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A range-wide assessment of populations of the dwarf wedgemussel (*Alasmidonta heterodon*)

A report to the U.S. Fish and Wildlife Service

by

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SUMMARY

The purpose of this study is to provide comparable estimates of the population sizes of the major remaining populations of the dwarf wedgemussel, Alasmidonta heterodon, a small, inconspicuous mussel listed as endangered by USFWS. Thirteen streams from New Hampshire to North Carolina were studied. At 1 - 9 sites on each stream, we assessed A. heterodon populations using both timed searches and quadrats, and measured the shell lengths of all living dwarf wedgemussels that we found. My conclusions are:

- all populations of A. heterodon that we studied are vulnerable to loss because of their small ranges, low population densities, linear ranges, or some combination of these three factors;

- all populations of A. heterodon that we studied are sparse, with mean densities typically $<0.01/m^2$ to $0.05/m^2$. These populations are much sparser than those that have been shown to suffer from low fertilization rates in other species. Low or declining density per se may therefore be a threat to populations of A. heterodon.

- all populations that we studied are nonetheless reproducing, as shown by the recent presence of young animals or gravid females;

- furthermore, all but one of the populations that we studied probably include hundreds to tens of thousands of animals, so these populations are too large to be strongly affected by many of the conservation problems of small

populations (e.g., inbreeding, demographic stochasticity, etc.). The one exception among the streams we studied is Aquia Creek, Virginia, which may contain as few as a few dozen adults.

- without considering the specific threats faced by these populations, the most robust populations of A. heterodon probably are those with both relatively high densities and relatively large ranges. Populations in this category include those in the Connecticut (NH), Ashuelot (NH), Neversink (NY), and Shelton/Tar (NC) Rivers (and perhaps the Little River (NC) as well). Aquia Creek (VA) clearly contains the least robust of the populations in this study, while populations in McIntosh Run (MD), the Po River (VA), Crooked Creek (NC), Swift Creek (NC), Moccasin Creek (NC), and Turkey Creek (NC) occupy an intermediate position.

- it is possible to obtain fairly precise estimates of actual mussel densities using an ANCOVA model based on catch-per-unit-effort data from timed searches.

INTRODUCTION

The primary goal of this study is to provide comparable (and if possible, absolute) estimates of the population sizes of the major remaining populations of the dwarf wedgemussel, _Alasmidonta heterodon_. _A_. _heterodon_ is a small, inconspicuous mussel formerly known from about 70 sites in streams between North Carolina and New Brunswick (Clarke, 1981; USFWS, 1993). Apparently never a common animal (e.g., Ortmann, 1919), _A_. _heterodon_ has declined to the point that it was listed as endangered by the USFWS in 1991. It is now known from 25 - 30 streams, most of which are thought to support small populations. The status and trends of these populations usually is given in terms like "poor," "good," "declining," "stable," etc., based on the experience of the biologist monitoring the population. Methods and terminology for describing mussel populations differ among biologists and across states, making it difficult to compare populations of _A_. _heterodon_ in different regions (or at different times). Quantitative estimates of the sizes of these populations have been made only for the Neversink River (Strayer and Ralley, 1993, and unpublished). The present study attempts to describe the major remaining populations of _A_. _heterodon_ using a standardized, repeatable (although imperfect) procedure.

THE STUDY SITES

Our study was set up to include the 10 - 12 streams thought by USFWS to support the largest remaining populations of _A_.

heterodon, namely: Connecticut River (NH), Ashuelot River (NH), Neversink River (NY), McIntosh Run (MD), Aquia Creek (VA), Po River (VA), Tar River (NC), Crooked Creek (Tar basin, NC), Swift Creek (Neuse basin, NC), Little River (Neuse basin, NC), Turkey Creek (NC), and Moccasin Creek (NC). Based on a preliminary examination of streams in North Carolina and on discussions with John Alderman, who has extensive experience with the North Carolina populations of A. heterodon, we decided to add Shelton Creek (NC) and de-emphasize Crooked Creek. We visited the streams according to the following schedule: reconnaissance of North Carolina sites, including Tar River, Shelton Creek, Crooked Creek, Swift Creek, Little River, and Moccasin Creek; 31 May - 2 June; Connecticut River: 25 - 28 August; Ashuelot River: 1 - 3 August; Neversink River: 9 and 14 June; 6, 7, 12, and 14 July; McIntosh Run: 19 - 20 July; Aquia Creek: 23 - 24 July; Po River: 21 - 22 July; Tar River: 25 - 26 June; Shelton Creek: 24 and 26 June; Crooked Creek: 21 June; Swift Creek: 23 June; Little River: 20 and 22 June; Turkey Creek: 19 and 21 June; Moccasin Creek: 18 and 22 June.

METHODS

We established 1 - 9 study sites on each stream. Locations of sampling sites are given in Appendix 2. Study sites typically encompassed the entire width of the stream, and ran for 100m (large streams) to 200m (small streams). Study sites usually were chosen in accessible reaches (often near bridges) for which we had no specific prior knowledge about the density of _A_. _heterodon_. The densities recorded in these study sites were therefore taken to represent the average density in the stream as a whole. In some streams, known mussel beds were thought to contain large populations of _A_. _heterodon_. These streams were stratified into bed and non-bed areas, and some study sites were deliberately set up in mussel beds. The midchannel of the Connecticut River was too deep to examine by our methods, so work on this river was confined to areas within 15m of the shore.

Within each study reach, I carried out a timed search for mussels while wading. This search usually took about 1 hour, and included both visual and tactile searches, as appropriate. All live mussels encountered were counted, regardless of species, and the length of all living individuals of _A_. _heterodon_ was measured to the nearest 0.1mm, using vernier calipers. At the end of the search, I recorded a subjective estimate of visibility at the site using a 1 - 10 scale, where 10 indicates that 100% of the bottom was clearly visible; 1 indicates that about 10% of the bottom was clearly visible, etc. At a few sites, the timed search while wading was omitted because of time limitations or because I felt that so much silt would be stirred up that a timed search while snorkeling (see below) would be impossible.

Following the timed search while wading, I put on a mask and snorkel and repeated a timed search of the study site. During this search, which usually took about an hour, I counted all living mussels encountered, regardless of species, and counted and measured all living A. heterodon seen. At the end of the search, a subjective index of visibility (1 - 10 scale, as above) was chosen. Timed searches while snorkeling were not done at some sites because of excessive turbidity.

These timed searches of course turn up only a small fraction of the mussels living in the study site, and merely provide an index of population density. Also, it is very important to remember that the CPUE generated in this study are comparable only to each other, and not to CPUE generated by other biologists (or even by the author under other circumstances). For example, a CPUE of 3 mussels/hr in this study does not correspond to a CPUE of 3 mussels/hr reported in some other study.

In addition to the timed searches, we estimated actual mussel density within the study site by searching $0.25 m^2$ quadrats. Quadrats were searched by sight and, where necessary, by feel. We used an adaptive cluster sampling design (Thompson, 1992), stratified at some sites into nearshore and midchannel strata. Typically, 30 to 100 primary quadrats were placed at random, then additional quadrats were searched according to the requirements of adaptive cluster sampling. Values for the condition varied among sites, and were set following an initial reconnaissance of each site. The estimator $\hat{\mu}_2$ was used for the mean.

Six indices of population density were derived from these data. The catch rates from the two timed searches (in units of mussels/hour) provide comparable, quantitative indices of population density, even though they are not in terms of the actual density of the population and are subject to variance from difference in visibility across sites, etc. The estimated mean density of mussels in quadrats provides a third index of population density, independent of the timed searches. While comparable among sites, quantitative, and expressed in terms of absolute density of the population, this index has fairly large errors and high detection limit, so that sparse populations are easily overlooked. Populations of A. heterodon usually are sparse, so quadrat-based estimates are limited in application.

In an attempt to use the best features of the timed searches and the quadrats, we developed a model (see appendix) to predict actual mussel densities from the catch-per-unit effort (CPUE) data from timed searches. Three such indices are derived here: one based on searches while wading, one based on searches while snorkeling, and one based on the combined results of both timed searches. These indices can detect fairly sparse populations and have acceptably small errors (see appendix), and probably offer the best estimates of A. heterodon densities.

A. heterodon is known to occur at all of our study sites except for PO3, which had not been surveyed previously (P. Stevenson, pers. comm.). Nevertheless, populations were too sparse at many sites to be detected by our sampling program, which had a detection limit much higher than those of conventional mussel surveys, which are designed to cover a lot of ground and detect rare species. Because many populations of A.

heterodon are thought to cover a fairly large area, even a population that was undetectable by our sampling program could be substantial. A formal analysis of the detection limits (i.e., the largest population likely to remain undetected, given the intensity of sampling), would require a consideration of the joint probabilities of not finding any A. heterodon in either timed searches or quadrats. I am not aware of any method for such an analysis, nor am I capable of deriving one. Instead, I used the following crude procedure to get an idea of the largest possible population that could have remained undetected. At each site where no A. heterodon were found, I calculated the density that would have been estimated if just one A. heterodon had been found in a timed search. I repeated this procedure for each study site on the stream, averaged the estimated densities, then divided by the number of study sites on the stream. This procedure should give the density that would have been estimated if just one A. heterodon had been found at one (average) study site. This is not exactly the same as the minimum detectable density, but it is straightforward to calculate and is interpretable, and shows that substantial populations of A. heterodon could live in some of the streams where we found none.

All estimates and statements in this report refer to individuals of A. heterodon that are visible at the sediment surface. Young animals of A. heterodon (i.e., less than ca. 25mm and 3-years old) were rarely seen (Figs. 1 - 3) and presumably buried out of sight beneath the sediment surface. In addition, in at least some unionid populations, substantial numbers of adults are buried beneath the sediment surface (Amyot and Downing, 1991). Our population estimates are therefore low to the extent that part of the population is buried.

RESULTS

The six indices of the density of A. heterodon populations are given in Table 1.

Catch rates in timed searches

Catch rates were uniformly low in areas not previously identified as mussel beds, ranging from 0 to 13 A. heterodon/hour, with means of 1.0/hour and 2.2/hour while wading and snorkeling, respectively. In areas previously known to be mussel beds, catch rates were 0 - 20 mussels/hour, with means of 4.1/hour and 8.8/hour while wading and snorkeling, respectively. Mussel population densities were below detection in 20 of the 38 sites searched while wading, 19 of the 47 sites searched while snorkeling, and 14 of the 31 sites searched by both methods. In general, catch rates were a little (but not significantly) higher in searches while snorkeling than while wading (Fig. A4). These catch rates are very low when compared to those of other species at the study sites, which often reached several hundred to more than a thousand mussels per hour (appendix 3).

