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Prey-driven control of predator assemblages: zooplankton abundance drives aquatic beetle colonization

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Abstract. Trophic interactions are critical determinants of community structure and ecosystem function. In freshwater habitats, top predators are traditionally viewed as drivers of ecosystem structure, shaping populations of consumers and primary producers. The temporary nature of small water bodies makes them dependent on colonization by many organisms, particularly insects that form highly diverse predator assemblages. We conducted mesocosm experiments with naturally colonizing populations of aquatic beetles to assess how prey (zooplankton) abundances influenced colonization and assemblages of natural populations of aquatic beetles. We experimentally demonstrate that zooplankton populations can be proximate regulators of predator populations and assemblages via prey-density-dependent predator recruitment. Our results provide support for the importance of prey populations in structuring predator populations and the role of habitat selection in structuring communities. We indicate that traditional views of predators as drivers of ecosystem structure in many systems may not provide a comprehensive picture, particularly in the context of highly disturbed or ephemeral habitats.

Key words: community assembly; Dytiscidae; food web; habitat selection; Hydrophilidae; predator–prey; trophic cascade; zooplankton.

Introduction

Communities are structured by three primary factors: predation (top-down), resources (bottom-up), or competition (parallel; Pimm et al. 1985, McQueen et al. 1986). How these factors interact and influence communities has been extensively studied in a variety of systems (Hairston et al. 1960, Power 1992, Ernest et al. 2000, Horswill et al. 2016). Predator-driven effects have been viewed as the dominant force in many systems, including intertidal (Paine 1966), freshwater (Carpenter et al. 1985), and terrestrial (Hairston et al. 1960). Resource-driven effects are dominant in marine systems (Aebischer et al. 1990, Ware and Thomson 2005, Frederiksen et al. 2006). Evidence for competition-driven control of populations is mixed (Sih et al. 1985, Meserve et al. 2003). However, no one factor is likely to control community structure in any given system, and there is considerable variability in the relative strengths of trophic processes. This variability has been attributed to shifting control (Meserve et al. 2003), complex non-linear relationships (Ernest et al. 2000), or missing links, such as non-lethal effects of predators (Peckarsky et al. 2008, Orrock et al. 2010).

Predators' effects reverberate throughout foods webs and play critical roles in structuring populations, communities, and ecosystems (Power 1990, Holt and Polis 1997, Sih et al. 1998). Direct consumption reduces abundance of some prey, while others may increase due to competitive release (Paine 1966). Changes in identity and/or abundances of top predators can lead to trophic cascades that shift predation pressures across a food web and alter biomass of primary producers (Carpenter et al. 1985, Power 1990, Polis et al. 2000). Predators, via both direct and indirect effects, can have positive, negative, or neutral effects on diversity (Menge and Sutherland 1976, Huston 1979, Shurin and Allen 2001).

We are becoming increasingly aware that these various effects on diversity can result from both lethal and non-lethal processes (Schmitz et al. 1997). Non-lethal processes play important roles in shifting prey habitat use and performance, but both lethal and non-lethal effects are important drivers of community structure. In particular, habitat selection can have dramatic effects on species distributions and resulting communities (Anderson and Shugart 1974, Resetarits and Wilbur 1989, Vonesh et al. 2009, Kraus and Vonesh 2010, Resetarits and Pintar 2016). Predators have non-lethal effects on habitat selection by prey and resulting prey distribution and abundance, whereas habitat selection by predators leads to lethal effects on prey.

Effects of predators on lower trophic levels have perhaps been best studied in freshwater systems (Brett and Goldman 1996, Hulot et al. 2014). Lentic systems, with their discrete boundaries and relatively closed nature, are well-suited to studies of population dynamics and community structure. Zooplankton are important consumers of primary production and significant food resources for predators in lentic systems (Elser and

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Goldman 1991). Predators strongly control zooplankton populations and weakly control phytoplankton, whereas resources strongly control phytoplankton and weakly control zooplankton (McQueen et al. 1989, Hulot et al. 2014). In these systems, fish are often top predators, and the transition from fish to fishless habitats is a defining characteristic. Many fishless habitats are temporary and undergo a seasonal/drying filling cycle, which makes them obligately dependent on recurrent colonization of both predators and prey (Wilbur 1980, Wellborn et al. 1996).

In fishless habitats, the primary predators are insects, such as beetles, odonates, and hemipterans, or other organisms with complex life cycles (e.g., larval salamanders; Schneider and Frost 1996, Wilbur 1997). Colonization by aquatic beetles and hemipterans can quickly influence communities as the aquatic adults select habitats both for themselves and their offspring. Odonates and many salamanders select habitats only for their offspring, and thus there is a time lag between oviposition and full development of larval predatory capabilities. Most aquatic beetles are strong dispersers and can form diverse assemblages in fishless habitats, but dispersal is energetically costly, and emphasis is placed on initial colonization as secondary dispersal may occur only if conditions dramatically change (Zalom et al. 1979, Jeffries 1994, Zera and Denno 1997, Bilton 2014). Colonizing beetles select habitats based on perceived risk, by avoiding predators such as fish, and their perceived reward, by choosing habitats with more available resources (Binckley and Resetarits 2005, 2009).

Beetles from the primary families in aquatic systems (Dytiscidae, Gyrinidae, Haliplidae, Helophoridae, Hydraenidae, Hydrochidae, Hydrophilidae) occupy trophic levels that vary with both family and life stage (Merritt et al. 2008). Haliplid larvae and adults are herbivorous, noterid larvae are omnivorous and adults predaceous, hydraenid larvae and adults are scavengers, and gyrinid larvae are predaceous but adults are both predators and opportunistic scavengers. Hydrochids and helophorids are less well understood, but may be scavengers (Epler 2010).

Dytiscids and hydrophilids are the dominant beetles in many lentic habitats. Larval dytiscids and hydrophilids are predaceous, and adult hydrophilids are omnivores/scavengers, whereas adult dytiscids are primarily predaceous (Testa and Lago 1994, Larson et al. 2000). Dytiscids capture prey ranging from zooplankton to other aquatic insects and conspecifics, to larval amphibians and small fish (Yee 2010, Culler et al. 2014). Dytiscid effects on zooplankton can be similar to fish effects, altering population sizes, community structure, behavior, and individual body size, while also causing trophic cascades by releasing phytoplankton and periphyton from grazing pressure (Arts et al. 1981, Herwig and Schindler 1996, Cobbaert et al. 2010). Effects of hydrophilid adults on aquatic communities are less well understood.

Studies of trophic interactions have traditionally focused on how changes to the resource base (bottom-up) or predator assemblages (top-down) affect food web dynamics (Hunter and Price 1992, Power 1992). The direct effects of intermediate trophic levels, especially on higher trophic levels, are poorly understood. Work in predator–prey systems often assumes that both predators and prey move between habitat patches in response to movements of the other (Sih 1984, Abrams 2007). This is seldom the case in lentic systems, where many organisms cannot disperse across the terrestrial matrix. Very little is known regarding how variation in prey abundances affects critical habitat selection processes and colonization dynamics of predators, or the resulting community structure, particularly in the context of speciose predator assemblages. The role of habitat selection, and how variation in characteristics of organisms at intermediate trophic levels and habitat selection interact, are important for understanding the dynamics of predation and community assembly.

