.0	0.0002
Tar River/Shelton Creek	1	7.6	0.1
Lasmigona subviridis			
Little River	17.7	na	1.8
Pyganodon cataracta			
Connecticut River	na	0.0005	0
Ashuelot River	0.02	1.6	0.04
Po River	2.0	0	0.002
Tar River/Shelton Creek	na	0.3	0
Strophitus undulatus			
Connecticut River	na	0.001	0.00002
Ashuelot River	5.6	3.6	0.1
Neversink River	1.6	2.6	0.0003
Aquia Creek	0	0.8	0.007
Po River	0.9	3.0	0.1
Tar River/Shelton Creek	0	0.4	0.004
Crooked Creek	1.2	5.0	0.2
Little River	0	1.0	0
Moccasin Creek	0	1.5	0.001
Villosa constricta			
Moccasin Creek	1.0	0.5	0.02

[a] Because of taxonomic uncertainty in *Elliptio*, we refer to all lanceolate forms as *E. "lanceolata"* and all other forms as *E. complanata*

(Amyot and Downing 1991, Balfour and Smock 1995). Our population estimates are therefore low to the extent that part of the population was buried.

Results

Catch rates for *A. heterodon* were uniformly low (0–4 mussels/h) for both kinds of timed searches (Table 2). In contrast, catch rates of other mussel species sometimes reached more than 1000/h and often exceeded 100/h (Table 3). Densities observed in quadrats were likewise low (0–0.06/m^2, Table 2), although densities of other mussel species often exceeded 1/m^2 (Table 3). In spite of these low densities, we estimate

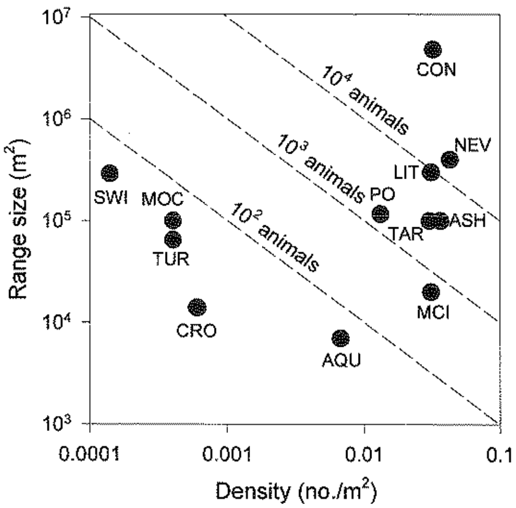

FIG. 1. Range size and mean density index (both logarithmically scaled) of studied populations of *Alasmidonta heterodon*. Streams are identified by the first three letters of their names (cf. Table 2). Dashed reference lines show population sizes implied by various combinations of density and range size. Densities for Crooked, Moccasin, Swift, and Turkey creeks are estimated upper bounds on population density (see text). Range size for the Po River based on this survey and Neves (1995).

that several of the populations of *A. heterodon* contained more than 1000 animals (Fig. 1).

Alasmidonta heterodon was not detected by any of our sampling methods in 4 streams in North Carolina (the sole animal that we saw in Crooked Creek was in an "edge unit", so it is not included in density calculations; Thompson 1992). Estimated maximum undetectable densities for these streams ranged from 0.0001 to $0.0006/m^2$.

All of the populations we studied contained animals of a wide range of sizes (Fig. 2). Animals smaller than 25 mm were rarely seen, and presumably were buried out of sight (cf. Amyot and Downing 1991), but all of the populations contained animals < 30 mm long. According to the growth curves calculated by Michaelson and Neves (1995), these animals probably were 3- to 5-y-old. There were no striking differences in size structure among the populations.

Discussion

All of the populations of *A. heterodon* that we studied had several features in common. All had low densities. Although these populations are thought to be the densest, largest remaining populations of *A. heterodon*, densities ranged from below detection (ca. $0.001–0.0001/m^2$) to $0.04/m^2$ (Table 2). In only 1 small mussel bed did we find densities approaching $0.5/m^2$. Populations of other unionid species often are $1–10/m^2$ in favorable habitats, and may reach well above $100/m^2$ in dense aggregations (e.g., Table 3, Miller and Payne 1993, Strayer and Ralley 1993, Strayer et al. 1994). Our findings support earlier statements (Ortmann 1919, Clarke 1981) that *A. heterodon* usually forms sparse populations. Low density may be a natural feature of *A. heterodon* populations or may have resulted from pervasive human influences that began before the early 20th century, when most systematic observations of mussel populations began. Unfortunately, no historical data on population density are available for any *A. heterodon* population (other than the data for the Neversink River in 1991—Strayer and Ralley 1993), so we cannot rigorously assess temporal trends in population density for this species.

