

**OPEN SYSTEMS IN COMMUNITY ECOLOGY: DISPERSAL, DIVERSITY, AND
ECOSYSTEM PROPERTIES**

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Abstract

**SARAH CHRISTINE LEE: Open systems in community ecology: dispersal, diversity,
and ecosystem properties
(Under the direction of John F. Bruno)**

A large fraction of community ecology has focused on processes that operate within communities to control species richness; however, most natural localities are open to dispersal. Dispersal can mediate community structure and functioning by introducing novel species and promoting coexistence at multiple spatial scales. Using experiments, I tested the effects of dispersal in complex, multi-trophic communities. Results suggest that dispersal of novel species is an important determinant of species richness, community composition and ecosystem properties across a range of environmental conditions. Dispersal also promoted coexistence in a network of communities with different environmental conditions, possibly by subsidizing failing populations with individuals of successful populations. Together, these results broaden our understanding of community and ecosystem-level effects of dispersal beyond terrestrial plant communities and highlight mechanisms of coexistence that may be unique to mobile animals.

To Pamela and Tan Lee,
who have given me everything

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INTRODUCTION

A large fraction of community ecology has focused on processes that operate within communities to control species richness (e.g., disturbance, predation, and competition for resources; Tilman 1982; Huston 1999). However, most natural localities are open to input of organisms from the surrounding environment via dispersal. The ecologically relevant unit of dispersal is a “propagule,” which is a colonizing organism or vegetative structure capable of establishing a self-sustaining population. Depending on a species’ life history, a propagule can be a pregnant female, a mating pair, seeds, or spores. By linking disjunct populations, dispersal of propagules between communities can control the dynamics of populations, communities, and ecosystems. Experimental evidence also suggests that the spatial characteristics of a group of interacting communities (a metacommunity, *sensu* Wilson 1992) can mediate species composition (Gonzalez 1998), interspecific interactions (Kareiva 1987; Bengtsson, 1989) and energy fluxes (Polis et al. 1998). Theoretical investigations have identified mechanisms that may structure metacommunities (Holyoak et al. 2005 and references therein); among these, dispersal-mediated mechanisms are of particular interest.

Each species’ dispersal ability, combined with the spatial distribution of habitat, determines the rate at which each species immigrates to a given patch (Nathan & Muller-Landau 2000). In this context, “patch” refers to a discrete area of habitat (Leibold et al. 2004). Post-arrival, whether a species becomes a member of the resident local community may depend on the degree of species saturation. Saturation occurs when local processes limit the number of species in a community (Terborgh & Faaborg 1980; Cornell & Lawton 1992;

Kneitel & Chase 2004; He et al. 2005). Theoretically, species can be excluded via local processes such as competition, predation, parasitism, or disturbance; however, resource partitioning and interspecific competition are frequently invoked as processes that act in concert to keep species richness at a saturation point (Ricklefs and Schluter 1993 and references therein). Local processes do not limit species richness of an unsaturated community; instead, unsaturated communities are limited by the availability of propagules and open to colonization by new species.

Propagule limitation occurs where species that could coexist in a locality are absent because propagules do not arrive at that locality in sufficient numbers; this can result in unsaturated communities. Propagule limitation can result from geographic barriers to migration or dispersal; for example, oceans are physical barriers to terrestrial organisms and surrounding land prevents dispersal of freshwater fishes. Biological barriers can also generate propagule limitation. Interspecific interactions such as predation can increase propagule mortality while species' intrinsic reproductive limitations can interact with stochastic population dynamics to prevent successful colonization via Allee effects (Taylor & Hastings 2005) Whether or not communities are likely to ever reach saturation remains an unresolved yet fundamental ecological question with direct consequences for our understanding of important phenomena, such as species invasions and climate-driven range expansions

One approach to determining whether or not communities are saturated is to graphically examine the relationship between richness sampled at “local” and “regional” scales. The advantages and shortcomings of this approach have been discussed intensively (Cornell & Lawton 1992; Huston 1999; Srivastava, 1999; Loreau 2000; Shurin et al. 2000;

Mouquet et al. 2003; He et al. 2005; Hillebrand 2005). Another approach is to experimentally determine whether local species richness is limited by propagule availability (Tilman 1997; Turnbull et al. 2000; Foster & Tilman 2003). If local richness increases when propagule supply is experimentally increased, the community is propagule-limited or unsaturated. In this case, dispersal is critical because presumably propagule limitation would disappear if all species in a region could disperse to all local communities.

Even if a local community is not propagule-limited, dispersal between communities can mediate meta-scale (i.e., including multiple habitat patches linked by dispersal) community structure (Tilman 1994; Kneitel & Chase 2004). A metacommunity is defined as an interactive group of local communities linked by dispersal of one or more species (Wilson 1992). For example, similar species may coexist at the metacommunity scale via source-sink dynamics (Brown & Kodric-Brown 1977; Mouquet & Loreau 2003). Early formulations of source-sink effects focused on the role of rapid (i.e., on the same time scale as competitive interactions) dispersal in allowing fugitive species to persist in a multi-patch system by being superior colonizers (Levin 1974). Dispersal can also reduce extinction rates in target communities, thus increasing species richness at equilibrium (rescue effect, *sensu* Brown & Kodric-Brown 1977). Rescue effects operating on population demography are referred to as mass effects (Shmida & Ellner 1984). Mass effects occur where input of individuals from habitats where there is positive population growth (i.e., “sources”) can maintain populations in “sinks” that would otherwise go extinct. The result is species remain present in patches where they would otherwise be rapidly excluded (Shmida & Ellner 1984; Pulliam 1988). At the community level, sources and sinks can be generated by spatial heterogeneity in either fitness or abiotic environmental conditions such that competitive rankings vary across a

metacommunity (Amarasekare & Nisbit 2001). Thus source-sink dynamics refer to spatial heterogeneity and dispersal mediating coexistence by maintaining different competitive outcomes among local habitats and providing spatial refuges from competitive exclusion (Muko & Iwasa 2000).

For my dissertation research, I explored the consequences of propagule limitation and dispersal in heterogeneous landscapes for community structure and ecosystem properties. This research addresses fundamental gaps in our understanding of communities open to dispersal and advances our basic understanding of the factors limiting species richness. Despite evidence that propagule supply can determine structure and function of some marine communities (Roughgarden et al. 1988; Connolly & Roughgarden 1998), there are no experimental tests of community-level propagule limitation in marine systems. I also investigated the effects of dispersal and environmental heterogeneity on species coexistence at multiple spatial scales.

Chapter 1: Propagule supply controls grazer community structure and primary production in a benthic marine ecosystem

Early theories of species diversity proposed that communities at equilibrium are saturated with species due to limited niche space (MacArthur 1965); however, propagule-addition experiments in terrestrial plant communities suggest that propagule-limitation is widespread and that many communities are naturally unsaturated (Tilman 1997; Foster & Tilman 2003; Mouquet et al. 2004). Although most relevant research has been focused at the population level (Turnbull et al. 2000), experiments in plant communities suggest that many communities are unsaturated and that species richness can be increased by adding propagules of new species.

Together with my advisor, I experimentally tested for community saturation and measured the effects of propagule supply on community structure in a benthic marine system (Lee & Bruno 2009). We manipulated propagule supply (arrival of individuals of numerous species) of mobile grazers in experimental mesocosms over multiple generations and, unlike all previous tests, we examined the cascading effects of propagule supply on prey (macroalgae) biomass. We found little evidence for saturation, despite the absence of processes such as disturbance and predation that are thought to alleviate saturation in nature. Increasing propagule supply increased the total number of species and made rare species more abundant. Perhaps surprisingly, given the strong effect of propagule supply on species richness, supply-related changes in body size and composition suggest that competitive interactions remained important. Grazer supply also had strong cascading effects on primary production, possibly due to dietary complementarity modified by territorial behavior. These results indicate that propagule supply can directly influence the diversity and composition of communities of mobile animals. Furthermore, the supply of consumer propagules can have strong indirect effects on prey and on fundamental ecosystem properties.

Chapter 2: Effects of propagule supply and resource availability on local species richness in mobile marine grazer communities

In many ecological communities, biodiversity and the demography of individual species are strongly determined by propagule availability (Gaines & Roughgarden 1985; Caley et al 1996; Hughes & Tanner 2000; Clark et al. 2007; Stohlgren et al. 2008; Lee & Bruno 2009). Experimental evidence indicates that the strength of propagule limitation of biodiversity can vary with habitat productivity (Huston 1999; Foster et al. 2004), presumably

because the factors regulating species richness and abundances shift along gradients of resource availability. To date these experiments have been conducted almost exclusively in terrestrial habitats, likely due to the relative ease of obtaining and manipulating plant seeds. However, large-scale associations between oceanographic regime, recruitment rates, and community dynamics (Connolly et al. 2001; Menge et al. 2003; Navarrete et al. 2005,) suggest that the strength of propagule limitation in marine habitats depends on environmental context.

Together with my advisor, I tested the environmental context-dependency of propagule supply effects by manipulating primary productivity (i.e. rate of algal prey growth) and grazer propagule supply in a flow-through mesocosm system. We also examined secondary effects of grazer propagule supply on algal prey communities. Increasing light availability increased both algal biomass and species richness. Despite this increase in food availability and diversity, algal resource availability had no effect on grazer propagule limitation. Instead we found that grazer propagule supply had strong positive effects on grazer richness, at all resource levels. These results highlight important differences in resource use between sessile producers and mobile grazers and suggest fundamental differences in how consumers and plants respond to resource enrichment.

Chapter 3: An experimental test of source-sink dynamics in a multi-trophic-level metacommunity

Models of source-sink dynamics predict that dispersal can promote local species coexistence in heterogeneous environments by subsidizing populations in “sinks” that would otherwise go extinct without individuals from habitats where there is positive population

growth (i.e., “sources”, Brown & Kodric-Brown 1977; Shmida & Ellner 1984; Mouquet & Loreau 2003; Mouquet et al. 2005). Species turnover (i.e., beta richness *sensu* Lande 1996) between local communities may also be influenced by dispersal because increased dispersal homogenizes species composition and eliminates spatial refugia for poor competitors. Metacommunity species richness appears to be maximized at low to intermediate dispersal when local communities are dominated by the best local competitor and declines as weak competitors at the metacommunity are driven extinct in all habitats. The effect of dispersal on species richness across spatial scales is mirrored by changes in composition; dominance shifts from good local competitors to good metacommunity competitors with increasing proportion of dispersal (Mouquet & Loreau 2003). Together with several colleagues, I examined source-sink dynamics in a model community with multiple trophic levels to test the effects of source-sink dynamics on species richness at multiple spatial scales.

We generated population sinks by manipulating temperature (a factor known to influence competition and persistence in this system) and coupled sources and sinks by directly manipulating immigration. As predicted, increasing the amount dispersal among local communities with differing temperature regimes promoted local coexistence and homogenized composition within metacommunities. Even with 50% of the individuals in communities dispersing every few generations, we did not see negative effects of dispersal on local diversity or diversity across the entire metacommunity, possibly because the rate of competitive exclusion of superior competitors at the metacommunity level was small enough that extinction did not occur in local “sinks” before another dispersal event occurred. Our results support the hypothesis that source-sink dynamics can promote local coexistence in the presence of metacommunity-scale heterogeneity and highlight the need for future

investigations of source-sink effects in communities shaped by dispersal between varying habitats.

Summary

Research presented here challenges long-held beliefs about processes limiting species richness in local communities. These results broaden our understanding of propagule limitation beyond terrestrial plant communities and highlights mechanisms of coexistence that may be unique to mobile animals. By determining how dispersal affects species coexistence in multi-trophic local and meta-communities, we may better understand and predict how changes in habitat distribution and isolation will affect the processes shaping natural communities.

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CHAPTER 1:
**PROPAGULE SUPPLY CONTROLS GRAZER COMMUNITY STRUCTURE AND
PRIMARY PRODUCTION IN A BENTHIC MARINE ECOSYSTEM**

Abstract

Early theories of species diversity proposed that communities at equilibrium are saturated with species. However, experiments in plant communities suggest that many communities are unsaturated and that adding propagules of new species can increase species richness. We experimentally tested for community saturation and measured the effects of propagule supply on community structure in a benthic marine system. We manipulated propagule supply (arrival of individuals of numerous species) of mobile crustacean grazers in experimental mesocosms over multiple generations and, unlike all previous tests, we examined the cascading effects of propagule supply on prey (macroalgae) biomass. We found little evidence for saturation, despite the absence of processes such as disturbance and predation that are thought to alleviate saturation in nature. Increasing propagule supply increased the total number of species and made rare species more abundant. Perhaps surprisingly, given the strong effect of propagule supply on species richness, supply-related changes in body size and composition suggest that competitive interactions remained important. Grazer supply also had strong cascading effects on primary production, possibly due to dietary complementarity modified by territorial behavior. Our results indicate that propagule supply can directly influence the diversity and composition of communities of

mobile animals. Furthermore, the supply of consumer propagules can have strong indirect effects on prey and on fundamental ecosystem properties.

Introduction

Elton argued over fifty years ago that “the number of different kinds of animals that can live together in an area of uniform type rapidly reaches a saturation point” (Elton 1950). Just as saturated liquids contain as much solute as can be dissolved without precipitation, saturated communities are thought to include the maximum number of species that coexist without local extinction. Classical niche theory invokes resource partitioning and interspecific competition as processes that act in concert to keep species richness at a saturation point (MacArthur 1965). Under this niche-based definition, resources are underutilized in unsaturated communities, allowing new species to colonize and persist until resident species monopolize all available resources. Theory predicts that when species attempt to colonize an already saturated community, there is an unsustainable amount of overlap in resource use – inferior competitors will be driven extinct, returning the community to the saturation point. Thus defined, species diversity at saturation is the stable equilibrium point to which communities are naturally attracted. Whether or not communities are likely to ever reach saturation remains an unresolved yet fundamental ecological question (Elton 1950; Terborgh & Faaborg 1980; Cornell and Lawton 1992; Loreau 2000) with direct consequences for our understanding of important phenomena, such as species invasions and climate-driven range expansions (Stachowicz & Tilman 2005).

A community is predicted to be saturated given sufficient homogeneity of resources in space and time (Loreau 2000) and in the absence of external sources of mortality that

weaken competition, e.g., disturbance or predation (Caswell & Cohen 1993). Even under these stringent conditions, a community will be open to colonization at equilibrium if it is isolated from propagules of novel species (MacArthur & Wilson 1967). A propagule is the ecologically relevant unit of dispersal, defined as a colonizing organism or vegetative structure capable of establishing a self-sustaining population. Depending on a species' life history, a propagule can be a pregnant female, a mating pair, seeds or spores. Propagule limitation occurs if species that could coexist in a locality are absent because propagules do not arrive at that locality in sufficient numbers, resulting in unsaturated communities (Chesson 1998).

Community saturation can be tested directly by increasing propagule supply experimentally, i.e., by increasing or decreasing the number of potential colonists arriving at suitable habitat (Tilman 1997). As supply is augmented and propagule limitation is relaxed, a subsequent increase in richness indicates that the local community was not saturated. In contrast, failure to colonize or the competitive displacement of resident species indicates that richness was not limited by propagule supply and the community may have been saturated. Propagule-addition experiments in terrestrial plant communities suggest that propagule-limitation is widespread and that many communities are naturally unsaturated (Tilman 1997; Foster et al. 2004; Mouquet et al. 2004; Gross et al. 2005), although most relevant research has been focused at the population level (Turnbull et al. 2000; Clark et al. 2007). Populations below carrying capacity can respond to increased propagule supply with increases in population size. Thus population-level "saturation" occurs when supplying additional propagules does not increase a species' abundance, whereas community-level saturation requires that species richness remains the same when propagules are added.

Virtually all community-level propagule addition experiments have focused on terrestrial plants (Tilman 1997; Foster & Tilman 2003; Foster et al. 2004; Mouquet et al. 2004; Gross et al. 2005; but see Shurin 2000), thus the generality of these propagule supply experiments to other trophic levels or other systems remains unclear. However, decades of research have demonstrated that propagule supply structures many marine populations (Gaines & Roughgarden 1985; Gaines & Bertness 1992; Doherty & Fowler 1994; Caley et al. 1996; Hughes & Tanner 2000) and can influence composition of marine communities (Sale 1991). Research on rocky shores suggests that propagule supply correlates with changes in community structure and mediates interspecific interactions strength (Connolly et al. 2001; Menge et al. 2003; Navarrete et al. 2005) but covarying changes in environmental conditions make inference about community saturation impossible. Despite empirical evidence that propagule supply influences marine community structure and theoretical analyses suggesting that propagule supply may determine diversity in some marine communities (Warner & Chesson 1985; Chesson 1998; Chave et al. 2002), the potential for saturation at the community level remains to be tested experimentally in a marine system.

