



Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes

James R. Vonesh, Johanna M. Kraus, J. Shoshana Rosenberg and Jonathan M. Chase

J. R. Vonesh (jrvonesh@vcu.edu), J. S. Rosenberg and J. M. Chase, Tyson Research Center, Washington University in Saint Louis, 6750 Tyson Valley Rd., Eureka, MO 63025, USA. JMC also at: Dept of Biology, Washington Univ. in Saint Louis Campus Box 1229, One Brookings Drive, St. Louis, MO 63130-4899, USA. – J. M. Kraus and JRV, Dept of Biology, Trani Center for Life Sciences, Virginia Commonwealth Univ., 1000 West Cary Street, Richmond, VA 23284-2012, USA.

Top predators are known to play an important role in the assembly of communities via two mechanisms: (1) by altering the colonization (or emigration) patterns of prey through behavioral habitat selection, and (2) by altering vital rates (e.g. mortality, birth) of prey after colonization. While both these mechanisms act to determine assembly, research has focused on either their combined overall effects (confounding them), or examined them singly. As a result, it remains unclear how these mechanisms act to sequentially shape community structure. In this study, we experimentally disentangle habitat selection and post-colonization effects of predaceous fish to test their independent and combined influence on the assembly of insect and larval amphibian communities in experimental freshwater habitats. Specifically, we ask, ‘do the behavioral choices of colonists continue to structure aquatic communities even after post-colonization processes have occurred?’ Like previous studies, we found that colonization was strongly reduced by the presence of fish cues. More importantly, these effects of fish on prey colonization behavior combined independently with post-colonization processes to determine the overall effect of predators on community assembly. Although habitat selection and predation both reduced abundance and biomass of most taxa in the post-colonization communities, these factors had qualitatively different effects on aspects of trophic structure. Habitat selection altered the ratio of secondary to primary consumer abundance and biomass, while post-colonization predation drove strong trophic cascades not observed in response to habitat selection. Our results suggest that behavioral choices regarding habitat selection can have lasting and unique effects on the structure of aquatic communities.

A central challenge in community ecology is to understand how exogenous and endogenous processes combine to affect community assembly (Beylea and Lancaster 1999, Shurin and Allen 2001, Cadotte et al. 2006). Exogenous factors include dispersal (Lewin 1986, Roughgarden et al. 1987, Morin 1995), colonization (Resetarits et al. 2005), and allochthonous input (Polis et al. 1997), while endogenous factors include intrinsic birth/death processes, predation and competition (Hairston et al. 1960, Polis and Strong 1996). Many studies of community assembly have shown a strong impact of endogenous factors in determining species composition and structure of local communities (e.g. species-sorting perspective; Leibold et al. 2004). However, variation in the strength of exogenous processes across a landscape clearly can also drive variability in assembly (Caffey 1985, Polis and Strong 1996, Resetarits 2005, McCauley 2007). There is growing evidence that adaptive habitat selection (Fretwell and Lucas 1970) can be an important mechanism in producing this variation across multiple spatial scales, specifically by altering an organism’s colonization rates in habitats with varying characteristics (Wilson and Osenberg

2002, Blaustein et al. 2004, Binckley and Resetarits 2005, Resetarits et al. 2005). However, the degree to which habitat selection can structure communities post-colonization, when strong endogenous factors might be at play, is less clear.

The importance of habitat selection for community assembly depends upon how habitat selection interacts with post-colonization processes. Because colonization and post-colonization occur sequentially, the former establish the community context under which the later play out. Initial differences due to habitat selection should persist if these processes combine independently. For example, differences in abundance among habitat patches due to avoidance of a particular habitat characteristic would not change when endogenous sorting processes acted on the communities. Conversely, post-colonization processes may erase initial differences created during colonization. For example, Morin (1984) found competitive differences due to colonization order (i.e. priority effects) were erased by subsequent predation by fish. Thus, our ability to determine the role of habitat selection in structuring communities post-colonization depends fundamentally upon our

ability to disentangle the behavioral choices made during colonization from the post-colonization processes.

In lentic systems, where terrestrial or dispersing adults are often able to make choices about where to deposit their aquatic young (Chesson 1984, Resetarits and Wilbur 1989) or to colonize themselves (Resetarits 2001), both habitat selection (Resetarits et al. 2005) and post-colonization species sorting (Wellborn et al. 1996) are strongly impacted by predatory fish. For example, abundance and diversity of aquatic beetles have been shown to be up to 80% lower in aquatic communities containing caged (non-lethal) fish due to habitat selection (Binckley and Resetarits 2005). Because responses to predator cues can vary among colonizing taxa and trophic levels (Åbjörnsson et al. 2002, Binckley and Resetarits 2005), effects of fish on habitat selection also have the potential to alter species interactions and food web structure, although not much data has been collected to test this prediction. Post-colonization predation by fish or the threat of it (i.e. subsequent non-consumptive effects; Preisser et al. 2005) can also have large impacts on species abundance, species interactions and aquatic community structure, and because predatory fish have a tendency to show size- or species-specific preferences for prey (Brooks and Dodson 1965, McPeck 1998, Zimmer et al. 2002, Garcia and Mittelbach 2008), post-colonization effects of fish can also impact food web structure. Wellborn et al. (1996) suggest that habitats containing predatory fish will be dominated by small, inactive prey because of predation pressure on invertebrate top predators and large, active prey.

Despite the importance of habitat selection and post-colonization responses to fish for community assembly, previous studies simultaneously examining their impacts are limited because they do not employ an experimental design that enables them to disentangle these effects (Åbjörnsson et al. 2002, Garcia and Mittelbach 2008). Here we use a two-step experiment to examine how habitat selection in response to fish determines community structure in the context of subsequent post-colonization effects of predators. Specifically, we examined the effects of colonization and oviposition behavior by insects and amphibians on lentic communities in the presence/absence of green sunfish *Lepomis cyanellus* relative to when the cues that elicit these behaviors were experimentally eliminated. We manipulated the presence of non-lethal caged fish in pools to quantify shifts in habitat selection due to fish cues. Colonists and eggs from these pools were then transferred regularly (i.e. enabling us to manipulate the effect of habitat selection on colonization and oviposition) to post-colonization treatment pools in which we manipulated free-roaming (i.e. potentially lethal) fish. By experimentally isolating the behavioral effect of habitat selection from post-colonization effects on community assembly, this design allows us to answer the questions: 1) do initial behavioral choices that occur during colonization fundamentally alter post-colonization community structure (compared to communities formed independently of those choices)? 2) Are differences in initial communities resulting from habitat selection modified by the post-colonization effects of a top predator? 3) How do the effects of habitat selection behavior on food webs (specifically predator-prey ratios and trophic cascades) compare with those of post-colonization effects of predation?