We conducted two mesocosm experiments that allowed us to determine how colonization and assemblage structure of aquatic beetles was influenced by zooplankton abundance over time. Our first experiment examined whether beetles preferred new vs. old ponds by simulating water conditions of newly filled ponds. These ponds had no preexisting zooplankton populations, thus relative zooplankton abundances were determined by actual pond age and our manipulation of water age. The follow-up experiment focused specifically on effects of zooplankton inoculation on beetle colonization under otherwise equivalent conditions. We predicted that adult dytiscids (predaceous) would colonize pools with higher zooplankton abundances, but were unsure if the omnivorous hydrophilids would preferentially colonize a treatment in either of the experiments.

Materials and Methods

Field site

Our experiments were conducted at the University of Mississippi Field Station (UMFS; 34°25′4″ N, 89°23′32″ W) near Oxford, Mississippi, USA from February until December 2015. UMFS consists of 318 ha of forests, fields, ponds, wetlands, and streams within the Eocene Hills of the Interior Gulf Coastal Plain. A diverse assemblage of aquatic beetles is known from UMFS, with 115 recorded species, 94 of which have been observed in our experimental mesocosms (M. R. Pintar and W. J. Resetarits, Jr., *unpublished data*).

Mesocosms

We established mesocosms using plastic wading pools (1 m diameter, 0.2 m deep, 110 L, $N = 24$). We added 0.5 kg of dry hardwood leaf litter (primarily *Quercus* spp. and *Fagus grandifolia*) and filled pools with unchlorinated well water. To separate colonizing beetles from the leaf litter and allow for efficient collection, pools were covered with window screening (1.3 mm^2, 1.13 mm opening) that was depressed below the water surface. In both experiments, the treatment of the first pool of the first block was randomly assigned, and then treatment was alternated between pools and by block so no pools of the same treatment were adjacent. Pools were separated from each other by 1 m edge-to-edge. Beetles were exhaustively collected once weekly, preserved in ethanol, and identified to species, with the exception of *Paracymus*, *Hydrochus*, and *Desmopachria*. *Paracymus* were not identified to species because of high abundance and small size, but those at UMFS are primarily *P. subcupreus*. Only males of the small *Hydrochus* species we collected are identifiable to species, and we only collected females. Beetles in the subgenus *Desmopachria* of the genus *Desmopachria* are very small and difficult to identify (only males are identifiable), but one individual from the subgenus *Pachriodesma* was identified to species.

Water change experiment

On 5 February 2015, we set up a 6 × 4 (N = 24) rectangular array in a field at UMFS. Two treatments were arranged with rows (N = 4, south-north from nearby ponds to forest edge) as blocks. The two treatments were (1) controls that retained the original water on a weekly basis (Old) and (2) pools that had most of their water and constituent zooplankton removed weekly and replaced with zooplankton-free well water (New) to simulate influx of water to existing ponds. Water used to initially fill and refill pools originated from the same source well. In addition to refilling New pools, all Old pools were topped off with water weekly to maintain equal volumes, which disturbed the water in each pool to a similar degree as occurred in the New pools. None of the pools were inoculated with pond water. Assemblages of zooplankton, phytoplankton, and algae nonetheless develop in uninoculated pools (Cáceres and Soluk 2002, Louette and De Meester 2005). Beetle collections began on 12 February, but cold temperatures and ice precluded sampling on 19 and 26 February and 5 March.

Following the collection on 26 March, we changed water in the New pools weekly by bailing from above the screen to prevent the loss of leaf litter. Replacement of water in New pools served two purposes: (1) to maintain water quality similar to that of recently filled pools and (2) to continually maintain low zooplankton abundances. Both zooplankton and water quality change over time in mesocosms, and some organisms (*Hyla* treefrogs) prefer water with conditions similar to those of newly filled pools (Pintar and Resetarits 2017*a*). We conducted the last water change on 7 May, and continued to collect beetles weekly and top off all pools as necessary until termination of the experiment on 21 October. Because our initial focus was on simulating newly filled ponds, and we were not primarily interested in zooplankton, we conducted limited zooplankton sampling. On 30 April (near the end of water changes), 22 June (after water changes had stopped and ponds presumably equilibrated), and 16 October (at the end of data collection) we collected two 400-mL water samples from separate locations in each pool, filtered them through 80-μm mesh into 50-mL centrifuge tubes, and preserved them with Lugol's solution. All zooplankton in each sample were counted and identified to order.

Inoculation experiment

On 22 October we set up six linear blocks of four pools each in six sites separated by >315 m distributed across UMFS (N = 24). Two pools in each block were inoculated with two 470-mL aliquots containing zooplankton collected from fishless ponds at UMFS, and the other two pools served as uninoculated controls. Pools underwent natural dynamics without water changes or other disturbances, except for weekly beetle collections. During collections, separate fine mesh nets were used for Control and Inoculated pools to prevent transfer of zooplankton between pools of different treatments. Final beetle collection was 10 December. Zooplankton samples were collected on 7 and 21 November in the same manner as in the water change experiment.

Data analysis

We analyzed the effect of treatment over time and block using univariate repeated-measures ANOVAs on species richness and abundances of all beetles, Dytiscidae, Hydrophilidae, and individual species with total abundances >75. We aggregated data from multiple weeks for assemblage analyses due to our exhaustive weekly sampling and temporal variation in dispersal of natural beetle populations. These temporal groups were based on our experimental procedures and patterns of beetle colonization. In the water change experiment, there were three groups: Period 1 (9 April–14 May), during which we actively changed the water; Period 2 (28 May–23 July), when the effects of the water changes persisted; and Period 3 (5 August–21 October), the latter part of the experiment during which the effects of the water changes subsided. There were two groups in the inoculation experiment: Early (29 October–5 November), when we observed clear differences in the total beetle abundances between treatments, and Late (19 November–10 December), when we did not observe differences in total beetle abundances. We analyzed the effect of treatment on total beetle, dytiscid, and hydrophilid assemblages using PERMANOVAs set to 999 permutations and type III SS. Repeated-measures PERMANOVA can only analyze one fixed and one random factor, so we did not run this analysis, as there were large block effects in several of our analyses from both experiments. We used SIMPER to determine which species contributed most to the dissimilarity between treatments within the aggregated temporal groups and highlighted differences between treatments in SIMPER results using univariate ANOVAs on each species in each group.

We used repeated-measures ANOVAs to analyze abundances of all zooplankton and orders Cladocera, Copepoda, Ostracoda, and Rotifera from both experiments. To directly compare beetle colonization to zooplankton abundance, we used multiple regression to relate beetle abundance to zooplankton abundance with block as a factor for beetle species and families with $N > 25$ in each corresponding sampling date. These regression analyses were only conducted with beetle data from sampling dates closest to the zooplankton sampling dates. In the water change experiment, beetles collected on 30 April, 25 June, and 14 October were paired with zooplankton collections from 30 April, 22 June, and 16 October, respectively. In the inoculation experiment, beetle collections from 5 and 19 November were paired with zooplankton collections from 7 and 21 November, respectively. There were no zooplankton-order-specific responses by beetles, so we used total zooplankton abundances in all regression analyses.

All analyses were conducted on square root transformed ($\sqrt{X + 0.5}$) count data using $\alpha = 0.05$. PRIMER 7 and the PERMANOVA+ add-on were used to conduct PERMANOVAs and SIMPER using the Bray-Curtis Index and to construct NMDS plots (Anderson et al. 2015, Clarke and Gorley 2015); all other analyses were conducted in R v. 3.3.1 (R Core Team 2016).

RESULTS

Water change experiment

A total of 6,763 beetles representing 55 species in five families colonized the water change experiment (Table 1). Pools were also colonized by several Hemiptera, but abundances were too low for meaningful analysis: *Belastoma lutarium* ($N = 1$), *Hesperocorixa* (18), *Limnoporus canaliculatus* (5), *Notonecta irrorata* (13), and *Sigara* (38). One Old pool failed (drained) on 20 May and was excluded from repeated-measures analyses.

