Research Article

The ecological consequences of nonindigenous *Corbicula fluminea* establishment on a benthic macroinvertebrate community

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Abstract

The frequently high abundances achieved by the nonindigenous Asian clam, *Corbicula fluminea,* has caused concern regarding the potential negative ecological impact the clams may have on native benthic macroinvertebrate communities. This study examined the ecological consequences of *C. fluminea* establishment on the benthic macroinvertebrate community in a New Hampshire, USA, river by comparing the benthic community before and after establishment and comparing sites with and those without *C. fluminea*. The nonmolluscan benthic communities were sampled using a ponar grab and compared using community metrics of macroinvertebrate densities, taxa richness, Shannon diversity, Hilsenhoff Biotic Index, and Bray-Curtis similarities cluster analysis and MSD ordination. Native bivalves were sampled by divers excavating 0.25 m² quadrats and compared using abundance and size-frequency distributions. No consistent significant difference was seen when comparing macroinvertebrate metrics before *vs.* after *C. fluminea* establishment or when comparing sites with and without *C. fluminea* for any of the metrics used. Metrics were often similar or improved at sites with *C. fluminea* relative to years before establishment or when compared to reference sites lacking *C. fluminea*. Bray-Curtis cluster analysis and MDS ordination failed to separate sites with *vs.* those without *C. fluminea*. Similarly, native bivalve abundances, namely *Elliptio complanata* and Sphaeriidae, were similar at sites with *vs.* sites without *C. fluminea*. *Elliptio complanata* size-frequency distributions did not differ significantly when compared across sites with and without *C. fluminea*. Rather than having negative consequences on the benthic macroinvertebrate community as many have proposed, it appears that *C. fluminea* may either have no effect or positive effects on the macrobenthos.

Key words: Asian clam, invasive species, diversity, abundance, community metrics, ecosystem engineering, native bivalves

Introduction

The potential ecological consequences of nonindigenous Asian clam, *Corbicula fluminea* (O. F. Müller, 1774), populations have been discussed for years (Cooper et al. 2005; Ilarri and Sousa 2012; Sickel 1973; Sousa et al. 2005, 2008a; Strayer 1999, Vaughn and Hakenkamp 2001). The frequently high population abundances achieved when *C. fluminea* invade a new area have led many to conclude that *C. fluminea* negatively impact abundance and diversity of benthic macroinvertebrate communities, including native bivalves, in North America (*e.g.,* Hakenkamp et al. 2001; Strayer 1999;

Sousa et al. 2008a; Vaughn and Hakenkamp 2001; Williams et al. 1993). The potential impact of *C. fluminea* on indigenous benthic communities continues to be of concern as these clams expand their range northward in North America and Europe (*e.g.,* Bódis et al. 2012; Caffrey et al. 2011; Domagala et al. 2004; Mackiewicz 2013; Morgan et al. 2003, 2004; Simard et al. 2012; Smagula 2016). Unfortunately, little empirical evidence is available documenting the impact, or lack thereof, of the nonindigenous *C. fluminea* on benthic invertebrate communities (Ilarri and Sousa 2012; Strayer 1999; Vaughn and Hakenkamp 2001). As *C. fluminea* expand their range northward, more evidence is needed to elucidate the impact of *C. fluminea* on indigenous benthic communities.

Originally native to southeast Asia, *C. fluminea* has been introduced to North and South America, Europe, Africa, and the Pacific islands (*e.g.*, Ilarri and Sousa 2012; Clavero et al. 2012; Morgan et al. 2003; Müller and Baur 2011; Strayer 1999; McMahon 1999, 2002; McMahon and Bogan 2001). *Corbicula fluminea* has experienced considerable geographic dispersion in just the past few decades (Ilarri and Sousa 2012; McMahon 1999; Morgan et al. 2003; Sousa et al. 2008a). In North America, live *C. fluminea* were first documented in British Columbia in 1924 (Counts 1981). By 1953, the clams had spread through much of the U.S., especially the Southeast (McMahon 1983; Simard et al. 2012), and can now be found in most of the lower 48 states and Hawaii (Strayer 1999). *Corbicula fluminea* have continued to spread in North America expanding their range northward into cooler waters once thought too cold for their survival (Smagula 2016; A. Benson, USGS *pers. comm.* 21 August 2017). For example, *C. fluminea* have recently spread into numerous areas of Colorado, Connecticut, Massachusetts, Minnesota, Michigan, New Hampshire, New York, and Utah where low water temperatures and ice cover are common (Colwell et al. 2017; Cordeiro et al. 2007; Morgan et al. 2003; Richards 2018; Smith et al. 2018; Wick 2017; USGS 2019; T. Richardson *pers. observ.* July and August 2017). Asian clams were first reported in Connecticut in 1990 (Morgan et al. 2003) and appeared in Massachusetts by 2001 (Colwell et al. 2017). By 2007 Asian clams had appeared in New Hampshire in the Merrimack River (Smagula 2018) and in Vermont by 2016 (Colwell et al. 2017). Asian clams have since spread into the greater southeastern area of New Hampshire including the numerous sites in the Merrimack River and in several lakes (T. Richardson *pers. observ.* July and August 2017).

The reasons for the northern range extension of *C. fluminea* into areas with low water temperatures and winter ice formation is a matter of considerable scientific uncertainty. Often, such expansion has been attributed to thermal plumes from cooling water discharge (Morgan et al. 2003, 2004; Simard et al. 2012). Compared to other bivalve species, *C. fluminea* has a limited temperature tolerance and has been widely perceived to be limited

in range due to intolerance of cold water ≤ 2 °C and warm water > 36 °C (Cairns and Cherry 1983; Mattice and Dye 1976; McMahon 1979, 1983, 2002; Rosa et al. 2012; Smith et al. 2018; Verbrugge et al. 2012; Werner and Rothhaupt 2008a). For example, French and Schloesser (1991) saw extirpation of complete *C. fluminea* populations due to winter mortality in the St. Clair River, Michigan and Smith et al. (2018) suspected back-to-back harsh winters contributed to overwinter mortality in the Fox River in Wisconsin. However, Müller and Baur (2011) found ≥ 75% survival when *C. fluminea* was exposed to 0 °C water for up to 4 weeks and that 17.5% of clams survived 0 °C exposure for 9 weeks. Similarly, populations of Asian clams were able to rebound after harsh winter conditions caused a die-off in Lake Constance, Germany (Werner and Rothhaupt 2008a). The rebound was attributed to reproduction from the few surviving individuals. Additionally, Morgan et al. (2004) concluded that the effects of thermal discharge on winter survival in the Connecticut River were minimal. Cordiero et al. (2007) saw successful overwintering of Asian clams throughout Colorado in the absence of warm water discharges. In a study examining *C. fluminea* distribution and thermal discharge, Castañeda (2012) cited human population density as being a more important factor than thermal discharge in *C. fluminea* establishment and density. This evidence combined with known distribution expansion into areas with low water temperature and ice formation suggests that *C. fluminea* have the genetic variability and capacity for adaptation to withstand cold winter temperatures and are able to establish in a much wider range of rivers and lakes than previously assumed.

Corbicula fluminea populations are known to frequently reach abundances > 1,000 clams/m^2 and may exceed 5,000 clams/m^2 in some locations (*e.g.,* Caffrey et al. 2011; Morgan et al. 2004; Simard et al. 2012; Sousa et al. 2008b; Strayer 1999; Vaughn and Spooner 2006). Such high Asian clam abundances have led some researchers to suggest that these clams could have a negative impact on the abundance and diversity of the indigenous benthic community including native unionid bivalves (Cordeiro et al. 2007; Strayer 1999; Sousa et al. 2008c; Vaughn and Hakenkamp 2001; Williams et al. 1993). With few exceptions, the potential negative ecological consequences of *C. fluminea* establishment on the ecosystems they invade have not been confirmed or validated. For example, Vaughn and Hakenkamp (2001) point out establishment of *C. fluminea* has only been speculated to have negatively impacted native bivalve abundance and distribution. Strayer (1999) recognizes that evidence for impacts of *C. fluminea* on native bivalves is derived largely from examining non-overlapping spatial distributions of bivalves or, less frequently, from changes in populations of native bivalves over time. Most of this evidence is anecdotal making it difficult to ascertain the impacts of *C. fluminea* on native bivalves. Studies that investigated the interaction between native unionids

and *C. fluminea* have suggested no significant effects of the clams on native bivalves or other invertebrates at Asian clam densities < 100 clams/m^2 up to 3,000/m^2 (Belanger et al. 1990; Beran 2006; Karatayev et al. 2003; Leff et al. 1990). For example, Karatayev et al. (2003) found no significant correlations between low *C. fluminea* densities (36–43 clams/m^2) or the density of their shells and any invertebrate taxon studied. An experiment by Hakenkamp et al. (2001) indicated that *C. fluminea* at densities near 1,900 clams/m^2 had no effect on benthic protists and invertebrates. Unfortunately, most studies of *C. fluminea* impacts on native assemblages of benthic organisms are indirectly correlative or largely examined non-overlapping spatial distributions of bivalves or investigated changes in populations over time following *C. fluminea* establishment (*sensu* Strayer 1999).