Quadrats

Densities of A. heterodon were below detection in 38 of the 56 sites sampled by quadrats. Mean densities were only 0.024/m^2

at sites not previously identified as mussel beds and 0.076/m^2 at sites previously identified as mussel beds. The maximum density seen was 0.39 A. heterodon/m^2 at a site in the Neversink River previously known to support a dense population of A. heterodon. In contrast, densities of other mussel species at our study sites often exceeded 10/m^2 (appendix 3).

Size structure of the populations

Shell lengths of living A. heterodon ranged from 18.9mm to 56.0mm (Figs. 1 - 3). Most animals were 30 - 40mm long. There were no striking differences in size structures among the populations. Most populations had similar mean lengths (32 - 35mm) and ranges of lengths. Populations in McIntosh Run and especially the Ashuelot River contained a broader range of sizes than the other populations.

It is not possible to infer precise ages from the size structure of these populations. Based on the age-length keys of Michaelson (1993), most of the animals that we saw were probably 4 - 8 years old. All of the sites at which we detected A. heterodon apparently contained fairly young (<5 year-old) animals, showing evidence of recent reproduction.

Results from each study site

Aquia Creek, Virginia

Previous work on Aquia Creek found that A. heterodon was found chiefly between former County Route 643 upstream to the mouth of Cannon Creek, a distance of only 0.5 km (Michaelson, 1993). We set up eight study reaches, each 100m or 200m long, which covered the entire reach between old Route 643 and Route 610, a distance of 1.2 km.

We found no _A_. _heterodon_ in any of the 454 quadrats we searched in Aquia Creek. Catch rates in timed searches (while snorkeling) ranged from 0 - 5.1 _A_. _heterodon_/hr with means of 0.2/hr below Cannon Creek and 4.6/hr above Cannon Creek. The total population of _A_. _heterodon_ in the study reach is estimated to be about 50 animals.

This population has evidently declined considerably since Michaelson's study in 1992. Michaelson was able to find dozens of live _A_. _heterodon_ for microhabitat studies (as well as dozens of spent shells) between Cannon Creek and old Route 643, while we found only one live animal and five very old spent valves in this reach. Apparently, some unknown cause (flooding?, Tim Stamps, pers. comm.) has nearly eliminated _A_. _heterodon_ between Cannon Creek and old Route 643. _Elliptio_ was still abundant in this reach (0.45/m^2) in 1994, though. Between Cannon Creek and Route 610, the population of _A_. _heterodon_ has a moderate density (0.03/m^2), and contains young animals (Fig. 6), but is small. The estimate of 50 animals may be too low, though, as there is no reason to believe that _A_. _heterodon_ does not live above the Route 610 bridge. The creek is so small (ca. 5 m wide) at Route 610 that the size and extent of this unknown, upper part of the population probably are small.

Ashuelot River, New Hampshire

The population of _A_. _heterodon_ in the Ashuelot River is thought to extend from the Route 12A bridge to the Surry Mountain Dam, a distance of 7.2 km (Cutko, 1993). Based on the monitoring data from 1991 - 93 presented by Cutko (1993), we stratified the reach into three sections: high density (Cutko's segment 2a), moderate density (Cutko's segment 1, 2b, 3 - 7), and low density (Cutko's segments 8 - 11). We set up three study reaches in the high density section, three in the moderate density section, and one in the low density section.

Catch rates ranged from 0 - 4.1 A. heterodon/hr in timed searches while wading and 1 - 13/hr in timed searches while snorkeling. Weighted means for the entire 7.2 km reach were 2.3/hr and 3.0/hr, respectively. Estimated densities ranged from 0.002 - 0.3/m^2, with a weighted reachwide mean of 0.05 A. heterodon/m^2. The total population was estimated to include about 6,000 animals. We found many young A. heterodon in the Ashuelot.

Connecticut River, New Hampshire

This population is thought to reach from the mouth of the Ottauquechee River to Weathersfield Bow, a distance of about 27 km (Fichtel, 1993). According to Fichtel (1993), much of the population of A. heterodon is thought to occur in a few more or less discrete beds. Accordingly, we set up study reaches in five of these known mussel beds, as well as at four sites where the mussel fauna was unknown to us.

Catches in the known mussel beds ranged from 0 - 11.6 A. heterodon/hr (searches while wading) and 1.1 - 10.8/hr (searches while snorkeling). Actual densities in these beds were estimated to be 0 - 0.06/m^2 (by quadrats) or 0.003 - 0.09/m^2 (estimated indirectly from timed searches). We estimated that about 400 A. heterodon lived in these discrete beds.

A. heterodon was found in two of the four study reaches where the mussel fauna was previously unknown to us. Catch rates were 3.7/hr and 11/hr (searches while snorkeling); no searches on foot were made at these two sites. Actual densities were estimated to be 0.05/m^2 and 0.12/m^2 (direct estimates from quadrats) and 0.02/m^2 and 0.08/m^2 (indirect estimates from timed searches). Many young animals were found in the Connecticut.

Estimating the total number of A. heterodon in the Connecticut River presents special problems. All of our work was done within 15 m of the shore. Deeper water near the center of the channel is difficult or impossible to search using the methods we employed and is thought to contain relatively few mussels (Chris Fichtel, pers. comm.). If we assume that all mussels in the Connecticut River live with 15 m of shore, we estimate that 20,000 A. heterodon live in the river. If we assume that mussel densities are the same in the middle of the river as near the shore, we estimate that 100,000 A. heterodon live in the river.

Crooked Creek, North Carolina

A. heterodon is thought to occupy a 1.6 - 3.2 km reach of Crooked Creek (USFWS, 1993). We visited one site on Crooked Creek, at which we set up two study reaches.

A. heterodon was not detected in 2 hr of timed searches at this site. A single A. heterodon (36.1 mm long, apparently 4-yr old) was seen in one of the 111 quadrats searched. Because the quadrat containing this animal was an edge unit (Thompson, 1992), it was not used in calculating density, so the formal estimate of A. heterodon density at this site is 0. Nevertheless, according to my approximate estimate of detection limits, a population of several hundred A. heterodon could exist in Crooked Creek without our detecting them, given our level of effort and the estimated extent of the population.

Little River, North Carolina

This population is thought to extend over 16 - 32 km of stream (USFWS, 1993). We surveyed three study sites in the Little River.

On our float survey of 1 June 94, which ran from the bridge just above the Wake-Johnston County line to Johnston County Route 1722, a group of six of us found six living A. heterodon among several thousand living unionids.

A. heterodon was not detected in quadrats (total n = 91) or timed searches (total of 213 min) at two of our study sites on the Little River. At the third site, we recorded a catch of 4 A. heterodon/hr in a timed search while wading and an absolute density of $0.17/m^2$ in quadrats. Density estimated using the ANCOVA model from timed searches was $0.5/m^2$, which seems too high to be reasonable.

Our estimate of the total size of the Little River population is poor, because of the small number of sites surveyed and the large among-site variance in densities. Nevertheless, our estimates range from 10,000 animals (based on the quadrat densities and a range of 16 km) to 70,000 animals (based on the timed search indirect estimate and a range of 32 km). From impressions gained on the float trip, where populations of *A. heterodon* seemed small and scattered, I would guess that even the lower of these two estimates is too high.

McIntosh Run, Maryland

A. heterodon is known to live in a 5-km long reach of this small stream. We set up five study reaches in McIntosh Run.

Catch rates and estimated densities in McIntosh Run were moderate. Catch rates were 0 - 2.9/hr (searches while wading) and 0 - 3.7/hr (searches while snorkeling). Densities estimated from quadrats were 0 - $0.08/m^2$ (mean = $0.04/m^2$) and those taken from timed searches were 0 - $0.11/m^2$ (mean = $0.03/m^2$). Some young animals were taken from McIntosh Run. Our estimate of the total population of *A. heterodon* in McIntosh Run is about 900 animals. The population is therefore moderately dense (for an *A. heterodon* population) and apparently reproducing, but limited in extent and only of modest overall size.

Moccasin Creek, North Carolina

A. heterodon is thought to occupy a 10 - 11 km long reach of Moccasin Creek (USFWS, 1993). We participated in a float survey of the reach from the Route 231 bridge down to Buckhorn Reservoir on 2 June 94, and set up three study reaches on the creek.

A group of five of us picked up five living A. heterodon during the float survey, all between the County Route 1733 (Antioch Church Road) and the reservoir. Above the Route 1733 bridge, we found only a single spent shell of A. heterodon.

We did not detect A. heterodon in any of our study reaches on Moccasin Creek, either in timed searches (total of 232 minutes) or in quadrats (total $n = 161$). Nevertheless, my analysis suggests that a population as large as 1500 animals could have escaped detection.

Neversink River, New York

The population of A. heterodon in the Neversink extends over about 9 km of river (Strayer and Ralley, 1991, 1993, and unpublished). We set up study reaches in two known mussel beds and in four areas where mussel densities previously were unknown.

In known mussel beds, population densities estimated from quadrats were $0.015/m^2$ and $0.4/m^2$. In the four areas where mussel densities had been unknown, quadrat-based densities were $0 - 0.1/m^2$ (mean = $0.04/m^2$), while catch rates were 1 - 3/hr based on searches while wading and 0 - 3/hr based on searches while snorkeling. Many young animals were seen in the Neversink (Fig. 5). Our estimate of the total population size was about 20,000 animals, similar to a previous estimate of 50,000 animals based on independent data collected in 1991 (Strayer and Ralley, 1993, and unpublished).

Po River, Virginia

Before this study, A. heterodon was known from only one site on the Po River (Phil Stevenson, pers. comm.). We found it at the next bridge crossing upstream, and are assuming that the species is found throughout the 6-km reach between the bridges. We surveyed three sites on the Po.

Catch rates on the Po were 0 - 3/hr (searches while wading) and 0 - 1.1/hr (searches while snorkeling). We found two living _A. heterodon_ in quadrats, but both were in edge units (Thompson, 1992), so the density estimated from quadrats was 0. Densities calculated by the ANCOVA model from timed search data were 0 - $0.12/m^2$ (mean = $0.05/m^2$). Some of the animals collected recently from the Po were young (Fig. 6). Because of great uncertainty about the extent of the population in the Po and the small number of sites we examined, our estimate of population size (about 5,000 animals) is highly uncertain. If the population is shown to reach beyond the Route 608 and Route 648 bridges, the population may be larger than we estimate.

Shelton Creek and Tar River, North Carolina

I will treat these two streams together because they have many characteristics in common and because they are close together, so close that the populations in the two streams may communicate. Both of these populations are thought to extend over long reaches of stream: 16 - 24 km in the Tar River (USFWS, 1993), and perhaps 6 - 9 km in Shelton Creek. Nevertheless, both streams have very variable widths and contain large reaches that probably do not contain _A. heterodon_ (long, stony riffles, beaver ponds). Thus, it is difficult to make even an approximate estimate of the area to which observed densities apply or the size of the population. We studied one site in the Tar that was known to contain a dense A. heterodon population, along with three other sites (one on the Tar and two on Shelton Creek) where mussel densities were previously unknown.