Low density may in itself be a severe, but poorly understood, threat to *A. heterodon* populations. In the only study of its kind, Downing et al. (1993) showed that female unionids may not be fertilized unless they are very close to a conspecific male mussel. In fact, they found virtually no fertilized females of *Elliptio complanata* in populations sparser than $10/m^2$ in a Quebec lake. Apparently *A. heterodon* can reproduce successfully at a much lower density. Nevertheless, Downing's work suggests that some (many?) of the low-density parts of *A. heterodon* populations may be incapable of reproduction. This possibility urgently needs further investigation.

Another property shared by most of the *A. heterodon* populations that we studied is that they have reproduced recently. We found animals that probably were 3–5 y old in every stream where we saw *A. heterodon*. Furthermore, other investigators recently found young or gravid *A. heterodon* in some streams where we did not detect the species: Turkey and Moccasin creeks (young animals and gravid females in Turkey Creek in 1992–1994, J. Alderman, personal communication), and Swift Creek (gravid females seen in 1994, J. Alderman, personal communication).

Despite their low densities, many of the populations of *A. heterodon* that we studied were

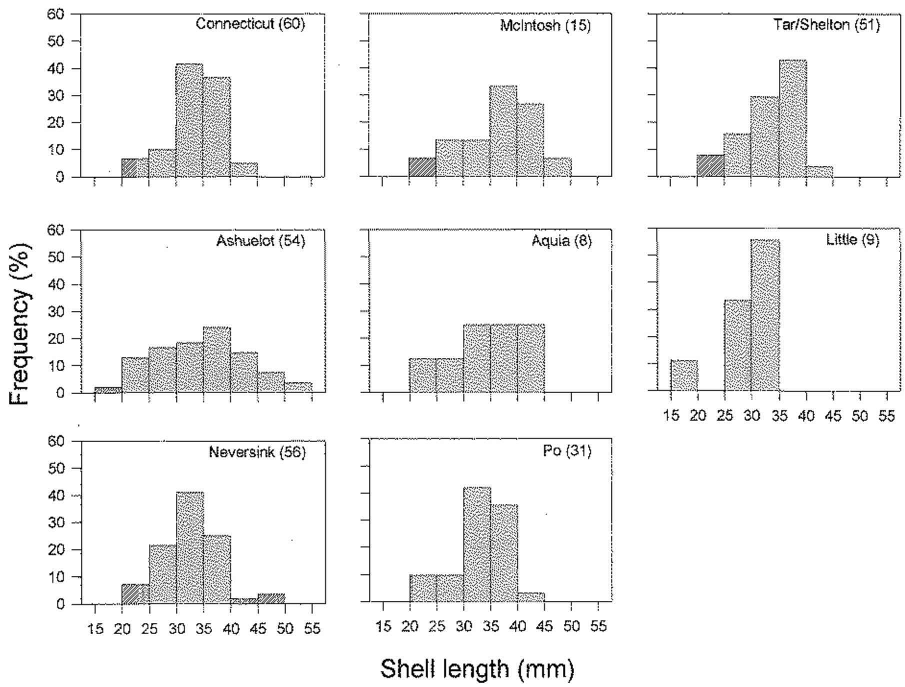

FIG. 2. Frequency of sizes of specimens of *Alasmidonta heterodon* collected at the study sites. The number of specimens measured is in parentheses following the name of the stream. Data for Po River include 21 living specimens measured by Phil Stevenson in December 1993 and April 1994. Sites arranged in order from north to south.

large (10^3–10^5 animals) (Fig. 1). To a first approximation (see below), these populations are too large to be strongly affected by many of the conservation problems of small populations (e.g., inbreeding, demographic stochasticity; Caughley 1994). Furthermore, these large populations probably are large enough to provide a modest supply of animals for reintroductions at other sites and laboratory studies of ecology and genetics.

A major assumption of the preceding paragraph is that all of the individuals of *A. heterodon* in a stream belong to a single panmictic population. This assumption probably is violated to some degree because in most streams *A. heterodon* occurs in more or less distinct, widely separated patches. Until we know more about the metapopulation structure of unionid populations (cf. Vaughn 1993), it will be hard to make definitive statements about how many animals are required for a population to be large or viable.

