Oecologia (2015) 178:1159–1168
DOI 10.1007/s00442-015-3310-x

POPULATION ECOLOGY - ORIGINAL RESEARCH

The role of host abundance in regulating populations of freshwater mussels with parasitic larvae

Wendell R. Haag[1] · **James A. Stoeckel**[2]

Received: 18 July 2014 / Accepted: 19 March 2015 / Published online: 14 April 2015

Abstract Host–parasite theory makes predictions about the influence of host abundance, competition for hosts, and parasite transmission on parasite population size, but many of these predictions are not well tested empirically. We experimentally examined these factors in ponds using two species of freshwater mussels with parasitic larvae that infect host fishes via different infection strategies. For both species, recruitment and larval survival were positively related to host abundance, but there was no apparent minimum host threshold and positive population growth occurred when an average of one fish per mussel was present. Recruitment increased rapidly with an initial increase in host abundance but appeared to approach an asymptote at moderate host abundance. Recruitment and larval survival did not differ according to whether mussel species occurred alone or in combination, providing no evidence for competition for hosts via acquired immunity. However, larval survival of the species that attracts hosts with a lure was higher than the species that infects hosts passively, but lower survival of the latter strategy was offset by higher fecundity, which resulted in comparable recruitment between the two species. The lack of evidence for competition for hosts or host saturation suggests that mussel recruitment is limited primarily by fecundity and larval transmission efficiency. Despite the lack of a minimum host abundance threshold, high variation in recruitment in all treatments suggests that population growth at low host abundance is limited by stochasticity. These results show that host–parasite interactions in natural situations may differ substantially from predictions based on models or laboratory findings.

Keywords Recruitment · Acquired immunity · Competition · Frequency-dependent transmission · Fecundity

Introduction

The abundance of parasites is regulated to a large degree by the abundance of their hosts. Persistence of parasite populations depends on a minimum host abundance threshold below which there is a low probability of transmission to hosts, and parasite abundance is expected to increase with increased host availability (Anderson and May 1978; Holt et al. 2003). These relationships are often non-linear, and parasite abundance may reach an asymptote as host carrying capacity is reached or when transmission is maximized (Arneberg et al. 1998). Many other factors mediate host–parasite relationships. Transmission strategies that are density-independent (e.g., frequency-dependent transmission; see below) can substantially lower persistence thresholds compared with density-dependent strategies (Ryder et al. 2007). The degree of specialization in host use can influence parasite population size with generalists often being more abundant or more widespread (Garnick 1992).

Communicated by Steven Kohler.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3310-x) contains supplementary material, which is available to authorized users.

✉ Wendell R. Haag
whaag@fs.fed.us

[1] Center for Bottomland Hardwoods Research, US Forest Service, Oxford, MS 38655, USA

[2] School of Fisheries, Aquaculture, and Aquatic Science, Auburn University, 203 Swingle Hall, Auburn, AL 36849, USA

Parasite fecundity can influence population dynamics in complex ways depending on parasite life history and virulence (Kaitala et al. 1997). Finally, many hosts harbor multiple parasite species, and competitive interactions between parasites can alter population dynamics (Pederson and Fenton 2007).

Freshwater mussels (order Unionoida) are a diverse and important component of freshwater ecosystems worldwide. They are unique among bivalves in having larvae (glochidia) that are obligate parasites on fishes. Metamorphosis from the larval stage to free-living juveniles occurs while glochidia are encapsulated on fishes (typically lasting 2–6 weeks) and is dependent on acquisition of nutrients from the host (Barnhart et al. 2008). Host specificity varies among species from generalists to specialists that can metamorphose on only one or a few closely related species. Mussels transmit glochidia to fishes with an array of strategies that reflect patterns of host use (Haag 2012). Many generalists release glochidia in mucus webs that entangle fishes indiscriminate of species. In contrast, most specialists have strategies that target feeding or other behaviors of their hosts. One such strategy is the display of lures consisting of modifications of the mantle of females. Specialists on large, piscivorous fishes have lures that resemble minnows or other large prey items, and specialists on smaller, benthic fishes have lures that resemble mayfly larvae, fish eggs, or snails. Another important feature of this relationship is that infected fishes may acquire temporary immunity to subsequent glochidial infections and thus become unavailable as hosts (Dodd et al. 2006). Acquired immunity is a common feature of parasitic relationships, and by limiting the host parasite burden, can reduce the severity of intra- or interspecific competition between glochidia or chances of host death (Brown and Grenfell 2001).

How host abundance and immune status contribute to the regulation of mussel abundance is poorly known. An epidemiological model predicted a relatively high minimum host abundance threshold for mussel population persistence followed by exponential population growth with increasing host abundance, but depending on the strength of acquired immunity, mussels could deplete the pool of suitable hosts (Strayer 2008). Another modeling study showed that competition for hosts could be intense (due presumably to acquired immunity or other immunological factors), and species with shared hosts could coexist only if their transmission efficiencies were equivalent (Rashleigh and DeAngelis 2007). The few observational studies show positive relationships between mussel and host abundance in some cases (Haag and Warren 1998; Mulcrone 2004), and fish abundance was the most important variable in explaining mussel abundance in Illinois streams (Cao et al. 2013). In the latter study, mussel abundance reached an asymptote with increasing fish abundance, but the explanatory power of fish abundance varied among mussel species suggesting that many factors influence these relationships.

Differences in transmission efficiency among infection strategies may influence mussel host–parasite relationships. Haag and Warren (1998) found a positive relationship between mussel and host abundance for some species, but they found no such relationship for specialists that use mantle lures. Frequency-dependent parasite transmission occurs via sexual contact or a vector that actively searches for hosts (Thrall et al. 1995; O'Keefe 2005). Mantle lures can be considered frequency-dependent transmission because they attract, or "search for" hosts, while release of glochidia in mucus webs is density-dependent and based on chance encounters with hosts. By releasing mussels from a density-dependent relationship with hosts, the mantle lure strategy may reduce the host abundance threshold, allowing these species to persist in habitats with low or variable fish abundance, such as headwater streams (Haag and Warren 1998).