In the pool previously known to support A. heterodon we found a catch rate of 14.8/hr (search while snorkeling) and estimated densities of $0.04/m^2$ (direct estimate from quadrats) and $0.24/m^2$ (indirect estimate from timed searches). At other sites in the Tar and Shelton, we found catch rates of 0 - 4.8/hr, and densities of $0 - 0.08/m^2$ (mean = $0.03/m^2$). Several young animals were found in the Tar. Because of difficulties described above, it is difficult to estimate the size of the population in the Tar and Shelton. Nevertheless, I believe the population is fairly large, perhaps on the order of 10^3 - 10^4 animals.

Swift Creek, North Carolina

The A. heterodon population in Swift Creek is thought to extend over 24 km (USFWS, 1993). We studied two sites on Swift Creek.

We did not detect living or dead A. heterodon in our timed searches (total = 232 minutes) or quadrats (total n = 135) on Swift Creek. Nevertheless, I estimate that a large population (up to 3000 animals) could have gone undetected, given our level of effort and size of the creek.

Turkey Creek, North Carolina

A. heterodon has been found over a 9 km reach of Turkey

Creek (USFWS, 1993). We studied three sites in that reach.

We did not find any living or dead _A_. _heterodon_ in our timed searches (total = 225 minutes) or quadrats (total n = 281) on Turkey Creek. I estimate that a population as large as 2000 animals could have gone undetected, based on our sampling effort.

DISCUSSION

All of the populations of _A_. _heterodon_ that we studied have several features in common. All are sparse. Although these populations are thought to be the densest, largest remaining populations of _A. heterodon_, densities generally range from below detection (ca. $0.01/m^2$) to $0.1/m^2$ (Table 2). Only the densest local populations exceed $0.1/m^2$, and the highest density we observed was less than $0.5/m^2$. 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. Our findings support earlier statements (Ortmann, 1919; Clarke, 1981) that _A_. _heterodon_ usually forms sparse populations. It is unclear whether low density is a natural feature of _A. heterodon_ populations or is caused by pervasive anthropogenic impacts that began before the early 20th century, when most systematic observations of mussel populations began.

Low density _per se_ may 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 essentially 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 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 questions needs further investigation.

Despite their low densities, most of the populations of _A_. _heterodon_ that we studied were large (10^3 - 10^5 individuals) (Table 3). 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, etc.; Caughley, 1994). Exceptions include Aquia Creek, which now contains only a few dozen individuals (i.e., visible individuals), and several of the North Carolina streams (Crooked Creek, Swift Creek, Turkey Creek, Moccasin Creek), where populations of _A_. _heterodon_ were too sparse to be detected by our methods. Populations in these latter streams might nevertheless be relatively large (Table 3).

A major assumption of the preceding paragraph is that all of the individuals of _A_. _heterodon_ in a stream belong to a single population. Because _A_. _heterodon_ occurs in more or less distinct patches over a large area in most streams, this assumption is unlikely to be met, so population dynamics and genetic structure of _A_. _heterodon_ could be very different from those of a single, well mixed population. 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.

A third property shared by most of the A. heterodon populations that we studied is that they all are reproducing (or have reproduced recently). Of course, it is obvious for a short-lived animal like A. heterodon (maximum life span <15 yr; Michaelson, 1993) that the existence of any living animals implies recent reproduction. More than this, though, we found animals that probably were 3 - 5 years old in most populations. Young or gravid animals have recently been found in streams at which we did not detect A. heterodon as well: Turkey and Moccasin Creeks (young animals in 1992; CZR, 1993; gravid females in Turkey Creek in 1994; J. Alderman, pers. comm.), and Swift Creek (gravid females seen in 1994; J. Alderman, pers. comm.).

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

In contrast, there are marked differences among the populations in population density, range size, population size, and the nature and severity of threats to the populations. Although all of these issues are important in predicting the long-term viability of a population, the subject of specific threats is outside the scope of the present study and will not be considered further here. Known threats to A. heterodon populations were briefly summarized by USFWS (1993).

As mentioned previously, none of the known populations of A. heterodon is very dense. Nevertheless, it is possible to distinguish a group of streams where population density is only moderately low (mean of about $0.03/m^2$, with patches $>0.1/m^2$) from those where the population density is very low (mean probably $<0.01/m^2$) (Table 4). The position of Crooked, Swift, Moccasin and Turkey Creeks is provisional but probably correct.

The ranges occupied by A. heterodon populations are well known for some populations but not for others. Determining and monitoring range limits for all major populations should be a high priority to follow the status and trends of these populations. Using the best available information, it is possible to divide the ranges of A. heterodon populations into three categories: fairly large (ca. 10^2 ha), small (ca. 10^1 ha), and very small (ca. 10^0 ha) (Table 5). Of course, the A. heterodon population actually occupies only a small part of these ranges. Nevertheless, this classification of range sizes contrasts populations that probably contain relatively few local populations, all close to one another and thereby highly vulnerable to many threats, from widespread populations that probably contain many local populations that are somewhat separated and thereby more buffered against some threats.

Because of considerable uncertainties in estimating both the density and range of A. heterodon populations, estimates of population size are subject to large errors. Nevertheless, it is clear that the populations of A. heterodon included in this study vary in size over two or three orders of magnitude. It may be useful to classify A. heterodon populations by size into three categories: moderately large (ca. 10^4 animals), small (ca. 10^3 animals), and very small (ca. 10^2 animals) (Table 6). Once again, it is difficult to place the North Carolina streams where densities of A. heterodon were below our detection limits. Because A. heterodon is routinely encountered over broad geographic ranges in these streams (CZR, 1993; Alderman, pers. comm.; Strayer, pers. obs.), it seems very unlikely that these populations are as small as the one in Aquia Creek. On the other hand, if these populations included more than a few thousand animals, we should have detected them. Thus, a provisional classification with the small (ca. 10^3 animals) populations seems most appropriate.

Nevertheless, it might be best not to focus too much attention on population size, but rather concentrate on its components: population density and local range size. I have suggested that the size of most populations of A. heterodon included in this study probably is adequate to overcome most of the dangers associated with small population size per se. Only the Aquia Creek population (and probably some of the A. heterodon populations not included in this study) appears small enough to suffer from these dangers. On the other hand, low population density might well affect fertilization success and thereby population viability in most of the A. heterodon populations. This possibility clearly needs more study. Furthermore, the small, linear range occupied by most A. heterodon populations makes them especially vulnerable to many threats, including pollution, habitat alteration, and disease.

In the absence of specific information about metapopulation structure and dynamics of A. heterodon, it seems reasonable to suppose that the most robust populations would be those with a relatively high density and a large, branched range. No population except perhaps the Shelton/Tar population meets these three criteria. Thus, all populations in this study appear to be vulnerable because of low densities, small ranges, linear ranges, or some combinations of these factors. Populations in the Connecticut, Ashuelot, Neversink, and Shelton/Tar Rivers (and perhaps the Little River), which have the highest densities and largest ranges (Fig. 4), probably are in the best condition. The population in Aquia Creek clearly is less robust than the remaining populations in this study, while populations in McIntosh Run, the Po River, Crooked Creek, Swift Creek, Moccasin Creek, and Turkey Creek occupy an intermediate rank (Fig. 4).

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Table 1. Indices of population density of *A. heterodon* at the study sites. nd = not determined.

Site	CPUE (Foot)	CPUE (Mask)	Density (no/0.25m^2)			
			Quadrats	CPUE (Foot)	CPUE (Mask)	CPUE (Combined)
CON1	0	0	0	0	0	0
CON2	0	4.6	0	0	0.014	0.011
CON3	0	0	0	0	0	0
CON4	11.6	10.8	0.0113	0.026	0.020	0.023
CON5	nd	11	0.0312	nd	0.019	nd
CON6	1.7	1.1	0	0.0041	-0.0020	0.00077
CON7	nd	4	0.0141	nd	0.016	nd
CON8	nd	3.7	0.0137	nd	0.0046	nd
CON9	3.1	6.1	0.0138	0.021	0.020	0.021
ASH1	nd	6	0	nd	0.049	nd
ASH2	1	13	0.026	0.047	0.082	0.082
ASH3	1.9	7.9	0.061	0.044	0.063	0.055
ASH4	2.4	5	0	0.0033	0.0057	0.0041
ASH5	0	1.2	0	0	0.0038	0.00042
ASH6	4.1	1	0	0.0091	0.0011	0.0019
ASH7	3.5	3	0	0.010	0.0060	0.0072
NEV1	2.07	0	0.0043	0.0069	0	0.00052
NEV2	1.43	3	0	0.0012	-0.0009	-0.00018
NEV3	1	3	0.0268	0.015	0.025	0.019
NEV4	3	1	0.0133	0.031	0.016	0.024
NEV5	nd	nd	0.0969	nd	nd	nd
NEV6	nd	20	0.0037	nd	0.022	nd
MCI1	1	nd	0.02	0.028	nd	nd
MCI2	0	nd	0.01	0	nd	nd
MCI3	nd	nd	0	nd	nd	nd

Site	CPUE (Foot)	CPUE (Mask)	Density (no/0.25m^2)			
			Quadrats	CPUE (Foot)	CPUE (Mask)	CPUE (Combined)
MCI4	2.9	3.7	0.0196	0.013	0.02	0.015
MCI5	0	0	0	0	0	0
AQU1	nd	0	0	nd	0	nd
AQU2	0	0	0	0	0	0
AQU3	nd	0	0	nd	0	nd
AQU4	nd	1	0	nd	-0.0012	nd
AQU5	nd	0	0	nd	0	nd
AQU6	nd	4.4	0	nd	0.0038	nd
AQU7	nd	5.1	0	nd	0.0090	nd
AQU8	nd	4.3	0	nd	0.010	nd
PO1	3	1.1	0	0.035	0.025	0.030
PO2	0.7	nd	0	0.0049	nd	nd
PO3	0	0	0	0	0	0
SHE1	1	2.1	0.0212	0.014	0.022	0.020
SHE2	nd	0	0	nd	0	nd
TAR1	nd	14.8	0.0111	nd	0.060	nd
TAR2	nd	4.8	0	nd	0.00096	nd
TAR3	nd	4.3	0	nd	0.0051	nd
CRO1	0	0	0	0	0	0
CRO2	0	0	0	0	0	0
LIT1	4	nd	0.0414	0.12	nd	nd
LIT2	0	0	0	0	0	0
LIT3	0	0	0	0	0	0
SWI1	0	0	0	0	0	0
SWI2	0	0	0	0	0	0
MOC1	0	0	0	0	0	0
MOC2	0	0	0	0	0	0

Site	CPUE (Foot)	CPUE (Mask)	Density (no/0.25m^2)			
			Quadrats	CPUE (Foot)	CPUE (Mask)	CPUE (Combined)
MOC3	0	nd	0	0	nd	nd
TUR1	0	0	0	0	0	0
TUR2	0	nd	0	0	nd	nd
TUR3	0	nd	0	0	nd	nd

Table 2. Weighted mean indices of population densities of *A. heterodon* in the study streams, along with approximate range size, based on USFWS (1993) and text.