Rather than negatively impacting indigenous benthic communities, some authors have suggested that *C. fluminea* may actually have a positive effect through ecosystem engineering (Gutiérrez et al. 2003; Jones and Gutiérrez 2007; Sousa et al. 2009). *Corbicula fluminea* movement within the top layer of sediments leads to bioturbation. Such bioturbation contributes to substantial changes in abiotic conditions like dissolved oxygen, redox potential, amount of organic matter, and particle size in a manner typically enhancing habitat conditions for other organisms (Ilarri and Sousa 2012; Werner and Rothhaupt 2007). Additionally, invasive bivalve species tend to have positive impacts on invertebrate density, biomass, and species richness through enhanced habitat heterogeneity, provide refugia from predators and abiotic stress, fluid transport and organic matter accumulation, and sediment reworking (Gutiérrez et al. 2003; Sousa et al. 2009 and references therein). In general, studies on the ecosystem engineering of bivalves, including *C. fluminea*, suggest they may either have no effect on native benthic invertebrates or mainly positive effects on native benthic invertebrates. As *C. fluminea* continue to spread northward into previously unoccupied areas, it becomes increasingly important to determine what impacts, positive or negative, the clams may have on indigenous benthic communities in these areas.

The purpose of this study was to determine if any negative effect of *C. fluminea* presence on native benthic invertebrates and native bivalves could be detected. To achieve this, multiple community metrics (*e.g.*, density, richness, diversity, and resilience) were enumerated. The metrics were used to compare sites with and without *C. fluminea* across years as well as before and after invasion by *C. fluminea*. It was hypothesized that if *C. fluminea* negatively affect native species there should be a detectable decrease in native species abundance, richness, diversity, and thus a reduction in resilience to disturbance. A lack of a decrease in these metrics would suggest that *C. fluminea* invasion is not negatively impacting native invertebrate species.

Materials and methods

Study Site

The current study was conducted in Hooksett Pool, Amoskeag Pool downstream of Hooksett Dam, and at reference sites in Garvins Pool located immediately upstream of Hooksett Pool all in the Merrimack River, New Hampshire, USA. The Merrimack River is a relatively large river with average discharge at Goffs Falls below Manchester, NH near 215 m³/sec during the time of the study (USGS 2020). Channel width ranged from approximately 100 m in Garvins Pool to near 230 m in lower Hooksett Pool with depth at the study sites ranging from 2–4 m (Normandeau 2012). *Corbicula fluminea* was first detected in the Merrimack River in 2007, 40 km downstream of Hooksett Pool (Smagula 2018) and were first documented in Hooksett Pool in 2011 by Normandeau Associates, Inc., (Normandeau 2012). Normandeau performed analyses of benthic macroinvertebrates during 1972, 1973, and 2011. During the 2011 sampling, *C. fluminea* was found in areas of Hooksett Pool downstream of Merrimack Station, a coal-fired electricity generating facility in Bow, New Hampshire, at densities as high as 2,400 clams/m². Hooksett Pool is an approximately 8 km stretch of the Merrimack River extending from Garvins Falls Dam to Hooksett Dam (Figure 1). Hooksett Pool begins some 45 km from the river's headwaters and ends approximately 120 km upriver of the mouth of the Merrimack at the Atlantic Ocean near Newburyport, Massachusetts, USA. Merrimack Station is located on Hooksett Pool approximately midway between Hooksett and Garvins Falls Dams.

Quantitative Macroinvertebrate Sampling

Quantitative macroinvertebrate sampling was used to determine the current extent of the distribution and abundance of *C. fluminea,* and composition and abundance of benthic macroinvertebrates within Hooksett Pool. In 1972, Normandeau (2012) established permanent sampling transects and stations in Hooksett Pool upstream and downstream of Merrimack Station (Figure 1). These same sample locations were again sampled in 1973 and 2011 with additional reference stations added in 2011 upstream in Garvins Pool. A station downstream in Amoskeag Pool with habitat comparable to Hooksett Pool was added in 2011 for a downstream comparison outside of Hooksett Pool. During 2014 and 2016, the quantitative benthic macroinvertebrate sampling used these same stations and repeated the sampling procedure used in Hooksett and Garvins Pools conducted in 1972, 1973, and 2011 (Normandeau 2012). In 2011, 2014, and 2016, *C. fluminea* were not found in Garvins Pool or upstream of Merrimack Station in Hooksett Pool. As a result of the current study using the same sampling locations, the benthic communities before and after *C. fluminea* establishment in Hooksett Pool could be directly compared. Furthermore,
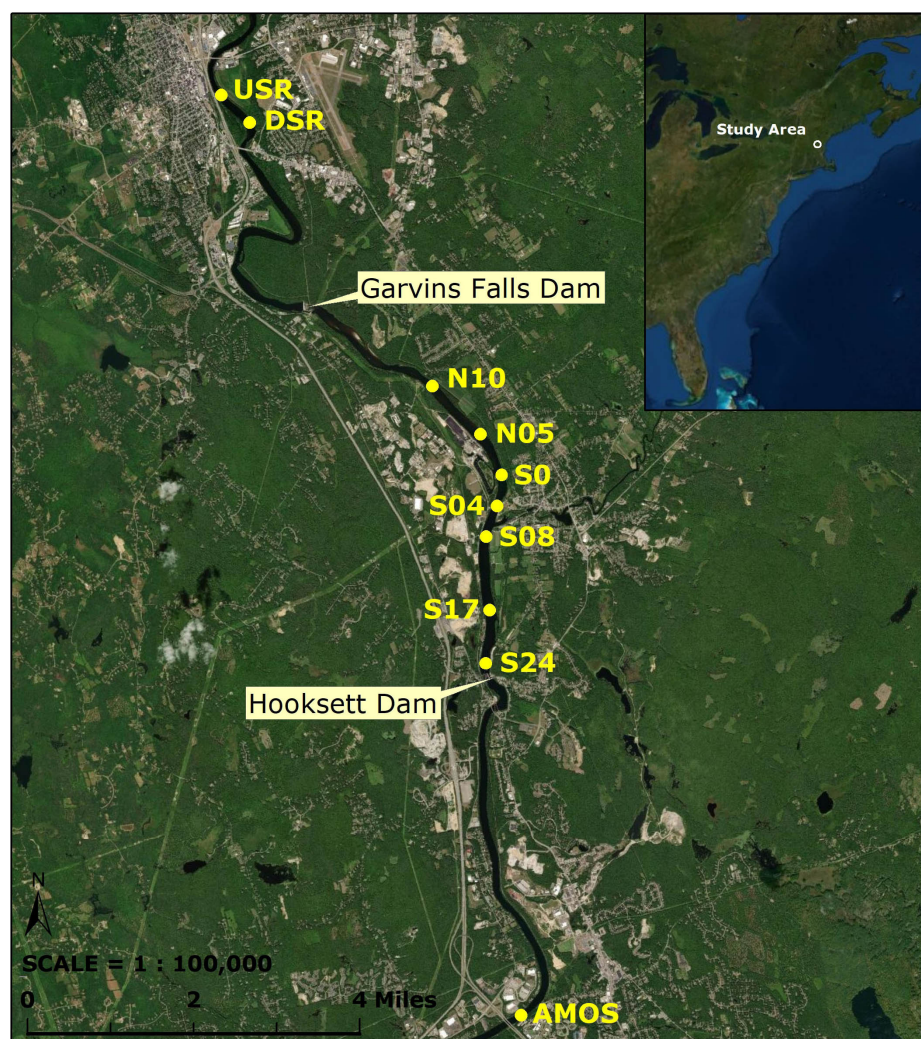
Figure 1. Satellite image with location of sampling stations in Garvins and Hooksett Pools in the Merrimack River, NH (USR = 43.2025 latitude, −71.5288 longitude; AMOS = 43.0421 latitude, −71.4579 longitude). Map was produced using www.arcgisonline.com.

using the 2014 and 2016 data from these stations, the benthic community from upstream reference areas and areas lacking *C. fluminea* could be directly compared to downstream areas with *C. fluminea*. Such before and after *C. fluminea* establishment, and presence *vs.* absence studies provided strong comparisons for assessing the ecological impact of *C. fluminea* establishment on the indigenous benthic invertebrate community.

At each station a transect line perpendicular to Merrimack River flow was established. Along each river bank-to-bank transect line three, one quarter distance locations were sampled: West, Middle, and East. A 23 × 23 cm standard ponar grab sampler was used to collect five replicate samples in 2014 and three replicate samples in 2016 at each of the three locations along each transect (Normandeau 2012). For the 2014 and 2016 study, the following ten stations were sampled (listed from upstream to downstream): Garvins Pool Stations USR and DSR (reference stations), Hooksett Pool Stations N-10 and N-5 upstream of Merrimack Station, and S-0, S-4, S-8, S-17, S-24 and Amoskeag Pool, AMOS downstream of Merrimack Station

(Figure 1). The substrata in Garvins, Hooksett, and Amoskeag Pools at the sampling transects were similar and uniformly sand and silt with some cobble/gravel mixture (*unpublished data*).

A total of 150 replicate samples were taken in 2014 and 90 were taken in 2016. Each replicate sample was initially sieved in the field through a 0.6 mm mesh sieve, preserved in an individual sample container, labeled with a unique sample number, replicate number, collection date, station and location. Samples were taken to the laboratory for sorting, identification, and enumeration of macroinvertebrates. The GPS coordinates of each station and location sampled were recorded on the field data sheet along with the sample label information.

In 2014, three of the five replicate samples from each station and location were randomly selected for further processing in the laboratory. In 2016, two of the three replicate samples were randomly selected for further processing. The remaining two samples from 2014 and the single remaining sample for 2016 were archived for potential future use if necessary. Each of the selected replicate samples was sorted, invertebrates identified to the lowest distinguishable taxon, and each taxon enumerated. All laboratory sorting, identification, and counting were subjected to a quality control (QC) inspection to insure an average outgoing quality limit of 10% or better. This QC inspection indicates that the data originating from laboratory processing were certified by independent statistical re-inspection at a sampling frequency to document that less than one record (one line of data) out of every ten records was outside of the established precision and accuracy for all contents of that record.