A large body of host–parasite theory exists, but few manipulative experiments have examined these relationships in natural situations, particularly regarding interactions between parasites with shared hosts. Variation in host specificity and infection strategies makes freshwater mussels a valuable system in which to study host–parasite interactions. Freshwater mussels also are highly imperiled and their decline may be related to declines or changes in host fish assemblages. We conducted a manipulative experiment in ponds to examine the relationship between host abundance and mussel recruitment and population growth in two species that differ in host breadth, fecundity, and host infection strategy. One species was a generalist that infects fishes with a density-dependent strategy (mucus webs), and the other was a specialist that infects fishes with a frequency-dependent strategy (mantle lures). We also examined how potential competitive interactions for a shared host between these two species mediate the host–parasite abundance relationship. Specifically, we tested the following predictions:

1. When species occur alone, recruitment should be positively related to host abundance, but the host threshold should be lower for the species that infects hosts in a frequency-dependent fashion (mantle lures) than for the species with density-dependent transmission (mucus webs). When host abundance is not limiting, recruitment should be equivalent between species or should be limited only by the fecundity of each species.
2. When species occur together, each at a density equal to that in single-species ponds, we expect three possible outcomes:

(a) If acquired immunity reduces infection by glochidia of the other species but the probability of transmission (H_o) is equal between species, recruitment of each species at a given host density should be mutually inhibited such that it is about half that in single-species ponds. This is because the number of available hosts is halved due to the presence of an equal number of the competing species. Even when the number of hosts is not limiting, recruitment for each species will be lower than in single-species ponds because the number of hosts with acquired immunity is doubled, and these fishes act as a sink for glochidia.

(b) If acquired immunity exists but H_o is unequal between species, recruitment will be higher for the species with the higher H_o. We predicted that mantle lures, which attract hosts, have higher H_o than mucus webs, which rely on chance encounters with hosts.

(c) If acquired immunity does not exist, population growth of each species in mixed-species ponds should be equal to that seen in single-species ponds regardless of differences in H_o.

Materials and methods

Study system and study species

We conducted the study in twelve 0.1-ha earthen ponds at the South Auburn Fisheries Research Station (SAFRS) near Auburn, Alabama, in 2009 and 2011. All ponds were 56 × 18 m with average depth of about 1 m (maximum 2 m). Ponds were fed from a reservoir that lacks mussels, and water exited the ponds through a screened outlet. Prior to the experiments, we drained all ponds and allowed them to dry to reduce existing populations of aquatic organisms. No mussels were present prior to the experiments in most ponds, but in 2009, ponds 4 and 9 (Online Resource 1) had small numbers of *Utterbackia imbecillis* and *Corbicula fluminea*, respectively. Both species survived pond drying. A few *C. fluminea* were found in pond 9 after the experiment, and *U. imbecillis* reproduced in pond 4 and young of year (YOY) mussels were found after the experiment. *C. fluminea* does not have parasitic larvae and probably had little effect on recruitment of our test species. We assumed that *U. imbecillis* did not influence our results for two reasons. First, glochidia of *U. imbecillis* can undergo direct development in addition to parasitizing fishes (Dickenson and Sietman 2008). Second, pond 4 had the highest recruitment of either test species in the ten-fish treatment (see below), and recruitment of *U. imbecillis* was nine times higher than mean recruitment across test species at this host level. This suggests that recruitment of *U. imbecillis* occurred largely independent of fish abundance and had little effect on our test species. No bivalves other than our test species were found in any pond in 2011. We used 19-mm-mesh heavy-duty plastic netting and steel fence posts to cordon off a 12 × 18-m section at the end of each pond opposite the outflow, and experiments were conducted within this 216-m^2 area. While the ponds were dry, we buried the netting about 0.15 m to prevent escapement of fishes or mussels. This smaller enclosure allowed us to create desired conditions of fish and mussel density using fewer animals and facilitated greater sampling efficiency, but it also ensured high water quality because of circulation with the entire pond volume.

We used two mussel species in the experiments, the pondmussel, *Ligumia subrostrata*, and the giant floater, *Pyganodon grandis*. Both are adapted to lentic habitats and are common in the south central US, but their host use and infection strategies differ. Pondmussels are specialists on sunfishes (Centrarchidae) (Stern and Felder 1978; W. R. Haag, unpublished data), and attract hosts mainly by displaying mantle lures (Gascho Landis et al. 2012). The mantle lure consists of small papillae that are fluttered to reveal the gravid gills, which resemble a cluster of fish eggs; this behavior may exploit the egg-feeding behavior of sunfishes (Corey et al. 2006; Haag 2012). The floater is a host generalist whose glochidia can metamorphose on nearly any fish species; the glochidia are released in large mucus webs (Trdan and Hoeh 1982; Haag 2012). Fecundity also differs substantially between these species: average fecundity of pondmussels is about 75,000, but it exceeds 400,000 for floaters (Haag 2013). Both species are long-term brooders in which eggs are fertilized in the autumn and glochidia are brooded over the winter and released in late winter or early spring. We collected gravid females of both species in Lafayette County, Mississippi, in November and December to ensure that they were gravid but had not yet released glochidia. Mussels were held in ponds at SAFRS until initiation of the experiments; holding ponds were not used in the experiments.

We used bluegill (*Lepomis macrochirus*) as a host for mussels. Bluegill is a suitable host for both species, is easily maintained in ponds, and can be obtained from commercial hatcheries in uniformly sized lots, which minimized variation in glochidial infection due to fish size. We purchased bluegills of 8- to 15-cm total length (American Sportfish Hatchery, Montgomery, AL). We chose this size because: (1) fish were too large to escape through the netting demarcating the experimental enclosures, (2) fish were large enough to have switched from plankton feeding to benthic feeding and thus were likely to respond to mantle lures of pondmussels, and (3) using subadult fishes allowed higher stocking densities in the experimental enclosure. Bluegill reproduced in the ponds, but YOY individuals did not appear until after the main host infection period and these YOY individuals probably fed on plankton until late summer; consequently, recruitment of YOY fishes was not expected to alter host availability during the experiment.

