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EFFECTS OF REGIONAL SPECIES POOL DYNAMICS ON METACOMMUNITY STRUCTURE AND ECOSYSTEM FUNCTION

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Kristin Emily France

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of
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TABLE OF CONTENTS

DEDICATION

This tome is dedicated first to my family, especially my parents, Roger and Carolyn France, and my sister, Karin, whose love and support helped me complete it.

Second, this is dedicated to all of my dear friends, especially the women of my incoming class, Lindy Dingerson, Jennifer Miselis, Courtney Schupp, Amy Shields, and Yuan Zhao; and Anne Mary Myers, the long-time friend who first pointed out that I had a prodigious talent for getting muddy in the field, and more importantly, saw it as a virtue.

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LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

ABSTRACT

Theory and small-scale experiments predict that biodiversity losses can decrease the magnitude and stability of ecosystem services such as production and nutrient cycling. Most of this research, however, has been isolated from the immigration and emigration (dispersal) processes that create and maintain diversity in nature. Since common anthropogenic drivers of biodiversity change, such as habitat fragmentation, species introductions, and climate change, are mediated by these understudied processes, it is unclear how environmental degradation will affect ecosystem services. This dissertation examines how diversity interacts with spatial processes to affect the magnitude and stability of ecosystem functions, using seagrass communities as a model system, by: 1) determining the relationship between diversity of mobile, generalist grazers and resistance to colonization by similar consumers; 2) testing the interactive effects of mobile grazer diversity and dispersal on the magnitude and predictability of ecosystem properties in seagrass metacommunities, or networks of patches connected by dispersal; 3) examining possible mechanisms for dispersal modification of relationships between diversity and ecosystem properties in these experimental metacommunities; and 4) testing whether grazer diversity and dispersal increase resistance to and recovery from the addition of macroalgae, which can outcompete seagrass and cause hypoxic stress for invertebrates.

Diverse communities were more resistant to colonization, but the order of species arrivals affected competition outcomes. As predicted, grazer metacommunities assembled from diverse species pools were more diverse at all scales, had larger grazer populations, and usually kept their primary food resource, epiphytic algae, at lower abundances than metacommunities assembled from smaller species pools. Contrary to theoretical predictions, increasing the number of mobile grazer species in these metacommunities increased spatial and temporal variability of producers and grazers. Effects of diversity on stability also differed qualitatively between patch and metacommunity scales. Moreover, allowing grazers to move among and select patches reduced diversity effects on production and modified relationships between grazer diversity and stability. Finally, dispersal significantly increased resistance to and recovery from the addition of macroalgae. Counter to theory, diversity did not. None of the existing theories for dispersal modification of biodiversity-ecosystem function relationships or consumer-resource metacommunity dynamics completely explained the patterns observed in these experiments. Effects of diversity and dispersal on ecosystem functions were complex, but seemed to be influenced by habitat choice and synchronization of grazer and epiphyte dynamics among patches. Overall, these results emphasize the importance of incorporating both spatial processes and trophic interactions into the study of biodiversity-ecosystem function relationships. This information is critical for conserving diversity and managing ecosystem services in light of the ongoing and projected changes to regional species pools caused by anthropogenic disturbance.

EFFECTS OF REGIONAL SPECIES POOL DYNAMICS ON METACOMMUNITY STRUCTURE AND ECOSYSTEM FUNCTION

INTRODUCTION

Anthropogenic habitat fragmentation, species introductions, and climate change, the three main drivers of diversity change around the globe, affect diversity patterns at multiple spatial scales. In the last decade, scientists have demonstrated that biodiversity loss at fine spatial scales, namely experimental plots or microcosms, can negatively affect the magnitude and predictability of important ecosystem services, such as production and nutrient cycling. Most of this research, though, has been conducted in isolation from spatial processes, such as immigration, disturbance, and foraging, which create and maintain diversity. Since all three drivers of diversity-change create spatial mosaics, and are mediated by dispersal of organisms, we have very limited ability to predict how they will affect ecosystem function in natural communities. Likewise, we do not know if coarser-scale patterns of diversity, such as patch heterogeneity (beta diversity), species turnover along environmental gradients (Whittaker's beta diversity)(Whittaker 1972), or the diversity of regional species pools (the set of species occurring in a region that is capable of reaching and surviving in a given location regional diversity), can also affect ecosystem function across landscapes. In order to mitigate biodiversity change, design reserves, and manage ecosystem functions that may be essential to societies, we need to understand how communities are responding to these relatively rapid changes in diversity at all spatial scales.

Regional species pools are dynamic in ecological time, primarily due to anthropogenic disturbances. Three of the major anthropogenic influences on ecosystems, habitat loss and fragmentation, climate change, and non-native species introductions, have the potential to affect regional species pools, or "the set of species occurring in a certain region that is capable of coexisting in the target community. A region is a reasonably large area of the Earth's surface, with a more or less uniform physiography and climate, from which species are expected to reach the target community" (Zobel 1997). Each of these three disturbance sources can affect the size of the regional species pool through extinctions and/or introductions. Habitat loss and non-native species introductions have been identified as the two biggest threats to global biodiversity (Wilcove et al. 1998), and (Sala et al. 2000) predict that land use and climate change will be the biggest drivers of diversity change in terrestrial systems. Habitat loss through conversion to human dominated landscapes can cause species loss from local communities and even catastrophic extinctions from regions (Brook et al. 2003). Climate change may facilitate non-native species invasions (Stachowicz et al. 2002). Introduced species can cause extinctions, they are themselves species additions, they can hybridize with native species to create entirely new species, and they may even facilitate further invasions (reviewed in Mooney and Cleland 2001).

Even when these anthropogenic forces do not cause extinctions, they can influence the abundance and distribution of species across a region, which can affect the dynamics of the pool of individuals dispersing throughout that region as well as the aggregate properties or ecosystem functions of the region. Habitat fragmentation can cause a decline in the abundance and distribution of species in a metacommunity (individuals in a regional collection of communities connected by dispersal over ecological time scales)[1] (Golden and Crist 1999, Gonzalez and Chaneton 2002, Zartman 2003), and has also been

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[1] Definition adapted from Hubbell 2001. The concept was originally outlined by (Wilson 1992).

shown to decrease community biomass (a common proxy for aggregate ecosystem function) in the remaining patches (Gonzalez and Chaneton 2002). Species ranges are already shifting in response to climate change; they are not shifting uniformly (Parmesan and Yohe 2003), however, so regional species pools are dynamic as they have not been in studied ecological time. Introduced species can restrict ranges and abundances of natives, potentially diminishing and eliminating functional roles of native species in local communities (Mooney and Cleland 2001). How the balance of these processes affect patterns of diversity both within and between patches can depend on the mechanisms of extinction and invasion (Cassey et al. 2006, Byrnes et al. 2007).

Finally, and perhaps most importantly, regional species pools may be increasing, rather than decreasing. Recent work suggests that human breakdown of biogeographic barriers and increased long distance dispersal of both terrestrial and aquatic organisms are leading to a net increase in regional species richness despite the perceived threat of invasions to biodiversity (Rosenzweig 2001, Sax et al. 2002, Davis 2003, Sax and Gaines 2003). This observed increase has been predicted by theory and models, some of which also predict a corresponding increase in richness in local communities (Brown 1995, Hraber and Milner 1997, Lockwood et al. 1997, Rosenzweig 2001). The burgeoning field of biodiversity and ecosystem function research, however, including investigations of the relationship between species richness and invasibility, continues to focus on the effects of biodiversity reductions at local scales. Although the demonstrated positive relationships between species richness and ecosystem function are generally curvilinear (reviewed in Kinzig et al. 2001, Loreau et al. 2002), it is not at all clear if, on average, adding and removing a species has the same effect (but different in sign) on ecosystem function. Indeed, some research indicates that additions and removals are unlikely to have countervailing effects. The few studies that have modeled species loss have found that removal of one species can cause cascading extinctions, and that re-introductions of removed species often fail, indicating that the removal and addition of a given species to regional pools may not have straightforward compensatory effects on community structure and stability (Borrvall et al. 2000, Lundberg et al. 2000). Furthermore, patterns of species loss and gain may increase trophic skew, as higher trophic levels tend to be lost first (Byrnes et al. 2007, Lotze et al. 2007).

The structure of regional species pools should influence local community structure and function. Ecologists have long debated the relative roles of regional diversity and local processes in determining the diversity of local communities (Ricklefs 1987, Ricklefs and Schluter 1993). While regional richness may not generally set the realized limit of species richness in local communities, it sets the upper limit by definition. There is also a fair amount of evidence suggesting that processes such as immigration that link regional species pools to local communities can play the most important role in determining local community structure. This evidence comes from both biogeographical data like local-regional richness curves and from local scale manipulative experiments. To begin with, null models of local abundance and richness based on random draws from a regional species pool are often close matches to real data (Gotelli and Graves 1996). This suggests that species abundance distributions are determined primarily by chance immigration rather than interactions between organisms. Hubbell (2001) recently advanced a neutral theory of biodiversity that predicts equilibrium species abundance distributions in both the metacommunity (regional pool of individuals) and local communities using only speciation rate and metacommunity size or local community size and immigration rate, respectively. His model fits data from a wide range of community types remarkably well, which also suggests that size and dynamics (speciation rate) of the regional pool are fundamental determinants of species abundance distributions. Furthermore, the main biogeographical evidence for a limit to local diversity due to species interactions, or "community saturation" has recently been cast into doubt. Ecologists had previously interpreted asymptotic local-regional richness curves as evidence of community saturation (Terborgh and Faaborg 1980). Recent corrections of methods used to create those curves and test for "saturation" (Caley and Schluter 1997, Srivastava 1999, Fox et al. 2000, Loreau 2000, Hillebrand and Blenckner 2002, Hillebrand 2005) have cast serious doubt on this evidence.[2] Meta-analyses correcting for the non-independence of local and regional richness have found a significant relationship between the two variables (reviewed in Zobel 1997). In fact, regional richness can often explain a large proportion (>75%) of variance in local richness (Gaston 2000). It can partly explain differing rates of species loss and species retention in fragmented habitats (Tellería et al. 2003). Recent work also suggests that species- area relationships scale consistently from fine-scales to regional scales (Fridley et al. 2006). In sum, there is little biogeographical evidence for limits to local richness imposed by species interactions. Broad-scale patterns suggest that regional pool size is a fundamental determinant of local richness.

There is also a substantial amount of evidence from small-scale studies that dispersal limitation and immigration can structure communities (Cadotte 2006), including

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[2] Note that some of these same studies, and others, have also shown that systems with strong interactions can produce linear or weakly curvilinear relationships (Fox *et al.* 2000; Loreau 2000a; Shurin & Allen 2001). Consequently, lack of an asymptote does not prove the absence of community saturation either.

grasslands (Tilman 1997, Symstad and Tilman 2001, Vandvik and Goldberg 2006), other plant communities (reviewed in Turnbull et al. 2000), wetlands (Freestone and Harrison 2006), inquiline communities (Kneitel and Miller 2003), coral reef fish (Schmitt et al. 1999), intertidal and subtidal invertebrates and algae (Hunt and Scheibling 1997, Connolly and Roughgarden 1998, Berlow 1999, Smith and Witman 1999), and forests (but see Webb and Peart 2001, Wootton 2001). Dispersal and corridors between patches have also increased species richness in multiple habitat fragmentation experiments (Debinski and Holt 2000). Oberdorff et al. (1998) used streams, which have distinctly limited colonist pools, to look at the relationship between local richness and regional richness, and found that similar habitats with richer colonist pools had proportionally richer local communities, in terms of species richness, total density, and total biomass. They suggest, therefore, that regional processes have a strong influence on local communities in these systems. Valone and Hoffman (2002) used temporal variation in the species richness of seed supply to determine the effect of regional species pool size on local communities, and also found that increasing regional pool size increased mean density and local richness. On an even larger scale, Mora et al. (2003) recently examined coral reef species distributions and found that dispersal from a major speciation center, the Indo-Pacific, seems to explain species richness patterns on both regional and local scales in the Pacific basin. Certainly, dispersal limitation may structure some communities more than others. The extent or distance of dispersal and disturbance frequency should mediate the relative influence of regional and local processes in structuring local communities (Palmer et al. 1996).

We do not know what effects regional species pool dynamics or dispersal have on biodiversity-ecosystem function relationships. Biodiversity and ecosystem function research has been largely limited to local community scale experimental manipulations; regional processes such as immigration, disturbance, and habitat fragmentation have rarely been considered, and when considered, are usually strictly controlled. In addition to this exclusion of regional processes, as Gonzalez and Chaneton (2002) point out, most biodiversity experiments have used a static approach, and the "temporal aspect of community disassembly has been largely missing from biodiversity-function studies." Limited empirical and modeling studies have demonstrated that community assembly and regional processes, such as dispersal and disturbance, can affect the relationship between biodiversity and ecosystem function at local scales (Gonzalez and Chaneton 2002, Fukami and Morin 2003, Mouquet and Loreau 2003, Cardinale et al. 2004, Chase and Ryberg 2004, Houseman and Gross 2006, Matthiessen and Hillebrand 2006). Other work has suggested that relationships between biodiversity and ecosystem function may depend on scale (Chase and Leibold 2002, Cardinale et al. 2004, Chase and Ryberg 2004) or environmental context (Cardinale et al. 2000, Cardinale and Palmer 2002). Recent reviews of the literature have explicitly called for an incorporation of regional processes into biodiversity and ecosystem function research, recognizing that the underlying processes which mediate local diversity may affect biodiversity-ecosystem function relationships (Srivastava 2002, Giller et al. 2004, Srivastava and Vellend 2005). Furthermore, between patch diversity (beta diversity) fostered by landscape heterogeneity may affect ecosystem function (Bengtsson et al. 2002). Beta-diversity can be affected by dispersal (Mouquet and Loreau 2003) and disturbance regimes, and is often profoundly influenced by anthropogenic modifications of the environment, such as agriculture (reviewed in Benton et al. 2003). Few ecologists have investigated the effects of regional species pool dynamics on beta diversity in models or real ecosystems, and little is known about beta diversity's effects on ecosystem function.

Conservation decisions are, by necessity, being made in the absence of information on how regional processes might affect ecosystem function. Conservation biologists know that dispersal can be important for maintaining populations in a fragmented landscape, by facilitating gene flow and rescuing local populations from extinction due to disturbance, stochastic population dynamics or competitive exclusion. Consequently, corridors or other strategies for improving connectivity among remaining patches of habitat, have become common elements of terrestrial conservation design (Debinski and Holt 2000). Likewise, in the marine realm, where many species have widely passively dispersing larval stages, connectivity between protected patches is a major focus of reserve design (Botsford et al. 2001, Lockwood et al. 2002, PISCO 2002, Gaines et al. 2003, Lubchenco et al. 2003, Guichard et al. 2004). Indeed, connectivity between protected areas and unprotected and fishable areas is an oft-used justification for the institution of marine reserves: production from protected areas is supposed to spill over into the unprotected matrix (PISCO 2002, Balmford et al. 2004, Sanchirico et al. 2006). However, evidence supporting the use of corridors has been largely conceptual, and is often motivated by single-species conservation goals. Effects of connecting patches may not be limited to targeted populations, or a simple increase in species richness. Corridors can preserve important plant-animal interactions like seed dispersal and pollination (Tewksbury et al. 2002), but can also facilitate seed predation and shift the relative importance of these interactions for different species, potentially altering community composition (Orrock et al. 2003, Orrock and Damschen 2005). Dispersal can also have directly negative impacts on population viability by synchronizing dynamics among patches (Hastings 1993, Ranta et al. 1995, Ranta et al. 1997, 1998, Ruxton and Rohani 1998, Blasius et al. 1999, Shimada and Ishihama 2000) or fixing harmful alleles under high frequencies of disturbance (Orrock 2005). Since connectivity between patches and landscapes may have direct effects on ecosystem function, independent of its effects on diversity, it is not clear that conservation strategies designed to maximize diversity will necessarily ensure maximal or stable ecosystem services. Understanding how processes such as dispersal and disturbance mediate or modify relationships between diversity and ecosystem function is essential for the conservation of both.

Consequently, for my PhD dissertation, I conducted an integrated study of relationships between regional biodiversity, community assembly and disassembly, and ecosystem function in marine ecosystems. In **Chapter I**, which was published in *Oikos* (France and Duffy 2006a), I investigated the relationship between biodiversity and invasibility in a partially open seagrass mesocosm system. This chapter demonstrates the importance of community assembly history to relationships between diversity and invisibility. **Chapter II**, which was published in *Nature* (France and Duffy 2006b), examines whether or not relationships between diversity and ecosystem function "scale up" to metacommunities, or networks of patches connected by dispersal. This chapter is the first experimental demonstration of the effects of biodiversity on ecosystem function at more than one scale, as well as one of the first tests of the effects of dynamic biodiversity (derived from regional species pool size and dispersal among local communities rather than static, imposed richness levels) on ecosystem function. In **Chapter III**, I consider possible mechanisms by which dispersal could have modified relationships between biodiversity and ecosystem function in the experiment discussed in Chapter II. Mechanisms examined include competition-colonization tradeoffs; metacommunity source-sink dynamics, or "mass effects"; effects on individual populations which might explain effects on aggregate properties; and synchronization. This chapter illustrates that dispersal can have subtle but important effects on the magnitude and predictability of ecosystem properties even when most previously proposed mechanisms for dispersal effects are not operating. Since Chapters II and III suggested, surprisingly, that both diversity and dispersal could de-stabilize ecosystem functions within metacommunities under normal conditions, I examined their effects on disturbed metacommunities in **Chapter IV**. These complex responses of metacommunities to species richness, dispersal, and spatially discrete disturbance, demonstrate the importance of incorporating both spatial processes and trophic interactions into the study of biodiversity-stability relationships. This information is critical for conserving diversity and managing ecosystem services in light of the likely changes to regional species pools caused by anthropogenic disturbance.

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CHAPTER 1:
CONSUMER DIVERSITY MEDIATES INVASION SUCCESS AT MULTIPLE TROPHIC LEVELS

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ABSTRACT

Theory and recent experiments, mostly focused on plants, indicate that biodiversity can reduce invasion success, but diversity effects on mobile animal invasion have received little attention. We tested effects of mobile crustacean grazer diversity (species richness) on the establishment of invaders at multiple trophic levels in flow-through seagrass mesocosms. On average, increasing diversity of resident grazers reduced population growth and biomass of experimentally introduced grazers. This increase in invasion resistance was concurrent with reductions in food and habitat availability and increases in resident density, paralleling previous results with plants. In many cases, mixtures of resident species resisted invasion better than did any single resident species, arguing that interactions among residents, rather than a sampling mechanism, explained diversity effects on invasion. Higher grazer diversity also generally reduced biomass of naturally recruiting invertebrates and algae and shifted epiphytic community dominance from algae to sessile invertebrates. Exploitation competition, then, appears to contribute to the diversity effect on invasion in both plant and animal systems. Our results further suggest that resident competitive advantage may also be at work in multi-trophic level systems. Thus, negative effects of local diversity on invasion appear general, and trophically mediated processes can also strongly influence invader success and identity in multi-trophic level systems.

INTRODUCTION

Invasions are one of the primary threats to endangered species, community structure, and ecosystem functioning (Vitousek et al. 1996, Wilcove et al. 1998, Mack et al. 2000, Pimentel et al. 2000). Several community properties, including species richness and species composition, can influence a community's resistance to invasion (Levine and D'Antonio 1999, Alpert et al. 2000, Miller et al. 2002, Brown and Fridley 2003). Elton (1958) originally proposed that communities with higher species richness are more stable and therefore less vulnerable to invasions. Recent theory has built on Elton's arguments, suggesting that species-rich communities should be less invasible than depauperate communities because niche differences among resident species result in greater overall resource use, leaving fewer resources for invaders (MacArthur 1970, Tilman 2004, Naeem et al. 2000). The relationship between diversity and invasibility has, however, continued to resist generalization. For example, while most local-scale experiments have found that invasibility decreases with plot richness, the opposite relationship has been found in both models and larger-scale observational studies (Levine and D'Antonio 1999, Levine 2000, Hector et al. 2001, Fridley et al. 2004).

Despite strong interest in the relationship between biodiversity and invasibility, empirical research has been conducted in a limited number of systems, primarily terrestrial plant assemblages and aquatic microcosms. Although pioneering experiments on this problem were conducted in a marine fouling community (Stachowicz et al. 1999, Stachowicz et al. 2002), work in marine systems is otherwise extremely limited. This is despite widespread invasion pressure on marine ecosystems from ballast water exchange, ship hulls, and aquaculture (Ruiz et al. 2000, Naylor et al. 2001, Wonham et al. 2001). Furthermore, most studies have focused on plants or other sessile organisms at basal trophic levels (but see Miller et al. 2002, Shurin 2000). Effects of consumer diversity on ecosystem structure and function, however, may be different from those of plant diversity (Duffy 2002, Holt and Loreau 2002, Naeem 2002). For example, competitive exclusion may be less frequent in mobile consumers than in sessile organisms (Peterson 1979), whereas interference competition may be more prevalent. Finally, like plants, consumers can affect habitat structure and resource availability for organisms at other trophic levels, which might mediate invasion dynamics at those levels via indirect effects. Yet few studies have examined effects of diversity at one trophic level on invasion success at other levels (McGrady-Steed et al. 1997, Duffy et al. 2003).

In this study, we examined how species richness and identity of native crustacean grazers affects establishment success of other native grazers and organisms at lower trophic levels in *Zostera marina* (eelgrass) mesocosms. Our experiment tested consumer effects on establishment by other native species both to explore processes of community assembly and as a model of diversity effects on invasion by non-natives. Several lines of evidence suggest that our approach using native "invaders" can also inform understanding of diversity effects on non-native invasion. First, the search for consistent ecological differences between "natives" and "non-natives" has been largely inconclusive (reviewed in Mack et al. 2000). In fact, regional-scale studies frequently find positive relationships between native and non-native richness (reviewed in Levine & D'Antonio 1999; Sax and Gaines 2003). These patterns suggest that the processes governing community structure in native species assemblages are often similar, on average, to those governing the incorporation of introduced species into native assemblages. A second line of support for our approach is that experiments testing plant diversity effects on invasion have found comparable results when using native and non-native species as experimental invaders (Crawley et al. 1999, Hector et al. 2001, Troumbis et al. 2002). Indeed, a long-term study of old-field succession concluded that "invasions by native and exotic species did not fundamentally differ" (Meiners et al. 2004). Consequently, "invasion dynamics" may be thought of as a specific subset of community assembly processes, and study of native species community assembly should help inform studies of exotic species invasion dynamics.

We employed two novel design components to examine the effects of biodiversity on invasion success. First, by using all possible resident:invader pairs drawn from a pool of four species, we tested the potential role of differing assembly sequence (priority effects, or resident competitive advantage) in mediating invasion dynamics. Second, by measuring success of both experimentally stocked grazer invaders and "volunteer" invaders that naturally recruited into the flow-through mesocosms, we tested the effects of mobile consumer diversity on invasion and establishment of a wide range of sessile and mobile taxa at different trophic levels.

MATERIALS AND METHODS

Study system and experimental design

Zostera marina (eelgrass) is the most widespread and abundant marine macrophyte in the northern hemisphere, and it supports many commercially important species (Hemminga and Duarte 2000). The dominant primary consumers in many eelgrass beds are small crustacean mesograzers, which feed preferentially on epiphytic micro- and macroalgae and can have important indirect, positive effects on eelgrass (Neckles et al. 1993, Duffy et al. 2001). Numerous sessile invertebrates also frequently grow on eelgrass blades, and can have negative effects on the host macrophytes. Early settlement stages of some of these sessile invertebrates are consumed by mesograzers (Duffy and Harvilicz 2001, Duffy et al. 2003).

The experiment was conducted in outdoor, flow-through seagrass mesocosms on the VIMS Ferry Pier, York River estuary, Gloucester Point, Virginia, USA. The mesocosms were semi-transparent buckets filled with 13.5 L of water, fitted with 250-μm mesh drain holes and covered with a layer of neutral-density plastic screen to approximate natural light levels. The submerged mesocosm wall surface area available for colonization by invertebrates was approximately 0.2 m^2. Fifteen pre-weighed *Z. marina* shoots were planted in 8 cm of sand within the mesocosms. This eelgrass shoot density falls within the range observed locally (Orth and Moore 1986). Prior to planting, the shoots were spun 20 times in a salad spinner and then massed to determine an initial grass wet mass for each mesocosm.

We used four native grazers in the experiment: ampithoid (a mixture of *Ampithoe longimana* and *Cymadusa compta*) and *Gammarus mucronatus* amphipods, and *Erichsonella attenuata* and *Idotea baltica* isopods. The relative abundances of these four taxa fluctuate markedly in time and space, but usually comprise a large fraction of the mesograzer assemblage in York River seagrass beds (Duffy et al. 2001, Parker et al. 2001), and therefore are likely to be the most important potential competitors influencing invasion of other grazer species. The same four grazer taxa were used as invaders in the experiment. All of these crustaceans have sexual reproduction, overlapping generations and direct development, and all feed on epiphytic algae and associated detritus (Duffy et al. 2003). At summer temperatures, generation times in our system can be as short as three weeks for amphipods (Fredette and Diaz 1986) and one month for isopods (Kouwenberg and Pinkster 1985, Jormalainen and Tuomi 1989). *A. longimana* and *C. compta* are in the same family, with similar life histories and feeding, and are difficult to distinguish when alive, so they were stocked as one taxonomic unit.

Our experimental design sought to test the influence of resident grazer presence, species identity, and species richness on establishment of invaders. To do so, we established four simultaneous experiments, with parallel designs, to test invasion success by each of the four grazer species into communities containing the remaining three species (Fig. 1). For each of the four invading grazer species, we established five treatments spanning a range in resident grazer richness, including no grazers (controls), each of the three remaining species alone (resident monocultures), and all three remaining species together (resident mixtures). Each of these five resident assemblage treatments was then experimentally invaded by the designated invader species. Consequently, there were a total of 20 treatments, each replicated five times (100 mesocosms total). Treatments were randomly assigned to one of ten large tanks and one of 12 positions (mesocosm) within that large tank.

Mesocosms were stocked with the resident communities on 23 July 2002. With the exception of the grazer-free controls, 30 individual reproductively mature adult grazers were placed in each mesocosm (30 of a given species for monocultures, and 10 of each species for mixtures). Since roughly half of the grazers stocked were adult females carrying embryos, populations began to grow immediately and rapidly. We allowed grazer populations to grow for four weeks, by which time a previous experiment showed that grazers reached carrying capacity (Duffy and Harvilicz 2001). At that point we "invaded" each mesocosm with ten reproductively mature adults of the designated invading species. After another month, all organisms retained by a 0.5-mm sieve were harvested. During this time, invader density increased by several- to 100-fold in controls, and some invasions failed completely (all invading individuals died, see **Results**). Nearly all of the planted eelgrass was consumed at the end of this 8-week period in a few mesocosms, so the experiment was terminated and harvested at this time to prevent population crashes. Note that the loss of grass biomass over the course of the experiment is not necessarily a mesocosm artifact; *Z. marina* often disappears during the late summer months in the York River estuary as well (personal observation).

The mesocosms were continuously replenished with filtered York River water. The filtration system (pool sand filter + 150 μm-mesh) excluded most juvenile amphipod and isopod grazers, but allowed passage of microscopic propagules of other invertebrates and algae. We refer to organisms that recruited into the tanks via the flow-through seawater system as "volunteer invaders". These were allowed to recruit throughout the experiment.

Prior to stocking experimental invaders (at 4 weeks) and at the end of the experiment (8 weeks), we estimated biomass of epiphytic algae by measuring epiphytic chlorophyll. Algae were negligible on the blades at the beginning of the experiment. Algae were scraped off of three haphazardly chosen blades from each mesocosm, pooled, collected on a glass fiber filter, and extracted in 20 ml of 90% acetone at –20°C for 24 hours. Chlorophyll *a* was determined spectrophotometrically (Parsons et al. 1984) and normalized to leaf blade area.

At the end of the experiment, all epifaunal invertebrates, algae and eelgrass retained by a 0.5 mm mesh sieve were separated, identified, dried to constant mass, ashed at 450 °C, and massed again. Amphipod and isopod grazers were separated into size classes using a stack of nested sieves, identified, and counted. Ash-free dry mass (AFDM) of amphipods was estimated using these size class data and empirically derived relationships between crustacean body size and biomass (Edgar 1990). Isopods did not uniformly size-fractionate through sieving, so were ashed and massed directly.

For stocked invaders, invasion success was measured as net invader population growth (final abundance/initial abundance) and final biomass. For volunteer invaders, invasion success was estimated as final abundance or final biomass.

Statistical Analyses

Our primary interest was testing the influence of resident diversity on invasion success. For statistical purposes, the five resident treatments invaded by a given grazer species were considered one experiment and analyzed with a 1-way, fixed-factor ANOVA. Thus, separate one-way ANOVAs were conducted for each of the four parallel experiments invaded by a different species. We could not use a single ANOVA design for the entire experiment because identity of resident species necessarily differed systematically and non-independently among invader treatments, and would have rendered such an analysis non-orthogonal. Each of the four ANOVAs tested the effects of resident grazer presence, identity, and species richness on invasion success as follows. Again, each experiment included five levels of resident community (Fig. 1): control (no grazer residents), three resident monocultures, and one resident mixture. For each of the four experiments, we partitioned the treatment sum of squares (SS) from the ANOVA into two orthogonal *a priori* contrasts, after Duffy et al. (2005): (1) the overall effect of resident grazers was tested as the contrast of grazer-free controls vs. the remaining four grazer treatments (three monocultures and one mixture, contrast DF=1); (2) the effect of resident species richness was tested as the contrast of the resident mixture vs. the remaining three monocultures (contrast DF=1); this tests whether or not the mixture of resident species was more resistant, on average, than the monocultures. Since the variances in our model are additive, after these two contrasts, the only variation remaining that is due to the treatment is variation among the monocultures. Consequently, we used this portion of the treatment SS remaining after accounting for the previous two contrasts to calculate an F-statistic (DF=2) for the effect of resident identity.

This identity F-statistic tests whether resident species differ in their ability to resist invasion. Once each of the four experiments had been analyzed, we obtained a single estimate, across all four experiments, of the overall influence of resident presence, richness, and identity on invasion success by combining the p-values for each contrast across the four experiments using the approach of Sokal and Rolf (Sokal and Rohlf 1995), pp. 794-797).

The analyses above test whether richness and identity of residents affect invasion, but do not indicate which resident species are responsible, nor whether richness effects result from sampling or complementarity (Huston 1997, Hector 1998). To determine whether particular resident species dominated effects on invasion success (a "sampling effect"), we ran a separate multiple regression for each of the four stocked invader species, including all five treatments which that species invaded. Each regression modeled invader population growth as the response, and used the final abundance of each of the three remaining (resident) species as predictors. Both response and predictor variables were transformed by $\log_{10}(x)$ to meet the assumption of homogeneous variances. The predictors were not correlated (maximum absolute value of significant $r=0.205$). To stringently assess whether richness effects derived from interactions among species, we calculated D_{max} for invasion resistance. D_{max}, the overyielding criterion, measures the difference between the observed total response in mixture (yield) and the maximal response in monoculture, as a proportion of the maximal response in monoculture (Loreau 1998).

Competition for food and substratum may mediate resident effects on invasion. To estimate the strength of exploitation competition among grazer species, we measured the loss of available habitat and surface area for growth of algal food as loss of eelgrass to grazer consumption. Final eelgrass AFDM was subtracted from initial AFDM, the latter estimated as 0.097*initial wet mass (g). We tested whether eelgrass biomass, resident grazer biomass, and resident grazer density differed in mixtures vs. monocultures using one-way ANOVAs with *a priori* contrasts for each of the four invader experiments, as described above. As an index of resource limitation, resident density was calculated as mg resident grazers/(mg macroalgae+eelgrass).

Since the analyses just described treated the four invader species separately, they could not rigorously test the overall influence of invader identity, or the interaction of resident and invader identity, on community development. To do so, we conducted two-way ANOVAs, using only the resident monoculture treatments, with factors resident grazer identity (fixed factor, 4 levels) and stocked invader identity (fixed factor, 4 levels). There were five replicates of each treatment combination. Our experiment did not include treatments with residents and invaders of the same species (e.g. *Erichsonella* invading mesocosms with resident *Erichsonella*) because it would have been impossible to determine invasion success in such a combination. Therefore, we used data from the controls (e.g. *Erichsonella* invading a community initially free of grazers) for these treatment combinations in the ANOVAs. As invaders reached high population densities during their four weeks in the mesocosms (see **Results**), we considered that these initially grazer-free controls should closely approximate the state of mesocosms that had had residents of the same species for the full eight weeks of the experiment. These two-way ANOVAs were conducted only for volunteer invaders and community-level responses (i.e., not for population growth of the stocked invader species or for density or biomass of the resident grazers).

Finally, we explored whether the sequence of community assembly influenced the outcome of competition by examining whether resident grazer species had a consistent competitive advantage over invaders. To do so, we used a continuous version of the Bradley-Terry paired comparison model that was developed to detect and estimate home field advantages in team competitions (Harville and Smith 1994). We considered each mesocosm with a single resident species and single invader species as a game (12 matchups, each replicated five times; see Fig. 1), and used the difference in performance between the residents (home team) and the invaders (visiting team) as the difference in score. By comparing the fit of the following model to one without a home field advantage term using Akaike's Information Criterion (AIC), we were able to determine whether residents had a competitive advantage over invaders:

$$y_{ijk} = R_{\text{resident } j} - R_{\text{invader } i} + H_j + E_{ijk.}$$

Y_{ijk} is the difference in net population growth between species j and species i. $R_{\text{resident } j}$ and $R_{\text{invader } i}$ are dummy variables for the resident competitive abilities (R_j=1 when the species is a resident, –1 when it is an invader, and 0 when it is not present in a mesocosm; R_i=1 when the species is an invader, -1 when it is a resident, and 0 when it is not present). H_j is a dummy variable for the home field advantage of species j (H_j=1 when species j is a resident, 0 otherwise). By assuming that the errors (E_{ijk} where k is the number of replicates of each resident:invader matchup) are normally distributed, this can be fit as an ordinary regression model (Harville and Smith 1994, Clarke and Norman 1995). We fit this regression model to several measures of differences in competitive ability between residents and invaders (y_{ijk}): difference in net population growth (final abundance/initial abundance), final biomass, final biomass with a handicap for residents (final biomass divided by 2), and final abundance. Using the sums of squares for the two models, we tested the null hypothesis that home field advantage = 0. The formula for the F-statistic for this hypothesis test is described in Harville and Smith (1994). We used SAS (SAS 2001) to fit the regression models (Agresti 2002, Weiss *pers. comm.*).

RESULTS

The experimental gradient in resident grazer diversity was maintained in the final grazer abundances (mean Shannon-Weaver index: controls=0.096; ampithoids=0.171; *E. attenuata*=0.310; *G. mucronatus*=0.118; *I. baltica*=0.204; mixtures=0.354). This diversity gradient overlaps the range found in York River seagrass beds (mean=0.378, range=0.125-0.594) (Duffy et. al. unpublished data). All four species of stocked invaders established populations in the initially grazer-free control treatments, indicating that the invading density was sufficient. Thirty-eight species of invertebrates, in addition to the stocked amphipods and isopods, invaded the mesocosms during the 8-week experiment, including anemones, bivalves, crabs, gastropods, nudibranchs, polychaetes, and tunicates. Seven species of macroalgae and two macroscopically different mixed microalgal assemblages (predominantly green or predominantly brown diatoms) colonized the experiment.

Both richness and identity of resident grazers strongly affected population growth and biomass of invading grazers (Fig. 2, Table 1). The overall effect of resident richness (i.e. combining the four experiments with different experimental invaders) was significant for both invader population growth ($p<0.025$) and invader biomass ($p<0.001$; Table 1). Resident richness also significantly reduced invasion success in the separate analyses for three of the four invaders (Appendix 1-1). This negative effect of resident species richness on invasion was generally consistent despite clear variation in invasion success among the four stocked invader species (Fig. 2). All four mixtures overyielded, or resisted invasion better than the maximal monoculture (D_{max} was greater than zero). Within the initially grazer-free controls, invading isopods (*E. attenuata* and *I. baltica*) reached significantly lower final biomass and population growth than the amphipods (ampithoids and *G. mucronatus*) (one-way ANOVA $p<0.001$, followed by Tukey's tests; Fig. 2).

The presence of grazers reduced the total biomass of volunteer epifaunal invertebrates (those invading through the seawater supply, Fig. 3a, Table 1). The aggregate biomass of these volunteer invaders was not significantly reduced at higher resident grazer species richness but was strongly affected by resident identity (Table 2). In contrast, the number of volunteer invertebrate species was unaffected by the presence, identity, or richness of resident grazers (Fig. 3c, Table 2).