Stream	CPUE (hr^{-1}) (wading)	CPUE (hr^{-1}) (snorkeling)	Density (m^{-2}) (quadrats)	Density (m^{-2}) (CPUE)	Range (ha)
Connecticut R.	0.004	3.7	0.04	0.02	500
Ashuelot R.	2.3	3.0	0.004	0.05	10
Neversink R.	1.9	1.9	0.05	0.04	40
McIntosh Run	1.0	1.8	0.04	0.04	2
Aquia Creek	0	1.3	0	0.006	0.7
Po River	1.2	0.6	0	0.01	≥7
Shelton/Tar	1.0	2.3	0.03	0.03	3-30
Crooked Creek	0	0	0	0	1
Little River	1.3	0	0.06	0.16	30
Swift Creek	0	0	0	0	30
Moccasin Creek	0	0	0	0	10
Turkey Creek	0	0	0	0	6

Table 3. Estimated population size of *A. heterodon* in the study streams. Data are very approximate (see text).

Stream	Population size
Connecticut River	20,000-100,000
Ashuelot River	6,000
Neversink River	20,000
McIntosh Run	900
Aquia Creek	50
Po River	>5,000
Shelton/Tar	1,000-10,000 (?, see text)
Crooked Creek	<900
Swift Creek	<3,000
Little River	10,000-70,000 (?, see text)
Moccasin Creek	<1,500
Turkey Creek	<2,000

Table 4. Study streams grouped by density of A. *heterodon* populations. See Tables 1 and 2 for details and supporting data.

A. Moderately sparse populations (ca. $0.03/m^2$)

Connecticut River
Ashuelot River
Neversink River
McIntosh Run
Shelton Creek/Tar River

Little River (?)

B. Very sparse populations ($<0.01/m^2$)

Aquia Creek
Po River
Crooked Creek
Swift Creek
Moccasin Creek
Turkey Creek

Table 5. Study streams grouped by approximate range covered by *A. heterodon* populations. See Table 2 for supporting data.

A. Fairly large (ca. 10^2 ha) ranges

Connecticut River
Neversink River
Shelton Creek/Tar River

B. Small (ca. 10^1 ha) ranges

Ashuelot River
Po River
Swift Creek
Little River
Moccasin Creek
Turkey Creek

c. Very small (ca. 10^0 ha) ranges

McIntosh Run
Aquia Creek
Crooked Creek

Table 6. Study streams grouped by approximate size of _A. heterodon_ populations. See Tables 1 and 2 for details and supporting data.

A. Moderately large (ca. 10^4 animals)

Connecticut River
Ashuelot River
Neversink River

Po River (?)
Shelton Creek/Tar River (?)
Little River (?)

B. Small (ca. 10^3 animals)

McIntosh Run

Crooked Creek (?)
Swift Creek (?)
Moccasin Creek (?)
Turkey Creek (?)

C. Very small (ca. 10^2 animals)

Aquia Creek

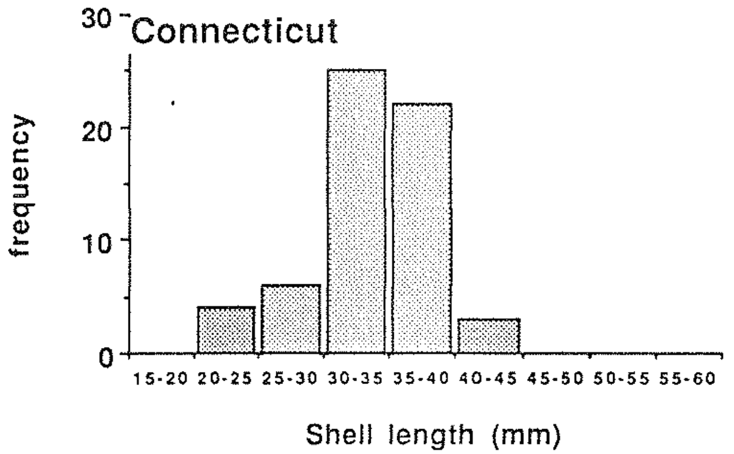
FIGURE LEGENDS

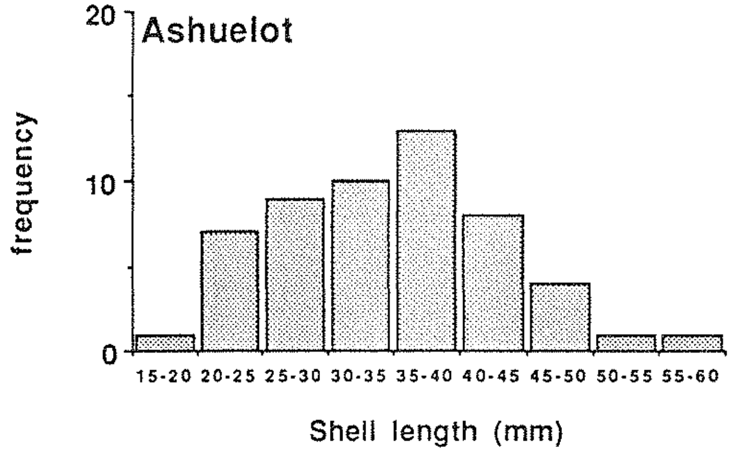
Fig. 1. Frequency distribution of shell lengths of living *A. heterodon* observed in the Connecticut, Ashuelot, and Neversink Rivers.

Fig. 2. Frequency distribution of shell lengths of living *A. heterodon* observed in McIntosh Run, Aquia Creek, and the Po River. Figure for the Po River includes a number of animals measured by Phil Stevenson in early 1994, as well as those seen in the present study.

Fig. 3. Frequency distribution of shell lengths of living *A. heterodon* observed in Shelton Creek, the Tar River, and the Little River.

Fig. 4. Estimated population size and range size of various populations of *A. heterodon*. Note logarithmic scale. Data are very approximate.


Connecticut
frequency
30
20
10
0
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)


Ashuelot
frequency
20
10
0
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)

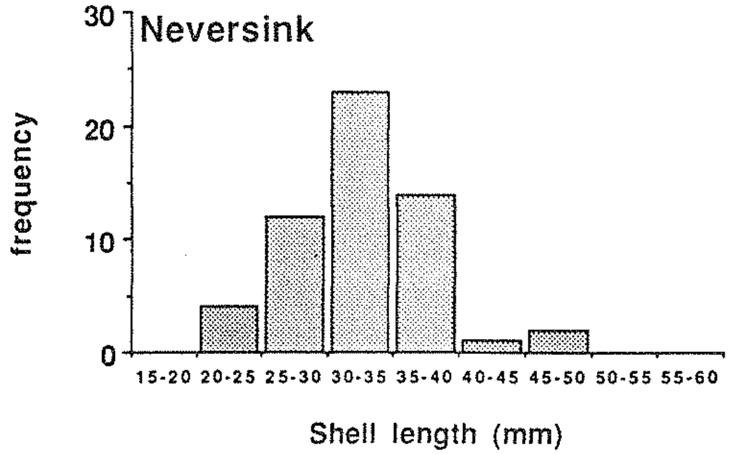
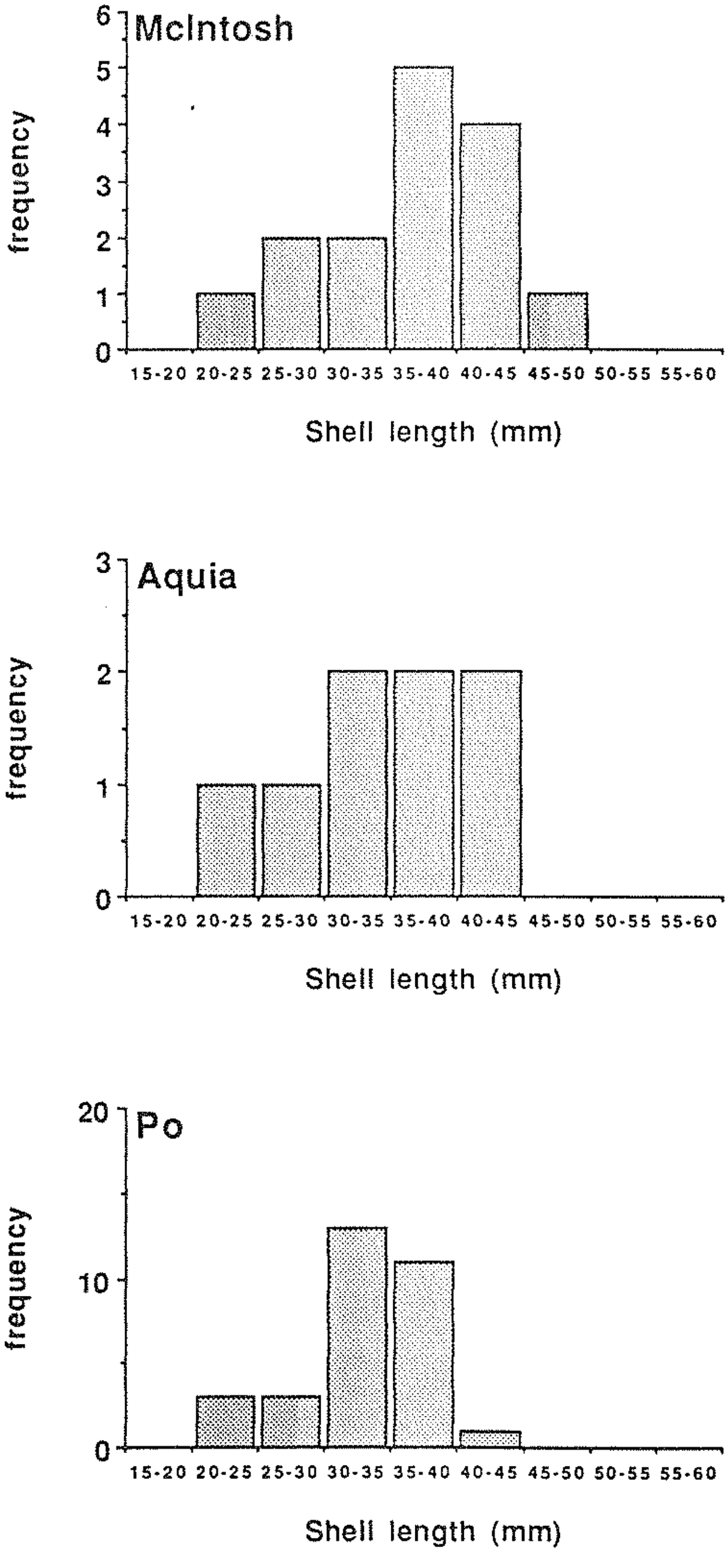
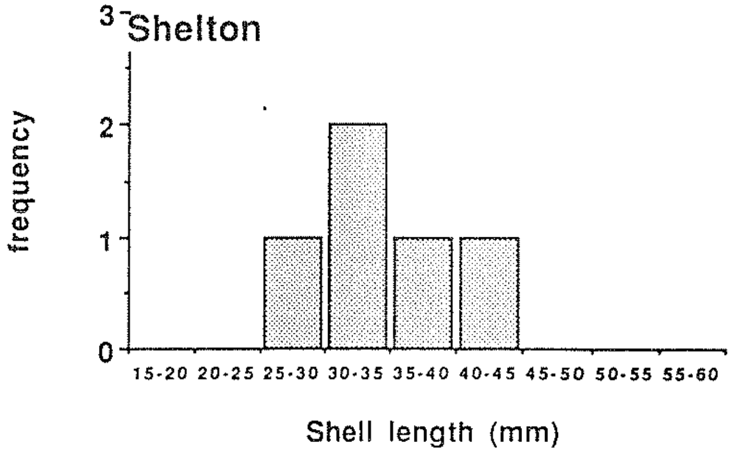
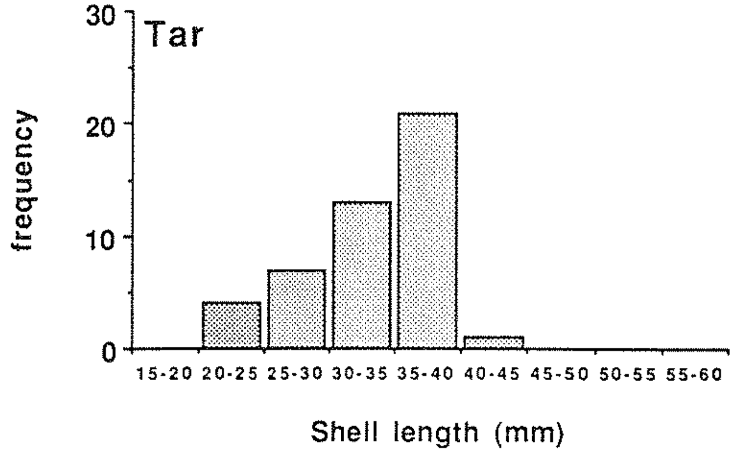
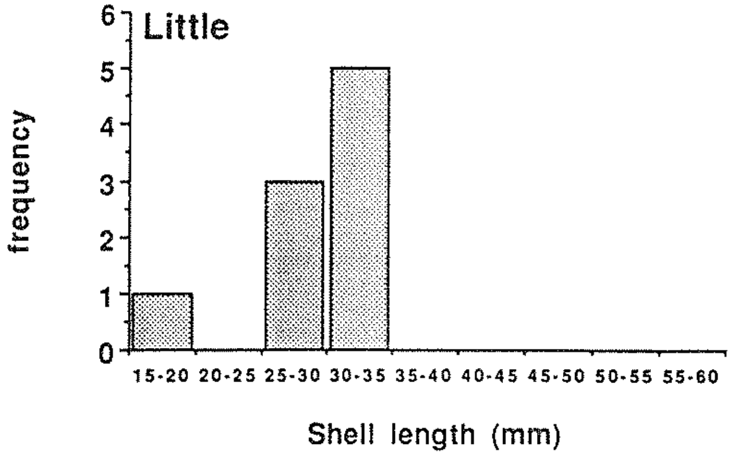