The experiment

We used a full factorial experiment to evaluate how mussel recruitment and population growth were related to three factors: host abundance, mussel species identity, and interactions between mussel species (Online Resource 1). Four ponds were randomly assigned as pondmussel only, four were assigned as floater only, and four ponds were assigned as pondmussel + floater. In each pond, we stocked nine to ten randomly selected gravid females of the indicated species; pondmussel + floater ponds received nine to ten individuals of each species. For each set of four ponds, we randomly assigned ponds to one of four host abundances: 10, 50, 200, and 500 fish. These abundances corresponded to about 1, 5, 20, and 50 host fishes per female mussel, respectively, fish densities ranging from 463 (ten fish) to 23,148 (500 fish) fish ha^{-1}, and fish biomass of 12.4–618.1 kg ha^{-1}, based on the predicted mass of a 11.5-cm bluegill [the midpoint of the length range of fishes in our experiment (Schneider et al. 2000)].

The experiment was conducted in 2009 and repeated in 2011. In both years, we stocked bluegill from mid-December to early January and stocked mussels about 2 weeks later. We maintained bluegill on commercial fish food, fed three times weekly throughout the experiment.

Experiments were terminated in November so that YOY mussels were near maximum size for the year. Because we did not know the size range of YOY individuals, in 2009 we sampled the first few ponds with a suction dredge and processed all material across a graduated series of sieves (minimum mesh size 2.5 mm). We found no individuals less than 28-mm length, a size that is easily detected by hand sampling, and we sampled all remaining ponds in 2009 and all ponds in 2011 by feeling through the substrate with our hands. We found few dead YOY mussels by hand sampling (<1 %). In both years, we drained the ponds after sampling to retrieve remaining mussels. We allowed ponds to dry until July and searched the pond bottoms approximately monthly during this time. Most remaining mussels were recovered by the end of January, but living individuals were found as late as March, and dead shells were recovered until June. We observed minimal evidence of predation on mussels during or after the experiment, and because of the lengthy period of sampling after draining the ponds, we assumed that total counts of YOY mussels represented absolute levels of recruitment during the experiment.

We estimated fish abundance in the ponds to determine if fish densities remained constant during the experiment. After draining ponds in 2009, we counted bluegill in each pond using a cohort size method to exclude YOY fishes. Final fish densities were much lower than stocking densities in four ponds and we omitted these ponds from analysis. Omitted ponds in 2009 included the following treatment combinations: pondmussel only, 50 fish; pondmussel + floater, ten fish; pondmussel + floater, 200 fish; floater only, 200 fish (Online Resource 1). We attribute these fish losses to herons, kingfishers, and mergansers, which were often observed near the ponds. We do not know when predation occurred, but affected ponds had low recruitment, regardless of fish abundance, suggesting that substantial losses occurred during the glochidial release period. To prevent predation in 2011, we covered all ponds with 5-cm-mesh bird netting. We monitored fish abundance during the 2011 experiment by trapping instead of counting fish at the end of the experiment. Trapping showed no evidence of substantial declines in stocking densities in any pond in 2011. However, one 500 fish pond (pondmussel + floater, 500 fish) had nearly complete mussel-recruitment failure in 2011 unlike all other ponds at this host level, which had consistently high recruitment. This pond had no apparent water quality problems, but we excluded it from analyses due to its inordinate influence.

Data analysis

We combined results of the 2009 and 2011 experiments for data analysis. There was no difference in the grand mean of recruitment between years (ANOVA, log-transformed recruitment, $F_{1,22} = 0.17$, $P < 0.687$). Omitting five ponds that suffered fish predation or other anomalies (see previous) left 19 ponds and 24 recruitment observations (Online Resource 1). Sample sizes (number of recruitment observations) for main effects were five to seven for each fish abundance level, 12 for each species, and ten to 14 for mixed- and single-species treatments. We evaluated the effects of host abundance, mussel species identity, and species combination (single or mixed species) on mussel recruitment with a three-factor general linear model including all main effects, second-order interactions, and the third-order interaction. The response variable, mussel recruitment, was log transformed to meet assumptions of normality and homogeneity of variance; the independent variables species identity, host abundance, and species combination were treated as fixed class variables. Significance of all comparisons was based on type III sums of squares. Because the model provided no support for an influence of species identity or species combination (see "Results"), we omitted these factors and used the combined data set for all species and species combinations to investigate the form of the relationship between host abundance and mussel recruitment, both of which were log transformed and treated as continuous variables. We evaluated several linear and non-linear relationships based on coefficients of determination and residuals.

We also calculated population growth rate (λ year^{-1}) for all ponds based on final adult population size and the number of recruits produced. We used this measure simply as an additional way to visualize the effect of host abundance on mussel populations, but we performed no statistical tests involving λ because in our experiment it is equivalent to the magnitude of recruitment.

We also estimated glochidial survival to the YOY stage to account for differences in fecundity between the two species. We estimated fecundity of each adult female mussel stocked in the ponds using existing length–fecundity relationships (Haag 2013). Total glochidial production in each pond was then estimated as the sum of the fecundity of all individuals stocked in the pond, and proportional glochidial survival was calculated as the number of recruits ÷ total glochidial production. We evaluated the effects of host abundance, mussel species identity, and species combination on glochidial survival with a three-factor general linear model identical to that used to analyze recruitment with the exception that the response variable (survival) was logit transformed.

Results

Mussel recruitment occurred in all ponds that did not suffer fish predation or other anomalies; even in the five ponds that were omitted from the final data set, most produced some YOY individuals, and only one had complete recruitment failure (pondmussel, 50 fish, 2009). Recruits of both species reached a large size by the end of their first year, but there was a significant difference in recruit size between the two species (ANOVA, $F_{1,19} = 8.42$, $P = 0.0092$; ponds with less than five recruits omitted). Across all treatments, YOY pondmussels averaged 50.2 mm (range 28.1–69.5 mm) and floaters averaged 61.2 (35.1–87.5) mm.