Native Freshwater Bivalve Quantitative Sampling

Compared to other benthic invertebrates, freshwater bivalves in the family Unionidae are typically found in low abundance and are not sampled adequately by the ponar method (T. Richardson *pers. observ.*). Quantitative sampling using divers to excavate 15 cm of substratum from a quadrat of known area (usually 0.25 m^2) is preferred for assessing unionid abundance (Miller and Payne 1993). Diver sampling was used coincident with the 2014 and 2016 quantitative macroinvertebrate sampling to adequately quantify the abundance of native bivalves found in Hooksett Pool during November/December 2014 and July 2016. The quantitative unionid samples were taken in the same stations and locations after quantitative benthic macroinvertebrate ponar grab sampling was completed. Care was taken that the diver quadrats were established adjacent to, but not within the exact footprint of the substratum disturbed by ponar sampling. Only stations N-10, S-0, S-4, and S-24 were sampled by divers for native bivalves in 2014 and 2016. At each station and location, two quantitative samples were taken for a total of 24 samples in 2014 with only one sample per station (n = 12) in 2016. Each sample was taken by randomly placing a 0.25 m^2

quadrat on the river bottom, excavating the substratum to a depth of 15 cm, and placing the quadrat contents in a 19-L plastic pail. In the laboratory, one of the two replicate samples in 2014 from each station and location was randomly selected for further processing. The remaining sample was archived for potential future use if necessary. Each of the 12 replicate samples to be processed was immediately sieved first over a 25 mm mesh sieve followed by 6 mm mesh then finally a 3 mm mesh sieve. All bivalves (unionids and sphaeriids) were removed, identified, and counted.

Data Analyses

Data from the quantitative macroinvertebrate samples were used to calculate densities of *C. fluminea* for each sample. These samples were also used to compute density, taxa richness, Shannon Community Diversity Index, and Hilsenhoff Biotic Index (HBI) of the benthic macroinvertebrate community for each sample using standard methods. At sites with Asian clams, *C. fluminea* was excluded from macroinvertebrate estimates for direct comparisons to the benthic macroinvertebrate community at sites without *C. fluminea*. The Shannon Community Diversity Index focuses on quantifying the uncertainty in predicting the species identity of an individual that is taken at random from the data set; similar communities will have similar Shannon Diversity. The HBI estimates the overall pollution tolerance of the community in a sampled area, weighted by the relative abundance of each taxonomic group, *i.e.,* the HBI takes into account resiliency of the community. Lower HBI's indicate a less pollution tolerant benthic community and, therefore, a "healthier" benthic community *i.e.,* reflects the community response to *C. fluminea* presence.

Data analyses of abundance and community metrics comparing stations or years were conducted using QI-Macro (2015) 2-way ANOVA with replication. Each null hypothesis tested was that there were no differences among stations or among years in the metric of interest. When comparing among year differences, only the two stations with highest *C. fluminea* abundances were used because the greatest potential for *C. fluminea* influence should have been at those stations. Similarly, when comparing among stations, only data from 2014 and 2016 were used because these should have reflected the greatest potential for *C. fluminea* impact on the benthic community and provided the most complete data set across all stations. When significant terms existed, single factor ANOVA with *post hoc* comparison was used to determine significant differences among station or year means. *Post-hoc* ANOVA comparisons of means were conducted with LSD comparisons. LSD *post hoc* comparisons were chosen as the least conservative estimate to show differences among sites or years with and without *C. fluminea*. Size-frequency distributions of native bivalves were analyzed using Kolmogorov-Smirnoff. Non-normal data sets were also analyzed using conservative nonparametric statistics (Kruskal-

Wallis or Friedman as appropriate) and produced similar results with respect to the null hypotheses tested using parametric statistics. All statistical analyses used α = 0.05 to test for significant differences.

Additionally, multivariate analyses were performed using data from the 90 quantitative macroinvertebrate samples from 2014. Prior to multivariate analyses, the taxon-mean counts per ponar grab sample were computed across the three replicate grab samples from each station and location. This reduced the input dataset for multivariate analyses to the mean count per taxon and grab sample for 30 station-locations. Data handling and preparation for multivariate analyses were completed using SAS software (version 9.3). Multivariate analyses were then performed using PRIMER v6 (Plymouth Routines in Multivariate Ecological Research) software, following standard techniques for the evaluation of spatial patterns in the distribution of faunal assemblages (Clarke 1993; Warwick 1993; Clarke and Green 1988; Clarke and Warwick 2001). These analyses included classification (cluster analysis) by hierarchical agglomerative clustering with group average linking and ordination by non-metric multidimensional scaling (MDS). Bray-Curtis Similarity was used as the basis for both classification and ordination. Prior to analyses, faunal abundance data (*i.e.*, mean count per taxon and grab sample) were square-root transformed to ensure that all taxa, not just the numerical dominants, would contribute to similarity measures. Bray-Curtis Community Similarity cluster analysis separates sites with dissimilar benthic invertebrate community composition. Likewise, MDS Ordination based on Bray-Curtis Similarity clusters separates sites with differences in community similarity. The "similarity profile test" (SIMPROF) was used to provide statistical support for the identification of faunal assemblages (*i.e.*, selection of cluster groups). SIMPROF is a permutation test of the null hypothesis that the groups identified by cluster analysis (samples included under each node in the dendrogram) do not differ from each other in multivariate structure. The "similarity percentages" (SIMPER) analysis was used to identify contributions from individual taxa to the overall dissimilarity between cluster groups. This analysis was used to identify the contribution of macroinvertebrate taxa (including *C. fluminea*) to the overall dissimilarity between cluster groups.

Results

Corbicula fluminea

Corbicula fluminea densities were compared among years only for the three sites with clams for which there was complete data for 2011, 2013, 2014, and 2016, *i.e.,* S-0, S-17, and S-24. Stations USR, DSR, N-10, and N-5 had no *C. fluminea* at the time of this study. *Corbicula fluminea* densities differed significantly among years (2-way ANOVA; $F_{3,\,72} = 7.0753$, $p < 0.0003$) fluctuating over an order of magnitude from 2011 to 2016 (Figure 2). In 2011,
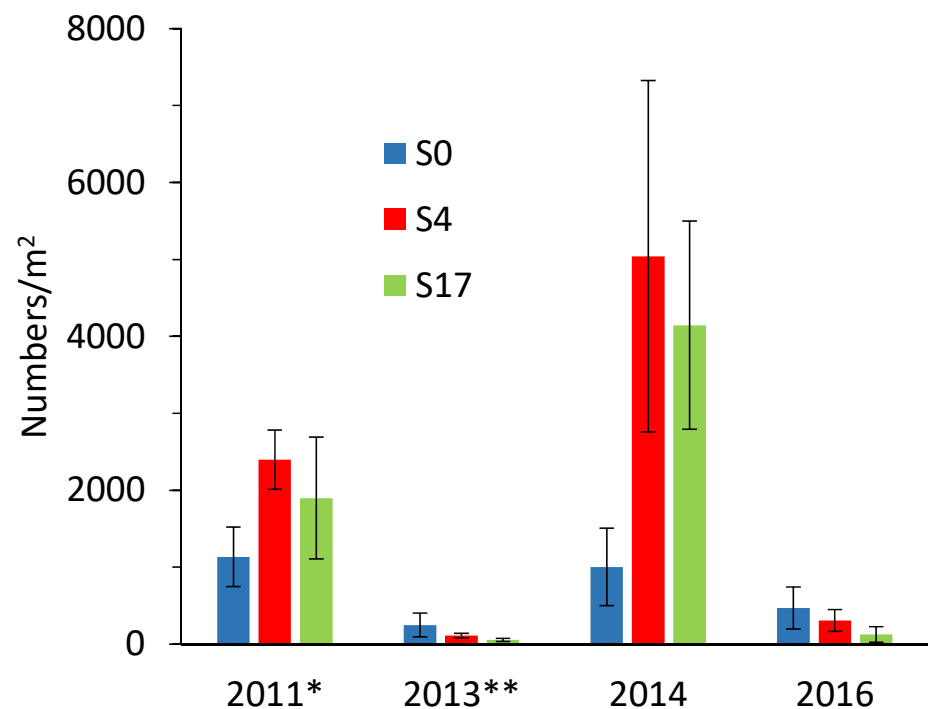
Figure 2. Mean (± standard error) *C. fluminea* densities at three sampling stations for which multi-year data are available on Hooksett Pool, Merrimack River, NH. S-0, S-4 and S-17 were the only sites for which all years were represented. *First year *C. fluminea* were observed in Hooksett Pool. **Data for 2013 are unpublished, with permission from New Hampshire Department of Environmental Services.

when clams were first sampled in Hooksett Pool, clam densities averaged 1,811 (± 325.9 standard error) clams·m^{-2} and declined to 123 (± 39.7 SE)·m^{-2} in 2013. By 2014, clam densities rebounded to a high of 3,397 (± 929.2 SE)·m^{-2} only to fall again to 302 (± 107.1 SE)·m^{-2} in 2016 (Figure 2). Clam densities did not differ significantly among stations (2-way ANOVA; $F_{2, 72} = 1.7745$, $p = 0.177$) and there was no station-by-year interaction (2-way ANOVA; $F_{6, 72} = 1.2684$, $p = 0.283$) suggesting density fluctuation among years was similar among stations.