Material and methods

Study area and experimental design

The experiment was conducted at Washington University's Tyson Research Center near St. Louis, MO between 26 May and 6 July 6, 2006. Forty-eight 1.52 m diameter plastic wading pools were arranged in six blocks with eight pools each. Two nearby man-made ponds served as a source of colonists. Each pool received ~200 l of well water, 200 g dried oak-hickory leaf litter to provide nutrients and cover, and a 500 ml inoculum of pond water. We used a two step experimental approach to first quantify any shifts in habitat selection in response to predator cues and then to evaluate how these initial differences played out in the presence and absence of predators (Fig. 1). Each treatment consisted of a colonization pool which was shaded with fiberglass screening but open to the environment and a tightly covered post-colonization pool into which only colonists from the first pool were transferred after they

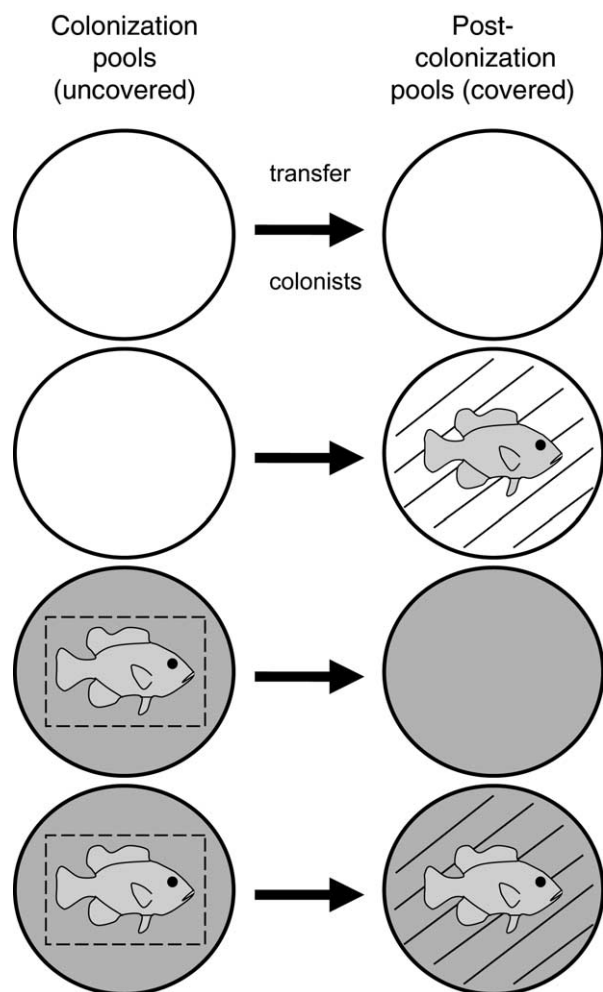


Figure 1. Experimental set-up. Colonization pools contained caged green sunfish (*Lepomis cyanellus*) or no fish, while post-colonization pools contained either a free-roaming sunfish or no fish. White circles = no caged fish during colonization, grey circles = caged fish during colonization, open circles = no free-roaming fish post-colonization, slashed circles = free-roaming fish post-colonization.

were quantified. In colonization pools, we manipulated the presence of two 'non-lethal' green sunfish, *Lepomis cyanellus* (total length (TL), mean \pm SD): 67.75 ± 15.5 mm), which were housed in 25×30 cm cages with fiberglass-covered windows to allow detection of fish chemical cues, but to prevent actual predation (empty cages and food were placed in control pools). In post-colonization pools, we manipulated the presence of two free-roaming lethal green sunfish (TL: 67.70 ± 5.61 mm). Treatments were randomly assigned within blocks. Green sunfish are effective colonizers and are common in shallow ponds, lakes and sluggish pools and backwaters of streams and rivers throughout central North America (Lee 1980, Stuber et al. 1982).

To quantify initial colonization we sampled each colonization pool twice a week for four weeks by scanning the water surface for egg clutches and larger organisms and taking seven standardized sweeps of the pool using an aquarium net (net size: 20×15.5 cm, mesh size: $400 \mu\text{m}$) to sample larvae and other smaller organisms which were identified and counted. We removed remaining colonists by continuously sweeping the pool for 3 min, and transferred the combined colonists (i.e. sample + remaining) to corresponding post-colonization pools.

At the end of four weeks, we sampled the resulting communities in the post-colonization pools. Filamentous algae were sampled by filtering 4906 cm^3 water in each pool. Periphyton was sampled from a 416-cm^2 area on submerged plastic buckets. Both types of algal samples were dried and weighed. We sampled the amphibian and insect populations using two sweeps across the entire diameter of each pool with an aquarium net (net size: 17×25 cm, mesh size: $400 \mu\text{m}$). We also spent 10 min searching for rare species not collected in the sweeps. All animals were preserved in 90% ethanol for later counting and identification, dried and weighed. Taxa were assigned to trophic groups based on taxonomic family-level generalization about feeding habits (Merritt and Cummins 1996).

Statistical analyses

We used a 2×2 factorial design to test for effects of caged fish (habitat selection, HS) and free roaming fish (predation, PR) on colonizing and post-colonization community characteristics (diversity, abundance, biomass and trophic structure). Due to low numbers, data were summed over time instead of being treated as repeated measures (i.e. replicate = pool). We tested both communities (Colonizing and Final) for main effects of HS, PR and the interaction among these treatments. Since initial communities were not yet exposed to lethal free roaming predators, a main effect of PR in the colonizing community would indicate bias in the original tank assignment (we found none). A main effect of HS in the initial communities indicates a non-lethal effect of fish on habitat selection. Main effects of HS and PR in the final communities are interpreted respectively as persistent effects of the behavioral response to the caged predator in pools containing either a free roaming fish or no fish and total effects (i.e. consumptive and non-consumptive) of fish on post-colonization community composition.

All data were analyzed using a generalized linear mixed model approach (GLIMMIX in SAS 9.2). GLMMs fit

statistical models to data using maximum and pseudo-likelihood where the error distribution is not necessarily normal and the model contains random effects (Pinheiro and Bates 2000, Venables and Ripley 2002). For count data we assumed Poisson error distribution unless data were over dispersed, in which case models were fit assuming a negative binomial error distribution (White and Bennetts 2005, Ver Hoef and Boveng 2007), while biomass and taxa density data or their square-root transformations were analyzed assuming a normal error distribution. Block was included in the model if it increased overall fit. All pairwise comparisons were tested using Tukey's test of honestly significant differences (HSD). Taxa richness was estimated using sample-based rarefaction scaled to abundance using EcoSim (Gotelli and Entsminger 2007) to make pair-wise comparisons between treatments at a common abundance (Magurran 2004).