When propagule supply determines diversity and species' relative abundances, effects of supply are likely to propagate through the ecosystem. Experimental changes in diversity have predictable effects on ecosystem-level properties such as resource-use efficiency and total community biomass (Cardinale et al. 2006). Therefore, supply-driven changes in diversity could also influence ecosystem functioning. Evidence from plant communities supports this prediction; increasing propagule supply increased abundance, percent cover (Foster & Tilman 2003; Mouquet et al. 2004), and biomass (Zeiter et al. 2006) in manipulated communities. Yet, it remains unclear how alleviating propagule limitation

among consumers will affect lower trophic levels and ecosystem properties. Theoretical evidence suggests that plant biomass is strongly influenced by the rate of herbivore propagule supply and that the outcome of plant-herbivore interactions depends on relative supply rates (Loreau & Holt 2004). Increasing rates of propagule supply could increase rates of consumption via at least three mechanisms: 1) by increasing the probability that a highly efficient grazer will establish a population (a sampling effect), 2) by increasing grazer complementary resource use via increases in species richness (Bruno et al. 2008), or 3) through facilitative interactions (Dethier & Duggins 1984).

We manipulated the propagule supply of mobile marine mesograzers (Duffy 1989) in experimental communities to test for propagule limitation and local saturation of species richness and to measure the effects of propagule supply on trophic interactions and ecosystem properties. Specifically, we tested (i) whether species richness was saturated in a model community of mobile marine grazers, if saturation was dependent on a persistent source of propagules, and (iii) whether grazer propagule supply has cascading effects on functioning at lower trophic levels. We used communities of mobile grazers consisting primarily of crustaceans and mollusks feeding on a combination of macroalgae, microalgae, and algal detritus (Cruz-Rivera & Hay 2000) that disperse as juveniles and adults via drifting and rafting. Our experiment integrates several research questions by examining fundamental constraints on local species richness in a model multi-trophic system open to immigration and emigration. Spatial models have revealed that recurrent immigration can affect the stability of population sizes and consumer-prey interactions (Holt 2002; McCann et al. 2005), suggesting that a persistent supply of grazer propagules may have different effects than a

single addition of propagules. We addressed this by concurrently manipulating the magnitude and frequency of propagule supply to the mesograzer community.

Methods

Experimental design

All experiments were conducted at the University of North Carolina at Chapel Hill's Institute of Marine Sciences in Morehead City, NC. In July 2004 we established 54, 4L flow-through mesocosms supplied with gravel-filtered seawater from Bogue Sound, NC and shaded to reproduce field light conditions. We manipulated magnitude (4 levels of Magnitude: Small, Med-Lo, Med-Hi, Large) and frequency of grazer propagule additions (2 levels of Frequency: Single and Multiple) in a fully factorial design. The experiment was performed in flow-through mesocosms to control potentially confounding factors such as sampling scale, habitat complexity and flow regime and to ensure homogeneity of resources. We also included control mesocosms in which no additional grazers were added to developing communities. Six mesocosms were randomly assigned to each of the 9 treatments and every mesocosm included an artificial seagrass mimic made of frayed polypropylene (Edgar 1991). All mimics were pre-conditioned with seawater filtered by a 100 μ m filter to prevent epifaunal colonization for 3 days preceding the experiment; this allowed epiphytic algal propagules to settle and provide food for grazers. Grazers were collected from nearby habitats, added to a large holding tank and added to the experimental mesocosms according to the assigned treatments by volume (i.e., Med-Lo, Med-Hi, and Large treatments received 2, 4, and 8 times the volume of grazers added to Small treatments, respectively). Samples of propagule additions were preserved and later identified (N=20).

Grazers were initially added in the Single and Multiple frequency mesocosms in volumes determined by assigned level of supply Magnitude. Grazers were experimentally added to mesocosms in Multiple treatments weekly. Throughout the experiment, the ratio between supply magnitude treatments remained the same, although the total volume varied with availability. Some grazer propagules also colonized all mesocosms naturally via the sea water supply, thus providing a continual source of food for grazers and allowing grazer communities to develop in no addition controls. At the end of six weeks (2-3 generations for most grazer species) all grazers were collected and preserved. Algae that had settled and grown in the mesocosms were collected and wet mass measured after excess water was removed via spinning (Bruno et al. 2005). Grazers were identified to lowest possible taxonomic group; some common species were lumped by genera due to the large number of juvenile individuals. The number of gravid females was also recorded. Samples were dried to constant mass at 60°C, ashed at 450°C, and massed again to obtain ash-free dry weights.

Statistical analyses

The effects of supply Magnitude, Frequency, and Magnitude x Frequency interaction on grazer abundance, richness, evenness, Shannon-Weiner diversity, ash-free dry weight and algal biomass were analyzed via separate, fully-crossed two-factor ANOVA ($n = 6$). Effect size (ω^2) was calculated for all significant treatments (Graham & Edwards 2001). Response variables were transformed as necessary to meet the assumptions of ANOVA. For species present in sufficient abundance, separate two-factor ANOVA testing the effects of supply Magnitude and Frequency on log-transformed total abundance and percent gravid females.

To compare species composition between experimental communities, we conducted multivariate analyses on a matrix of Bray-Curtis similarities generated from 4th root transformed abundances (Clarke 1993). The effects of supply Magnitude and Frequency on compositional similarity were investigated using analysis of similarities (ANOSIM) and protected pairwise tests were performed to test for differences between levels (N=6). A hierarchical agglomerative cluster analysis with group average linking was performed on similarities to delineate samples with greater than 80% similarity in species composition. To visualize differences in composition among treatment levels, a non-metric multi-dimensional scaling algorithm was performed on similarities with 50 iterations and the 2-dimensional configuration that best preserved similarity rankings (i.e., had the lowest stress value) was used to generate an multi-dimensional scaling analysis (MDS) ordination plot.

We tested the effect of our supply treatments on the body-size distributions of the four most abundant species (N=3). Body-size distributions were obtained by counting the number of individuals retained by each of a nested series of sieves (2.8, 2.0, 1.4, 1.0, 0.71, 0.50 mm). Statistical comparison of body-size distributions by a 2-factor ANOSIM (factors = Magnitude, Frequency) performed on untransformed Euclidean distances.

Although the identity of individuals in our random propagule additions is unknown, we used preserved samples to estimate the richness of experimental treatments. Using EstimateS 8 (Colwell 2006), we generated sample-based rarefaction curves to estimate species richness as a function of accumulated samples and thus the number of species added in each propagule addition treatment (Figure A.2).

Results

Supply effects on diversity and composition

Final grazer diversity depended on the volume of propagules added (hereafter, Magnitude) and whether or not additions occurred once or recurrently (Frequency). Increasing the magnitude of propagule supply had a strong positive effect on grazer Shannon-Weiner diversity (Figure 1.1A) explaining nearly 40% of observed variation (Table 1.1). In protected post-hoc comparisons, communities receiving the greatest number of propagules had significantly higher diversity than all other treatments ($P < 0.05$ for each of the following: Large vs. Med-High, Large vs. Med-Low, Large vs. Small). Grazer diversity was also higher in treatments receiving propagule additions weekly versus a single time, although the addition Frequency effect was weaker than the effect of magnitude (Table 1.1). Interestingly, the lack of significant interaction term indicates that the positive effects of supply magnitude were not dependent on a continuous supply of propagules. The effect of propagule supply on diversity was due to concurrent increases in both the representation of less abundant species (i.e., greater evenness Figure 1.1B) and in species richness (Figure 1.1C). Communities receiving multiple propagule additions had more individuals than those receiving a single addition and this effect was greatest in high magnitude treatments (Figure 1.1D, Table 1.1).

Multivariate analysis of similarities in species composition among treatments indicated that supply also influenced species identity and relative abundances (ANOSIM: Magnitude, Global $R = 0.25$, $P < 0.001$; Frequency, Global $R = 0.35$, $P < 0.001$; Figure 1.2). Composition in the smallest magnitude treatments differed from composition in medium-high and large supply treatments (protected post-hoc comparisons; Small vs. Med-High: $R = 0.33$, $P < 0.003$; Small vs. Large: $R = 0.64$, $P = 0.001$). These results were reinforced by

hierarchical cluster analysis; at 80% similarity, communities receiving the least propagules formed groups distinct from the majority of communities receiving the greatest volume of propagules (Figure 1.2A). These composition differences among supply treatments were driven by rare species (i.e., those with abundance below 10% of total community abundance).

In addition to overall differences in grazer community composition, propagule supply had significant population-level effects. Nine species were absent in no-addition control communities despite the large number of individuals present in that treatment, indicating strong effects of propagule-limitation on species composition (Figure 1.1C). Other abundant species tended to increase in population size as the magnitude and frequency of propagule supply increased (Figure 1.3B-I, Table A.1). In contrast, two rare species, *Jassa falcata* and *Microprotopus raneyi*, were absent only in large supply treatments. The most abundant taxon, amphitoid amphipods, was significantly less abundant in large magnitude supply treatments than in all other propagule magnitude treatments (Figure 1.4a, Tukey's HSD, $P < 0.05$). This reduction in abundance had no significant effect on total amphitoid biomass (Magnitude: $F_{3, 16} = 0.008$, $P > 0.99$; Frequency: $F_{1, 16} = 0.0008$, $P > 0.97$; $M \times F$: $F_{3, 16} = 1.06$, $P > 0.39$) because increasing the magnitude of propagule supply significantly increased the proportion of large-bodied amphitoids (ANOSIM: Magnitude, Global $R = 0.20$, $P < 0.05$, Figure A.2). However, supply did not significantly affect body-size of three other abundant species, *Dulichchiella appendiculata*, *Elasmopus levis*, or *Paracerceis caudata*. There was a marginally significant positive effect of supply Magnitude on the proportion of gravid (i.e., egg-bearing) amphitoids (Magnitude: $F_{3, 40} = 2.5$, $P = 0.07$; Frequency: $F_{1, 40} = 0.004$, $P > 0.95$; $M \times F$: $F_{3, 40} = 0.52$, $P > 0.65$).

Ecosystem properties

Grazer propagule supply affected ecosystem properties at multiple trophic levels. Adding grazer propagules increased the final biomass of grazers, especially in those treatments receiving the largest and most frequent additions (Figure 1.1E, Table 1.1). Grazer supply also had cascading effects on primary production via changes in grazing intensity (Figure 1.1F). Final macroalgal biomass decreased with increasing magnitude of propagule supply, however frequency of additions had no significant effect (Table 1.1).

Discussion

Despite conditions that favored competitive exclusion, we found no evidence for saturation of grazer species richness or diversity – both were strongly dependent on the magnitude and frequency of propagule supply, indicating propagule limitation at the community level. For species richness and diversity, comparison of communities receiving propagules at different frequencies (i.e., Single vs. Multiple) suggests that our communities were open to new species throughout our experiment. The effect of recurrent propagule additions remained constant and positive across the gradient of diversity represented in the Single treatments (Figure A.2), as indicated by the lack of a significant interaction between supply Magnitude and Frequency treatments (Figure 1.1A-B). In other words, initially high supply magnitude did not affect invasibility by subsequently added propagules. In contrast, increased frequency of propagule additions had a disproportionate effect on grazer abundance and biomass in communities receiving the greatest magnitude of propagule supply (Figure 1.1D, Figure 1.1F), possibly due to stabilizing effects of recurrent immigration on

population dynamics at high immigration rates (Holt 2002). These results demonstrate that the abundance and species richness of this experimental grazer community were propagule-limited.

Relieving propagule limitation caused significant changes in identity and relative abundances of grazer species. Similar to studies in terrestrial plant communities, changes in community composition were largely driven by the absence of rare species in the no addition controls (Foster & Tilman 2003). In our communities, four rare species (each less than 10% total abundance) were absent in Control and Small Magnitude supply treatments either because they were not strongly represented in randomly drawn additions or because colonization rates might not have exceeded rates of stochastic extinction. Of these, three species, *Melita dentata*, *Gammarus mucronatus*, and *Lembos smithi*, were also absent in field samples (see Methods), suggesting that they are locally rare. Interestingly, results from our MDS analysis (Figure 1.2) suggest that whether propagule limitation is relieved by an increase in the number propagules arriving or by more frequent arrivals, the impact on community composition is essentially the same.

By altering grazer species richness, composition and abundance, grazer propagule supply indirectly affected primary production (Figure 1.1E). Algal standing stock declined with the magnitude of grazer propagule supply, but was not affected by supply Frequency. Several mechanisms might explain the effects of grazer propagule supply on algal biomass. It could be due increased per capita consumption driven by a shift from small- to large-bodied individuals (Figure A.1); however, supply only affected the body size of amphipod amphipods and not the three other most abundant species whose abundance decreased with increasing supply (Figure 1.3). Alternatively, grazer assemblages may have consumed more

algae in high supply treatments because these assemblages were more diverse. Negative effects of consumer diversity on prey or resource abundances are well-documented (Bruno et al. 2005; Cardinale et al. 2006; Duffy et al. 2007; Bruno et al. 2008) in experimental manipulations of species identity and richness. Despite strong effects of Frequency on total grazer abundance and richness (Figure 1.1C-D), supply Frequency did not affect algal biomass in the largest Magnitude treatments. We speculate that this may be due to antagonistic interactions among grazers that limit algal consumption. An important group of grazers, amphitoid amphipods, construct and inhabit tubes that provide substrate for epiphytic algae. In the largest Magnitude treatments, our results suggest that there was strong intraspecific competition among amphitoids (see *Propagule limitation in mobile grazers*). Due to territorial behavior and interference competition, grazers may not have had access to algae growing on tubes, preventing algal biomass from dropping below ~10 g wet mass (Figure 1.1F). Based on these results, we surmise that mobile grazer behavior may modify positive effects of species richness on resource use efficiency.

Propagule limitation in mobile grazers

Methodologically, we gave every opportunity for competitive exclusion to occur; the communities persisted for multiple generations in an environment free of disturbance and predation. Still, our communities were unsaturated with species. There are at least three possible explanations. First, there may not have been enough time for species to be driven extinct by competitive exclusion. In other words, we may be observing oversaturated communities that have not yet reached equilibrium. But if time increased the probability of saturation, we would have expected to see that the effects of supply on diversity and richness

were weaker in communities receiving a Single addition (i.e., communities with the greatest time between propagule additions and the end of the experiment). This was not the case; supply effects did not vary significantly with the frequency of propagule additions (non-significant Magnitude x Frequency interactions, see Results). The behavior and life histories of mobile mesograzers also suggest that our study was of appropriate duration. Dispersal occurs rapidly and extensively in this guild; studies of mesograzer colonization observed a daily turnover rate of 30% of resident individuals in natural seagrass habitats (Edgar 1992). High mobility, combined with an experimental design that allowed emigration from mesocosms (and thus allowed both exploitative and interference competition to occur) suggest that competitive dynamics should occur rapidly in this system (Duffy & Harvilicz 2001).

A second possibility is that mobility and habitat selection behavior among these grazers increases the likelihood of propagule limitation because species leave suboptimal habitats that could nevertheless support viable populations. Stream insects have been observed to abandon habitats and enter the water column in association with poor food quality (Kohler 1985); this behavioral response to resource limitation could weaken competition and prevent saturation. Ampithoid amphipods, the numerically dominant taxa in all treatments, were least abundant in communities receiving the most propagules (Figure 1.3A). As population sizes decreased, there was a concurrent shift to larger-bodied individuals (Figure A.1) such that total ampithoid biomass did not vary with propagule supply. This result may be due to self-thinning via density-dependent mortality, as observed in sessile plant populations (Weiner 1990); however, it is more likely that shifts in abundance and size structure are driven by emigration to avoid strong intraspecific competition for food

or tube-building space. As propagule supply increased there was also a trend toward greater representation of gravid amphipod females (15.2% gravid in Small vs. 21.4% gravid in Large magnitude treatments, $P > 0.07$). Previous work suggests that juvenile and small adult amphipods are more likely to abandon habitats than mature adults because smaller individuals are poor competitors (Franz & Mohamed 1989). Together, our results suggest that increasing propagule supply may drive strong intraspecific competition and emigration from areas with unfavorable resources rather than interspecific competition that could lead to competitive exclusion and saturation.