Of the five most frequent volunteer invaders, all were significantly reduced by the presence of grazers, and two were affected by the characteristics of the resident grazer community. Invasion success (biomass) of the sea slug *Haminoea solitana,* the second most frequent volunteer and the only volunteer herbivore, was reduced by resident grazer richness and strongly affected by resident grazer identity (Fig. 3e, Table 1). The abundance of *Molgula manhattensis*, a solitary tunicate and the fourth most frequent invader, was significantly reduced by resident grazer richness and affected by resident grazer identity (Fig. 3f, Table 1). The first and third most frequent volunteers, *Hydroides dianthus*, a tube-dwelling polychaete, and *Corophium volutator*, a detritivorous amphipod, were unaffected by resident richness or identity (data not shown).

Grazers significantly reduced biomass and species richness of invading algae, relative to initially grazer-free controls, although resident *G. mucronatus* tended to increase algal biomass (Fig. 3b,d). Algal biomass was also significantly reduced by resident grazer richness and strongly affected by resident grazer identity (Figs. 2b,d; Tables 1,2, Appendix 1-1).

Identity of the invading grazer species significantly affected only two of the eight response variables examined: the invasion success of one of the volunteer invaders, *Molgula manhattensis* (Table 2) and the number of successfully invading algal taxa (Table 2). Interactions between resident and invader identity were highly significant for two of the volunteer invaders, *H. solitana* and *M. manhattensis* (Table 2).

Multiple regressions conducted separately for each of the four stocked invader species showed that reduced success of *E. attenuata* invasions was attributable primarily to *I. baltica* (overall regression $p<0.001$, adjusted $R^2=0.556$; *I. baltica* $p<0.001$; other residents $p>0.716$), and ampithoid invasion was marginally negatively affected by *G. mucronatus* (overall regression $p=0.080$, $R^2=0.159$; *G. mucronatus* $p=0.056$; other residents $p>0.172$). There were no significant effects of any particular species on *G. mucronatus* and *I. baltica* invasions.

Summed biomass of all resident grazers, i.e., potential competitors for the invaders, was significantly higher, on average, in grazer mixtures than in monocultures (Fig. 3i, Table 2). Habitat and substrate availability were reduced at high resident richness, as eelgrass lost significantly more biomass, on average, in mixtures than in the monocultures. In contrast, eelgrass mass loss did not differ, on average, between monocultures and controls (Fig. 3h, Table 2). As an index of resource limitation for invading grazers, we examined density of resident grazers per gram plant. Resident density was marginally non-significantly greater in mixtures than in monocultures on average (Fig. 3j, Table 2), and was also affected by resident species identity. The resident densities measured in our mesocosm experiment are comparable to those found in the field if grazer abundance is normalized to all available surface area, including mesocosm walls (mean across treatments=0.067 mg residents/cm^2 area, field mean=0.11 mg/cm^2 eelgrass), but are higher than the maximum observed field density if only plant surface area is considered (mean across treatments=0.328 mg/cm^2, field max=0.20 mg/cm^2; field data from Duffy and Harvilicz 2001).

The fit of the regression model including home-field advantage was highly significant, explained more than 50% of the variance in the competitive outcomes between residents and invaders, and was better than that of the model without home-field advantage, regardless of the competition measure used (Table 3). Residents had a significant competitive advantage over invaders (see F test for comparing model to null model without home field advantage, Table 3). In other words, for a given grazer species, performance against a given competitor was greater when the focal species was a resident than when it was an invader. We also compared invader biomass in controls (no competitors, 4 weeks of population growth) to resident biomass in monocultures (competitors for 4 weeks out of 8 weeks of population growth) to determine whether invader populations had time to reach carrying capacity in the absence of competitors. Amphipod populations that invaded control treatments reached population sizes equal to those of their conspecifics that had been residents in monocultures for 8 weeks (invader biomass, resampling two-tailed p= 0.0896 for ampithoids, p=0.8569 for *G. mucronatus*), suggesting that the 4-week invasion period was sufficient for amphipods to reach carrying capacity in the absence of competitors. Isopods, however, had significantly lower population sizes in controls than in monocultures (resampling one-tailed *E. attenuata* p= 0.0004, *I. baltica* p=0.0007), suggesting that they did not reach carrying capacity during the 4-week invasion period. Although these data advise caution in inferring resident competitive advantage, they suggest it is likely, at least for the amphipods.

DISCUSSION

We found that resident grazer species richness significantly decreased establishment of other mobile grazers, including both experimentally stocked amphipods and isopods as well as "volunteer" sea slugs that recruited naturally from planktonic larvae. This pattern was consistent for three of the four experimental grazer invaders analyzed separately, and was strongly significant when results were pooled across the four invader species. Moreover, multiple regressions revealed that no single resident species dominated the inhibitory effects on invaders, strongly suggesting that invasion resistance was a general effect of diverse resident assemblages rather than a sampling effect due to presence of a particularly strong interactor. This consistency is particularly noteworthy given the marked differences among invader species in potential population growth rates, as observed in competitor-free controls (Fig. 2a), and the differences among resident species in ability to resist invaders. Thus, our finding that mobile consumer diversity reduced invasion success of other species at the same trophic level appears robust.

A second line of evidence for the generality of diversity effects on invasion in our experiment comes from naturally recruiting "volunteer" invaders. Grazer species richness significantly reduced the success of two of the most frequent volunteer invaders, one of which (*H. solitana*) is a mobile grazer and therefore a potential competitor, and marginally reduced the aggregate biomass of all naturally recruiting invaders. Most of these volunteers were sessile organisms probably affected by grazers ingesting or disturbing their newly settled recruits. More diverse grazer assemblages tended to shift the system from algal dominance towards sessile invertebrate dominance, as seen before (Duffy et al. 2003).

The most straightforward explanation for reduced invasion success at high resident richness in our experiment appears to be stronger competition for resources, namely food and habitat. Several lines of evidence support this possibility. First, as expected, invasion success of stocked grazers was greater in the competitor-free controls (Fig. 2), suggesting that competition mediated invasion success, at least in part. Second, as in other studies where more diverse assemblages use resources more fully (Tilman 1997, Naeem et al. 2000, Duffy et al. 2003), food consumption tended to be greater in the grazer mixtures than in monocultures. Specifically, algal biomass was significantly reduced by grazer richness, and both macro- and micro- algal biomass were quite low in all mixtures relative to controls, confirming that consumption pressure was high (Figs. 3b&g, Table 2). Intense consumption in grazer mixtures is further indicated by the significantly greater loss of eelgrass biomass in these treatments compared with monocultures (Fig. 3h, Table 2), since grazers usually only consume eelgrass when epiphytic algae, their preferred food source, is limited (Jernakoff et al. 1996, Valentine and Duffy in press). These results for mobile consumers parallel those from both plant and zooplankton assemblages, where species richness and aggregate biomass of native "invading" species decreased with increasing species richness of residents (Kennedy et al. 2002, Shurin 2000, Troumbis et al. 2002). Finally, habitat availability, i.e., eelgrass leaf area, was also reduced by grazer richness. Seagrass blades simultaneously serve as surfaces for feeding, resting, building tube dwellings, and reproducing as well as substrate for the mesograzers' main food source, epiphytic microalgae. There is some evidence for behaviorally mediated competitive exclusion among eelgrass-associated grazers when plant habitat is limiting (Nagle 1968), and both field experiments and energetic estimates suggest that mesograzer production often may be limited by diffuse competition in the field (Edgar 1990, 1993). Eelgrass biomass was lowest, and resident density tended to be highest, in mixtures (Figs. 3h,j; Table 2). This parallels findings of many plant studies that more diverse assemblages have more neighboring individuals or greater biomass (Naeem et al. 2000, Kennedy et al. 2002, Troumbis et al. 2002), presumably leaving less room and resources for invaders. Thus, the pattern emerging from our data on mobile consumers and previous studies is that resource limitation and competition are greater in more diverse assemblages.

The importance of resident density in influencing invasion success in our experiment is further supported by evidence of resident competitive advantage, or the advantage conferred simply by being there first. We suspected that residents might have such an advantage in our system because at least two of the grazers, *I. baltica* and *G. mucronatus*, consume juveniles of other grazer species as well as conspecifics (J. G. Douglass unpublished data). We found that residents did have a competitive advantage: each species had significantly greater success as a resident than as an invader, regardless of which species it was paired with (Table 3). Although this apparent resident competitive advantage might be explained by invaders having insufficient time to reach their maximum population size, this seems unlikely. Only isopod invaders failed to reach carrying capacity in the absence of competition after four weeks of growth, suggesting that isopod invaders might be at a disadvantage. Yet half of the match-ups were isopod-

isopod. Furthermore, our calculation of the difference between resident performance and invader performance could be considered biased (conservatively) towards invaders, since we divided final population size by initial population size (30 for residents and 10 for invaders) and populations increased by more than an order of magnitude. Finally, we found significant resident competitive advantage even when we "handicapped" residents by halving their final biomass (Table 3). Our demonstration of resident competitive advantage is consistent with considerable theoretical (e.g. Lotka 1932; Case 1990) and empirical (Shurin 2000, review in Morin 1999) evidence that the outcome of competition and/or invasion can depend on initial conditions, including relative abundances and the order of arrival. This evidence of resident competitive advantage lends support to the idea that the diverse assemblages resisted invasion due to higher aggregate resident biomass and density, in keeping with Elton's (1958) original hypothesis.

The invasion resistance that we observed was not primarily mediated by the presence of a single species—that is, by a sampling effect—as it has been in some studies (McGrady-Steed et al. 1997, Hodgson et al. 2002). Several pieces of data confirm that no one resident species dominated the inhibition of invasion in our study. First, although *I. baltica* was the resident species most resistant to grazer invasion in monoculture (Fig. 2), it did not dominate the mixtures where it was present. Second, every resident species used in the experiment was absent from one of the 3-species resident mixtures. If invasion resistance was primarily conveyed by one species, then the mixture lacking that species should have lower invasion resistance relative to the other three mixtures. This was not the case for most variables (Fig. 3). Perhaps most importantly, multiple regressions examining the dependence of invader population growth on the abundance of each resident species were only significant for two of the four stocked grazer invaders, and the resident species with the greatest effect was different in these two cases. Finally, D_{max}, a stringent index for overyielding, was positive for all four mixtures.

Experiments such as ours have potential implications for understanding how native biodiversity influences exotic invasion. These implications depend, however, on the assumption that the native species used as "invaders" are suitable proxies for exotic invaders. The course of any particular real invasion will of course be influenced by the idiosyncratic traits of both residents and invader. Nevertheless, several lines of evidence suggest that native and non-native species often establish in communities by similar mechanisms, and thus that using non-natives as invaders would not have changed the outcome of our experiment dramatically. First, searches for consistent trait differences between natives and non-natives, with the exception of organisms that invade unaccompanied by predators or pathogens, have been largely unsuccessful (reviewed in Mack et al. 2000). Second, the mechanisms apparently responsible for the richness effect on invasion in our experiment, reduced food and habitat availability and increased density of competitors, should similarly reduce success of native and non-native grazers. Third, our four native grazer invaders had different population growth rates and degrees of omnivory, but were similarly deterred by richness of co-occurring native grazers. Finally, most small marine crustaceans, in contrast to terrestrial insects, are generalists, and, at least in seagrass beds, are readily consumed by most predators (Edgar and Shaw 1995). Although we appreciate the importance of studying how specific non-native invaders infiltrate communities, these considerations suggest that studying invasion dynamics of native species can provide important insights into the more logistically and ethically difficult questions of non-native invasions.

More generally, our experiment suggests that some mechanisms hypothesized to explain diversity effects on invasibility and community assembly in plants also apply to mobile consumers, and thus may be general. Our results suggest that three mechanisms of diversity effects may be important in mediating invasion success. First, species richness can reduce invasion success of some invaders by decreasing resource availability at a given point in time through complementary resource use (in our experiment, food and habitat availability) (Table 1). Second, species-rich communities can reduce invasion success of a diverse suite of invaders because they contain species that are better at deterring a particular invader (the sampling effect). For example, in our experiment, *H. solitana* was primarily deterred by ampithoid residents (Fig. 3e, Table 1). Across the whole experiment, the proportion of variance in invasion success explained by different components of the resident community (grazer presence, richness, and identity) also varied widely for the different invaders, suggesting that the best defense against invasion is a species-rich, intact community (data not shown). Finally, species-rich communities may stand a better chance of reducing invasion success through time by increasing average resource utilization through time (Davis et al. 2000, Davis and Pelsor 2001, Stachowicz et al. 2002). While our experiment does not test this, we note that our grazers show different seasonal abundance patterns (Parker et al. 2001, Duffy et al. 2001), which should produce more complete resource use through time as shown for space use by sessile invertebrates (Stachowicz et al. 2002). Our demonstration of resident competitive advantage highlights the importance of having competitors present, regardless of their size or competitive ability, to impede invasion.

In summary, as resident grazer diversity increased in the eelgrass system, food and habitat availability decreased, aggregate grazer biomass increased, and invasion success of both experimentally introduced grazers and naturally recruiting mobile (*H. solitana*) and sessile organisms was reduced. These effects could not be attributed to any particular resident species by way of a sampling effect. We found these significant effects of consumer species richness on invasibility despite using a low (albeit near natural) level of maximum diversity, studying invaders with different population growth capacities, and allowing trophic interactions and some natural recruitment to occur. Further work is necessary to determine the importance of invasion resistance conveyed by biodiversity relative to other factors, such as disturbance, resource availability, and propagule supply (Elton 1958, Crawley 1987, Huston 1994, Levine and D'Antonio 1999, Stohlgren et al. 1999, Davis et al. 2000, Levine 2000, Brown and Peet 2003). Our results, however, argue for the generality of a negative relationship between diversity and invasibility at the neighborhood scale, and they support straightforward and common mechanisms of exploitative resource competition as producing these relationships.

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TABLES

Table 1. Effects of grazer presence, species richness, and identity on invasion success and community development, pooled across all four invaders. Letters in last three columns indicate which invaders had significant effects in separate analyses by invader species (see Appendix 1-1), and correspond to the first letter of the invading genus or family. Letters in italics indicate marginally significant effects (p= approximately 0.05).

	Chi square of combined p-values (-2 sum ln(P))			Significance of Chi-square			Invader Identity		
Response Variable	Grazers	Richness	Identity	Grazers	Richness	Identity	Grazers	Richness	Identity
Invader population growth	19.16	19.55	27.60	**<0.025**	**<0.025**	**<0.001**	**A**	**E,I**	**E,I**
Invader biomass	35.27	31.58	19.79	**<0.001**	**<0.001**	**<0.025**	**A,G**	**E,G,I**	**G,I**
Volunteer richness	2.46	4.33	4.93	**NS**	**NS**	**NS**			
Volunteer biomass	17.28	15.44	24.75	**<0.05**	**NS**	**<0.01**	**E,G**	**E**	**A,E**
H. solitana biomass	40.32	23.39	43.57	**<0.001**	**<0.01**	**<0.001**	**A,E,I**	**E,I**	***A*,E,G,I**
M. manhattensis abundance	43.91	34.39	27.07	**<0.001**	**<0.001**	**<0.001**	**A,E,G**	**A,E**	**E,G**
Algae richness	35.75	11.00	14.22	**<0.001**	**NS**	**NS**	**E,G,I**		***I***
Algae biomass	31.79	20.45	20.10	**<0.001**	**<0.01**	**<0.01**	**E,G,I**	***G*,I**	**I**
Epiphytic chlorophyll	44.26	4.46	35.41	**<0.001**	**NS**	**<0.001**	**A,G,*I***		**A,G**
Resident biomass	NA	23.33	9.35	**NA**	**<0.01**	**NS**		**A,E**	
Change in *Zostera* biomass	12.84	23.46	28.62	**NS**	**<0.01**	**<0.001**	**A**	**A,E**	**A**
Resident density	NA	15.38	18.59	**<0.0001**	**NS**	**<0.025**	**E,I**	**E**	***G*,I**

Table 2. Interactive effects of resident identity and invader identity. Data from monocultures only (see Fig. 1 and text). MS and p-values are from 2-way ANOVAs of resident and invader identity.

	Resident Identity (df=3)		**Invader Identity (df=3)**		**Resident*Invader (df=9)**		**Overall Model**		
Response Variable	MS	P	MS	P	MS	P	MS	P	MSE
Volunteer richness	3.79	0.7347	3.52	0.7562	3.99	0.9026	3.85	0.9626	8.88
Volunteer biomass	0.21	**0.0012**	0.01	0.8938	0.07	0.0638	0.09	**0.0084**	0.04
H. solitana biomass	3.09	**0.0001**	0.45	0.0897	1.17	**0.0001**	1.41	**0.0001**	0.20
M. manhattensis abundance	9.49	**0.0001**	31.42	**0.0001**	31.42	**0.0001**	14.01	**0.0001**	0.81
Algae richness	2.00	**0.0348**	3.36	**0.0031**	1.05	0.1341	1.70	**0.0043**	0.66
Algae biomass	6.23	**0.0001**	1.01	0.2258	1.61	**0.0214**	2.41	**0.0002**	0.68
Epiphytic chlorophyll	85.04	**0.0001**	0.21	0.9957	17.08	0.0893	27.30	**0.0019**	9.59
Change in *Zostera* biomass	3.33	**0.0001**	0.43	0.3174	0.49	0.2165	1.05	**0.0014**	0.36

Table 3. Regression models and hypothesis tests for resident competitive advantage. F tests for comparing models were calculated as: $F(I \text{ vs } 0) = (SSE_0 - SSE_1)/((SS_1 - SS_2 + SSE_2)/56)$ and $F(II \text{ vs } 0) = (SSE_0 - SSE_2)/((SSE_2)/53)$, after Harville and Smith (1994).

	No Resident Advantage (0) (null hypothesis)		
	Regression		
Response Variable	R2	P	AIC
Population Growth	0.438	<0.0001	295.9
Biomass	0.198	0.0053	630.9
Biomass w/ resident handicap	0.105	0.0935	567.8
# of indiv.	0.164	0.0161	698.7

	Resident Advantage (I) same for all species				
	Regression			F test (I vs 0)	
Response Variable	R2	P	AIC	F (1,50)	P
Population Growth	0.474	**<0.0001**	293.9	3.91	0.054
Biomass	0.753	**<0.0001**	562.3	125.68	**<0.0001**
Biomass w/ resident handicap	0.702	**<0.0001**	504	111.83	**<0.0001**
# of indiv.	0.696	**<0.0001**	640.1	97.71	**<0.0001**

	Resident Advantage (II) different for all species				
	Regression			F test (I vs 0)	
Response Variable	R2	P	AIC	F (1,50)	P
Population Growth	0.531	**<0.0001**	293	2.65	**<0.05**
Biomass	0.761	**<0.0001**	566.2	31.23	**<0.0001**
Biomass w/ resident handicap	0.776	**<0.0001**	497.9	35.32	**<0.0001**
# of indiv.	0.745	**<0.0001**	635.4	30.25	**<0.0001**

FIGURE LEGENDS

Figure 1. Experimental design. A = ampithoids, E = *Erichsonella attenuata*, G = *Gammarus mucronatus*, I = *Idotea baltica,* Con = control (no residents). Each of the 20 treatments was replicated 5 times. Invaders were introduced one month after residents.

Figure 2. Effects of resident grazer identity and richness on **(a)** population growth and **(b)** final biomass of experimentally stocked grazer invaders. Controls (white bars) had no stocked residents prior to invasion. Mixtures (black bars) contained all three species other than the invader. Population growth= $N_{final}/N_{initial}$. The line at y=1 indicates the threshold of invasion failure (net negative population growth). Error bars show ± 1 SE (n=5). See Tables 1 and 2 for statistical analysis.

Figure 3. Effects of resident grazer identity and richness on naturally recruiting ("volunteer") species and on resource availability. **1st row:** Total ash-free dry biomass of naturally recruiting **(a)** invertebrates and **(b)** algae. **2nd row:** Taxon richness of naturally recruiting **(c)** invertebrates and **(d)** algae. **3rd row:** Two of the five most abundant naturally recruiting invertebrates, **(e)** *Haminoea solitana*, a gastropod grazer, and **(f)** *Molgula manhattensis*, a solitary tunicate. **4th row:** Resource availability: **(g)** Final epiphytic chlorophyll a, normalized to leaf blade area and **(h)** loss of eelgrass biomass. **4th row:** Resident grazer community **(i)** biomass and **(j)** density. Error bars show ± 1 SE. Data for controls (n=20) and resident monocultures (n=15) are pooled across invader species while data for each resident mixture composition (and therefore each invader, n=5) are presented separately to allow the reader to compare a response in the monoculture of a given resident to the response in the mixture missing that species. See Tables 1 and 2 for statistical analysis.

Figure 1

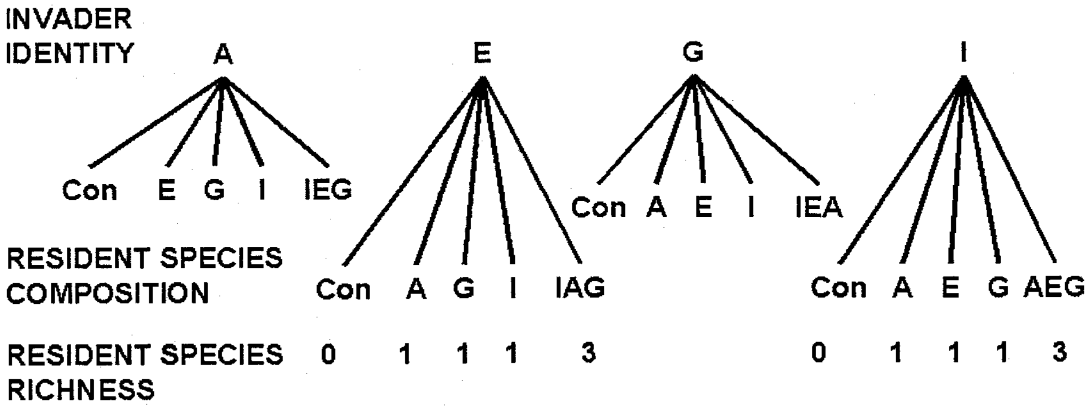

INVADER IDENTITY
A
E
G
I
Con E G I IEG
Con A E I IEA
RESIDENT SPECIES COMPOSITION
Con A G I IAG
Con A E G AEG
RESIDENT SPECIES RICHNESS
0 1 1 1 3
0 1 1 1 3

Figure 2

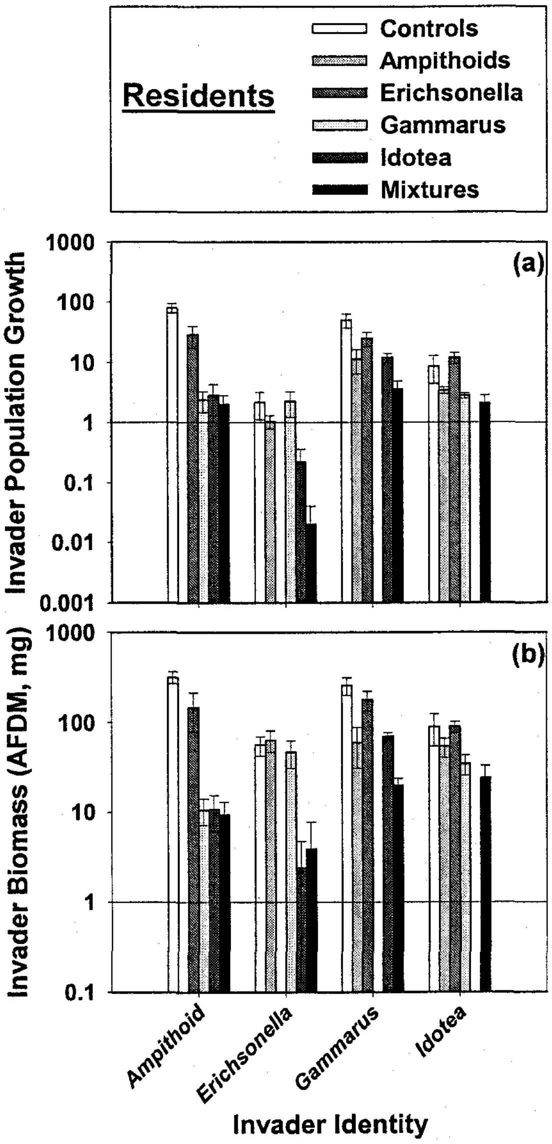
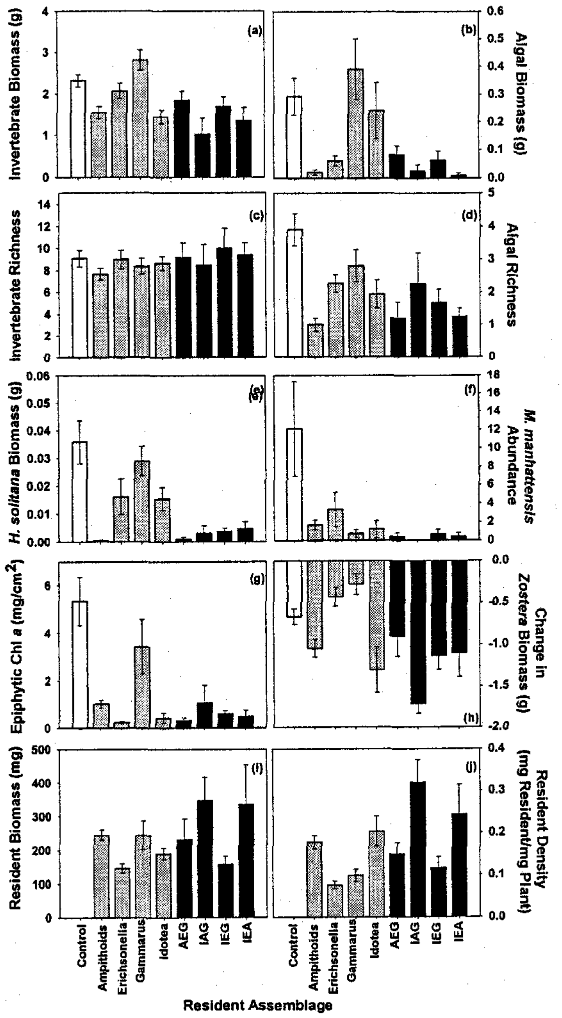

Residents
Controls
Ampithoids
Erichsonella
Gammarus
Idotea
Mixtures
(a)
Invader Population Growth
1000
100
10
1
0.1
0.01
0.001
(b)
Invader Biomass (AFDM, mg)
1000
100
10
1
0.1
Ampithoid
Erichsonella
Gammarus
Idotea
Invader Identity

Figure 3



Invertebrate Biomass (g)
Algal Biomass (g)
Invertebrate Richness
Algal Richness
H. solitana Biomass (g)
M. manhattensis Abundance
Epiphytic Chl a (mg/cm2)
Change in Zostera Biomass (g)
Resident Biomass (mg)
Resident Density (mg Resident/mg Plant)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
Control
Ampithoids
Erichsonella
Gammarus
Idotea
AEG
IAG
IEG
IEA
Resident Assemblage

Appendix 1-1. Effects of grazer presence, species richness, and identity on invasion success and community development for each of the four experiments (one for each invader) conducted concurrently. SS and p-values are from one-way ANOVAs for each invader, partitioned as described in the text. The total SS is the total sum of squares for the whole model (model SS + error SS).

Invader=Ampithoids

	Grazers (df=1)		**Richness (df=1)**		**Identity (df=2)**		**TOTAL**		
Response Variable	SS	P	SS	P	SS	P	SS	P	MSE
Invader population growth	11.765	**0.0041**	0.000	0.9981	7.465	0.1685	41.657	**0.0118**	22.427
Invader biomass	11.792	**0.011**	0.000	0.9917	9.234	0.1873	51.093	**0.0255**	1.503
Volunteer richness	0.645	0.8179	14.933	0.2746	2.533	0.8514	267.115	0.8221	249.200
Volunteer biomass	0.027	0.834	2.044	0.0787	8.290	**0.0251**	22.264	**0.0108**	11.903
Haminoea biomass	1.483	**0.0085**	0.544	0.0931	1.429	**0.0554**	7.214	**0.0054**	3.693
Molgula abundance	5.550	0.0854	16.041	**0.0058**	3.463	0.392	61.509	**0.0182**	35.774
Algae richness	0.018	0.907	2.743	0.1584	4.933	0.178	34.615	0.2389	26.933
Algae biomass	0.609	0.3994	2.691	0.0849	4.240	0.0714	24.739	0.0964	17.284
Epiphytic chlorophyll	107.620	**0.0001**	1.844	0.5434	16.287	0.0033	228.337	**0.0014**	101.477
Resident biomass	NA	NA	0.190	**0.0078**	0.010	0.9607	0.547	**0.0571**	0.356
Change in Zostera biomass	0.464	**0.0263**	0.921	**0.0029**	7.441	**0.0001**	10.581	**0.0001**	1.707
Resident density	NA	NA	0.005	0.7959	0.647	**0.0573**	1.970	0.0709	1.556

Invader=*Erichsonella*

	Grazers (df=1)		**Richness (df=1)**		**Identity (df=2)**		**TOTAL**		
Response Variable	SS	P	SS	P	SS	P	SS	P	MSE
Invader population growth	3.021	0.175	9.277	**0.0232**	11.825	**0.0403**	52.598	**0.018**	28.919
Invader biomass	8.575	0.0764	17.983	**0.0138**	8.780	0.2672	80.690	**0.0263**	2.442
Volunteer richness	6.422	0.4082	1.856	0.6545	0.133	0.9924	179.333	0.9102	170.600
Volunteer biomass	2.520	**0.0354**	3.179	**0.0198**	9.773	**0.0019**	24.567	**0.0007**	9.334
Haminoea biomass	0.703	**0.0152**	0.987	**0.0052**	4.365	**0.0001**	7.861	**0.0001**	1.878
Molgula abundance	23.849	**0.0001**	4.240	**0.0001**	40.275	**0.0001**	68.456	**0.0001**	0.927
Algae richness	41.408	**0.0003**	2.654	0.2753	0.933	0.4418	85.958	**0.0042**	39.950
Algae biomass	3.598	**0.0457**	1.560	0.1753	3.254	0.2287	23.166	0.0683	14.954
Epiphytic chlorophyll	8.249	0.3636	4.497	0.5002	36.743	0.2316	229.831	0.3104	180.855
Resident biomass	NA	NA	0.467	**0.0013**	0.125	0.1726	0.591	**0.0047**	0.445
Change in Zostera biomass	0.692	0.2329	3.347	**0.0139**	3.696	0.1078	16.263	**0.0136**	8.654
Resident density	NA	NA	0.260	**0.0133**	0.034	0.6022	0.788	0.0657	0.494

Appendix 1-1 (cont'd)

Invader=*Gammarus*

	Grazers (df=1)		**Richness (df=1)**		**Identity (df=2)**		**TOTAL**		
Response Variable	SS	P	SS	P	SS	P	SS	P	MSE
Invader population growth	0.354	0.5565	0.940	0.3414	0.618	0.1867	21.705	0.748	19.726
Invader biomass	1.593	**0.0002**	1.083	**0.0011**	0.935	**0.0291**	5.113	**0.0001**	0.075
Volunteer richness	0.010	0.9693	0.817	0.7283	8.533	0.4939	140.960	0.8371	131.600
Volunteer biomass	2.345	**0.0299**	0.404	0.3434	0.969	0.2795	12.302	0.11	8.583
Haminoea biomass	0.666	0.1357	0.047	0.6838	3.318	**0.0092**	9.539	**0.0216**	5.509
Molgula abundance	41.809	**0.0001**	1.405	0.3507	15.880	**0.0338**	89.852	**0.0002**	30.758
Algae richness	37.210	**0.0014**	3.750	0.2541	12.400	0.1519	107.760	**0.0064**	54.400
Algae biomass	8.060	**0.0012**	2.404	**0.0536**	4.084	0.095	25.978	**0.0018**	11.430
Epiphytic chlorophyll	188.376	**0.0001**	0.473	0.7483	5.439	**0.0001**	283.745	**0.0001**	89.456
Resident biomass	NA	NA	0.087	0.3596	0.677	0.0633	0.764	0.0878	1.564
Change in Zostera biomass	0.314	0.4657	0.992	0.2009	1.929	0.2972	14.580	0.2618	11.345
Resident density	NA	NA	0.134	0.1637	0.302	0.166	1.458	0.1184	1.286

Invader=*Idotea*

	Grazers (df=1)		**Richness (df=1)**		**Identity (df=2)**		**TOTAL**		
Response Variable	SS	P	SS	P	SS	P	SS	P	MSE
Invader population growth	0.174	0.1727	0.777	**0.0072**	1.014	**0.0008**	3.704	**0.0033**	1.739
Invader biomass	0.284	0.1307	0.950	**0.0092**	0.353	**0.0346**	3.874	**0.0262**	2.287
Volunteer richness	0.160	0.9035	0.267	0.8757	28.133	0.2042	240.960	0.6189	212.400
Volunteer biomass	0.755	0.2006	0.021	0.8281	1.305	0.3161	10.697	0.3387	8.617
Haminoea biomass	5.203	**0.0001**	1.264	**0.0252**	5.095	**0.0068**	15.885	**0.0001**	4.323
Molgula abundance	0.757	0.341	1.634	0.1673	0.000	NA	18.302	0.5689	15.912
Algae richness	12.960	**0.0452**	2.400	0.3689	19.600	0.0685	91.760	**0.0397**	56.800
Algae biomass	4.800	**0.0057**	2.285	**0.0454**	6.221	**0.0278**	23.343	**0.0014**	10.035
Epiphytic chlorophyll	46.977	0.0674	5.174	0.5283	33.606	0.2683	336.990	0.188	251.232
Resident biomass	NA	NA	0.009	0.6521	0.008	0.8887	0.016	0.9403	0.664
Change in Zostera biomass	0.087	0.57	0.000	0.9955	0.890	0.1902	0.977	0.4622	5.205
Resident density	NA	NA	0.192	0.1247	0.770	**0.0317**	2.129	**0.0195**	0.073

CHAPTER 2:
DIVERSITY AND DISPERSAL INTERACTIVELY AFFECT PREDICTABILITY OF ECOSYSTEM FUNCTION

published as: France, K. E. and J. E. Duffy. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*. **441:** 1139-1143.

Theory and small-scale experiments predict that biodiversity losses can decrease the magnitude and stability of ecosystem services such as production and nutrient cycling[1,2]. Most of this research, however, has been isolated from the immigration and emigration (dispersal) processes that create and maintain diversity in nature[3-5]. Since common anthropogenic drivers of biodiversity change, such as habitat fragmentation, species introductions, and climate change, are mediated by these understudied processes[5-7], it is unclear how environmental degradation will affect ecosystem services[3,4]. We tested the interactive effects of mobile grazer diversity and dispersal on the magnitude and stability of ecosystem properties in experimental seagrass communities that were either isolated or connected by dispersal corridors. Here we show that, contrary to theoretical predictions[2,8-11], increasing the number of mobile grazer species in these metacommunities increased spatial and temporal variability of primary and secondary production. Moreover, allowing grazers to move among and select patches reduced diversity effects on production. Finally, effects of diversity on stability differed qualitatively between patch and metacommunity scales. Our results indicate that declining biodiversity and habitat fragmentation synergistically influence the predictability of ecosystem functioning.

Broadening the spatial scope of biodiversity-ecosystem functioning (BD-EF) research to metacommunities, i.e., groups of patches connected by dispersal of organisms, adds two components of diversity: beta-diversity, or heterogeneity in species composition among patches, and gamma diversity, or diversity of the entire metacommunity[12]. Limited evidence suggests that, at these broader spatial scales, the functional consequences of diversity may be different[13,14]. Furthermore, effects of dispersal among patches on ecosystem properties have rarely been considered, despite dispersal's demonstrated importance in maintaining diversity, particularly in fragmented habitats[5,10,15]. Given recent predictions that the mechanism of diversity maintenance strongly influences relationships between biodiversity and ecosystem function[15,16], and the increasingly fragmented character of most habitats, scaling up BD-EF research to metacommunities is critical for its application to conservation.

Here, we test how diversity, dispersal, and spatial scale interactively affect properties of experimental multi-trophic seagrass (*Zostera marina*) ecosystems. We assembled metacommunities with low (3 spp.) and high (8 spp.) grazer species richness, simulating loss of rare species from a species pool. Each metacommunity had five patches which were either interconnected by dispersal corridors or unconnected (see Methods). Dispersal was extremely rare among unconnected patches and moderate among connected patches. Each patch received 30 mobile crustacean grazers (15 male-female species pairs), and the species composition of this founding community was determined by random draws from the appropriate species list (3 vs 8 spp.). Initial metacommunity-wide richness of grazers was set at either three or eight species, but both the relative abundances of species within metacommunities and the species richness within patches varied. We allowed this initial random assembly plus subsequent dispersal and species interactions to influence grazer diversity over the six- week experiment. This enabled us to determine how multiple spatial components of biodiversity affect ecosystem properties in both connected and unconnected metacommunities.

We tested four hypotheses: (1) Increasing metacommunity richness will increase mean patch richness[15,17] and beta-diversity of grazers[18]. (2) Allowing dispersal will increase mean patch richness[5,15] and decrease beta diversity[17] of grazers. Based on these predicted diversity patterns, and on previously documented links between diversity and ecosystem properties[1], we expected that (3) grazer abundance and grazing pressure will increase with metacommunity richness and dispersal[13,15-17]. Since increasing richness often increases the predictability of ecosystem properties[2,8-11], even in multi-trophic systems[19] and in metacommunities[15], we hypothesized that (4) increasing metacommunity richness should increase predictability of ecosystem properties among and within patches.