Temporal variation in dispersal of natural beetle populations resulted in significant effects of time in all repeated-measures analyses. In all these ANOVAs, we saw significant time × treatment interactions for all beetles, Dytiscidae, the four most abundant dytiscid species, *Helophorus linearis*, and one hydrophilid (*Enochrus ochraceus*; Appendix S1: Table S1). There was significantly higher colonization of Old pools by these groups and species while the water changes were being conducted and for up to two months after (Figs. 1, 2).

PERMANOVA revealed that treatment had a significant effect on total beetle and dytiscid assemblages in Periods 1 and 2 and on hydrophilids in Period 2 (Appendix S1: Table S2, Fig. 3). There were no significant assemblage differences in Period 3. Differences in Periods 1 and 2 were driven by dytiscid species, with abundant Hydrophilidae also contributing (Table 2). However, only one hydrophilid had significantly higher colonization in Old pools within these groups: *Berosus*

TABLE 1. Species and abundances of colonizing beetles for both the water change (WC) and inoculation (IN) experiments.

	Experiment	
Species	WC	IN
Dytiscidae ($S = 32$)	3,211	643
Acilius fraternus	0	1
Acilius mediatus	0	5
Agabus disintegratus	7	3
Agabus punctatus	0	9
Bidessonotus inconspicuus	1	0
Celina angustata	1	0
Celina hubbelli	1	0
Copelatus caelatipennis	1	0
Copelatus chevrolati	19	6
Copelatus glyphicus	1,006	94
Desmopachria spp.	19	0
Desmopachria seminola	1	0
Hydaticus bimarginatus	2	0
Hydrocolus deflatus	6	36
Hydrocolus oblitus	26	69
Hydroporus pseudoniger	11	12
Hydroporus rufilabris	476	153
Hydrovatus pustulatus	2	0
Ilybius biguttulus	3	0
Ilybius gagates	4	2
Laccophilus fasciatus	199	170
Laccophilus maculosus	6	0
Laccophilus proximus	995	62
Mediorhantus calidus	11	2
Neobidessus pullus	54	1
Neoporus blanchardi	2	10
Neoporus undulatus	1	1
Platambus flavovittatus	7	0
Thermonectus basillaris	7	4
Thermonectus nigrofasciatus	2	1
Uvarus granarius	328	2
Uvarus lacustris	14	0
Haliplidae ($S = 3$)	5	10
Haliplus triopsis	2	0
Peltodytes dunavani	3	0
Peltodytes sexmaculatus	0	10
Helophoridae ($S = 2$)	180	51
Helophorus linearis	177	51
Helophorus marginicollis	3	0
Hydrochidae ($S = 1$)	1	2
Hydrochus	1	2
Hydrophilidae ($S = 21$)	3,366	1,600
Berosus exiguus	28	0
Berosus infuscatus	242	84
Berosus peregrinus	4	1
Berosus striatus	12	0
Cymbiodyta chamberlaini	22	76
Cymbiodyta vindicata	1	2
Enochrus cinctus	3	0
Enochrus consors	5	1
Enochrus ochraceus	252	490
Enochrus perplexus	23	1
Enochrus pygmaeus	8	75

Table 1. (Continued)

Species	Experiment WC	Experiment IN
Enochrus sayi	3	0
Helochares maculicollis	9	143
Hydrochara brevipalpus	1	0
Hydrophilus triangularis	1	0
Laccobius teneralis	1	0
Paracymus	1,868	253
Tropisternus blatchleyi	4	5
Tropisternus collaris	22	58
Tropisternus lateralis	855	411
Tropisternus natator	2	0

Note: *S* indicates number of species from that family.

exiguus in Period 2, which were present in only low abundances. The large contribution of species with similar means in each treatment could be due to a statistical artifact (Warton et al. 2012).

There were significant time × treatment interactions and main effects of time in the total zooplankton, cladoceran, copepod, and rotifer analyses (Appendix S1: Table S3). Overall zooplankton abundances were initially 47 times higher in Old pools while water changes were being conducted than in New pools, and abundances remained higher in Old pools for over a month after water changes ended before becoming equivalent between treatments late in the experiment (Fig. 4a). Thus, observed differences between Old and New water treatments corresponded to periods where zooplankton abundance was significantly higher in the Old treatments, and disappeared when zooplankton populations equilibrated between Old and New pools.

In the June beetle/zooplankton regression, we observed a strong positive relationship between zooplankton abundance and abundances of dytiscids, with more dytiscids in pools that contained more zooplankton, regardless of treatment, but there was no relationship with hydrophilids (Fig. 5; Appendix S1: Fig. S1). We observed similar patterns for the April and October samples, but abundances were much lower for these dates, so these figures are included in the supplemental material (Appendix S1: Figs. S2, S3).

Inoculation experiment

A total of 2,306 beetles representing 36 species in five families colonized the zooplankton inoculation experiment (Table 1). Pools were colonized by several Hemiptera, but abundances were again too low for analysis: *Hesperocorixa* ($N = 36$), *Notonecta irrorata* (53), and *Sigara* (39). We observed significant effects of time and block in all repeated-measures ANOVAs, however we observed significant time × treatment interactions in only the dytiscid and *Laccophilus fasciatus* (the most abundant dytiscid) analyses (Fig. 6; Appendix S1: Table S4). Other less abundant dytiscids (e.g., *Hydroporus rufilabris*) had similar but non-significant patterns (Fig. 6f). Abundances of these groups were initially higher in Inoculated pools before equilibrating between treatments (Fig. 6). However, there were significant

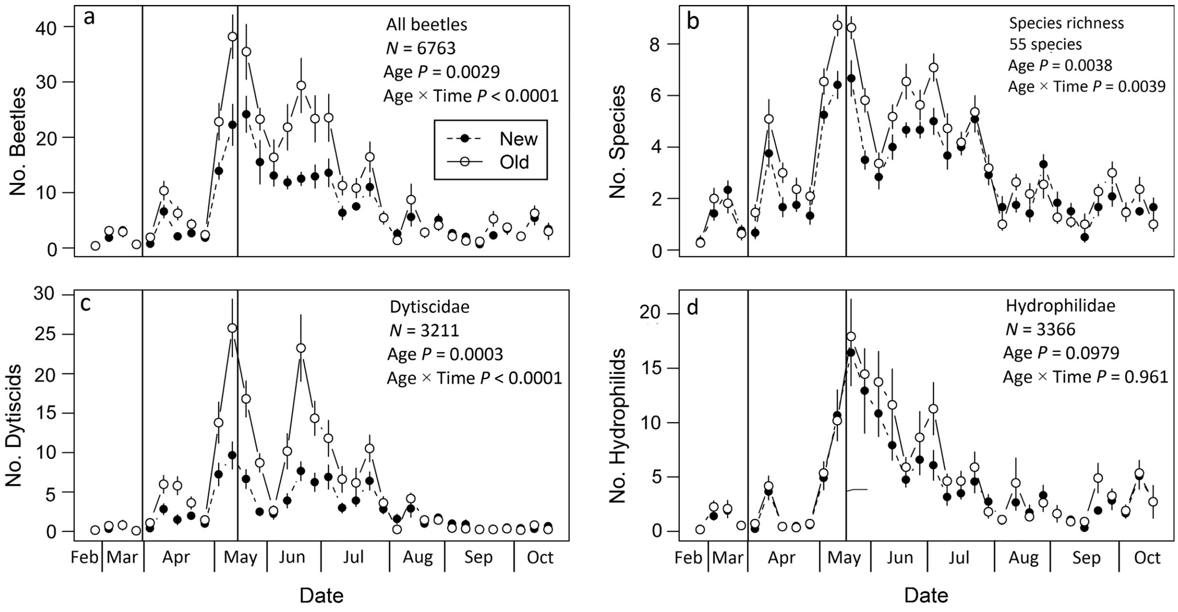


Fig. 1. (a) Total beetle abundance, (b) species richness, (c) dytiscid abundance, and (d) hydrophilid abundance over time in Old and New pools in the water change experiment (means ± SE). First vertical line, start of water changes; second vertical line, end of water changes. *N* indicates number of individuals represented in the corresponding graph with *P* values for the effect of Age (treatment) and the Age × Time interaction in the repeated-measures ANOVA (full results in Appendix S1: Table S1).