A third possibility is that natural variability in propagule supply on short time scales keeps these communities unsaturated. In marine systems, natural variability in propagule supply can have dramatic impacts on resident communities (Gaines & Roughgarden 1985; Doherty & Fowler 1994; Caley et al. 1996; Hughes & Tanner 2000). However, experimental tests have focused predominantly on population-level effects of propagule limitation at a particular life stage (i.e., recruitment or settlement). Further, among marine and terrestrial experiments there is usually a strong seasonal component to dispersal (e.g., when seeds or larvae are produced) and the period of dispersal is short relative to species generation times. Unlike plants and sessile marine species, for which dispersal is a single, predictable event in an individual's life, our experimental organisms may disperse multiple times, multiple dispersal events occur per generation, and there are several generations per season (France & Duffy 2006). Because propagules are arriving on time scales similar to (or even shorter than) those of demographic processes, propagule supply strongly influences local community dynamics (Shurin & Srivastava 2005). In other words, the equilibrial dynamics necessary for saturation to occur may be prevented in a community with near constant dispersal. As a

consequence, we would expect to see similar unsaturated patterns in other systems where demographic rates are comparable to dispersal rates.

It is important to recognize that in an unsaturated community, not all species will be able to colonize successfully. Stochastic niche theory, which integrates the effects of propagule supply into a niche-based model of community assembly, predicts that the majority of propagules reaching a community will ultimately fail to produce viable populations due to demographic stochasticity (Tilman 2004). Several rare species found in samples of our propagule additions were not found in any of our experimental communities. These results are consistent with the only other work manipulating propagule supply in a community of mobile animals, in which communities were not saturated but several added species were unable to invade (Shurin 2000). Alternatively, novel colonists in propagule additions may exclude some resident species but still increase overall species diversity if the number of successful species is greater than the number of species lost. Although our experimental communities did not reach an apparent richness limit, two species were absent only in large magnitude supply treatments. Species released from propagule-limitation via experimentally increased supply may have suppressed competitive subordinates. Resource availability may also have affected establishment (Tilman, 2004). Algal biomass was low in communities receiving the greatest supply (Figure 1.1F) and these conditions may have been insufficient to sustain populations of *Jassa* or *Microprotopus*. Our results emphasize that lack of saturation does not infer lack of competition or population regulation in our communities, but instead that competitive exclusion does not decrease or limit species diversity.

Conclusions

Our experiment suggests that propagule-limitation occurs even in relatively open systems in which dispersal occurs frequently and rapidly. We also found strong cascading effects of propagule supply on lower trophic levels, which had not been documented previously. Our results suggest that supply alters ecosystem functioning by increasing consumption of resources and that these effects are strong enough to persist despite emigration. Additionally, our findings reinforce the idea that population regulation and competition can shape unsaturated communities via changes in composition without limiting species richness and that propagule limitation does not preclude density-dependent interactions (Chesson 1998). These results emphasize the role propagule supply plays in maintaining diverse communities and suggest that supply effects at one trophic level may cascade throughout food webs.

Tables.

Table 1.1. Results of ANOVA and calculated effect size (ω^2)

Effects of propagule supply magnitude and frequency on grazer Shannon-Weiner diversity, species richness, Pielou's evenness, abundance and biomass and algal production.

Response	Effect	df	<i>F</i>	<i>P</i>	ω^2
Grazer diversity	Supply magnitude	3, 40	13.9	<0.0001	39.2
	Supply frequency	1, 40	12.2	<0.01	11.3
	M x F	3, 40	1.31	NS	
Grazer richness	Supply magnitude	3, 40	3.2	<0.05	11.1
	Supply frequency	1, 40	7.9	<0.01	11.6
	M x F	3, 40	0.5	NS	
Grazer evenness	Supply magnitude	3, 40	10.4	<0.0001	35.7
	Supply frequency	1, 40	7.6	<0.01	6.7
	M x F	3, 40	1.3	NS	
Grazer abundance	Supply magnitude	3, 40	1.4	NS	
	Supply frequency	1, 40	14.5	<0.001	12.0
	M x F	3, 40	4.7	<0.01	8.3
Algal biomass	Supply magnitude	3, 40	6.8	<0.001	25.5
	Supply frequency	1, 40	1.8	NS	
	M x F	3, 40	2.0	NS	
Grazer biomass	Supply magnitude	3, 40	7.48	<0.001	19.8
	Supply frequency	1, 40	21.7	<0.0001	21.0
	M x F	3, 40	4.37	<0.01	10.3

Figures.

Figure 1.1. Effects of propagule supply on grazer community structure and ecosystem properties (means \pm S.E.).

Magnitude treatments indicated along x-axis. Frequency treatments indicated by symbol: ●, multiple; ○, single. Controls in which supply was not augmented indicated by ▲. (A) Grazer Shannon-Weiner diversity, (B) Grazer Pielou's coefficient of evenness, (C) Grazer species richness, (D) Total abundance of grazer individuals, (E) Grazer ash-free dry weight (AFDW), (F) Algal wet mass.

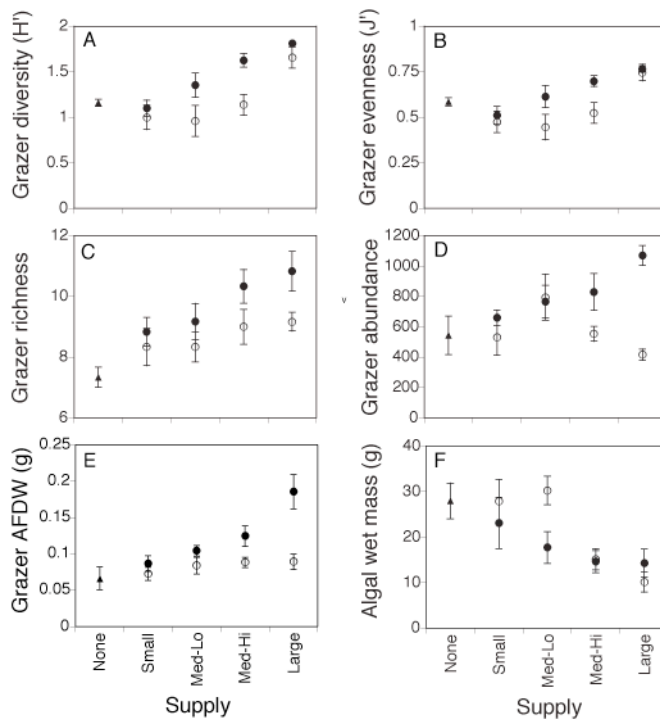


Figure 1.2. Non-metric ordination of experimental communities based on species identity and abundance.

Ordination derived from multi-dimensional scaling analysis of Bray-Curtis similarities (Stress = 0.2). Samples enclosed within circles have greater than 80% similarity in composition (see *Methods*). (A) Communities coded by supply magnitude treatment, (B) Communities coded by supply frequency treatment.

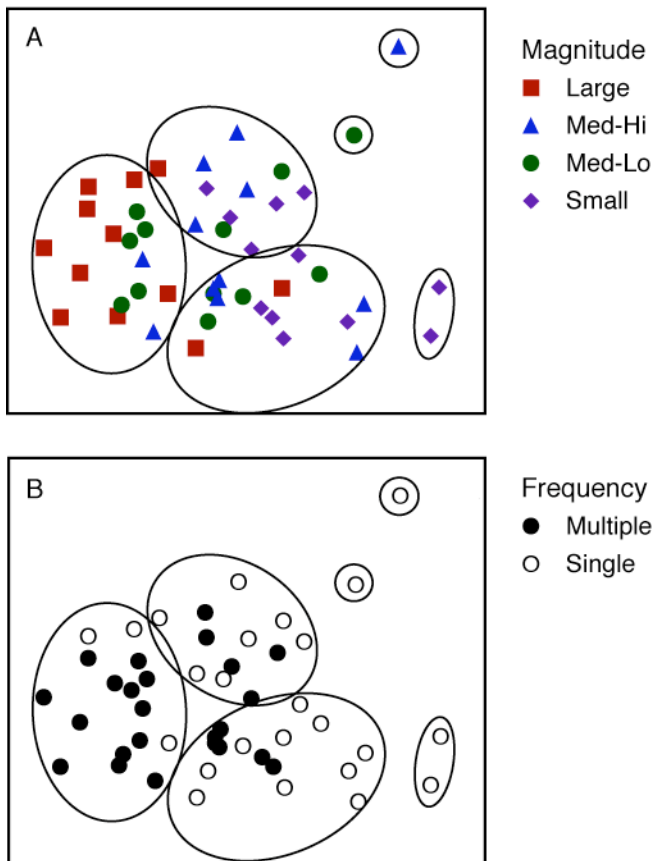
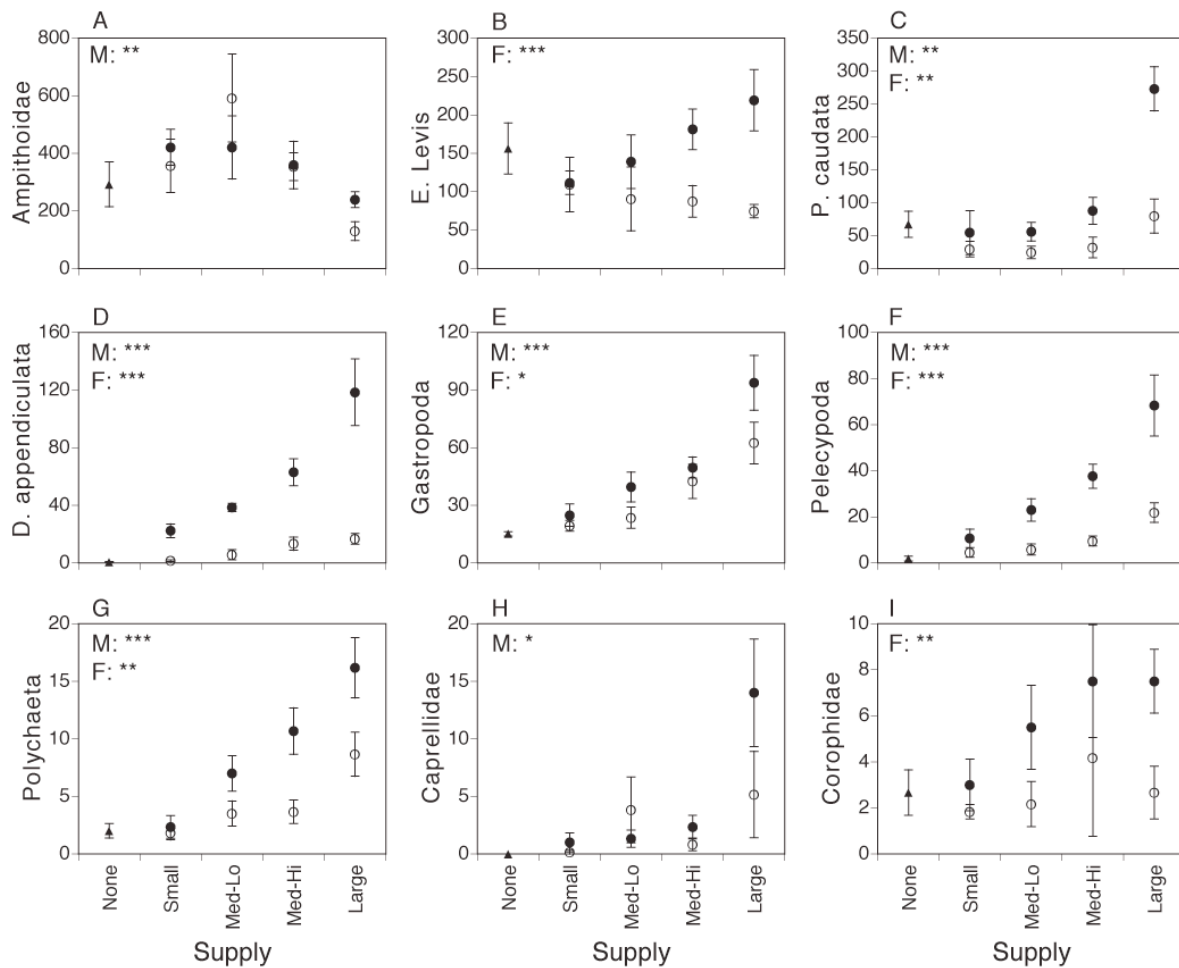


Figure 1.3. Effect of propagule supply on individual species' abundances (means \pm S.E.).

Results from 2-factor ANOVA (Factors = Magnitude, Frequency, N=6) performed on log-transformed abundances indicated by asterisk (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Only significant tests are shown. There were no significant Magnitude \times Frequency interactions.

Magnitude treatments indicated along x-axis. Frequency treatments indicated by symbol: ●, multiple; ○, single. Controls in which supply was not augmented indicated by ▲.



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CHAPTER 2:

EFFECTS OF PROPAGULE SUPPLY AND RESOURCE AVAILABILITY ON LOCAL SPECIES RICHNESS IN MOBILE MARINE GRAZER COMMUNITIES

Abstract

Though the importance of propagule limitation in determining local species richness is widely recognized, how resource availability could affect the strength of propagule effects is less clear. Despite the central nature of this question, the effect of resource availability on propagule limitation has been tested exclusively with terrestrial plants. We tested the environmental context-dependency of propagule supply effects by manipulating primary productivity (i.e. rate of algal prey growth) and grazer propagule supply in a flow-through mesocosm system. We also examined secondary effects of grazer propagule supply on algal prey communities. Increasing light availability increased both algal biomass and species richness. Despite this increase in food availability and diversity, algal resource availability had no effect on grazer propagule limitation. Instead we found that grazer propagule supply had strong positive effects on grazer richness, at all resource levels. These results highlight important differences in resource use between sessile producers and mobile grazers and suggest fundamental differences in how consumers and plants respond to resource enrichment.

Introduction

Many ecological communities are unsaturated with regard to the number of species that could potentially inhabit them (Srivastava & Lawton 1998; Foster & Tilman 2003; Stohlgren et al. 2008; Lee & Bruno 2009). Thus, in many cases, local species richness is ultimately determined by propagule availability instead of being limited by competition for resources, as is the prevailing paradigm (Stohlgren et al. 2008). Though the importance of propagule limitation has been demonstrated, experimental evidence indicates that the strength of propagule limitation varies with habitat productivity (Foster et al. 2004; Stein et al. 2008), presumably because the factors regulating species richness shift along gradients of resource availability (Partel et al. 2000). However, it has proven difficult to reconcile these results with theoretical predictions of how competition and resource availability should affect community responses. Consequently, the environmental context-dependency of propagule limitation remains unclear (Harrison & Cornell 2008) despite its importance in determining community assembly and invasion dynamics (Lockwood et al. 2005).

The interactive effects of propagule limitation and resource availability on local species richness can generate at least three hypothetical relationships (Fig.1, also Foster et al. 2004,). First, propagule limitation could be constant across a resource gradient resulting in equal, positive effects of propagule addition at all resource levels (Fig.1a). This hypothesis does not preclude effects of resource enrichment on local richness; rather it posits that no resource environment is more amenable to the establishment of novel species than another. Evidence from seed additions in grassland communities indicates that, while biomass removals and fertilizer additions can impact species richness, these effects do not modify

propagule limitation of richness (Wilsey & Polley 2003; Stevens et al. 2004; Gross et al. 2005).

A second group of general models of community assembly predict that propagule establishment should be more successful when per capita resource availability is greater (Tilman 1988; Davis et al. 2000; Tilman 2004) (Fig.1b). Here, available resources reflect niches unoccupied by resident species, allowing novel species to survive vulnerable life stages. Observed patterns of species invasions support these models and suggest that habitats with high resource availability are more likely to gain species via invasions (Burke & Grime 1996; Davis et al. 2000; Davis & Pelsor 2001; Thompson et al. 2001; Jiang & Morin 2004). Short-term increases in resource availability have also strengthened the effects of experimental propagule addition on plant community richness. Several studies have demonstrated that removing biomass from potential competitors (via clipping of live tissue) and increasing light availability (by removing litter) increases the positive effect of propagule additions on species richness (Lord & Lee 2001; Xiong et al. 2003; Foster et al. 2004). In these cases, increasing resource availability enhanced propagule effects by decreasing local competitive intensity.