MATERIALS AND METHODS

Study system

Zostera marina (eelgrass) is the most widespread and abundant marine macrophyte in the northern hemisphere, and it supports many commercially important species[27]. The dominant primary consumers in many eelgrass beds are small crustacean grazers, which feed on epiphytic algae and can have important indirect, positive effects on eelgrass[27]. We manipulated diversity of these grazers, which all have overlapping generations, direct development, and summer generation times of 3-4 weeks.

Mesocosm system

The experiment was conducted in outdoor, flow-through 13.5-L eelgrass mesocosms. Filtered seawater from the York River estuary, Virginia, USA, was delivered in pulses to mesocosms shaded to approximate natural light levels. Fifteen pre-weighed Z. marina shoots were planted in each mesocosm. Filters excluded grazers, but allowed passage of propagules of other invertebrates and algae[28,29]. We grouped mesocosms into metacommunities consisting of five patches (individual mesocosms) each. For half of the 20 metacommunities, patches within the metacommunity were connected to a central hub via clear 2.2 cm vinyl tubing. These dispersal corridors were 5 cm long, so grazers had an equal chance of dispersing to all other patches within the metacommunity. All grazer species could swim rapidly through the dispersal corridors, but dispersal between patches was relatively infrequent, and species differed in their dispersal inclinations (Table S1). There was no active dispersal between unconnected patches, but these patches were linked into a metacommunity by sharing a common water supply, which was the source of propagules of all species other than the manipulated grazers.

Experimental design

We used a fully-crossed, two-factor ANOVA design with metacommunity richness and dispersal as the two factors. Metacommunity richness had two levels, low (3 spp.) and high (8 spp.). The low richness species pool was a subset of the high richness species pool, consisting of the three most abundant grazers in the field at the time of the experiment (Table S4). The high richness pool included approximately 75% of the crustacean grazer species known from the lower Chesapeake Bay region (Table S4). Each treatment combination (metacommunity richness x dispersal) was replicated five times. The initial grazer community inoculated into each mesocosm was 15 reproductively mature male-female pairs, species composition of which was determined by random draws of pairs of individuals from the designated species pool (Table S4). Each metacommunity initially contained the full complement of species from the whole pool, but most individual mesocosms did not. The experiment ran for 47 days, long enough for at least two complete generations of most species in addition to the founding generation, population increases approaching two orders of magnitude, and achievement of carrying capacity[29,30].

Sampling ecosystem properties

At two-week intervals, we estimated biomass of epiphytic algae as epiphytic chlorophyll[28]. Mid-way through the experiment (day 26), we sampled grazers by sweeping a dipnet at mid-depth 10 times, and counting and identifying the grazers captured. We estimated spatial variability of ecosystem properties as the coefficient of variation (CV) of each response variable across the five patches in a metacommunity. Spatial variability was initially zero, and resulted from a combination of random variation in colonization through the flow-through system and subsequent interactions with the grazer community. We also estimated temporal CV of epiphytic chlorophyll (three time points) and grazer abundance (two time points). At the end of the experiment, all organisms retained by a 0.5 mm mesh sieve were separated, identified, dried to constant mass, ashed at 450 °C, and massed again.

Statistical analyses

To determine whether dispersal erased the signature of initial composition, we analyzed the relationship between initial and final relative abundance for each species using a GLM with dispersal as a class predictor (Table S1). For response variables measured within patches, we analyzed data using a GLM with three factors: grazer metacommunity richness and dispersal, which were fully crossed, and metacommunity ID, which was nested within the fully crossed design. When the p-value for metacommunity ID was >0.25, we ignored that factor and ran a fully-crossed, two-way ANOVA with metacommunity richness and dispersal (n=25). For response variables determined at the metacommunity level, data were analyzed using a fully factorial two-way ANOVA with metacommunity richness and dispersal as the factors (n=5). We also analyzed the relationship between final grazer diversity and ecosystem properties using a GLM with final Shannon-Weaver (S-W) diversity of grazers as a continuous predictor and dispersal as a class predictor. Patch S-W was used for responses in patches, and metacommunity S-W was used for metacommunity responses and spatial heterogeneity.

Selection effects

To determine whether effects of grazer metacommunity richness were due to the presence of a particular grazer species, we ran backwards elimination multiple regressions of each response variable against the final abundance of each grazer species. Backwards elimination regression showed that different combinations of species were significant contributors to the decrease in each food resource (Fig. 2); there was not a single species or a single combination of species that significantly explained all effects. Furthermore, the effects of metacommunity richness could not be explained simply by the presence of additional species in the high richness metacommunities; species also present in the low richness metacommunities contributed to all of the diversity effects observed. Species that were significant contributors to the spatial heterogeneity of algal, invertebrate, and *Z. marina* biomass were also not the same species responsible for the increase in beta-diversity.

Diversity measures

Beta-diversity was calculated as: Beta-diversity = 1 – (UV/(U+V+UV)) where U is the relative abundance of the shared species in patch 1 and V is the relative abundance of the shared species in patch 2[1]. Beta diversity was calculated for every possible pair of patches in a metacommunity and the mean was used as the datum from that metacommunity in the analyses.

Synchrony

Synchrony was calculated as the sum of the covariances of epiphyte abundance through time for each possible pair of patches within a metacommunity[2,3]. To determine whether or not diversity and dispersal affected synchrony, we used these summed covariances as the response variable in a GLM with S-W diversity as a continuous predictor and dispersal as a class predictor. Results are not shown, but synchrony marginally significantly decreased with diversity in unconnected communities, and dispersal increased synchrony.

RESULTS AND DISCUSSION

Both metacommunity richness and dispersal of grazers influenced grazer diversity (Fig. 1). As predicted, increasing initial metacommunity richness increased final grazer diversity at all scales: within patches (alpha diversity), between patches (beta diversity), and within entire metacommunities (gamma diversity)[15,17]. Grazer dispersal increased compositional similarity among patches, decreasing beta and gamma diversity without affecting alpha diversity in the patches (Fig. 1). Both local extinctions and colonizations occurred, at varying rates for different species (Table S1). Dispersal was frequent enough that all but one grazer species successfully founded populations in patches where they were not initially present, colonizing 25-100% of such patches. But dispersal was not so frequent that it erased the stamp of initial composition, since final proportional abundances of most species were significantly predicted by initial proportional abundances (Table S1). This evidence of colonization, extinction, and moderate dispersal rates confirms that our connected patches functioned as true metacommunities. Effects of this active dispersal on diversity in our experiment parallel the effects of passive dispersal observed for protozoans and other zooplankton[20,21], suggesting that the dispersal effects on metacommunity diversity we found may be robust.

Metacommunity richness and dispersal of grazers also affected net production at multiple trophic levels. Mean grazer abundance increased with grazer richness both within patches (Table S2) and in entire metacommunities (Fig. 2a), as predicted[13,15-17]. Concomitantly, the larger grazer populations in richer metacommunities more effectively cropped biomass of primary producers, including macroalgae, cyanobacteria, the foundation species *Zostera,* and its epiphytic algae (Fig. 2c-f, Table S2). These metacommunity richness effects cannot be explained by "selection effects" (i.e. presence of a particular species at higher diversity), because several species from both small and large pools significantly contributed to these trends (see Supplementary Methods). Thus, even in a system with random assembly, immigration, and emigration, species richness pervasively influenced community and ecosystem properties.

Compared to diversity, grazer dispersal had relatively modest effects on ecosystem properties. Contrary to our prediction[5,15], dispersal did not increase mean grazer diversity or abundance within patches (Fig. 1, 2a). Nonetheless, dispersal did affect grazing impact, allowing grazers to actively seek patches with preferred food and abandon patches with undesirable food. Specifically, connecting patches decreased the biomass of edible macroalgae and recruits of the tunicate *Molgula manhattensis* (Fig. 2c,d). In contrast, dispersal increased the biomass of less preferred cyanobacteria and *Z. marina*, at least in the less diverse communities (Fig. 2e,f). During the first 28 days of the experiment, this dispersal-mediated shift in grazing impact actually enhanced epiphyte biomass accumulation within connected patches (Table S2). Furthermore, connecting patches reduced the enhancement of secondary production by diversity seen in isolated patches. Specifically, total grazer abundance increased with grazer diversity, but the slope of this relationship was reduced by grazer dispersal (Fig. 2b, Table S3). In the absence of dispersal, diversity led to more effective and thorough grazing; however, when grazers could actively select favorable patches, they may have limited their own population growth by indirectly facilitating the colonization of limited substrate by less palatable algae[22]. Hence, active dispersal and habitat selection by multiple generations of grazers can affect ecosystem properties and modify the effects of biodiversity on ecosystem properties, underscoring a key difference between assemblages with single vs. multiple trophic levels.

Also contrary to our expectations[2,8-11], higher metacommunity richness increased ecosystem variability both among and within patches. Whereas the similarity hypothesis predicts that increasing diversity increases compositional similarity, thereby increasing the predictability of ecosystem function across space[11], we found that more diverse grazer metacommunities produced greater spatial variability in ecosystem properties, including algal and sessile invertebrate biomass accumulation (Fig. 1b, Fig. 3b-d). This increased spatial variability probably stemmed from variability in grazer community composition (increased beta-diversity) in the more diverse metacommunities (Fig. 1b), supporting the hypothesis that compositional similarity and spatial predictability of ecosystem function are positively related[11]. However, these results also suggest that when species are lost from entire landscapes, and not just local communities, declining diversity may increase patch compositional similarity, producing a negative relationship between diversity and predictability in space. The contrast between our results and previous experiments[11,23,24] highlights the importance of examining how different biodiversity loss scenarios affect ecosystem function, and recognizing that higher diversity does not necessarily increase the predictability of ecosystem functioning in space as it often does in time.

Metacommunity grazer richness also affected temporal variability of ecosystem properties, but in surprising, scale- and dispersal- dependent ways. First, temporal variabilities of both grazer abundance and epiphyte load were generally lower in metacommunities than in patches (Fig. 3e-h). At the patch scale, increasing grazer richness increased temporal variability of grazer abundance (Fig. 3e), contradicting predictions that diverse competitive assemblages will have lower temporal variability of aggregate properties[2,8-10,15]. Our results are consistent, however, with recent theory predicting that biodiversity can reduce stability of biomass in multi-trophic food webs with strongly generalist grazers, like ours[19], and that mobile consumers can de-stabilize production in patchy landscapes[25].

In contrast to patch-scale patterns, at the metacommunity scale diversity stabilized both grazer and epiphyte abundance, at least in the absence of dispersal (grey bars, Fig. 3 g,h), confirming predictions[2,8-10,15]. Since the patches in these unconnected metacommunities were isolated, the reduced variability of their summed properties at high diversity, even while individual patch variability was increased, must be due to asynchronous fluctuations. Asynchrony is often invoked as a mechanism stabilizing aggregate properties within patches at high diversity[8]. Similarly, spatial variability of species composition, or beta-diversity, may create asynchrony of ecosystem properties among patches, stabilizing ecosystem properties at the metacommunity scale (see conceptual diagram, Supp. Fig. 1). Dispersal may decrease beta-diversity and spatial heterogeneity (Figs. 2, 3) and increase synchrony, potentially eliminating this stabilizing effect (Supp. Fig. 1). In our experiment, grazer diversity did reduce synchrony of epiphyte abundance among patches, but only without dispersal (data not shown; see Supplementary Methods). This conceptually supports the spatial insurance hypothesis for metacommunities[15], but also demonstrates that diversity can contribute insurance via spatial variation even in the absence of dispersal.

The contrast between predicted stabilizing effects of diversity and dispersal, and our findings that diversity more often made ecosystem properties less predictable in space and time, highlights a potentially fundamental difference in processes mediating BD-EF relationships in single versus multi-trophic ecosystems: the influence of active food and habitat selection by mobile consumers. At the metacommunity level, grazer dispersal eliminated the stabilizing effect of diversity on ecosystem properties (Fig. 3g,h), and at the patch level, grazer dispersal consistently increased temporal variability (Fig. 3e,f). Both results contradict the spatial insurance hypothesis, which is based on equilibrium metacommunities of sessile organisms with passive dispersal[15]. In communities of mobile animals where dispersal is active and competitive exclusion is rare, connecting patches may allow both rapid recruitment to optimal habitat and emigration after resource depletion, inflating temporal variability within a given patch and enhancing spatial heterogeneity. This hypothesis is also consistent with our finding that, at least in less diverse communities, dispersal enhanced grazer impacts on edible algae but reduced impacts on inedible algae (Fig. 2c,e). Habitat selection, then, might be a means by which species interactions, including those that mediate production, transcend the local scale and affect patterns at metacommunity scales[25,26].

Biodiversity-stability theory, like most ecological theory, assumes equilibrium[2,8-10,15]. Although our communities experienced colonization, extinction, and reached carrying capacity, they probably did not reach compositional equilibrium. Therefore, the increased temporal variability we observed in response to both diversity and dispersal might be due to transient dynamics. In nature, however, grazer composition shifts and seagrass patches change in size and location over timescales comparable to the length of our experiment, due to seasonal dynamics and disturbances (personal observation). Since such non-equilibrium phenomena are important in most natural ecosystems, we believe our results are broadly relevant. Furthermore, running the experiment for longer would probably increase the importance of dispersal, which eliminated the predicted and observed stabilizing effects of diversity (Fig. 3e-h). Consequently, our results probably differed from diversity-stability predictions because we used mobile consumers that can actively choose patches and affect spatial heterogeneity of resources, rather than sessile organisms with passive dispersal.

Our experiment demonstrates that the stabilizing effect of biodiversity can be modified by both dispersal and scale, supporting previous theory and empirical research demonstrating that both dispersal and scale can modify the effect of biodiversity on the magnitude of productivity[14-17]. Furthermore, our results indicate that increasing diversity will not necessarily increase the predictability of ecosystem functioning in space as it often does in time. There may be tradeoffs, then, between maximizing diversity across landscapes and stabilizing ecosystem services in time. However, our experiment also corroborates, for the first time, theory predicting that diversity can enhance reliability of ecosystem services through a spatial mechanism[15]: spatial heterogeneity created by more diverse metacommunities of grazers stabilized ecosystem properties at the metacommunity scale. Clearly, the spatial and temporal processes that influence diversity within natural landscapes can substantially influence the ways that biodiversity mediates ecosystem functioning. Integrating these influences is critical to effective management of ecosystem services in response to habitat fragmentation and other drivers of biodiversity change.

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Supplementary Information is linked to the on-line version of the paper at www.nature.com/nature.

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FIGURE LEGENDS

Figure 1. Species pool size affects grazer diversity at multiple spatial scales. Grey bars=no dispersal corridors; black bars=dispersal corridors. (a) Mean (± s.e.m.) patch diversity (Shannon-Weaver, SW, n=25 for each bar). (b) Beta-diversity (see Supplementary Methods-Diversity Measures, n=5 for each bar). (c) Metacommunity SW diversity (n=5 for each bar). R=richness; D=dispersal; † p <.1, * p<.05, ** p <.01, *** p <.001, ****p<.0001.

Figure 2. Metacommunity richness and dispersal affect the magnitude of ecosystem production at multiple trophic levels. (a) Mean (±s.e.m.) grazer abundance increased with diversity, but (b) this relationship was modified by dispersal. Open symbols = no dispersal, closed symbols = dispersal. n=50 for each set. More diverse (and denser) grazer communities more effectively reduced biomass of (c) edible macroalgae, (d) *M. manhattensis* recruits, (e) less edible cyanobacteria, and (f) *Z. marina*, the foundation species. Connecting patches allowed grazers to concentrate on preferred food (c,d), facilitating accumulation of less preferred food (e,f). n=5 for each bar. Symbols as in Fig. 1.

Figure 3. Diversity effects on ecosystem variability are modified by dispersal and spatial scale. Spatial variation (CV) (± s.e.m.) among the five patches within a metacommunity for (a) grazer abundance, (b) biomass of *Molgula manhattensis*, the most frequent sessile invertebrate invader, (c) edible algae biomass (macroalgae), and (d) inedible algae biomass (cyanobacteria). n=5 for each bar. Temporal variation (CV) (± s.e.m.) of (e, g) grazer abundance (n=10) and (f, i) epiphyte load (n=25) within patches and within whole metacommunities. Symbols as in Fig. 1.

Figure 1

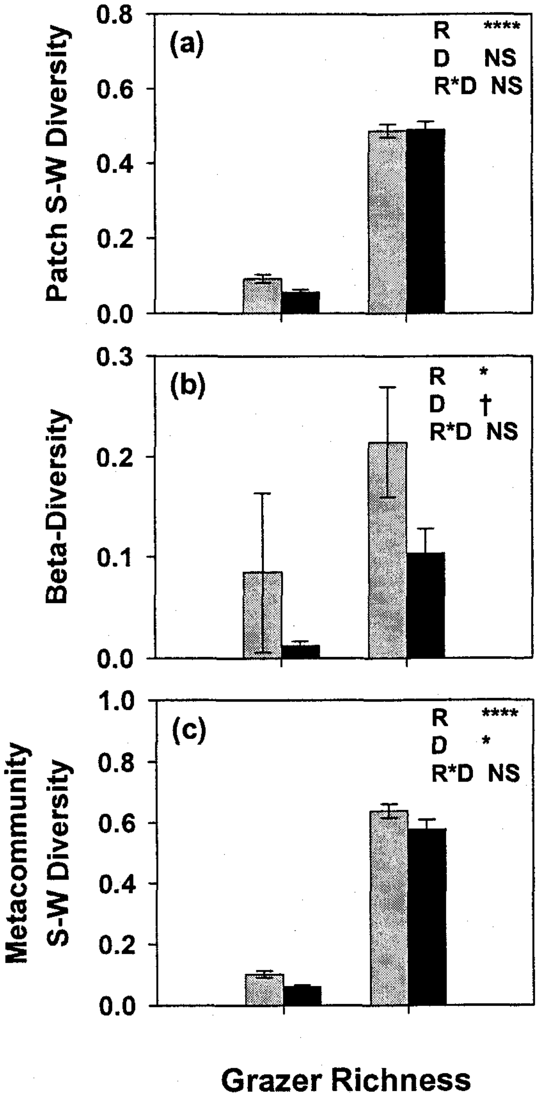
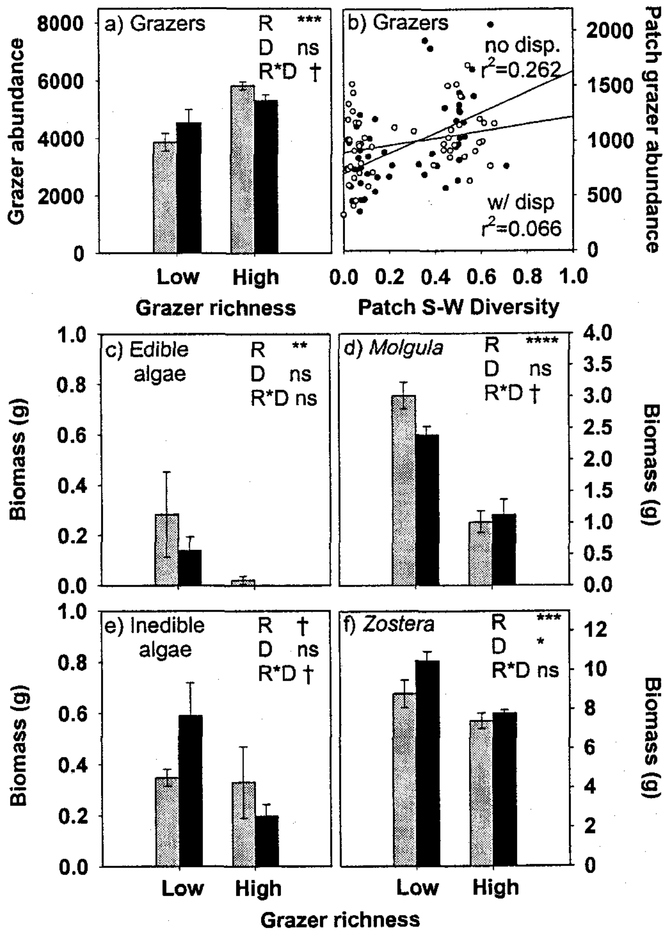
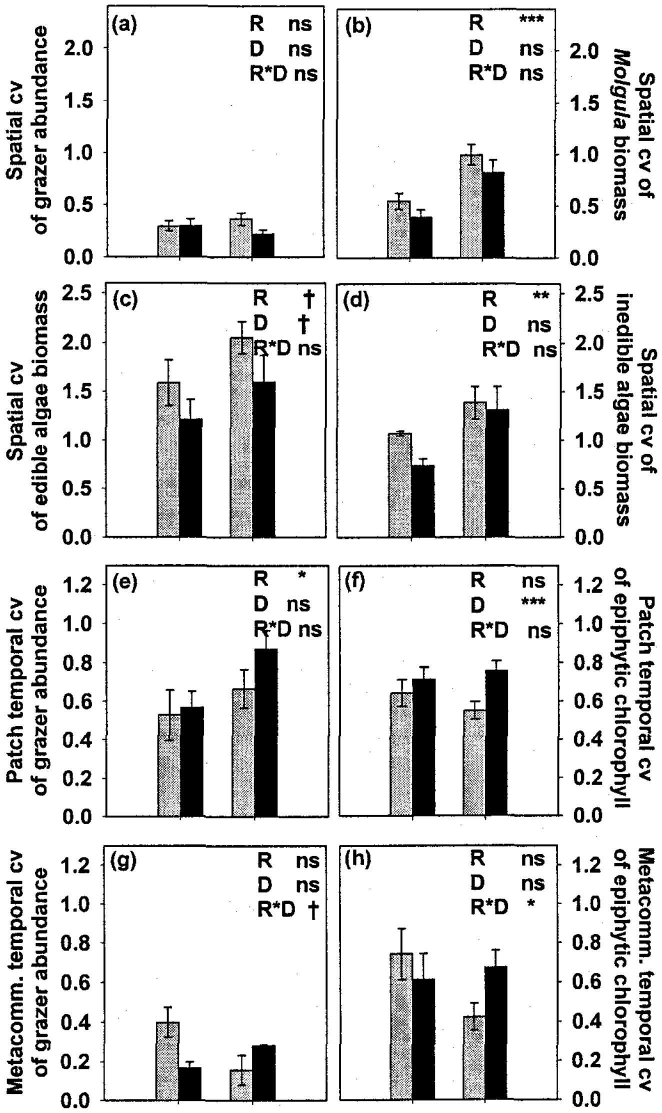

Patch S-W Diversity
0.8
0.6
0.4
0.2
0.0
(a)
R ****
D NS
R*D NS
Beta-Diversity
0.3
0.2
0.1
0.0
(b)
R *
D †
R*D NS
Metacommunity S-W Diversity
1.0
0.8
0.6
0.4
0.2
0.0
(c)
R ****
D *
R*D NS
Grazer Richness

Figure 2

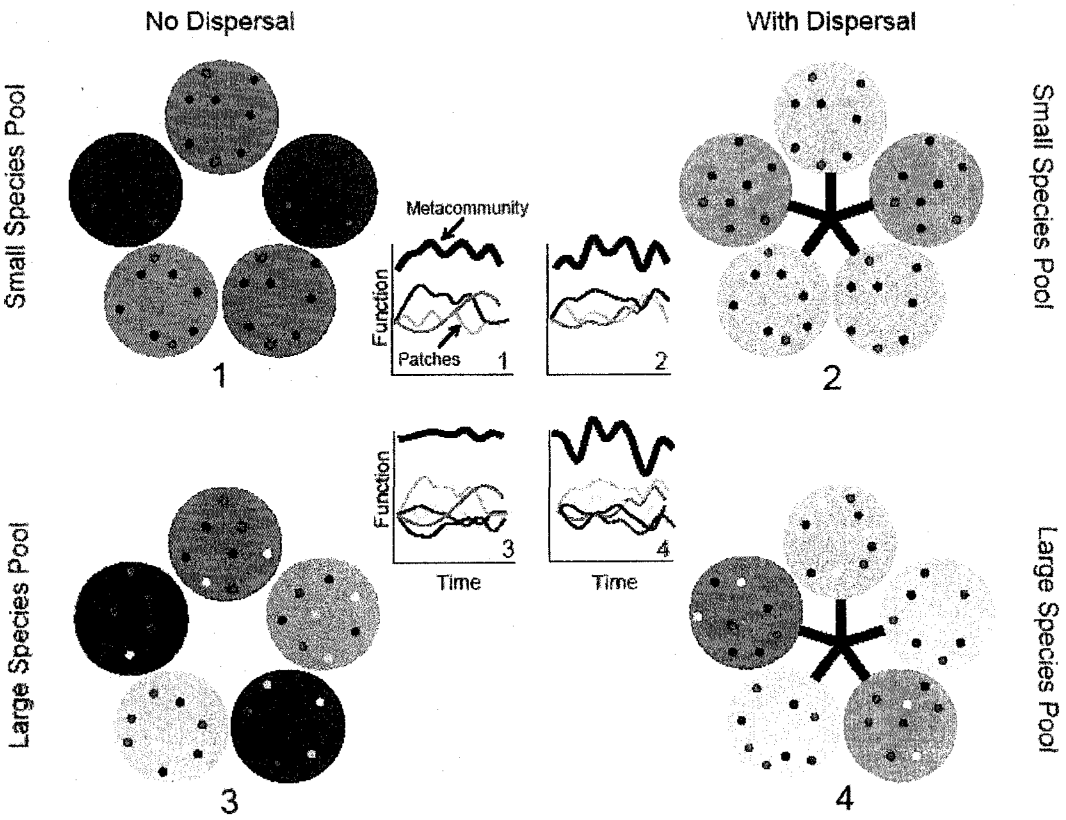


a) Grazers
R ***
D ns
R*D †
Grazer abundance
8000
6000
4000
2000
0
Low
High
Grazer richness
b) Grazers
no disp.
r²=0.262
w/ disp
r²=0.066
0.0 0.2 0.4 0.6 0.8 1.0
Patch S-W Diversity
Patch grazer abundance
2000
1500
1000
500
0
c) Edible algae
R **
D ns
R*D ns
Biomass (g)
1.0
0.8
0.6
0.4
0.2
0.0
d) Molgula
R ****
D ns
R*D †
Biomass (g)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
e) Inedible algae
R †
D ns
R*D †
Biomass (g)
1.0
0.8
0.6
0.4
0.2
0.0
f) Zostera
R ***
D *
R*D ns
Biomass (g)
12
10
8
6
4
2
0
Low
High
Low
High
Grazer richness

Figure 3


(a)
R ns
D ns
R*D ns
Spatial cv of grazer abundance
(b)
R ***
D ns
R*D ns
Spatial cv of *Molgula* biomass
(c)
R †
D †
R*D ns
Spatial cv of edible algae biomass
(d)
R **
D ns
R*D ns
Spatial cv of inedible algae biomass
(e)
R *
D ns
R*D ns
Patch temporal cv of grazer abundance
(f)
R ns
D ***
R*D ns
Patch temporal cv of epiphytic chlorophyll
(g)
R ns
D ns
R*D †
Metacomm. temporal cv of grazer abundance
(h)
R ns
D ns
R*D *
Metacomm. temporal cv of epiphytic chlorophyll
0.0
0.5
1.0
1.5
2.0
2.5
0.2
0.4
0.6
0.8
1.2

Appendix 2-1.



Supplemental Figure 1: Conceptual diagram of effects of species pool size and dispersal on spatial and temporal variability of ecosystem properties. Large circles represent patches, and each cluster of five patches is a metacommunity. Small circles within the patches represent individual grazers; colors signify species. Each combination of grazers consumes resources differently, creating spatial heterogeneity, as shown by the contrast between patch colors within a metacommunity. Patches of the same color are similar in species composition and grazing efficiency; consequently they have the same temporal fluctuations and are shown by the same color line on the graphs. Graphs show the fluctuations through time of a hypothetical ecosystem function, such as primary productivity, within each patch (thin lines, color matches patch color) and within the metacommunity as a whole (thick line, summed function of individual patches).

Increasing the number of species in the species pool used to assemble metacommunities leads to greater spatial variability in grazer species composition, which enhances spatial heterogeneity of the grazers' resources and the variety of temporal patch trajectories. This greater variety of patch trajectories stabilizes metacommunity function through time.

Dispersal decreases spatial variability and increases synchrony (temporal fluctuations in graphs are more in phase). This eliminates the stabilizing effect of metacommunity richness.

Supplemental Methods:

Selection effects. To determine whether effects of grazer metacommunity richness were due to the presence of a particular grazer species, we ran backwards elimination multiple regressions of each response variable against the final abundance of each grazer species. Backwards elimination regression showed that different combinations of species were significant contributors to the decrease in each food resource (Fig. 2); there was not a single species or a single combination of species that significantly explained all effects. Furthermore, the effects of metacommunity richness could not be explained simply by the presence of additional species in the high richness metacommunities; species also present in the low richness metacommunities contributed to all of the diversity effects observed. Species that were significant contributors to the spatial heterogeneity of algal, invertebrate, and *Z. marina* biomass were also not the same species responsible for the increase in beta-diversity.

Diversity measures. Beta-diversity was calculated as: Beta-diversity = 1 – (UV/(U+V+UV)) where U is the relative abundance of the shared species in patch 1 and V is the relative abundance of the shared species in patch 2[1]. Beta diversity was calculated for every possible pair of patches in a metacommunity and the mean was used as the datum from that metacommunity in the analyses.

Synchrony. Synchrony was calculated as the sum of the covariances of epiphyte abundance through time for each possible pair of patches within a metacommunity[2,3]. To determine whether or not diversity and dispersal affected synchrony, we used these summed covariances as the response variable in a GLM with S-W diversity as a continuous predictor and dispersal as a class predictor. Results are not shown, but synchrony marginally significantly decreased with diversity in unconnected communities, and dispersal increased synchrony.

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Supplementary Table 1 (Table S1): Effects of dispersal on extinction, colonization, and final composition compared with initial composition. Extinctions were instances where initial abundance was >0 and final abundance was 0; colonizations were instances where initial patch abundance was 0 and final abundance was >0. Comparisons of initial and final relative abundances of each species were made using a GLM with initial relative abundance as a continuous predictor and dispersal as a class predictor. Table cells are (F-statistic, p-value).

	Extinction rate		**Colonization rate**	**R2**	**F, p-value**			
Species	**No Disp**	**W/ Disp**	**W/ Disp**		**Initial Composition**	**Dispersal**	**Comp *Disp**	**Overall**
Erichsonella attenuata	0.38	0.45	0.2	0.3037	**9.97, 0.0028**	2.21, 0.1438	**5.92, 0.0189**	**6.69, 0.0008**
Gammarus mucronatus	0	0	1	0.4625	**28.35, <0.0001**	2.99, 0.0907	1.63, 0.2082	**13.19, <0.0001**
Idotea baltica	0.08	0.09	0.67	0.208	**7.27, 0.0098**	0.59, 0.4471	**8.30, 0.0060**	**4.27, 0.0096**
Ampithoe valida	0	0.05	0.4	0.1238	**6.04, 0.0178**	0.15, 0.7046	0.53, 0.4692	2.17, 0.1048
Cymadusa compta	0	0	1	0.4073	**21.01, <0.0001**	1.31, 0.2585	**5.23, 0.0268**	**10.54, <0.0001**
Dulichiella appendiculata	0.11	0.21	0.75	0.2516	**13.09, 0.0007**	0.15, 0.7047	1.26, 0.2676	**5.15, 0.0037**
Elasmopus levis	0.22	0.17	1	0.1407	**7.42, 0.0091**	0.50, 0.4851	0.64, 0.4295	**2.51, 0.0703**
Paracerceis caudata	0.67	0.85	0	0.0457	1.48, 0.2300	0.28, 0.6023	0.60, 0.4422	0.79, 0.5082

Supplementary Table 2 (Table S2): Effects of metacommunity richness and dispersal on patterns of diversity and ecosystem properties within patches and metacommunities. Data were analyzed using a GLM. Metacommunity ID is fully nested within the interaction term. When the p-value for it exceeded 0.2, we removed it from the analysis, changing the model d.o.f. from 7 to 3. Table cells are (F-statistic, p-value). When data were not normally distributed, they were log-transformed.

Response Variable	Metacommunity Richness (df=1)	Dispersal (df=1)	Metacomm. Richness * Dispersal (df=1)	Meta-community ID (df=4)	Total (df=7,3)
Patch (n=25 for each combination of treatments, n=100 total)					
Grazer species richness	**64.93, <0.0001**	0.9, 0.3441	**3.2, 0.0768**	4.05, 0.0045	**29.08, <0.0001**
Grazer Shannon-Weaver diversity	**700.19, <0.0001**	1.05, 0.3090	1.49, 0.2257	NS	**234.69, <0.0001**
Log grazer abundance	**24.05, <0.0001**	0.10, 0.7568	0.92, 0.3391	4.08, 0.0044	**5.99, <0.0001**
Epiphytic chl *a* (week 2)	**33.44, <0.0001**	**10.93, 0.0014**	**3.61, 0.0604**	7.53, <0.0001	**7.48, <0.0001**
Epiphytic chl a (week 4)	0.24, 0.6227	**4.02, 0.0477**	0.1, 0.7532	NS	1.46, 0.2317
Epiphytic chl *a* (week 6)	0.14, 0.7130	0.53, 0.4695	1.59, 0.2108	NS	0.76, 0.5219
Log total algal biomass	**20.91, <0.0001**	0, 0.9482	1.0, 0.3197	NS	**7.3, 0.0002**
Edible algae biomass (macroalgae)	**7.65, 0.0068**	1.29, 0.2583	0.75, 0.3874		**3.23, 0.0258**
Inedible algae biomass (cyanobacteria)	**4.85, 0.0301**	0.28, 0.6011	**3.17, 0.0781**	NS	**2.76, 0.0461**
Z. marina biomass	**19.05, <0.0001**	**4.98, 0.0280**	1.93, 0.1682	NS	**8.65, <0.0001**
Invertebrate biomass	**38.16, <0.0001**	1.87, 0.1752	0.09, .7637	NS	**13.37, <0.0001**
Log *M. manhattensis* biomass	**10.93, 0.0014**	**6.96, 0.0098**	**8.52, 0.0044**	3.51, 0.0104	**7.42, <0.0001**
Temporal CV of grazer abundance	**4.56, 0.0397**	1.44, 0.2386	0.63, 0.4308	NS	2.21, 0.1039
Temporal CV of epiphytic chl *a*	0.14, 0.7107	**11.31, 0.0011**	1.89, 0.1726	1.64, 0.1708	**2.00, 0.0629**
Metacommunity (n=5 for each combination of treatments, n=20 total)					
Grazer species richness	**77.04, <0.0001**	1.04, 0.3226	0.04, 0.8408	N/A	**26.04, <0.0001**
Grazer Shannon-Weaver diversity	**647.44, <0.0001**	**5.95, 0.0267**	0.24, 0.6333	N/A	**217.88, <0.0001**
Grazer beta-diversity	**4.94, 0.0411**	**3.39, 0.0844**	0.15, 0.7063	N/A	**2.82, 0.0720**
Grazer abundance	**19.78, 0.0004**	0.05, 0.8305	**3.73, 0.0715**	N/A	**7.85, 0.0019**
Total algal biomass	**9.91, 0.0062**	0.08, 0.7828	0.61, 0.4477	N/A	**3.53, 0.0390**
Edible algae biomass (macroalgae)	**4.96, 0.0406**	0.84, 0.3731	0.49, 0.4942	N/A	2.10, 0.1408
Inedible algae biomass (cyanobacteria)	**4.43, 0.0514**	0.25, 0.6227	2.90, 0.1078	N/A	2.53, 0.094
Z. marina biomass	**17.69, 0.0007**	**4.62, 0.0472**	1.79, 0.1997	N/A	**8.03, 0.0017**
Invertebrate biomass	**27.06, <0.0001**	1.32, 0.2670	0.06, 0.8028	N/A	**9.48. 0.0008**
M. manhattensis biomass	**67.71, <0.0001**	1.68, 0.2129	**3.42, 0.0831**	N/A	**24.27, <0.0001**
Spatial CV of grazer abundance	0.01, 0.9239	1.67, 0.2147	1.96, 0.1811	N/A	1.21, 0.3377
Spatial CV of epiphytic chl *a* (week 2)	1.32, 0.2683	2.42, 0.1397	0.30, 0.5904	N/A	1.34, 0.2952
Spatial CV of epiphytic chl a (week 4)	0.39, 0.5418	0.46, 0.5088	0, 0.9776	N/A	0.28, 0.8376
Spatial CV of epiphytic chl *a* (week 6)	0.02, 0.8841	0.79, 0.3879	1.5, 0.2388	N/A	0.77, 0.5281
Spatial CV of total algal biomass	**10.38, 0.0053**	1.31, 0.2688	0.24, 0.6318	N/A	**3.98, 0.0270**
Spatial CV of edible algae biomass	**3.67, 0.0736**	**3.44, 0.0820**	0.03, 0.8564	N/A	2.38, 0.1078
Spatial CV of inedible algae biomass	**8.80, 0.0091**	1.84, 0.1937	0.79, 0.3884	N/A	**3.81, 0.0310**
Spatial CV of *Z. marina* biomass	1.68, 0.2128	1.29, 0.2732	0.74, 0.4016	N/A	1.24, 0.3287
Spatial CV of invertebrate biomass	**4.17, 0.0581**	0.8, 0.3843	1.63, 0.2201	N/A	2.2, 0.1279
Spatial CV of *M. manhattensis* biomass	**21.65, 0.0003**	3.01, 0.1020	0, 0.9468	N/A	**8.22, 0.0015**
Temporal CV of grazer abundance	1.25, 0.3262	0.91, 0.3943	**10.34, 0.0324**	N/A	4.17, 0.1009
Temporal CV of epiphytic chl *a*	1.42, 0.2502	0.31, 0.5863	**3.07, 0.0991**	N/A	1.60, 0.2288

Supplementary Table 3 (Table S3): Effects of final grazer diversity on ecosystem properties at both patch- and metacommunity- scales. Data were analyzed using a GLM with grazer Shannon-Weaver (S-W) diversity as a continuous predictor and dispersal as a class predictor. Local response variables were regressed against local grazer S-W and metacommunity response variables were regressed against metacommunity S-W. Table cells are (F-statistic, p-value).