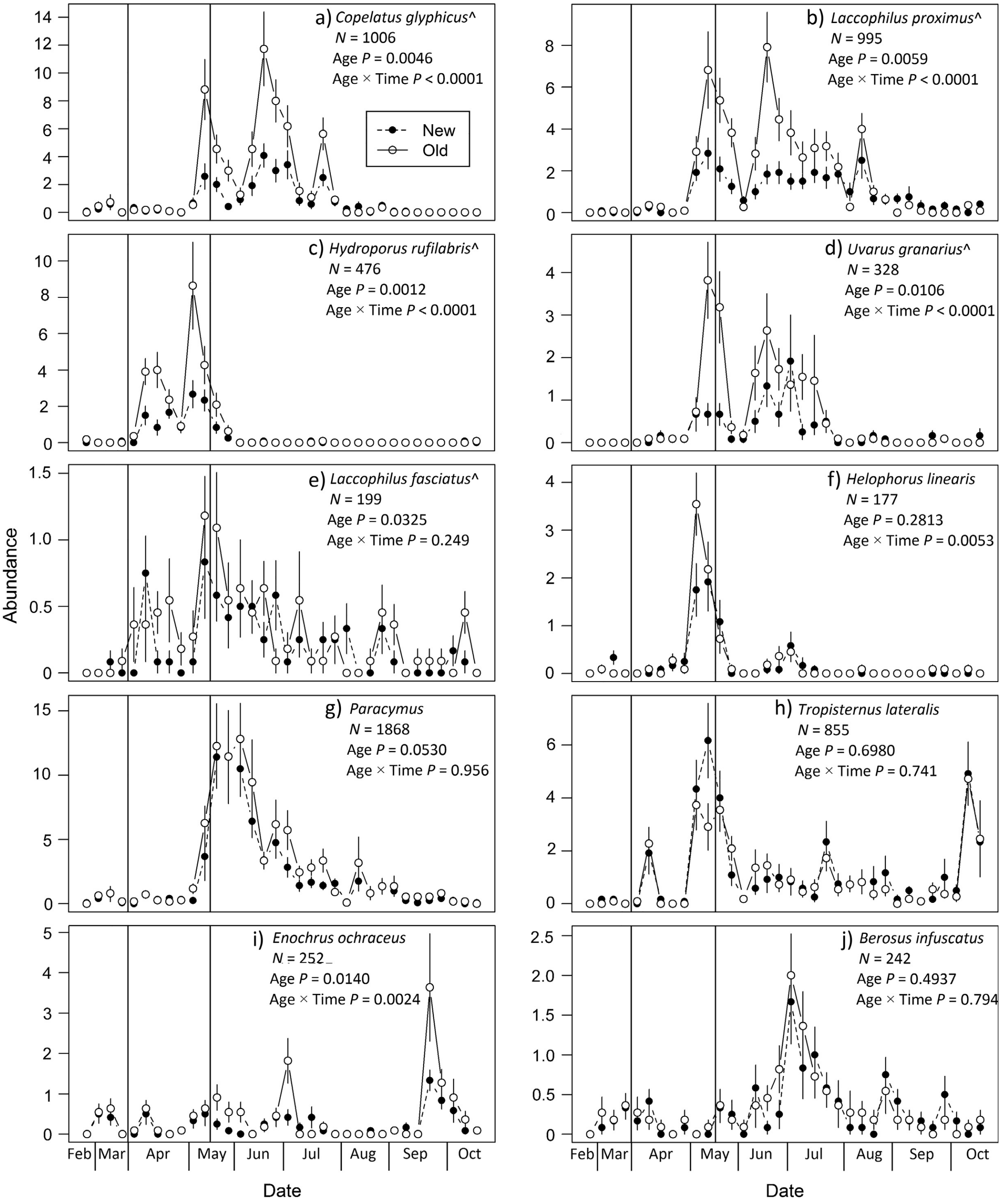


FIG. 2. Abundances of the 10 most numerous colonizing species over time in Old and New pools in the water change experiment (means ± SE). First vertical line, start of water changes; second vertical line, end of water changes. An up arrow ^ indicates Dytiscidae. *N* indicates number of individuals represented in the corresponding graph with *P* values below for the effect of Age (treatment) and the Age × Time interaction in the repeated-measures ANOVA (full results in Appendix S1: Table S1).

main effects of treatment in the analyses of all beetles, Dytiscidae, and the three most abundant dytiscids, reflecting higher colonization of Inoculated pools during the first two weeks when abundances of all dispersing beetles were much greater. Hydrophilids were the dominant colonizers in this experiment, but there were no significant effects of treatment or an interaction for this family (Fig. 6; Appendix S1: Table S4).

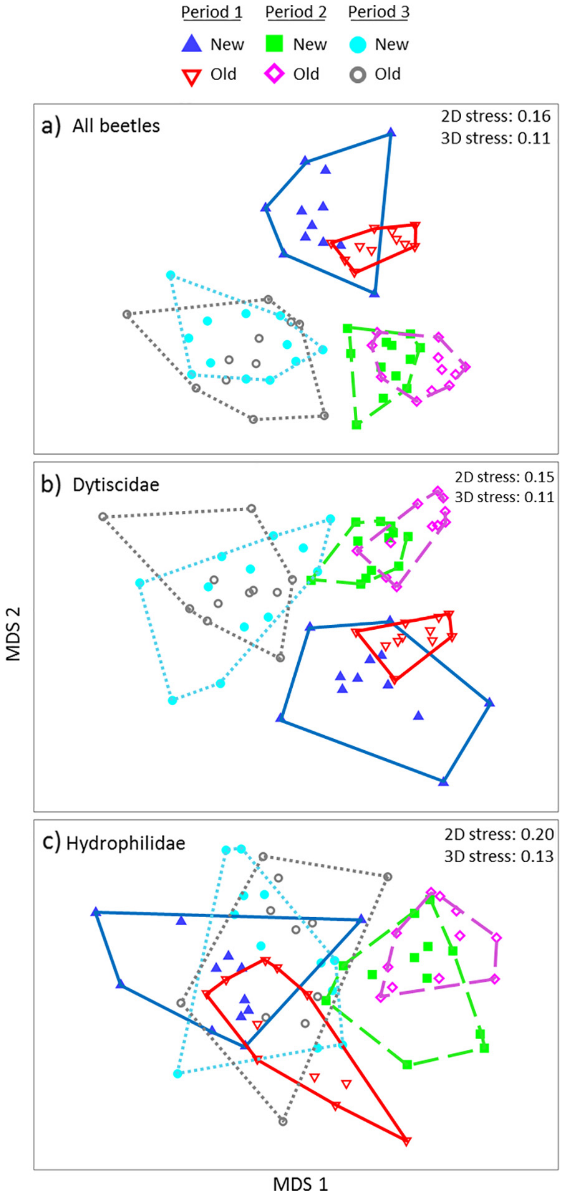


FIG. 3. Nonmetric multidimensional scaling (NMDS) plots of (a) all beetles, (b) Dytiscidae, and (c) Hydrophilidae in the water change experiment. Points are sorted by group and treatment, and outlined in minimum convex polygons. Full PERMANOVA results are in Appendix S1: Table S2. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2. The 10 species contributing most to dissimilarity among beetle assemblages in the water change experiment as determined by SIMPER.