Recruitment was strongly and positively related to host abundance ($F_{3,8} = 29.11$, $P < 0.0001$), but species identity and species combination were not significant factors (species identity, $F_{1,8} = 0.03$, $P = 0.8756$; species combination, $F_{1,8} = 0.41$, $P = 0.5382$; Fig. 1; Online Resource 1). The host abundance × species combination interaction was marginally significant ($F_{3,8} = 3.33$, $P = 0.0770$), but sums of squares indicated a weak influence of this model

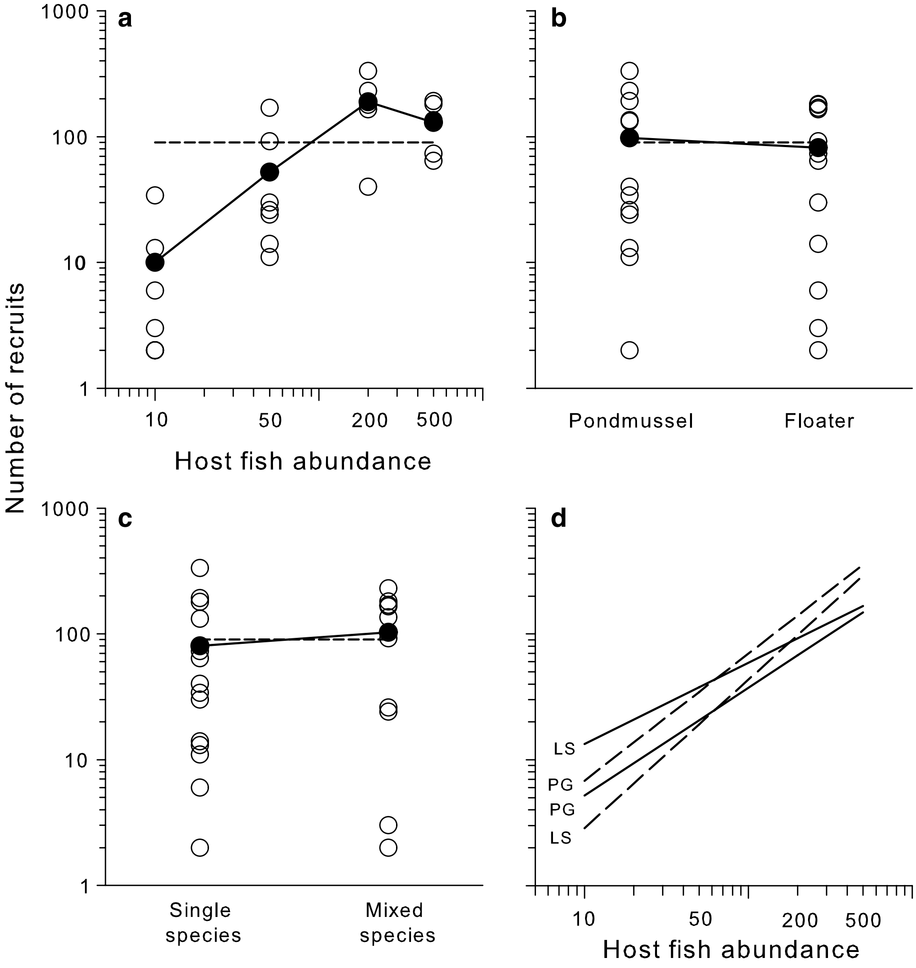

Fig. 1 **a**–**c** Main effects plots showing mussel recruitment in relation to host abundance ($n = 5$–7 for each treatment level), species identity ($n = 12$ for each species), and species combination (mixed species, $n = 10$; single species, $n = 14$). *Open circles* are results from individual ponds, and *solid circles* are means for each treatment level. *Horizontal dotted lines* are grand means across all treatment levels. **d** Interaction plot showing regression lines for each treatment combination (species identity × species combination); pondmussel (*LS*), floater (*PG*). *Solid lines* Single-species treatments, *dotted lines* mixed-species treatments

term compared to host abundance (Online Resource 1); all other interaction terms in the model were non-significant ($F = 0.96$–2.19, $P = 0.1774$–0.4591). A reduced model including only main effects similarly gave no support for an effect of species identity or species combination.

For the combined data set of all recruitment observations (both species), the linear relationship between raw recruitment and host abundance was significant, but it explained little of the variation in recruitment ($P = 0.0064$, $R^2 = 0.241$) and residual plots suggested that a curvilinear function would more accurately depict the relationship. Models using either log-transformed recruitment or log-transformed host abundance both improved model fit ($R^2 = 0.355$, 0.416, respectively), but a log–log transformation provided the best fit to the data ($P < 0.0001$, $R^2 = 0.634$, log recruitment $= 0.836 \times$ log host abundance $+ 0.02$), suggesting that the rate of increase in recruitment decreased with increasing host abundance. Residuals from this relationship were normally distributed (Shapiro–Wilk test, $W = 0.946$, $P = 0.220$), there were no influential observations (Studentized residuals between -1.451 and 1.981), and there was no evidence of heteroscedasticity (Levene's test, $F_{3,20} = 1.30$, $P = 0.3028$). Despite the overall good fit of this model, residuals suggested that it overestimated recruitment at the highest host abundance level (500 fish). A three-parameter logistic model provided further improvement in fit ($R^2 = 0.734$) and suggested that recruitment began to approach an asymptote at moderate levels of host abundance between about 50 and 200 fish and did not increase appreciably at higher host abundance (Fig. 2a).

Although there was no statistical support for a difference in the variance of recruitment across levels of host abundance sufficient to affect parametric statistical tests, coefficients of variation indicated a decrease in the variability of recruitment as host abundance increased (Fig. 2b). This pattern was the inverse of that seen for the magnitude of recruitment: variability in recruitment declined abruptly with an initial increase in host abundance but began to stabilize at a moderate level of host abundance between about 50 and 200 fish. Mean recruitment per fish also showed more variability at low host abundance. Across all host abundance levels, mussel populations produced an average of less than one recruit (0.818) per fish. However, patterns of per fish recruitment varied among host abundance levels (Fig. 2c) and suggested a decline in both the magnitude and variability in mean number of recruits per fish with increasing host abundance.