Finally, the ranges of most populations of *A. heterodon* are linear, consisting of an unbranched segment of stream. Such linear populations are especially vulnerable to loss because they have no spatial refuge from threats occurring upstream of the population or in the watershed. Only 2 of the populations studied may have branched ranges (Tar/Shelton and Turkey/Moccasin), and even here the extent of communication between the 2 branches is unclear.

The populations that we studied differed in size over about 3 orders of magnitude (Fig. 1). It is tempting to equate population size with viability and thereby rank the largest populations as the most viable. We have suggested, though, that many populations of *A. heterodon* are too large to be threatened by low population sizes per se. Instead, populations may be threatened more or less independently by low density (discussed above) and small ranges. The ranges occupied by *A. heterodon* populations are known only roughly for some populations; determining and monitoring range limits for all major populations should be a high priority. Nevertheless, range sizes apparently span 3 orders of magnitude (Table 1, Fig. 1). At the lower end of this span are populations such as the one in Aquia Creek, which probably contains only a few local subpopulations, all close to one another and thereby highly vulnerable to many threats. More widespread populations (e.g., the one in the Connecticut River) probably contain many local subpopulations that are somewhat separated and thereby more buffered against some threats. The most robust populations of *A. heterodon* may be those with both relatively dense populations and large ranges. Viewed from this perspective, the most robust remaining populations are those in the Connecticut, Neversink, Little, Tar (including Shelton Creek), Ashuelot, and Po rivers (Fig. 1). Nevertheless, all populations in our study appear to be vulnerable to loss because of low densities, small ranges, linear ranges, or some combinations of these factors.

The North Carolina streams where densities of *A. heterodon* were below our detection limits present special problems for both monitoring and management. Despite the effort we expended, we could obtain only the most fragmentary information (i.e., approximate upper limits to population density) about these populations. Even if we were able to devote more time to these streams, we probably could not estimate population sizes or densities with enough precision to satisfactorily assess temporal trends due to natural or human-induced forces (Strayer et al. 1996). The extremely low density of these populations ($<0.001/m^2$) thus severely limits our ability to understand their functioning and dynamics. The low density and small size of these populations are worrisome from a conservation viewpoint as well. Are these populations poised on the knife edge of extirpation? This question is especially significant because most of these sparse populations are in the Neuse River basin, where streams are under pressure from residential and industrial development and logging. Furthermore, if these southern populations of *A. heterodon* are generally differentiated from northern populations, losses of populations from the Neuse basin may represent an important loss of genetic diversity in the species.

Our study highlights both strengths and weaknesses of a standardized, quantitative approach to assessing mussel populations. We were able to assess major remaining populations of *A. heterodon* using a consistent and objective set of measures (Table 2; Fig. 1). The resulting ranking of populations is strikingly different from previous rankings made by different biologists using different methods and criteria (Fig. 3). Because our methods are repeatable, our results can be used to assess changes in *A. heterodon* populations through time. Further, because we were able to estimate actual population size, we were able to suggest that small population size in itself probably isn't a major threat to some populations of *A. heterodon*. On the other hand, our methods are much more expensive in terms of time and effort than less formal approaches to population assessment (Strayer et al. 1996). Furthermore, the quality of the data (precision, sensitivity) may still be inadequate to meet the needs of biologists and managers, especially for the extremely sparse populations often of most interest to conservationists (Strayer et al. 1996). Perhaps the most serious shortcoming of all current methods of population assessment is that we still don't have enough information on the structure and functioning of mussel populations to link measurable quantities like population density and size to properties of direct importance to conservation issues, such as population viability and sensitivity to environmental degradation.

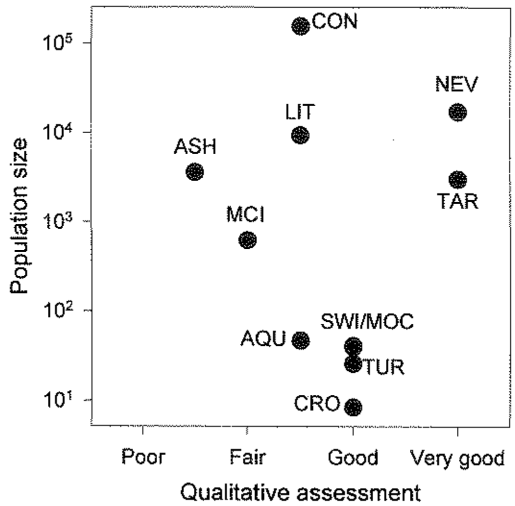

FIG. 3. Comparison of the qualitative assessments of *Alasmidonta heterodon* populations given by US FWS (1993) with population sizes estimated in this study. Each point represents one stream. The data for the four smallest populations are estimated upper bounds on population size (see text).