There is also abundant evidence for a third hypothetical relationship, in which propagule effects on richness decline with resource availability (Fig.1c) and competitive intensity may increase with resource availability (Rosenzweig 1995; Waide et al. 1999; Dodson et al. 2000; Mittelbach et al. 2001; Rajaniemi 2003; Chase & Leibold 2002). Propagule additions in high productivity or fertilized habitats often have weaker effects on richness than additions to unenriched communities (Foster 2001; Houseman & Gross 2006). Diminished propagule effects in high productivity habitats are likely driven by the same

mechanisms driving ubiquitous patterns of suppressed species richness under high productivity conditions (Rosensweig 1995; Waide et al. 1999; Dodson et al. 2000; Mittelbach et al. 2001; Chase & Leibold 2002). For example, propagules may be less successful in enriched habitats either because there is less environmental heterogeneity and thus fewer combinations of limiting factors and reduced niche dimension (Tilman 1982; Harpole & Tilman 2007) or because higher overall rates of population growth in high productivity habitats would result in more rapid competitive exclusion without any change in niche dimensions (Grime 1979; Huston 1999).

Despite the central nature of this question, the effect of resource availability on propagule limitation has been tested exclusively among terrestrial plants and revealed conflicting and inconclusive patterns. Unlike plants, many animals exhibit behavior and consume living, demographically dynamic prey suggesting that the relationship between resource availability and propagule limitation may vary significantly between plant and animal communities. Observational evidence suggests that propagule limitation is common in marine communities and tightly linked to productivity (Menge et al. 1997; 2003); however, this relationship has yet to be tested experimentally. We tested the environmental context-dependency of propagule supply effects by manipulating primary productivity (i.e., rate of algal prey growth) and grazer propagule supply in a flow-through mesocosm system. We also examined secondary effects of grazer propagule supply on algal prey communities. Specifically we asked 1) is species richness of grazer communities limited by propagule supply and 2) how does propagule-limitation of species richness vary across a gradient of resource availability?

Methods

Study system

We manipulated propagule supply of a suite of small mobile grazers, dominated by amphipod and isopod crustaceans (hereafter referred to as mesograzers, Nelson 1979; Duffy 1989) that feed on epiphytic algae. Mesograzers are an important food source for secondary consumers (e.g., crabs and fish) and drive seasonal changes in macroalgal community structure (Duffy and Hay 2000). Mesograzers have short, overlapping generation times on the order of 3-4 weeks. Unlike many marine organisms that disperse as minute larvae, the amphipods and isopods in our system brood their larvae and disperse primarily as juveniles and adults, thus allowing us to manipulate propagule supply by adding juveniles and adults collected from algae in the field. Thus, our manipulations of easily collected juveniles and adults are relevant to and represent realistic differences in propagule supply. It is important to note that the gravel-filtration system removes most but not all mobile epifauna propagules; this baseline community is reflected in the Control treatments. The filtration system mimics natural propagule limitation by restricting the abundance and species richness of Control communities, which are analogous to a collection of natural communities with strong biological or physical filters limiting immigration.

Experimental design

The experiment was conducted at the University of North Carolina at Chapel Hill's Institute of Marine Sciences in July 2005. We established 42, 4L flow-through mesocosms supplied with gravel-filtered seawater from Bogue Sound (34°42'W, 76°46' N). To test whether the effects of propagule supply vary with resource availability, we manipulated

grazer propagule supply and algal resource availability in a fully factorial design. In these mesocosms we manipulated the volume of grazers reaching each mesocosm (2 levels of grazer propagule supply: no addition and propagule addition). We collected nearby seagrass and algal material and transferred the attached grazers to a seawater reservoir before adding them to propagule Addition treatments at the beginning of the experiment. We manipulated resource availability by limiting the growth of grazers' primary food resource, epiphytic algae, via light reduction (3 levels of resource: Low, Medium, High). Algal propagules and nutrients were supplied via constantly replenished water from Bogue Sound. Light was manipulated via window screening to an average of 950, 1400, and 2150 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ under full sun in Low, Medium, and High treatments, respectively. Summertime full sun levels at 1m depth in the field range from 1000-1500 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$. Therefore, our High light treatment represented higher availability than average field conditions. Seven mesocosms were assigned to each of the 6 treatments and every mesocosm included an artificial seagrass mimic made of frayed polypropylene. All mimics were pre-conditioned with seawater processed by a 100 μm filter for 3 days preceding the experiment; this allowed epiphytic algal propagules to settle. At the end of 4 weeks all grazers were collected and preserved. Macroalgae that had settled and grown in the mesocosms was collected and excess water was removed via spinning. Algae were identified to species and wet mass was recorded for each mesocosm. Grazers were identified to lowest possible taxonomic group; some common species were lumped by genus due to the large number of juvenile individuals. The number of gravid females was also recorded.

Statistical analyses

Summary statistics of grazer community structure (total abundance, richness, evenness, Shannon-Weiner diversity) were calculated for all experimental communities based on grazer taxonomic identity and abundance. The effects of propagule supply, resource availability and supply-resource interaction on grazer abundance, richness, evenness, diversity and algal biomass were analyzed via separate two-factor ANOVA ($n = 7$) with resource availability as a continuous factor and propagule supply as a categorical factor in R (R Development Core Team 2008). Effect size (ω^2) was calculated for all significant treatments (Graham & Edwards 2001). Response variables were transformed as necessary to meet the assumptions of ANOVA. For species present in great enough abundance, separate two-factor ANOVA were performed to test the effects of propagule supply and resource availability on square-root transformed total abundance and percent gravid females.

To compare taxonomic abundances between experimental communities, we conducted multivariate analyses using analysis of similarities (ANOSIM) of Bray-Curtis similarity coefficients generated from 4th root transformed abundances (Clarke & Warwick 2001). The effects of supply and resource availability on compositional similarity were investigated using analysis of similarities (2-factor ANOSIM, $N=7$). A hierarchical agglomerative cluster analysis with group average linking was performed on similarities to delineate samples with greater than 60% similarity in species composition after transformation. In order to visualize differences in composition among treatment levels, a non-metric multi-dimensional scaling algorithm was performed on similarities with 50 iterations and the 2-dimensional configuration that best preserved similarity rankings (i.e., had the lowest stress value) was used to generate an ordination plot.

Results

Algal community response

Total algal biomass strongly increased with increased light availability ($\omega^2=51.1$), making our light treatments a successful manipulation of resource availability to grazers (Table 2.1, Figure 2.2A). Algal biomass also declined as grazer supply increased (Table 2.1, Figure 2.2A). Algal species richness tended to increase with light ($P=0.06$, Figure 2.2C). In control communities both algal evenness (J') and diversity increased with light, whereas in communities receiving grazer propagules, algal evenness and diversity decreased with light (Figure 2.2). Individual algal species responded differently to light and propagule supply (Figure 2.3, Table 2.1).

Grazer community response

Grazer species richness was controlled by grazer propagule supply and was virtually unaffected by light and algal resource availability (Table 2.1, Figure 2.4C). In contrast, grazer abundance was dependent on the interactive effects of resource availability and supply; algal resource availability boosted grazer abundance, but only in communities to which grazer propagules were added (Figure 2.3A, Table 2.1).

Abundance of the crustaceans *Elasmopus levis*, *Paracerceis caudata*, *Dulichella appendiculata*, and the gastropod *Bittium varium* increased significantly with increasing propagule supply but were not affected by algal resource availability (Figure 2.5, Table 2.2). Supply effects on amphipod abundance were dependent on resource availability; positive effects of supply were greatest in high resource treatments. Unlike other species,

Amphilocheus sp. abundance decreased with propagule additions and increased significantly with resource availability.

Multivariate analysis of similarities in grazer species composition among treatments indicated that propagule supply strongly influenced species identity and relative abundances (ANOSIM: Global $R = 0.61$, $P < 0.001$, Figure 2.6B). Resource availability had only marginal and statistically insignificant effects on composition (ANOSIM: Global $R = 0.06$, $P < 0.12$, Figure 2.A). These results were reinforced by hierarchical cluster analysis; at 60% similarity, communities receiving propagule additions formed a single group, distinct from communities without added propagules.

Discussion

Grazer richness was strongly propagule-limited under all resource conditions; propagule additions uniformly increased grazer species richness by 50%. There was no evidence that resource availability influenced grazer species richness (Figure 2.4C) or composition (Figure 2.6) despite strong positive effects of light manipulations on algal biomass and richness (Figure 2.2A, 2.2C, Table 2.1). Our results support the view that no resource environment is more or less amenable to the establishment of novel species (Figure 2.1A) and stand in stark contrast with experiments with primary producers where resource availability has had strong effects on local species richness (Worm et al. 2002; Hillebrand et al. 2007) and plant-based theoretical predictions (Figure 2.1B, 2.1C) that competitive exclusion and niche availability should vary with productivity (Grime 1979; Huston 1999; Tilman 2004).

We found that grazer abundance, but not species richness, responded to resource manipulations. We expected that resource availability might modify the effects of propagule supply via resource effects on population densities because resource competition can regulate amphipod and isopod population density on short time scales (Edgar 1990; Duffy 2001). In fact, the effect of resource availability on grazer density was weak and dependent on propagule supply (Figure 2.4A, Table 2.1). This result suggests that abundant algal resources did not lead to high rates of grazer population growth in the absence of additional propagules, refuting the hypothesis that increased resource availability enhances exclusion by accelerating population dynamics (Huston 1999, Figure 2.1C). Although competitive exclusion might not occur in 1-2 generations, if competition were more intense in low resource availability habitats (as predicted by Davis et al. 2000; Tilman 2004, Figure 2.1B) or in high resource availability habitats (as predicted by Grime 1979; Huston 1999, Figure 2.1C), we would expect to see grazer evenness decrease with resource availability as species were driven extinct. Instead, high productivity did not appear to increase dominance of any particular grazer species (Figure 2.4D), although there was evidence that abundance of single taxa, *Amphilocheus spp.*, was reduced in propagule addition treatments (Table 2.2, Figure 2.5). It is possible that *Amphilocheus* is competitively inferior to species that are propagule limited. There is, however, no indication that *Amphilocheus* were suppressed more strongly in any resource treatments (Table 2.2).

Consumer-prey dynamics

In many marine and aquatic ecosystems, light can limit macrophyte production (Binzer et al. 2006). By increasing experimentally increasing light beyond ambient field

conditions, we increased both algal biomass and species richness (Figure 2.2, Figure 2.7). Surprisingly, the positive effect of light on algal resource abundance and diversity did not enhance grazer richness despite evidence that more diverse prey can support a more diverse suite of consumers (Duffy 2002; Olsen et al. 2007; Stachowicz et al. 2007). Instead of a bottom-up diversity effect, our results suggest that grazers exerted significant control on algal communities (Table 2.1, Figure 2.7). Changes in grazer community structure drive significant changes in producer diversity and standing biomass (Duffy et al. 2003; Raberg & Kautsky 2007; Bruno et al. 2008). Grazer propagule supply significantly affected abundance of three algal species, probably because of light-driven shifts in the algal palatability and differences in grazer preference (Hillebrand 2005). A meta-analysis of freshwater algal systems indicates that light effects on biomass diminished in the presence of grazing (Hillebrand 2005), which is clearly the case for *Enteromorpha* (Figure 2.5). High light conditions favor easily ingested algae (Hillebrand 2005), which may also be low in food quality due to changes in algal tissue stoichiometry (Urabe et al 2002). Nutritional requirements vary within the mesograzer guild; *Ectocarpus siliculosus* is the best growth medium for certain grazers, whereas mixed algal and animal diet most beneficial for others. *Polysiphonia sp.* and *Enteromorpha flexuosa* have less nutritional quality (Cruz-Rivera and Hay 2000). Grazers appear to actively avoid consuming *Polysiphonia* (Figure 2.5, Duffy and Hay 2000), leading to high biomass in communities with grazer propagule additions. Despite a shift to an unpalatable prey species, *Polysiphonia*, with increasing light and propagule supply, grazer abundance was highest in high light, propagule addition communities. This provides further evidence that the type of resources available did not limit grazer communities and emphasizes the complexity of multitrophic systems.

Resource use by mobile animals

Why did we find that resource availability had no effect on grazer species richness or propagule limitation? Possibly because of fundamental differences in how plants and animals use resources. Plants consume inorganic nutrients whose renewal rate is positive and donor-controlled whereas animals consume dynamic resources that can be driven extinct (Ives et al. 2005; Duffy et al. 2007). Plants that are superior resource competitors are those with the highest resource conversion efficiency, i.e., those that use fewer resources than their neighbor to obtain the same amount of new biomass (Tilman 1982; Ives et al. 2005). Competitively dominant animals are often those with the greatest capture rate, which are able to use more resources than their neighbor, but not necessarily with greater conversion efficiency. Thus, despite higher grazer population growth rates in high resources, competition may have been alleviated under high resource conditions.

Another potential difference between plant and animal systems arises from how niche heterogeneity is generated. Differences in niche availability are hypothesized to drive both positive and negative effects of resource availability on propagule effects (Tilman 1982; 2004). In primary producer communities, niche heterogeneity can be generated by variation in limiting resource identity and resource patchiness (Harpole & Tilman 2007). In mobile grazer communities, niche heterogeneity may be best characterized by algal prey diversity and composition. In our experiment, the greatest levels of algal diversity tended to occur in high light treatments (Figure 2.2B, $P = 0.06$). The trend for greater algal diversity in high productivity communities may have represented a wider range of niches for grazer species, however this did not translate to differences in grazer richness (see *Consumer-prey*

dynamics). Our results emphasize an important difference between animal and plant communities. Niche dimensionality in animals is defined largely by what is present (i.e., which prey species, in what abundance, in what physiological condition) whereas in plants, emphasis is placed on what is absent (i.e. number of limiting resources, Harpole & Tilman 2007) and resource consumption at the lowest resource levels is thought to determine species survival. Consequently, the hypothesis that high primary productivity reduces animal species richness and propagule-limitation via reduced niche heterogeneity will apply in animal communities only if high productivity is negatively related to prey diversity or variability.

Conclusions

In this experiment, propagule supply had strong positive effects on grazer richness at all resource levels. These results highlight important differences in resource use between sessile producers and mobile grazers and suggest that the mechanisms maintaining productivity-richness relationships in grazer communities are likely to be distinct from those in plant communities. Unlike plants, grazers consume resources that have their own interspecific interactions and demography. Grazer resource use and competitive ability are also dependent on a complex behaviors, including territoriality, intraguild predation, and optimal foraging. Our results emphasize that how grazer behavior modifies propagule limitation and resource competition remains an open question.

Tables.

Table 2.1. Results of 2-factor ANOVA testing the effects of resource and supply on grazer and algal community structure

Response	Effect	df	SS	<i>F</i>	<i>P</i>	ω^2
Grazer diversity	Resource	1	0.20	2.28	0.14	37.3
	Supply	1	1.19	13.7	0.0006	
	Resource x Supply	1	0.07	0.83	0.37	
	Error	38	3.29			
Grazer richness	Resource	1	2.93	0.48	0.48	35.1
	Supply	1	130	22.3	0.0001	
	Resource x Supply	1	0.81	0.14	0.71	
	Error	38	222			
Grazer evenness	Resource	1			NS	
	Supply	1			NS	
	Resource x Supply	1			NS	
	Error	38				
SqRt (Grazer abundance)	Resource	1	56	2.28	0.14	65.8
	Supply	1	1200	49.2	0.0001	
	Resource x Supply	1	106	4.32	0.04	
	Error	38	930			
SqRt (total algal biomass)	Resource	1	69	36	0.0001	51.1
	Supply	1	52	27	0.0001	19.1
	Resource x Supply	1	0.81	0.42	0.52	
	Error	38	73			
Algal diversity	Resource	1	0.51	7.09	0.01	18.0
	Supply	1	0.09	1.31	0.26	
	Resource x Supply	1	0.54	7.50	0.009	19.3
	Error	38	2.74			
Algal richness	Resource	1	2.78	3.74	0.06	11.9
	Supply	1	0.38	0.51	0.48	
	Resource x Supply	1	0.41	0.54	0.47	
	Error	38	28.3			

Algal evenness						
Resource	1	0.46	4.64	0.04	10.7	
Supply	1	0.010	0.10	0.76		
Resource x Supply	1	1.05	10.5	0.002	28.2	
Error	38	3.80				
Ectocarpus						
Resource	1	209	7.08	0.01	9.3	
Supply	1	2190	74.4	0.0001	56.1	
Resource x Supply	1	76.1	2.58	0.12		
Error	38	1120				
SqRt (Polysiphonia)						
Resource	1	6.23	3.92	0.05	9.8	
Supply	1	15.6	9.86	0.003	14.7	
Resource x Supply	1	4.21	2.66	0.11		
Error	38	60.3				
SqRt(Enteromorpha)						
Resource	1	46.3	47.3	0.0001	38.9	
Supply	1	26.7	27.2	0.0001	11.0	
Resource x Supply	1	38.8	39.6	0.0001	17.6	
Error	38	37.2				

Table 2.2. Results of 2-factor ANOVA testing the effects of resource and supply on grazer species (fixed, nominal effects)

Response	Effect	df	SS	F	P	ω^2
SqRt (<i>Elasmopus</i>)						
	Resource	1	3.19	0.14	0.70	
	Supply	1	360	16.5	0.0002	
	Resource x Supply	1	57.9	2.64	0.1123	
	Error	38	833			
SqRt (<i>Ampithoidae</i>)						
	Resource	1	74.5	10.14	0.0029	
	Supply	1	611	83.27	0.0001	
	Resource x Supply	1	108	14.72	0.0005	
	Error	38	279			
SqRt (<i>Paracerceis</i>)						
	Resource	1	0.0002	0.00	0.99	
	Supply	1	60.72	9.05	0.0046	
	Resource x Supply	1	0.18	0.027	0.87	
	Error	38	255			
SqRt (<i>Dulichella</i>)						
	Resource	1	0.47	0.08	0.78	
	Supply	1	554	97.7	0.0001	
	Resource x Supply	1	2.60	0.46	0.50	
	Error	38	773			
SqRt (<i>Amphilocheus</i>)						
	Resource	1	26.6	5.63	0.0227	
	Supply	1	34.1	7.21	0.0107	
	Resource x Supply	1	5.89	1.25	0.27	
	Error	38	179			
SqRt (<i>Bittium</i>)						
	Resource	1	6.42	3.71	0.0613	
	Supply	1	104	60.2	0.0001	
	Resource x Supply	1	4.52	2.62	0.1139	
	Error	38	65.6			

Figures.