Response Variable	Grazer S-W (df=1)	Dispersal (df=1)	Grazer S-W * Dispersal (df=1)	R2	Total (df=3)
Patch (n=100)					
Grazer abundance	**19.30, <0.0001**	**3.52, 0.0638**	**4.52, 0.0361**	0.189	**7.37, 0.0002**
Log total algal biomass	**16.18, 0.0001**	0.33, 0.5669	0.69, 0.4083	0.156	**5.92, 0.0010**
Edible algae biomass (macroalgae)	**3.67, 0.0585**	1.87, 0.1861	0.42, 0.5183	0.054	1.82, 0.1496
Inedible algae biomass (cyanobacteria)	**3.80, 0.0542**	2.48. 0.1184	2.67, 0.1059	0.073	**2.51, 0.0634**
Z. marina biomass	**12.92, 0.0005**	0.19, 0.6653	1.53, 0.2197	0.175	**6.73, 0.0004**
Invertebrate biomass	**24.68, <0.0001**	0.84, 0.3624	0.03, 0.8537	0.224	**9.13, <0.0001**
Log *M. manhattensis* biomass	**19.24, <0.0001**	0.31, 0.5811	0.28, 0.5979	0.168	**6.42, 0.0005**
Temporal CV of grazer abundance	2.43, 0.1279	0.10, 0.7499	0.27, 0.6086	0.101	1.34, 0.2753
Temporal CV of epiphytic chl *a*	0.17, 0.6849	0.85, 0.3579	0.72, 0.3980	0.168	2.57, 0.0591
Metacommunity (n=20)					
Grazer abundance	**20.57, 0.0003**	**3.51, 0.0795**	**3.50, 0.0798**	0.601	**8.04, 0.00017**
Algal biomass	**9.50, 0.0071**	0.03, 0.8718	0.42, 0.5266	0.382	**3.29, 0.0478**
Edible algae biomass (macroalgae)	0.63, 0.4369	**3.46, 0.0812**	0.35, 0.5649	0.269	1.96, 0.1608
Inedible algae biomass (cyanobacteria)	0.54, 0.4723	0.08, 0.7862	**3.64, 0.0745**	0.350	2.87, 0.0688
Z. marina biomass	**18.34, 0.0006**	**4.41, 0.052**	1.69, 0.2120	0.603	**8.12, 0.0016**
Invertebrate biomass	**24.83, 0.0001**	0.40, 0.5347	0.09, 0.7668	0.620	**8.70, 0.0012**
M. manhattensis biomass	**48.11, <0.0001**	**5.31, 0.0350**	2.32, 0.1472	0.766	**17.48, <0.0001**
Spatial CV of grazer abundance	0.01, 0.9255	0.05, 0.8176	1.68, 0.2137	0.172	1.11, 0.3750
Spatial CV of epiphytic chl *a* (week 2)	3.17, 0.0941	0.00, 0.9749	0.49, 0.4920	0.287	2.15, 0.1138
Spatial CV of epiphytic chl a (week 4)	0.04, 0.8456	0.00, 0.9722	1.41, 0.2530	0.226	1.55, 0.2391
Spatial CV of epiphytic chl *a* (week 6)	0.00, 0.9682	1.02, 0.3282	1.15, 0.2499	0.072	0.41, 0.7472
Spatial CV of total algal biomass	**8.44, 0.0103**	0.41, 0.5313	0.03, 0.8649	0.376	**3.22, 0.0510**
Spatial CV of *Z. marina* biomass	0.06, 0.8080	2.31, 0.1484	1.02, 0.3278	0.535	**6.13, 0.0056**
Spatial CV of invertebrate biomass	**3.16, 0.0946**	1.12, 0.306	0.65, 0.4303	0.218	1.48, 0.2569
Spatial CV of *M. manhattensis* biomass	**17.38, 0.0007**	0.52, 0.4816	0.00, 0.9628	0.557	**6.70, 0.0039**
Temporal CV of grazer abundance	0.32, 0.6036	**6.19, 0.0676**	**5.94, 0.0714**	0.651	2.49, 0.1994
Temporal CV of epiphytic chl *a*	1.12, 0.3063	1.06, 0.3179	2.72, 0.1184	0.210	1.42, 0.2741

Supplementary Table 4 (Table S4): Initial patch and metacommunity composition. Cells are numbers of male-female pairs.

			Large Species Pool												
			Small Species Pool												
Metacommunity ID	**Patch ID**	**Dispersal?**	***Gammarus mucronatus***	***Erichsonella attenuata***	***Idotea baltica***	***Ampithoe valida***	***Cymadusa compta***	***Dulichiella appendiculata***	***Elasmopus levis***	***Paracerceis caudata***	**Total # of Grazers**	**Initial Patch Richness**	**Initial Patch S-W Diversity**	**Initial Metacommunity S-W Diversity**
1	1		3	5	7	0	0	0	0	0	30	3	0.453	0.472
1	2		4	6	5	0	0	0	0	0	30	3	0.471	
1	3		9	2	4	0	0	0	0	0	30	3	0.403	
1	4		6	5	4	0	0	0	0	0	30	3	0.471	
1	5		8	6	1	0	0	0	0	0	30	3	0.383	
2	6		4	1	1	3	3	0	1	2	30	7	0.785	0.896
2	7		2	0	2	1	3	3	2	2	30	7	0.825	
2	8		1	1	2	1	2	2	3	3	30	8	0.865	
2	9		4	2	1	3	1	2	1	1	30	8	0.840	
2	10		0	2	2	2	2	2	2	3	30	7	0.840	
3	11	+	2	10	3	0	0	0	0	0	30	3	0.374	0.475
3	12	+	4	2	9	0	0	0	0	0	30	3	0.403	
3	13	+	7	4	4	0	0	0	0	0	30	3	0.461	
3	14	+	3	5	7	0	0	0	0	0	30	3	0.453	
3	15	+	6	5	4	0	0	0	0	0	30	3	0.471	
4	16	+	1	3	3	0	2	2	1	3	30	7	0.810	0.890
4	17	+	1	3	1	0	4	1	2	3	30	7	0.785	
4	18	+	1	1	3	1	2	0	3	4	30	7	0.785	
4	19	+	4	1	3	2	0	2	2	1	30	7	0.800	
4	20	+	2	0	2	2	3	3	2	1	30	7	0.825	
5	21	+	5	5	5	0	0	0	0	0	30	3	0.477	0.474
5	22	+	8	5	2	0	0	0	0	0	30	3	0.421	
5	23	+	6	4	5	0	0	0	0	0	30	3	0.471	
5	24	+	1	8	6	0	0	0	0	0	30	3	0.383	
5	25	+	6	6	3	0	0	0	0	0	30	3	0.458	
6	26	+	3	3	3	2	0	1	2	1	30	7	0.810	0.887
6	27	+	2	2	0	0	3	4	2	2	30	6	0.760	
6	28	+	2	0	3	2	1	4	2	1	30	7	0.800	
6	29	+	3	2	5	1	2	0	1	1	30	7	0.767	
6	30	+	2	3	2	1	2	3	0	2	30	7	0.825	
7	31		1	7	7	0	0	0	0	0	30	3	0.387	0.465
7	32		6	7	2	0	0	0	0	0	30	3	0.430	
7	33		8	6	1	0	0	0	0	0	30	3	0.383	
7	34		5	7	3	0	0	0	0	0	30	3	0.453	
7	35		9	2	4	0	0	0	0	0	30	3	0.403	
8	36		2	1	2	3	1	4	1	1	30	8	0.840	0.891
8	37		2	3	2	1	2	2	2	1	30	8	0.880	
8	38		0	3	2	2	1	2	1	4	30	7	0.800	
8	39		1	4	4	1	2	1	1	1	30	8	0.815	
8	40		2	2	1	2	2	2	1	3	30	8	0.880	
9	41	+	5	8	2	0	0	0	0	0	30	3	0.421	0.473
9	42	+	4	7	4	0	0	0	0	0	30	3	0.461	
9	43	+	6	5	4	0	0	0	0	0	30	3	0.471	
9	44	+	6	3	6	0	0	0	0	0	30	3	0.458	
9	45	+	7	4	4	0	0	0	0	0	30	3	0.461	
10	46		6	5	4	0	0	0	0	0	30	3	0.471	0.462
10	47		7	6	2	0	0	0	0	0	30	3	0.430	

10	48		5	8	2	0	0	0	0	0	30	3	0.421	
10	49		3	5	7	0	0	0	0	0	30	3	0.453	
10	50		4	9	2	0	0	0	0	0	30	3	0.403	
11	51	+	4	1	0	2	4	2	0	2	30	6	0.735	0.889
11	52	+	1	0	4	2	0	3	2	3	30	6	0.744	
11	53	+	0	0	1	4	3	3	2	2	30	6	0.744	
11	54	+	2	2	2	3	2	1	2	1	30	8	0.880	
11	55	+	2	2	3	2	1	3	2	0	30	7	0.825	0.879
12	56		1	1	3	1	0	5	1	3	30	7	0.752	
12	57		3	2	1	0	0	4	2	3	30	6	0.744	
12	58		2	4	1	1	1	1	3	2	30	8	0.840	
12	59		2	2	2	2	1	2	2	2	30	8	0.895	
12	60		0	2	2	2	2	1	4	2	30	7	0.815	
13	61		6	6	3	0	0	0	0	0	30	3	0.458	0.477
13	62		3	6	6	0	0	0	0	0	30	3	0.458	
13	63		4	4	7	0	0	0	0	0	30	3	0.461	
13	64		6	3	6	0	0	0	0	0	30	3	0.458	
13	65		5	7	3	0	0	0	0	0	30	3	0.453	
14	66	+	2	2	3	1	0	1	3	3	30	7	0.810	0.881
14	67	+	3	2	3	1	2	3	1	0	30	7	0.810	
14	68	+	1	2	6	2	0	0	2	2	30	6	0.704	
14	69	+	4	1	1	0	3	1	5	0	30	6	0.687	
14	70	+	3	4	0	2	1	2	1	2	30	7	0.800	
15	71	+	5	8	2	0	0	0	0	0	30	3	0.421	0.469
15	72	+	5	8	2	0	0	0	0	0	30	3	0.421	
15	73	+	5	4	6	0	0	0	0	0	30	3	0.471	
15	74	+	6	5	4	0	0	0	0	0	30	3	0.471	
15	75	+	4	6	5	0	0	0	0	0	30	3	0.471	
16	76		1	5	1	3	1	0	1	3	30	7	0.752	0.893
16	77		1	3	0	1	4	3	2	1	30	7	0.810	
16	78		3	0	1	3	3	0	3	2	30	6	0.754	
16	79		4	1	3	1	1	1	2	2	30	8	0.840	
16	80		4	0	3	1	0	2	3	2	30	6	0.744	
17	81	+	6	5	4	0	0	0	0	0	30	3	0.471	0.474
17	82	+	5	5	5	0	0	0	0	0	30	3	0.477	
17	83	+	8	3	4	0	0	0	0	0	30	3	0.438	
17	84	+	4	8	3	0	0	0	0	0	30	3	0.438	
17	85	+	5	5	5	0	0	0	0	0	30	3	0.477	
18	86		3	0	3	2	0	2	1	4	30	6	0.744	0.879
18	87		2	1	5	1	0	1	2	3	30	7	0.767	
18	88		1	1	4	0	2	4	2	1	30	7	0.775	
18	89		0	3	2	2	3	3	2	0	30	6	0.769	
18	90		1	2	2	2	3	4	1	0	30	7	0.800	
19	91		4	4	7	0	0	0	0	0	30	3	0.461	0.475
19	92		4	7	4	0	0	0	0	0	30	3	0.461	
19	93		5	6	4	0	0	0	0	0	30	3	0.471	
19	94		4	5	6	0	0	0	0	0	30	3	0.471	
19	95		9	5	1	0	0	0	0	0	30	3	0.371	
20	96	+	2	1	3	4	3	1	1	0	30	7	0.785	0.896
20	97	+	2	2	1	1	3	3	2	1	30	8	0.865	
20	98	+	3	0	3	1	2	2	3	1	30	7	0.810	
20	99	+	2	3	2	1	2	2	2	1	30	8	0.880	
20	100	+	2	1	3	0	5	2	2	0	30	6	0.727	

CHAPTER 3:

MECHANISMS FOR DISPERSAL MODIFICATION OF ECOSYSTEM PROPERTIES WITHIN EXPERIMENTAL SEAGRASS METACOMMUNITIES

ABSTRACT

Habitat fragmentation, climate change and species invasions are changing biodiversity at both local and regional scales. Dispersal of individuals can mediate how all three of these changes to regional biodiversity affect diversity in networks of local communities, or metacommunities. But there is little theory or empirical evidence to suggest how dispersal or other metacommunity processes might affect the relationships between biodiversity and ecosystem function (BD-EF). We tested the interactive effects of grazer diversity and dispersal (patch connectivity) on the magnitude and predictability of ecosystem properties in experimental seagrass metacommunities. Previous analyses of this experiment suggested that dispersal had limited effects on the magnitude of community-level or aggregate properties but could modify BD-EF relationships and de-stabilize grazer and algal abundance. Here we examined how dispersal affected the temporal and spatial variability of individual grazer and resource populations. We investigated several possible mechanisms for the observed dispersal modification of BD-EF: competition-colonization tradeoffs, metacommunity source-sink dynamics, effects on individual metapopulations, and synchronization of metacommunity dynamics. We did not find evidence of competition-colonization tradeoffs among the eight species of grazers. Instead, the best competitors were the best dispersers, and dispersal rarely affected relative competitive performance. Likewise, dispersal had limited effects on the spatial and temporal variability of individual grazer species. We think the best remaining explanation for the reduction of grazer abundance in diverse metacommunities by dispersal is that dispersal indirectly reduced carrying capacity by allowing the accumulation of less edible algae. Selective foraging and/or a decrease in consumption pressure within patches during the first weeks of the experiment, mediated by mass effects, could have increased accumulation of less edible algae. Overall, dispersal tended to homogenize other ecosystem components across space, synchronize resource dynamics, and reverse the effects of diversity on the magnitude and predictability of ecosystem properties. Our experiment illustrates that dispersal can have subtle but important effects on the magnitude and predictability of ecosystem properties even when most previously proposed mechanisms for dispersal effects are not operating.

INTRODUCTION

In the last decade, research has shown that biodiversity losses may affect both the magnitude and stability of ecosystem processes such as production, decomposition, and nutrient cycling at the scale of local patches (e.g. Naeem et al. 1994, Tilman et al. 1996, McGrady-Steed et al. 1997, Loreau et al. 2001, Tilman et al. 2001, Hooper et al. 2005). Recent reviews of the BD-EF field have pointed out that three of the major challenges to making BD-EF research relevant to conservation are 1) scaling up to landscapes, 2) studying BD-EF relationships within foodwebs, rather than simply within trophic levels, and 3) separating the direct effects of habitat fragmentation, species introductions, and climate change on ecosystem function from their indirect effects on ecosystem function mediated by their effects on diversity (Giller et al. 2004, Srivastava and Vellend 2005).

As a first step towards meeting these challenges, we tested how diversity and dispersal interactively affect the magnitude, spatial variability, and temporal variability of ecosystem properties in experimental multi-trophic seagrass (*Zostera marina*) metacommunities. We manipulated metacommunity-wide species richness (gamma diversity) of mobile crustacean grazers by randomly assembling founding communities of grazers from two different species pools: one with three species and one with eight species. This mimicked loss of rare species from a regional species pool. Initial metacommunity-wide richness of grazers was set at either three or eight species, but both the relative abundances of species within metacommunities and the species richness within individual patches varied. We allowed this initial random assembly plus subsequent dispersal and species interactions to influence grazer diversity over the six weeks of the experiment. This design allowed us to simultaneously consider how metacommunity richness affected diversity within and between patches, to indirectly examine how beta-diversity affected ecosystem function, and to examine how dispersal might modify BD-EF relationships in metacommunities.

We found that, although dispersal only slightly affected diversity patterns and only modestly influenced aggregate ecosystem properties at any scale, dispersal still 1) significantly reduced the effect of grazer diversity on grazer abundance and 2) eliminated the few temporally stabilizing effects of diversity that we observed, increasing temporal variability of grazers and epiphytes (France and Duffy 2006b). Here we follow up on these findings by examining evidence for several mechanisms by which dispersal could mediate BD-EF relationships. These include: 1) competition-colonization tradeoffs, 2) source-sink metacommunity dynamics and mass effects, 3) sampling effects on variability due to dispersal favoring species with high or low population variability, 4) increasing synchronization of dynamics among patches, and 5) diminishing spatial variability of individual populations.

Both competition-colonization tradeoffs and source-sink metacommunity dynamics could explain how dispersal reduces the effects of diversity on grazer abundance that we observed in our experiment (France and Duffy 2006b). First, a tradeoff between competitive ability and dispersal ability is a common premise of many metacommunity models (summarized in Mouquet et al. 2005) and has been demonstrated in plant and parasitoid assemblages (Tilman 1994, Tilman et al. 1994, Lei and Hanski 1998). Under such a tradeoff, and assuming that productivity is directly positively related to competitive ability (Tilman et al. 1997, Loreau 1998, Mouquet et al. 2002), dispersal could decrease production because species that maximize production will not be the same species favored by high dispersal. So, dispersal could simultaneously increase diversity and decrease production if it helps maintain poorer competitors within patches.

Second, dispersal could help maintain species in patches where they perform poorly through source-sink dynamics or mass effects (net flow of individuals to a patch from other patches with larger populations) (Shmida and Wilson 1985, Amarasekare and Nisbet 2001, Mouquet et al. 2005). Again, if dispersal maintains poorly performing species, then total resource acquisition and production could be reduced by dispersal (Loreau and Mouquet 1999, Bond and Chase 2002, Mouquet and Loreau 2002). However, if patches differ considerably in resource availability or other environmental conditions, the effect of dispersal on ecosystem function might depend on scale. In this case, mass effects could decrease positive relationships between diversity and ecosystem function within patches by sustaining species in unfavorable patches with reproductive output from more favorable patches. Conversely, at the metacommunity scale, these dynamics could still yield predominantly positive relationships between biodiversity and ecosystem function. This is because dispersal could ensure that species best-suited to each patch will reach those patches, leading to positive BD-EF at the metacommunity scale – a kind of niche complementarity acting through space (Bond and Chase 2002). In our experiment, dispersal reduced the slope of the relationship between diversity and grazer abundance at both patch and metacommunity scales (France and Duffy 2006b), suggesting that competition-colonization tradeoffs or mass effects might be mediating BD-EF.

In addition to decreasing the effect of diversity on grazer abundance in our experiment, dispersal also increased temporal variability of grazers and epiphytes (France and Duffy 2006b). There are several possible explanations for this. First, dispersal could increase temporal variability of both grazers and epiphytes if it allows a grazer species with high temporal variability to spread and dominate throughout the metacommunity (Loreau et al. 2003). Alternatively, dispersal could stabilize individual metapopulations within the metacommunity by enabling new individuals from patches with successful populations to subsidize populations in patches of poorer quality or lower reproductive success (the "rescue effect"). Relatively small subsidies for each grazer species could substantially reduce temporal variability of their aggregate abundance. Somewhat similarly, if patches are heterogeneous and that heterogeneity changes through time, dispersal could decrease temporal variability of metacommunities by enabling dispersing species to find suitable habitat, averaging out environmental variation across patches (Holt 1993, Gonzalez and Holt 2002, Loreau et al. 2003). This spatial averaging effect can buffer ecosystem processes.

In contrast to these potentially stabilizing benefits of dispersal, if dispersal reduces the time lag between population dynamics of consumers and their resources in a patchy landscape, dispersal could de-stabilize ecosystem processes (Neubert et al. 2002). This could explain why dispersal increased temporal variability of epiphytes and eliminated stabilizing effects of consumer diversity (France and Duffy 2006b). As metapopulation researchers have recognized, dispersal could also de-stabilize metapopulations of individual species by synchronizing population dynamics (Hastings 1993, Ranta et al. 1995, Ranta et al. 1997, 1998, Ruxton and Rohani 1998, Blasius et al. 1999, Shimada and

Ishihama 2000). We suggest similarly that dispersal-mediated synchronization of dynamics among patches might increase temporal variability of ecosystem processes in metacommunities (France and Duffy 2006b). As others have recognized, asynchronous population fluctuations among patches can be an important stabilizer for consumer-resource dynamics in metacommunities (De Roos et al. 1991, McCauley et al. 1993, 1996). In general, all of these potential dispersal effects on individual species could affect variability of aggregate ecosystem properties within metacommunities. Limited theoretical work suggests that, within metacommunities, dispersal can also de-synchronize and/or de-stabilize dynamics, depending on fecundity and interspecific competition (Neuhauser 2002), the number of patches (Ylikarjula et al. 2000), and which trophic levels disperse between patches (Koelle and Vandermeer 2005). Some of these predicted mechanisms for direct effects of dispersal on stability might explain the striking de-stabilizing effects of dispersal we observed.

Finally, consideration of multiple trophic levels (two in our case), adds additional complexity. When dispersing consumers can substantially affect their resources at lower trophic levels, such as habitat-forming plants, dispersal might mediate the stability of ecosystem properties at the metacommunity-scale by affecting the degree of spatial heterogeneity of resources and structure among patches. In our experiment, beta-diversity, or variability among patches in grazer species composition, was the component of diversity most affected by dispersal, and it was reduced (France and Duffy 2006b). Previously, we suggested that patch heterogeneity may stabilize metacommunity temporal dynamics in the same way that species diversity can stabilize patch temporal dynamics (France and Duffy 2006b): the greater the differences in species composition among patches, the greater the chance that patches will fluctuate asynchronously. This can stabilize dynamics and ecosystem properties at the metacommunity scale, analogous to the "portfolio effect" of diversity within a patch (Doak et al. 1998), where the fluctuations of different species cancel each other out, rendering community abundance more stable. So, grazer dispersal could synchronize grazer dynamics across patches through 1) population connectivity, as discussed in the previous paragraph, *and* 2) by homogenizing the environmental conditions among patches which, in turn, mediate grazer dynamics. The importance of spatial heterogeneity for the stability of ecosystem processes was recognized early on in BD-EF research (Frank and McNaughton 1991), but has received relatively little attention since. Though we know spatial heterogeneity can affect BD-EF (Cardinale et al. 2000), most metacommunity BD-EF theory has imposed spatial heterogeneity that dictates local and between-patch species composition (Mouquet and Loreau 2002, Loreau et al. 2003, Mouquet and Loreau 2003). This makes it difficult to predict how between-patch diversity per se (in the absence of abiotic heterogeneity) might affect the spatial and temporal variability of ecosystem function.

Here we examine evidence for mechanisms by which dispersal could have affected the magnitude and predictability of ecosystem properties in our experimental metacommunities, independent of dispersal effects on diversity. Competition-colonization tradeoffs and mass effects might explain the reduction in the dependence of grazer abundance on grazer diversity seen in the experiment. Selection of species with high population-level temporal variability by dispersal, synchronization of dynamics among patches, and reductions in spatial heterogeneity might each have eliminated the stabilizing effects of diversity we documented.

MATERIALS AND METHODS

Study system

Seagrasses are important foundation species in marine environments, and often harbor high diversity of invertebrates and fishes (Hemminga and Duarte 2000, Williams and Heck 2001). While seagrasses often form large contiguous beds, natural processes such as new recruitment and growth, storms, bioturbation by large animals, and disease, can create patches as small as $0.5m^2$ (Robbins and Bell 1994, Hovel and Lipcius 2001). Seagrass habitats worldwide are disappearing at alarming rates (Duarte 2002, Orth et al. 2006) due to nutrient and sediment pollution, disease, and possibly food-web alteration (Williams and Heck 2001). The Chesapeake Bay, where we conducted our work, has lost more than half of its underwater grass cover since the early 20th century, with much of this loss occurring in the last several decades (Orth and Moore 1984, Orth et al. 2005). The dominant species found in the lower Chesapeake Bay, *Zostera marina* (eelgrass), is the most widespread and abundant marine macrophyte in the northern hemisphere, and supports many commercially important species (Hemminga and Duarte 2000, Heck et al. 2003). The dominant primary consumers in many eelgrass beds are small crustacean mesograzers, which feed preferentially on epiphytic micro- and macroalgae and can have important indirect, positive effects on eelgrass (Neckles et al. 1993, Valentine and Duffy 2006).

We tested the interactive effects of grazer richness and dispersal using a fully-factorial design. We manipulated metacommunity richness by changing the size of the species pool of these crustacean grazers used to assemble the grazer metacommunities. The small species pool was a subset of the large species pool, and included the three most abundant grazers in the field at the time of the experiment (two isopods, *Erichsonella attenuata* and *Idotea baltica,* and an amphipod, *Gammarus mucronatus*). The large pool of eight species included approximately 75% of the epifaunal crustacean grazer species known from the lower Chesapeake Bay region (Wass 1972), and included the three species from the small pool as well as four more amphipods, *Ampithoe valida*, *Cymadusa compta*, *Dulichiella appendiculata*, and *Elasmopus levis*, and one additional isopod, *Paracerceis caudata.* All of these crustaceans have sexual reproduction, overlapping generations and direct development, and all feed on epiphytic algae and associated detritus (Duffy and Hay 2000, Duffy et al. 2003). At summer temperatures, generation times in our system can be as short as three weeks for some amphipods (Fredette and Diaz 1986) and one month for isopods (Kouwenberg and Pinkster 1985, Jormalainen and Tuomi 1989). These species can all swim and crawl along eelgrass blades, but differ in their swimming ability and activity level (personal observation, Duffy and Hay 1994). Dispersal distances and frequencies for these organisms are not well-known; however, all species used have been observed to disperse 10s-100s of meters by swimming or drifting on tidal currents to new seagrass patches (Matich et al. in prep. Virnstein and Curran 1986). Both drift macroalgae and eelgrass detritus wrack are potential long-distance (up to 10s of km) dispersal vectors (Holmqvist 1994, Brooks and Bell 2001, Harwell and Orth 2002).

The experiment was conducted in outdoor, flow-through seagrass mesocosms at the Virginia Institute of Marine Science, Gloucester Point, Virginia, USA. The mesocosms were semi-transparent buckets that held 13.5 L of water, fitted with 250-μm mesh drain holes. Seawater from the York River estuary was filtered by passing through a sand filter and then 500 micron mesh bags, and delivered to each mesocosm in pulses via vinyl tubing angled to create turbulent flow. The mesocosm arrays were shaded with a layer of neutral-density fiberglass screen to approximate natural light levels. Fifteen pre-weighed *Z. marina* shoots were planted in each mesocosm. This eelgrass shoot density falls within the range observed locally (Orth and Moore 1986). Prior to planting, the shoots were spun 20 times in a salad spinner and then massed to determine an initial grass wet mass for each mesocosm.

Each experimental metacommunity consisted of five of these mesocosms clustered together and indirectly connected by sharing a common flow-through water supply. A trapezoidal trough periodically dumped seawater into a common basin drained by tubing to each mesocosm within the metacommunity. Hereafter, we call a mesocosm a "patch" and a group of five mesocosms a "metacommunity."

Experimental design

We used a fully-crossed, two-factor ANOVA design with grazer metacommunity richness and dispersal as the two fixed factors. Metacommunity richness had two levels, low (three spp.) and high (eight spp.). Dispersal regime also had two levels: no dispersal between patches, and some dispersal (mesocosms connected with corridors). Metacommunities with dispersal had all five patches connected to a small central hub via 5 cm long corridors of clear vinyl tubing. We used this configuration so that grazers leaving one patch had an equal chance of dispersing to all of the other patches within the region. Entrances to the corridors were 3 cm from the water surface and 2.2 cm in diameter, or 5-20x the width of adult amphipods and isopods. All grazer species could swim through the dispersal corridors, but varied in their dispersal "inclinations". Active (voluntary) dispersal could not occur between unconnected patches. Passive dispersal may have occasionally occurred by transfer via sampling and maintenance equipment. Each of the four treatment combinations (metacommunity richness x dispersal regime) was replicated five times, for a total of 20 metacommunities and 100 patches.

At the start of the experiment, each patch was inoculated, or "colonized", by 30 individuals (15 male-female pairs of reproductively mature adults). We determined the species composition of these founding communities by randomly drawing pairs of individuals from the designated species pool. Each species had an equal chance of being chosen at each draw. Thus, although initial metacommunity-wide richness of grazers was set at either three or eight species, both the relative abundances of species within metacommunities and the species richness within patches varied. We allowed this initial random assembly plus subsequent dispersal and species interactions to influence grazer diversity over the six weeks of the experiment. The initial composition for each patch is available in the on-line supplementary information of France & Duffy (2006b). The experiment ran for 47 days, which was long enough for nearly two complete generations of most grazer species in addition to the founding generation, population increases approaching two orders of magnitude (France and Duffy 2006b), and achievement of carrying capacity.

In a few mesocosms, nearly all of the planted eelgrass was consumed or had senesced at the end of this 47-day period, so the experiment was terminated and harvested at this time to prevent grazer population crashes. Note that the loss of grass biomass over the course of the experiment is not necessarily a mesocosm artifact: *Z.*

marina is near the southern edge of its range in the Chesapeake Bay (Green and Short 2003), and often declines precipitously during the late summer months in the York River estuary as well (Duffy et al. unpublished data, Orth and Moore 1986).

Sampling ecosystem properties

At two-week intervals, we estimated biomass of epiphytic algae, the grazers' main food source, by measuring epiphytic chlorophyll. Algae were negligible on the blades at the beginning of the experiment. Algae were scraped off of three haphazardly chosen blades from each mesocosm, pooled, collected on a glass fiber filter, and extracted in 20 ml of 90% acetone at –20°C for 24 hours. Chlorophyll *a*, *b*, *c* and carotenoid pigments were determined spectrophotometrically (Parsons et al. 1984) and normalized to leaf blade area.

Mid-way through the experiment (day 26), and immediately prior to the end of the experiment (day 42), we sampled grazer species composition in each local community by sweeping a small aquarium dipnet through the mesocosm at mid-depth 10 times. We counted the number of individuals of each species of amphipod and isopod captured by the net and then returned them to their mesocosms. The capture efficiency of this method differs among species, underestimating the relative abundance of *D. appendiculata* and *E. levis* while overestimating the relative abundance of isopods (*I. baltica* and *E. attenuata*), but patterns predicted by the final sweep sampling were largely borne out in the actual final counts. Proportional abundance in the final sweep sample was a significant predictor ($p<.05$) of final proportional abundance for all species except *A. valida* (mean r^2 across species =.275, range .06-.67). At the end of the experiment, all epifaunal invertebrates, algae and eelgrass retained by a 0.5 mm mesh sieve were separated, identified, dried to constant mass, ashed at 450 °C, and massed again.

We estimated spatial variability of ecosystem properties as the coefficient of variation (CV) of each response variable across the five patches in a metacommunity. While there are many indices used to characterize variability, CV is most often used for comparing variability between samples with different means (Cottingham et al. 2001, Morin and McGrady-Steed 2004, Steiner et al. 2005). Spatial variability was initially zero for all properties except *Z. marina* mass and grazer richness and composition, whose initial spatial variability was recorded. Spatial heterogeneity in our system results from a combination of random variation in colonization of algae and non-grazing invertebrates through the flow-through system, as well as subsequent interactions with the grazer community. We also estimated temporal CV of epiphytic pigments (three time points) and grazer abundance (two time points).

Extinction and colonization

Extinction frequency was estimated as the ratio of patches where a species was initially present, but absent at the end of the experiment, divided by the number of patches where it was initially present. Colonization frequency was estimated as the number of patches where a species was initially absent but present at the end of the experiment, divided by the number of patches where a species was initially absent.

Aggregation

To determine whether dispersal affected species distributions across the metacommunity, we estimated both intra- and inter-specific aggregation (Ives 1988, 1991, Sevenster 1996). Intraspecific aggregation was estimated as:

$$J = \left(\frac{\sum_{r=1}^{N} e_r}{N^2} \cdot \sum_{r=1}^{N} \frac{n_r (n_r - 1)}{e_r} \right) - 1$$

where n_r is the abundance of species a in patch r, N is the number of patches, and e_r is the carrying capacity of patch r. We calculated intraspecific aggregation for each species stocked in the experiment within each metacommunity (which consisted of five patches each). We assumed that carrying capacities were equal, so set $e_r=1$.

Interspecific aggregation was estimated as:

$$C_{xy} = \left(\frac{\sum_{r=1}^{N} e_r}{N_x N_y} \cdot \sum_{r=1}^{N} \frac{n_{xr} n_{yr}}{e_r} \right) - 1$$

where x and y are the two species being examined, n_{xr} is the abundance of species x in patch r, N_x is the total abundance of species x in the metacommunity, and e_r is the carrying capacity (of individuals) of patch r. We again assumed that $e_r=1$ for all patches, and calculated interspecific aggregation within each metacommunity for every possible pair of stocked species.

Synchrony

To examine the effect of dispersal on metacommunity dynamics, we estimated the degree of synchrony among patches for epiphytic chlorophyll (the proxy for epiphyte biomass). We calculated synchrony as the sum of the covariances of epiphytic chlorophyll *a* for all possible pairs of the five patches within each metacommunity. We chose this metric over other candidates because it is often used to detect the portfolio effect of diversity, i.e. the increased likelihood that the more species present in a community, the more likely it is that some population dynamics will be out of phase, stabilizing aggregate community abundance (Doak et al. 1998, Tilman 1999, Steiner et al. 2005). Since we were looking for the analogous buffering effect of patch differences (rather than species differences), here we calculated covariances among patches rather than among species. Other metrics, such as average Pearson or cross-correlation coefficients, are more commonly used to detect population synchrony among patches within metapopulations, but these are not ideal when considerable asynchrony is present, and are unaffected by variation in amplitude of fluctuations (Bjørnstad et al. 1999, Liebhold et al. 2004). We wanted variation in amplitude of fluctuations to affect the synchrony metric. Synchrony (and asynchrony) of high amplitude dynamics in a natural system with considerable noise seems less probable than synchronization of low amplitude dynamics. So, we wanted to use a metric that yielded higher values of synchrony for that rarer scenario. Given the limitations of these metrics and the small number of time points we have for our data, we also visually inspected the time course of epiphytic chlorophyll within individual patches for each metacommunity.

Statistical analyses

Competitive performance of each species was estimated as the difference between final and initial relative abundance within a patch, and was evaluated separately for isolated and connected patches.

Effects of dispersal and grazer species identity on the magnitude and variability of final grazer abundances were determined using a two-way ANOVA with grazer species and dispersal as fixed factors (n=25 per dispersal treatment for final abundance and temporal variability, n=5 per dispersal treatment for spatial variability). Effects of diversity and dispersal on epiphyte pigments within patches were analyzed using a General Linear Model (GLM) with three factors: grazer metacommunity richness, dispersal, and metacommunity ID. Richness and dispersal were fully-crossed, and metacommunity ID was nested within the fully crossed design. When the p-value for metacommunity ID was >0.25, we ignored that factor and ran a fully-crossed, two-way ANOVA with metacommunity richness and dispersal (n=25 for each treatment combination). For spatial heterogeneity and metacommunity-level responses of epiphyte pigments, data were analyzed using a fully factorial two-way ANOVA with metacommunity richness and dispersal as the factors (n=5 for each treatment combination).

We analyzed relationships between final, realized grazer diversity and ecosystem properties for unconnected and connected patches using linear regression. To detect whether effects of dispersal on these relationships were significant, we used a GLM with dispersal as a class predictor and Shannon-Weiner diversity (S-W) as a continuous predictor. Patch S-W was used as the predictor for responses in patches, and metacommunity S-W was used for metacommunity responses and spatial heterogeneity. These results partially appear in the supplementary information of France and Duffy (2006b), and are summarized in Table 4. In Table 4, we indicate whether or not the slope of the relationship was increased, reduced, inverted, or unchanged by dispersal. To qualify as other than a “no change”, the slope had to change by ≥25% of the maximum absolute value, and at least one of the regressions had to explain more than 5% of the variance. Likewise, we tallied whether or not the intercept changed more than 25% and in what direction.