Results

The presence of caged green sunfish had a dramatic effect on oviposition and colonization of pools. Pools without fish received nearly seven times more colonists (i.e. eggs, larvae and adults) as those with fish ($F_{1,20} = 20.98$, $p < 0.001$, Fig. 2a, Appendix 1, Table A1). The most common groups of taxa that oviposited in these pools all tended to avoid fish, including *Culex* and *Anopheles* mosquitoes, chironomid midges, and grey treefrogs (*Hyla chrysoscelis*), (Appendix 1, Fig. A1). Other taxa (e.g. adult hydrophilid beetles) showed similar patterns of abundance, but numbers were too small for separate statistical analyses (Appendix 1, Table A1). Although they avoided fish, these taxa have been found in both fishless and fish ponds in an independent survey of natural ponds within the region (Chase unpubl.). The composition of taxa sampled from pools with and without caged fish was somewhat similar: 75% of the taxa overlapped among HS treatments (compared with 97% overlap within treatments). Taxa density (i.e. number of taxa samples not corrected for abundance, sensu Gotelli and Colwell 2001) was also nearly twice as high in fishless pools ($F_{1,15} = 24.96$, $p < 0.001$, Fig. 2c). However, when the influence of abundance was controlled through rarefaction, pools with and without fish had similar richness: number of taxa in fish treatments fell within the 95% CI of no fish treatments at the same abundance level (Appendix 2, Fig. A2a).

In post-colonization communities, both habitat selection and subsequent predator effects reduced total abundance (HS: 56% of controls, $F_{1,15} = 19.87$, $p < 0.001$; PR: 80%, $F_{1,15} = 53.02$, $p < 0.001$, Fig. 2b), biomass (HS: 80%, $F_{1,15} = 5.99$, $p = 0.03$; PR: 92%, $F_{1,15} = 49.73$, $p < 0.001$, Fig. 2e), and taxa density (HS: 19%, $F_{1,15} = 4.54$, $p = 0.05$; PR: 41%, $F_{1,15} = 28.36$, $p < 0.001$; Fig. 2d). Overall, there was no interaction between habitat selection and subsequent predator effects on these measures (abundance: $p = 0.14$, biomass: $p = 0.85$, richness: $p = 0.49$); however, we included the interaction term in subsequent taxon-specific analyses because it was part of our initial design. In addition, including block improved the fit of model for total abundance, biomass and taxa density driven primarily by spatial heterogeneity in colonization by

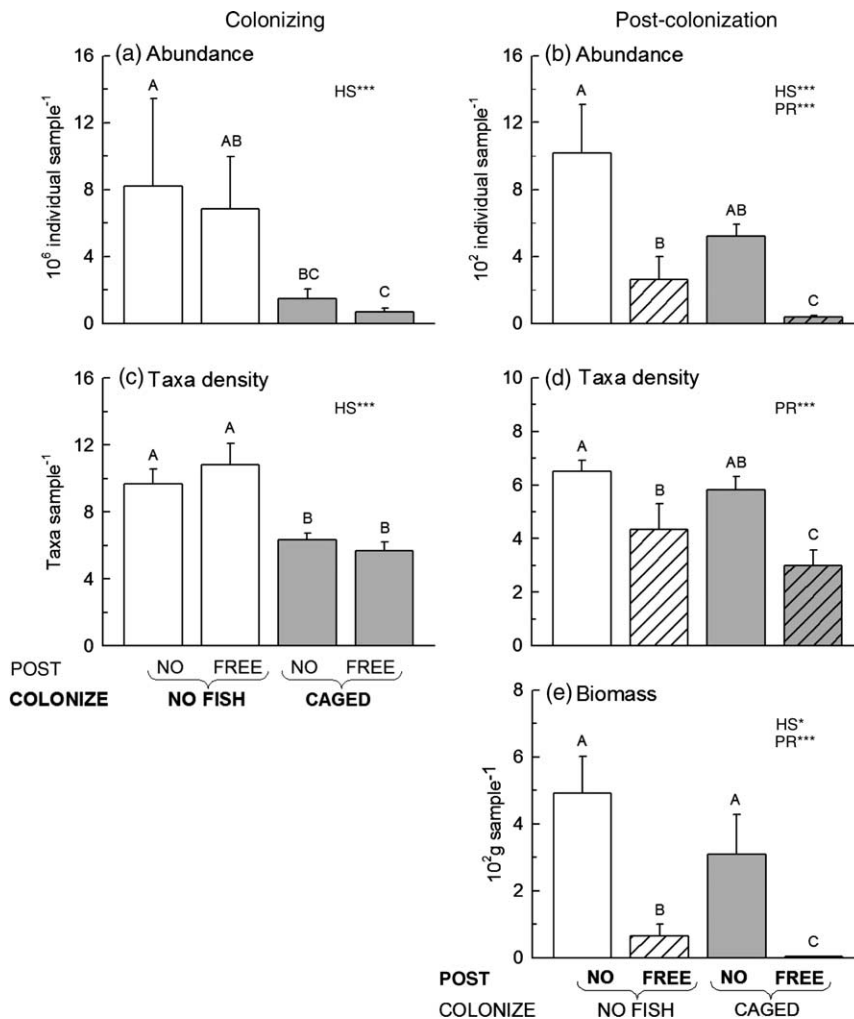


Figure 2. Community-wide response (mean \pm 1 SE) to predators during colonization (left, $n = 12$) and post-colonization (right, $n = 6$): (a) number of individuals (eggs, larvae and adults) sampled colonizing pool⁻¹, (b) number of individuals (eggs, larvae and adults) sampled final pool⁻¹, (c) no. of taxa sampled colonizing pool⁻¹, (d) no. of taxa sampled final pool⁻¹, (e) colonist biomass (10² g sample⁻¹) final pool⁻¹. For all graphs, dipteran egg masses were counted and converted to individual egg numbers using 150 eggs clutch⁻¹ for Culicidae and 1000 eggs clutch⁻¹ for chironomids (Vonesh unpubl.). White bars = no caged fish, grey bars = caged fish, open bars = no free-roaming fish, slashed bars = free-roaming fish. PR = main effect of free-roaming predators in post-colonization pools. HS = main effect of habitat selection in post-colonization community in response to caged fish in initial community. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Labels indicate statistically different treatments (Tukey LSD, $p < 0.05$).

chironomids and *H. chrysoscelis*. The relative effects of habitat selection and predation at the community-level are generally echoed in the responses of individual taxa for which there were sufficient data to conduct statistical analyses (Appendix 1, Fig. A1). Finally, identity of taxa sampled from pools with a history of caged fish was somewhat similar to those sampled in pools without this history: 83% of the taxa overlapped between HS and No HS treatments. In contrast, free swimming fish led to taxa sorting post-colonization: only 50% of taxa were found in pools with and without free-swimming fish.