Figure 2.1. Three hypothesized relationships between resource availability and propagule limitation.

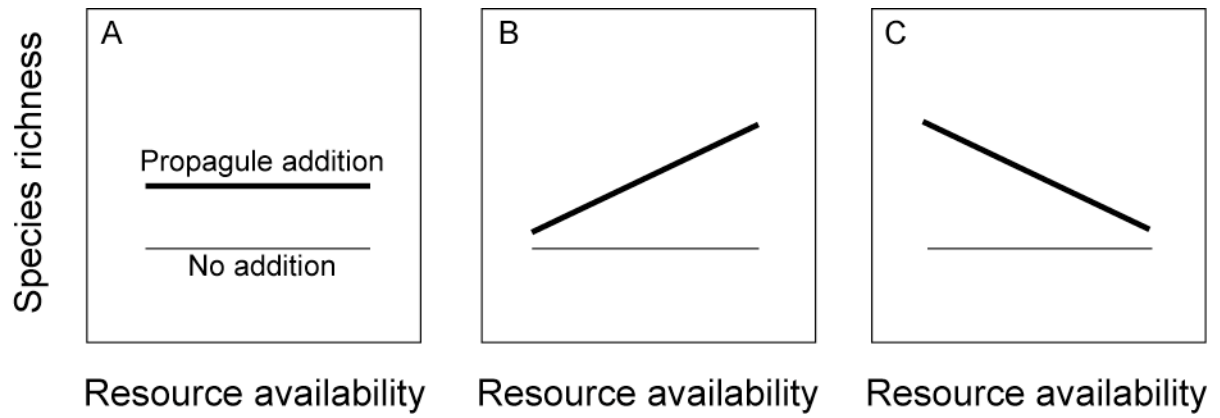


Figure 2.2. Effects of propagule supply and light availability on algal community structure (means \pm S.E.).

Resource availability treatments indicated along x-axis. Propagule addition treatments indicated by symbol: ●, propagule addition; ○, no addition. (A) Algal wet mass, (B) Algal Shannon-Weiner diversity, (C) Algal species richness, (D) Algal Pielou's coefficient of evenness.

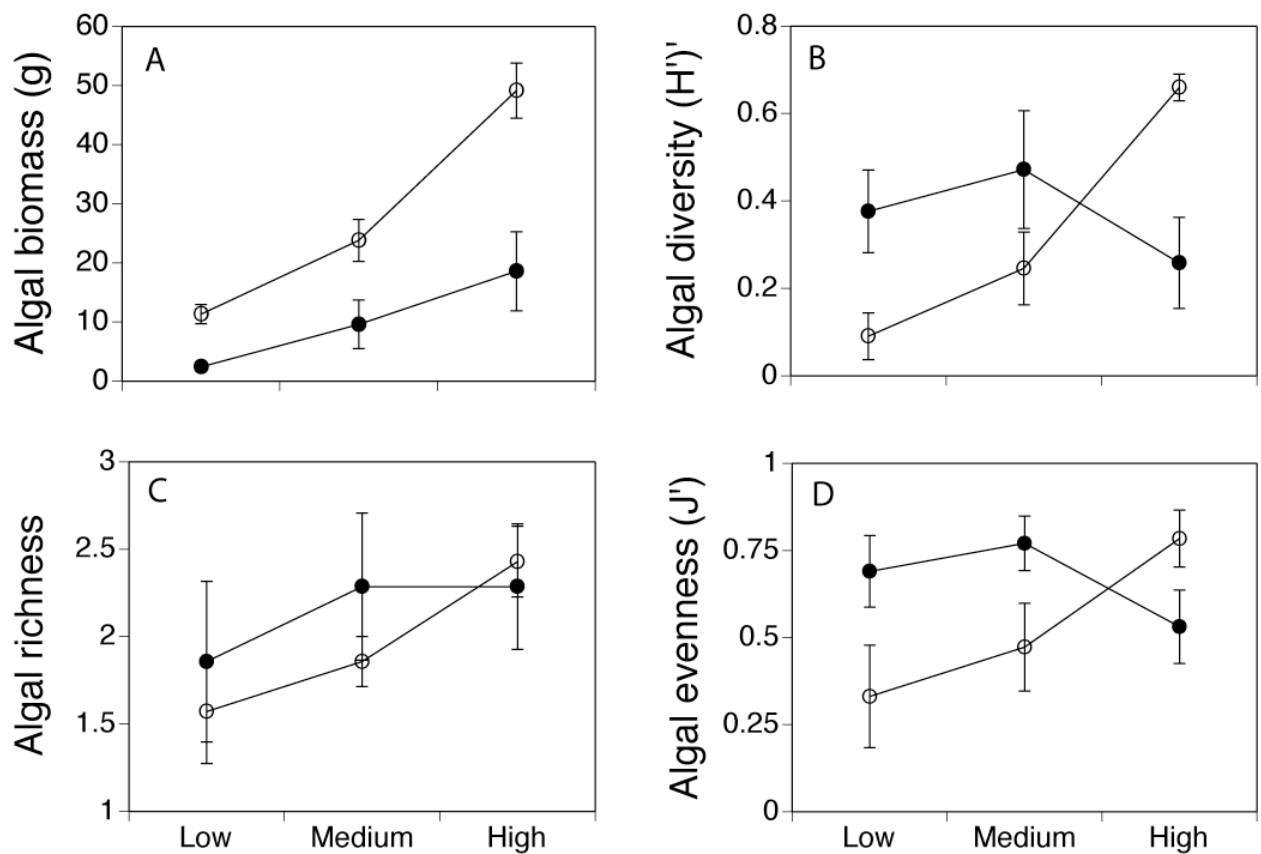


Figure 2.3. Effect of propagule supply on individual algal species (means \pm S.E.).

Propagule addition treatments indicated by symbol: ●, propagule addition; ○, no addition.

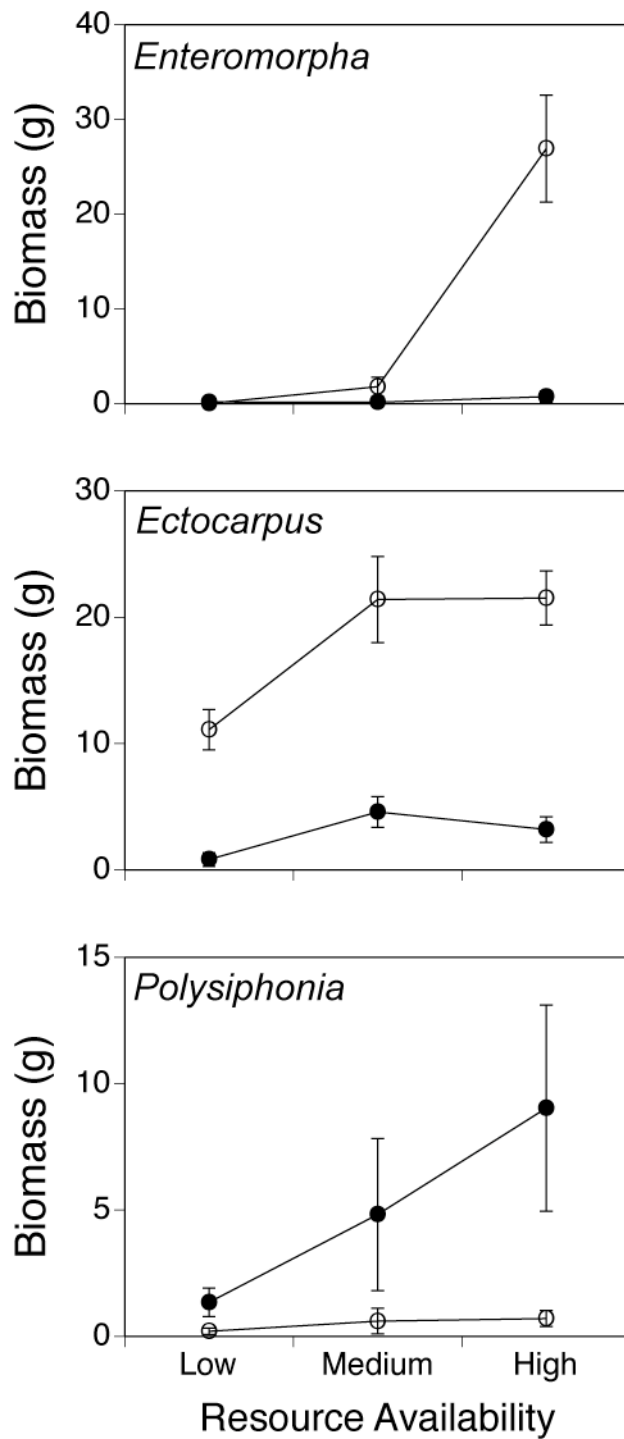


Figure 2.4. Effects of propagule supply and resource availability on grazer community structure (means \pm S.E.).

Resource availability treatments indicated along x-axis. Propagule addition treatments indicated by symbol: ●, propagule addition; ○, no addition. (A) Grazer wet mass, (B) Grazer Shannon-Weiner diversity, (C) Grazer species richness, (D) Grazer Pielou's coefficient of evenness.

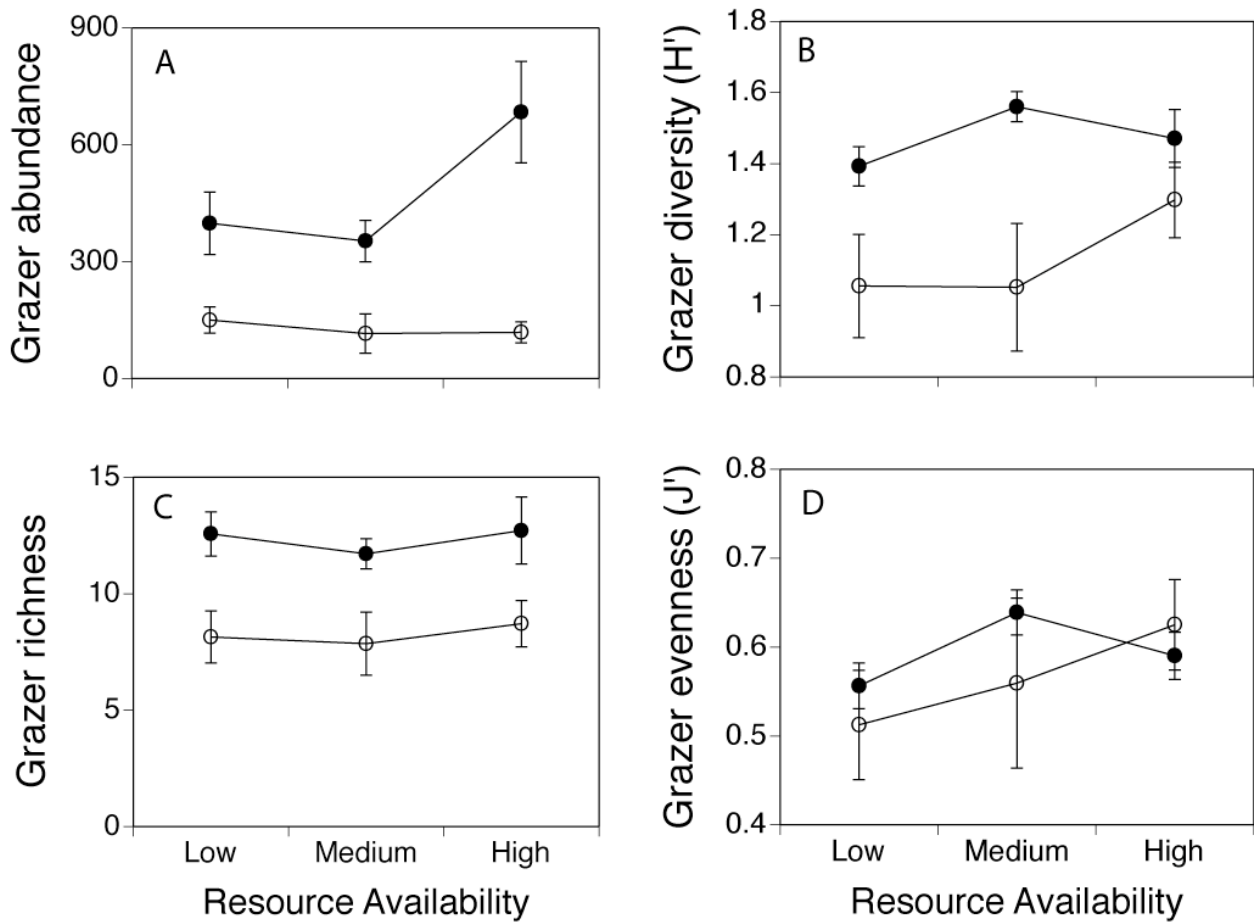


Figure 2.5.

Effect of propagule supply on individual grazer species (means \pm S.E.).

Propagule addition treatments indicated by symbol: ●, propagule addition; ○, no addition.