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Literature Cited

ALLAN, J. D., AND A. S. FLECKER. 1993. Biodiversity conservation in running waters. BioScience 43:32–43.

AMYOT, J.-P., AND J. A. DOWNING. 1991. Endo- and epibenthic distribution of the unionid mollusc *Elliptio complanata*. Journal of the North American Benthological Society 10:280–285.

BALFOUR, D. L., AND L. A. SMOCK. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. Journal of Freshwater Ecology 10:255–268.

BRUCE, P. C. 1993. Resampling Stats®: the "new statistics" user guide, IBM version 3.14. Resampling Stats, Arlington, Virginia.

CAUGHLEY, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

CLARKE, A. H. 1981. The tribe Alasmidontini (Unionidae: Anodontinae) Part I: *Pegias, Alasmidonta,* and *Arcidens.* Smithsonian Contributions to Zoology 326:1–101.

CUTKO, A. 1993. Inventory and monitoring of the dwarf wedgemussel (*Alasmidonta heterodon*) in New Hampshire. 1993 Performance Report to New Hampshire Fish and Game Department, Concord.

CVANCARA, A. M., R. D. NORBY, AND J. B. VAN ALSTINE. 1976. Mollusks of the Sheyenne River, North Dakota, U.S.A.: present and past. Malacological Review 9:25–38.

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

FICHTEL, C. 1993. Inventory, monitoring and conservation planning for the dwarf wedgemussel (*Alasmidonta heterodon*) in the Connecticut River. 1993 Performance Report to the U.S. Fish and Wildlife Service, Hadley, Massachusetts.

GREEN, R. H., AND R. C. YOUNG. 1993. Sampling to detect rare species. Ecological Applications 3:351–356.

HOEH, W. R., AND R. J. TRDAN. 1985. Freshwater mussels (Pelecypoda: Unionidae) of the major tributaries of the St. Clair River, Michigan. Malacological Review 18:115–116.

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.

MILLER, A. C., AND B. S. PAYNE. 1993. Qualitative versus quantitative sampling to evaluate population and community characteristics of a large-river mussel bed. American Midland Naturalist 130: 133–145.

NEVES, R. J. 1993. A state-of-the-unionids address. Pages 1–10 *in* K. S. Cummings, A. C. Buchanan, and L. M. Koch (editors). Conservation and management of freshwater mussels. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

NEVES, R. J. 1995. A survey of the freshwater mussel fauna at Proposed Corridor A and Modified Corridor C crossings of the Po River and unnamed tributaries, Spotsylvania County, Virginia. Final Report for the Virginia Department of Transportation, Richmond, Virginia.

ORTMANN, A. E. 1919. A monograph of the naiades of Pennsylvania. Part III. Systematic account of the genera and species. Memoirs of the Carnegie Museum 8:1–384.

STRAYER, D. L., AND J. RALLEY. 1991. Freshwater mussels (Unionoida) of the upper Delaware River basin, New York. American Malacological Bulletin 9:21–25.

STRAYER, D. L., AND J. RALLEY. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. Journal of the North American Benthological Society 12:247–258.

STRAYER, D. L., D. C. HUNTER, L. C. SMITH, AND C. K. BORG. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. Freshwater Biology 31:239–248.

STRAYER, D. L., S. CLAYPOOL, AND S. J. SPRAGUE. 1996. Assessing unionid populations with quadrats and timed searches. *In* K. S. Cummings, A. C. Buchanan, and L. M. Koch (editors). The conservation and management of freshwater mussels II: initiatives for the future. Upper Mississippi River Conservation Committee, Rock Island, Illinois (in press).

THOMPSON, S. K. 1992. Sampling. John Wiley, New York.

US FWS (FISH AND WILDLIFE SERVICE). 1993. Dwarf wedge mussel (*Alasmidonta heterodon*) recovery plan. US FWS, Hadley, Massachusetts.

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. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

WILLIAMS, J. D., M. L. WARREN, K. S. CUMMINGS, J. L. HARRIS, AND R. J. NEVES. 1993. Conservation status of the freshwater mussels of the United States and Canada. Fisheries 18(9):6–22.

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