Neversink
frequency
30
20
10
0
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)

Fig. 2


McIntosh
frequency
0
1
2
3
4
5
6
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)
Aquia
frequency
0
1
2
3
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)
Po
frequency
0
10
20
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)


Shelton
frequency
3
2
1
0
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)


Tar
frequency
30
20
10
0
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
Shell length (mm)


Little
frequency
6
5
4
3
2
1
0
15-20
20-25
25-30
30-35
35-40
40-45
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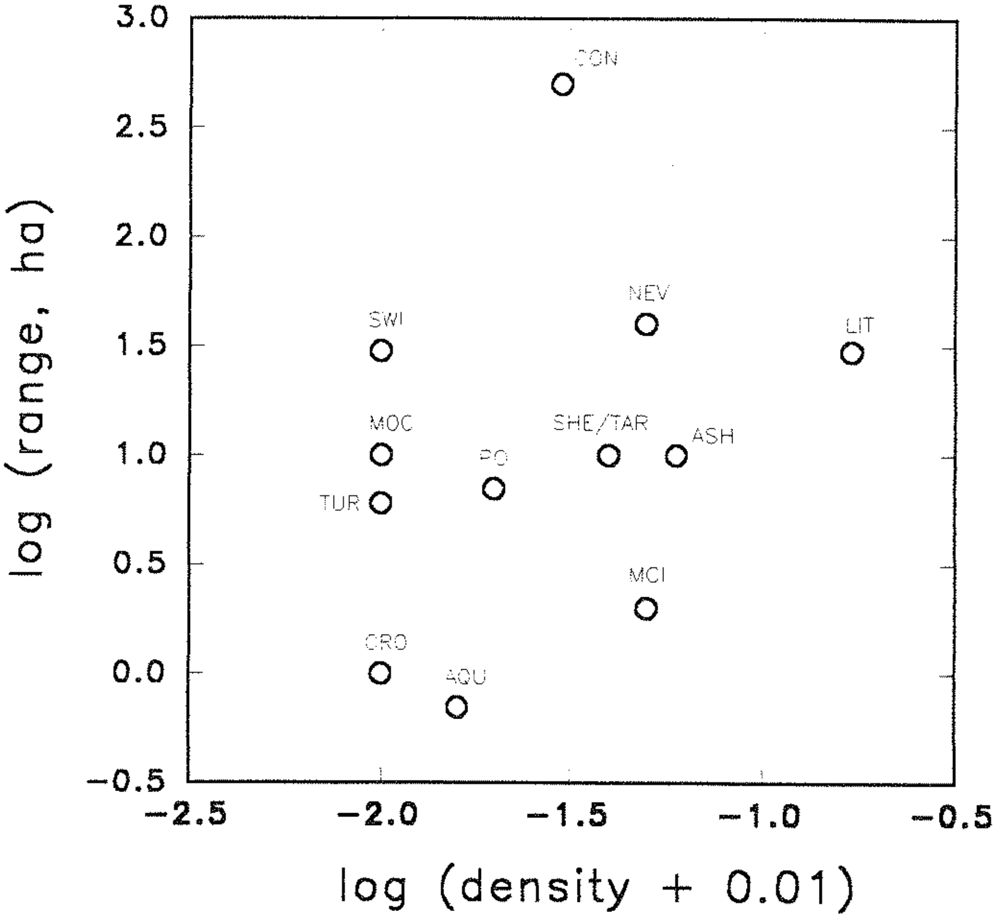
50-55
55-60
Shell length (mm)


CON
NEV
SWI
LIT
MOC
SHE/TAR
ASH
PO
TUR
MCI
CRO
AQU
3.0
2.5
2.0
1.5
1.0
0.5
0.0
−0.5
−2.5
−2.0
−1.5
−1.0
−0.5
log (range, ha)
log (density + 0.01)

Appendix 1: predicting densities of mussel populations from timed searches.

The results of mussel surveys often are given as catch-per-unit-effort (CPUE) from timed searches (e.g., Cvancara et al., 1976; Hoeh and Trdan, 1985; Mackie and Topping, 1988; Strayer and Ralley, 1991), based on the tacit assumption that CPUE and actual mussel densities are at least loosely correlated. Nevertheless, it is widely recognized that many factors including the experience of the observer, the size and behavior of the mussel species, the depth and clarity of the water, sunlight intensity and direction, wind speed, and mode of search might affect the relationship between CPUE and mussel density, to the extent that some malacologists question the utility of presenting CPUE data. Despite the widespread use of CPUE data to assess mussel populations, there have been no formal tests of the relationship between CPUE and mussel density. The purpose of this study was to examine the relationship between CPUE and mussel density and see whether CPUE data would be used to estimate mussel density, under the best possible circumstances.

Our approach was to simultaneously estimate CPUE and actual density over a wide range of study sites. Because we wanted the tightest possible correlation between CPUE and mussel density, all timed searches were made by one individual (DLS), thereby eliminating what we suspect to be substantial variation due to the experience and searching approach of the observer.

Field methods for determining CPUE and mussel density are described in the main body of the paper. Because variance in both CPUE and density estimates rises with the mean, data were transformed (ln x + 1 for CPUE, ln x + 0.01 for density) before statistical analysis. We then used analysis of covariance (ANCOVA) to try to predict mussel density from CPUE, mussel species, and site of collection. We ran the analyses with three different estimates of CPUE: catch rates while wading, catch rates while snorkeling, and the sum of these two catch rates. We used the NOINT option in SAS (1987) to force the intercept through 0, -2 (i.e., catch rates and densities of 0). To estimate densities from the resulting log-log ANCOVA model, we corrected the predicted long-density values before back-transformation (e.g., Spruegel, 1984).

The relationships between CPUE and mussel densities are shown in Figs. A1-A3. There are strong but noisy correlations between CPUE and mussel density (r^2 = 0.91=0.93). Mussel species and site of collection also are significant covariates, but account for relatively little of the variation in the CPUE-density regression (Table A1).

Standard errors associated with individual predictions generally fell between 0.7 and 0.8 ln-units, corresponding to a 90% confidence interval spanning a range of about 12-fold. CPUE data from timed searches can therefore be used to make rough estimates of population densities under the controlled conditions of this study.

Because of potentially large differences among observers, our results cannot be directly extrapolated to other situations. (In fact, because we used a different search strategy in this study than in other survey work we've done (e.g., Strayer and Ralley, 1991), the CPUE-density relationships we generated here do not even apply to our own previously published CPUE data. Each study seeking to use CPUE data to estimate mussel densities must test and calibrate its own CPUE-density model.

Table A1. Results of ANCOVA models to predict mussel density from CPUE, mussel species, and site. Values in parentheses are p-values.