Macroinvertebrates

When comparing stations, benthic macroinvertebrate density (minus *C. fluminea*) differed among stations (2-way ANOVA; $F_{9,130} = 2.3617$, $p = 0.017$), but did not differ between 2014 and 2016 (2-way ANOVA; $F_{1, 130} = 3.6340$, $p = 0.059$) (Figure 3). There was no significant station-by-year interaction (2-way ANOVA; $F_{9, 130} = 1.5388$, $p = 0.141$). In general, invertebrate density was the same or higher among many stations with *vs.* those without *C. fluminea* (Figure 3). There was no significant difference (LSD; $p > 0.05$) among many of the stations with *C. fluminea* compared to those sites without clams in both 2014 and 2016. In 2014, invertebrate density was significantly higher at station S-17 (ANOVA; $F_{9, 89} = 2.0874$, $p = 0.040$; LSD, $p < 0.05$), one of the stations with the highest *C. fluminea* densities, than at any of the stations without clams including two reference stations
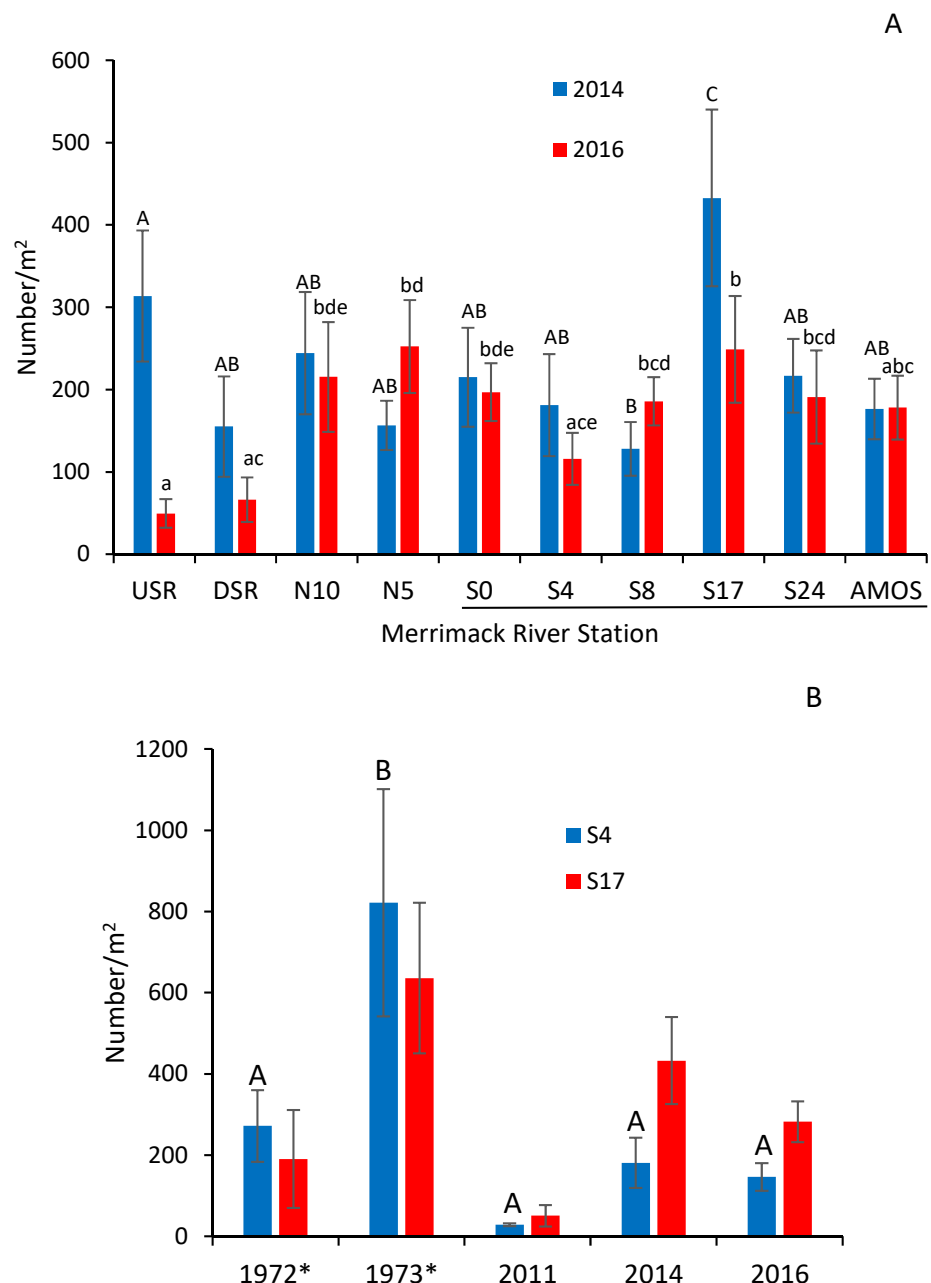
A

B

Figure 3. Mean (± standard error) of benthic invertebrate density by station (A) and year (B). Densities do not include *C. fluminea*. Underlined sites are sites known to have *C. fluminea* present. S-4 and S-17 are sites with highest *C. fluminea* density. * = years prior to *C. fluminea* establishment. Means with different letters are significantly different (LSD; $p < 0.05$); uppercase letters are for 2014, lowercase for 2016.

(Figure 3). In 2016, densities among stations differed (ANOVA; $F_{9, 59}$ = 2.4035, $p = 0.024$; LSD, $p < 0.05$) with some of the lowest invertebrate abundances at the two reference stations.

Comparing differences among years at the two stations with highest *C. fluminea* densities (S-4 and S-17), benthic invertebrate densities (minus *C. fluminea*) differed among years (2-way ANOVA; $F_{4, 62}$ = 9.134, $p = 0.00001$), but were similar between the two stations (2-way ANOVA; $F_{1, 62}$ = 0.6415, $p = 0.426$) (Figure 3). There was no significant station-by-year interaction (2-way ANOVA; $F_{4, 62}$ = 1.2435, $p = 0.302$). At S-4, densities differed
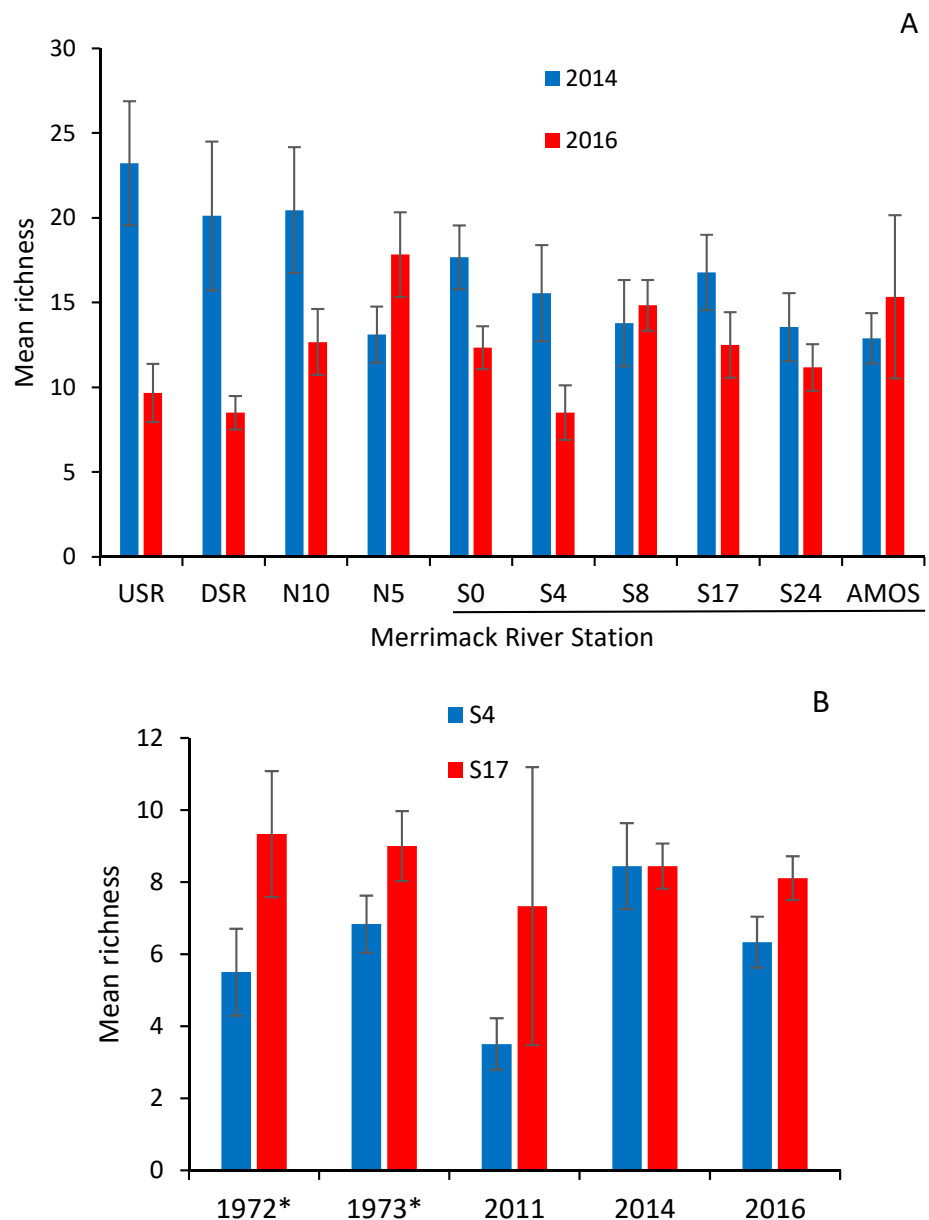
Figure 4. Mean (± standard error) taxa richness of benthic invertebrates by station (A) and year (B). Taxa richness estimates do not include *C. fluminea*. Underlined sites are sites known to have *C. fluminea* present. S-4 and S-17 are sites with highest *C. fluminea* densities. * = years prior to *C. fluminea* establishment.

among years (ANOVA; $F_{4, 35} = 5.7651$, $p = 0.001$; LSD, $p < 0.05$), but were similar in 1972, 2011, 2014, and 2016 (LSD; $p > 0.05$); densities were significantly higher in 1973 (LSD; $p < 0.05$) (Figure 3). At S-17, invertebrate densities were not significantly different among years (ANOVA; $F_{4, 35} = 2.4933$, $p = 0.063$).