Both habitat selection and predation altered trophic structure in post-colonization communities (Fig. 3, 4). Free roaming fish reduced abundance and biomass of primary consumers (included Anura: Hylidae, *Hyla chrysoscelis*; Diptera: Chironomidae, Culicidae, *Anopholes* sp., *Culex* sp.; Ephemeroptera: Baetidae, Pulmonata: Physidae,

Physella sp., Planorbidae; abundance: $F_{1,15} = 19.03$, $p < 0.001$; biomass: $F_{1,15} = 46.94$, $p < 0.001$; Fig. 3c-d) and predators (included Coleoptera: Hydrophilidae; Diptera: Chaoboridae, *Chaoborus* sp., Tipulidae, Ceratopogonidae, *Bezzia* sp., Stratiomyidae, *Odontomyia* sp.; Hemiptera: Gerridae; Megaloptera: Corydalidae; abundance: $F_{1,15} = 53.23$, $p < 0.001$; biomass: $F_{1,15} = 19.96$, $p < 0.001$; Fig. 3a-b). Habitat selection, on the other hand, reduced primary consumer abundance and biomass (abundance: $F_{1,15} = 10.98$, $p = 0.005$; biomass: $F_{1,15} = 5.84$, $p = 0.03$) but did not affect secondary consumers (abundance: $F_{1,15} = 0.04$, biomass: $F_{1,15} = 2.69$, $p > 0.05$). As a result, the proportional abundance of secondary to primary consumers is on average five times higher ($F_{1,20} = 8.74$, $p = 0.007$) and biomass thirteen times higher in the post-colonization community ($F_{1,20} = 10.89$, $p = 0.003$) due to initial habitat selection (Fig. 3e-f). In contrast, post-

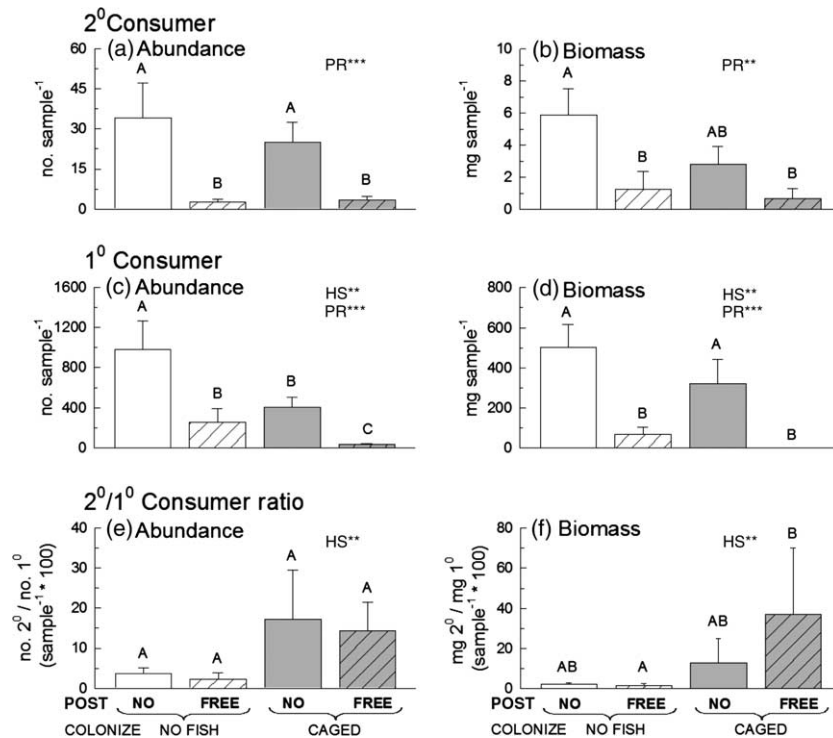


Figure 3. Numerical (mean \pm 1 SE no. sample⁻¹) and biomass (mean \pm 1 SE mg sample⁻¹) response of (a–b) 2° consumers, (c–d) 1° consumers, (e–f) and the ratio of 2° to 1° consumers (units = ratio sample⁻¹ \times 100) to fish and history of fish (habitat selection) in post-colonization communities. 2° consumers include predaceous colonists, 1° consumers include herbivores and detritivores (see text for list of taxa included in each category). Bar shading, letters, and replicates as in Fig. 2.

colonization predation had no effect on the consumer ratio (abundance: $F_{1,20} = 0.35$, $p = 0.56$, biomass: $F_{1,15} = 2.33$, $p = 0.15$).

Habitat selection, predation and their interaction all significantly affected the abundance of herbivores (i.e. all primary consumers except Chironomidae were included, see above) in final pools (HS: $F_{1,20} = 23.98$, $p < 0.001$; PR $F_{1,20} = 53.11$, $p < 0.001$; HS \times PR: $F_{1,20} = 11.50$, $p = 0.003$; Fig. 4a). However, only the presence of predators post-colonization significantly reduced herbivore biomass (PR: $F_{1,15} = 47.26$, $p < 0.001$; Fig. 4b). Post-colonization predation also increased the standing biomass of periphyton by 392% ($F_{1,15} = 14.51$, $p = 0.002$; Fig. 4d) and filamentous algae by 1549% ($F_{1,15} = 10.73$, $p = 0.005$; Fig. 4c). Habitat selection, in contrast, had a marginal effects on filamentous algae ($F_{1,20} = 3.14$, $p = 0.09$) and had no effect on periphyton ($F_{1,15} = 0.04$, $p = 0.84$).

Discussion

Consistent with previous studies, we observed large, community-wide shifts in colonization due to habitat selection in response to fish predators. Pools with caged predators received 86% fewer colonists (i.e. eggs and adults) representing 30% fewer taxa than pools without predators. Previous studies have reported a similar reduction in abundance and taxa density in response to predator cues (Binckley and Resetarits 2005) while others found no such effect (Åbjörnsson et al. 2002, Eitam et al. 2002). In our

case, when the influence of abundance was controlled through rarefaction, pools with and without fish had similar richness during colonization. Thus, the differences in the number of taxa observed appeared to be driven by colonization rates (i.e. changes in abundance) rather than changes in richness per se. Since previous studies did not account for differences in abundance among treatments, it is unclear whether differences they found (or lack thereof) in taxa density also simply arose due to differences in colonization rates among treatments.

While a growing number of studies have documented such large shifts in habitat selection in response to predator cues, few have explicitly examined if initial differences in the colonizing community have consequences for aquatic community structure after exposure to the subsequent effects of predators post-colonization. Interestingly, we found that initial differences in colonization and oviposition habitat selection persisted to the end of the study. Habitat selection lowered final abundance by 56% and biomass by 80% in the post-colonization community and marginally reduced the number of taxa sampled by 19%. These effects of habitat selection per se on final communities were qualitatively similar to those of subsequent exposure to free-roaming predators (i.e. both types of effects reduced). However, post-colonization effects of fish were 60 to 200% larger than those of habitat selection: the presence of fish in post-colonization communities reduced abundance by 80%, biomass by 92%, and taxa density by 41%. While the magnitude of habitat selection and post-colonization predator effects may vary among taxa (e.g.