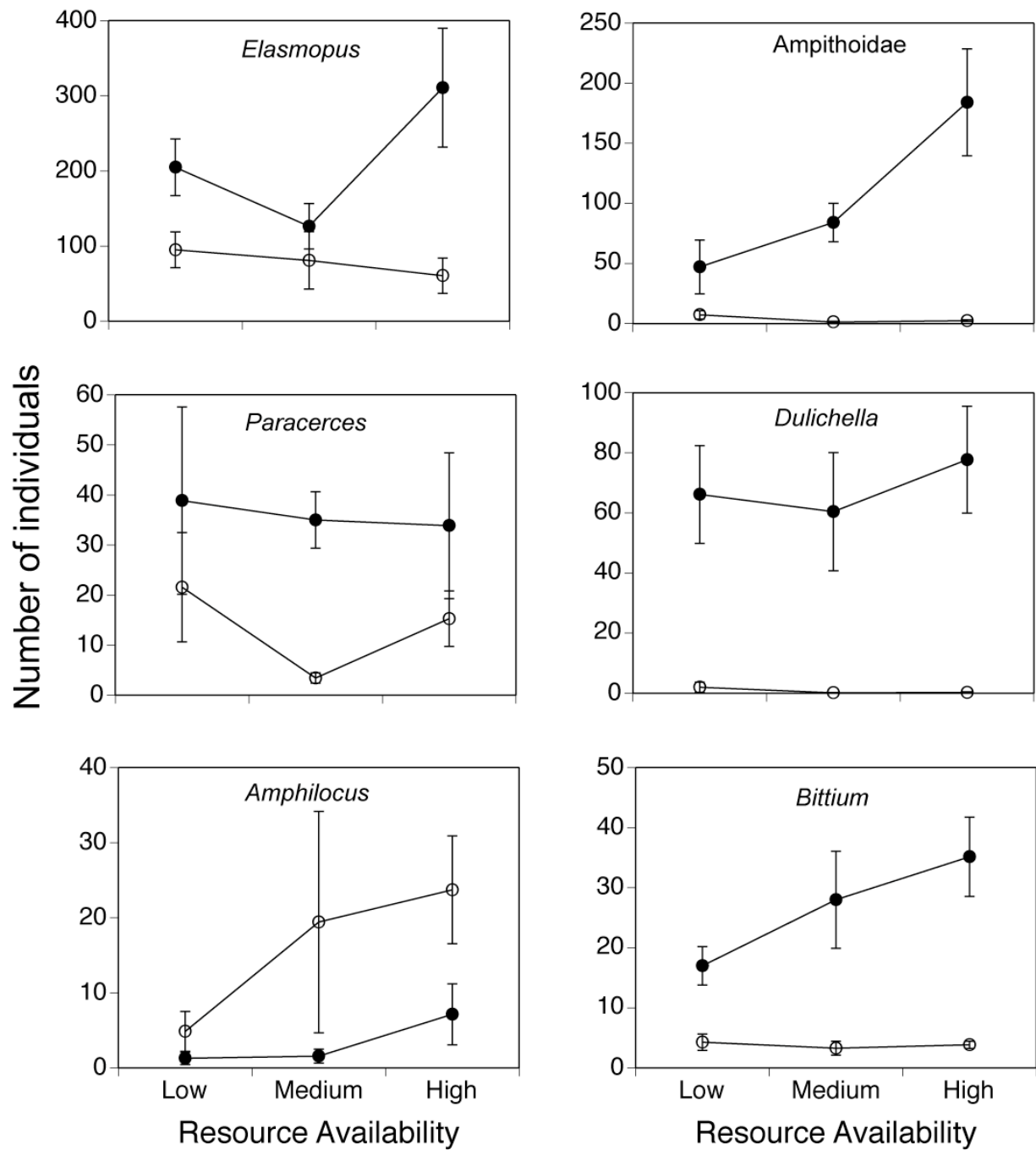


Figure 2.6. Non-metric ordination of experimental communities based on species identity and abundance.

Ordination derived from multi-dimensional scaling analysis of Bray-Curtis similarities (Stress = 0.2). Samples enclosed within circles have greater than 60% similarity in composition (see *Methods*). (A) Communities coded by resource availability treatment, (B) Communities coded by propagule supply treatment; ●, propagule addition; ○, no addition.

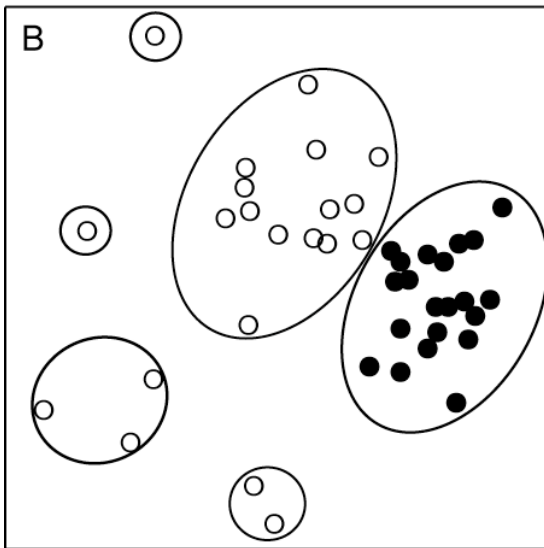
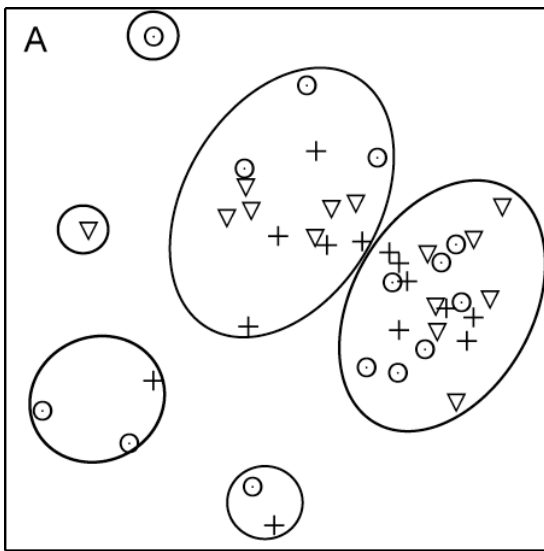
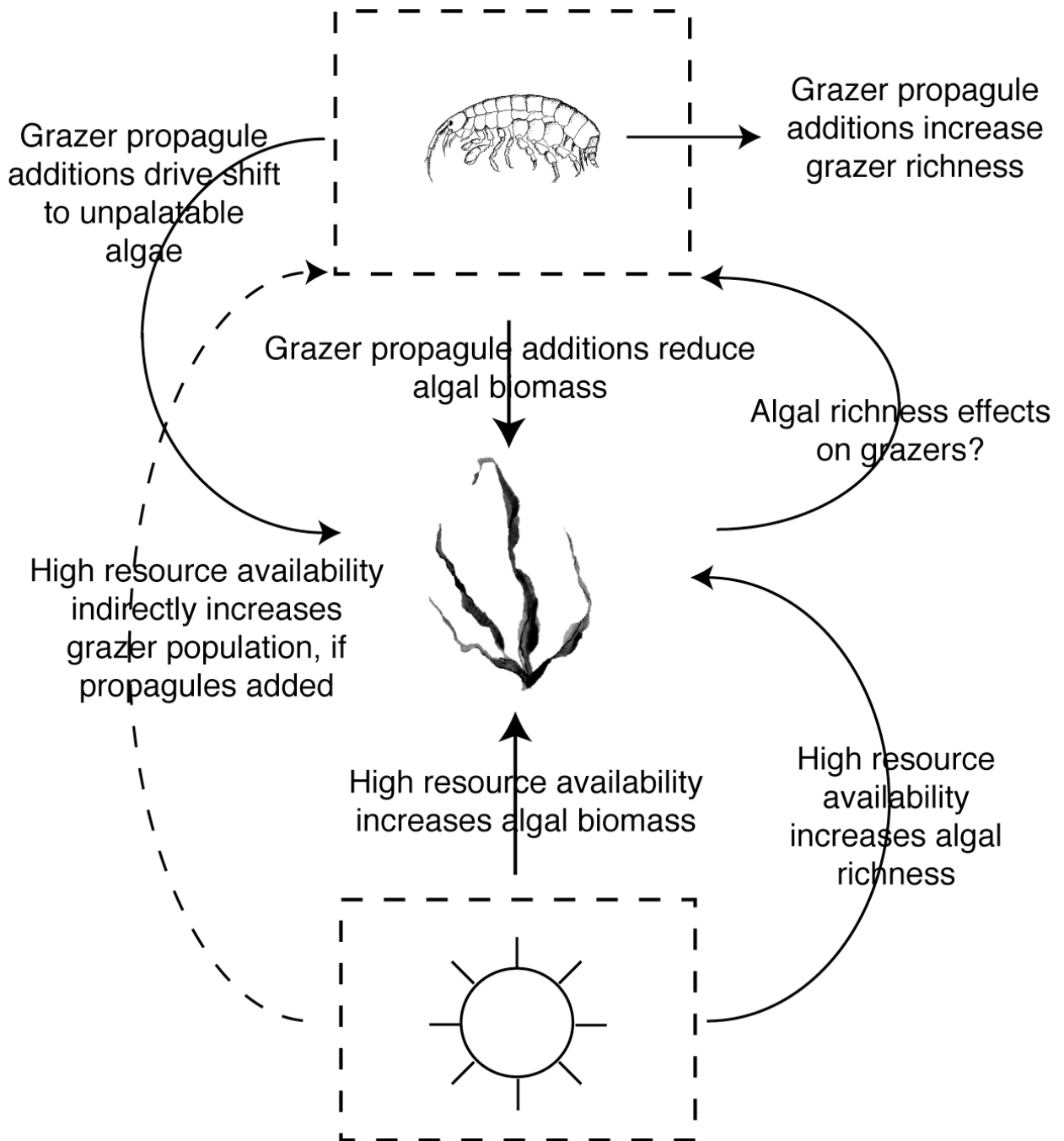


Figure 2.7. Schematic summary of results



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CHAPTER 3

AN EXPERIMENTAL TEST OF SOURCE-SINK DYNAMICS IN A MULTI-TROPHIC-LEVEL METACOMMUNITY

Abstract

Models of source-sink dynamics predict that dispersal can promote local species coexistence in heterogeneous environments by subsidizing populations in “sinks” that would otherwise go extinct without individuals from habitats where there is positive population growth (i.e., “sources”). Here we examine source-sink dynamics in a model community with multiple trophic levels. We generated population sinks by manipulating temperature (a factor known to influence competition and persistence in this system) and coupled sources and sinks by directly manipulating immigration. We examined the relationship between dispersal and species richness, relative abundances, resource use and demographic synchrony. As predicted, increasing the amount dispersal among local communities with differing temperature regimes promoted local coexistence and homogenized composition within metacommunities. However, even with 50% of the individuals in communities dispersing every few generations, we did not see negative effects of dispersal on local diversity or diversity across the entire metacommunity. Species dominance shifted from a strong local competitor in the absence of dispersal to a generally weaker competitor when 50% of the community underwent dispersal. Basal resources (bacteria) were most abundant at intermediate dispersal levels (10%), indicating that resource use by bacterivores may have

declined in the presence of higher levels of dispersal. Dispersal had a slight positive effect on temporal synchrony of communities. Our results support the hypothesis that source-sink dynamics can promote local coexistence in the presence of metacommunity-scale heterogeneity and highlight the need for future investigations of source-sink effects in communities shaped by dispersal between varying habitats.

Introduction

Metacommunity theory provides a predictive framework for understanding community structure and dynamics at multiple spatial scales (Leibold et al. 2004; Holyoak et al. 2005). A metacommunity is defined as an interactive group of local communities linked by dispersal of one or more species (Wilson 1992). The metacommunity perspective focuses, in part, on spatial mechanisms for coexistence. Dispersal between local communities can promote local and metacommunity species coexistence by altering competitive outcomes. For example, trade-offs between competitive and colonization ability allow poor competitors that are good dispersers to persist at the metacommunity level even though they cannot coexist at the local level with better competitors (Leibold et al. 2004; Mouquet et al. 2005). However, given spatial heterogeneity within a metacommunity, species can coexist without invoking trade-offs in life history traits via source-sink dynamics. Dispersal can also promote species coexistence by altering outcomes of predator-prey interactions (Holyoak and Lawler 1996), allowing predators and prey to coexist across a metacommunity when they are unable to coexist within local patches.

Early formulations of source-sink effects focused on the role of rapid (i.e., on the same time scale as competitive interactions) dispersal in allowing fugitive species to persist

in a multi-patch system by being superior colonizers (Levin 1974). Dispersal can also reduce extinction rates in target communities, thus increasing species richness at equilibrium (rescue effect, *sensu* Brown & Kodric-Brown 1977). Rescue effects operating on population demography are referred to as mass effects (Shmida & Ellner 1984). Mass effects occur where input of individuals from habitats where there is positive population growth (i.e., “sources”) can maintain populations in “sinks” that would otherwise go extinct. The result is species remain present in patches where they would otherwise be rapidly excluded (Shmida & Ellner 1984; Pulliam 1988). At the community level, sources and sinks can be generated by spatial heterogeneity in either fitness or abiotic environmental conditions such that competitive rankings vary across a metacommunity (Amarasekare & Nisbit 2001). Spatial heterogeneity would thus promote coexistence by maintaining different competitive outcomes among local habitats, thus providing spatial refuges from competitive exclusion (Muko & Iwasa 2000).

Although several numerical models have examined source-sink dynamics for a single or two competing species (e.g., Pulliam 1984; Muko & Iwasa 2000; Hoopes et al. 2005), few have made clear predictions for species-rich communities. A notable exception is Mouquet and Loreau’s (2003) investigation of the community structure and functioning in source-sink metacommunities with spatial heterogeneity. Similar to previous work, this model predicts that local species richness is greatest at intermediate levels of dispersal. They argued that without dispersal, the best competitor for local conditions dominates and at very high dispersal, the species that is most successful under all conditions dominates (i.e., the best metacommunity-scale competitor). Species turnover (i.e., beta richness *sensu* Lande 1996) between local communities declines as increased dispersal homogenizes species composition

and eliminates spatial refugia for poor competitors (Mouquet & Loreau 2003; Mouquet et al. 2005) – a result also supported by earlier models (Brown & Kodric-Brown 1977; Shmida & Ellner 1984). Metacommunity species richness appears to be maximized at low to intermediate dispersal when local communities are dominated by the best local competitor and declines as weak competitors at the metacommunity are driven extinct in all habitats. The effect of dispersal on species richness across spatial scales is mirrored by changes in composition; dominance shifts from good local competitors to good metacommunity competitors with increasing proportion of dispersal (Mouquet & Loreau 2003). There are few models of metacommunity dynamics for systems containing two or more trophic levels, although Caswell's (1978) models show that the coexistence of predators and two competing prey can be enhanced by metacommunity dynamics.

By changing species richness and composition, dispersal in source-sink systems is also predicted to affect ecosystem properties and demographic variability. If good local competitors are also the species with the highest rate of intrinsic increase in a given environment, increasing dispersal will reduce productivity and abundance as species composition shifts toward predominance by good metacommunity competitors (Mouquet & Loreau 2003). Even in the absence of a strong relationship between local competitive ability and reproductive rate, local biomass production may decline at high dispersal levels if biomass is maximized at highest species richness (Matthiessen & Hillebrand 2006). Regardless of whether production is decreasing or increasing, dispersal should also increase demographic synchrony in time and space (Levin 1974).

Previous work examining the effect of dispersal on community structure at multiple scales has largely upheld the above predictions (Kneitel & Miller 2003; Cadotte 2006b,

Cadotte et al. 2006); however, there have been few experimental studies including spatial heterogeneity in biotic or abiotic conditions and thus allowing an examination of source-sink dynamics (Cadotte 2006a). Of those including spatial heterogeneity, dispersal manipulations have focused on the effects of dispersal presence or frequency but not the proportion of community dispersing (Fox 2007). This is an important distinction in tests of source-sink dynamics because many models and predictions are predicated on rapid dispersal altering competitive outcomes. Robust tests of existing models of source-sink dynamics should manipulate dispersal without confounding effects of timing, for example by controlling the proportion of a community that disperses without varying the frequency of dispersal events (e.g., once per generation vs. once per 10 generations).

Here we examine source-sink dynamics in a model community with multiple trophic levels including a basal level of edible bacteria, nine species of protist bacterivores, and five species of omnivorous or predatory protists. Environmental heterogeneity between local communities was introduced by creating controlled temperature differences among local communities, and the proportion of community members that dispersal was directly manipulated by mixing and transferring different volumes drawn from local communities. We used freshwater aquatic microcosms to test the following four hypotheses. As the proportion of dispersal between local communities increases, (Hypothesis 1) - local species richness is maximized at intermediate dispersal levels, beta species richness declines monotonically and metacommunity diversity declines at high levels of dispersal; (Hypothesis 2) - species dominance and composition shift from good local competitors to good metacommunity competitors; (Hypothesis 3) - productivity and resource use declines; and (Hypothesis 4) - and demographic synchrony increases.

Methods

Biological communities

Each local community was constructed by adding 100 mL of nutrient medium and two wheat seeds as a slow-release carbon source into loosely capped 200 mL Pyrex bottles. Nutrient medium was a 50:50 vol:vol mix of soil/water medium and Protist Pellet Medium (Carolina Biological Supply, Burlington, NC, USA) as described in McGrady-Steed et al. (1997). To standardize initial bacterial conditions, sterile medium was inoculated with a common suite of four bacteria (*Serratia marcescens* Bizio, *Bacillus subtilis* Ehrenberg and *B. cereus* Frankland and Frankland and *Proteus vulgaris*) 3 days prior to dividing the medium into the microcosms. All microcosms began with the same food web composition, and were established by sequentially inoculating microcosms with bacterivores (3 days after bacteria), followed by top predator/omnivores (3 days after bacteria) to allow for the establishment of sufficient prey prior to introducing consumers. Bacterivores included *Chilomonas* sp., *Tetrahymena thermophila*, *Paramecium tetraurelia*, *Spirostomum teres*, *Colpoda magna*, *Halteria* sp., and *Colpidium striatum* and predator/omnivores included *Blepharisma americanum*, *Euplotes* sp., *Didinium nasutum*, *Stentor coeruleus*, and *Dileptus cygnus*. The bacterivore *Uronema* was present in many stock cultures of different species as an additional food source, and hence was added at small densities to all treatments. Trophic positions were determined by published accounts (Foissner & Berger 1996), direct observation, and known culture requirements. All microcosms were housed in incubators without light to prevent colonization by algae. All protists came from either the Rutgers Display Garden Pond (New

Brunswick, NJ, USA) or the Carolina Biological Supply Company. Approximately once a week, 10 mL of the microcosm was removed and replaced with sterile nutrient medium to reduce the effects of accumulating waste products.