All statistical analyses were conducted using SAS (SAS 2001).

RESULTS

Grazer abundance and competition

Since competition-colonization tradeoffs might explain the effects of dispersal on ecosystem function that we previously observed, we determined whether or not dispersal affected competitive outcomes. We examined grazer population growth and changes in relative abundances over the course of the experiment to determine which species were the best competitors and whether or not the competitive hierarchy changed when patches were connected. Dispersal did not affect net population growth (species F=33.29, p <0.0001; dispersal F=0.14, p=0.7074; interaction F=1.47, p=0.1766), and none of the effects on individual species were significant (Table 2), although dispersal tended to increase net population growth of the best competitor, *G. mucronatus*, and the large isopod, *I. baltica* (Fig. 1i; Table 2).

Initial proportional abundance significantly predicted final proportional abundance for all grazer species except *P. caudata* (Fig. 1h), which went extinct in most patches. *G. mucronatus* was clearly the best competitor, and both *E. levis* and *C. compta* increased in proportional abundance in more than half of the replicates. *D. appendiculata* occasionally managed to dominate patches, either when allowed to disperse (three of the six points clustered well above the 1:1 line in the *D. appendiculata* panel) or in patches with *G. mucronatus* initially absent (the other three points). *E. attenuata* and *P. caudata* were the poorest competitors.

Dispersal had limited effects on the relationship between initial and final abundance. Interactive effects of initial abundance and dispersal on final proportional abundance were only significant ($p<.05$) for three of the eight species: *E. attenuata*, *I. baltica* and *C. compta* (Table 1). Dispersal tended to decrease the fit of the final:initial relative abundance relationship (when significant) for all species except *D. appendiculata*. Generally, dispersal reduced the slope of the relationship (Fig. 1).

Colonization and extinction

We could not directly measure grazer dispersal rates without disrupting the communities. At the end of the experiment, however, we found that dispersal had occurred: at least seven of the eight originally stocked grazer species migrated to patches where they were not initially present, colonizing 25-100% of such patches, depending on the species. Even with dispersal, though, final proportional abundance of seven of the eight grazer species was significantly explained by initial proportional abundance (Table 1), suggesting that dispersal did not erase effects of initial relative abundance.

Extinction risk decreased with the number of founding individuals (Fig. 2a). 18% of founding populations consisting of a single male-female pair ultimately failed, while only 8% of those started with eight individuals did. All species except *G. mucronatus* and *C. compta* went extinct in some patches where they were initially present, at rates ranging from 2% to 73%, depending on the species. *G. mucronatus*, *C. compta* and *E. levis* were the most successful colonizers (Fig. 2b). As expected, overall, extinction frequency was inversely proportional to colonization frequency (Fig. 2b; without dispersal: slope=-0.456, std. error=0.1648, $R^2=0.5607$, p=0.0325; with dispersal: slope=-0.607, std. error=0.1788, $R^2=0.6578$, p=0.0146). Oddly, though, for all species except *E.*

levis and those that never went extinct, extinction risk tended to increase when patches were connected and dispersal was possible (Fig. 2b), though this trend was non-significant.

Contrary to the hypothesis of a competition-colonization tradeoff, the best colonizers were also the best competitors (Fig. 2d), and dispersal had little effect on species competitive performances (Fig. 2c). The relationship between competition and colonization was unaffected by the presence of dispersal corridors (Fig. 2d).

Mass effects

Mass effects, i.e. a net flow of individuals from high density to low density patches, could also have decreased the relationship between diversity and ecosystem properties. If dispersal created mass effects, we would expect dispersal to homogenize total grazer densities among patches and/or reduce intraspecific aggregation for some species. Dispersal did marginally significantly reduce mean grazer density within patches assembled from the more diverse species pool (Fig. 3; GLM: richness MS=0.257, p=0.0006; dispersal MS=0.058, p=0.095; interaction MS=0.050, p=0.1218). Dispersal also tended to reduce intraspecific aggregation of the more mobile species (Fig. 4a; *C. compta*, F=7.03, p=0.0468; *G. mucronatus*, F=11.69, p=0.0091). Interspecific aggregation patterns were also affected by dispersal, but the effect depended on the identity of the species involved. Interspecific aggregation in the presence of dispersal was strongly and negatively related to interspecific aggregation in the absence of dispersal. Moreover, the effect of dispersal switched sign with decreasing aggregation. Pairs of species that were most aggregated in unconnected metacommunities tended to become less aggregated when grazers were allowed to move between patches, while pairs of species that were less aggregated in the absence of dispersal tended to become more aggregated when allowed to move between patches (Fig. 4b,c; regression on re-sampled data $p<0.0001$). Several species pairs were significantly affected by dispersal. Associations between *G. mucronatus* and two other species, *C. compta* (MS=.322, F=32.38, p=0.0005) and *A. valida* (MS=.990, F=11.06, p=0.0105), became less negative when the grazers were allowed to disperse (Fig. 4b). In contrast, positive aggregations of *A. valida* with *C. compta* (MS=.654, F=5.37, p=0.0491) and *E. attenuata* (MS=6.64, F=11.59, p=0.0093) were eliminated and even reversed by dispersal.

Variability of grazer populations

We examined the effects of dispersal on the temporal and spatial variability of each species to determine whether any one species could explain the marginal increase in temporal variability of aggregate grazer abundance found when patches were connected (France and Duffy 2006b). Temporal variability of individual species abundances, however, was unaffected by dispersal (Table 2). Temporal variability of relative abundance of the most mobile/dispersive species, *G. mucronatus*, was decreased by dispersal (Table 2).

Spatial variability (among patches) of most species tended to increase over the course of the experiment regardless of dispersal (Fig. 5). Overall, the consistency of changes in spatial variability through time between non-connected and connected metacommunities is remarkable. The final spatial variability (determined from the final destructive harvest) of the most mobile species (*G. mucronatus* and *C. compta*) was marginally reduced by dispersal (Fig. 5; Table 2).

Grazing

Allowing grazers to move among patches increased the total biomass (chlorophyll) of epiphytes in the first four weeks of the experiment, as estimated based on epiphytic chlorophyll (France and Duffy 2006b). We hypothesized that this was because dispersal enabled the grazers to selectively forage, or emigrate from patches where less edible algae became established. If this was the case, we might expect effects of dispersal on different components of the algal community to differ. Dispersal did indeed affect the chlorophyll pigments differently (Fig. 6, Table 3). The mass of chlorophyll *b*, found in green algae and prochlorophytes, as well as higher plants (Van den Hoek et al. 1995, Miller 2004), remained relatively unaffected by dispersal, whereas chlorophylls *a* (found in all photosynthetic organisms) and *c* (found in diatoms and dinoflagellates, among other organisms) were significantly increased by dispersal in the first few weeks of the experiment (Fig. 6a-d; statistics in Table 3). Carotenoids, present in a wide range of algae, were also initially increased by dispersal, but that algal component was subsequently rapidly consumed. We also calculated the fractions of epiphyte biomass that each pigment represented, and these data show that dispersal significantly decreased the fractions of chlorophylls b and c (data not shown). Importantly, among marine phytoplankton and algae, there is little to no overlap between taxa that contain chlorophyll *b* and taxa that contain chlorophyll *c* (Van den Hoek et al. 1995, Miller 2004). So, although we cannot completely resolve which functional groups of algae created the patterns shown in Fig. 6, allowing grazer dispersal clearly affected epiphytic community composition through time.

Spatial variability of most components of the epiphyte community tended to increase over the course of the experiment, just as spatial variability of grazer abundance did (data not shown). Connecting patches did not generally diminish spatial variability, as we originally expected. Instead, within the more diverse metacommunities, dispersal increased the spatial variability of chlorophyll b and carotenoids (Fig. 7). In fact, dispersal often reversed or eliminated the effects of grazer diversity on spatial variability of food resources (Tables 3&4). Furthermore, allowing grazers to move between patches increased the synchrony of epiphyte biomass dynamics among patches (Fig. 6e, note different scales). In unconnected metacommunities, epiphytic chlorophyll *a* within different patches had low and, in one metacommunity, negative covariance through time, but epiphyte loads in connected patches had overwhelmingly positive covariances (Fig. 6e; w/o dispersal, R^2=0.1228, p=0.3208; w/ dispersal, R^2=0.0009, p=0.9346; GLM diversity F=0.02, p=0.8879, dispersal F=0.93, p=0.35, diversity*dispersal F=0, p=0.9776). Visual inspection confirmed that dispersal tended to make the time course of epiphyte abundance more similar among patches (Appendix 3-1).

Interactive effects of diversity and dispersal

We examined the effect of dispersal on the relationships between grazer diversity and the magnitude and stability of ecosystem properties. Although only some effects of dispersal were significant, we tallied the direction of the effect of dispersal on the slope of diversity-function relationships (increased absolute value, decreased absolute value, reversed, or no change). Results are shown in Table 4 with significant interactions bolded and in red. Dispersal tended to reverse the effects of diversity on the magnitude and predictability of ecosystem function. When it did so, it tended to eliminate BD-EF relationships more often than strengthen them.

DISCUSSION

Our experiment demonstrated that connecting patches decreased the effect of grazer diversity on grazer abundance within both patches and metacommunities (France and Duffy 2006b). If dispersal allowed less successful species to persist in metacommunities where patches were connected, either through competition-colonization tradeoffs or mass effects, grazer abundance and grazing efficacy could be reduced, explaining the pattern we observed. However, our present analysis found no evidence of competition-colonization tradeoffs among the eight species we used in our experiment. Dispersal did tend to homogenize grazer density among patches in diverse metacommunities, creating a kind of mass effect, but it primarily affected the best competitor rather than the poorer competitors. Consequently, these mass effects are unlikely to entirely explain the effect of dispersal on BD-EF we observed. We think the best remaining explanation for the reduction of grazer abundance in diverse metacommunities by dispersal is that dispersal indirectly reduced carrying capacity by allowing the accumulation of less edible algae. Selective foraging and/or a decrease in consumption pressure within patches during the first weeks of the experiment, mediated by mass effects, could have increased accumulation of less edible algae.

We also found previously that dispersal increased temporal variability of grazer and epiphyte abundance, and that it eliminated the stabilizing effects of grazer diversity on grazer and epiphyte abundance at the metacommunity scale. Here we show that this is not due to the effects of dispersal on any one species, and that it is more likely due to synchronization of both grazer and epiphyte dynamics among patches.

Competition-colonization tradeoffs

We found no evidence of competition-colonization trade-offs for these generalist, mobile grazers. Instead, our estimates of competitive and colonization abilities were positively related in the grazer species we studied (Fig. 2d). The best competitors, *G. mucronatus*, *C. compta*, and *E. levis*, remained the best competitors even when grazers could move among habitat patches, and in fact were the best colonizers as well. Likewise, *E. attenuata* and *P. caudata* were the least successful competitors and colonizers. These performances are consistent with previous studies comparing invasion success and species performance in monocultures vs. mixtures in this system (Duffy et al. 2001, Duffy et al. 2003, Duffy et al. 2005, France and Duffy 2006a). Likewise, the comparative colonization abilities we observed mostly matched our predictions based on the swimming ability and structure affinity of these grazers. *G. mucronatus* is ubiquitous in a wide range of estuarine habitats in Chesapeake Bay, and is often observed swimming within our mesocosms and in the plankton (Williams and Bynum 1972). *E. levis* has also been observed at low abundances within estuarine plankton (Williams and Bynum 1972). While *C. compta* is a tube-dwelling amphipod, it has been demonstrated to utilize drift algae at night, suggesting that it is willing to leave seagrass blades for alternative habitat (Brooks and Bell 2001). In contrast, *E. attenuata* is a long, thin, stick-like isopod well-suited for crawling along eelgrass, and it often flails clumsily when knocked off of grass blades (personal observation). *P. caudata* is roly-poly and a rather slow swimmer.

Furthermore, field evidence suggests that *P. caudata* may be limited by dispersal and/or recruitment, and have trouble increasing from low numbers (S. Marion, pers. comm.).

It is important to note that our estimated colonization frequency is the product of several processes: innate dispersal inclination, affected by behavior and relative strength of structural associations; swimming ability, often correlated with dispersal inclination and structure association; intrinsic population growth rates and/or Allee effects (reductions in population growth rates at low densities) that differ among species; and finally, competitive ability. Since we determined colonization frequencies based on species presence in patches where they were initially absent, these data clearly incorporate colonization success in an already settled habitat as well as dispersal inclination and ability, which might bias our results away from finding a competition-colonization tradeoff. However, we used forgiving criteria for "colonization"; population growth was not required, simply presence of a single individual where there had been none. Also, on average, 15% of final colonizations were in place *and* detected in the first half of the experiment by non-destructively sampling the grazer populations, even though this sampling only captures about 10% of the population and only adults were identified (because the identification had to be done with the naked eye). This suggests that much of the movement between patches was done by the founding generation before populations were at carrying capacity.

Both theory and evidence for competition-colonization tradeoffs are stronger for plants than for animals. For example, large seeds often yield more successful plants, but those large seeds travel less far, or, because large seeds are costly, the plant produces fewer of them (Turnbull et al. 2004) and references therein). However, for mobile grazers, particularly those that interact with ephemeral or patchy resources, it is not clear that the ability to acquire resources, or to compete, is different from the ability to move to and become established within new habitats. Empirical evidence for competition-colonization tradeoffs is limited, particularly among animals (Amarasekare 2003, Kneitel and Chase 2004). Most studies with insects, reasonable terrestrial analogs for our grazers, have failed to find a tradeoff between competitive and dispersal abilities (Harrison et al. 1995, Amarasekare 2000a, c). Some consumers do exhibit a trade-off between the ability to find new patches and consume resources down to low levels once there (see references in Kneitel and Chase 2004). Since grazers are important components of all ecosystems, it may be time to re-examine the utility of this tradeoff assumption for constructing general mathematical and conceptual models for biodiversity maintenance, particularly since mechanisms of biodiversity maintenance can affect predictions of the effects of diversity on ecosystem function (Moore et al. 2001, Cardinale et al. 2004).

Competition-colonization tradeoffs, then, cannot explain the reduction of aggregate grazer abundance by dispersal that we observed. Since the best competitors in isolated patches were also the best dispersers, one might expect metacommunity-wide grazer populations to *increase* with dispersal, as the competitive dominant could disperse to all patches. This may have been the case in low diversity metacommunities, but not in high diversity metacommunities, where grazer populations were reduced by dispersal (France and Duffy 2006b).

Mass effects and rescue effects

We also found little evidence for source-sink dynamics or mass effects within our connected metacommunities. The scope for source-sink dynamics in our system was limited because patches did not differ intrinsically in favorability for any species (Mouquet et al. 2005, Mouquet et al. 2006). Still, initial variation in the species composition of the founding communities, combined with priority and Allee effects, could essentially create "source" and "sink" habitats that would differ for each species. Models have shown that heterogeneity in initial abundances, even in the absence of environmental heterogeneity, can generate source-sink dynamics (Amarasekare 2000b, Yu and Wilson 2001, Levine and Rees 2002). However, we found little evidence of rescue effects provided by dispersal. Extinction rates of the less common species were actually increased by dispersal, though not significantly (Fig. 2b; paired t-test for all species p=0.1201). Likewise, only the performances of the dominant species were improved by dispersal (Fig. 1). Local richness was unaffected by dispersal (France and Duffy 2006b), further suggesting that dispersal did not generally "rescue" species. In our system, where priority effects are important (France and Duffy 2006a), stochasticity of population dynamics and environmental factors, along with seasonal changes, might be important mechanisms generating co-existence. Therefore, dispersal might actually reduce diversity by reducing the patch differences generated by these mechanisms. Furthermore, in our system, dispersal by either the dominant or other grazer species may have indirectly made entire metacommunities slightly more sink-like, by facilitating growth of less edible species throughout the metacommunity (France and Duffy 2006b).

Dispersal did tend to facilitate spread of the most competitive grazer species, reducing their intraspecific aggregation (Fig. 4a) and their spatial heterogeneity (Fig. 5), and thereby reducing metacommunity-wide diversity and beta-diversity (France and Duffy 2006b). This spatial homogenization is also somewhat evident across all species in the patterns of interspecific aggregation. With dispersal, the association of most species pairs became closer to a random distribution (Fig. 4b). Such spatial homogenization could be considered a kind of mass effect, where the most competitive and dispersive grazers spread from areas of high founding density to low founding density. Here, the mass effects are driven by stochastic variation in population densities among patches, rather than resource heterogeneity across patches. In models, such spatial averaging facilitated by dispersal has reduced temporal variability (Loreau et al. 2003). However, in our system, dispersal tended to increase temporal variability of aggregate grazer abundance (France and Duffy 2006b), even though it had little or no effect on temporal variability of individual species (Table 2).

This difference between prediction and our results probably reflects differences between producers, the subject of most theoretical models, and consumers that interact with a dynamic resource. In our system, the "best" patches, in terms of resource availability, probably fluctuated through time. Over the course of the experiment, algae colonized, senesced or were consumed, and new recruits from a dynamic pool outside of the mesocosm system re-colonized. By allowing more mobile grazers to move among patches and exploit this dynamic and patchy resource, dispersal corridors could inflate temporal variability of grazer abundance within patches, which tended to occur in our experiment. Similar inflationary effects of dispersal on temporal variability have been observed in metapopulation models (Holt 1992). Note that one might expect this active foraging to aggregate grazers, increasing spatial variability. Others have observed that if consumers aggregate too well on resources, it can synchronize patches and destabilize dynamics (Murdoch et al. 1992). However, we did not detect pronounced aggregation of grazers, at least in the limited "snapshots" we took at the mid-point and at the final harvest (Figs. 4,5; France & Duffy 2006b). Still, we think grazer interactions with a spatially and temporally patchy resource remain the best explanation for why dispersal increased the temporal variability of grazer abundance in our experiment.

Synchronization

In addition to destabilizing grazer dynamics, connecting patches de-stabilized epiphyte dynamics. By either enabling selective foraging among patches or decreasing overall consumption pressure within patches through mass effects (Fig. 3), dispersal allowed the accumulation of less edible algae, increasing temporal variability of epiphyte dynamics within patches (Fig. 6a-d) and the spatial variability of some pigments (Fig. 7). As modeling results have suggested, generalist consumers can destabilize producer dynamics (Thébault and Loreau 2005), and mobile consumers can actually have "an inordinate destabilizing effect" on systems when their activities strongly couple local habitats (McCann et al. 2005). By coupling patches, grazers can increase temporal variability at the metacommunity scale as well as the patch scale. Consistent with these theoretical predictions, in our system, grazer dispersal did tend to couple patches. Connecting patches synchronized epiphyte dynamics among patches within a metacommunity, which de-stabilized epiphyte abundance still further, at least in diverse systems (Fig. 6, Appendix A).

Homogenization

In addition to synchronizing epiphyte dynamics, dispersal blurred the otherwise pervasive (France and Duffy 2006b) effects of grazer diversity on temporal and spatial patterns of resources. Although dispersal did not affect the spatial heterogeneity of grazer abundance at the times we sampled, it nevertheless tended to homogenize ecosystem properties across space, blurring the differences between patches created by diverse grazer communities. This probably occurred due to dispersal's homogenization of species composition: dispersal reduced beta diversity (France and Duffy 2006b) and tended to randomize species co-occurrences (Fig. 4b). Dispersal inverted the slope of the relationship between grazer diversity and the magnitude and variability of ecosystem properties for 15 out of 43 variables examined (Table 4). Ten of those instances were at least marginally significant changes. Dispersal only strengthened the effects of diversity in eight cases. It may be that, by facilitating the spread of the more successful species, dispersal minimized differences in patch dynamics created by initial random assembly. We think it is important to note that dispersal effects on diversity itself, which were essentially non-existent, could not have predicted these effects of dispersal on ecosystem properties. Neither could dispersal's effects on individual grazer species. The effects of dispersal on the spatial heterogeneity of the grazers themselves could not even have predicted the homogenizing effects of dispersal on other ecosystem properties. But the combined effects of connecting patches in this multi-trophic grazing system led to increased similarity among patches for many response variables, and increased the variability of both grazers and epiphytes.

Since dispersal often eliminated the differences in ecosystem properties between high and low richness metacommunities, it is possible that maintaining connectivity among patches in a fragmented landscape could ameliorate losses of production due to changes in biodiversity, at least for mobile grazers. This potential benefit, is, of course, in addition to the well-recognized benefits of connectivity for maintaining individual populations (Brown and Kodric-Brown 1977, Gonzalez et al. 1998). But it is not clear that all systems will have highly successful competitors that are also the most effective short and long-range dispersers. And, while connecting patches often blurred the differences between species-rich and species- poor communities in terms of overall production, it usually did so by *both* increasing the magnitude and stability of ecosystem properties in species-poor communities *and* decreasing them in species-rich communities (Table 4, Fig. 6e) (France and Duffy 2006b). Dispersal essentially eliminated the few temporally stabilizing effects of diversity we observed. As other authors have pointed out, the level of connectivity among patches required to maintain individual populations may simultaneously reduce landscape-wide diversity by reducing beta-diversity and/or total landscape diversity (Forbes and Chase 2002). There may be similar dispersal-mediated tradeoffs between maintaining local diversity and landscape-wide stability of ecosystem properties.

Our finding that dispersal-mediated reductions in beta-diversity and/or biotically generated heterogeneity de-stabilized metacommunities through time might also apply to other systems, particularly if those reductions lead to increased synchronization, as they did, in a limited fashion, in our system. First, spatial heterogeneity has long been recognized as an important mechanism for maintaining diversity (e.g. Levins 1979, Huston 1994, Rosenzweig 1995), and has been shown to be important for maximizing diversity of metacommunities (Mouquet et al. 2006). Losses of this heterogeneity could jeopardize diversity. Second, for mobile consumers, regional spatial heterogeneity provides not only opportunities for niche partitioning, but can help mobile consumers compensate for temporal variability of resources at a local scale (Fryxell et al. 2005). Restricting consumer movement to fewer areas and homogenizing habitats could de-stabilize grazing interactions (Van de Koppel et al. 2005). Our experiment suggests that this may be an important consideration when trying to manage for both diversity and predictability of ecosystem services.

While metapopulation researchers have widely recognized that synchronization is a likely and often detrimental consequence of dispersal among patches within metapopulations (Hastings 1993, Ranta et al. 1995, Ranta et al. 1997, 1998, Ruxton and Rohani 1998, Blasius et al. 1999, Shimada and Ishihama 2000), the consequences of synchronization for ecosystem function in metacommunities have not yet been much explored. One modeling study suggested that decreasing the distance between patches could sometimes *de*synchronize population dynamics, particularly when the benefits for dispersal conveyed by increasing proximity vary among trophic levels (Koelle and Vandermeer 2005). We believe that the latter condition was true in our experiment, because dispersal of producers through the corridors was either impossible (eelgrass) or limited by currents (epiphytes). However, we found that consumer dispersal increased synchrony in metacommunities, which might be explained through either of two mechanisms: 1) by coupling resource dynamics between patches within grazer generations and, 2) in the longer term, by homogenizing species composition, thereby increasing the likelihood that patches will respond similarly to exogenous temporal fluctuations. Our time course data is limited, however, and more explicit tests of the effects of dispersal on synchronization and consequences for metacommunity-scale function are clearly needed.

Finally, we emphasize that the composition and movement of mobile consumers can generate spatial heterogeneity (e.g. Pickett et al. 2000, Adler et al. 2001, Bakker et al. 2003, Flecker and Taylor 2004). Spatial heterogeneity is often imposed or abiotically generated in models, but biotically generated heterogeneity can have different consequences for the persistence of communities (Shurin et al. 2004). Mouquet et al. (2006) recently suggested that metacommunity diversity is maximized when both dispersal and spatial heterogeneity are at intermediate levels. Our work supports previous work (examples cited above) pointing out that dispersal of mobile grazers can interact with spatial heterogeneity. Since it is common for mobile consumers to integrate resources over coarser spatial scales than environmental heterogeneity is manifested at (e.g. Polis et al. 1997, Ritchie 1998), such interactive effects between dispersal and spatial heterogeneity might be common, and may have important consequences for the predictability of ecosystem functions in both space and time.

Overall, our experiment illustrates that dispersal can have subtle indirect effects on the magnitude and predictability of ecosystem properties even when most of the previously proposed mechanisms for dispersal effects are not prominently operating. Amongst our grazers, there were no competition-colonization tradeoffs, at least at this experimental scale. Likewise, source-sink dynamics were not operating, perhaps due to limited spatial heterogeneity in resource supply relative to natural systems. We think it noteworthy that dispersal modified relationships between diversity and most ecosystem properties measured, even in our system where dispersal arguably had a lesser community-structuring role than is observed in many systems. Also, in the absence of strong dispersal-mediated community structuring, grazing-mediated community structuring seems to have considerable potential to impact the predictability of ecosystem properties in both space and time.

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TABLES

Table 1. The predictability of final relative abundances of grazer species based on initial relative abundances, with and without dispersal (regression lines plotted in Fig. 1). General Linear Model table cells are the p-value of the dispersal effect. Regression table cells are R^2 value, p-value.

Response Variable	**GLM effect of Disperal p-value**	**GLM effect of Diversity*Dispersal p-value**	**Regression No Dispersal R^2, p-value**	**Regression With Dispersal R^2, p-value**
Erichsonella attenuata	.1438	**.0189**	**.3144, .0037**	.0423, .3240
Gammarus mucronatus	.0907	.2082	**.5470, <.0001**	**.2289, .0155**
Idotea baltica	**.04**	**.006**	**.3418, .0021**	.001, .8797
Ampithoe valida	.7046	.4692	.1129, .1006	.1269, .0805
Cymadusa compta	.2585	**.0268**	**.4344, .0003**	**.1621, .0460**
Dulichiella appendiculata	.2626	.2676	.0844, .1588	**.4468, .0003**
Elasmopus levis	.4851	.4295	**.1661, .0431**	.1034, .1170
Paracerceis caudata	**Whole model not significant**		.0390, .3442	.0311, .3994

Table 2. Effects of dispersal on each grazer species. Data were analyzed using General Linear Models. Table cells are (MS, F-statistic, p-value).

Response Variable	Net Population Growth (total df=48)	Temporal CV of Abundance (total df=48)	Temporal CV of Relative Abundance (total df=48)	Spatial CV of Abundance (mid-pt) (total df=9)	Spatial CV of Abundance (final) (total df=9)
Species					
A. valida	1990, 1.89, .1754	.001, 0.01, .9168	.280, 1.42, .2390	.034, 0.37, .5580	.005, 0.02, .8874
C. compta	311, 0.10, .7541	.001, 0.02, .887	.216, 2.33, .1334	.000, 0, .9687	**.402, 6.63, .0329**
D. appendiculata *	9383, 1.21, .2778	.013, 0.16, .6898	.003, 0.01, .9063	.012, 0.03, .8607	0, 0, .9644
E. levis	1234, 0.70, .4084	0, 0, .9907	.127, 0.72, .3991	.113, 0.36, .5793	.057, 0.45, .5226
E. attenuata **	1.35, 0.99, .3254	.012, 0.07, .7985	.028, 0.28, .6021	.241, 1.22, .3011	.015, 0.08, .7882
G. mucronatus	2116, 0.48, .4914	.006, 0.18, .6757	**.882, 7.03, .0108**	**.374, 8.57, .0191**	**.281, 9.76, .0141**
I. baltica	1457, 1.51, .2254	.09, 0.48, .4926	0, 0, .9894	.132, 1.23, .3003	.029, 0.14, .7144
P. caudata ***	.014, 0.03, .8734	.034, 0.85, .3610	.016, 0.33, .5696	N/A	N/A

* Net population growth df=43.
** Net population growth df=42.
*** Net population growth df=45.

Table 3. Effects of metacommunity richness and dispersal on epiphyte pigments. Data were analyzed using a General Linear Model. Metacommunity ID is fully nested within the interaction term. When the p-value for it exceeded 0.2, we removed it from the analysis, changing the model degrees of freedom from 7 to 3. Table cells are (MS, F-statistic, p-value). NS= p-values > 0.30.

Response Variable	Metacommunity Richness (df=1)	Dispersal (df=1)	Metacommunity Richness * Dispersal (df=1)	Metacommunity ID (df=4)	Total (df=7,3)
Patch (n=25 for each combination of treatments, n=100 total)					
Epiphytic chl *a* (wk 2)	**33.44, <0.0001**	**10.93, 0.0014**	**3.61, 0.0604**	7.53, <0.0001	**7.48, <.0001**
Epiphytic chl *b* (wk 2)	**.178, 7.44, .0076**	**.0786, 3.29, .0730**	.027, 1.13, .29	.211, 8.85, <.0001	**0.126, <.0001**
Epiphytic chl *c* (wk 2)	**2.11, 27.19, <.0001**	**.908, 11.68, .0009**	**0.33, 4.25, .0422**	.5447, 7.00, <.0001	**0.635, <.0001**
Epiphytic carotenoids (wk 2)	**13.9, 25.78, <.0001**	**5.39, 9.97, .0022**	**1.64, 3.03, .0852**	15.6, 7.22, <.0001	**3.64, <.0001**
Epiphytic chl *a* (wk 4)	NS	**4.02, 0.0477**	NS	NS	1.46, 0.2317
Epiphytic chl *b* (wk 4)	.157, 2.65, .107	.156, 2.62, .1089	**.22, 3.71, .0573**	.204, 3.43, .0117	**0.123, .0558**
Epiphytic chl *c* (wk 4)	NS	NS	NS	NS	0.357, .4247
Epiphytic carotenoids (wk 4)	.00039, 2.6, .1103	NS	.0002, 1.32, .254	.00064, 4.3, .0031	**0.0005, .0035**
Epiphytic chl *a* (wk 6)	NS	NS	1.59, 0.2108	NS	0.76, 0.5219
Epiphytic chl *b* (wk 6)	.042, 2.16, .1446	NS	.0413, 2.12, .149	.0853, 4.38, .0028	**0.053, .0138**
Epiphytic chl *c* (wk 6)	NS	.0307, 1.3, .2571	NS	NS	0.027, .3556
Epiphytic carotenoids (wk 6)	NS	NS	NS	NS	0, .9628
Temporal CV of epi. chl *a*	NS	**11.31, 0.0011**	1.89, 0.1726	1.64, 0.1708	**2.00, 0.0629**
Temporal CV of epi. chl *b*	NS	NS	NS	NS	1.94, .8266
Temporal CV of epi. chl *c*	NS	1.85, 0.1766	**3.25, .0745**	NS	0.11, .1716
Temporal CV of epi. carot.	NS	1.148, 1.58, .2118	NS	NS	0.60, .4810
Metacommunity (n=5 for each combination of treatments, n=20 total)					
Epiphytic chl *a* (wk 2)	**271.1, 3.86, .0671**	NS	NS	N/A	130.2, .1784
Epiphytic chl *b* (wk 2)	NS	NS	NS	N/A	0.079, .9126
Epiphytic chl *c* (wk 2)	2.398, 1.55, .2315	**8.833, 5.7, .0297**	NS	N/A	**4.00, .0894**
Epiphytic carotenoids (wk 2)	NS	**36.409, 3.29, .0886**	NS	N/A	17.05, .2426
Epiphytic chl *a* (wk 4)	NS	308.2, 2.09, .1673	NS	N/A	111.5, .5344
Epiphytic chl *b* (wk 4)	NS	NS	NS	N/A	0.07, .9677
Epiphytic chl *c* (wk 4)	6.259, 2.18, .1592	NS	NS	N/A	2.21, .5269
Epiphytic carotenoids (wk 4)	.00232, 1.69, .2117	NS	.00181, 1.32, .2671	N/A	0.001, .3863
Epiphytic chl *a* (wk 6)	NS	NS	NS	N/A	9.65, .6872
Epiphytic chl *b* (wk 6)	NS	NS	NS	N/A	0.047, .8211
Epiphytic chl *c* (wk 6)	NS	NS	**.664, 4.2, .0572**	N/A	.225, .2727
Epiphytic carotenoids (wk 6)	NS	NS	NS	N/A	0, .6199
Temporal CV of epi. chl *a*	NS	.084, 1.42, 0.2502	**.180, 3.07, 0.099**	N/A	1.60, .2288
Temporal CV of epi. chl *b*	.094, 1.39, .2563	NS	NS	N/A	0.037, .6577
Temporal CV of epi. chl *c*	NS	NS	.0563, 1.78, .201	N/A	0.030,.4345
Temporal CV of epi. carot.	.0074, 1.26, .2785	.0121, 2.06, .1705	.009, 1.53, .2344	N/A	0.010, .2253
Spatial CV of epi. chl *a* (wk 2)	NS	**.238, 7.11, .0169**	**.140, 4.17, 0.058**	N/A	3.76, 0.0323
Spatial CV of epi. chl *b* (wk 2)	NS	NS	.597, 1.92, .1844	N/A	0.31, .4136
Spatial CV of epi. chl *c* (wk 2)	NS	**.0649, 3.73, .0714**	NS	N/A	0.024, .2853
Spatial CV of epi. carot.(wk 2)	**NS**	.136, 2.14, .1633	.143, 2,24, .1537	N/A	0.11, .2009
Spatial CV of epi. chl *a* (wk 4)	NS	NS	NS	N/A	0.28, 0.8376
Spatial CV of epi. chl *b* (wk 4)	.497, 2.12, .1651	NS	NS	N/A	0.18, .5356
Spatial CV of epi. chl *c* (wk 4)	NS	NS	NS	N/A	0.019, .8852
Spatial CV of epi. carot.(wk 4)	NS	1.90, 2.36, .1443	1.50, 1.85, .1922	N/A	1.18, .2615
Spatial CV of epi. chl *a* (wk 6)	NS	NS	.116, 1.4, .2579	N/A	0.77, 0.5281
Spatial CV of epi. chl *b* (wk 6)	NS	NS	**48.52, 5.16, .037**	N/A	18.31, .1626
Spatial CV of epi. chl *c* (wk 6)	NS	NS	NS	N/A	9.97, .7847
Spatial CV of epi. carot.(wk 6)	.319, 1.17, .2953	NS	NS	N/A	0.14, .6701

Table 4. Effects of dispersal on the relationships between biodiversity and the magnitude and predictability of ecosystem functions. Table cells are slope of the biodiversity-ecosystem function (BD-EF) relationship, p-value, R^2, determined by general linear regression. The BD-EF column indicates whether the slope of the BD-EF relationship for that response variable was positive, negative, or changed from one to the other by dispersal. The "Direction" column indicates the effect of dispersal on the slope of the BD-EF relationship (+ for an increase in the absolute value of the slope); bolded values indicate a significant effect of dispersal. Changes in slope that exceeded 25% of the higher value were counted as changes in direction, provided each regression line still explained at least 5% of variance in both instances. When regressions were significant but did not meet the latter criteria, they were still counted. The intercept column indicates whether or not dispersal increased or decreased the intercept by >25%.