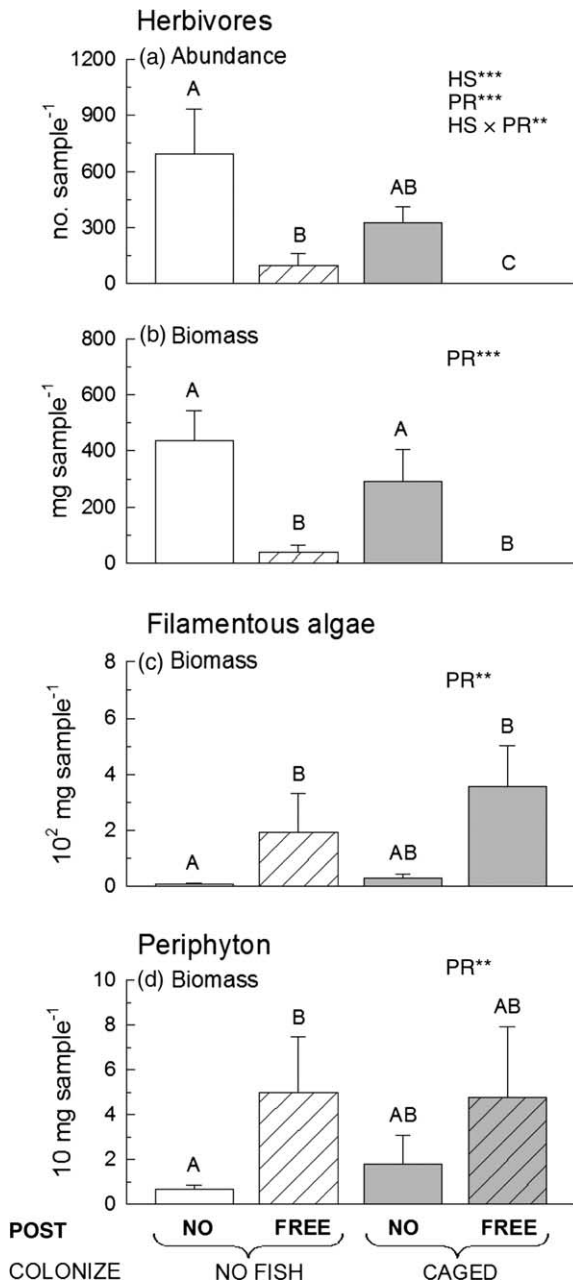


Figure 4. Habitat selection and post-colonization effects of fish on post-colonization (a) abundance (mean \pm 1 SE no. sample⁻¹) and (b) biomass (mean \pm 1 SE mg sample⁻¹) of herbivores pool⁻¹, and their cascading effects on standing biomass of (c) filamentous algae (100 mg sample⁻¹) and (d) periphyton (10 mg sample⁻¹). Bar shading, letters, and replicates as in Fig. 2.

novel predators to which the prey are naïve; Salo et al. 2007) or environmental context (e.g. habitat complexity, number of refugia), an important point from this study is that the effects of habitat selection persisted even in the presence of strong post-colonization effects. This pattern may be due to the fact that, with one exception (herbivore abundance), post-colonization effects of fish on the aquatic community (i.e. taxa abundance, biomass and richness) were independent of the effects of habitat selection. Thus, with respect to these community attributes, fish effects on

colonization tended to reinforce the post-colonization effects of fish predators.

While the effects of habitat selection and post-colonization predators on abundance, biomass and diversity were qualitatively similar, their effects on other aspects of food web structure in the post-colonization communities differed (specifically, consumer ratios and trophic cascades). Habitat selection strongly shifted the relative abundance and biomass of consumers in post-colonization communities towards secondary consumers by reducing primary consumer abundance and biomass. In contrast, free-roaming fish predators reduced both abundance and biomass of secondary and primary consumers and had no effect on consumer ratios. These food webs, characterized by relatively greater secondary consumer abundance and/or biomass, may experience higher levels of intraguild interactions (e.g. competition, intraguild predation) with potential consequences for food web stability (McCann and Hastings 1997, Vandermeer 2006) and higher levels of indirect effects of predators on basal resources via intermediate consumers (Finke and Denno 2005). Thus, in this regard, initial habitat selection altered a basic element of aquatic food web structure by altering consumer ratios (Elton 1927). Åbjörnsson et al. (2002) also observed a strong effect of predator cues on consumer ratios, but in their case the abundance and biomass of secondary consumers shifted with no response among primary consumers in communities sampled after three months. In other words, habitat selection appears to have resulted in communities with relatively fewer (not more) predators. We think the differences between our studies likely arise from differences in the pool of colonizing species. Our most numerically dominant predator were small (but active) fly larvae (*Chaoborus*), whereas their pools supported much greater abundance of larger, pelagic adult backswimmers (Hemiptera: Notonectidae) and aquatic beetles (i.e. more likely food for fish).

Although habitat selection altered consumer ratios, it had little effect on trophic cascades within the post-colonization communities: the moderate effect of habitat selection on herbivore abundance had marginal effects on algal biomass. In contrast, free-roaming fish predators had large cascading effects on resource abundance. Free-roaming fish reduced herbivore abundance and biomass by >80% compared to fishless pools. In addition, fish in post-colonization pools may have reduced or otherwise altered foraging activity of herbivores (Peacor and Werner 1997, Luttbegg et al. 2003, Schmitz 2008) and increased nutrient recycling rates (Glaholt and Vanni 2005). While our study design was not intended to separate these direct and indirect kinds of post-colonization fish predator effects, collectively they resulted in a trophic cascade that increased the standing biomass of periphyton and filamentous algae by approximately 400 and 1500%, respectively. This pattern suggests that the post-colonization effects of fish on herbivore biomass, apparently by consuming or behaviorally reducing feeding of larger herbivores, was a stronger driver of rates of herbivory than a reduction in the numbers of herbivores due to habitat selection. Stav et al. (2000) observed similar results: lethal predators elicited a strong trophic cascade while shifts in habitat selection alone did not affect the standing stock of algae. Thus, while habitat

selection and subsequent predation were qualitatively similar in their effects on abundance, diversity, and biomass, each factor also affected aquatic communities in unique ways, increasing the diversity of top predator effects on aquatic communities beyond that of either process alone.

The roles of endogenous and exogenous processes in shaping community assembly is an old and ongoing debate in ecology. While the importance of predation in organizing lentic communities is widely acknowledged, most studies have focused on the effects of predators on post-colonization species sorting processes. Recent studies have highlighted that oviposition and colonization site selection in response to predator cues may also play an important role in determining the abundance and diversity of colonists (Resetarits 2001, Eitam and Blaustein 2004, Binckley and Resetarits 2005). Few studies, however, have evaluated whether these initial differences in colonization persist, or attempted to evaluate the relative importance of initial habitat selection versus post-colonization effects of predators on resultant communities. In our study, both types of processes had important effects on community assembly and structure: habitat selection and predation both reduced abundance, biomass and number of taxa, but habitat selection altered the ratio of secondary to primary consumers, while post-colonization effects of predators resulted in a trophic cascade. Thus, it is important to integrate both processes in order to understand effects of predators on community assembly and structure. While we have focused on the multiple roles of predators in community assembly, factors such as the presence of conspecifics, competitors or pathogens may interact with predators to affect both habitat selection and subsequent species sorting processes. Future studies should examine the interplay between these multiple, potentially interacting factors, to continue to construct a more holistic view of the major drivers of community assembly.