Dispersal treatments

All local communities had initially similar species compositions (see *Methods: Biological communities*). Microcosms (local communities) were housed in unlighted incubators at four different temperatures (22, 24, 30, 32 °C). Each metacommunity consisted of four local communities with one local community at each temperature to introduce meta-scale environmental heterogeneity (Fig.1). At 4 day intervals a proportion (by volume) of each local community was experimentally dispersed (Dispersal, 4 levels: no dispersal, 1%, 10%, and 50%). Dispersal events between local communities were accomplished by removing a fixed volume of each local community within a metacommunity, thoroughly pooling and mixing those volumes, and equally dividing and redistributing it between local communities. There were 5 replicate metacommunities at each of the four dispersal levels, for a total of 20 metacommunities and 80 local communities (bottles).

Sampling

To facilitate sampling, communities were initially assembled and sampled in two temporal blocks, staggered by 1 day apart. No blocking effects were statistically detectable and blocks are not included in the analyses described below. Communities developed for 5 days after predator/omnivore additions before the first dispersal event occurred. Sampling of communities began two days after the initial dispersal event (i.e., “Day 1” is the first

sampling event, 7 days after omnivore/predator addition). Thereafter, sampling occurred at 4 day intervals, always 2 days after each dispersal event. Density of each non-bacterial species was estimated for every local community by counting individuals from a small sample volume (0.09–0.30 mL, determined gravimetrically) removed from a thoroughly mixed microcosm. Protists were counted live using a Nikon SMZ-U dissecting microscope. Samples were diluted by a known amount if protest densities were too high to count accurately in the initial sample. This occurred in two sorting blocks, offset by 1 day. After 31 days, population size of each protest species was determined for every local community and total microcosm volume was scanned for rare species. Bacterial abundance was determined for each local community at the end of the experiment using acridine orange direct counts via fluorescence microscopy (Hobbie et al. 1977). All fixed samples were stored at 4°C until counts were performed by collecting cells (from formalin-fixed samples) directly on Irgalin black stained Nucleopore filters as previously described (Hobbie et al. 1977). Biomass of bacterivores and omnivore/predators was estimated using published values for average biovolumes (McGrady-Steed & Morin 2000; Fukami 2004; Cadotte et al. 2006).

Statistical analyses

Local richness and abundances was the average of all four local communities within a metacommunity to avoid pseudoreplication. Beta richness was defined as the difference in species richness at the metacommunity level and local richness (Lande 1996) and CV was calculated as the ratio of the standard deviation to the mean. The temporal dynamics of dispersal effects on species richness at different spatial scales were examined using repeated

measures ANOVA. The effects of proportion of dispersal on final richness, abundance, and biomass were tested with single factor ANOVAs.

To compare species abundances between experimental communities, we conducted multivariate analyses using analysis of similarities (ANOSIM) of Bray-Curtis similarity coefficients generated from square root transformed abundances (Clarke & Warwick 2001). The effects of dispersal on compositional similarity of averaged local communities were investigated using analysis of similarities (ANOSIM, $N=5$).

Results

Species richness patterns

Approximate equilibrium dynamics were reached 16 days (16-32 generations) after the first dispersal event (Fig.2). Initial declines in richness at all spatial scales (i.e., local, beta, and metacommunity) stabilized by day 16. Dispersal had a marginally significant effect on mean local species richness over time (Fig.2, Table 1), but did not affect beta or metacommunity species richness (Table 1). Dispersal also had strong effects on temporal variability in local richness and weak effects on spatial variability ($P < 0.087$, Table 1).

In a final census, we found that increasing the proportion of dispersal drove greater homogenization of local communities within the metacommunity (i.e., beta richness declined in response to dispersal, Fig.3). Local species richness was significantly less in no dispersal treatments than in any dispersal treatment in post-hoc comparisons; this effect was highly significant (Table 1). Metacommunity species richness remained equivalent across dispersal levels (Fig.3, Table 1).

Local and metacommunity composition

Relative abundances of each species changed with dispersal levels (Fig.4). Comparisons within each species reveal that *Paramecium tetraurelia* (a good competitor) decreased in relative abundance from no dispersal versus 1, 10 and 50% dispersal, and *Halteria* sp. (a weak competitor) increased such that the no dispersal and 50% dispersal treatments were significantly different (but neither is different from 1 or 10% treatments).

We found, on average, a weak nonsignificant trend of protist species composition in response to dispersal (ANOSIM conducted on square-root transformed local densities: Global $R = 0.085$, $P = 0.113$) and post-hoc comparisons revealed that the strongest differences were between no dispersal and 50% dispersal treatments ($P = 0.04$).

By the end of the experiment, dispersal had subtle effects on metacommunity-scale abundance of bacteria (Fig.5) as well as nonsignificant trends for the biomass of bacterivores ($P = 0.0978$) and omnivore/predators ($P = 0.0686$) within local communities (Table 1). Biomass of omnivore/predators in local communities responded to temperature differently depending on the proportion of the community dispersing; in the absence of dispersal there were no predators in any 28 and 32°C microcosms (Fig.5). This effect was ameliorated somewhat by dispersal. In 10 and 50% dispersal treatments omnivore/predators were present in most microcosms.

Discussion

Our results largely support several the predictions of source-sink metacommunity theory (Mouquet & Loreau 2003; Mouquet et. Al 2005). As predicted, increasing the proportion of dispersal between temperature regimes promoted local coexistence and homogenized composition within metacommunities (Hypothesis 1). However, even with

50% of the community dispersing every few generations, we did not see negative effects of dispersal on metacommunity or local diversity (Fig.3). Species dominance shifted from a strong local competitor (*Paramecium*) in the absence of dispersal to a generally weaker competitor (*Halteria*) when 50% of the community was dispersing (Hypothesis 2; Fig.4), suggesting that dispersal provided a refuge from competition for the competitively inferior *Halteria*. Basal resources (bacteria) were most abundant at intermediate dispersal levels (10%), indicating that resource use by bacterivores may have declined in the presence of dispersal (Hypothesis 3; Fig.5), although there was not a clear relationship between dispersal and bacterivore or omnivore/predator production. Local richness was most variable in the absence of dispersal (supporting Hypothesis 4), although there was no effect of dispersal on the temporal CV of local abundance ($P = 0.777$).

A previous meta-analysis of dispersal experiments indicated that the presence of dispersal generally increases local richness and diversity and often drives decreases in metacommunity diversity (Cadotte 2006a). Among studies, dispersal rate had a loosely unimodal relationship with local species richness, as predicted in source-sink models (Amarasekare & Nisbit 2001; Mouquet & Loreau 2003; Mouquet et al. 2005). High levels of dispersal can depress richness by causing a metacommunity to function as one large community, thus removing spatial refugia (Levin 1974; Amarasekare & Nisbit 2001). Contrary to most other studies, our experiment included a very high level of dispersal: 50% of a local community dispersing once every 4-8 generations (Cadotte 2006a). Nevertheless, we did not observe disproportionately high extinctions in response to this treatment. One possibility is that mass effects were strong enough to overcome negative interactions that would cause extinction because there was only weak competitive asymmetry at the

metacommunity level (Amarasekare & Nisbit 2001). In other words, if populations had strong local advantages in “source” populations then, even with global distribution of superior competitors, the rate of competitive exclusion of superior competitors at the metacommunity level was small enough that extinction did not occur in local “sinks” before another dispersal event occurred.

Another possibility is that predators increased coexistence in high dispersal metacommunities. Experiments testing the effect of dispersal on predator-prey interactions have found that predators can both destabilize and stabilize coexistence (Huffaker 1958; Holyoak 2000, Cadotte & Fukami 2005) and may reduce the positive effects of dispersal (Kneitel & Miller 2003 but see Robinson & Edgemon 1989). If metacommunities were functioning as single large communities, predators may have persisted because they functionally existed in a greater area with a larger prey base. These effects should depend on how specialized and area dependent predators are (Holt 2002). By the end of our experiment, omnivore/predator species were entirely absent from no dispersal communities in 28 and 32°C microcosms and from 1% dispersal, 32°C microcosms (Fig.5). If omnivore/predators stabilized coexistence of bacterivore prey, then these effects were likely greatest in high dispersal treatments.

In our experiment, equal proportions of predator and prey populations dispersed. Although this may be unrealistic in some systems, there are relevant analogues. For example, in many marine systems both prey and predators disperse as minute larvae in the pelagic environment (e.g., seastar/gastropod predators and mussel/barnacle prey in rocky intertidal systems). Our experimental test of source-sink models is particularly apt for these systems because (1) many larvae essentially enter a common pool of dispersers and are

redistributed by oceanographic forces (Roughgarden et al. 1988) and (2) larvae produced in favorable habitats (“sources”) may be transported to unsuitable habitats (“sinks”).

Theoretical models of these systems suggest that spatial heterogeneity at the metacommunity level can promote coexistence where competitive outcomes are decided by lottery (Chesson 1985; Iwasa & Roughgarden 1986; Muko & Iwasa 2000). By directly manipulating dispersal, we remove the potential species to have differential dispersal rates, thus providing a strong test of lottery models in which dispersing individuals are chosen by random draw to occupy vacant sites (Shmida & Ellner 1984).

In summary, direct manipulation of dispersal within model communities reveals that that dispersal effects may happen at relatively low proportions when dispersal occurs on similar time scales to species interactions. Our results affirm that source-sink dynamics can promote local coexistence in species-rich, multi-trophic communities and highlight the utility of the metacommunity approach in complex systems. Metacommunity models of marine communities characterized by multiple scales of interaction suggest that integrating the effect of dispersal on coexistence can improve marine reserve design (Guichard et al. 2004). In order to reach two major goals of marine conservation (i.e., maximizing biodiversity and system productivity), it may be necessary to integrate metacommunity dynamics into our current understanding of marine systems.

Tables.

Table 3.1. Results of ANOVA on the effect of dispersal on species richness at different spatial scales, temporal and spatial variability, and abundance at different trophic levels.

To test effects of richness and coefficients of variance (CV) over time, a repeated measures (RM) ANOVA was used.

Response variable		df.	<i>F</i>	<i>P</i>
Mean local richness over time (RM ANOVA)				
	Dispersal	3	3.12	0.0556
	Time	8	58.53	<0.0001
	Dispersal × time	24	2.60	0.0007
Beta richness over time (RM ANOVA)				
	Dispersal	3	3.74	0.0327
	Time	8	10.80	<0.0001
	Dispersal × time	24	0.51	0.1295
Metacommunity richness over time (RM ANOVA)				
	Dispersal	3	0.29	0.8319
	Time	8	45.92	<0.0001
	Dispersal × time	24	1.33	0.2218
Final mean local richness (ANOVA)				
	Dispersal	3	8.28	0.0015
Final beta richness (ANOVA)				
	Dispersal	3	4.75	0.0149
Final metacommunity richness (ANOVA)				
	Dispersal	3	1.12	0.3703
Temporal CV of local richness (ANOVA)				
	Dispersal	3	6.97	0.0004
	Temperature	3	1.53	0.2145
	Dispersal × temperature	9	0.84	0.5866
Spatial CV over time (RM ANOVA)				
	Dispersal	3	2.61	0.0870
	Time	8	8.41	<0.0001
	Dispersal × time	24	0.85	0.6611
Log(Metacommunity final bacteria abundance) (ANOVA)				
	Dispersal	3	3.91	0.0286
Metacommunity final bacterivore abundance (ANOVA)				
	Dispersal	3	2.49	0.0978
Log(Metacommunity final omnivore/predator biomass) (ANOVA)				

	Dispersal	3	2.88	0.0686
Log(Mean local Omnivore/predator:Bacterivore biomass) (ANOVA)				
	Dispersal	3	3.0605	0.0584

Figures.

Figure 3.1. Schematic of experimental design.

Rectangles represent temperature treatments and circles represent individual bottles. Each bottle contained a “local community”. A metacommunity consisted of 4 bottles (one from each temperature treatment) that shared a fixed volume of individuals and medium during dispersal events.

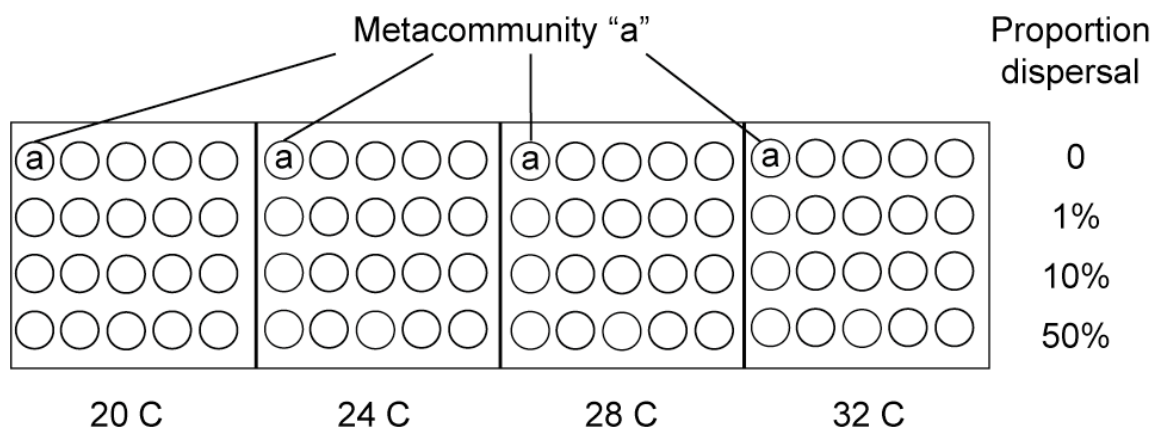


Figure 3.2. Mean (\pm S.E.) local species richness over time.

Sampling of communities began on “Day 1,” 5 days after predator/omnivore addition and two days after the initial dispersal event.

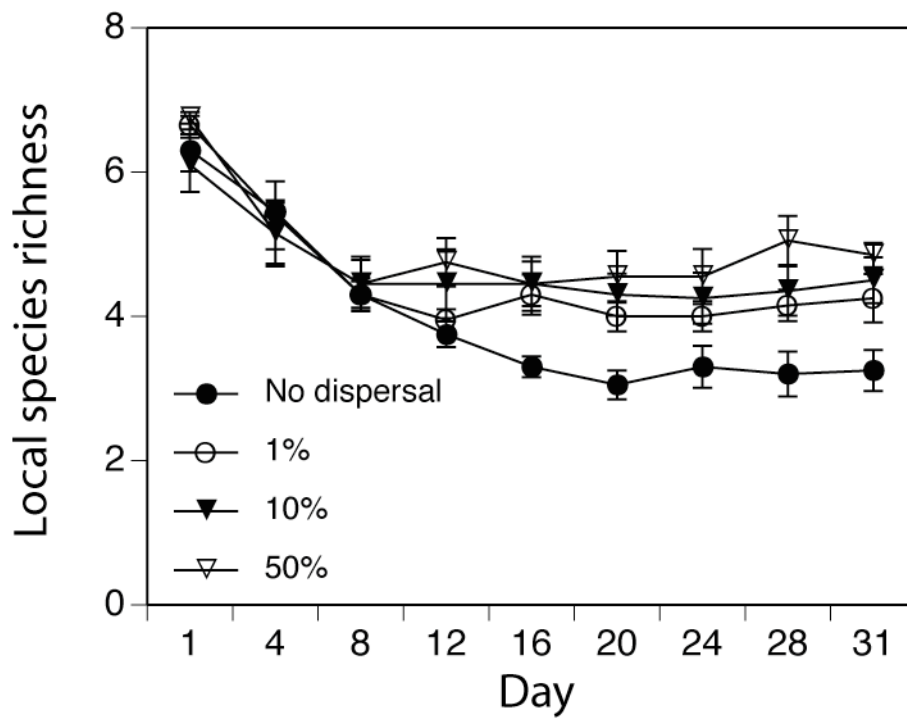


Figure 3.3. Final local, beta, and metacommunity species richness (mean \pm S.E.).