Indigenous macroinvertebrate taxa richness showed little difference among stations in both 2014 and 2016 (Figure 4). Benthic invertebrate taxa richness did not differ among stations (2-way ANOVA; $F_{9, 130} = 0.8096$, $p = 0.608$), but did differ between years (2-way ANOVA; $F_{1, 130} = 12.604$, $p = 0.001$) and there was a significant station-by-year interaction (2-way ANOVA; $F_{9, 130} = 2.3312$, $p = 0.018$).

There was no significant difference among years in taxa richness at the two stations with highest *C. fluminea* densities (S-4 and S-17) (2-way ANOVA; $F_{4, 62}$ = 1.3055, p = 0.278); benthic invertebrate taxa richness was the same in 2011, 2014 or 2016 following *C. fluminea* establishment compared to 1972 or 1973 prior to *C. fluminea* establishment (Figure 4). Taxa richness did differ significantly between the two stations (2-way ANOVA; $F_{1, 62}$ = 5.7813, p = 0.019) with taxa richness higher at S-17 than S-4. There was no significant station-by-year interaction (2-way ANOVA; $F_{4, 62}$ = 0.7094, p = 0.589).

The Shannon Community Diversity Index for the benthic invertebrate community differed significantly among stations (2-way ANOVA; $F_{9, 130}$ = 1.9735, p = 0.047), between years (2-way ANOVA; $F_{1, 130}$ = 25.6028, p = P = 0.000001), and there was a significant station-by-year interaction (2-way ANOVA; $F_{9, 130}$ = 2.0219, p = 0.042) (Figure 5). Shannon Diversity was higher at all stations in 2014 than in 2016. However, when looking within individual years, Shannon diversity was the same among many stations with *vs.* those without *C. fluminea* (Figure 5). In 2014, Shannon Diversity differed significantly among stations (ANOVA; $F_{9, 89}$ = 2.3243, p = 0.022) although stations S-0, S-4, and S-17 with *C. fluminea* were not significantly different (LSD; p >0.05) when compared to the stations lacking *C. fluminea* (N-5, N-10, and the two reference stations DSR and USR) without *C. fluminea* (Figure 5). Shannon diversity for stations S-8, S-24, and AMOS did not differ from N-5 and S-8 also did not differ from the DSR reference station (LSD; p > 0.05). There was no significant difference in Shannon Diversity among stations in 2016 (ANOVA; $F_{9, 59}$ = 0.3358, p = 0.099) (Figure 5).

Shannon Community Diversity Indices at S-4 and S-17 did not differ among years (2-way ANOVA; $F_{4, 62}$ = 1.7198, p = 0.157) suggesting community diversity was the same in 2011, 2014, and 2016 following *C. fluminea* establishment compared to 1972 or 1973 prior to *C. fluminea* establishment (Figure 5). Shannon diversity did differ between stations (2-way ANOVA; $F_{1, 62}$ = 9.7174, p = 0.003) with S-17, the site with highest *C. fluminea* density, having higher diversity. There was no significant year by stations interaction (2-way ANOVA; $F_{4, 62}$ = 1.2216, p = 0.311).

Hilsenhoff Biotic Index (HBI) estimated for the invertebrate community differed significantly among stations (2-way ANOVA; $F_{9, 130}$ = 2.3000, p = 0.020), between years (2-way ANOVA; $F_{1, 130}$ = 239.66, p = < 0.0001), and there was a significant interaction between 2014 and 2016 among stations (2-way ANOVA; $F_{9, 130}$ = 27.7200, p = P < 0.0001). Overall, HBI's were lower for 2016 than for 2014 (Figure 6). Examining individual years, HBI did not differ significantly among stations in 2016 (ANOVA; $F_{9, 59}$ = 1.1515, p = 0.346), but did differ significantly among stations in 2014 (ANOVA; $F_{9, 59}$ = 4.1532, p = 0.00002). In 2014, HBI at many stations with *C. fluminea* were similar (LSD; p > 0.05) to stations lacking clams (Figure 6). The lowest
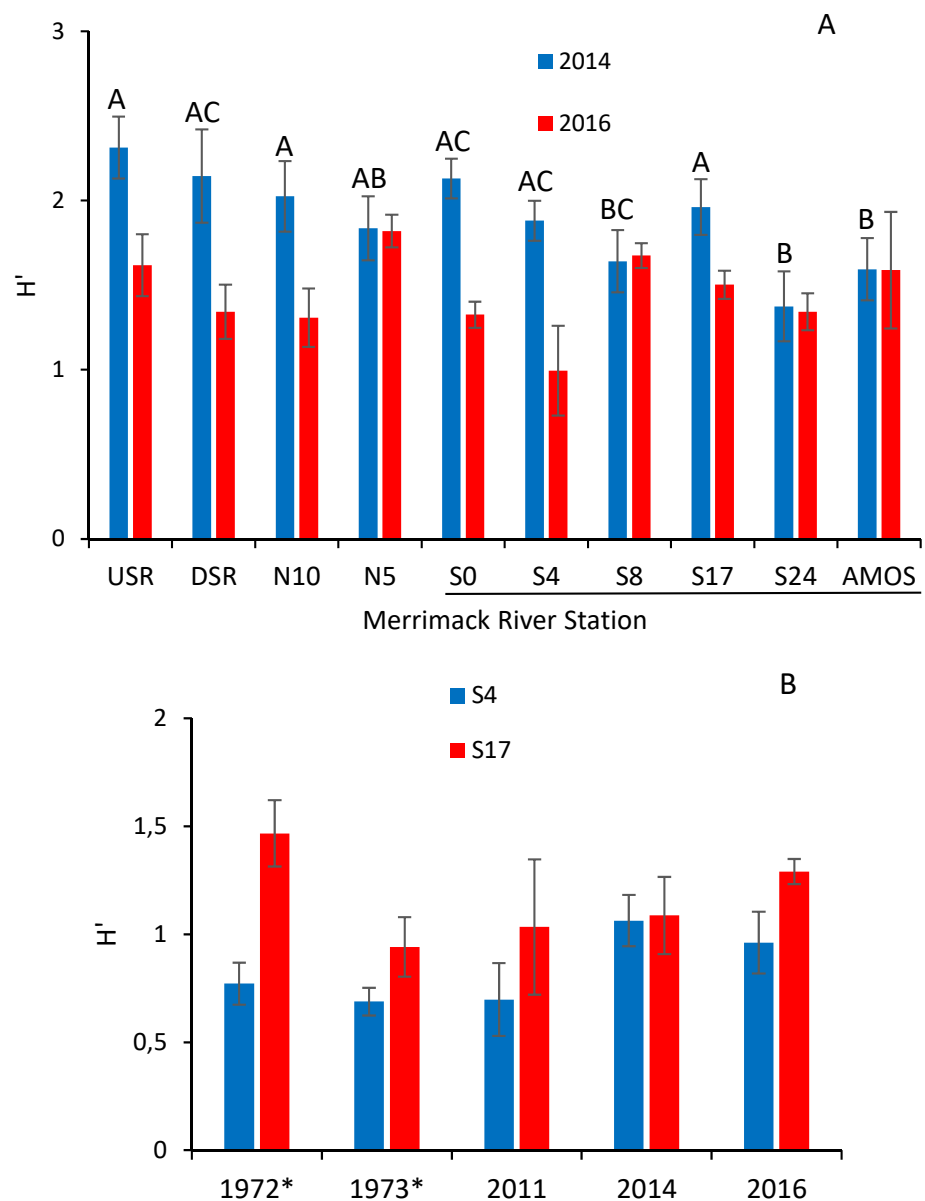
Figure 5. Mean (± standard error) Shannon Diversity Index of benthic invertebrates by station (A) and year (B). Shannon diversity indices do not include *C. fluminea*. Underlined sites are sites known to have *C. fluminea* present. S-4 and S-17 are sites with highest *C. fluminea* densities. * = years prior to *C. fluminea* establishment. Means with different letters are significantly different (LSD; $p < 0.05$).

HBI's were at Stations S-4 (high *C. fluminea* abundance), and USR and N-5 (each with no *C. fluminea* present). HBI was highest at S-8 and AMOS (LSD; $p < 0.05$), both with *C. fluminea*, but S-8 and AMOS were similar to DSR and N-10, both lacking *C. fluminea* (LSD; $p > 0.05$).