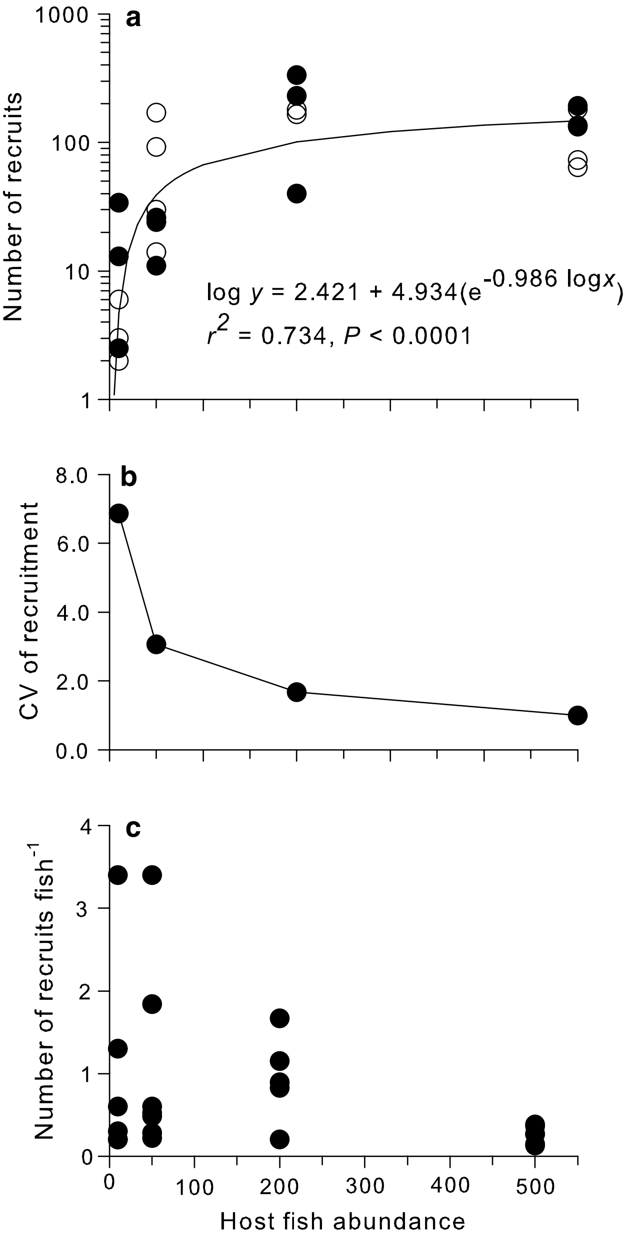

Fig. 2 **a** Three-parameter logistic model showing the relationship between host fish abundance and mussel recruitment (both mussel species combined, $n = 24$). *Solid circles* are pondmussels and *open circles* are floaters. **b** Coefficient of variation (*CV*) of recruitment in relation to host fish abundance (both species combined). **c** Number of recruits per fish in relation to host fish abundance (both species combined)

Population growth rate (λ year^{-1}) was similar for both species and was positive in all ponds. For pondmussels, λ ranged from 1.2 to 34.3, and for floaters, λ ranged from 1.2 to 19.1. Across both species, λ averaged 2.0, 6.2, 19.9, and 14.0 in 10, 50, 200, and 500 host ponds, respectively. Despite the potential for rapid population growth, survival from the glochidial stage to the recruit stage was extremely low for both species and averaged 0.00577 % across species and host abundance levels. Mean estimated individual fecundity in our study was 132,331 for pondmussels and 535,690 for floaters. Similar to recruitment, glochidial survival was strongly and positively related to host abundance

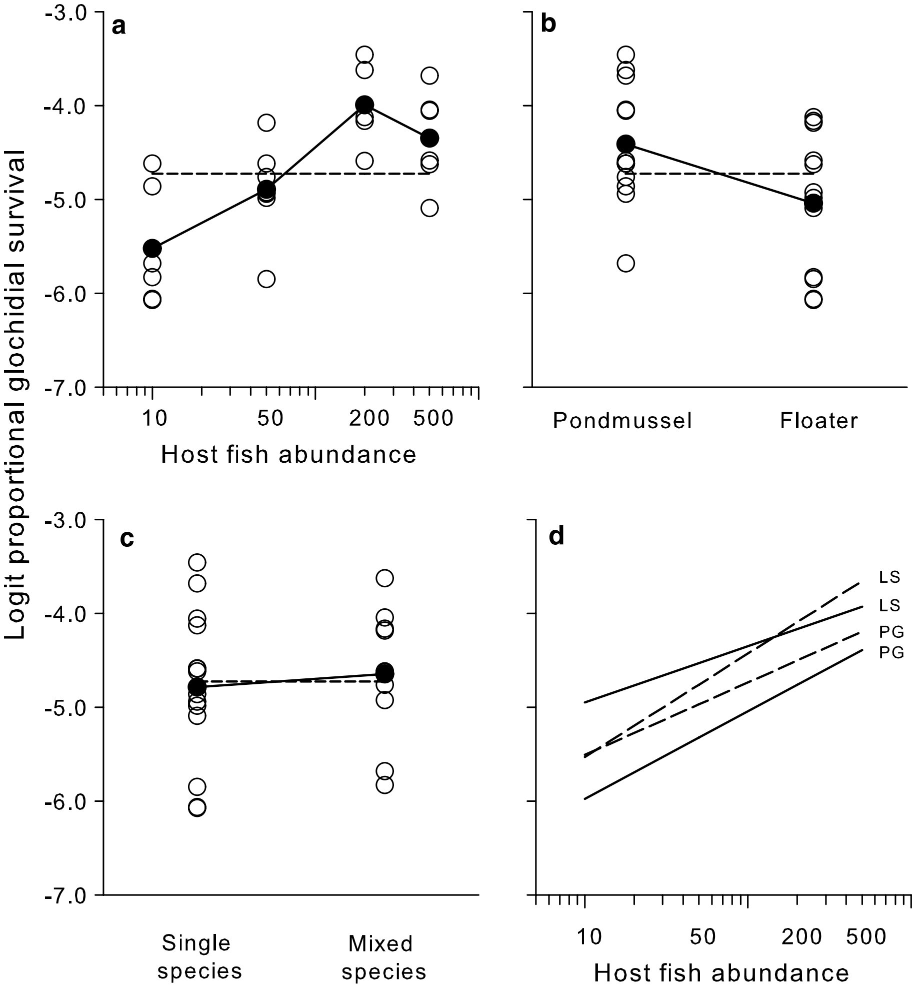

Fig. 3 **a**–**c** Main effects plots showing survival from the glochidial to the recruit stage in relation to host fish abundance ($n = 5$–7 for each treatment level), species identity ($n = 12$ for each species), and species combination (mixed species, $n = 10$; single species, $n = 14$). *Open circles* are results from individual ponds, and *solid circles* are means for each treatment level. *Horizontal dotted lines* are grand means across all treatment levels. **d** Interaction plot showing regression lines for each treatment combination (species identity × species combination). *Solid lines* Single-species treatments, *dotted lines* mixed-species treatments. For abbreviations, see Fig. 1