Species	Average abundance New	Average abundance Old	Contributing percent
Period 1			
Hydroporus rufilabris^	9.83	**25.08**	10.19
Copelatus glyphicus^	3.58	**11.00**	8.98
Paracymus	5.75	9.58	7.48
Tropisternus lateralis	12.67	9.58	7.37
Uvarus granarius^	1.67	**4.92**	7.37
Laccophilus proximus^	5.08	**10.33**	7.32
Helophorus linearis	4.17	6.00	5.39
Laccophilus fasciatus^	1.83	**3.58**	5.30
Enochrus ochraceus	1.42	1.83	4.77
Hydrocolus oblitus^	0.42	1.25	4.30
Period 2			
Copelatus glyphicus^	17.67	**43.00**	12.95
Laccophilus proximus^	13.17	**32.00**	10.39
Paracymus	43.83	57.64	10.17
Uvarus granarius^	5.75	**11.36**	8.65
Berosus infuscatus	5.25	6.55	5.58
Tropisternus lateralis	7.75	9.55	5.38
Enochrus ochraceus	1.83	3.73	4.90
Neobidessus pullus^	2.33	1.73	4.67
Berosus exiguus	0.58	**1.55**	4.48
Helophorus linearis	1.00	1.09	4.00
Period 3			
Paracymus	6.33	9.64	13.58
Tropisternus lateralis	13.25	11.09	11.59
Berosus infuscatus	2.50	2.18	8.14
Enochrus ochraceus	3.25	6.36	7.15
Laccophilus fasciatus^	1.00	1.64	6.87
Laccophilus proximus^	7.58	6.82	6.39
Copelatus glyphicus^	1.33	0.45	6.35
Tropisternus collaris	0.33	0.64	4.54
Uvarus granarius^	0.67	0.27	4.36
Copelatus chevrolati^	0.33	0.27	3.57

Notes: Contributions are broken down between New and Old treatments and by sampling period (see *Methods*). Species are listed in descending order of contributing percent. Average abundances are means of raw beetle numbers abundances in each group, and contributing percent was calculated from square-root-transformed data. An up arrow ^ indicates Dytiscidae; boldface type indicates significantly higher colonization in ANOVA.

In our Early group, there were significant effects of treatment on the total beetle and dytiscid assemblages, but not the hydrophilids (Appendix S1: Table S5). There were no significant effects of treatment among any beetle assemblages in the Late group. Differences in the Early group were driven by a mix of the abundant hydrophilid species as well as three dytiscids (Table 3). However, ANOVAs on the species within the Early group reveal significant differences in colonization between pool types for only the three dytiscids and one hydrophilid, *E. ochraceus*. In the Late group, a mix of species from both families contributed to differences between treatments, but there were no significant differences between treatments for any species. In all PERMANOVA analyses, we saw a large, significant effect of block, which makes visualization of differences using NMDS plots difficult (Appendix S1: Table S5, Fig. S4).

There were significant time × treatment interactions in the total zooplankton and copepod analyses: overall zooplankton abundances were initially five times higher in inoculated pools Early and equal between treatments

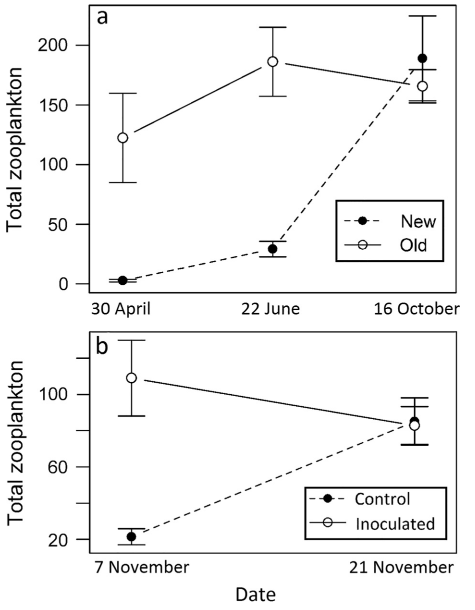


FIG. 4. Total zooplankton abundances over time in Old and New pools in the (a) water change experiment and in Inoculated and Control pools in the (b) inoculation experiment (means ± SE). Full ANOVA results are in Appendix S1: Table S3.

Late (Appendix S1: Table S3). Significant main effects of treatment in zooplankton, cladoceran, copepod, and rotifer analyses reflected higher abundances in inoculated pools (Fig. 4b). Abundance patterns of the three common orders followed the same patterns as that of all zooplankton. Ostracods were too rare ($N = 10$) for meaningful analysis, but were included in the total zooplankton ANOVA.

In regression analyses of beetles collected on 5 November and zooplankton collected on 7 November, we observed a significant relationship between dytiscid abundances and zooplankton abundances, but hydrophilids had no relationship with zooplankton abundance (Fig. 7a–f; Appendix S1: Fig. S5). Although there were fewer beetles during the 19 November collections, we still observed a significant relationship between dytiscid and zooplankton abundances, but still no relationship between hydrophilids and zooplankton (Fig. 7g, h; Appendix S1: S6). It is important to note that the 19/21 November collections occurred when there were no longer statistically significant differences between treatments in either dytiscid colonization or zooplankton abundance. On both sampling dates, dytiscids were more abundant in pools that contained more zooplankton, regardless of treatment.