Response Variable	No Dispersal Slope, p value, R2	Dispersal Slope, p value, R2	BD-EF	Direction of change	Intercept
Patch (n=25 for each combination of treatments, n=100 total)					
Log grazer abundance	**926.86, .0002, .2617**	**322.25, .0722, .0658**	**+**	-	+
Epiphytic chl *a* (week 2)	**2.16, .0377, .0905**	**4.43, .0062, .1457**	**+**	**+**	0
Epiphytic chl a (week 4)	.656, .7006, .0032	-2.29, .3978, .0149	**+ to -**	**N/A (R2 too low)**	+
Epiphytic chl *a* (week 6)	1.87, .1521, .0431	-.646, .333, .0195	**+ to -**	**N/A/↲**	+
Log total algal biomass	**-1.158, .0385, .0879**	**-1.76, .00006, .2181**	-	+	0
Edible algae biomass	-.083, .1949, .0355	-.018, .3235, .0207	-	N/A (R2 too low)	-
Inedible algae biomass (cyanobacteria)	-.014, .7615, .002	**-.134, .008, .1404**	-	N/A/created	+
Z. marina biomass	**-.628, .0725, .067**	**-1.001, .0007, .2163**	-	+	+
Invertebrate biomass	**-1.66, .0037, .166**	**-1.789, .0002, .2565**	-	0	0
Log *M. manhattensis* biomass	**-1.406, .0012, .2007**	**-1.1, .0077, .139**	-	-	0
Nereis biomass	-.01, .4203, .0145	**-.035, .0589, .0754**	-	N/A /created(R2 too low)	0
Botryllus biomass	-.048, .575, .0067	.144, .2124, .0322	- to +	N/A (R2 too low)	0
Temporal CV of grazer abundance	.264, .5109, .0244	.526, .1164, .300	+	N/A (R2 too low)	+
Temporal CV of epiphytic chl *a*	-12.729, .5144, .009	4.06, .8186, .0011	- to +	N/A/↲	+
Temporal CV of epiphytic chl *b*	-.08, .7203, .0028	-1.38, .5304, .0083	-	N/A (R2 too low)	-
Temporal CV of epiphytic chl *c*	-.269, .1714, .0394	**.232, .078, .0632**	**- to +**	↲	0
Temporal CV of epiphytic chl carot	-.103, .5555, .0074	-.383, .5971, .0059	-	N/A (R2 too low)	0
Metacommunity (n=5 for each combination of treatments, 20 total)					
Spatial CV of grazer abundance	.121, .4224, .0820	-.14, .3522, .1087	+ to -	↲	0
Spatial CV of epiphytic chl *a* (week 2)	**.7375, .0057, .6359**	.0128, .9568, .00004	**+**	**-/eliminated**	+
Spatial CV of epiphytic chl a (week 4)	-.35, .5572, .0446	.11164, .8019, .0083	- to +	N/A (R2 too low)	-
Spatial CV of epiphytic chl *a* (week 6)	087, .8444, .0051	-.375, .1476, .2432	+ to -	↲/created	+
Spatial CV of epiphytic chl *b* (week 2)	.2493, .1145, .2817	-.175, .3208, .1228	**+ to -**	↲	+
Spatial CV of epiphytic chl b (week 4)	.203, .1973, .1982	.158, .3667, .1027	+	-	+
Spatial CV of epiphytic chl *b* (week 6)	**-.832, .0149, .5442**	.343, .4555, .0818	**- to +**	**↲/eliminated**	-
Spatial CV of epiphytic chl *c* (week 2)	.1727, .361, .105	.2161, .1571, .2336	+	+	0
Spatial CV of epiphytic chl c (week 4)	-.069, .8826, .0029	.2774, .1952, .1999	- to +	↲/created	-
Spatial CV of epiphytic chl *c* (week 6)	.648, .2695, .1496	-.315, .6104, .0459	+ to -	↲	+
Spatial CV of epiphytic chl carotenoids (week 2)	**.600, .0770, .3398**	-.216, .4686, .0675	+ to -	↲/eliminated	+
Spatial CV of epiphytic chl carotenoids (week 4)	.373, .3432, .11226	.129, .8056, .008	+	N/A (R2 too low)	0
Spatial CV of epiphytic chl carotenoids (week 6)	-.1233, .7965, .0088	-.402, .6067, .0346	-	N/A (R2 too low)	+
Spatial CV of total algal biomass	**.900, .0576, .3801**	**1.014, .0878, .3208**	+	0	+
Spatial CV of edible algae biomass	.634, .5745, .0411	**-2.16, .0032, .6822**	**+ to -**	**↲/created**	+
Spatial CV of inedible algae biomass	**.6132, .0775, .3389**	.924, .1126, .2841	+	+	-
Spatial CV of *Z. marina* biomass	.091, .6059, .0348	.2114, .2374, .169	+	N/A/+	-
Spatial CV of invertebrate biomass	.081, .4387, .0766	.218, .1491, .2416	+	+	0
Spatial CV of *M. manhattensis* biomass	.800, .0115, .5708	.782, .0274, .4752	+	0	-
Spatial CV of *Nereis* biomass	**1.02, .0276, .4743**	.3733, .4949, .0601	+	-/eliminated	+
Spatial CV of *Botryllus* biomass	N/A	N/A		N/A	N/A
Temporal CV of Spatial CV of epi chl a	**-.451, .0465, .4089**	.1497, .5849, .0389	**- to +**	**↲/eliminated**	-
Temporal CV of Spatial CV of epi chl b	**-1.019, .00004, .8115**	.3195, .3656, .1031	**- to +**	**↲/eliminated**	-

Temporal CV of Spatial CV of epi chl c	.0468, .8957, .0023	**-.682, .0332, .4520**	+ to -	↲/created	+
Temporal CV of Spatial CV of epi chl carot	.155, .4749, .0656	.269, .2644, .1526	+	+	-
Temporal CV of grazer abundance	-.396, .2345, .586	**.250, .0717, .8618**	- to +	↲	-
Temporal CV of epiphytic chl *a*	**-.55828, .0825, .3299**	.12241, .6958, .02	- to +	**↲/eliminated**	-
Temporal CV of epiphytic chl *b*	-.1142, .6525, .0266	.05421, .8863, .0027	- to +	N/A (R2 too low)	0
Temporal CV of epiphytic chl *c*	-.191, .4886, .0618	.13818, .3853, .0954	- to +	↲	0
Temporal CV of epiphytic chl carotenoids	.059, .8767, .003	.180, 1.57, .235	+	+	**0**
Increased (+)				**8**	**17**
Reduced (-)				**4**	**12**
No Change (0) or too little variance explained				**16**	**13**
Reversed (↲)				**14**	**N/A**

Note:

-There were 12 instances where dispersal made BD-EF more negative (either reversed from a positive to a negative slope, increased the absolute value of an already negative slope, or decreased the absolute value of a positive slope).

-There were 14 instances where dispersal made BD-EF more positive (either reversed from a negative to a positive slope, increased the absolute value of an already positive slope, or decreased the absolute value of a negative slope).

FIGURE LEGENDS

Figure 1. **a-h:** Competitive performance with and without dispersal. Final proportional abundance vs. initial proportional abundance of each species in all patches where it was present. Empty dots are isolated patches; black dots are connected patches. Diagonal lines are 1:1 ratio; dots above the line represent populations that increased relative to their initial proportional abundance. Regression lines are shown where significant; dashed=isolated patches, solid=connected patches. **i:** Net population growth (final abundance/initial abundance) for each species. White bars=isolated patches; black bars=connected patches.

Figure 2. Extinctions and colonizations. **a)** Cumulative frequency of extinctions (black) and population increases (grey) by initial founding population size. Initial populations consisted of a variable number of reproductively mature male-female pairs. Extinction frequency decreased with increasing size of the founding population. Data for *P. caudata* are not included because *P. caudata*'s extinction rate was four times that of any other species. **b)** Colonization frequency vs. extinction frequency in isolated (light blue) and connected (dark blue) patches. Genus and species initials indicate points. Note that *G. mucronatus* and *C. compta* points (both with and without dispersal) are at (1,0). **c)** Competitive performance with and without dispersal, determined by the change in proportional abundance over the course of the experiment (y-x from Figure 1). **d)** Competition vs. colonization. Symbols as in **b)**. Competition and colonization as in **c)** and **b)**.

Figure 3. Grazer density with (black bars) and without (white bars) dispersal. Significant effects indicated in top left. † $p<.10$, * $p<.05$, ** $p<.01$, *** $p<.001$. Error bars are S.E..

Figure 4. Dispersal effects on **a)** intraspecific and **b)** interspecific aggregation within high richness metacommunities. In **b)**, species pairs are arranged in order of decreasing interspecific aggregation in unconnected metacommunities. Species pairs are listed as GenusspeciesGenusspecies. Species are listed below the x-axis in order of increasing dispersal ability for reference. The effect of dispersal on interspecific aggregation depended on the degree of aggregation in unconnected patches, shown more clearly in **c)**, where the difference between interspecific aggregation with and without dispersal was estimated by resampling the data 100 times for each species pair. Error bars are S.E..

Figure 5. Changes in the degree of spatial heterogeneity of individual species abundance **(a-h)** and aggregate grazer abundance **(i)** through time. Spatial heterogeneity estimated as the coefficient of variation of abundance among all five patches within a metacommunity. Empty dots are isolated patches; black dots are connected patches.

Figure 6. Time course of algal pigments, in μg/cm^2 eelgrass leaf blade, within patches. **a)** Chlorophyll *a*, common to most producers; **b)** chlorophyll *b*, found in higher plants, green algae and prochlorophytes; **c)** chlorophyll *c*, found in diatoms, dinoflagellates, cryptomonads and haplophytes; and **d)** carotenoids. Circles = low metacommunity richness; triangles = high metacommunity richness. Empty symbols are isolated patches; filled symbols are connected patches. **e)** Synchrony of epiphyte load among patches within a metacommunity through time. Empty symbols and dashed line = metacommunities without dispersal; filled symbols and solid line = metacommunities with dispersal.

Figure 7: Among-patch variation (C.V.) of epiphytic algal pigments through time. Data are from large species pool treatments only (n=5 for each point). Error bars are standard error.

Figure 1

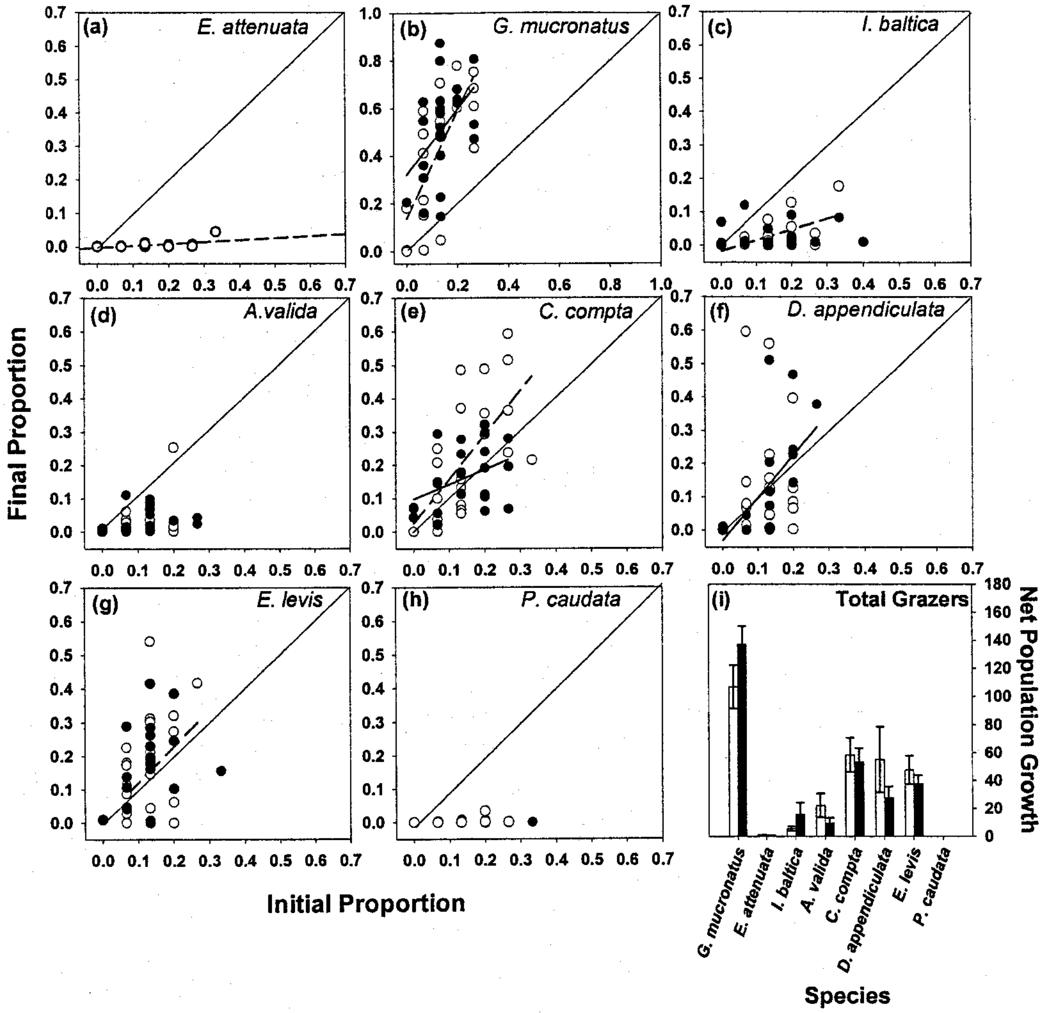
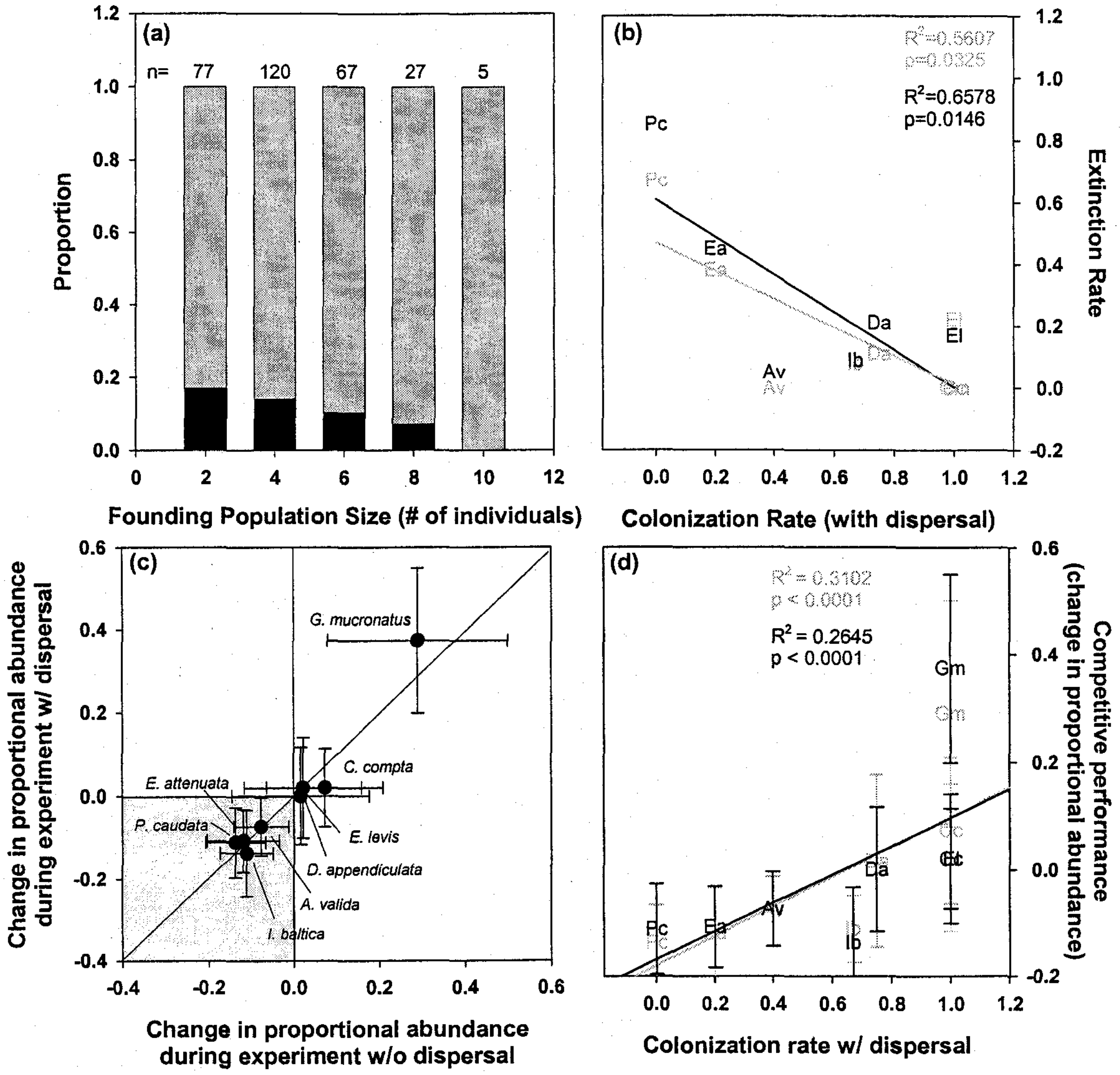

(a) E. attenuata
(b) G. mucronatus
(c) I. baltica
(d) A.valida
(e) C. compta
(f) D. appendiculata
(g) E. levis
(h) P. caudata
(i) Total Grazers
Final Proportion
Initial Proportion
Net Population Growth
Species
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7
0.0 0.2 0.4 0.6 0.8 1.0
0 20 40 60 80 100 120 140 160 180
G. mucronatus
E. attenuata
I. baltica
A. valida
C. compta
D. appendiculata
E. levis
P. caudata

Figure 2



(a)
n= 77 120 67 27 5
Proportion
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0 2 4 6 8 10 12
Founding Population Size (# of individuals)
(b)
R^2=0.5607
p=0.0325
R^2=0.6578
p=0.0146
Pc
Pc
Ea
Ea
Da
Da
Ib
El
El
Av
Av
Cc
Extinction Rate
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0.0 0.2 0.4 0.6 0.8 1.0 1.2
Colonization Rate (with dispersal)
(c)
G. mucronatus
C. compta
E. attenuata
P. caudata
E. levis
D. appendiculata
A. valida
I. baltica
Change in proportional abundance during experiment w/ dispersal
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.4 -0.2 0.0 0.2 0.4 0.6
Change in proportional abundance during experiment w/o dispersal
(d)
R^2 = 0.3102
p < 0.0001
R^2 = 0.2645
p < 0.0001
Gm
Gm
Cc
El
Da
Av
Ib
Ea
Pc
Pc
Competitive performance (change in proportional abundance)
0.6
0.4
0.2
0.0
-0.2
0.0 0.2 0.4 0.6 0.8 1.0 1.2
Colonization rate w/ dispersal

Figure 3

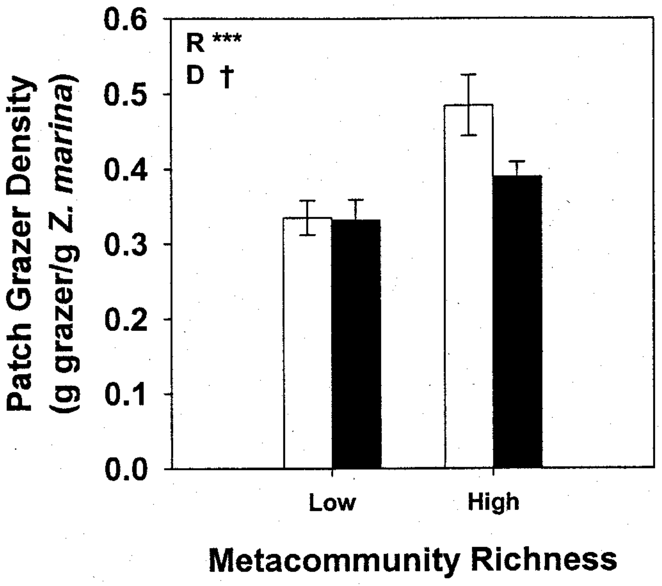

R ***
D †
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Patch Grazer Density
(g grazer/g *Z. marina*)
Low
High
Metacommunity Richness

Figure 4

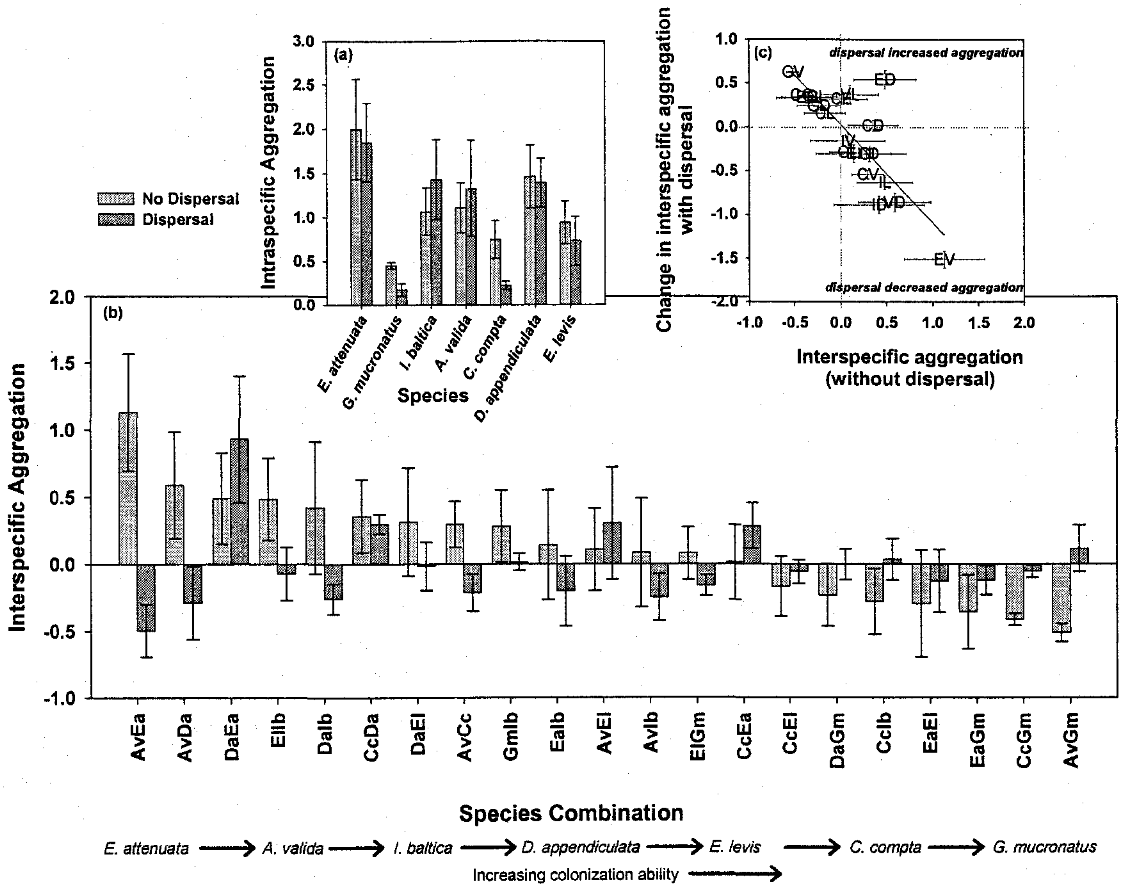

(a)
Intraspecific Aggregation
3.0
2.5
2.0
1.5
1.0
0.5
0.0
E. attenuata
G. mucronatus
I. baltica
A. valida
C. compta
D. appendiculata
E. levis
Species
No Dispersal
Dispersal
(b)
Interspecific Aggregation
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
AvEa
AvDa
DaEa
EIIb
DaIb
CcDa
DaEl
AvCc
GmIb
EaIb
AvEl
AvIb
ElGm
CcEa
CcEl
DaGm
CcIb
EaEl
EaGm
CcGm
AvGm
Species Combination
E. attenuata → A. valida → I. baltica → D. appendiculata → E. levis → C. compta → G. mucronatus
Increasing colonization ability →
(c)
dispersal increased aggregation
dispersal decreased aggregation
Change in interspecific aggregation with dispersal
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Interspecific aggregation (without dispersal)
GV
ED
CD
CV
IL
ID
VD
EV

Figure 5

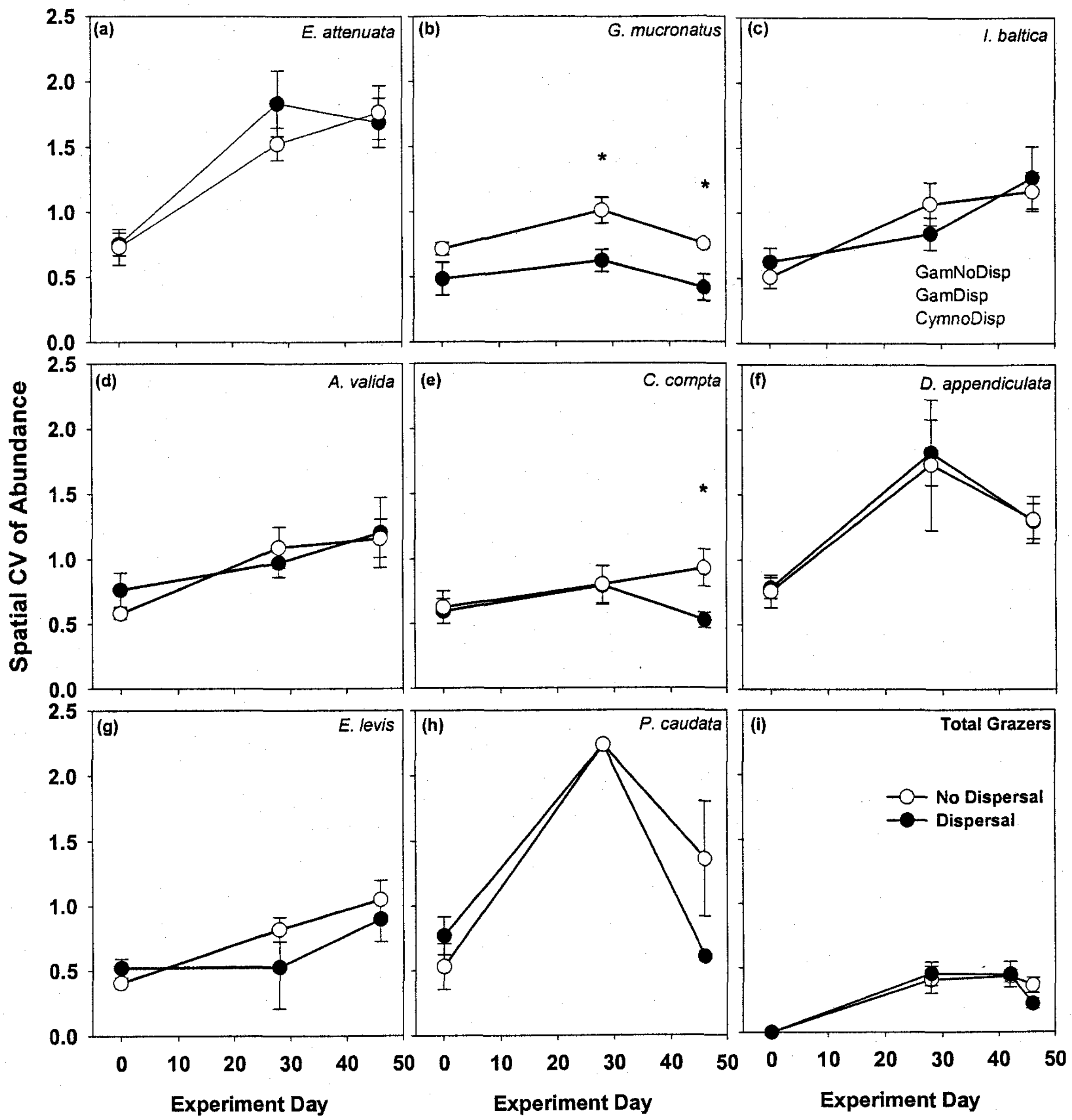
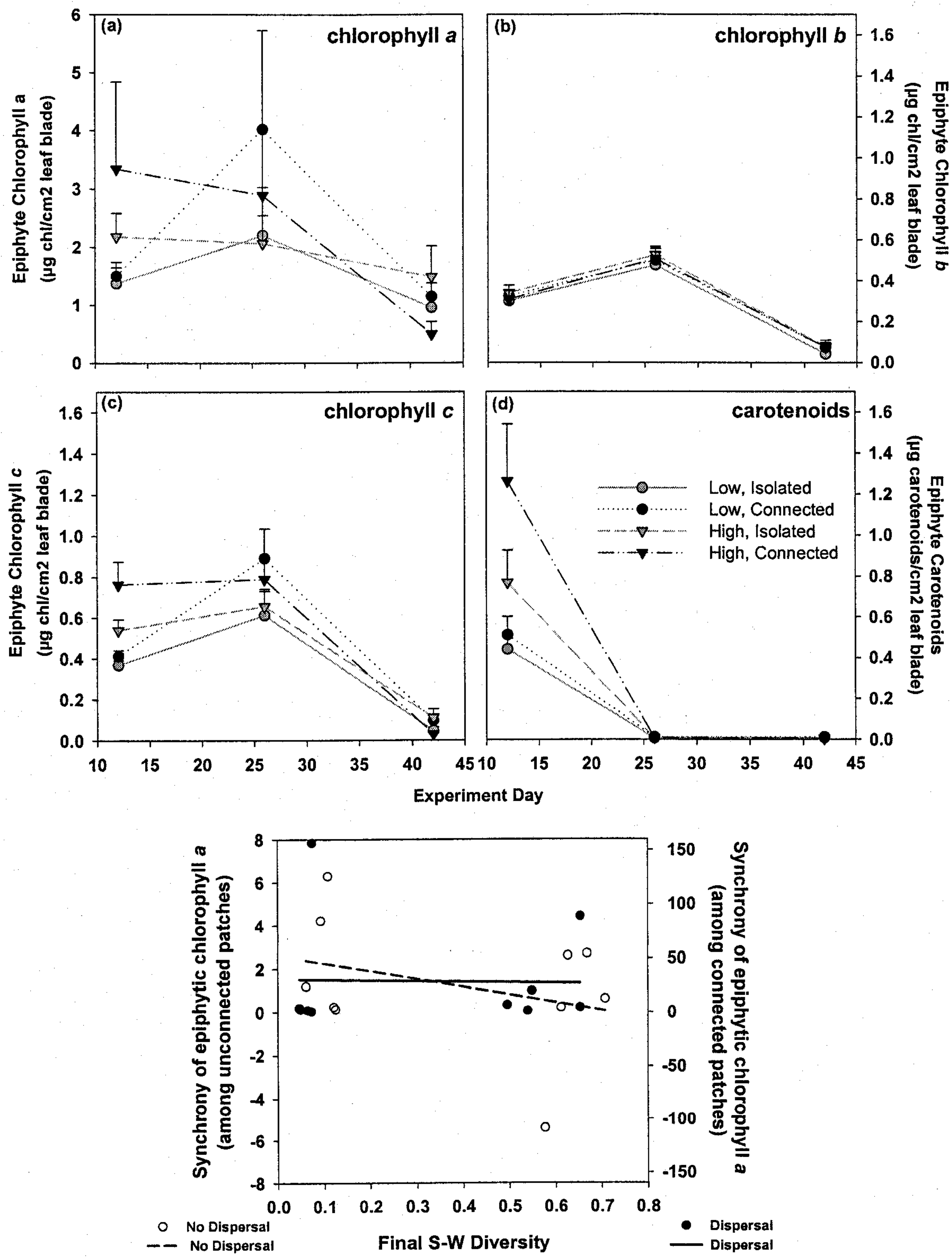
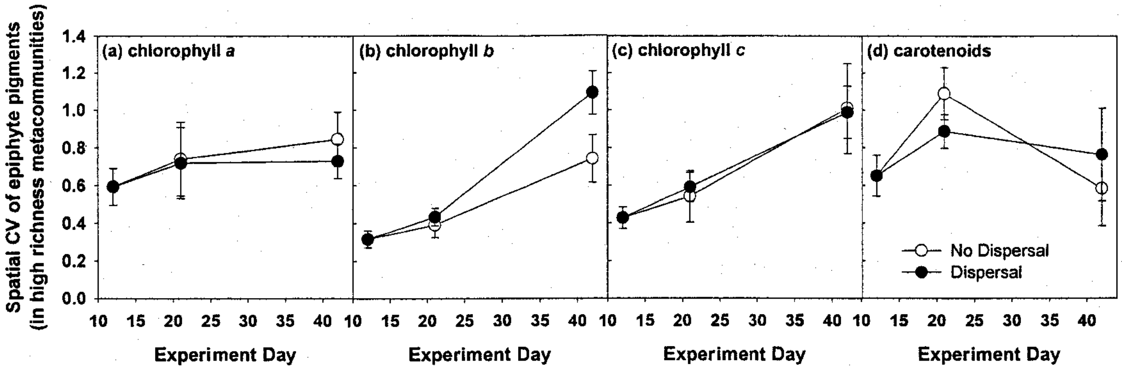

(a)
E. attenuata
(b)
G. mucronatus
(c)
I. baltica
GamNoDisp
GamDisp
CymnoDisp
(d)
A. valida
(e)
C. compta
(f)
D. appendiculata
(g)
E. levis
(h)
P. caudata
(i)
Total Grazers
No Dispersal
Dispersal
*
Spatial CV of Abundance
0.0
0.5
1.0
1.5
2.0
2.5
Experiment Day
0
10
20
30
40
50

Figure 6

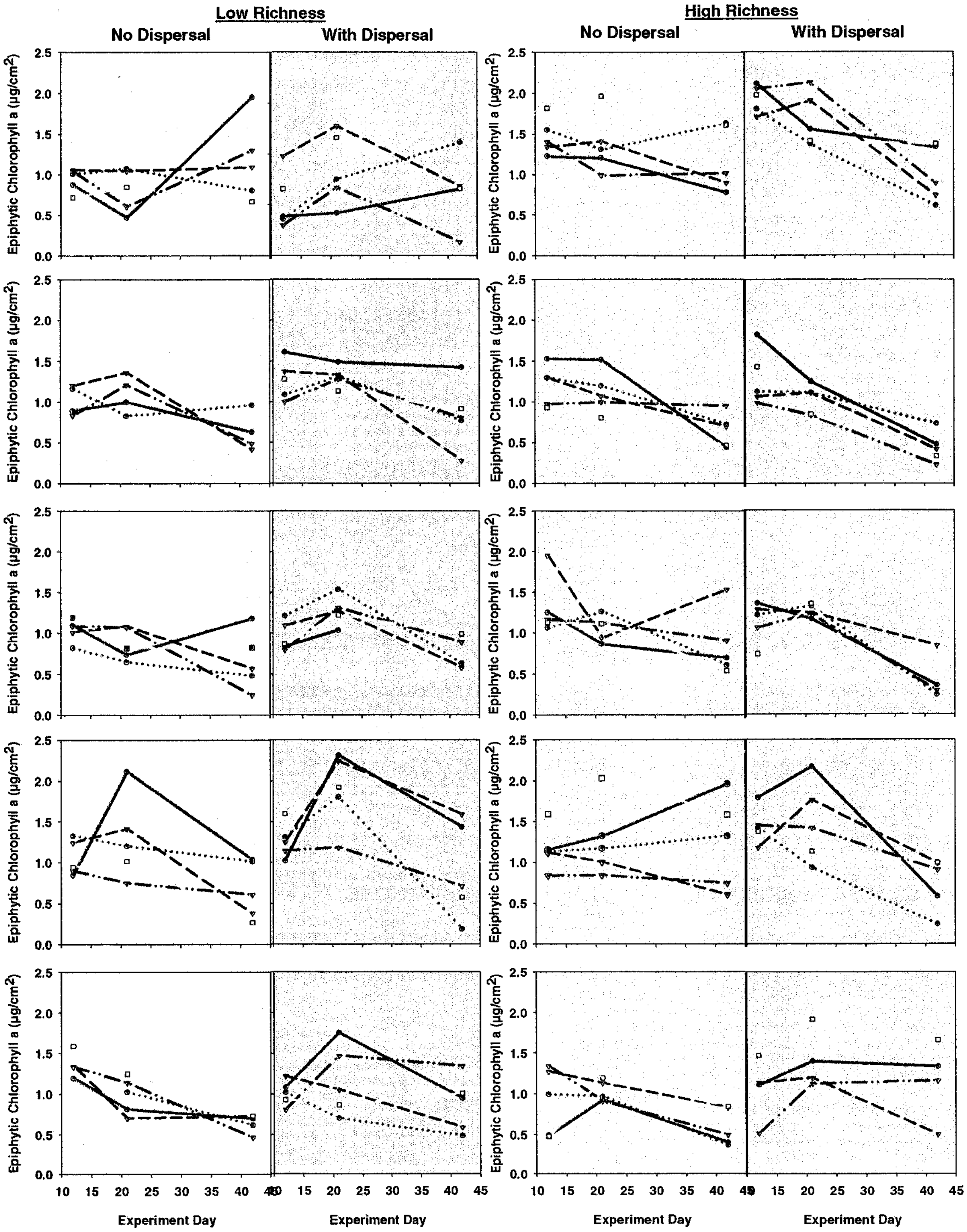


(a)
chlorophyll *a*
Epiphyte Chlorophyll a (µg chl/cm2 leaf blade)
0
1
2
3
4
5
6
(b)
chlorophyll *b*
Epiphyte Chlorophyll *b* (µg chl/cm2 leaf blade)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
(c)
chlorophyll *c*
Epiphyte Chlorophyll *c* (µg chl/cm2 leaf blade)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
(d)
carotenoids
Epiphyte Carotenoids (µg carotenoids/cm2 leaf blade)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Low, Isolated
Low, Connected
High, Isolated
High, Connected
10
15
20
25
30
35
40
45
Experiment Day
Synchrony of epiphytic chlorophyll *a* (among unconnected patches)
8
6
4
2
0
-2
-4
-6
-8
Synchrony of epiphytic chlorophyll *a* (among connected patches)
150
100
50
0
-50
-100
-150
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Final S-W Diversity
○ No Dispersal
– – No Dispersal
● Dispersal
— Dispersal

Figure 7


Spatial CV of epiphyte pigments (in high richness metacommunities)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
(a) chlorophyll *a*
(b) chlorophyll *b*
(c) chlorophyll *c*
(d) carotenoids
No Dispersal
Dispersal
10 15 20 25 30 35 40
Experiment Day

Appendix 3-1. Epiphyte biomass through time in each metacommunity, as estimated by epiphytic chlorophyll *a*. Each line represents a patch, and each panel is an individual metacommunity.