($F_{3,8} = 12.89$, $P = 0.0020$), but there also was a significant effect of species identity ($F_{1,8} = 7.03$, $P = 0.0292$; Fig. 3). Mean glochidial survival across host abundance levels was 0.00910 % (±0.00326 SE; range 0.00021–0.03493) for pondmussels and was 0.00245 % (±0.000824; range 0.00008–0.00749) for floaters. There was no significant effect of species combination ($F_{1,8} = 0.28$, $P = 0.6082$), and all interaction terms were non-significant ($F = 0.67$–1.33, $P = 0.2828$–0.5915; Online Resource 1). A reduced model omitting interaction terms gave stronger support for a significant effect of host abundance ($F_{3,18} = 11.64$, $P = 0.0002$) and species identity ($F_{1,18} = 9.25$, $P = 0.0070$) but there was no effect of species combination ($F_{1,18} = 0.56$, $P = 0.4643$).

Discussion

A positive relationship between host and parasite abundance is expected intuitively and from theory, but empirical tests of this prediction have had surprisingly varied results with many showing no relationship or even a negative relationship (e.g., Haukisalmi and Henttonen 1990; Arneberg 2001; Stanko et al. 2006). Most of these results are from correlative field studies, and deviations from theory are explained by confounding or overriding effects of environmental factors or host attributes (e.g., body size, life cycle). Perhaps because our experimental approach reduced many of these effects, mussel recruitment was strongly and positively related to host abundance, and this relationship was best described by a curvilinear function and appeared to approach an asymptote as predicted by theory. However, specific features of this relationship were surprising, and the extent to which our results supported other predictions varied.

We found no evidence for either species of a minimum host abundance threshold. Recruitment occurred consistently and population growth was positive even at low host abundance (ten fish), corresponding to an average of only one fish per mussel. Our experiments represented a natural setting, but fishes were confined with mussels in a relatively small area and this could be partially responsible for the lack of an observed threshold. However, the range of fish densities in our ponds corresponds well with the range seen in nature. Biomass of bluegill in 219 North American lakes averaged 56.0 kg ha^{-1} and ranged from 0.2 to 657.0 kg ha^{-1} (Carlander 1955). These average and maximum values are nearly identical to those of our 50-fish (61.8 kg ha^{-1}) and 500-fish treatments (618.1 kg ha^{-1}), respectively, but biomass in our ten-fish treatment (12.4 kg ha^{-1}) was substantially larger than the minimum reported value in the wild (0.2 kg ha^{-1}). The low bluegill biomass estimates reported by Carlander (1955) are extreme values and mostly from unproductive, oligotrophic lakes, a habitat in which pondmussels do not occur. Nevertheless, these values raise the possibility that minimum host thresholds may exist in the wild for host specialists like pondmussels in some cases. Host limitation may be less likely even in the wild for generalists like floaters, which can parasitize nearly any fish species. In a survey of 31 lakes worldwide, the minimum reported fish biomass (all species) was 7.3 kg ha^{-1} in an oligotrophic lake in Canada (Randall et al. 1995). This value corresponds closely to biomass in our ten-fish treatment (12.4 kg ha^{-1}), suggesting that floaters rarely encounter lower fish densities. In general, our results show that both the mantle lure and mucus web transmission strategies can infect hosts even when host density is at the low end of the range seen in nature.

For both strategies, recruitment increased rapidly with increasing host abundance but appeared to approach an asymptote quickly; recruitment was similar between 200- and 500-fish treatments, and recruitment in several 50-fish ponds was similar to those in higher abundance treatments. The form of this relationship cannot be specified precisely because of the high variability in recruitment, but our best-fitting model suggests that transmission is inefficient relative to glochidial production and does not increase appreciably when host abundance increases beyond moderate levels. The low survivorship from the glochidial to the recruit stage also supports the inefficiency of transmission. Even in 500-fish treatments, pondmussels and floaters produced an estimated 4,000 and 10,000 glochidia per fish, respectively, but they produced only 0.31 and 0.21 recruits per fish, showing that a large excess of glochidia existed in all host abundance treatments. Part of this high mortality probably occurs during metamorphosis and in the first few months after settlement. However, natural glochidial infections on fishes often are low (see below), and metamorphosis success often exceeds 50 % (Eads et al. 2010), suggesting that failure to infect a host represents by far the largest component of early mortality regardless of host abundance.

Our results provide tentative support for the prediction that transmission efficiency of the mantle lure strategy is higher than for mucus webs. These strategies were equivalent from a recruitment and population growth perspective, but mean survival from the glochidial to the recruit stage was nearly four times higher for pondmussels than for floaters, suggesting that the mantle lure strategy of pondmussels is more efficient than release of glochidia in mucus webs. Differences in metamorphosis success on fishes between the two mussel species also could contribute to differences in glochidial survival, but we were not able to measure this in our experiment. Regardless of the mechanism, differences in glochidial survival show that floaters must devote more energy to glochidial production to maintain population growth comparable to that of pondmussels, assuming that other life history parameters that influence population growth are equal; this imbalance in reproductive investment is accentuated by the fact that floater glochidia are about 40 % larger than pondmussel glochidia (Barnhart et al. 2008). These two strategies also illustrate an important tradeoff. Release of glochidia in mucus webs typically is associated with generalist host use (Haag 2012). Despite lower glochidial survival, this strategy has the benefit of enabling infection of a wide range of hosts regardless of host attributes such as feeding behavior, and in a diverse fish assemblage this substantially increases the available host resource (see previous discussion of host density in the wild). In contrast, the mantle lure transmission strategy of specialists—although potentially more efficient—is dependent on the presence of fish species for which that strategy has evolved to target.