Acknowledgements – Thanks to the Tyson Research Center Summer Research Program for Undergraduates (<http://tyson.wustl.edu/index.php>) and J. Chase and T. Knight labs at Washington University in St. Louis. J. Shurin and M. McCoy provided comments that improved the manuscript. Funding was provided by a Tyson Research Center postdoctoral assistantship to JRV and an HHMI/SURF fellowship to SR. Research was conducted according to IACUC protocol no. 20050173.

References

- Åbjörnsson, K. et al. 2002. The relative importance of lethal and non-lethal effects of fish on insect colonization of ponds. – *Freshwater Biol.* 47: 1489–1495.
- Beylea, L. R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. – *Oikos* 86: 402–416.
- Binckley, C. A. and Resetarits, W. J. 2005. Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. – *Biol. Lett.* 1: 370–374.
- Blaustein, L. et al. 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. – *Oecologia* 138: 300–305.
- Brooks, J. L. and Dodson, S. I. 1965. Predation, body size and composition of plankton. – *Science* 150: 28–39.
- Cadotte, M. C. et al. 2006. The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. – *Oecologia* 149: 150–157.
- Caffey, H. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. – *Ecol. Monogr.* 55: 313–332.
- Chesson, J. 1984. Effect of *Notonecta* (Hemiptera: Notonectidae) on mosquitoes (Diptera: Culicidae): predation or selective oviposition? – *Environ. Entomol.* 13: 531–538.
- Eitam, A. and Blaustein, L. 2004. Oviposition habitat selection by mosquitoes in response to predator (*Notonecta maculata*) density. – *Physiol. Entomol.* 29: 188–191.
- Elton, C. S. 1927. *Animal ecology*. – Univ. of Chicago Press.
- Finke, D. L. and Denno, R. F. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. – *Ecol. Lett.* 8: 1299–1306.
- Fretwell, S. D. and Lucas, H. L. 1970. On the territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – *Biotheoretica* 19: 16–36.
- Garcia, E. A. and Mittelbach, G. G. 2008. Regional coexistence and local dominance in *Chaoborus*: species sorting along a predation gradient. – *Ecology* 89: 1703–1713.
- Glaholt, J. R. and Vanni, M. J. 2005. Ecological responses to simulated benthic-derived nutrient subsidies mediated by omnivorous fish. – *Freshwater Biol.* 50: 1864–1881.
- Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – *Ecol. Lett.* 4: 379–391.
- Gotelli, N. J. and Entsminger, G. L. 2007. EcoSim: null models software for ecology. – Acquired Intelligence Inc. and Keesey-Bear.
- Hairston, N. G. et al. 1960. Community structure, population control and competition. – *Am. Nat.* 94: 421–425.
- Lee, D. S. 1980. *Lepomis cyanellus* (Rafinesque), green sunfish. – In: Lee, D. S. (ed.), *Atlas of North American freshwater fishes*. N. Carolina State Mus. Nat. Hist., pp. 591–592.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Lewin, R. 1986. Supply-side ecology: existing models of population structure and dynamics of ecological communities have tended to ignore the effect of the influx of new members into the communities. – *Science* 234: 25–27.
- Luttbeg, B. et al. 2003. Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. – *Ecology* 84: 1140–1150.
- Magurran, A. E. 2004. *Measuring biological diversity*. – Blackwell.
- McCann, K. and Hastings, A. 1997. Re-evaluating the omnivory-stability relationship in food webs. – *Proc. R. Soc. Lond. B* 264: 1249–1254.
- McCauley, S. J. 2007. The role of local and regional processes in structuring larval dragonfly communities. – *Oikos* 116: 121–133.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. – *Ecol. Monogr.* 68: 1–23.
- Merritt, R. W. and Cummins, K. W. 1996. *An introduction to the aquatic insects of North America* (3rd ed.). – Kendall/Hunt Publ., Dubuque, IA.
- Morin, P. J. 1984. Odonate guild composition: experiments with colonization history and fish predation. – *Ecology* 65: 1866–1873.
- Morin, P. J. 1995. Functional redundancy, non-additive interactions and supply-side dynamics. – *Ecology* 76: 133–149.
- Peacor, S. D. and Werner, E. E. 1997. Trait-mediated indirect interactions in a simple aquatic food web. – *Ecology* 78: 1146–1156.

- Pinheiro, J. C. and Bates, D. M. 2000. Mixed-effects models in S and S-plus. – Springer.
- Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – *Am. Nat.* 147: 813–846.
- Polis, G. A. et al. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Annu. Rev. Ecol. Syst.* 28: 289–316.
- Preisser, E. L. et al. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. – *Ecology* 86: 501–509.
- Resetarits, W. J. 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera : Hydrophilidae). – *Oecologia* 129: 155–160.
- Resetarits, W. J. 2005. Habitat selection behaviour links local and regional scales in aquatic systems. – *Ecol. Lett.* 8: 480–486.
- Resetarits, W. J. and Wilbur, H. M. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. – *Ecology* 70: 220–228.
- Resetarits, W. J. et al. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. – In: Holyoak, M. et al. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 374–398.
- Roughgarden, J. et al. 1987. Supply side ecology: the role of physical transport processes. – In: Gee, J. H. R. and Giller, P. S. (eds), *Organization of communities, past and present*. 27th Symp. Brit. Ecol. Soc., Blackwell, pp. 491.
- Salo, P. et al. 2007. Alien predators are more dangerous than native predators to prey populations. – *Proc. R. Soc. Lond. B* 274: 1237–1243.
- Schmitz, O. 2008. Effects of predator hunting mode on grassland ecosystem function. – *Science* 319: 952–954.
- Shurin, J. B. and Allen, E. G. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. – *Am. Nat.* 158: 624–637.
- Stav, G. et al. 2000. Influence of nymphal *Anax imperator* (Odonata: Aeshnidae) on oviposition by the mosquito *Culiseta longiareolata* (Diptera: Culicidae) and community structure in temporary pools. – *J. Vector Ecol.* 25: 190–202.
- Stuber, R. J. et al. 1982. Habitat suitability index models: green sunfish. – US Dept of the Interior, Fish and Wildlife Service, pp. 1–28.
- Vandermeer, J. H. 2006. Omnivory and the stability of food webs. – *J. Theor. Biol.* 238: 497–505.
- Venables W. N. and Ripley, B. D. 2002. *Modern applied statistics with S* (4th ed.). – Springer.
- Ver Hoef, J. M. and Boveng, P. L. 2007. Quasi-poisson vs negative binomial regression: how should we model over-dispersed count data. – *Ecology* 88: 2766–2772.
- Wellborn, G. A. et al. 1996. Mechanisms creating community structure across a freshwater habitat gradient. – *Annu. Rev. Ecol. Syst.* 27: 337–363.
- White, G. C. and Bennetts, R. E. 2005. Analysis of frequency count data using the negative binomial distribution. – *Ecology* 77: 2549–2557.
- Wilson, J. and Osenberg, C. W. 2002. Experimental and observational patterns of density-dependent settlement and survival in the marine fish, *Gobiosoma*. – *Oecologia* 130: 205–215.
- Zimmer, K. D. et al. 2002. Effect of fathead minnows and restoration on prairie wetland ecosystems. – *Freshwater Biol.* 47: 2071–2086.