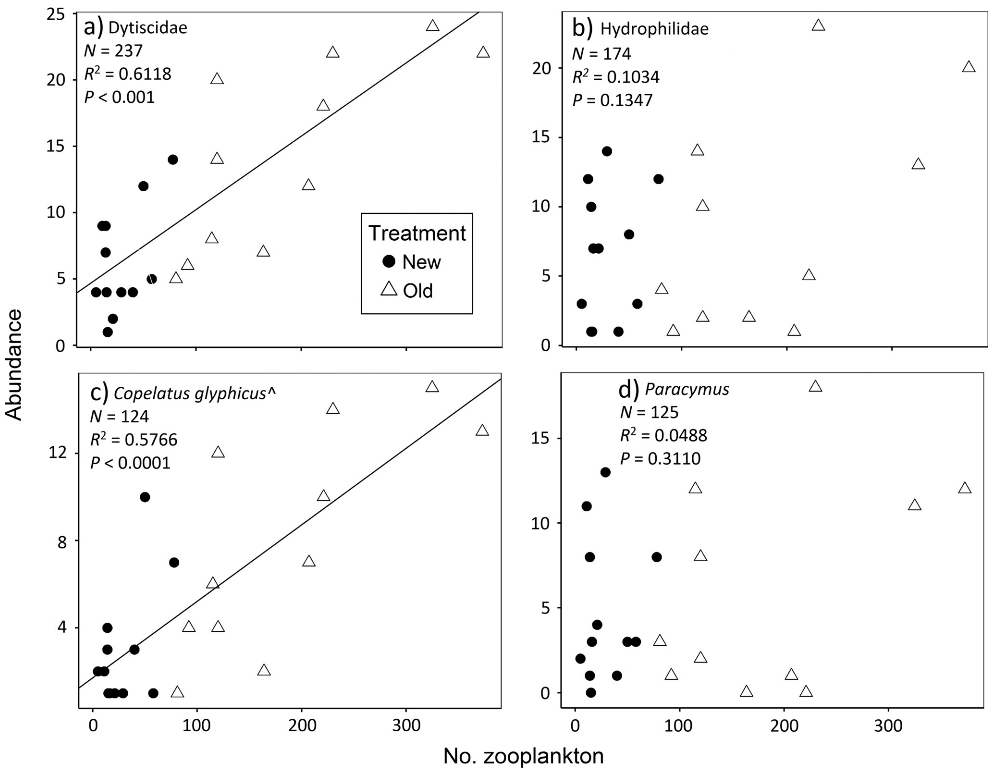


FIG. 5. Multiple regression of (a) dytiscids, (b) hydrophilids, (c) *Copelatus glyphicus*, and (d) *Paracymus* from the water change experiment against total zooplankton abundances in New and Old pools. Beetles were collected on 25 June and zooplankton on 22 June. Statistics are summaries of multiple regression results with P values for effects of zooplankton abundance. An up arrow ^ indicates Dytiscidae. N, total number of beetles for that sample date.

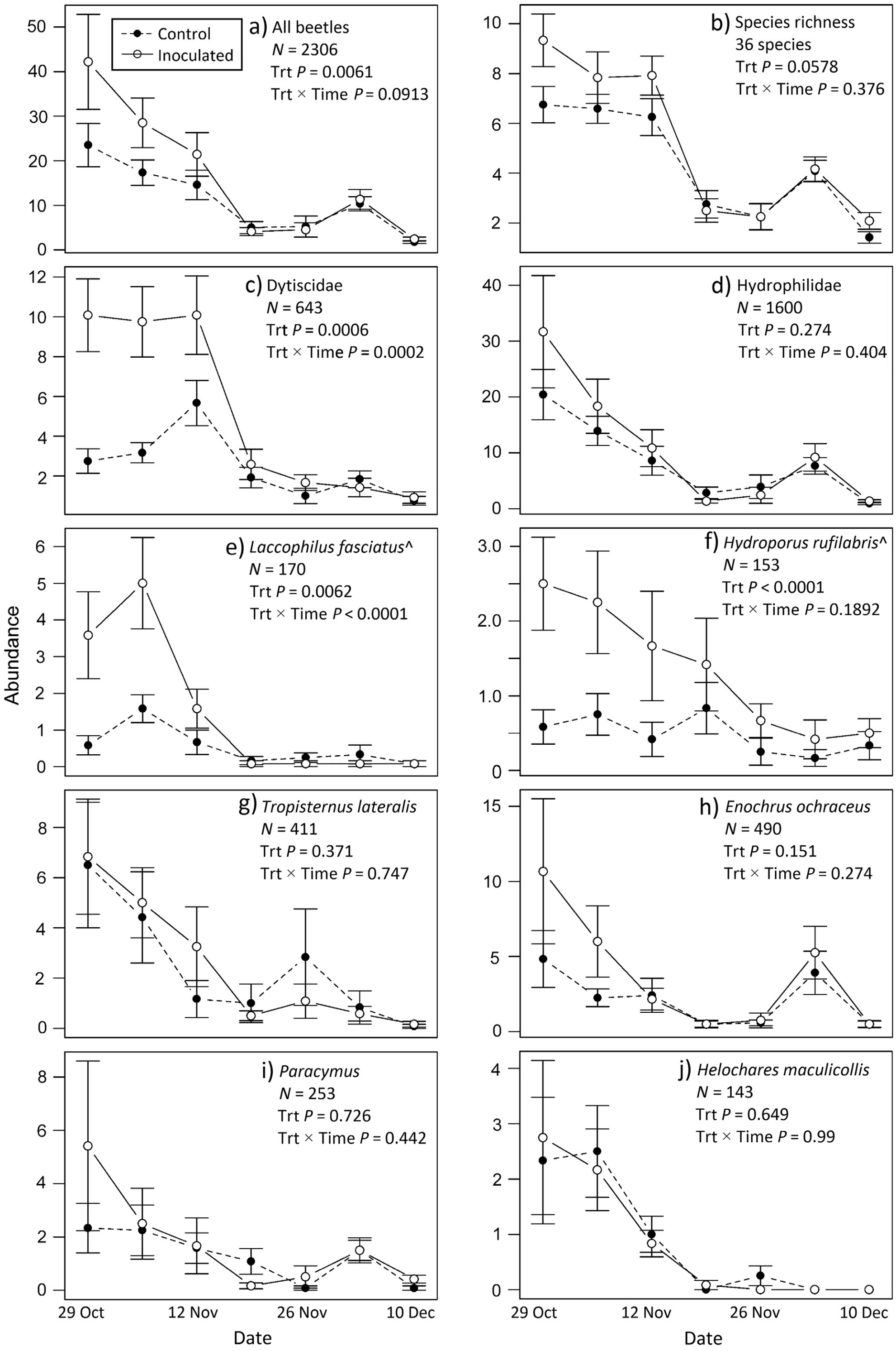


FIG. 6. (a) Abundances of all colonizing beetles, (b) species richness, and (c) abundances of dytiscids, (d) hydrophilids, (e, f) the two most abundant dytiscid species, and (g–j) the four most abundant hydrophilid species over time in Inoculated and Control pools in the inoculation experiment (means ± SE). An up arrow ^ indicates Dytiscidae. *N* indicates number of individuals represented in the corresponding graph, with *P* values below for the effect of Treatment (Trt) and the Trt × Time interaction in the repeated-measures ANOVA (full results in Appendix S1: Table S4).

TABLE 3. The 10 species contributing most to dissimilarity among beetle assemblages in the inoculation experiment as determined by SIMPER.

Species	Average abundance		Contributing percent
	Control	Inoculated	
Early			
Tropisternus lateralis	11.00	12.00	11.05
Enochrus ochraceus	7.08	**16.67**	9.36
Helochares maculicollis	4.83	4.92	8.48
Laccophilus fasciatus^	2.17	**8.58**	8.37
Paracymus	4.58	7.92	8.33
Hydroporus rufilabris^	1.33	**4.75**	7.20
Laccophilus proximus^	1.17	**2.75**	5.61
Berosus infuscatus	2.83	2.83	6.39
Enochrus pygmaeus	1.00	2.25	4.66
Tropisternus collaris	2.00	2.00	4.64
Late			
Enochrus ochraceus	5.50	7.00	11.95
Tropisternus lateralis	4.75	2.33	11.62
Hydroporus rufilabris^	1.58	3.00	8.90
Cymbiodyta chamberlaini	0.00	0.17	8.67
Paracymus	0.17	0.08	7.95
Helophorus linearis^	1.33	1.42	7.82
Hydrocolus oblitus^	0.83	0.92	6.49
Hydrocolus deflatus^	0.50	0.92	5.12
Laccophilus fasciatus^	0.83	0.33	5.04
Copelatus glyphicus^	0.67	0.42	4.84

Notes: Contributions are broken down between Inoculated and Control treatments and Early and Late sample groups (see *Methods*). Species are listed in descending order of contributing percent. Average abundances are means of raw beetle abundances in Early and Late groups, and contributing percent was calculated from square-root-transformed data. An up arrow ^ indicates Dytiscidae; boldface type indicates significantly higher colonization in ANOVA.