We also predicted that the mantle lure strategy would be of particular benefit at low host abundance, but we found no interaction between host abundance and species that would indicate this type of difference in host abundance thresholds. Rather, the lack of interaction suggested that mantle lures were associated with higher glochidial survival regardless of host abundance. Small differences in host thresholds among species could be important in long-term population dynamics, but our ability to detect such differences was limited because of high variation in recruitment within fish abundance levels. Differences also may be more apparent in the wild where host abundance is more spatially and temporally variable.

The lack of evidence for acquired immunity and competition for hosts in our experiments was particularly surprising and could be explained in at least two ways. First, floaters appeared to begin glochidial release a few weeks earlier than pondmussels; this is based on casual observations but it could have reduced the potential for competition for hosts. However, pondmussels begin displaying mantle lures and releasing glochidia at temperatures as low as 10 °C (Gascho Landis et al. 2012) and the host infection periods probably overlapped broadly between these two species. Furthermore, acquired immunity can last for at least 7 months (Dodd et al. 2006) and should have affected glochidial survival throughout our experiment. Alternatively, our results suggest that acquired immunity is not important in some natural situations. There is strong evidence for acquired immunity in the laboratory (e.g., Dodd et al. 2006), but these studies used high glochidial infection loads (mean ≈500 glochidia per fish) and multiple, successive infections to induce an immune response. In the wild, high infection loads are uncommon and most fishes often carry fewer than ten glochidia (e.g., Neves and Widlak 1988); in the laboratory, bluegill infected naturally by pondmussel glochidia carried similarly low infections with few individuals carrying high glochidial loads [mean ≈16 glochidia per fish; A. Gascho Landis, unpublished data]. These infection patterns suggest the classic overdispersion of parasite occurrence on hosts (Anderson and May 1978). Even though strong acquired immunity can be induced in the laboratory, glochidial infections high enough to induce immunity may be rare in the wild in many cases.

The lack of evidence for competition for hosts suggests that the host carrying capacity was not reached at any host abundance level. Acquired immunity or other types of host saturation at low host abundance could be invoked as an explanation for the sharp increase in recruitment that we observed between ten- and 200-fish treatments, but we found no evidence for an effect of species combination on recruitment or glochidial survival that would support such a mechanism. Furthermore, although the higher maximum number of recruits per fish at low host abundance suggests that some fishes were parasitized by glochidia from multiple mussels, the mean number of recruits per fish rarely exceeded two and was less than one in most ponds. In the laboratory, individual fishes routinely produce hundreds of mussel recruits from a single, heavy glochidial infection, and fish mortality is typically seen only at extremely high infection rates (Kaiser 2005; Howerth and Keller 2006). We have no information about glochidial burdens carried by individual fishes, but our results suggest that most fishes in our experiment carried burdens far lower than their carrying capacity, and hence, density-dependent effects such as host saturation were relatively unimportant.

The high variation in recruitment in all treatments shows that host infection has a large random component even in the relatively static conditions of our ponds. The higher variability at low host abundance suggests that stochastic processes are particularly important when hosts are rare. Although mussels successfully infected hosts even at low host abundance, λ was as low as 1.2 in ten-fish treatments. Such low growth may not be sustainable in the face of high intrinsic variability especially when compounded by predation and environmental stochasticity. At higher host abundance, population growth also was variable but was consistently high, suggesting that rapid population growth or long-term population persistence are dependent on moderate host abundance.

Except when hosts are extirpated or extremely rare (e.g., Smith 1985; Fritts et al. 2012), host abundance and associated density-dependent effects may have little impact on mussel population size and persistence. Previous model findings showing that mussel population growth is strongly controlled by acquired immunity and host abundance (Rashleigh and DeAngelis 2007; Strayer 2008) were not supported by our results, which gave no evidence of competition for hosts and suggested that recruitment and population growth are reduced only at low host densities and are relatively insensitive to large increases in host availability. Rather, our results suggest that recruitment may be limited primarily by fecundity and glochidial transmission efficiency in addition to environmental factors. Ultimately, population growth may be influenced to a greater extent by these factors—as well as other life history traits such as age at maturity, adult survivorship, and life span (see Haag 2012)—than to host abundance in all but the most extreme cases.

Our study is the first to examine the relationship between mussel and host fish abundance experimentally, and we show that host–parasite interactions in natural situations may differ substantially from predictions based on laboratory results. Nevertheless, the existence of competition for hosts or host saturation at some level underpins many proposed mechanisms for the radiation of the North American mussel fauna and for mussel assemblage structure (Strayer 2008; Haag 2012), and these relationships should be examined in other species and ecological contexts. Pondmussels and floaters represent two broadly divergent lineages, but acquired immunity can be stronger between closely related mussel species (Dodd et al. 2005). Similarly, other host attraction strategies may be more strongly dependent on high host fish abundance [e.g., broadcast of free glochidia or conglutinates (see Haag 2012)]. Our study also occurred under conditions of low adult mussel density (~ 0.05 m^{-2}). Large, dense aggregations of mussels such as mussel beds in large rivers may have a greater potential for saturation of the local host resource and manifestation of density-dependent effects such as acquired immunity. However, fish populations in large rivers are correspondingly larger, and mussel beds may be limited by disturbance or even physical space (Vannote and Minshall 1982; Strayer 1999) before host limitation occurs. The relative importance of these factors likely varies substantially among mussel species in accordance with the great diversity of life history and host-infection strategies seen in these animals.

Author contribution statement W. R. H. and J. A. S. contributed equally to this work.