Appendix 1. Taxa-level response to predaceous fish in colonization and post-colonization communities

Most of the colonization of the pools occurred through oviposition by amphibious or terrestrial adults who then left the pools (Table A1). The four most common groups of taxa that oviposited in these pools all tended to avoid fish, including *Culex* mosquitoes (primarily *Cx. pipiens*, but also including *Cx. salinarius*, *Cx. territans* at our site) (GLMM $F_{1,20} = 13.84$, $p = 0.001$), grey treefrogs (*Hyla chrysoscelis*) ($F_{1,20} = 32.86$, $p < 0.001$), *Anopheles* mosquitoes (primarily *An. quadrimaculatus*, but also *An. punctipennis* and *An. walkeri* at our site) ($F_{1,15} = 20.31$, $p < 0.001$), and chironomid midges ($F_{1,20} = 20.79$, $p < 0.001$). Other taxa (e.g. adult hydrophilid beetles) showed similar patterns of abundance, but numbers were too small for separate statistical analysis. *Chaborus* oviposition was not detected in colonization pools and so this group was only quantified in final pools (Fig. A1). Both habitat selection and subsequent predation by fish had strong effects on the abundance and biomass of most of the common taxa in the post-colonization communities, but the relative importance of these factors varied among species (Fig. A1). The

absolute reduction in post-colonization abundance due to habitat selection was 87% higher in chironomid midges relative to the reduction due to fish predation (HS $F_{1,15} = 20.34$, $p < 0.001$, PR $F_{1,15} = 7.72$, $p = 0.01$). Reduction by habitat selection was similar to predation reduction in *Culex* mosquitoes (HS reduction was 3.4% lower than PR, HS $F_{1,15} = 6.13$, $p = 0.02$, PR $F_{1,20} = 7.51$, $p = 0.01$), 53.3% lower than predation in *Hyla* tree frogs (HS $F_{1,15} = 5.16$, $p = 0.04$, PR $F_{1,15} = 39.03$, $p < 0.001$), 25.3% lower in *Anopheles* mosquitoes (HS $F_{1,20} = 5.81$, $p = 0.03$, PR $F_{1,20} = 22.23$, $p < 0.001$) and 82.0% lower in *Chaoborus* phantom midges (HS, $p > 0.05$, PR $F_{1,20} = 38.38$, $p < 0.001$). The reduction in biomass in response to habitat selection relative to free roaming fish were again higher for chironomids (+48%, PR $F_{1,15} = 5.85$, $p = 0.03$, HS $F_{1,15} = 9.68$, $p = 0.007$), lower for *Culex* (10%, HS $p > 0.05$, PR $p > 0.05$), *Hyla* (80%, HS $p > 0.05$, PR $F_{1,15} = 44.82$, $p < 0.001$), *Anopheles* (50%, HS $p > 0.05$, PR $F_{1,15} = 12.11$, $p = 0.003$), and *Chaoborus* (>100%, HS $p > 0.05$, PR $F_{1,15} = 18.24$, $p < 0.001$). There was no interaction between habitat selection and subsequent predation for any of the common taxa ($p > 0.05$).

Table A1. Mean (± 1 SD) abundance of all taxa sampled pool⁻¹ during colonization (i.e. summed over the experiment).

| Order | Family | Species | Stage | Morpho spp. | Abundance |
|---------------|--------------|--------------------------|-------------|-------------|----------------|
| Anura | Hylidae | <i>Hyla chrysoscelis</i> | eggs | 1 | 5449 (5023.5) |
| | | | tadpoles | 1 | 749.3 (918.9) |
| | Ranidae | <i>Rana clamitans</i> | eggs† | 1 | 361.9 (1773.0) |
| Coleoptera | Dytiscidae | unknown sp. | larvae | 1 | 0.04 (0.2) |
| | unknown | unknown sp. | adult | 15 | 1.5 (1.8) |
| | | | larvae | 2 | 0.2 (0.8) |
| Diptera | Chironomidae | unknown sp. | egg masses‡ | 1 | 27.0 (32.2) |
| | | | larvae | 1 | 101.0 (150.4) |
| | Chaoboridae | <i>Chaoborus</i> sp. | larvae | 1 | 4.0 (19.4) |
| | Culicidae | <i>Aedes</i> sp. | egg masses‡ | 1 | 22.9 (22.6) |
| | | | larvae | 1 | 149.3 (136.3) |
| | | <i>Anopheles</i> sp. | egg masses‡ | 1 | 7.3 (10.0) |
| | | | larvae | 1 | 185.8 (368.9) |
| | | <i>Culex</i> sp. | egg masses‡ | 1 | 7.0 (11.9) |
| | | larvae | 1 | 0.8 (1.7) | |
| Hemiptera | unknown | unknown sp. | larvae | 2 | 0.3 (0.6) |
| | Gerridae | unknown sp. | adult | 1 | 0.2 (0.5) |
| Ephemeroptera | Notonectidae | <i>Notonecta</i> sp. | adult | 2 | 0.2 (0.5) |
| Pulmonata | Baetidae | <i>Callibaetis</i> sp. | larvae | 1 | 0.04 (0.2) |
| | unknown | unknown sp. | adult | 1 | 0.1 (0.3) |

† Removed from analyses. Represents one breeding pair laying in one pool.

‡ For graphs and analyses dipteran egg masses are converted to eggs.