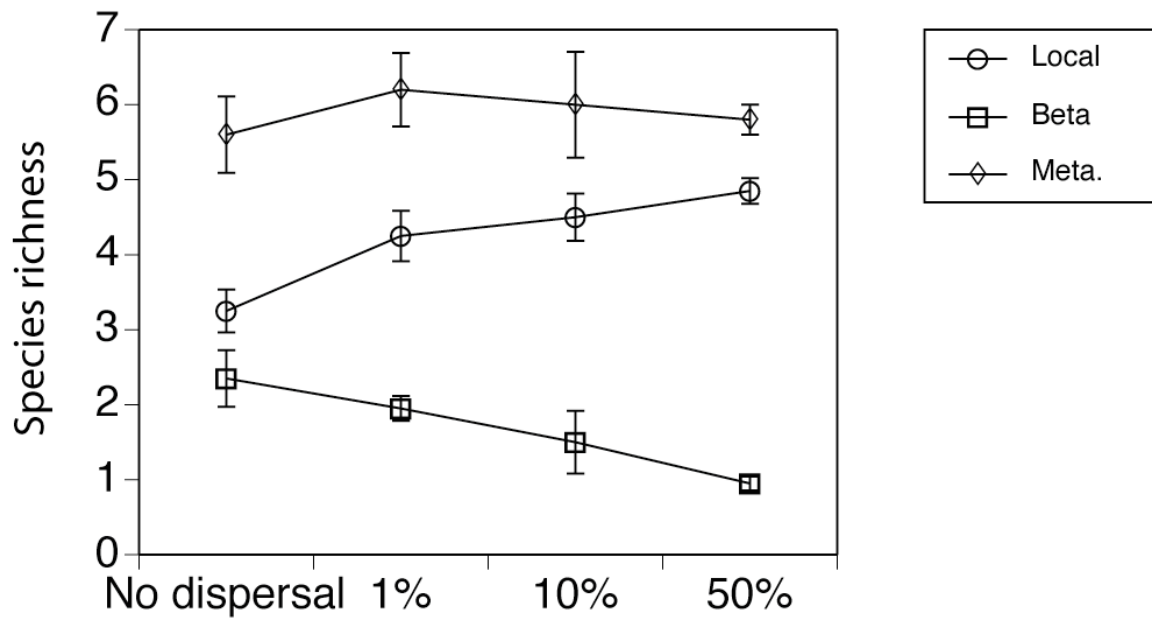


Figure 3.4. Final species relative abundances.

Different letters indicate significant differences in protected post-hoc analyses. Abbreviations are as follows: Pt = *Paramecium tetraurelia*, Ch = *Chilomonas* sp., Ur = *Uronema* sp., Eu = *Euplotes* sp., Ha = *Halteria* sp., Di = *Dileptus cygnus*, Sp = *Spirostomum teres*, Ci = *Colpoda magna*, St = *Stentor coeruleus*, Cs = *Colpidium striatum*.

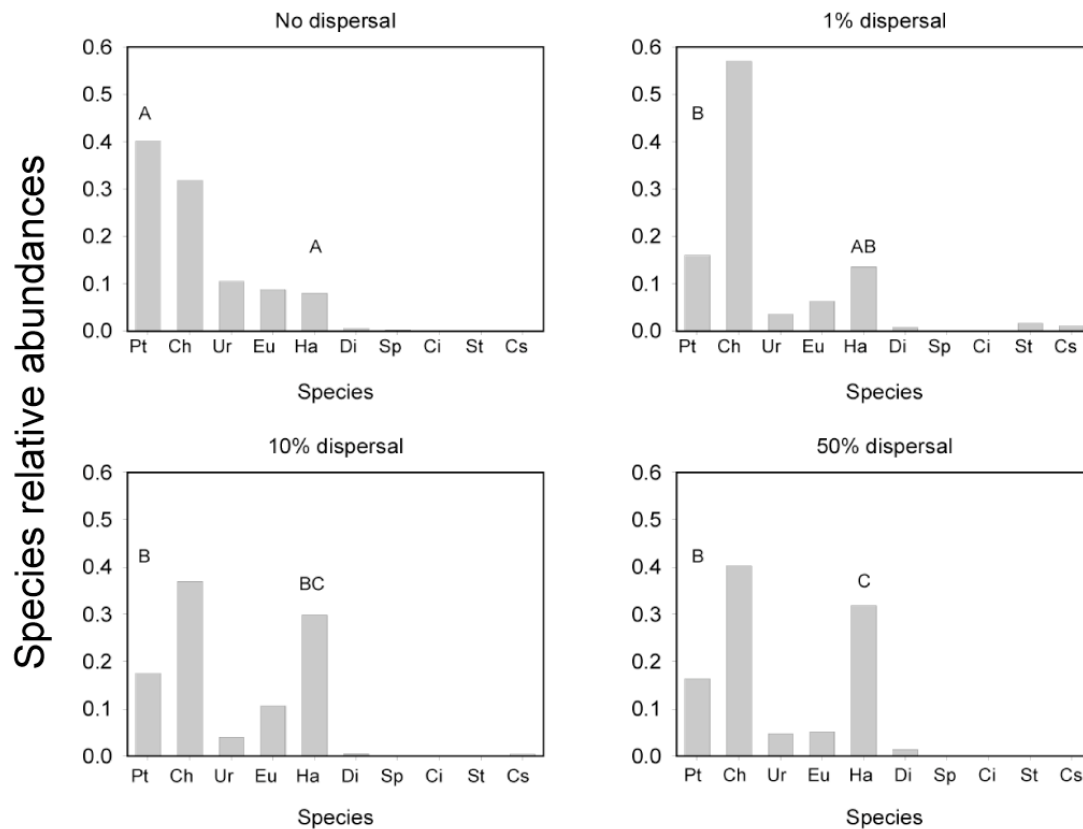
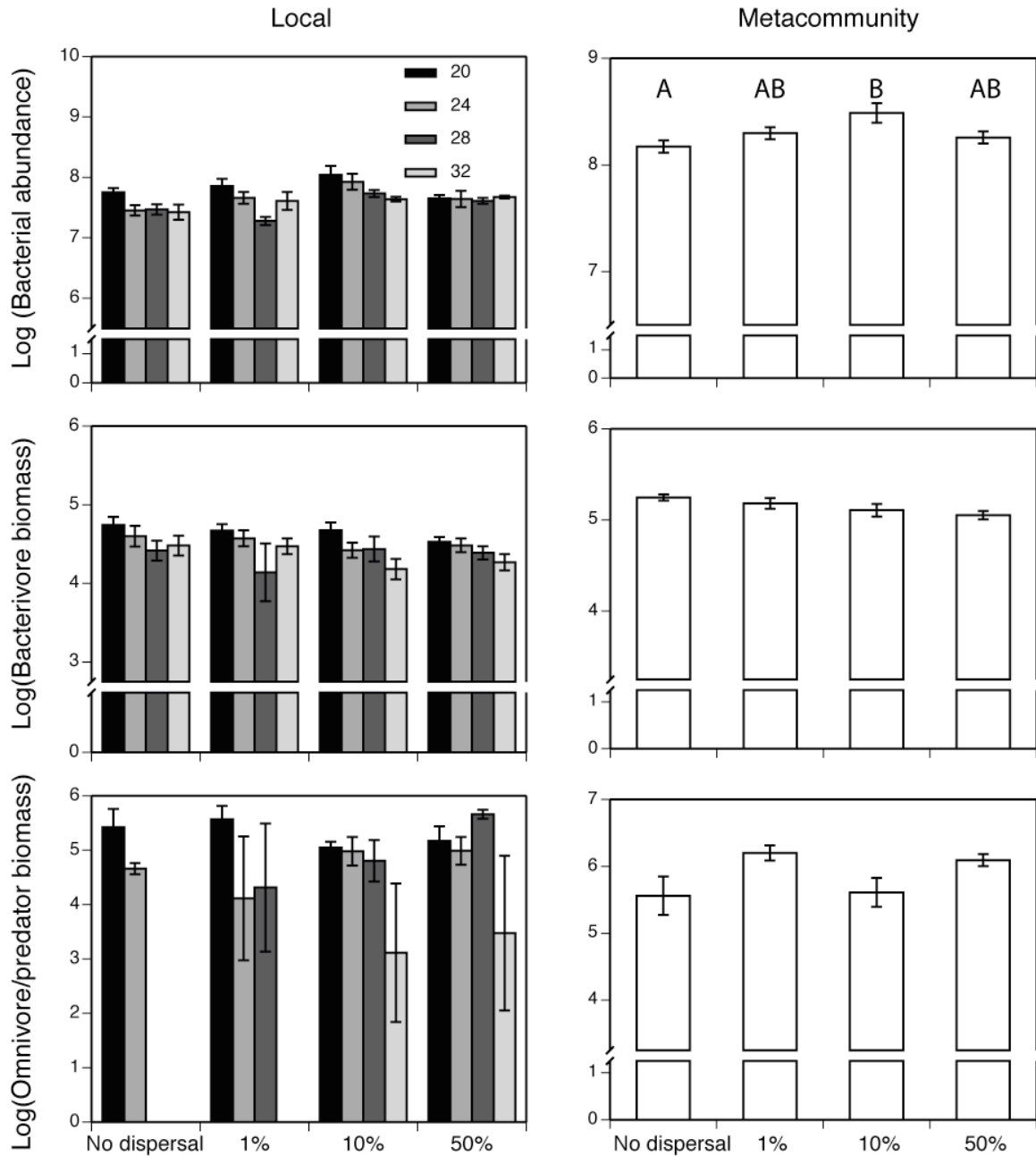


Figure 3.5. Final local and metacommunity level bacteria abundances, bacterivore biomass and omnivore/predator biomass (mean \pm S.E.).

Right panel: Bar color refers to temperature treatment. Left panel: Different letters indicate significant differences in protected post-hoc analyses.



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**APPENDIX: SUPPLEMENTARY ANALYSES AND FIGURES TO
CHAPTER 1**

**Propagule supply controls grazer community structure and primary production in a
benthic marine ecosystem**

This Appendix includes:

Supplementary Table

Supplementary Figures and Legends

**Table A.1. Results of 2-factor ANOVA testing the effects of supply size and frequency
on individual taxa abundance and percent gravid females.**

Only significant tests are listed.

Response	Effect	df	SS	<i>F</i>	<i>P</i>	ω^2
Log(Ampithoidae +1)	Supply size	3	5.8	4.8	<0.01	18.5
	Error	40	15.9			
Log(<i>Dulichella</i> +1)	Supply size	3	23.7	17.0	<0.0001	23.1
	Supply frequency	1	52.8	113.8	<0.0001	54.2
	Error	40	18.6			
Log(<i>Elasmopus</i> +1)	Supply frequency	1	5.7	16.8	<0.001	25.0
	Error	40	13.6			
Log(<i>Corophium</i> + 1)	Supply frequency	1	6.8	10.8	<0.01	17.3
	Error	40	25.4			
Log(Gastropoda +1)	Supply size	3	10.9	8.5	<0.001	31.4
	Supply frequency	1	1.9	4.4	<0.05	4.7
	Error	40	17.0			
Log(<i>Paracerceis</i> +1)						

	Supply size	3	19.1	4.8	<0.01	16.3
	Supply frequency	1	16.1	12.1	<0.01	15.9
	Error	40	53.0			
Log(Polychaeta +1)						
	Supply size	3	14.2	10.3	<0.0001	33.6
	Supply frequency	1	3.8	8.2	<0.01	8.7
	Error	40	18.4			
Log(Caprellidae +1)						
	Supply size	3	10.6	4.0	<0.05	15.3
	Error	40	35.0			
Log(Pelecypoda +1)						
	Supply size	3	21.8	14.8	<0.0001	33.1
	Supply Frequency	1	18.9	38.6	<0.0001	30.0
	Error	40	19.6			
% Ampithoidae gravid						
	Supply size	3	0.04	2.5	<0.07	
	Error	40	0.21			

Figure.A.1 Effect of propagule supply Magnitude and Frequency on proportion of amphipods in each size class (mean \pm 1 S.E., N = 3)

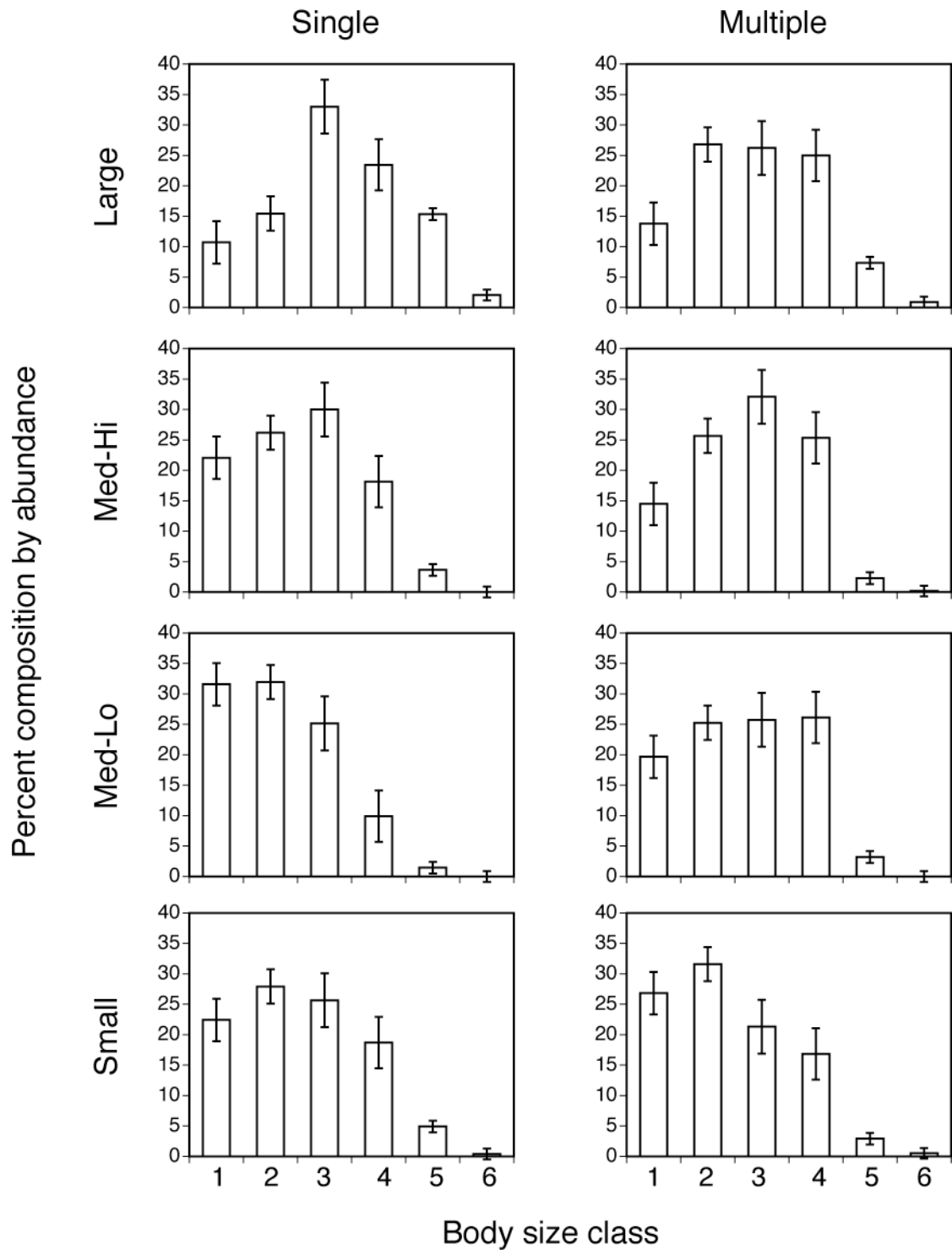


Figure A.2. Estimated number of species added and species richness observed in the field

Final grazer species richness increased significantly with the estimated number of species added ($R^2=0.24$, $N=30$, $P<0.006$; Supplement 3a). The mean number of species included in four treatment levels of grazer propagule supply was estimated using rarefaction analysis of samples taken from the initial propagule pool ($N=20$). In supply treatments receiving a single addition, small additions received an estimated 123.5 total individuals of 8.85 species; Med-Lo, 246.9 individuals of 10.25 species; Med-Hi, 493.8 individuals of 11.59 species; Large, 987.6 individuals of 12.8 species. A) MaoTao expected species richness (± 1 standard deviation) as a function of accumulated samples. B) Relationship between observed species richness and estimated number of species added for Single frequency propagule additions.