Acknowledgments We thank S. Nichols and M. Hart, who assisted with all aspects of the experiments. We also thank the following people for their various contributions to the study: M. Bland, A. Commens-Carson, D. Foree, A. Gascho Landis, R. Kennedy, T. Mosley,

G. Moyer, I. Palmer, N. Rankin, B. Staton, and M. Warren. This study was supported by the US Forest Service, Southern Research Station.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

Anderson RM, May RM (1978) Regulation and stability of host–parasite population interactions. I. Regulatory processes. J Anim Ecol 47:219–247

Arneberg P (2001) An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. Ecography 24:352–358

Arneberg P, Skorping A, Grenfell B, Read AF (1998) Host densities as determinants of abundance in parasite communities. Proc R Soc Lond Ser B Biol Sci 265:1283–1289

Barnhart CE, Haag WR, Roston W (2008) Adaptations to larval parasitism in the Unionoida. J N Am Benthol Soc 27:370–394

Brown SP, Grenfell BT (2001) An unlikely partnership: parasites, concomitant immunity and the host defence. Proc R Soc Lond Ser B Biol Sci 268:2543–2549

Cao Y, Huang J, Cummings KS, Holtrop A (2013) Modeling changes in freshwater mussel diversity in an agriculturally dominated landscape. Freshwater Sci 32:1205–1218

Carlander KD (1955) The standing crop of fish in lakes. J Fish Res Bd Can 12:543–570

Corey CA, Dowling R, Strayer DL (2006) Display behavior of *Ligumia* (Bivalvia: Unionidae). Northeast Nat 13:319–332

Dickenson BD, Sietman BE (2008) Recent observations of metamorphosis without parasitism in *Utterbackia imbecillis*. Ellipsaria 10:7–8

Dodd BJ, Barnhart MC, Rogers-Lowery CL, Fobian TB, Dimock RV Jr (2005) Cross-resistance of largemouth bass to glochidia of unionid mussels. J Parasitol 91:1064–1072

Dodd BJ, Barnhart MC, Rogers-Lowery CL, Fobian TB, Dimock RV Jr (2006) Persistence of host response against glochidia larvae in *Micropterus salmoides*. Fish Shellfish Immunol 21:473–484

Eads CB, Bringolf RB, Greiner RD, Bogan AE, Levine JF (2010) Fish hosts of the Carolina heelsplitter (*Lasmigona decorata*), a federally endangered freshwater mussel (Bivalvia: Unionidae). Am Malacol Bull 28:151–158

Fritts AK, Fritts MW II, Peterson DL, Fox DA, Bringolf RB (2012) Critical linkage of imperiled species: Gulf sturgeon as host for purple bankclimber mussels. Freshwater Sci 31:1223–1232

Garnick E (1992) Niche breadth in parasites: an evolutionarily stable strategy model, with special reference to the protozoan parasite *Leishmania*. Theor Popul Biol 42:62–103

Gascho Landis AM, Mosley TL, Haag WR, Stoeckel JA (2012) Effects of temperature and photoperiod on lure display and glochidial release in a freshwater mussel. Freshwater Sci 31:775–786

Haag WR (2012) North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, Cambridge

Haag WR (2013) The role of fecundity and reproductive effort in defining life history strategies of North American freshwater mussels. Biol Rev 88:745–766

Haag WR, Warren ML Jr (1998) Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. Can J Fish Aquat Sci 55:297–306

Haukisalmi V, Henttonen H (1990) The impact of climatic factors and host density on the long-term population dynamics of vole helminthes. Oecologia 83:309–315

Holt RD, Dobson AP, Begon M, Bowers RG, Schauberet EM (2003) Parasite establishment in host communities. Ecol Lett 6:837–842

Howerth EW, Keller AE (2006) Experimentally induced glochidiosis in smallmouth bass (*Micropterus dolomieu*). Vet Pathol 43:1004–1007

Kaiser BE (2005) The effects of glochidiosis on fish respiration. Master thesis, Missouri State University, Springfield, MO

Kaitala V, Heino M, Getz WM (1997) Host parasite dynamics and the evolution of host immunity and parasite fecundity strategies. Bull Math Biol 59:427–450

Mulcrone RS (2004) Incorporating habitat characteristics and fish hosts to predict freshwater mussel (Bivalvia: Unionidae) distributions in the Lake Erie drainage, Southeastern Michigan. PhD dissertation, University of Michigan, Ann Arbor, MI

Neves RJ, Widlak JC (1988) Occurrence of glochidia in stream drift and on fishes of the Upper North Fork Holston River, Virginia. Am Midl Nat 119:111–120

O'Keefe KJ (2005) The evolution of virulence in pathogens with frequency-dependent transmission. J Theor Biol 233:55–64

Pederson AB, Fenton A (2007) Emphasizing the ecology in parasite community ecology. Trends Ecol Evol 22:133–139

Randall RG, Kelso JRM, Minns CK (1995) Fish production in freshwaters: are rivers more productive than lakes? Can J Fish Aquat Sci 52:631–643

Rashleigh B, DeAngelis DL (2007) Conditions for coexistence of freshwater mussel species via partitioning of fish host resources. Ecol Model 201:171–178

Ryder JJ, Miller MR, White A, Knell RJ, Boots M (2007) Host–parasite population dynamics under combined frequency- and density-dependent transmission. Oikos 116:2017–2026

Schneider JC, Laarman PW, Gowing H (2000) Length–weight relationships. In: Schneider JC (ed) Manual of fisheries survey methods II, chap 17. Michigan Department of Natural Resources, Fisheries special report 25. Michigan Department of Natural Resources, Ann Arbor, MI (not consecutively paginated)

Smith DG (1985) Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut river system. Freshwater Invertebr Biol 4:105–108

Stanko M, Krasnov BR, Morand S (2006) Relationship between host abundance and parasite distribution: inferring regulating mechanisms from census data. J Anim Ecol 75:575–583

Stern EM, Felder DL (1978) Identification of host fishes for four species of freshwater mussels (Bivalvia: Unionidae). Am Midl Nat 100:233–236

Strayer DL (1999) Use of flow refuges by unionid mussels in rivers. J N Am Benthol Soc 18:468–476

Strayer DL (2008) Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press, Berkeley

Thrall PH, Biere A, Uyenoyama MK (1995) Frequency-dependent disease transmission and the dynamics of the *Silene–Ustilago* host–pathogen system. Am Nat 145:43–62

Trdan RJ, Hoeh WR (1982) Eurytopic host use by two congeneric species of freshwater mussel (Pelecypoda: Unionidae: *Anodonta*). Am Midl Nat 108:381–388

Vannote RL, Minshall GW (1982) Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. Proc Natl Acad Sci USA 79:4103–4107