CHAPTER 4:
DISPERSAL MEDIATES STABILITY OF ECOSYSTEM PROPERTIES IN RESPONSE TO DISTURBANCE IN EXPERIMENTAL EELGRASS METACOMMUNITIES

ABSTRACT

Theory and small-scale experiments predict that biodiversity losses can decrease the stability of ecosystem services such as production and nutrient cycling. Diversity's role in mediating stability within metacommunities, or networks of patches connected by dispersal, however, is not clear. Since many forms of disturbance, such as habitat fragmentation and species introductions, are inherently spatial, it is unclear how biodiversity will affect stability of ecosystem services in response to those perturbations. We tested the effects of diversity and dispersal on metacommunity responses to a perturbation within one patch using experimental seagrass metacommunities. Although we have previously demonstrated positive relationships between diversity and ecosystem properties in this system, we did not find positive relationships between diversity and stability. Species-poor metacommunities had greater resistance to the perturbation, a macroalgal bloom. Increasing grazer diversity decreased temporal variability of grazer abundance and epiphyte biomass under some circumstances, but those effects were often disrupted or reversed by dispersal or perturbation. Dispersal effects were also complex. Although connecting patches decreased grazer abundance in undisturbed metacommunities, it increased grazer abundance in disturbed metacommunities, increasing resistance to negative effects of the macroalgal disturbance. Dispersal also occasionally de-stabilized undisturbed metacommunities, but usually stabilized grazer abundance in disturbed metacommunities. Our results emphasize the importance of incorporating both spatial processes and trophic interactions into the study of biodiversity-stability relationships. While diverse, connected communities may offer the greatest resistance to perturbations, tendencies for both diversity and dispersal to amplify temporal fluctuations of ecosystem services could increase the likelihood of state changes. Influences of diversity and spatial dynamics on both aspects of stability need to be considered to effectively conserve ecosystem services.

INTRODUCTION

The possible influence of biodiversity on stability is a long-standing controversy (Odum 1953, MacArthur 1955, Elton 1958, May 1972). The last decade of research generally supports a positive influence of diversity on stability, but the nature of that link is still debated, and empirical evidence is limited (reviewed in McCann 2000, Cottingham et al. 2001, Loreau et al. 2002). Biodiversity can affect the stability of community structure and ecosystem function in several ways. First, if temporal variations in abundance of different species within a trophic level are asynchronous, the variance of their aggregate abundance will be less than that of their individual abundances (statistical averaging or the "portfolio effect") (Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, Ives et al. 2000). This asynchrony can be increased by biological mechanisms as well: if species compete strongly, or have different responses to environmental variation, then they will have negative covariances (Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, Tilman 1999, Ives et al. 2000). Second, due to niche differentiation or simply differences among species, as species richness increases, there is a greater chance that some species will perform well in a new suite of environmental conditions; diversity provides insurance for a wide range of conditions (Yachi and Loreau 1999). Third, functional redundancy may increase as species richness increases, buffering ecosystem function if a few species go extinct (Naeem 1998, Loreau 2004). These mechanisms, alone and/or combined, may increase the resistance of an ecosystem to perturbations such as drought or other effects of climate change; increase predictability (the inverse of temporal variability) of ecosystem functions (Pimm 1984), and increase resilience, or "the ability of a community to return to a former state after exogenous disturbance" (definition from Lincoln et al. 1998).

Although all three of these types of stability have been well-defined within the literature, relationships between them are not well-established. Much of the controversy over biodiversity-stability relationships stems from the fact that different kinds of stability might be differently affected by diversity (Pimm 1984, McCann 2000). Still, different kinds of stability are often treated as conceptually interchangeable. Most of the convincing evidence for BD-stability relationships comes from measures of general stability, or the inverse of temporal variability (Tilman et al. 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, McGrady-Steed and Morin 2000, Stachowicz et al. 2002). Limited evidence exists for positive relationships between biodiversity and resistance (Tilman and Downing 1994, Boles et al. 2004, Hughes and Stachowicz 2004), resilience (Griffiths 2000, Reusch et al. 2005), or combinations of both resistance and resilience as recovery from a disturbance (Lepš et al. 1982, Mulder et al. 2001). There are also studies which have found positive relationships between diversity and one kind of stability, but not others (Allison 2004, Caldeira et al. 2005), and several which have found weak or even negative relationships between diversity and stability, particularly resistance (Loreau and Behera 1999, Wardle et al. 2000, Pfisterer and Schmid 2002, Downing unpublished data). Most of these experiments have been conducted within single trophic levels, and with plants. Demonstrated effects of diversity on stability within multi-trophic systems are even more limited and equivocal, with many studies, other than the seminal early papers (McGrady-Steed et al. 1997, Naeem and Li 1997, McGrady-Steed and Morin 2000), finding no or even negative effects of diversity on general stability, resistance (nutrient addition, Wojdak 2005; drought resistance, Wardle et al. 2000), and resilience (predation, Smedes and Hurd 1981). Furthermore, the statistical significance of positive biodiversity-stability relationships in those early papers has been questioned (e.g. Huston 1997 but see Morin and McGrady-Steed 2004).

Diversity's role in mediating any form of stability is even less clear within metacommunities, or networks of patches connected by dispersal. Theory is limited, but suggests that diversity could stabilize ecosystem function, namely production, in heterogeneous landscapes in ways similar to its effects in isolated patches. Diversity among patches (beta diversity) can provide spatial insurance, just as diversity within a patch provides insurance: the more species there are in a system, the more likely it is that one or several of them can survive and even thrive under current conditions, including dramatically altered ones (Loreau et al. 2003). For diversity to serve as spatial insurance, though, organisms need to move between patches. Dispersal among patches may be essential for system recovery after a perturbation. If local communities are connected, species that can handle the perturbation are more likely to reach the disturbed area (Nyström and Folke 2001, Bengtsson et al. 2002, Starzomski and Srivastava in press). Empirical evidence for positive relationships between diversity and stability of ecosystem function within metacommunities is almost entirely lacking, however. Preliminary evidence suggests that diversity can actually increase both spatial and temporal variability within metacommunities connected by dispersal (France and Duffy 2006b). Increased variability is usually equated with decreased stability (McCann 2000, Cottingham et al. 2001). There is good reason for this: larger population fluctuations can lead to greater risks of extinction, and larger fluctuations in ecosystem states could increase the risk of systems switching to an alternative state. It may be that stabilizing benefits of diversity are apparent only at longer time-scales than observed in this experiment, as the mechanisms described above may only operate under when communities experience a wide range of environmental conditions. Coordinately, while dispersal among patches can synchronize dynamics and therefore increase temporal variability at the metacommunity level (De Roos et al. 1991, Holyoak and Lawler 1996, Ruxton and Rohani 1998, Bull et al. 2006), it could be critical to facilitating recovery after a perturbation in one particular location. Finally, spatial insurance provided by beta-diversity and patch connectivity, as discussed above, might be most beneficial after a perturbation.

Consumer diversity might also stabilize resource diversity, even if it increases spatial and temporal variability of consumers under normal conditions (France and Duffy 2006b). First, environmental temporal variability can stabilize biomass within patches, by reducing covariance among individual populations (Gonzalez and Descamps-Julien 2004). This is one of the same mechanisms by which diversity can stabilize biomass. Within metacommunities, autocorrelated environmental temporal variability can increase abundance (Gonzalez and Holt 2002, Holt et al. 2003, Roy et al. 2005), which might, in turn, stabilize dynamics by decreasing risks of stochastic extinctions. This inflationary effect on abundance can persist even if patches are synchronized, but it is strengthened by asynchrony among patches (Roy et al. 2005). Although this inflationary effect has primarily been modeled and tested using abiotic variability and primary producers, biotically-mediated temporal variability, such as that generated by diversity and consumer-resource interactions, might also have this inflationary and potentially stabilizing effect. So, consumer diversity might stabilize resource metacommunity dynamics by increasing temporal variability within patches, particularly if it also increased asynchrony among patches.[3]

Since disturbances are often spatially discrete, incorporating space and connectivity between patches into predictions about the effects of diversity on all forms of stability is necessary. Habitat fragmentation, one of the major threats to diversity (Wilcove et al. 1998), is by nature a spatial phenomenon, and its effects are clearly mediated by dispersal. Furthermore, broad-scale perturbations can cause or interact with habitat fragmentation, compounding effects of both. For instance, although climate change is a broad scale phenomenon, nearshore temperature anomalies associated with it are often quite localized, and may facilitate disease on coral reefs, fragmenting reef habitat (Selig et al. in prep.). Similarly, eutrophication of marine and freshwaters is often due to non-point source pollution, yet, by facilitating macro- and micro- algal blooms, it can have local effects, leading to fragmentation of submerged aquatic vegetation.

Seagrass beds are one of the marine ecosystems threatened by the combined effects of eutrophication and fragmentation. Seagrasses are important foundation species in shallow marine habitats, supporting commercially important fisheries and often harboring higher diversity than adjacent, unvegetated areas, but they are threatened worldwide (Orth et al. 2006). Though seagrass beds are naturally patchy (Robbins and Bell 1994, Hovel and Lipcius 2001), they are becoming increasingly fragmented, particularly within the Chesapeake Bay (Orth and Moore 1983, Orth et al. 2002). Nutrient pollution can also

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[3] Note, though, that Gonzalez and Descamps-Julien (2004) manipulated both temperature variability and algal richness, and found that, at a given richness, increasing environmental variability decreased CV of biomass, but that richness still increased CV. These were within isolated patches.

contribute to the decline of eelgrass (Kemp et al. 2005) by shifting competitive dominance for light from seagrass to macroalgae, epiphytic microalgae, and phytoplankton (Kenworthy et al. 2006, Ralph et al. 2006). Macroalgal blooms are now a common disturbance within eelgrass beds, shading and occasionally replacing eelgrass (Fletcher 1996, Valiela et al. 1997). Mesograzers can partially mitigate these effects by preferentially feeding on epiphytic micro- and macroalgae (Neckles et al. 1993, Valentine and Duffy 2006). However, macroalgal blooms can increase hypoxia and anoxia within the sediments, stressing small invertebrates and shifting benthic community structure (Raffaelli et al. 1998).

We tested the interactive effects of grazer species richness and patch connectivity on experimental eelgrass metacommunity responses to disturbance in the form of an addition of macroalgae within one patch. Eelgrass (*Zostera marina* is an important estuarine foundation species throughout much of the northern hemisphere, and is the dominant seagrass species in the mid-Chesapeake Bay region. We have previously demonstrated positive relationships between grazer richness and grazer abundance, as well as corresponding negative relationships between grazer richness and abundance of their food resources, in this system (France and Duffy 2006b). With this experiment, we addressed the following questions: 1) Do species-rich grazer assemblages maintain larger abundances than species-poor assemblages when patches are perturbed by a macroalgal bloom? 2) Do corridors between perturbed and unperturbed patches facilitate recovery of grazer populations? 3) Do either grazer richness or dispersal affect the variability of ecosystem properties within the macroalgae laden patches, and/or the entire metacommunity?

MATERIALS AND METHODS

We manipulated grazer metacommunity richness by changing the size of the species pool used to assemble the grazer metacommunities. The small species pool was a subset of the large species pool, and included the three most abundant grazers in the field at the time of the experiment (two amphipods, *Gammarus mucronatus* and *Cymadusa compta*, and an isopod, *Idotea baltica*). The large pool included approximately 75% of the epifaunal crustacean grazer species known from the lower Chesapeake Bay region (Wass 1972), and included the three species from the small pool as well as four more amphipods, *Ampithoe valida*, *Dulichiella appendiculata*, *Elasmopus levis*, and *Melita nitida,* and one additional isopod, *Erichsonella attenuata*. All of these crustaceans have sexual reproduction, overlapping generations and direct development, and all feed on epiphytic algae and associated detritus (Duffy 1990, Duffy et al. 2003). At summer temperatures, generation times in our system can be as short as three weeks for amphipods (Fredette and Diaz 1986) and one month for isopods (Kouwenberg and Pinkster 1985, Jormalainen and Tuomi 1989). These species can all swim and crawl along the eelgrass blades, but differ in their swimming ability and dispersal inclination (Duffy and Hay 1994, France & Duffy in prep. (Chapter III)). Dispersal distances and frequencies for these organisms are not well-known. Both drift macroalgae and eelgrass detritus wrack are potential long-distance (up to 10s of km) dispersal vectors (Holmqvist 1994, Brooks and Bell 2001, Harwell and Orth 2002). All species used in the experiment have been observed to disperse 10s-100s of meters by swimming or drifting on tidal currents to colonize seagrass patches (Virnstein and Curran 1986, Duffy et al. unpublished data, Matich et al. unpublished data).

The experiment was conducted in outdoor, flow-through seagrass mesocosms at the Virginia Institute of Marine Science, Gloucester Point, Virginia, USA. The mesocosms were semi-transparent buckets filled with 13.5 L of water, fitted with 250-μm mesh drain holes. Filtered seawater from the York River estuary was delivered to each mesocosm in pulses via vinyl tubing angled to create turbulent flow. The mesocosm arrays were shaded with a layer of neutral-density plastic screen to approximate natural light levels. Fifteen pre-weighed *Z. marina* shoots were planted in the mesocosms. This eelgrass shoot density falls at the low end of the range observed locally over the past twenty years (Orth and Moore 1986), although it is in the middle of the range of densities observed within the past several years, when eelgrass declined precipitously in the lower Bay (Orth 2007, Duffy et al. unpublished data). Prior to planting, the shoots were spun 20 times in a salad spinner and then massed to determine an initial grass wet mass for each mesocosm.

The experimental metacommunities consisted of three of these mesocosms clustered together and indirectly connected by a common flow-through water supply. Hereafter, we call a mesocosm a "patch" and a group of three mesocosms a "metacommunity."

Experimental design

We used a fully-crossed, three-factor factorial design with grazer metacommunity richness, patch connectivity, and macroalgal addition as the three factors.

Metacommunity richness had two levels: low (3 spp.) and high (8 spp.). Patches within a metacommunity were either isolated or connected with corridors that the mobile grazers could swim through. These dispersal corridors were 5 cm of clear vinyl tubing connected to a small central hub so that grazers leaving one patch had an equal chance of dispersing to all of the other patches within the metacommunity. Entrances to the corridors were 3 cm from the water surface and 2.2 cm in diameter, or approximately 5-20x the width of adult amphipods and isopods. All grazer species could swim rapidly through the dispersal corridors, but dispersed at different frequencies, due to differences in encounter rates with the corridor entrances and propensity to swim into the corridors. There was no active dispersal between unconnected patches. Finally, metacommunities were either undisturbed or disturbed by an addition of macroalgae, mimicking a macroalgal bloom, to one of the three patches. Macroalgae, primarily *Ulva lactuca*, a common bloom species in Virginia (Tyler et al. 2001), was added at day 19, after the grazers had approached carrying capacity. We used 125 g wet weight of algae (after 25 spins in a salad spinner to standardize water removal) in each disturbed patch, or 2 kg/m^2. This falls within the range of macroalgal bloom densities observed in coastal Virginia (450-650 g dw m^{-2}) (Tyler et al. 2001)), and is consistent with densities used by other researchers to study the effects of macroalgal blooms (Hull 1987, Raffaelli et al. 1998, Cardoso et al. 2004). When added to the mesocosms, this biomass of macroalgae covered the water surface and filled approximately two-thirds of the water column within the mesocosms. Each of the eight treatment combinations (metacommunity richness x patch connectivity x macroalgal addition) was replicated seven times, for a total of 56 metacommunities and 168 patches.

At the start of the experiment, each patch was stocked with 30 grazers, that is, 15 reproductively mature male-female pairs. We determined the species composition of these founding communities by randomly drawing pairs of individuals from the designated species pool. Each species had an equal chance of being chosen at each draw. Initial metacommunity-wide richness of grazers was set at either three or eight species, but both the relative abundances of species within metacommunities and the species richness within patches varied. We allowed this initial random assembly plus subsequent dispersal and species interactions to influence grazer diversity over the six weeks of the experiment. The initial composition for each patch is available in Appendix 3-1. The experiment ran for 45 days, which was long enough for about two generations of grazers, in addition to the founding generation.

Sampling ecosystem properties

We sampled grazer species composition in each patch before (day 18) and after macroalgal addition (days 24, 32, and 39) by sweeping a small aquarium dipnet through the mesocosm at mid-depth 10 times. We counted the number of individuals of each species of grazer captured by the net and then replaced them all. By comparing final abundances to sampled abundances from immediately prior to harvest, we know that the capture efficiency of this method differs among species: it underestimates the relative abundance of the amphipods *D. appendiculata*, *E. levis* and *M. nitida*, while overestimating the relative abundance of isopods (*I. baltica* and *E. attenuata*) and the dominant species, *G. mucronatus* and *C. compta*. However, patterns observed in the final sweep sampling were largely borne out in the actual final counts (proportional abundance in the final sweep sample was a significant predictor of final proportional abundance for all species, and raw abundance was a significant predictor for all species except *E. levis*).

We estimated biomass of epiphytic algae, the grazers' main food source, by measuring epiphytic chlorophyll before (day 16) and after macroalgal addition (days 22, 30, and 44). The longer gap between sampling dates towards the end of the experiment was due to very low epiphyte accumulation; we waited to maximize the biomass sampled. At each sampling point, we harvested two artificial seagrass blades made of green curling ribbon that had been in the patches for at least a week. All blades harvested at a particular time had been in the experiment for the same length of time. These artificial blades were then frozen and later extracted in 20 ml of 90% acetone at –20°C for 24 hours. Chlorophyll *a*, *b*, *c* and carotenoid pigments were determined spectrophotometrically (Parsons et al. 1984) and normalized to leaf blade area. Clean ribbon undergoing the same extraction served as a blank, but the pigments in the ribbon dye do not absorb at the same wavelengths used to determine chlorophyll pigments.

To estimate whole-ecosystem metabolism, we also measured daytime production and nighttime consumption of oxygen within the mesocosms. Daytime measurements were taken between 10:00 and 14:30 on sunny days, and nighttime measurements were initiated at least 1 hour after sunset and taken between 21:30 and 03:00 on the same or adjacent days. The flow-through seawater system was turned off, and the water column in each patch was sealed off at the surface with transparent plastic bags anchored in place by flexible circles of tubing. Connections between patches were sealed off with caps. We measured dissolved oxygen at three time points using a Hach Portable LDO HQ10 Dissolved Oxygen Meter. Daytime production was underestimated in a few patches because the water became supersaturated with oxygen, and the meter only measures accurately below 20 mg/L. We chose this meter because of its accuracy and precision below 4.0 mg/L, because we were most interested in hypoxic stress caused by the macroalgal addition and wanted to be able to characterize slight differences in low oxygen levels.

At the end of the experiment, all epifaunal invertebrates, algae and eelgrass retained by a 0.5 mm mesh sieve were separated, identified, dried to constant mass, ashed at 450 °C, and massed again. Amphipod and isopod grazers were separated into size classes using a stack of nested sieves, identified, and counted. Ash-free dry mass (AFDM) of amphipods was estimated using these size class data and empirically derived relationships between crustacean body size and biomass (Edgar 1990).

We estimated spatial variability of ecosystem properties as the coefficient of variation (CV) of each response variable across the three patches in a metacommunity. The coefficient of variation is the traditional way of scaling variance relative to the mean within the biodiversity-stability field (May 1972, Tilman 1996). Spatial variability was initially zero for all properties other than eelgrass biomass and grazer composition. Spatial heterogeneity in our system results from a combination of random variation in colonization of algae and invertebrates (such as barnacles, anemones, tunicates, polychaetes, and nudibranchs) through the flow-through system, and subsequent interactions with the grazer community. We also estimated temporal CV of epiphytic pigments (four time points) and grazer abundance (four time points). We estimated synchrony among patches of both grazer abundance and epiphyte biomass for all metacommunities that were sampled at least three times during the experiment. After calculating the covariance of grazer abundance or epiphyte biomass for all three possible pairs of patches within a metacommunity, we summed those pairwise covariances to obtain an estimate of synchrony (Doak et al. 1998, Tilman 1999, Steiner et al. 2005).

Statistics

For metacommunity response variables (abundances summed across all patches within a metacommunity) and spatial variability of all response variables, data were analyzed using a fully-crossed 3-way General Linear Model design, with metacommunity richness, dispersal, and macroalgal addition as fixed factors. Each factor had two levels: low vs. high richness, no dispersal vs. dispersal, and no macroalgal addition vs. macroalgal addition. Data were log transformed to meet assumptions of normality and homogeneity of variance when necessary.

For response variables measured at the patch scale, we randomly chose one patch from each of the undisturbed metacommunities, and compared those patches to the patches which were actually subjected to the macroalgae addition within the disturbed metacommunities, using the 3-way GLM described above.

We also separately examined responses in patches directly subjected to the macroalgal addition, using a fully-crossed 2-way ANOVA (metacommunity richness*dispersal).

RESULTS

The summer of 2005 was one of the hottest summers on record for the Chesapeake Bay region. Water temperature exceeded 30°C, a critical threshold temperature for *Z. marina* (Marsh et al. 1986), for an unprecedented number of days (VIMS 2006). Under these conditions, eelgrass within the mesocosms, as well as in the field, failed to produce new growth and senesced. Eelgrass virtually disappeared within our mesocosms by the end of the experiment in early September, and disappeared in the field by October. While we often see nearly complete consumption of the eelgrass in treatments with high grazing pressure (Duffy et al. 2001, Duffy et al. 2003, Duffy et al. 2005), the simultaneous die-off of eelgrass within the mid-Chesapeake Bay in 2005 was unprecedented (Orth pers. comm.).

Diversity patterns

As expected, increasing the size of the grazer species pool used to assemble the metacommunities increased species richness and Shannon-Weaver diversity (S-W) within the patches for all combinations of dispersal and macroalgal addition (Fig. 1, 1st and 2nd rows; Table 1). Connecting patches had no significant main effects on S-W, but it tended to have opposite effects on diversity in disturbed metacommunities compared to undisturbed communities (Fig. 1, 2nd row; Table 1). Disturbance, i.e. adding macroalgae, reduced S-W diversity of metacommunities assembled from the large species pool (Fig. 1, 2nd row, right panel; Table 1). Finally, increasing the size of the species pool also significantly increased beta-diversity, or heterogeneity of species composition among patches (Fig. 1, 3rd and 4th rows). Adding macroalgae tended to homogenize species composition in high richness metacommunities, but increased composition differences among patches in low richness metacommunities (Fig. 1, 3rd and 4th rows). Dispersal tended to reduce beta-diversity, enabling most species to persist in most patches, particularly in disturbed metacommunities (Fig. 1, 3rd and 4th rows, right panels).

Grazers

As we have observed before (France & Duffy 2006b), in undisturbed and unconnected metacommunities, increasing grazer richness tended to increase grazer abundance and biomass, but this relationship was not significant in this experiment (Fig. 2a,d,f,i; Table 1). When patches were disturbed, grazer richness actually decreased grazer biomass ($p=0.0507$, Table 2, Fig. 2h) and resistance to the addition of macroalgae ($p=0.0181$, Table 1). Connecting these disturbed patches to undisturbed patches tended to increase grazer abundance ($p=0.0224$ at wk 5, $p=0.1676$ final; Table 2; Fig. 2c) and resistance to the macroalgae disturbance ($p=0.0609$; Table 2). Grazer dispersal tended to have opposite effects on grazer abundance and biomass in disturbed and undisturbed metacommunities (interaction $p=0.0717$, 0.1487, respectively; Table 1). Overall, adding macroalgae significantly reduced the number of grazers within the disturbed patches ($p=0.0198$, Fig. 2c), but because the remaining individuals were considerably larger (Appendix 3-6), adding macroalgae did not significantly affect grazer biomass (Fig. 2h).

Reductions in grazer populations in disturbed patches were evident, though not significant, by day 32, thirteen days after the macroalgal addition (Fig. 3, Table 2).

Grazer resistance to the macroalgae disturbance, or the change in grazer abundance from day 18 to day 32, was marginally significantly increased by dispersal (p=0.0609, Fig. 3, Table 2).

Producers

Contrary to expectation, eelgrass had the greatest biomass within the disturbed patches (p=0.002, Fig. 4, 1st row). Oddly, diverse grazer communities had higher biomass of blue-green algae and other microalgal mats (p=0.0314, Fig. 4, 2nd row).

Grazer richness increased microalgal biomass on the walls of the mesocosms in both undisturbed and disturbed patches (p=0.0397, Fig. 4, 4th row). Allowing grazers to disperse tended to increase epiphyte biomass on eelgrass (day 42, metacommunity-wide p=0.0743; Fig. 4, 3rd row; Fig. 5, days 23&42; Table 1). Adding macroalgae reduced epiphyte biomass on all sampling dates, as expected (Table 1, Fig. 5).

Temporal variability

Grazer richness did not stabilize grazer abundance in undisturbed patches (Fig. 6a), as we have found previously (France and Duffy 2006b). In contrast, more diverse grazer patches did have marginally significantly lower temporal variability of epiphyte biomass (p=0.0958, Table 1, Fig. 7a). Connecting patches tended to increase temporal variability of both grazer abundance and epiphytes (Figs 6d; 7a,d), as we have shown before (France and Duffy 2006b), but the effects in this experiment were not significant.

Disturbing patches by adding macroalgae altered some of the relationships between richness, dispersal, and temporal variability. First, dispersal and macroalgae interactively affected the temporal variability of grazer abundance at the metacommunity scale.

(p=0.0261, Table 1). Dispersal actually stabilized grazer abundance in disturbed metacommunities (Fig. 6e). Second, the macroalgal disturbance interacted significantly with grazer richness to affect epiphyte biomass at the patch scale (p=0.0656, Table 1). Epiphytes were more variable through time in diverse patches and metacommunities subjected to the macroalgae (Fig. 7c,e). Note that the figures and analyses include both pre- and post- macroalgal addition sampling points. Patterns were fairly similar if pre-macroalgal addition sampling points were excluded (App. 3-2, 3-3, & 3-4; Table 1).

Spatial variability

Metacommunity grazer richness significantly increased spatial variability (among patches) of grazer abundance (p=0.0354, Fig. 8a&b; Table 1). This pattern was even more marked in disturbed metacommunities, as grazer populations foundered more in the species-rich metacommunities.

Spatial variability of epiphyte biomass within metacommunities was generally increased by metacommunity richness as well (p=0.0818, Fig. 8, lower panels). It was also, not surprisingly, increased by adding macroalgae to one patch. Spatial variability of epiphyte biomass tended to decrease over the course of the experiment in undisturbed metacommunities and increase in disturbed metacommunities (Fig. 8c&d).

Grazer richness, dispersal and the addition of macroalgae had complex effects on spatial variability of epiphyte biomass (Fig. 8c&d). When we examined the average spatial variability of each metacommunity over the course of the experiment, the three-way interaction was significant (p=0.0048, Fig. 9a&b, Table 1). In undisturbed, low richness metacommunities, grazer dispersal tended to reduce the spatial variability of this primary food resource (Figs. 8c&9a). Grazer dispersal did not homogenize epiphyte biomass among patches in diverse grazer metacommunities though (Figs. 8c&9a). In disturbed metacommunities, allowing low richness grazer assemblages to move between patches increased spatial variability of epiphytes, while the dispersal of high richness grazer assemblages decreased spatial variability of epiphytes (Figs. 8d&9b). Disturbing one of the patches in a metacommunity also tended to reverse the effects of grazer richness on spatial variability of food resources: low richness grazer assemblages had higher spatial variability of epiphytes than high richness grazer assemblages. In general, though, grazer richness tended to increase spatial variability of food resources except in disturbed metacommunities with dispersal (Fig. 9a&b). Spatial variability of the biomass of microalgae growing on the mesocosm walls at the end of the experiment was not significantly affected by any of the factors (Fig. 9c&d).

Changes in the degree of spatial heterogeneity

Our experimental system is extremely dynamic, and the spatial pattern of resources changed continuously. To examine the effects of grazer richness, patch connectivity, and macroalgal disturbance on the rate of change of these patterns, we estimated the temporal variability of the degree of spatial heterogeneity by calculating the temporal CV of the spatial CV for each metacommunity. Interestingly, in unconnected metacommunities, grazer richness increased the temporal variability of the spatial pattern of grazers, both with and without disturbance ($p=0.0016$, Fig. 10a&b). However, when patches were connected by dispersing grazers, grazer richness led to a more consistent degree of spatial heterogeneity of grazer populations, even when the metacommunities were perturbed.

Eight species grazer metacommunities also had a more consistent degree of spatial heterogeneity of food resources under all conditions (Fig. 10c&d).

Synchrony

The effects of richness, dispersal and disturbance on the synchrony of grazers and epiphytes among patches largely mirrored their effects on metacommunity-wide temporal variability (Figs. 6 and 7, lower panels). Grazer richness tended to increase synchrony of grazers among patches (App. 4-1, Fig. 11a&b) and decrease synchrony of epiphytes (Fig. 11c&d). However, when macroalgae was added to one of the patches, richness increased synchrony of epiphytes among patches (Fig. 11d). Somewhat surprisingly, connecting patches did not significantly affect synchrony of grazers or epiphytes.

Ecosystem respiration

Immediately after we added the macroalgae, species-rich, connected patches were the only disturbed patches that had net positive oxygen production during the day (Fig. 12a). The effects of the macroalgae may have carried over into neighboring patches in diverse, connected metacommunities, as rates of net oxygen production were decreased in those patches (Fig. 12a). Three weeks after we added the macroalgae, all disturbed patches had net oxygen production during the day, but eight-species patches had marginally significantly less (Fig. 12b, Appendix 4-7). Dispersal significantly increased daytime oxygen production within disturbed patches (Fig. 12d, insert).

Sediment organic matter

Although there were no detectable effects of any of the factors on the organic carbon content of the sediments (Fig. 13, 1st row), there was an interactive effect of dispersal and macroalgae on the C:N ratio of the organic matter in the sediments (Fig. 13, 3rd row; Table 1). Dispersal also tended to reduce the spatial variability among patches of the quality of organic matter (Fig. 13, 4th row; Table 1). Metacommunity richness also affected the spatial variability of the C:N ratio, but the effect depended on disturbance (Fig. 13, 2nd row).

DISCUSSION

Diversity, dispersal, and effects of disturbance

The effects of the macroalgal addition were not as straightforward as we intended. In the field, macroalgal blooms often shade the eelgrass sufficiently to prevent growth, whereas eelgrass maintained dramatically higher biomass in disturbed patches in our experiment. We suspect that this difference in *Z. marina* biomass between undisturbed and disturbed patches was probably due to both a lack of senescence in disturbed patches as well as actual growth. *Z. marina* is near the southern end of its range in the Chesapeake Bay, and July and August 2005 had record breaking water temperatures accompanied by an unprecedented disappearance of eelgrass beds in September. We suggest that shading by the macroalgae reduced water temperatures in the mesocosms and prevented *Z. marina* senescence. Unfortunately, we only have anecdotal temperature data for mesocosms-when measuring dissolved oxygen, we noted that temperature was consistently lower underneath the macroalgal canopies in disturbed patches. An additional possible explanation for the higher eelgrass biomass is that the macroalgae provided additional food sources for the grazers both directly and indirectly by creating more substrate for epiphyte growth, preventing reduction of eelgrass biomass through overgrazing.

Either way, the macroalgae still lowered oxygen levels at night, and hypoxia stress was observed at night (most grazers were at the water surface, climbing out of the water and up onto the sides of the mesocosms). This stress is probably what reduced the number of grazers (Figs. 2&3), as intended. However, the remaining grazers in the species poor metacommunities were better able to take advantage of the macroalgal food source, and grew larger (Appendix 3-6). This increase in size in disturbed metacommunities may have been achieved by delaying reproduction or by not having to compete with new generations, which may have been more susceptible to low oxygen conditions. While we intended the macroalgae to have a direct negative effect on grazer abundance through increased nighttime hypoxia, effects of real macroalgal blooms, as well as other disturbances, are often equally complex. And, environmental conditions that are detrimental for some species enable other species to thrive. This is one of the underlying premises for the beneficial effects of diversity on resistance and resilience, as well as one of the reasons that periodic disturbances can help maintain diversity.

That said, the macroalgal addition altered the relationships between grazer richness, dispersal, and grazer and epiphyte abundance in three major ways. In disturbed metacommunities: 1) *low richness* metacommunities maintained higher aggregate abundance and biomass immediately after and throughout the remainder of the experiment; 2) dispersal *increased*, rather than decreased, grazer abundance; 3) patterns of temporal and spatial variability with respect to richness and dispersal differed from those in undisturbed metacommunities.

First, the low richness metacommunities actually had greater resistance to the macroalgal addition: species-poor grazer communities maintained higher aggregate abundance immediately after we added the macroalgae (Fig. 3, Table 2) and ultimately attained higher aggregate abundance and biomass (Fig. 2, Table 2) than species-rich grazer communities. Furthermore, differences between grazer abundance and biomass in undisturbed and disturbed patches were greater for species-rich patches (Fig. 2, Table 2). Diverse, disturbed metacommunities also had greater among-patch differences in sediment organic matter and the quality of organic matter in the sediments, suggesting that diverse communities of grazers did not manage to ameliorate the effects of the algal addition (Fig. 13). Day rates of net oxygen production, which were low or even negative in diverse patches, also suggest that diverse grazer assemblages were less capable of cleaning the macroalgae, causing it to decay, consuming oxygen (Fig. 12). This seems the most plausible explanation for lower rates of net oxygen production in those disturbed patches, as algal biomass was not lower (Figs. 4 and 5), grazer biomass was certainly not higher (Fig. 2), and biomass of other invertebrates (mainly *Nereis diversicolor* and *Molgula manhattensis*) was not higher (Appendix 3-5).

The three species metacommunities probably had greater resistance than the eight species metacommunities because they contained higher abundances of *G. mucronatus*, which was present in both species pools. Virtually all of the recovery of the grazer community and associated ecosystem properties can be attributed to *G. mucronatus*, which dominated disturbed patches and whose net population growth was increased by the addition of macroalgae (data not shown). *G. mucronatus* is a cosmopolitan species, with a wide salinity tolerance and remarkable hypoxia tolerance (Bousfield 1973, Sagasti 2000). As an example of these tolerances, we often find *G. mucronatus* in tiny pools of rainwater within our emptied mesocosms after they have sat outdoors over the winter (sometimes for over six months). Perhaps because of this robustness, *G. mucronatus* is a consistent and often dominant member of the dynamic grazer assemblages in the lower Chesapeake Bay throughout the year (Marsh 1970, Duffy et al. unpublished data). In another experiment, we recently observed that monocultures of *G. mucronatus* outperformed mixtures of three and five species subjected to both bottom-up (nutrient addition) and top-down (predator presence) press perturbations (Duffy et al. unpulbished data). So, we did observe response diversity, or variation in how species responded to the addition of macroalgae, which has previously explained a positive relationship between diversity and resistance to or recovery from a disturbance (Chapin III et al. 1997, Norberg et al. 2001, Elmqvist et al. 2003). In our experiment, though, both pools contained the species best equipped to resist hypoxic stress and take advantage of the additional food source. Our results highlight the importance of predicting realistic species loss patterns and examining their consequences (Srivastava 2002, Ives and Cardinale 2004, Solan et al. 2004, Zavaleta and Hulvey 2004, Larsen et al. 2005, Srivastava and Vellend 2005, Gross and Cardinale 2006).

A few other studies have demonstrated that species-poor communities can resist disturbance as well as, if not better than, species-rich communities. Species-poor communities can maintain higher biomass in response to drought or thermal stress, even though, under normal conditions, diversity leads to increased production (Pfisterer and Schmid 2002, Allison 2004), and some species-poor plant communities may also recover more quickly or extensively post-drought (Lepš et al. 1982). Other studies have found no differences between low and high diversity communities in response to disturbance (Petchey et al. 1999), even when diversity increased general stability (Caldeira et al. 2005, Dang et al. 2005). Dominant species can sometimes maintain ecosystem function when other species are lost from communities (Smith and Knapp 2003). Likewise, a few other studies have also showed that diversity can decrease general stability (Petchey et al.

2002, Gonzalez and Descamps-Julien 2004, France and Duffy 2006b). Theoretical studies have pointed out that a positive relationship between diversity and stability can depend on species having different responses, rather than highly correlated responses, to environmental fluctuations (Ives et al. 2000, Ives and Hughes 2002). Although the crustacean grazer species we used exhibit clear differences in their response to seasonal temperature and light fluctuations (Duffy et al. unpublished data), they probably respond similarly to epiphyte fluctuations and anoxia. Our estuarine organisms may actually be selected for tolerances of a wide range of environmental conditions, as estuaries are notoriously dynamic. Indeed, current seagrass epifaunal communities may have been recently selected for even wider tolerances, as loss of habitat through seagrass wasting disease, several hurricanes, and rising water temperatures have been accompanied by shifts in the grazer community within just the last several decades (Marsh 1970, Parker 1998, Orth 2007, Duffy et al. unpublished data). In other systems, where perturbations are less of a community structuring and selective force, diversity could still increase both the magnitude and the stability of ecosystem services.

The second major difference in disturbed patches is that grazer abundance was higher and more stable when the disturbed patches could be re-colonized by grazers from species-rich neighboring patches. After macroalgae were added, colonization clearly played a role in stabilizing grazer populations within those patches, as connected disturbed patches had higher grazer numbers than unconnected disturbed patches throughout the post-disturbance time period (Fig. 3, right panels). So, while dispersal has reduced grazer populations under normal conditions (France and Duffy 2006b), it increased grazer populations under disturbed conditions. The importance of dispersal for "rescuing" populations within patches where they are poorly performing has been long-recognized in metapopulation ecology (Brown and Kodric-Brown 1977, Gotelli 1991, Hanski 1991). While such rescue effects are often studied in model or empirical systems with relatively fixed spatial variability of patch quality, rescue effects could also certainly be important in facilitating amelioration of and recovery from a disturbance (Gyllenberg and Hanski 1997, Johst et al. 2002). Here, we demonstrate the importance of dispersal for mediating response to a spatially discrete disturbance within a multi-trophic metacommunity. Somewhat similarly, others have demonstrated that the effect of dispersal on metacommunity diversity can depend on disturbance, where dispersal reduces richness in the absence of disturbance but increases richness when the metacommunity is disturbed (Östman et al. 2006). As others have recognized, given the frequency of spatially discrete disturbances within ecosystems, connectivity is an important aspect of conservation designs targeting ecosystem services as well as diversity.