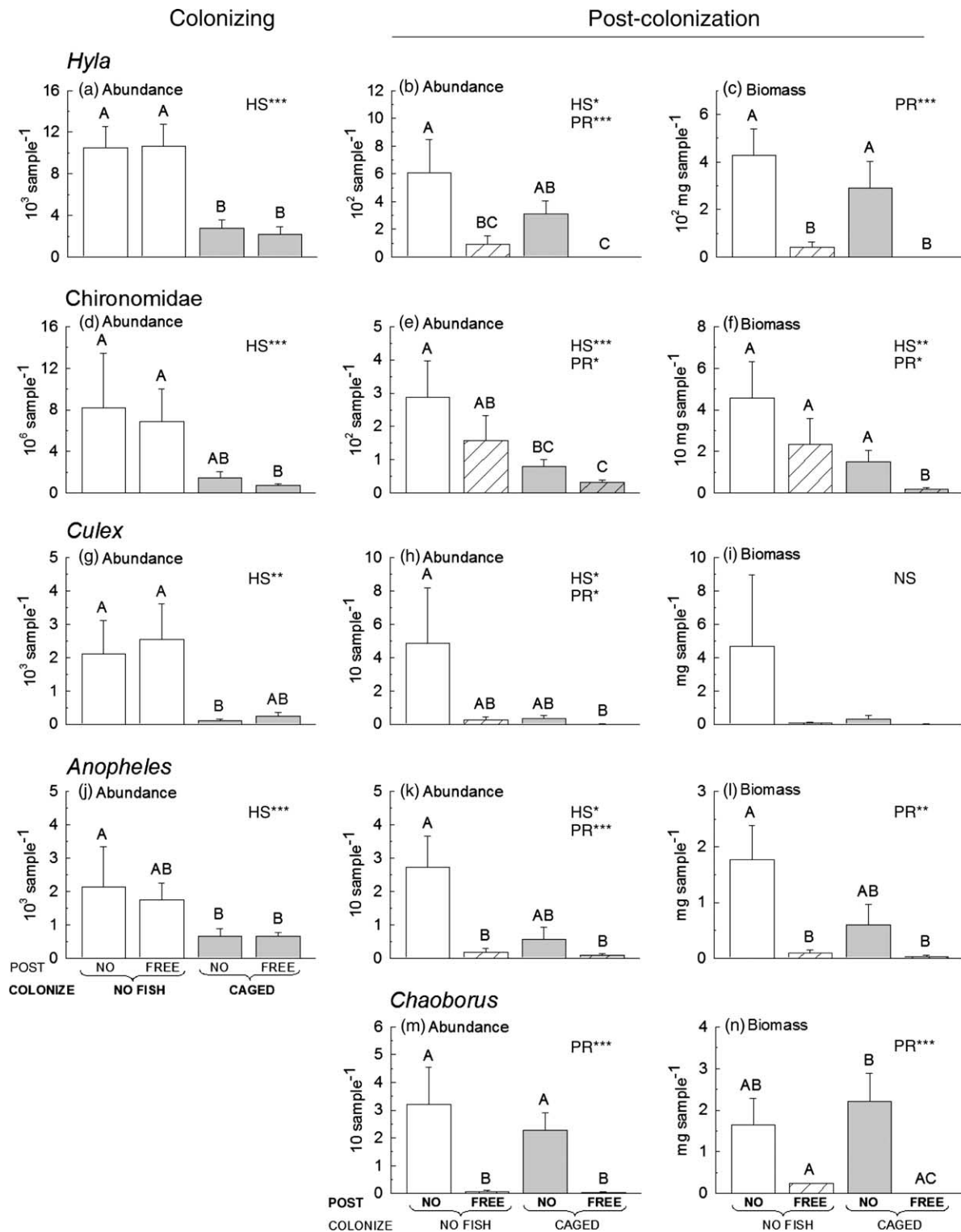


Figure A1. Habitat selection and post-colonization effects of fish on post-colonization abundance and biomass of common taxa sampled pool⁻¹: *Hyla* abundance during (a) colonization (1000 eggs and tadpoles sample⁻¹) and (b) post-colonization (100 tadpoles sample⁻¹) and (c) biomass post-colonization (100 mg of tadpoles sample⁻¹); Chironomidae abundance during (d) colonization (1 000 000 eggs and larvae sample⁻¹) and (e) post-colonization (100 larvae sample⁻¹) and (f) biomass post-colonization (10 mg of larvae sample⁻¹); *Culex* abundance during (g) colonization (1000 eggs and larvae sample⁻¹) and (h) post-colonization (10 larvae sample⁻¹) and (i) biomass post-colonization (mg of larvae sample⁻¹); *Anopheles* abundance during (j) colonization (1000 eggs and larvae sample⁻¹) and (k) post-colonization (10 larvae sample⁻¹) and (l) biomass post-colonization (mg of larvae sample⁻¹); *Chaoborus* abundance (m) post-colonization (10 larvae sample⁻¹) and (n) biomass post-colonization (mg of larvae sample⁻¹). HS = main effect of habitat selection in response to caged fish. PR = main effect of free-roaming predators in post-colonization pools. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Bar shading, letters, and replicates as in Fig. 2 in text.

Appendix 2. Sample-based rarefaction curves used to estimate taxa richness independent of number of individuals sampled pool^{-1} treatment^{-1}

Taxa richness was estimated through rarefaction using EcoSim (Gotelli and Entsminger 2007). Rarefaction is useful when comparing assemblages of difference abundance (Magurran 2004). We used sample-based rarefaction

scaled to abundance to make pair-wise comparisons between treatments at a common abundance (i.e. to control for the effect of abundance on richness estimates (Gotelli and Colwell 2001, Magurran 2004). If the observed diversity of the smaller community fell within the 95% of the rarefaction curve of the larger community, the communities were considered not to be significantly different in richness (Magurran 2004).

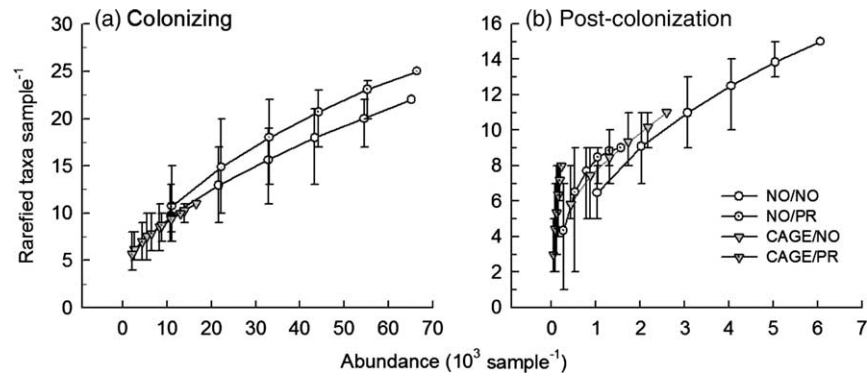


Figure A2. Sample-based rarefaction curves (mean no. of species \pm 95% CI per 1 sample, 2 samples etc.) scaled to abundance (mean no. individuals based on the number of samples chosen) to examine the a) effect of habitat selection on taxa richness in colonization pools ($n = 12$) and b) effect of habitat selection and post-colonization effects of fish on taxa richness in post-colonization pools ($n = 6$ samples total treatment^{-1}). White circle = no caged fish during colonization, grey triangle = caged fish during colonization, open circle or triangle = no free-roaming fish post-colonization, dot in circle or triangle = free-roaming fish post-colonization.