Search type	r^2	F (CPUE)	F (species)	F (site)
Wading	0.93 (<0.0001)	49.0 (<0.0001)	3.4 (0.006)	3.8 (<0.0001)
Snorkeling	0.91 (<0.0001)	72.5 (<0.0001)	1.8 (0.05)	3.0 (<0.0001)
Combined	0.93 (<0.0001)	39.4 (<0.0001)	1.8 (0.06)	3.8 (<0.0001)

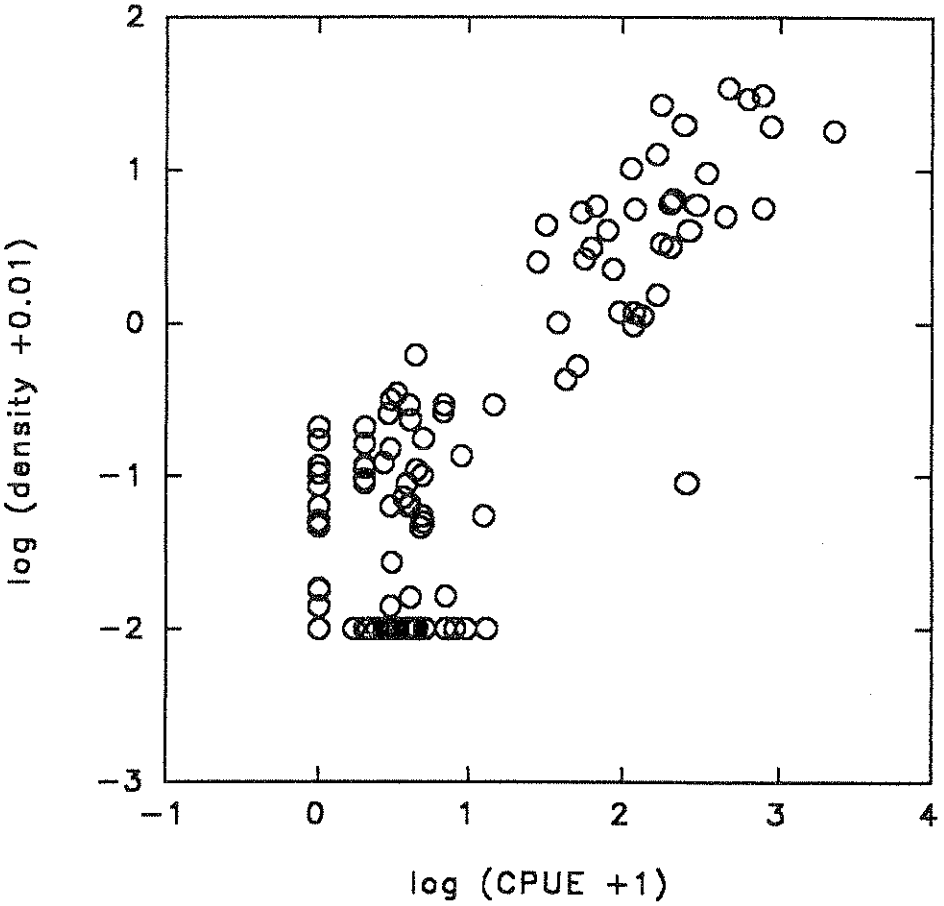
FIGURE LEGENDS (APPENDIX 1)

Fig. A1. Relationship between CPUE (wading) and population density. Each dot represents one mussel species at one site. Note that axes are logarithmic.

Fig. A2. Relationship between CPUE (snorkeling) and population density. Each dot represents one mussel species at one site. Note that axes are logarithmic.

Fig. A3. Relationship between CPUE (sum of wading and snorkeling searches) and population density. Each dot represents one mussel species at one site. Note that axes are logarithmic.

Fig. A4. Relationship between CPUE (wading) and CPUE (snorkeling).


2
1
0
−1
−2
−3
−1
0
1
2
3
4
log (density +0.01)
log (CPUE +1)

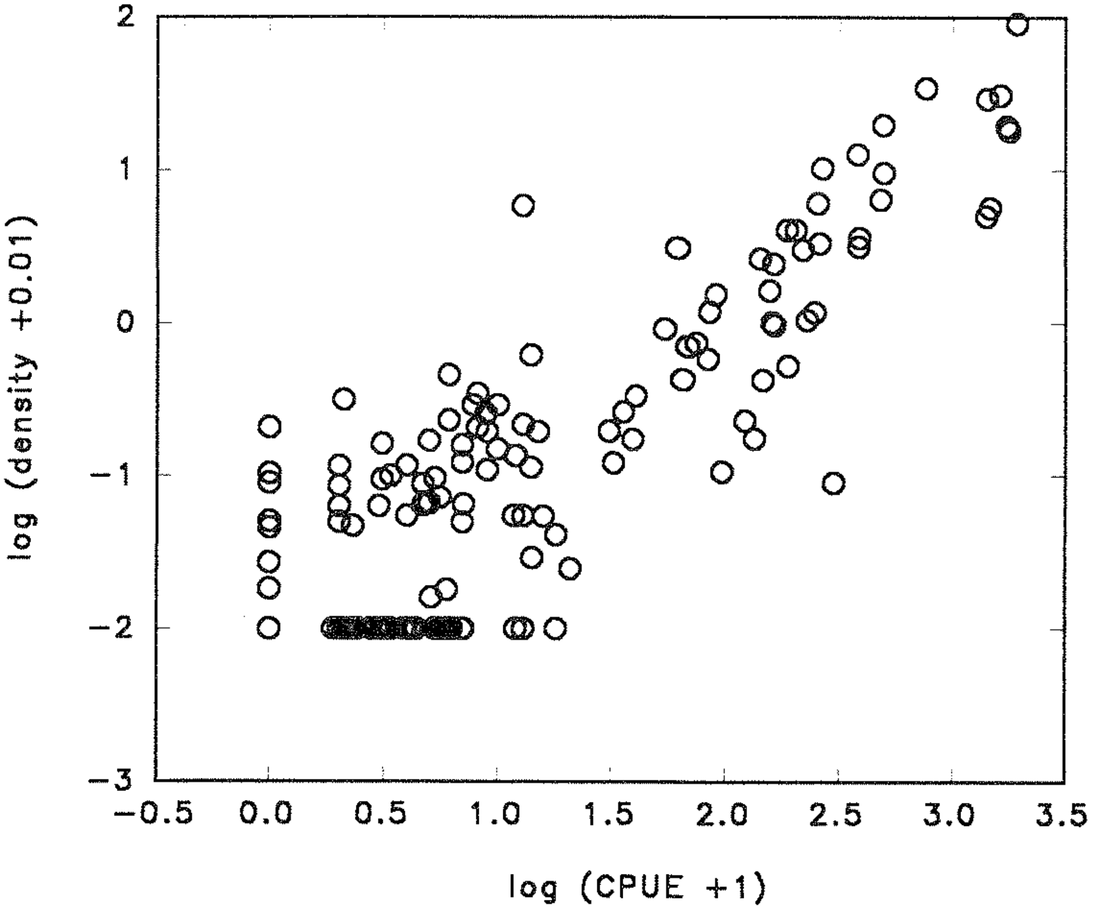
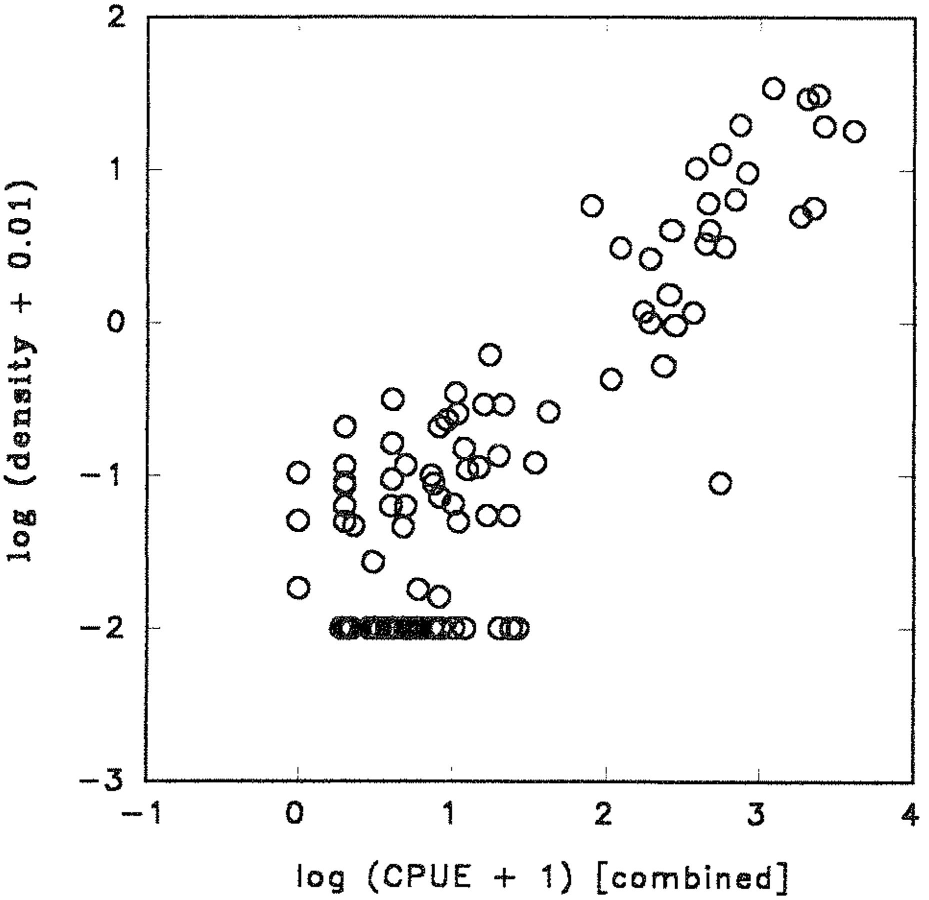
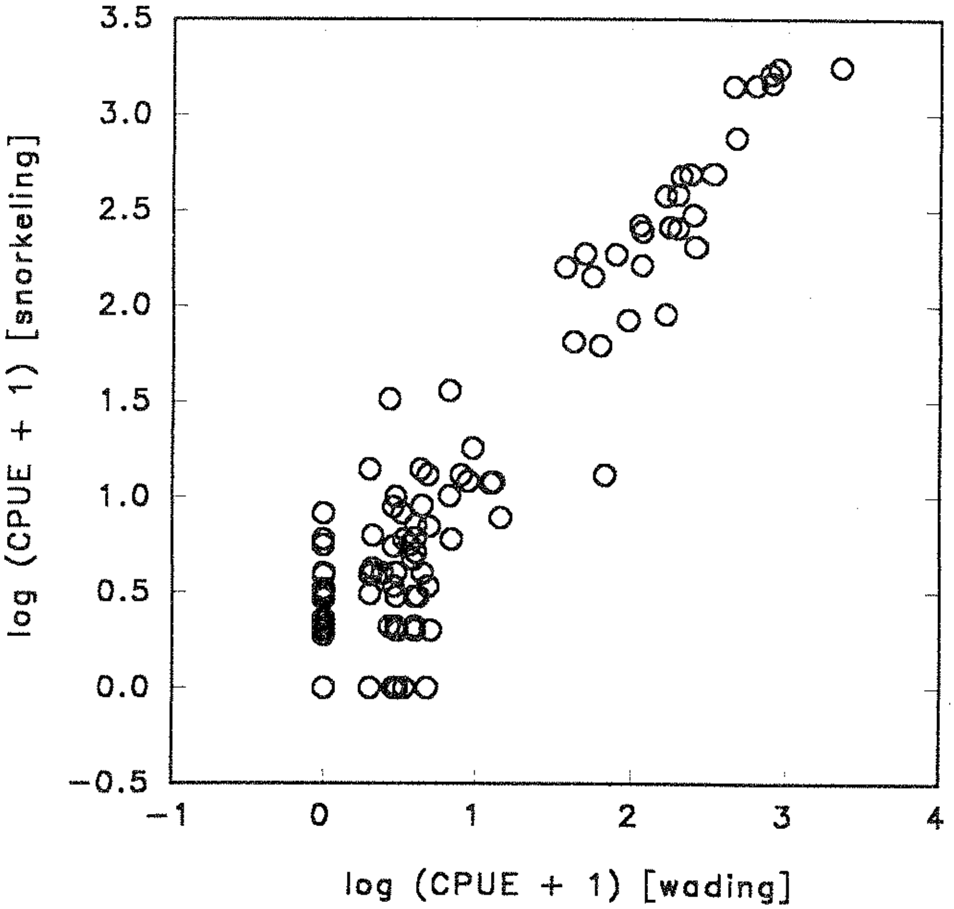

2
1
0
−1
−2
−3
−0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
log (density +0.01)
log (CPUE +1)

Fig. A5




3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
−0.5
−1
0
1
2
3
4
log (CPUE + 1) [snorkeling]
log (CPUE + 1) [wading]

Appendix 2. Locations of study sites.