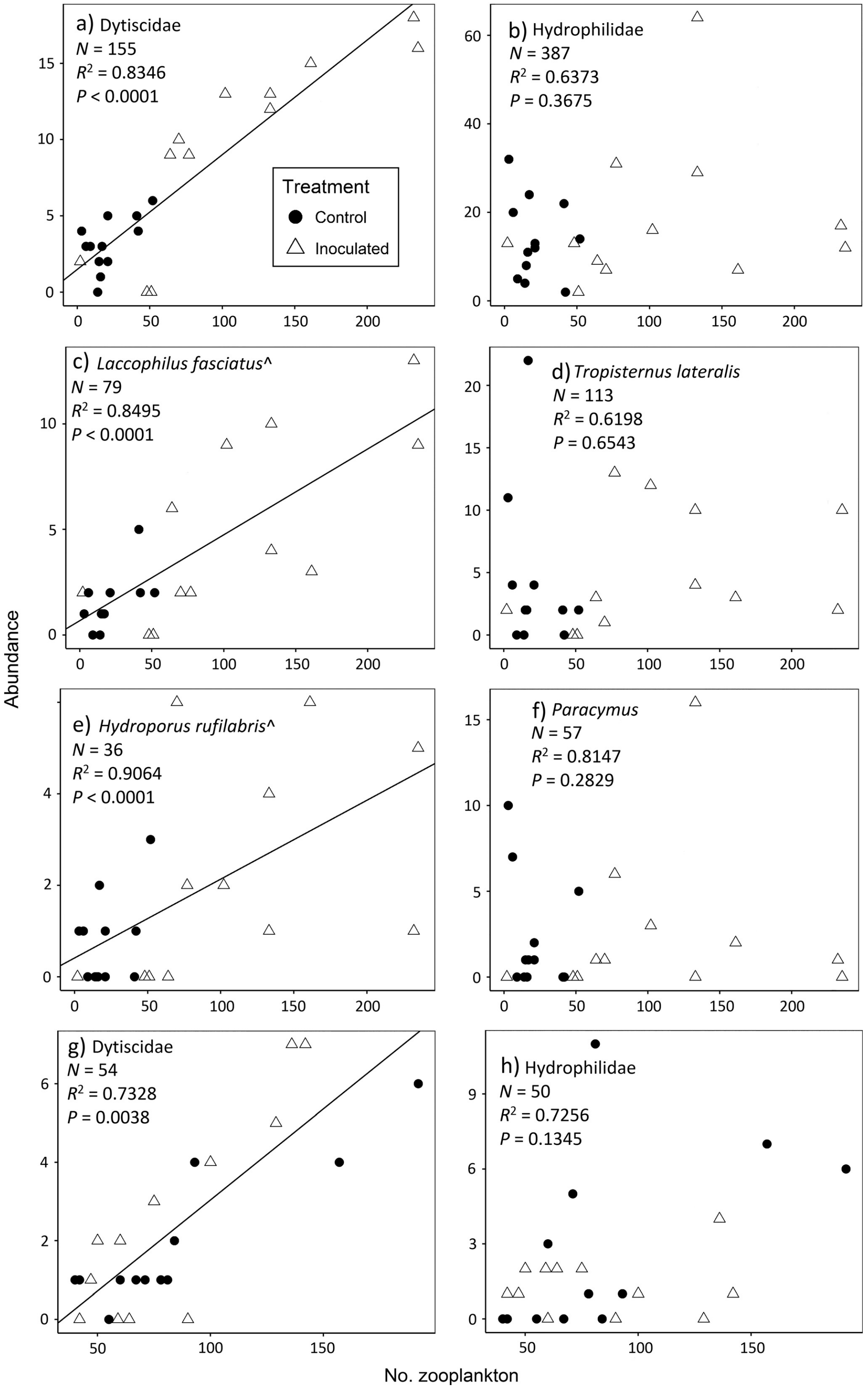
DISCUSSION

Predator–prey interactions and their consequences are a central focus in ecology. It is well documented that predators are attracted to areas with more prey, and evolve/develop appropriate prey acquisition strategies, whereas prey, of necessity, avoid predators and evolve/develop appropriate defenses (Sih 1984, Lima 1998). Studies have traditionally focused on interactions between small numbers of predator and prey species, or effects of one (or a small number) of predator species on larger assemblages of prey (Sih et al. 1998, Abrams 2007). Much of this work has been in systems where at least one, and often all, species involved are vagile and capable of moving between habitat patches at will, as in the context of optimal foraging theory and the ideal free distribution (Fretwell and Lucas 1970, Werner and Hall 1974, Charnov 1976). This kind of movement dynamics is not realistic for many natural systems, and we can learn a great deal about community assembly by studying the effects of prey abundances on predator habitat selection, colonization, and resulting community structure in more constrained systems. Our study system involved numerous prey species across four orders of zooplankton, 32 species of predaceous diving beetles (Dytiscidae), and 27 species of aquatic beetles from four other families (Table 1). Aside from low abundances of hemipterans, beetles were the only predators present in our pools.

Our data show that abundances of prey occupying middle trophic levels (zooplankton) can be the proximate regulator of the colonization dynamics and resulting abundances and species composition of predators (adult beetles) in lentic systems. We observed significant time × treatment interactions in both zooplankton abundances and colonization by dytiscid beetles: when zooplankton abundances were higher, there was increased colonization by aquatic beetles, predominately predatory dytiscids, but not hydrophilids. Over time, as zooplankton abundances equilibrated between treatments, colonization likewise equilibrated. This is supported by both zooplankton removal in the water change experiment, and addition in the inoculation experiment. Perhaps most interestingly, even given our limited number of zooplankton sampling dates, we found strong relationships between dytiscid and zooplankton abundances, with more dytiscids colonizing pools with more zooplankton. This relationship occurred regardless of treatment and whether or not there were significant differences in dytiscid or zooplankton abundances between treatments.

Zooplankton are important consumers of primary production and significant food resources for predators in freshwater systems (Elser and Goldman 1991). In fishless lentic systems, adult and larval dytiscids and larval hydrophilids are among the most important predators of zooplankton (Wilbur 1997, Arnott et al. 2006). Adult beetles have terrestrial pupation of their larvae, which makes populations entirely dependent on colonization from surrounding patches or terrestrial pupation sites. Resource variation in lentic systems does not immediately affect adult population size, as resources do not cause direct/immediate mortality, but rather drive patterns of colonization, dispersal, and fitness via

FIG. 7. Multiple regression of (a) dytiscids, (b) hydrophilids, (c) *Laccophilus fasciatus*, (d) *Tropisternus lateralis*, (e) *Hydroporus rufilabris*, and (f) *Paracymus* against total zooplankton abundances for beetles collected on 5 November and zooplankton collected on 7 November. Regression of (g) dytiscids and (h) of hydrophilids against total zooplankton abundances for beetles collected on 19 November and zooplankton collected on 21 November. Statistics are summaries of multiple regression results, with *P* values for effects of zooplankton abundance. High R^2 values are largely due to large, significant effects of block in the inoculation experiment. An up arrow ^ indicates Dytiscidae. *N* indicates number of beetles for that sampling date.


a) Dytiscidae
N = 155
R² = 0.8346
P < 0.0001
Treatment
● Control
△ Inoculated
b) Hydrophilidae
N = 387
R² = 0.6373
P = 0.3675
c) Laccophilus fasciatus^
N = 79
R² = 0.8495
P < 0.0001
d) Tropisternus lateralis
N = 113
R² = 0.6198
P = 0.6543
e) Hydroporus rufilabris^
N = 36
R² = 0.9064
P < 0.0001
f) Paracymus
N = 57
R² = 0.8147
P = 0.2829
g) Dytiscidae
N = 54
R² = 0.7328
P = 0.0038
h) Hydrophilidae
N = 50
R² = 0.7256
P = 0.1345
Abundance
No. zooplankton
0
50
100
150
200

differences in patch quality. Over short timescales resources can more strongly affect larval beetles, which cannot disperse to other patches. Resources are nonetheless critical to adults given the importance of initial colonization decisions, low likelihood of secondary dispersal, and effects on larval performance.