HBI at S4 and S17 (the two sites with the highest recorded *C. fluminea* abundances) was significantly different among years (2-way ANOVA; $F_{4, 62}$ = 5.7846, $p = 0.001$) (Figure 6). Overall, HBI at S4 was not significantly different than HBI at S17 (2-way ANOVA; $F_{1, 62}$ = 0.1954, $p = 0.660$) and there was no significant station-by-year interaction (2-way ANOVA; $F_{4, 62}$ = 1.4862, $p = 0.217$). In comparisons among years within stations, HBI at S-4 differed significantly among years (ANOVA; $F_{4, 35}$ = 1.0796, $p = 0.049$) with
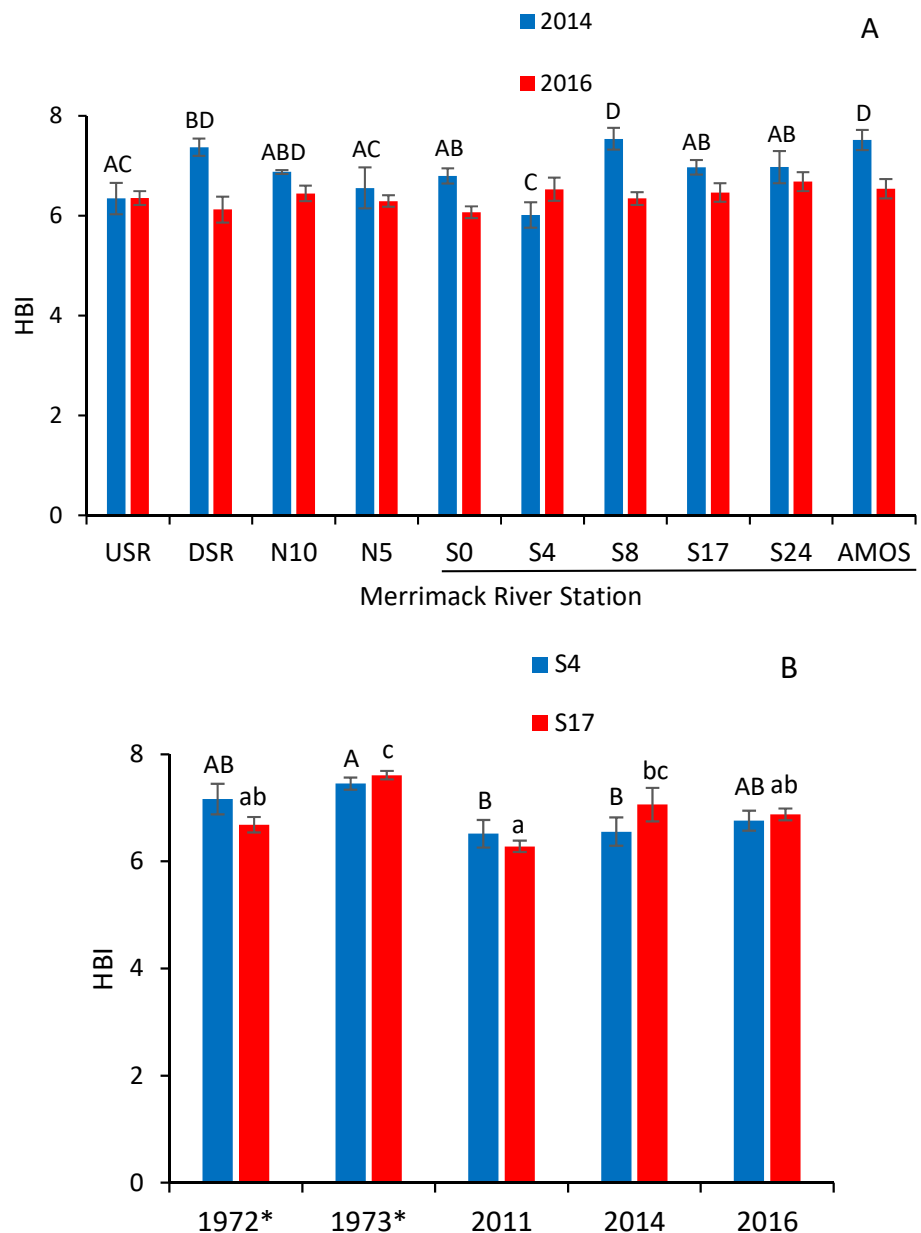
Figure 6. Mean (± standard error) Hilsenhoff Biotic Index of benthic invertebrates by station (A) and year (B). The HBIs do not include *C. fluminea*. Underlined sites are sites known to have *C. fluminea* present. S-4 and S-17 are sites with highest *C. fluminea* densities. * = years prior to *C. fluminea* establishment. Means with different letters are significantly different (LSD; p < 0.05).

2011 and 2014 HBI significantly lower than 1973 (LSD; p < 0.05); however, 2011 and 2014 HBI were similar to 1972, and 2016 (LSD; p > 0.05). Similarly, S-17 HBI differed among years (ANOVA; $F_{4, 35}$ = 4.9677, p = 0.003); 1972, 2011, and 2016 HBI were lower than 1973 indicating an improved biotic index (LSD; p < 0.05), but similar to 2014. S-17 HBI was similar between 1973 and 2014 (LSD; p > 0.05).

Bray-Curtis Community Similarity Indices cluster analysis indicated similar macroinvertebrate communities among stations with and without *C. fluminea* (Figure 7). The cluster analysis grouped stations into three significant groups; however, each of these significant groups contained stations with and without *C. fluminea*. Within each of the three significant
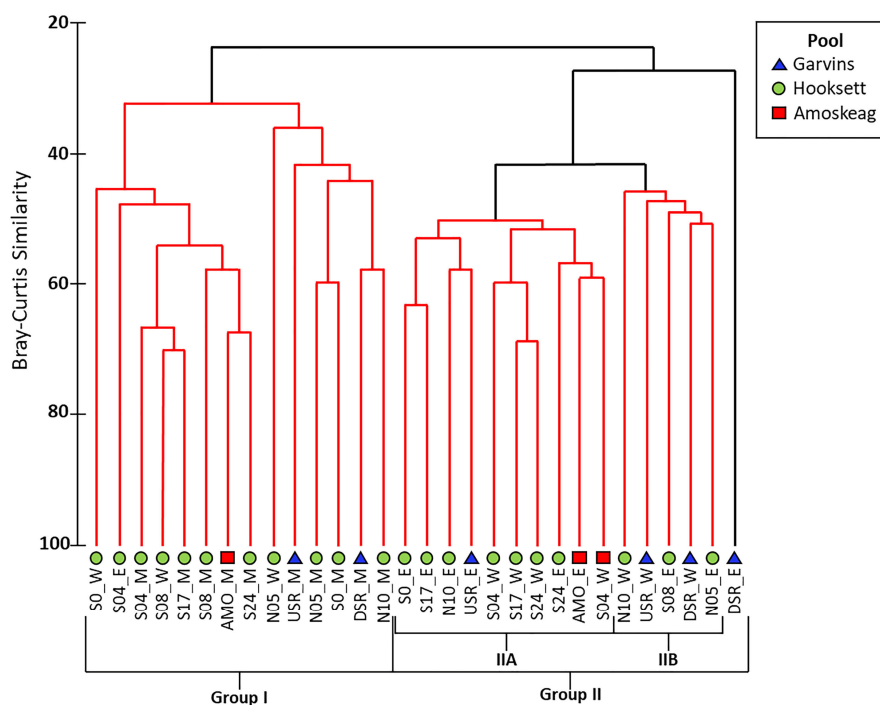
Figure 7. Cluster analysis results using Bray-Curtis similarities for the 2014 macroinvertebrate samples from the Merrimack River. Similarities include *C. fluminea* where present. The SIMPROF test results are indicated by the black and red lines on the dendrogram. Black lines on the dendrogram indicate statistically valid cluster groups, while red lines indicate branches of the dendrogram within which SIMPROF found no statistical evidence for sub-structure. In reference to sample position along each transect, E = east, M = middle, and W = west.
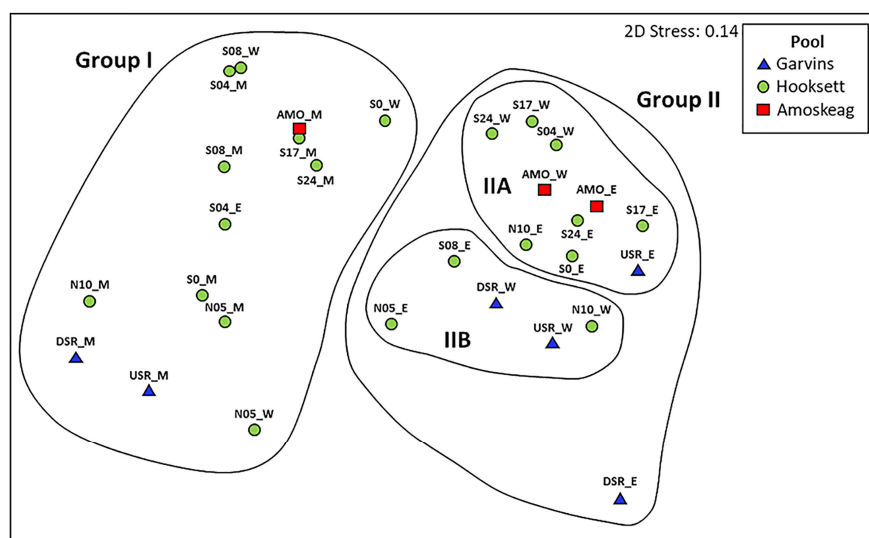

Figure 8. MDS ordination based on Bray-Curtis Similarities for the 2014 macroinvertebrate samples. Each point on the plot represents one of 30 station locations; similarity of species composition is indicated by proximity of points on the plot. Faunal assemblages (Groups I-II, and sub-groups) identified by cluster analysis are circled on the plot. In reference to sample position along each transect, E = east, M = middle, and W = west.

groupings, there was no statistical evidence for substructure or separation. MDS Community Ordination based on similarities confirmed the Bray-Curtis clusters and separated stations into the three Bray-Curtis clusters (Groups I and II and subgroups IIA and IIB). The MDS two-dimensional stress level of 0.14 (Figure 8) suggests a good ordination and 2-D separation

of the groups. Each of the Bray-Curtis clusters and MDS groups contained stations with and those without *C. fluminea*.