CON1: Connecticut River, east bank, approx. 3.1 km downstream of Sumner Falls.

CON2: Connecticut River, east bank, immediately downstream of Cornish covered bridge.

CON3: Connecticut River, east bank, state boat launch, approx. 0.5 km upstream of Cornish covered bridge.

CON4: Connecticut River, west bank, "Route 5 Cemetery site" of Fichtel (1993), approx. 3 km downstream of the Ascutney bridge.

CON5: Connecticut River, west bank, Wilgus State Park.

CON6: Connecticut River, east bank, immediately above the Cornish covered bridge.

CON7: Connecticut River, east bank, "Horseback Ridge site" of Fichtel (1993), approx. 2.2 km downstream of Cornish covered bridge.

CON8: Connecticut River, east bank, near Balloch.

CON9: Connecticut River, west bank, approx. 250m downstream of Sumner Falls.

ASH1: Ashuelot River below Surry Mountain Road (lower end of reach 2A of Cutko, 1993).

ASH2: Ashuelot River, reach 1 of Cutko, 1993; 150-286 m downstream of low-head dam below Surry Mountain Dam.

ASH3: Ashuelot River, reach 1 of Cutko, 1993; 50 - 125m downstream of low-head dam below Surry Mountain Dam.

ASH4: Ashuelot River, downstream 150m of reach 4 of Cutko, 1993.

ASH5: Ashuelot River, reach 7 of Cutko, 1993.

ASH6: Ashuelot River, lower part of reach 9 of Cutko, 1993.

ASH7: Ashuelot River, above Surry Mountain Road, upper part of reach 2A of Cutko, 1993.

NEV1: Neversink River at The Nature Conservancy's preserve, ca. 2 km below Graham Road.

NEV2: Neversink River above Route 209.

NEV3: Neversink River ca. 2 km above Neversink Drive, Huguenot.

NEV4: Neversink River below Neversink Drive, Huguenot.

NEV5: Neversink River below Graham Road, west bank.

NEV6: Neversink River ca. 0.5 km above Route 209.

MCI1: McIntosh Run below mouth of Burnt Mill Creek.

MCI2: McIntosh Run 350 - 550m downstream of McIntosh Road.

MCI3: McIntosh Run 80 - 280m downstream of McIntosh Road.

MCI4: McIntosh Run near Maypole Road (reach is 0 - 200m above Laurie MacIvor's blue-flagged water chemistry sampling station).

MCI5: McIntosh Run near Maypole Road (reach is 350 - 475m above Laurie MacIvor's blue-flagged water chemistry sampling station).

AQU1: Aquia Creek, 0 - 200, above old Route 643.

AQU2: Aquia Creek, 200 - 400m above old Route 643.

AQU3: Aquia Creek, 400 - 600m above old Route 643.

AQU4: Aquia Creek, 600 - 800m above old Route 643.

AQU5: Aquia Creek, 800 - 900m above old Route 643 (mouth of Cannon Creek is 900m above old Route 643 and 300m below Route 610).

AQU6: Aquia Creek, 200 - 300m below Route 610.

AQU7: Aquia Creek, 100 - 200m below Route 610.

AQU8: Aquia Creek, 1 - 100m below Route 610.

PO1: Po River below Route 608.

PO2: Po River below Route 648.

PO3: Po River above Route 208.

SHE1: Shelton Creek above U.S. 158.

SHE2: Shelton Creek at Sunset Drive.

TAR1: Tar River ca. 1 km below U.S. 158 (Michaelson's study site)

TAR2: Tar River below Moriah Road (Route 1141).

TAR3: Tar River above Moriah Road (Route 1141).

CRO1: Crooked Creek below Pearces Road (Route 1001).

CRO2: Crooked Creek above Pearces Road (Route 1001).

LIT1: Little River ca. 200m below Fowler Road (Route 2308).

LIT2: Little River above Route 1722 (Mudhound Road).

LIT3: Little River above Route 39.

SWI1: Swift Creek above Route 1501 (Bucket Jones Road).

SWI2: Swift Creek, ca. 100m above Route 1555 to ruined mill dam.

MOC1: Moccasin Creek below Route 231.

MOC2: Moccasin Creek ca. 400m above Route 1733 (Antioch Church Road)

MOC3; Moccasin Creek ca. 400m above Route 231.

TUR1: Turkey Creek along Bunn Road (Route 1128)

TUR2: Turkey Creek ca. 300m above Route 263 (westbound)

TUR3: Turkey Creek above Alt. Route 264.

Appendix 3. Master worksheet for 1994 heterodon project.

species abbreviations as follows:
AC=Anodonta cataracta
AH=Alasmidonta heterodon
AI=Anodonta implicata
AU=Alasmidonta undulata
AV=Alasmidonta varicosa
EC=Elliptio complanata and other non-lanceolate Elliptio spp.
EL=lanceolate Elliptio spp.
FM=Fusconaia masoni
LC=Lampsilis cariosa
LR=Lampsilis radiata
LS=Lasmigona subviridis
SU=Strophitus undulatus
VC=Villosa constricta

density is #/0.25 sq. m.
CPUE as number per hour
vis"=index of visibility
site codes as given in appendix 2

						density.........estimates			
							from timed searches		
	vis	vis		CPUE	CPUE		....		
Site	wading	mask	Specie	wading	mask	quadra	wading	mask	combined
MOC1	3	9	EC	79	185	1.01	1.914	1.417	1.778
MOC1	3	9	EL	3.4	13	0.151	0.072	0.111	0.117
MOC1	3	9	SU	0	3	0	0.017	0.028	0.023
MOC1	3	9	VC	0	1	0.013	0.009	0.019	0.013
MOC1	3	9	FM	0	1	0	0.004	0.006	0.003
MOC1	3	9	AU	0	0	0.010	0.024	0.007	0.008
MOC2	6	8	EC	62	61	0.768	0.948	0.696	0.782
MOC2	6	8	VC	1.9	0	0	0.010	0.007	0.009
MOC2	6	8	EL	0	1.3	0.009	0.009	0.026	0.015
TUR1	6	8	EC	262	202	1.01	1.080	0.809	0.942
TUR1	6	8	EL	3.2	2	0	0.012	0.013	0.015
TUR1	6	8	AU	0	1	0	-0.00	0.004	0.000
TUR2	1	.	EC	31	.	1.09	1.671	0	0
LIT1	3	.	EC	176	.	6.64	5.396	0	0
LIT1	3	.	LS	53	.	1.32	1.274	0	0
LIT1	3	.	AH	4	.	0.041	0.120	0	0
LIT1	3	.	EL	3	.	0.070	0.126	0	0
LIT2	6	8	EC	202	383	0.786	0.962	1.004	1.087
LIT2	6	8	AU	0	2.2	0	0.000	0.006	0.004
LIT2	6	8	LS	0	1.1	0	0.011	0.006	0.005
TUR3	2	.	EC	27	.	0.625	0.960	0	0
CRO1	6	10	EC	202	253	1.52	1.265	1.243	1.203

Appendix 3 (continued)

						density.........	....	....	estimates
							from timed searches		
	vis	vis		CPUE	CPUE		....		
Site	wading	mask	Specie	wading	mask	quadra	wading	mask	combined
CRO1	6	10	AU	2.4	0	0	0.017	0.002	0.008
CRO1	6	10	SU	0	2.9	0	0.000	0.016	0.006
CRO2	2	2	EC	67	12	1.46	3.193	0.690	1.541
CRO2	2	2	SU	2.3	7.2	0.084	0.087	0.161	0.098
CRO2	2	2	AU	0	7.2	0.049	0.052	0.180	0.110
MOC3	1	.	EC	86	.	0.563	1.041	0	0
MOC3	1	.	EL	2	.	0.001	0.024	0	0
MOC3	1	.	VC	1	.	0	0.005	0	0
MOC3	1	.	AU	0	.	0.040	0.008	0	0
MOC3	1	.	SU	0	.	0.001	0.004	0	0
LIT3	8	10	EC	460	757	8.6	5.285	6.538	6.452
LIT3	8	10	FM	2	0	0	0.016	0.009	0.014
LIT3	8	10	EL	1	0	0.049	0.042	0.028	0.036
LIT3	8	10	SU	0	2	0	0.017	0.047	0.028
LIT3	8	10	AU	0	0	0.023	0.024	0.021	0.015
SWI1	7	9	EC	118	244	0.292	0.756	0.564	0.651
SWI1	7	9	EL	1.1	5.3	0	0.006	0.013	0.012
SWI1	7	9	FM	1.1	3.2	0	-0.00	-0.00	-0.00
SWI1	7	9	AU	0	1.1	0	0.001	-0.00	-0.00
SWI2	5	8	EC	244	488	4.95	3.144	3.206	3.386
SWI2	5	8	AU	0	1	0	0.019	0.022	0.018
SHE1	6	6	EC	166	89	0.381	1.621	0.941	1.490
SHE1	6	6	LR	1	2.1	0.038	0.026	0.039	0.030
SHE1	6	6	AH	1	2.1	0.021	0.014	0.022	0.020
SHE1	6	6	SU	0	0	0.002	0.005	0.006	0.002
SHE2	.	9	EC	.	384	0.898	0	1.525	0
SHE2	.	9	LR	.	12	0.051	0	0.067	0
TAR1	.	9	EC	.	154	0.404	0	0.996	0
TAR1	.	9	AH	.	14.8	0.011	0	0.059	0
TAR1	.	9	SU	.	6	0.037	0	0.034	0
TAR1	.	9	LR	.	5.1	0.112	0	0.047	0
TAR2	.	6	EC	.	95	0.024	0	0.214	0
TAR2	.	6	LR	.	13.2	0.004	0	0.020	0
TAR2	.	6	AH	.	4.8	0	0	0.000	0
TAR2	.	6	AC	.	1.2	0	0	-0.00	0
TAR2	.	6	SU	.	1.2	0	0	-0.00	0
TAR3	.	10	EC	.	54	0.225	0	0.217	0
TAR3	.	10	AH	.	4.3	0	0	0.005	0
TAR3	.	10	LR	.	2.9	0	0	0.008	0
TAR3	.	10	LC	.	1.4	0	0	0.006	0
MCI1	5	.	EC	120	.	1.39	2.124	0	0
MCI1	5	.	AH	1	.	0.02	0.027	0	0
PO1	7	9	EC	335	492	2.39	3.035	4.121	3.627
PO1	7	9	AH	3	1.1	0	0.034	0.025	0.030
PO1	7	9	SU	2	1.1	0.075	0.025	0.028	0.024
MCI2	1	.	EC	134	.	0.278	0.978	0	0
MCI2	1	.	AH	0	.	0.01	0	0	0
MCI3	.	.	EC	.	.	0.511	0	0	0