We would expect increased colonization of pools with more zooplankton to place increased predation pressure on those populations, possibly creating a negative feedback loop (Möllmann et al. 2008). Whether this occurred in our system is undetermined, because we interrupted community assembly with each weekly sample, and there was significant temporal variation in natural colonization rates. However, even based on relatively few zooplankton samples, differences in zooplankton abundance between Old vs. New, and Inoculated vs. Control pools are relatively consistent (Fig. 4), until they ultimately converge. This suggests no top-down feedback or population regulation in our system. Inoculated pools reached stable levels quickly (within two weeks), whereas Control pools approached this same level after four weeks. This high capacity for passive dispersal by zooplankton allows for rapid colonization of small, isolated water bodies (Maguire 1963, Cáceres and Soluk 2002).

We see evidence of bottom-up regulation of zooplankton and in turn adult beetle populations in the water change experiment. With our weekly water changes, we removed from New pools not only zooplankton, but also dissolved nutrients and fine particulate organic matter. Conducting water changes for seven weeks should have reduced base resource levels, and in turn, reduced primary productivity and consumer (zooplankton) populations (Leibold 1999). If the effects of water changes were solely to reduce zooplankton populations, we would expect some recovery of populations in New pools by the second sampling date (22 June), over a month after water changes ended, given the equality of populations between treatments after four weeks in the inoculation experiment. Although we do not have zooplankton data between 22 June and 16 October, based on patterns of dytiscid colonization, we suspect zooplankton populations did not recover until at least late July. However, we see strong relationships between dytiscid abundance and zooplankton abundance throughout the course of the experiment with higher dytiscid abundances in pools with more zooplankton, regardless of treatment. Therefore, the differences in colonization between treatment likely cannot be attributed to disturbance, differences in water chemistry, or other such factors.

Interestingly, we did not observe consistent differences between treatments in colonization by the omnivorous hydrophilids. We saw significant time × treatment interactions for *Enochrus ochraceus* and *Helophorus linearis* (Helophoridae is closely related to Hydrophilidae) in the water change experiment and significantly higher colonization by *E. ochraceus* of Old pools (Appendix S1: Table S1). These patterns are weaker than for dytiscids, occur on only a few dates in *E. ochraceus* (Fig. 2i), and there is no relationship with zooplankton abundance as in dytiscids (Appendix S1: Fig. S5c). Across several colonization experiments, *E. ochraceus* responses have been enigmatic, exhibiting geographically and temporally variable colonization (Resetarits and Pintar 2016; *unpublished data*). Why we see significant differences with this particular hydrophilid in this experiment is unknown. Knowledge of species-level resource use is limited in aquatic beetles, but we would expect resource use and colonization responses to more closely mimic other adult hydrophilids than dytiscids.

If water changes removed sufficient nutrients or other resources to suppress zooplankton populations, it suggests that overall productivity was lowered, including decreased primary productivity. Similarly, our zooplankton inocula also undoubtedly contained phytoplankton and periphyton. Both of these processes should affect hydrophilid colonization, but we saw equal colonization of both treatments in both experiments among most hydrophilids. As scavengers, hydrophilids may directly respond to base resource in our pools (leaf litter; Pintar and Resetarits 2017*b*). We previously recorded resource-driven colonization of pools that vary in the type and quality of leaf litter only in hydrophilids, not dytiscids (Pintar and Resetarits 2017*c*). The trophic distance from the resource base to scavenging hydrophilids is shorter than to predaceous dytiscids, and colonization preferences of hydrophilids switched between litter types over a short time scale (two months). While many natural systems contain many other aquatic insects that could be food sources for beetles, we observed very few in our experiment and many that were present were removed during beetle sampling.

Variation in resources used by different taxa and the differing primacy of factors controlling patch quality places an emphasis on habitat selection decisions by colonizing adult beetles. Colonization in response to varying prey levels among dytiscid adults and not hydrophilids suggests that hydrophilids are primarily selecting habitats for themselves and not their predaceous offspring, which should perform better with greater zooplankton abundance. Preference of adult dytiscids for pools with more zooplankton matches the optimal habitat for both their predaceous offspring and themselves, maximizing expected fitness, whereas lower zooplankton abundances (while they persist) would reduce fitness for hydrophilids as a result of larval competition and cannibalism. Similar differences exist between these families in colonization preferences in the context of predation risk, reinforcing the idea that adult hydrophilids select habitats primarily for themselves (Resetarits and Pintar 2016, Pintar and Resetarits 2017*c*).

Variation in zooplankton populations drives differential family- and species-specific colonization of aquatic beetles, resulting in distinct assemblages between treatments in both experiments. Assemblages were more distinct temporally (Fig. 3), but significant differences existed between treatments early (groups 1, 2, and Early) in both experiments for all beetles and dytiscids, but not later (groups 3 and Late), or in hydrophilids. However, there was also considerable spatial overlap in the NMDS plots (Fig. 3). The degree of overlap is similar to that observed with other resource-driven colonization patterns, yet less distinct than those in the context of predation risk-driven colonization (Resetarits and Pintar 2016, Pintar and Resetarits 2017*c*). Nevertheless, based on our results, we would expect both primary resource and prey abundances to be important drivers of assemblage structure in small, ephemeral, fishless habitats. Species composition and those species contributing the most to differences between treatments varied over time in both experiments (Tables 2, 3), yet we still observed effects that tracked zooplankton abundances for dytiscids and not hydrophilids.

Distinct assemblages and higher species richness in pools with more zooplankton should produce functionally distinct communities in lentic systems across a gradient of prey availability. In contrast to most taxa of aquatic animals (including other insects), beetles can sustain highly diverse assemblages in small habitat patches (Larson 1985, Batzer and Wissinger 1996, Fairchild et al. 2000, 2003). Aquatic beetles (dytiscids in particular) are more morphologically and functionally diverse as adults than they are as larvae (Larson et al. 2000). Zooplankton are consumed by many adult dytiscids (and all larval dytiscids), and some adults have specialized morphologies for capturing zooplankton (Friis et al. 2003). Further work on zooplankton community structure in this context could prove interesting if increased beetle colonization alters zooplankton abundance and species composition via a feedback loop (Arnott et al. 2006).

Zooplankton are indicators of water quality and critical to the functioning of freshwater and marine food webs (Gannon and Stemberger 1978, Richardson 2008). Populations of these abundant consumers support countless other species in aquatic systems. Although their populations have traditionally been viewed as controlled by predator populations, we see that during the initial colonization phase of freshwater systems zooplankton determine the abundances of predators present and their assemblage structure within a patch. The effects observed in our system are analogous to remote effects of predators (Orrock et al. 2010) but in reverse, with prey-driven patterns of dispersal and colonization in predator populations. While predators may be more dominant drivers of community structure later in community assembly, the abundances and identities of the initial colonists are important, as they can shape future colonization patterns and successional dynamics (Alford and Wilbur 1985). It is important to understand the roles of prey population dynamics and habitat selection in structuring populations and metacommunities via prey-density dependent predator colonization, especially in the context of local and global environmental changes (Mortelliti et al. 2010, Doerr et al. 2011). Top-down and bottom-up control of community structure are only two of the possibilities for how variation in species composition and population density impact the function of natural ecosystems.

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