Native Freshwater Bivalves

Native bivalve species richness was relatively low in the diver excavated 0.25 m² quantitative samples in both 2014 and 2016. Of the 253 bivalves sampled in 2014, 250 were *Elliptio complanata* (Lightfoot, 1786) and three individuals were members of the family Sphaeriidae tentatively identified as *Pisidium* spp. In 2016, 232 native bivalves were collected: three *E. complanata* and 229 sphaeriids. *Corbicula fluminea* was the most abundant bivalve in the 0.25 m² samples with a total of 4,371 clams collected in 2014 and 630 collected in 2016. Overall, in 2014 *E. complanata* averaged 83 individuals·m⁻² (± 31.9 SE) and sphaeriids averaged 1 individual·m⁻² (± 0.5 SE). In 2016, *E. complanata* averaged 1 individual·m⁻² (± 0.7 SE) and sphaeriids averaged 63 individuals·m⁻² (± 17.7 SE). Based on the diver quadrat samples, *C. fluminea* averaged 1,457 individuals·m⁻² (1004.1 SE) in 2014 and 210 individuals·m⁻² (148.6 SE) in 2016.

Analysis of the 2014 0.25 m² samples indicated a significant difference among native bivalve species (2-way ANOVA; $F_{1, 16}$ = 7.6964, p = 0.014) with *E. complanata* more abundant than sphaeriids (Figure 9). However, there was not a significant difference among stations (2-way ANOVA; $F_{3, 16}$ = 1.6091, p = 0.227). Notably, *E. complanata* and sphaeriids, had densities at Station N-10, where no Asian clams occurred, similar to those of Station S-24, where Asian clams were abundant (Figure 9). Also, there was no significant station-by-species interaction (2-way ANOVA; $F_{3, 16}$ = 1.5045, p = 0.251) suggesting *E. complanata* and sphaeriid abundances were not affected differently by the presence of *C. fluminea*. In 2016, analysis showed a significant difference among native bivalve species (2-way ANOVA; $F_{1, 16}$ = 12.0965, p = 0.003); however, in 2016 sphaeriids were more abundant than *E. complanata* (Figure 9). Similar to 2014, in 2016 there was no significant difference among stations (2-way ANOVA; $F_{3, 16}$ = 0.9725, p = 0.430) and there was no significant station-by-species interaction (2-way ANOVA; $F_{3, 16}$ = 0.9571, p = 0.437).

Elliptio complanata densities differed between years (2-way ANOVA; $F_{1, 16}$ = 7.6934, p = 0.014) and were less abundant in 2016 than in 2014 (Figure 9). There was no difference in *E. complanata* densities among stations (2-way ANOVA; $F_{3, 16}$ = 1.5947, p = 0.230) and there was no station-by-year interaction (2-way ANOVA; $F_{3, 16}$ = 1.5177, p = 0.248). Sphaeriidae densities also differed between years (2-way ANOVA; $F_{1, 16}$ = 12.1092, p = 0.003) and were more abundant in 2016 than in 2014. There was no difference among stations (2-way ANOVA; $F_{3, 16}$ = 1.0043, p = 0.416) and no station-by-year interaction (2-way ANOVA; $F_{3, 16}$ = 0.9273, p = 0.450). There was no significant effect of *C. fluminea* density on native bivalve density.
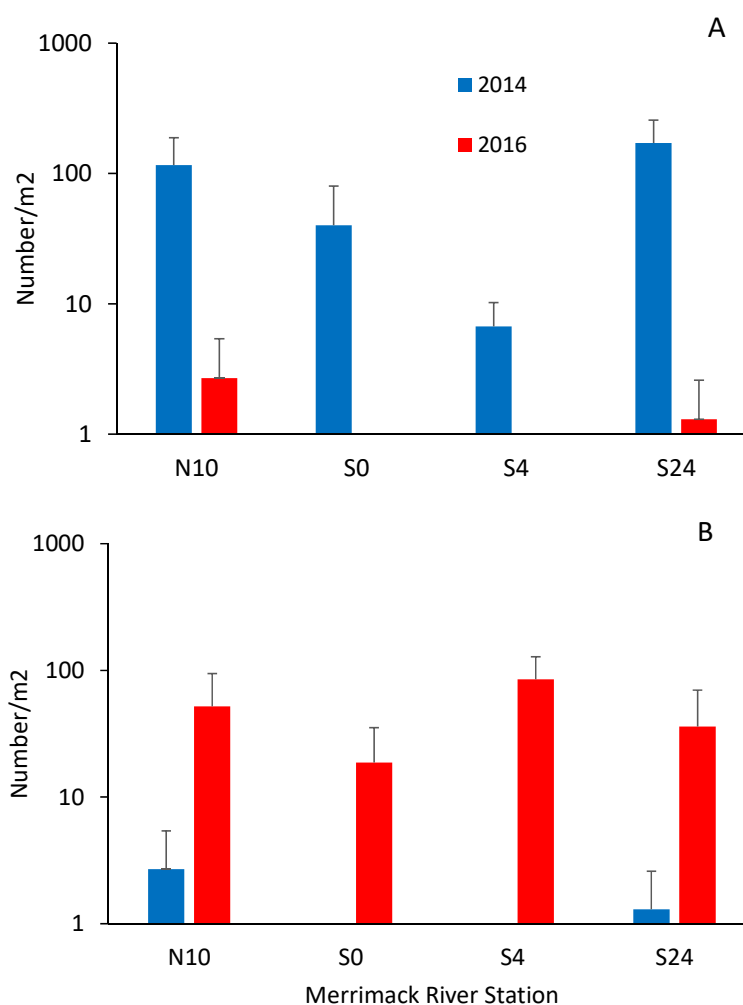
Figure 9. Mean (± standard error) density of *E. complanata* (A) and sphaeriids (B) at four Merrimack River Stations. Stations S-0, S-4, and S-24 have *C. fluminea*. Samples are 0.25 m² quadrates excavated to 15 cm substrate depth.

When pooling 2014 and 2016 *E. complanata* data from stations with *C. fluminea* and comparing the shell size-frequency distribution to data from stations without *C. fluminea*, population size-frequency structures were similar and did not differ significantly (Kolmogorov-Smirnov D_{stat} = 0.1288 < $D_{\alpha; 14, 14}$ = 0.1333; $p > 0.65$) (Figure 10).

Discussion

The potential ecological consequences of nonindigenous *C. fluminea* populations and their adaptations for rapid establishment have been discussed for years (Colwell et al. 2017; Cooper et al. 2005; Ilarri and Sousa 2012; McMahon 1983, 1999, 2002; Sickel 1973; Sousa et al. 2005, 2008a; Strayer 1999; Vaughn and Hakenkamp 2001). This study investigated the ecological impact of *C. fluminea* on the indigenous benthic community of Hooksett Pool, Merrimack River, New Hampshire, USA, in order to determine the ecological consequences of *C. fluminea* establishment on the benthic community. At the three stations in Hooksett Pool with multiple year data, *C. fluminea* densities fluctuated widely between 2011 and 2016.
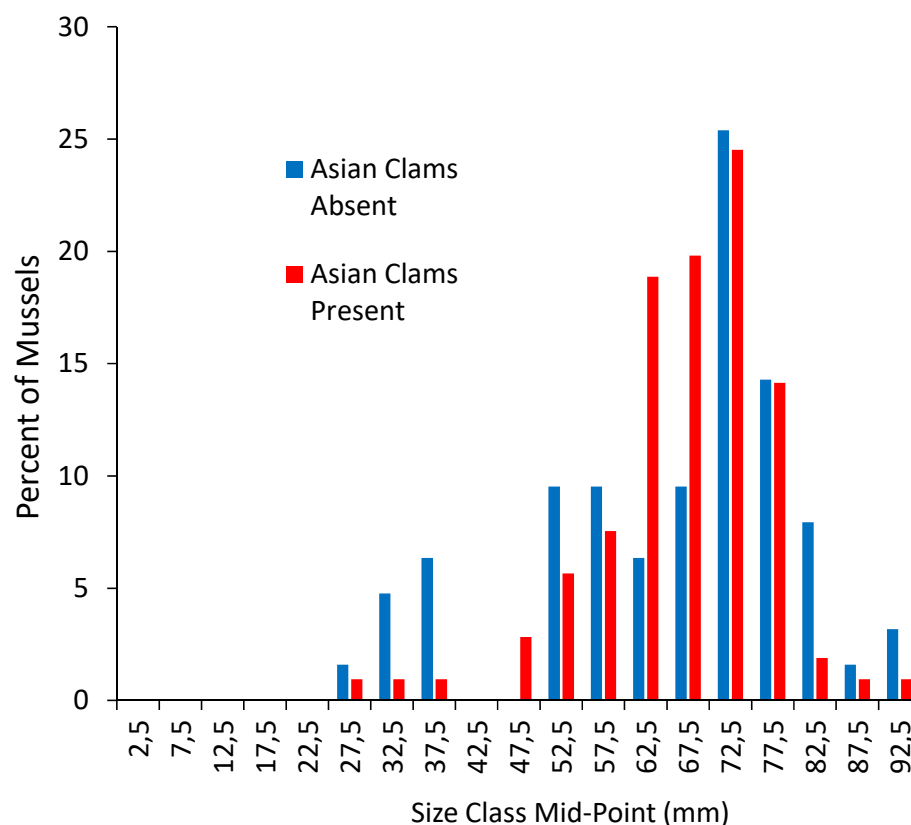
Figure 10. Size-frequency distribution of Eastern elliptio, *Elliptio complanata*, the predominant native bivalve in Hooksett Pool. Station N-10 was used for "*C. fluminea* Absent" and S-0, S-4, and S-24 were pooled for "*C. fluminea* Present." The two distributions are not significantly different (Kolmogorov-Smirnov $D_{stat} = 0.1288 < D_{\alpha, 14, 14} = 0.1333$, p > 0.65).