Appendix 3 (continued)

						density.........estimates	from timed searches		
Site	vis wading	vis mask	Specie	CPUE wading	CPUE mask	quadra	wading	mask	combined
MCI4	5	7	EC	94	83	0.294	0.748	0.624	0.675
MCI4	5	7	AH	2.9	3.7	0.019	0.012	0.019	0.015
MCI5	4	7	EC	56	141	0.655	1.010	1.076	1.017
PO2	1	.	EC	291	.	1.49	1.511	0	0
PO2	1	.	AC	6	.	0.001	0.007	0	0
PO2	1	.	AH	0.7	.	0	0.004	0	0
PO2	1	.	SU	0.7	.	0	0.003	0	0
PO3	4	7	EC	117	162	0.24	0.750	0.369	0.477
PO3	4	7	SU	0	5	0.002	-0.00	0.004	0.001
PO3	4	7	EL	0	3	0	0.001	0.005	0.003
AQU1	.	8	EC	.	120	0.054	0	0.095	0
AQU2	7	8	EC	254	298	0.020	0.036	0.039	0.036
AQU3	.	8	EC	.	144	0.104	0	0.175	0
AQU4	.	10	EC	.	226	0.259	0	0.631	0
AQU4	.	10	AH	.	1	0	0	-0.00	0
AQU5	.	10	EC	.	82	0.143	0	0.239	0
AQU6	.	10	EC	.	40	0.080	0	0.158	0
AQU6	.	10	AH	.	4.4	0	0	0.003	0
AQU6	.	10	SU	.	2.2	0	0	0.000	0
AQU7	.	10	EC	.	161	0.608	0	0.520	0
AQU7	.	10	AH	.	5.1	0	0	0.008	0
AQU7	.	10	SU	.	3.4	0	0	0.006	0
AQU8	.	9	EC	.	67	0.174	0	0.342	0
AQU8	.	9	AH	.	4.3	0	0	0.010	0
AQU8	.	9	SU	.	4.3	0.021	0	0.012	0
ASH1	.	10	EC	.	1921	22.8	0	7.661	0
ASH1	.	10	AU	.	14	0.046	0	0.107	0
ASH1	.	10	AC	.	8	0.046	0	0.050	0
ASH1	.	10	AH	.	6	0	0	0.048	0
ASH1	.	10	SU	.	4	0.04	0	0.041	0
ASH2	10	10	EC	619	1417	7.32	8.178	6.212	7.443
ASH2	10	10	SU	2	9	0.035	0.056	0.070	0.066
ASH2	10	10	AH	1	13	0.026	0.046	0.082	0.081
ASH2	10	10	AU	0	1	0.019	0.035	0.021	0.022
ASH2	10	10	AC	0	1	0.01	0.009	0.012	0.006
ASH3	7	10	EC	774	1626	7.78	7.077	7.137	7.098
ASH3	7	10	SU	13.5	6.8	0.07	0.116	0.061	0.084
ASH3	7	10	AU	5.8	9.1	0.07	0.094	0.085	0.091
ASH3	7	10	AH	1.9	7.9	0.061	0.043	0.062	0.055
ASH3	7	10	AC	1.9	4.5	0	0.017	0.036	0.021
ASH4	8	10	EC	874	1739	4.82	1.699	2.103	1.865
ASH4	8	10	SU	12	11	0	0.016	0.016	0.015
ASH4	8	10	AU	6	5	0	0.013	0.008	0.011
ASH4	8	10	AH	2.4	5	0	0.003	0.005	0.004
ASH5	6	10	EC	439	1409	1.25	1.935	3.134	2.591
ASH5	6	10	SU	3.8	0	0.009	0.015	-0.00	0.006
ASH5	6	10	AU	0	2.3	0	0.003	0.011	0.006
ASH5	6	10	AH	0	1.2	0	0.001	0.003	0.000

Appendix 3 (continued)

						density.........	.........estimates		
							from timed searches		
	vis	vis		CPUE	CPUE		....	....	....
Site	wading	mask	Specie	wading	mask	quadra	wading	mask	combined
ASH6	7	10	EC	790	1468	1.41	1.830	2.751	2.367
ASH6	7	10	AH	4.1	1	0	0.009	0.001	0.005
ASH6	7	10	SU	2.1	1	0	0.003	0.002	0.001
ASH6	7	10	AU	0	1	0	-0.00	0.003	-0.00
ASH7	7	10	EC	2266	1782	4.54	3.815	2.814	3.231
ASH7	7	10	AU	7.1	12	0	0.023	0.031	0.029
ASH7	7	10	SU	3.5	8	0.025	0.008	0.019	0.012
ASH7	7	10	AH	3.5	3	0	0.010	0.006	0.007
CON2	8	10	EC	179	258	0.828	1.437	0.946	1.200
CON2	8	10	AU	8	11.1	0.031	0.047	0.038	0.048
CON2	8	10	LR	2.7	4.6	0.015	0.034	0.026	0.026
CON2	8	10	AH	0	4.6	0	0	0.013	0.011
CON2	8	10	AC	0	0.9	0	-0.00	0.000	-0.00
CON3	.	10	EC	.	3.8	0.014	0	0.032	0
CON3	.	10	LR	.	1.3	0	0	0.002	0
CON4	8	10	EC	36.8	158	0.25	0.353	0.522	0.471
CON4	8	10	AH	11.6	10.8	0.011	0.026	0.019	0.023
CON4	8	10	LR	3.9	12	0.011	0.021	0.038	0.027
CON4	8	10	SU	3.9	2.4	0.022	0.009	0.004	0.005
CON4	8	10	AU	1.9	2.4	0	0.008	0.005	0.006
CON5	.	10	EC	.	30	0.046	0	0.163	0
CON5	.	10	AH	.	11	0.031	0	0.018	0
CON5	.	10	LR	.	9	.	0	0.029	0
CON5	.	10	SU	.	1	.	0	-0.00	0
CON6	6	9	EC	1.7	31.6	0.027	0.074	0.148	0.153
CON6	6	9	AH	1.7	1.1	0	0.004	-0.00	0.000
CON6	6	9	LR	0	2.1	0	0.003	0.005	0.002
CON6	6	9	AU	0	1.1	0	0.000	-0.00	-0.00
CON6	6	9	SU	0	1.1	0	-0.00	-0.00	-0.00
CON7	.	10	EC	.	217	0.746	0	0.988	0
CON7	.	10	LR	.	6	0.028	0	0.039	0
CON7	.	10	AH	.	4	0.014	0	0.015	0
CON7	.	10	AU	.	1	0	0	0.007	0
CON7	.	10	SU	.	1	0	0	0.005	0
CON7	.	10	AC	.	1	0	0	0.002	0
CON8	.	10	EC	.	38.8	0.041	0	0.181	0
CON8	.	10	AH	.	3.7	0.013	0	0.004	0
CON8	.	10	LR	.	1.8	0	0	0.005	0
CON8	.	10	AU	.	0.9	0	0	-0.00	0
CON9	7	10	EC	212	478	1.6	1.611	1.522	1.640
CON9	7	10	LR	41.5	64.1	0.105	0.175	0.186	0.172
CON9	7	10	AH	3.1	6.1	0.013	0.021	0.019	0.021
CON9	7	10	AC	3.1	6.1	0	0.005	0.016	0.009
CON9	7	10	SU	3.1	4.1	0.001	0.019	0.016	0.016
CON9	7	10	AU	3.1	5.1	0.055	0.027	0.022	0.026
NEV1	7	10	EC	49.7	186	0.129	0.439	0.653	0.588
NEV1	7	10	AH	2.07	0	0.004	0.006	-0.00	0.000
NEV1	7	10	AV	1.03	2.9	0	-0.00	0.001	0.000

Appendix 3 (concluded)

	vis	vis		CPUE	CPUE	density.........estimates from timed searches			
Site	wading	mask	Specie	wading	mask	quadra	wading	mask	combined
NEV1	7	10	SU	0	1.94	0	-0.00	0.004	-0.00
NEV2	3	8	EC	5.71	35	0.063	0.098	0.125	0.126
NEV2	3	8	AH	1.43	3	0	0.001	-0.00	-0.00
NEV2	3	8	SU	1.43	3	0	0.000	0.000	-0.00
NEV2	3	8	AV	8.57	17	0	0.008	0.008	0.008
NEV3	8	10	EC	113	264	2.57	1.359	1.744	1.657
NEV3	8	10	AH	1	3	0.026	0.015	0.024	0.019
NEV3	8	10	AI	1	0	0.02	0.021	0.018	0.017
NEV3	8	10	AV	4	6	0.01	0.021	0.026	0.024
NEV3	8	10	AU	1	0	0	0.019	0.007	0.010
NEV3	8	10	SU	2	3	0	0.019	0.027	0.021
NEV4	9	10	EC	166	377	3.18	1.876	2.639	2.356
NEV4	9	10	AH	3	1	0.013	0.031	0.016	0.023
NEV4	9	10	AU	0	1	0.026	0.012	0.021	0.013
NEV4	9	10	AV	2	2	0.013	0.016	0.013	0.014
NEV4	9	10	AI	2	1	0.013	0.033	0.042	0.038
NEV4	9	10	SU	3	2	0	0.028	0.026	0.026
NEV5	.	.	EC	.	.	0.549	0	0	0
NEV5	.	.	SU	.	.	0	0	0	0
NEV5	.	.	AH	.	.	0.096	0	0	0
NEV5	.	.	AU	.	.	0	0	0	0
NEV6	.	10	EC	.	73	0.183	0	0.230	0
NEV6	.	10	AV	.	133	0.041	0	0.065	0
NEV6	.	10	AH	.	20	0.003	0	0.022	0
NEV6	.	10	SU	.	17	0.007	0	0.021	0
NEV6	.	10	AU	.	3	0.011		0.003	0