When *C. fluminea* were first discover in Hooksett Pool in 2011 (Normandeau 2012), densities averaged nearly 1,800 clams·m^{-2}, declined to 123·m^{-2} in 2013, rebounded by 2014 to a high of nearly 3,400·m^{-2} only to fall again to about 300·m^{-2} in 2016. Such rapid population growth of *C. fluminea* following establishment or some density reduction event is not uncommon. *Corbicula fluminea* populations may rapidly reach high abundances, but a low juvenile survivorship and a high mortality rate throughout adult life leads to considerable annual, seasonal, and site-to-site variability and fluctuations in abundances and frequent population mortality events, especially in sites experiencing cold water temperatures (*e.g.,* French and Schloesser 1991; Ilarri et al. 2011; Morgan et al. 2003, 2004; Smith et al. 2018; Vohmann et al. 2010; Werner and Rothhaupt 2008a). Contributing to this variability is the relatively low physiological tolerances of the *C. fluminea* and its dependence on elevated fecundity for invasive success and rapid population recovery (McMahon 2002). Such elevated fecundity by *C. fluminea* is due, in part, to its high allocation of energy to growth and reproduction which is typical of such opportunistic and invasive species (McMahon 2002). The population of *C. fluminea* in Hooksett Pool appears to adhere to the typical population variability centered on the capacity of the clam to rapidly re-establish populations after density reduction (McMahon 2002).

Population variability notwithstanding, the frequently high population abundances achieved when *C. fluminea* invade a new area has led many to conclude that *C. fluminea* negatively impact abundance and diversity of benthic macroinvertebrates communities, including native bivalves (*e.g.,* Araujo et al. 1993; Hakenkamp et al. 2001; Strayer 1999; Sousa et al. 2005, 2008d; Vaughn and Hakenkamp 2001; Williams et al. 1993). However, experimental evidence for the impact of *C. fluminea* on benthic macroinvertebrates is rare (Vaughn and Hakenkamp 2001; Karatayev et al. 2005; Werner and Rothhaupt 2007, 2008b). Most studies rely on examination of spatial distributions, comparing systems with *C. fluminea* to systems lacking the clams. No studies use multiple community metrics or compare benthic communities before and after establishment of *C. fluminea* (*sensu* Sousa et al. 2008b). This study used density and commonly accepted macroinvertebrate community metrics to compare invertebrate communities with and without *C. fluminea*, and before *vs.* after *C. fluminea* establishment. Benthic macroinvertebrate density and community metrics in Hooksett Pool showed no clear pattern between areas with and those without *C. fluminea*. During 2014 and 2016, macroinvertebrate densities were the same or higher in areas with *C. fluminea*. Likewise, benthic invertebrate density at the two stations with highest *C. fluminea* densities (S-4 and S-17) was similar before and after *C. fluminea* establishment (1972 and 1973 *vs.* 2011–2016). Lacking a consistent significant difference in invertebrate density among stations with and without *C. fluminea* for either 2014 or 2016 and before and after Asian clam establishment suggests *C. fluminea* had no negative effect on the benthic macroinvertebrate community density. Like this study, Werner and Rothhaupt (2007) found no significant difference in macroinvertebrate density between experimental boxes with and without *C. fluminea* at densities similar to those found in Hooksett Pool. Werner and Rothhaupt (2007) also found that some macroinvertebrate species actually increased in abundance and attributed this positive affect to the addition of shell to the sandy substratum after mass mortality of *C. fluminea*. Similarly, using a combination of field and laboratory experiments, Hakenkamp et al. (2001) found that abundance of *C. fluminea* was negatively associated with the abundance of benthic bacteria and flagellates, but saw no effect on other protists or meiofauna. Taken together, this information strongly supports that benthic macroinvertebrate abundance in large rivers like the Merrimack River is not adversely affected by the establishment and persistence of *C. fluminea* and that Asian clams may actually have positive impacts on invertebrate abundance. Such evidence supports the assertions of Gutiérrez et al. (2003) and Sousa et al. (2009) that nonindigenous invasive species like *C. fluminea* may actually enhance abundance through ecosystem engineering, *i.e.*, organisms that can physically modify the environment.

Various metrics of benthic macroinvertebrate communities are often used to examine community responses to stressors (*e.g.,* pollution) by comparing them to reference sites and other areas lacking stressors or before and after some stressor is applied. In 2014 and 2016, benthic invertebrate taxa richness was similar between areas with and without *C. fluminea* and higher at some sites compared to reference sites. Shannon diversity was similar at many sites with *C. fluminea* compared to sites without clams including reference sites during 2014 and 2016. HBI during 2014 and 2016 was similar between sites with and those without *C. fluminea* and was even lower at some sites with clams compared to reference sites. Similarly, benthic invertebrate richness and diversity at the two stations with highest *C. fluminea* densities (S-4 and S-17) were similar before and after *C. fluminea* establishment (1972 and 1973 *vs.* 2011–2016). HBI was either similar or lower following *C. fluminea* establishment than prior to establishment. Bray-Curtis similarities cluster analysis and MDS based on Bray-Curtis similarities was unable to distinguish between macroinvertebrate communities at reference sites and other sites with *vs.* those without *C. fluminea* as was the case with Sousa et al. (2008c). Others have seen similar beneficial effects of introduced *C. fluminea* (Sousa 2008c, d; Werner and Rothhaupt 2007), but lacked the comparison of indices like Shannon diversity and HBI. The use of such community metrics is a powerful tool for assessing the effects that *C. fluminea* establishment and abundance may have on benthic invertebrate communities. The use of such metrics and the findings here conclusively support the idea that nonindigenous *C. fluminea* are not having a negative effect on macrobenthic communities and may possibly be enhancing the community through ecosystem engineering (Gutiérrez et al. 2003; Sousa et al. 2009).

In addition to the benthic macroinvertebrate community in general, specific concern has been raised about the effects *C. fluminea* may have on native bivalves, specifically members of the Unionidae (*e.g.,* Hakenkamp et al. 2001; Strayer 1999; Sousa et al. 2008c; Vaughn and Hakenkamp 2001; Williams et al. 1993). Using diver excavated samples, this study compared *E. complanata*, the dominant unionid in Hooksett Pool, and a sphaeriid clam at sites with and sites without *C. fluminea* in 2014 and 2016. Although differences among years were seen in native bivalve density, lack of a significant difference between sites with and without Asian clams supported that in 2014 and again in 2016 the presence *vs.* absence of *C. fluminea* had no impact on native bivalve densities. Size-frequency of *E. complanata* was also compared between sites with and without *C. fluminea* and no difference was observed. Native bivalve density was unaffected by presence of *C. fluminea* and *E. complanata* size-frequency distribution was similar between sites with and those without *C. fluminea*. However, *E. complanata* is the most widespread, ubiquitous, and common unionid species in New England and the effects of *C. fluminea* on rare species of Unionidae may

differ. Nonetheless, the frequently high abundances reached by *C. fluminea* has led to the supposition that *C. fluminea* may have greater impacts on native bivalves than any other nonindigenous species except for the zebra mussel, *Dreissena polymorpha* (Pallas, 1771) (Strayer 1999). This purported impact is generally thought to happen through competition (*e.g.,* depletion of phytoplankton and pedal feeding food resources, and space utilization/reduction); ingestion of sperm, glochidia and juveniles; and ammonia production and oxygen consumption following mass mortality events (see Strayer 1999 and references therein). However, Leff et al. (1990) found that while *C. fluminea* appeared to cause localized reduction of seston and rapidly cleared the sediment boundary layer of food, there was no evidence of a negative impact on the distribution of the native *E. complanata*. Similarly, in this study *C. fluminea* and native bivalves were abundant at the same sites and no effect of *C. fluminea* presence on native bivalve abundance was seen. Such overlapping distributions at sites with relatively high *C. fluminea* abundances suggest the clams are not crowding out native bivalves, and ammonia and oxygen consumption following die-offs appears to have not been an issue. Similarly, if *C. fluminea* were affecting native unionid bivalves through competitive interactions, a difference in population size structure between stations with and without *C. fluminea* might be expected. Competitive interactions through feeding would tend to lead to reduced growth and an overall smaller shell size-frequency distribution. Conversely, ingestion of sperm, glochidia or juveniles would tend towards a larger shell size-frequency distribution. Because *E. complanata* size-frequency distributions were not different between sites with and without *C. fluminea,* neither competition through feeding activities nor consumption of sperm and propagules seem to be affecting this native unionid.

As *C. fluminea* spread into previously unoccupied areas, the impacts, if any, that *C. fluminea* may have on indigenous benthic communities continues to be of concern. Before and after *C. fluminea* establishment, and presence *vs.* absence studies combined with community metrics provide strong evidence for assessing the ecological impact of *C. fluminea* establishment on indigenous macroinvertebrate communities. Clearly, in Hooksett Pool the presence of nonindigenous *C. fluminea* is not having negative consequences on the indigenous benthic macroinvertebrates or native bivalves as demonstrated through density and various community metrics. Indeed, *C. fluminea* may be beneficial to the native invertebrates through ecosystem engineering leading to more habitat heterogeneity, refugia from predators and abiotic stress, fluid transport and organic matter accumulation, and sediment reworking (see Gutiérrez et al. 2003; Sousa et al. 2009 and references therein). Nonetheless, Sousa et al. (2009) rightly point out that beneficial effects on some species may mask negative consequences experienced by declines in other species. However, similar or improved HBI metrics and the inability of community similarity indices to

separate communities with *C. fluminea* in this study indicate this is not the case in Hooksett Pool. Nonindigenous *C. fluminea* may not have the negative impacts on benthic macroinvertebrate communities as was once thought and, in some cases, may be having beneficial effects on the communities. Invasivity inherently implies that the nonnative species is causing harm to the indigenous community. Lacking any evidence of harm to the indigenous benthic invertebrate community, the Asian clam in the Merrimack River may not therefore be an invasive species *per se*, but may simply be an addition to the indigenous community.

Acknowledgements

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