Third, there were also several cases of a factor having opposite effects on variability under normal and disturbed conditions. **1)** Dispersal tended to decrease stability of grazers in patches under normal conditions but increased resistance and stability in disturbed patches. **2)** Increasing grazer richness stabilized epiphyte biomass through time except under disturbed conditions. **3)** Changing grazer richness had opposite effects on synchrony of grazers and epiphytes in undisturbed and disturbed metacommunities. **4)** Increasing grazer richness increased spatial variability of epiphyte biomass except under disturbed conditions.

The first two differences highlight the fact that temporal variability of a system is not necessarily an indicator of its resistance or resilience. Dispersal amplified temporal variability under normal conditions, yet decreased variability in patches subjected to the macroalgal bloom by facilitating resistance and/or a quick recovery of grazer populations (Figs. 2, 3, Table 2). And even though species-rich grazer communities stabilized their food resources under normal conditions, they failed to do so when one patch was disturbed with a macroalgal bloom that shaded the epiphytes (Fig. 7). Other studies have also found a disconnect between general stability and resistance to disturbance. For instance, in modeling studies, increasing species richness decreased variance of community biomass under normal conditions, but did not stabilize it in response to perturbation (Hughes and Roughgarden 2000). As mentioned above, Caldeira et al. (2005) also found that grassland diversity had no effect on responses to disturbance, despite increasing general stability. Of course, temporal variability is still an important characteristic of communities, and a valid indicator of stability. Systems with high variability of species abundances are more likely to have extinctions, and may be more likely to exceed thresholds and switch to alternate stable states. However, our experiment demonstrates that, in spatially heterogeneous habitats, temporal variability of abundance in patches may not translate to other scales or to ecosystem functions.

The third and fourth differences, opposing effects of grazer richness on synchrony and spatial variability in undisturbed and disturbed communities, can be largely explained by the comparatively poor performance of eight-species grazer metacommunities in response to the macroalgal bloom. Grazer populations declined in the disturbed patch, and when they could, fled to the undisturbed patches, dramatically decreasing synchrony among patches. Epiphyte dynamics were *more* synchronized within diverse, disturbed metacommunities for the same reason: macroalgae reduced epiphytes in the disturbed patch through shading, while grazer populations in undisturbed patches, inflated by refugees, also reduced epiphytes to lower levels.

Finally, we think it is interesting that diverse, connected metacommunities had the most consistent degree of spatial variability of both grazers and epiphytes, even when disturbed. We also observed this in a previous experiment with five patches per metacommunity (France & Duffy, unpublished data, Chapter III). The consistency of spatial variability through time was not due to low levels of spatial variability -- diverse grazer communities tended to increase spatial variability of most ecosystem properties. It seems that diverse grazer communities resisted homogenization and synchronization sufficiently to maintain different epiphyte time courses within different patches: epiphyte patterns in diverse metacommunities were less synchronized even in connected metacommunities, with widely divergent epiphyte loads for all sampling dates (Fig.11, Appendix 3-3). Since synchronization can de-stabilize populations, and therefore perhaps ecosystem functions, resistance to synchronization could be important for stabilizing ecosystem function in metacommunities. It will be interesting to explore whether diversity can indeed prevent synchronization in other situations and systems.

It is important to note that neither grazer richness nor dispersal were strongly stabilizing under any conditions, disturbed or undisturbed, in these experimental metacommunities. There are many possible explanations for why grazer richness did not stabilize abundance under normal conditions, as it has in previous experiments in other systems (Tilman 1996, McGrady-Steed et al. 1997, McGrady-Steed and Morin 2000, Valone and Hoffman 2003, Morin and McGrady-Steed 2004, Steiner et al. 2005). First, the mathematical neutral expectation that diversity will reduce variability of aggregate biomass depends on the assumption that species interactions have no effects on biomass (Doak et al. 1998). Clearly, in our system, species interactions and behavior matter. Second, we used fairly generalist mobile consumers, and recent theory suggests that diverse communities of generalist grazers could reduce stability of biomass (Thébault and Loreau 2003, 2005, 2006). In those studies, consumer diversity usually increased variability of producers as well, which we did not observe. Perhaps the complexity added by having a dynamic resource community caused that difference. Finally, an important difference between most models and our experiment is that our metacommunities were certainly not at equilibrium. Although our grazers reached carrying capacity and continued to experience births and deaths, the community was unlikely to reach equilibrium either in the experiment or in nature because seasonal change in this system is fast relative to demographic processes of most species. Furthermore, seagrass patches themselves are dynamic over these time scales due to disturbance by storms and foraging by large predators (i.e. rays) (Hovel and Lipcius 2002). Even if the effects of richness and dispersal on temporal and spatial variability that we observed were due to transient dynamics and community assembly processes, we think that they are important to consider. Transient dynamics and community assembly processes are important even in equilibrial metacommunities (Fukami and Morin 2003, Fukami 2004), and are likely to be increasingly important in community responses to disturbances in today's rapidly changing ecosystems. Nevertheless, a lack of equilibrium, or the short experimental duration relative to the time needed for a wide range of experimental conditions which might favor different species, might explain the differences between our results and others.

Comparison to Chapter II

Somewhat surprisingly, patterns in undisturbed metacommunities in this experiment differed from those in metacommunities in the experiment described in Chapters II and III (which were all undisturbed). In both experiments, grazer richness increased grazer abundance, biomass, and population growth, while dispersal reduced both slightly (Fig. 2, left side; population growth not shown). These patterns were significant and marked in the Chapter II experiment, but much less significant and noticeable in this disturbance experiment. Still, we expected that the higher grazer abundance in richer grazer treatments would correspondingly decrease biomass of epiphytes, the grazers' main food resource, as it has in other experiments with these grazers (Duffy et al. 2001, Duffy et al. 2003, Duffy et al. 2005, France and Duffy 2006b (Chapter II)). However, in this experiment, grazer richness did not decrease epiphyte biomass (Fig. 5, Table 1), and in fact, significantly increased algal growth on the walls of the mesocosms (Fig 4, 4th row), the biomass of microalgal mats (Fig. 4, 2nd row), and the biomass and abundance of *Molgula manhattensis,* a solitary tunicate (data not shown), all of which were reduced by grazer richness in other experiments (Duffy et al. 2001, Duffy et al. 2003, Duffy et al. 2005, France and Duffy 2006b). While we have often observed that grazer richness increases epiphyte biomass during the early days of an experiment, since some species have lower population growth rates, we have always found that diverse grazer communities more effectively reduce algal biomass by the end of the experiment.

We suspect that these differences between experiments are due to different "trajectories" of species loss among experiments. While previous experiments have used monocultures or quasi-random combinations of species at the low end of the richness gradient, here we eliminated the least common species to create the smaller species pool. Consequently, both the amphipods *Gammarus mucronatus* and *Cymadusa compta* were present in the small species pool, a combination which we have not used before. Both species are competitive dominants (France and Duffy 2006a, Chapter III, in prep.). *G. mucronatus* is one of the most abundant species in the field throughout most of the year, and *C. compta* is found in high abundances in the late summer months in the lower Chesapeake Bay (Duffy et al. unpublished data). In this experiment, the net population growth of these two species was an order of magnitude greater than for any of the other six species (data not shown). Although richness effects in some previous experiments could not be attributed to any one species or even a combination of species, these two species were previously combined only in high richness treatments. They may have driven relationships between richness and micro- and macro- algal biomass in those experiments. Alternatively, the record-breaking water temperatures in July and August could have favored the population growth of *C. compta* more than usual; *C. compta* is most abundant in seagrass beds in the lower Chesapeake Bay during July and August, the hottest months of the year (Duffy et al. unpublished data).

Summary

Although BD-stability reviews have carefully distinguished between different kinds of stability (Cottingham et al. 2001, McCann 2000), opposing effects of diversity on those different kinds of stability have perhaps been underemphasized. Here, we demonstrate that increasing grazer species richness did decrease both general stability and resistance to a macroalgal addition. However, dispersal decreased the general stability of both grazers and epiphytes, but increased resistance to and recovery from the macroalgal addition. Dispersal increased grazer abundance in patches subjected to the macroalgal addition, marginally improved the performance of eelgrass in those patches, and stabilized grazer abundance in those disturbed metacommunities. Grazer richness also had subtle benefits under disturbed conditions, despite its tendencies to decrease stability: species-rich, connected metacommunities had the lowest temporal variability of grazer abundance throughout the experiment. Species-rich, connected metacommunities also had the most consistent degree of spatial heterogeneity of both grazer abundance and epiphyte biomass. Overall, our results emphasize the importance of incorporating both spatial processes and trophic interactions into the study of biodiversity-stability relationships. While species-rich, connected communities may sometimes offer the greatest resistance to perturbations, tendencies for both grazer richness and dispersal to amplify temporal fluctuations of ecosystem services could increase the likelihood of state changes. Influences of diversity and spatial dynamics on both aspects of stability need to be considered in order to effectively manage and conserve ecosystems and the services they provide.

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TABLES

Table 1. Main and interactive effects of metacommunity richness, dispersal and disturbance on the magnitude and variability of ecosystem properties. Significant ($p < 0.05$) values are [illegible] and highlighted in red. Marginally significant ($0.05 < p < 0.10$) effects are in *italics* and highlighted in yellow. Data were analyzed using a fully-crossed 3-way GLM with all factors fixed. MS are Type III.

			Metacommunity Richness		Dispersal		Disturbance		Richness * Dispersal		Richness * Disturbance		Dispersal * Disturbance		Richness * Dispersal * Disturbance	
Response Variable	**Model d.o.f., Error d.o.f.**	**R2**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**
Patch (subsampled 1 patch from each metacommunity)																
Grazer S-W diversity	7, 32	.548	.350	[illegible]	.013	.4118	.098	[illegible]	.010	.4604	.019	.3166	.092	[illegible]	.043	.1355
Grazer abundance (FINAL)	7, 31	.123	1974	.9040	19582	.7045	811817	[illegible]	277963	.1593	22362	.6853	84796	.4318	6880	.8220
Grazer biomass	7, 33	.167	7706	.7442	11396	.6916	93844	.2591	20173	.5980	108933	.2248	237607	*.0767*	53.6	.9783
Grazer resistance (d32-d18)	7, 48	.165	26827	[illegible]	2.92	.9796	3.97	.9763	697	.6937	1466	.5683	2760	.4346	7092	.2130
Epi. chl. *a* (d 16)	7, 48	.343	13.2	[illegible]	0	.9790	5.48	[illegible]	.631	.3991	.103	.7325	.057	.7988	1.21	.2437
Epi. chl. a (d 22)	7, 48	.352	.969	.1157	.814	.1477	4.73	[illegible]	.481	.2636	1.46	[illegible]	.006	.8982	.042	.7412
Epi. chl. a (d 30)	7, 48	.234	.434	.2502	.171	.4682	3.77	[illegible]	.116	.5507	.034	.7459	.012	.8500	.006	.8811
Epi. chl. *a* (d 42)	7, 48	.255	.178	.5238	.333	.3839	5.13	[illegible]	.279	.4250	0	.9792	.027	.8016	.194	.5056
Wall chl. *a*	7, 48	.111	.009	[illegible]	0	.7656	0	.9791	0	.6679	.001	.4626	0	.7428	0	.7947
Microalgal mat biomass (mainly cyanobacteria)	7, 48	.145	.011	[illegible]	0	.9439	0	.5195	0	.6008	0	.7560	.004	.1784	.003	.2605
Change in *Z. marina* biomass	7, 48	.301	5.42	.2571	.085	.8864	. 68.9	[illegible]	.679	.6868	3.11	.3887	.809	.6598	2.80	.4140
Sediment C:N	7, 22	.362	.001	.9728	.362	.5851	1.35	.297	0	.9924	2.47	.1634	7.27	[illegible]	2.79	.1393
Temporal CV of grazer abundance- all sampling points	7, 32	.188	.015	.7067	.003	.8588	.413	.7636	.003	.8736	.228	*.0502*	.037	.5514	.002	.8775
Temporal CV of epi. chl *a*- all sampling points	7, 48	.308	.267	*.0958*	.001	.9121	1.10	[illegible]	.013	.7079	.329	*.0656*	.004	.8412	.067	.3995
Metacommunity																
Grazer S-W diversity	7,33	.507	.602	[illegible]	.012	.4728	.019	.3725	0.0000	.9641	.093	*.0520*	.001	.8051	.064	.1048
Grazer abundance beta-diversity	7,33	.447	.080	[illegible]	.0008	.6312	.005	.2402	.0004	.7181	.007	.1541	.0005	.6913	0.000	.9467
Final grazer abundance (d 45)	7,33	.224	86346	.6578	5809	.9084	1762710	*.0516*	179162	.5241	522781	.2793	149614	*.0717*	2598	.9387
Final grazer biomass (d 45)	7, 33	.135	21862	.8034	411371	.2842	42090	.7299	1917	.9412	232094	.4194	758880	.1487	296086	.3624
Avg spatial CV of grazer abund	7,48	.268	.117	[illegible]	.039	.2185	.146	[illegible]	.003	.7300	.045	.1865	.026	.3079	.004	.7075
Temporal CV of spatial CV of grazer abundance	7,48	.253	.004	.8388	.285	*.0749*	.001	.9109	.852	[illegible]	.008	.7587	.263	*.0864*	0	.9428
Epiphytic chlorophyll a (d 42)	7, 48	.482	.218	.5456	1.96	*.0743*	15.9	[illegible]	2.76	[illegible]	.443	.3897	1.39	.1307	.122	.6503
Spatial CV of sediment C:N	7, 22	.455	.0007	.6566	.0165	[illegible]	.0009	.6016	.009	.1103	.013	*.0596*	.007	.1661	.013	*.0631*
Spatial CV of epi chl *a* (d 42)	7, 48	.655	.049	.2135*	0	.8703	2.38	[illegible]	0	.9470*	.124	*.0515*	.002	.8064	.071	.1377
Avg spatial CV of epi. chl. *a*	7, 48	.586	.037	*.0818*	.002	.6486	.540	[illegible]	.009	.3956	.011	.3288	0	.9964	.101	[illegible]
Temporal CV of spatial CV of epi chl a	7, 48	.409	.622	[illegible]	.006	.7438	.782	[illegible]	0	.9722	.274	[illegible]	.011	.6561	.009	.6937
Temporal CV of grazer abund.- including before disturbance	7, 47	.257	.168	*.0829*	.020	.5475	.054	.3187	.116	.1472	.009	.6829	.282	[illegible]	.060	.2930
Temporal CV of epi. chl. *a* – including before disturbance	7, 48	.149	.036	.1972	.005	.6305	.002	.7425*	0	.9514	.021	.3247*	.002	.7814	.003	.7259
Synchrony of epiphytic chl *a*	7, 48	.153	.046	.7282	.616	.2069	.307	.3711	.123	.5700	1.72	[illegible]	.179	.4942	.522	.2448

Table 2. Effects of richness and dispersal on patches that were actually disturbed by the macroalgal addition. Significant ($p<0.05$) effects are **bolded**. Marginally significant effects are *italicized*. Data were analyzed using a fully-crossed two-way GLM with both factors fixed. MS are Type III.

			Metacommunity Richness		Dispersal		Richness * Dispersal	
Response Variable	**Model df, Error df**	**R2**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**
Patch Type III sum of squares								
Grazer abundance (wk 3)	3, 8	.196	631	.6129	2160	.3586	1656	.4185
Grazer abundance (wk 5)	3, 14	.366	1384	.2760	7093	**.0224**	26.7	.8772
Grazer abundance (wk 6)	3, 8	.481	24842	**.0268**	243	.7957	65.3	.893
Grazer abundance (FINAL)	3, 15	.167	76590	.4334	248454	.1676	28648	.6296
Grazer biomass	3, 15	.257	505259	*.0507*	20016	.6880	100381	.3738
Grazer resistance (wk 5- wk 2)	3, 14	.307	1253	.4385	8184	*.0609*	1083	.4707
Temporal CV of grazer abundance	3, 15	.119	.016	.6910	.012	.2464	.024	.5971

FIGURE LEGENDS

Figure 1. Final diversity patterns. **1st row, from left to right:** Patch species richness within **a)** undisturbed patches, **b)** undisturbed patches in disturbed metacommunities, and **c)** disturbed patches. Light grey = no dispersal corridors to the patch; dark grey = dispersal corridor to the patch. Unmarked bars are undisturbed patches, coarsely-hatched bars are undisturbed patches in disturbed metacommunities, and finely-hatched bars are disturbed patches. **2nd row:** Patch Shannon-Weaver diversity (S-W) of grazers, panels **d-f** as in 1st row. **3rd row:** Beta-diversity, or dissimilarity of species composition among patches, estimated using relative abundance of all species. Light grey = no dispersal corridors among patches within the metacommunity; dark grey = dispersal corridors among patches within the metacommunity. **g)** Unmarked bars are undisturbed metacommunities and **h)** coarsely-hatched bars are disturbed metacommunities. **4th row:** Beta-diversity estimated using solely presence-absence of all species within the metacommunity for **i)** undisturbed and **j)** disturbed metacommunities. Significant effects are shown to the right: R=richness, Dp=dispersal, Db=disturbance; † $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$, **** $p<0.0001$. Error bars are standard error (S.E.).

Figure 2. Final grazer abundance. **1st row, from left to right: a)** Grazer abundance within undisturbed patches, **b)** undisturbed patches in disturbed metacommunities, and **c)** disturbed patches. **2nd row, from left to right: d)** Grazer biomass (estimated) within undisturbed patches, **e)** undisturbed patches in disturbed metacommunities, and **f)** disturbed patches. **3rd row, from left to right:** Grazer abundance within **g)** undisturbed and **h)** disturbed metacommunities. **4th row, from left to right:** Grazer biomass (estimated) within **i)** undisturbed and **j)** disturbed metacommunities. Bars as described in Figure 1. Significant effects are shown to the right, as in Figure 1. Error bars are S.E..

Figure 3. Time course of grazer abundance. Panels, from left to right: undisturbed patches in undisturbed metacommunities; undisturbed patches in disturbed metacommunities; disturbed patches. Circles = 3 spp. pool; triangles = 8 spp. pool; open symbols = no dispersal; closed symbols = dispersal. Dashed line indicates when macroalgae were added to the disturbed patches. Error bars are S.E..

Figure 4. Effects on primary producers. Bar colors and shading as described in Figure 1. Significant effects shown on the right, as in Figure 1. All error bars are S.E. **1st row, from left to right:** Change in *Z. marina* biomass over the course of the experiment in undisturbed patches, undisturbed patches in disturbed metacommunities, and disturbed patches. **2nd row:** Inedible algae (blue-green mats and unidentified cohesive algal mats). **3rd row:** Epiphytic chlorophyll a, final week of the experiment. **4th row:** Final epiphyte biomass on mesocosm walls. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 5. Time course of epiphyte biomass, as estimated by mcg chlorophyll *a* per cm^2 leaf. Panels, from left to right: undisturbed patches in undisturbed metacommunities; undisturbed patches in disturbed metacommunities; disturbed patches. Circles = 3 spp. pool; triangles = 8 spp. pool; open symbols = no dispersal; closed symbols = dispersal. Red line indicates when macroalgae were added to the disturbed patches. Error bars are S.E.. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 6. Temporal variability of grazer abundance (coefficient of variation) within **(a-c)** patches (top row) and **(d-e)** metacommunities (bottom row). Panels as described above. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 7. Temporal variability of epiphyte biomass (coefficient of variation) within **(a-c)** patches (top row) and **(d-e)** metacommunities (bottom row). Panels as described above. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 8. Spatial variability (coefficient of variation) of **grazer abundance (top row)** and **epiphyte biomass (bottom row)** through time. Circles = metacommunities assembled from 3 spp. grazer pool; triangles = 8 spp. pool; open symbols = no dispersal; closed symbols = dispersal. Red line indicates when macroalgae were added to the disturbed patches. Statistics as described in Figure 1. Error bars are S.E..

Figure 9. Average spatial variability of **epiphytes on eelgrass (top row)** and **mesocosm walls (bottom row)**. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 10. Temporal variability of spatial heterogeneity of **(a,b)** grazers and **(c,d)** epiphytes in undisturbed and disturbed metacommunities. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 11. Synchrony of **(a,b)** grazer abundance and **(c,d)** epiphyte biomass among patches within a metacommunity. Synchrony is estimated as the sum of the covariances for each of the three possible pairs of patches within a metacommunity. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 12. Rates of **(a,b)** daytime oxygen production and **(c,d)** nighttime oxygen consumption within patches one week and three weeks after the addition of macroalgae. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 13. Sediment organic matter. **1st row, from left to right:** % total organic carbon in the sediments in undisturbed patches in undisturbed metacommunities, undisturbed patches in disturbed metacommunities, and actually disturbed patches. **2nd row:** Spatial heterogeneity (coefficient of variation) of sediment % organic carbon. **3rd row:** Approximate C:N ratio of sediment organic matter. Panels as in 1st row. **4th row:** Variation among patches in the quality of organic matter in the sediments. Bars and statistics as described in Figure 1. Error bars are S.E..

Figure 1

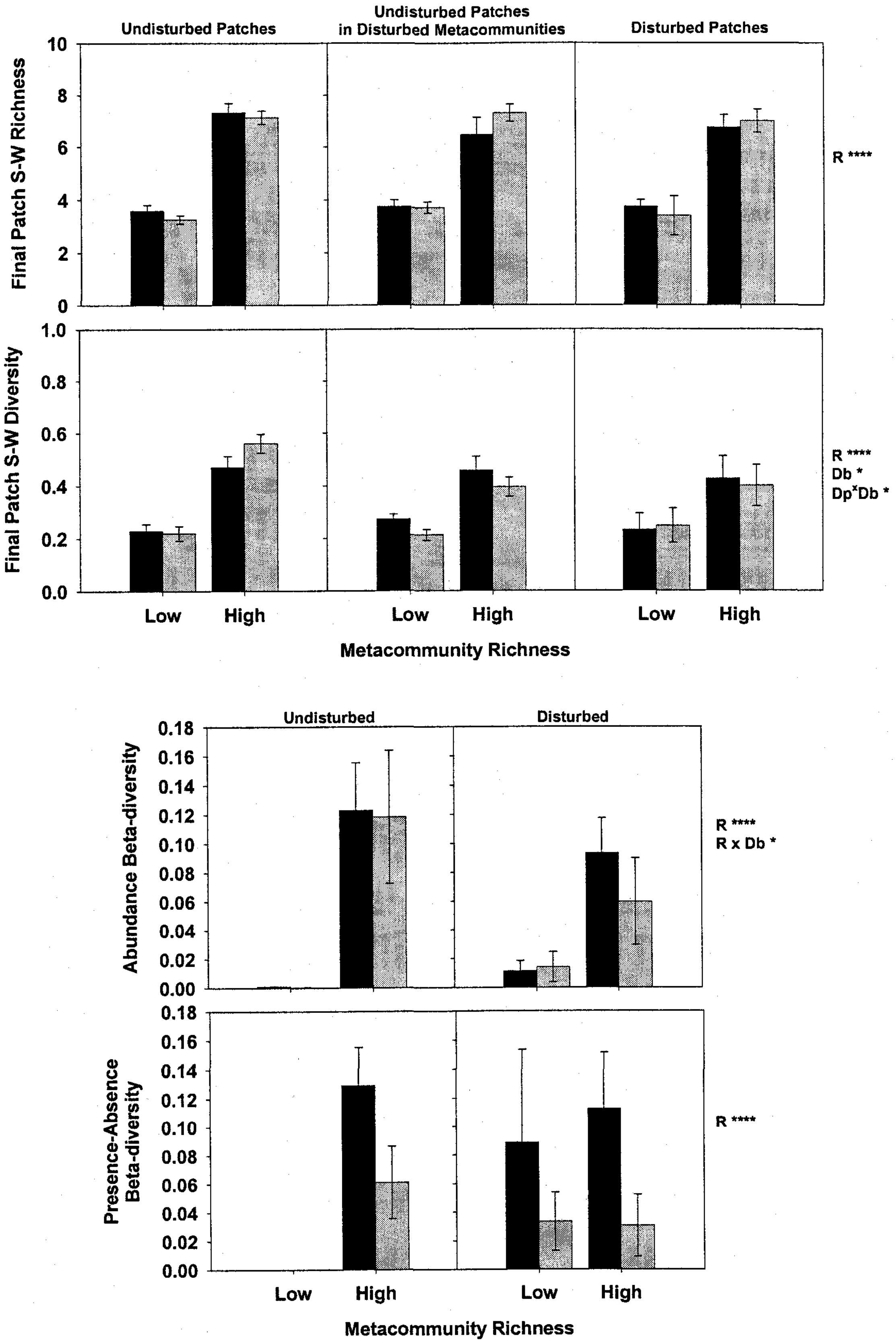

Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
Final Patch S-W Richness
10
8
6
4
2
0
R ****
Final Patch S-W Diversity
1.0
0.8
0.6
0.4
0.2
0.0
R ****
Db *
Dp^xDb *
Low
High
Low
High
Low
High
Metacommunity Richness
Undisturbed
Disturbed
Abundance Beta-diversity
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
R ****
R x Db *
Presence-Absence Beta-diversity
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
R ****
Low
High
Low
High
Metacommunity Richness

Figure 2

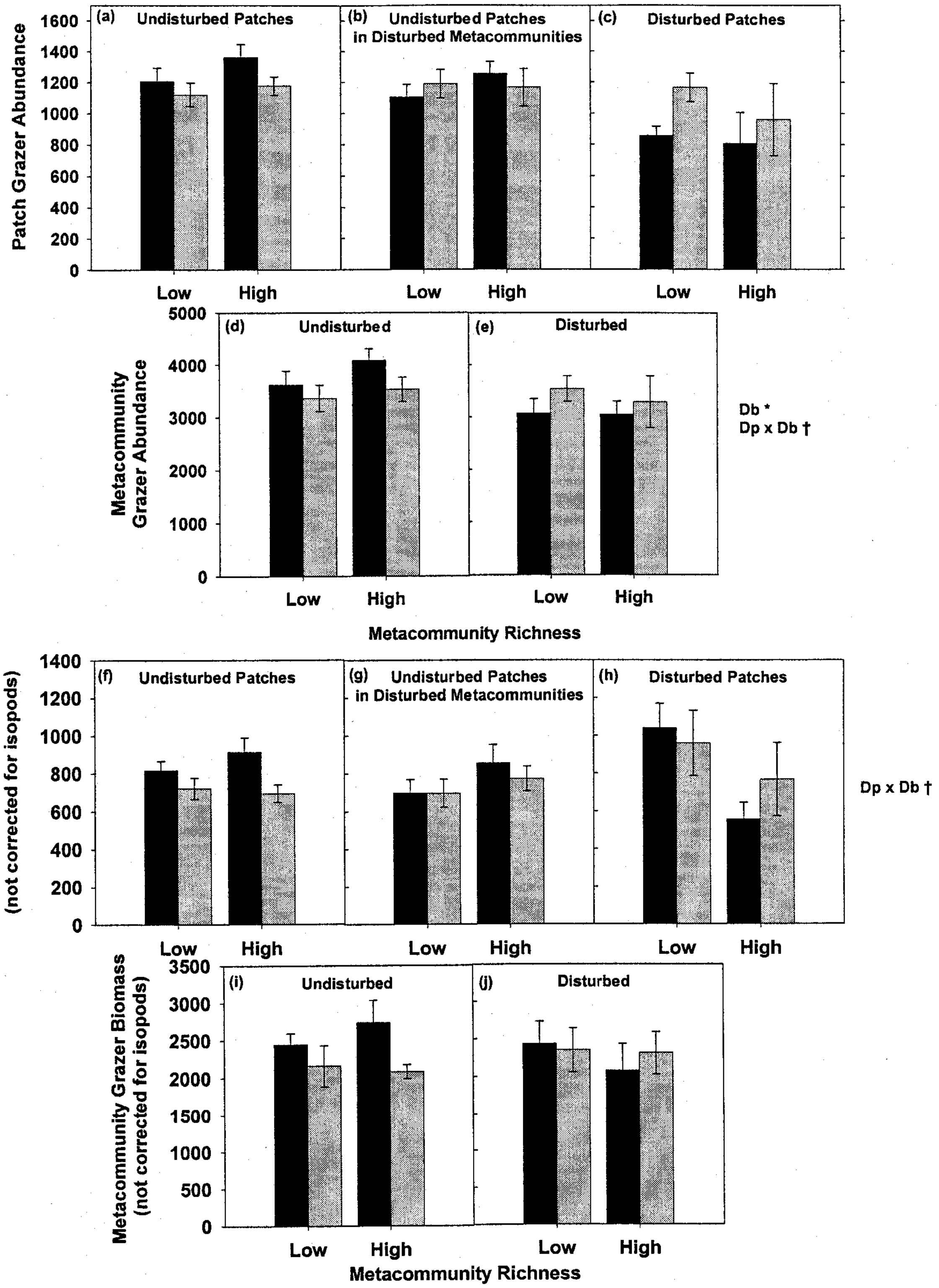

Patch Grazer Abundance
0
200
400
600
800
1000
1200
1400
1600
(a) Undisturbed Patches
(b) Undisturbed Patches in Disturbed Metacommunities
(c) Disturbed Patches
Low
High
Low
High
Low
High
Metacommunity Grazer Abundance
0
1000
2000
3000
4000
5000
(d) Undisturbed
(e) Disturbed
Low
High
Low
High
Db *
Dp x Db †
Metacommunity Richness
Patch Grazer Biomass (not corrected for isopods)
0
200
400
600
800
1000
1200
1400
(f) Undisturbed Patches
(g) Undisturbed Patches in Disturbed Metacommunities
(h) Disturbed Patches
Dp x Db †
Low
High
Low
High
Low
High
Metacommunity Grazer Biomass (not corrected for isopods)
0
500
1000
1500
2000
2500
3000
3500
(i) Undisturbed
(j) Disturbed
Low
High
Low
High
Metacommunity Richness

Figure 3

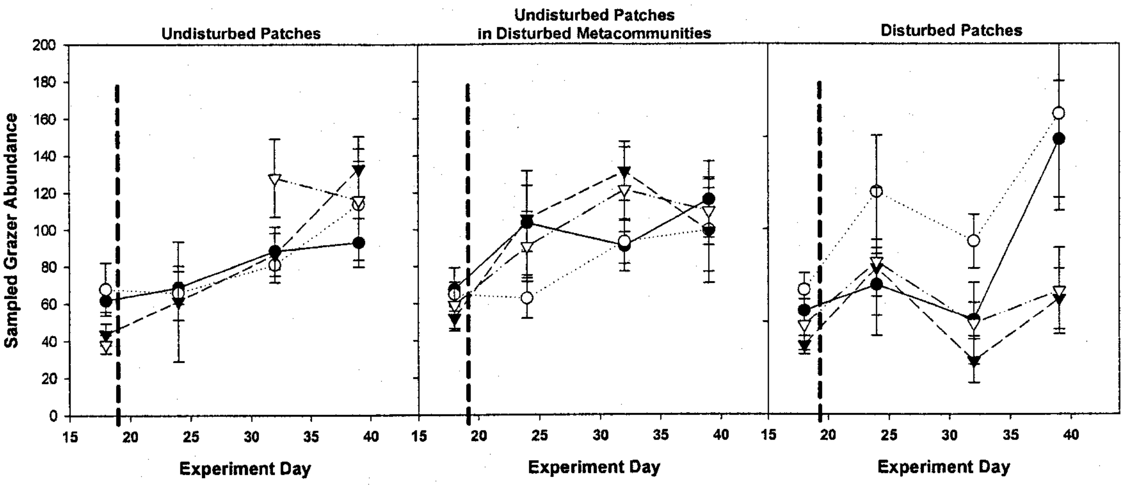

Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
Sampled Grazer Abundance
0
20
40
60
80
100
120
140
160
180
200
15
20
25
30
35
40
Experiment Day

Figure 4

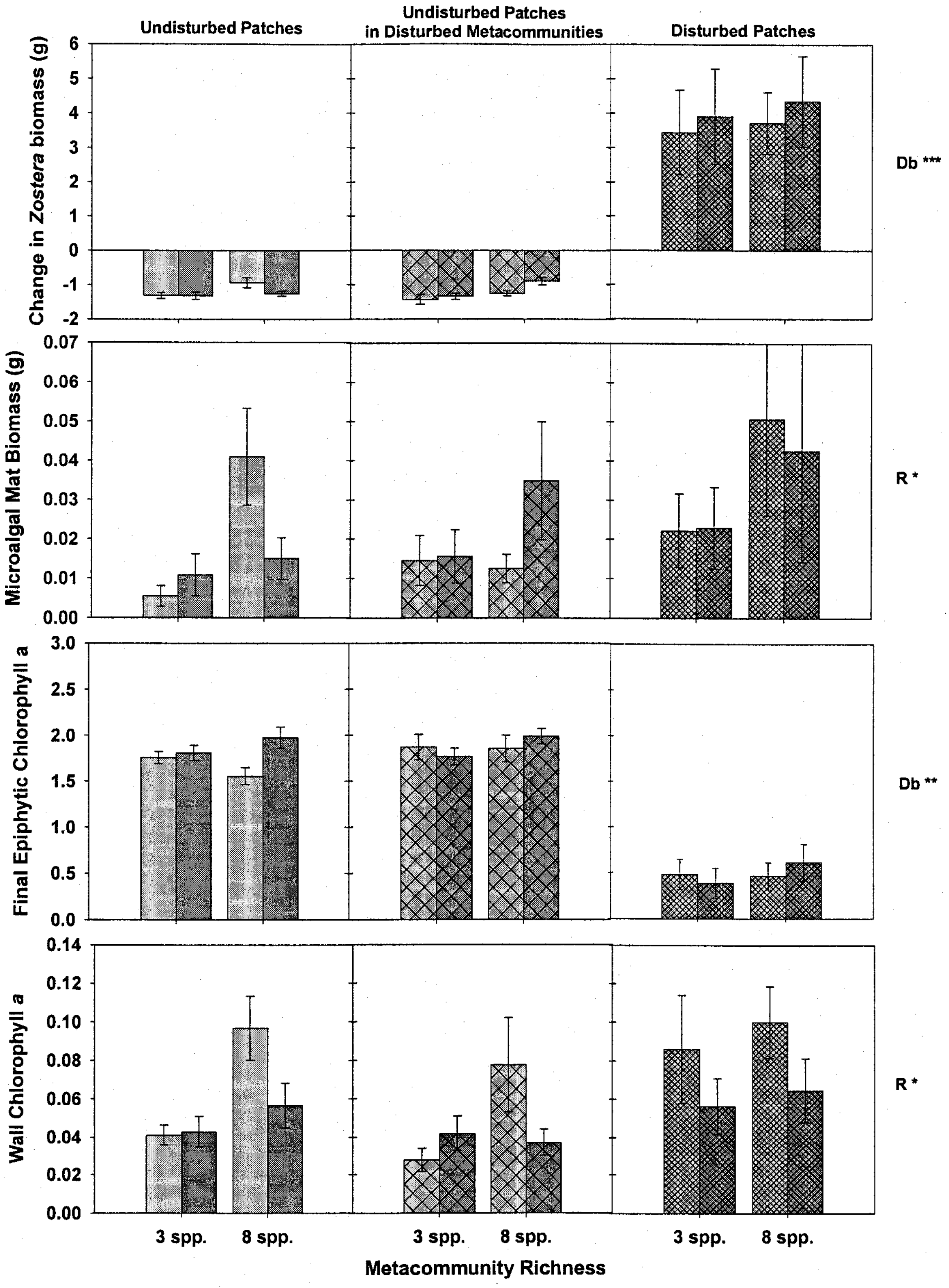
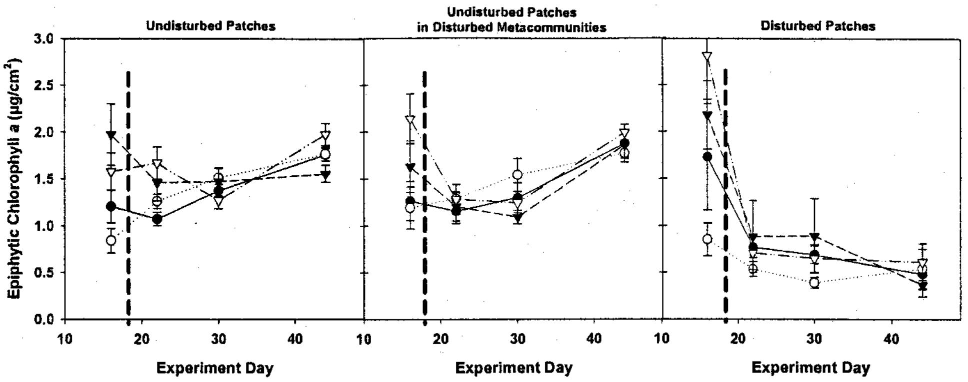
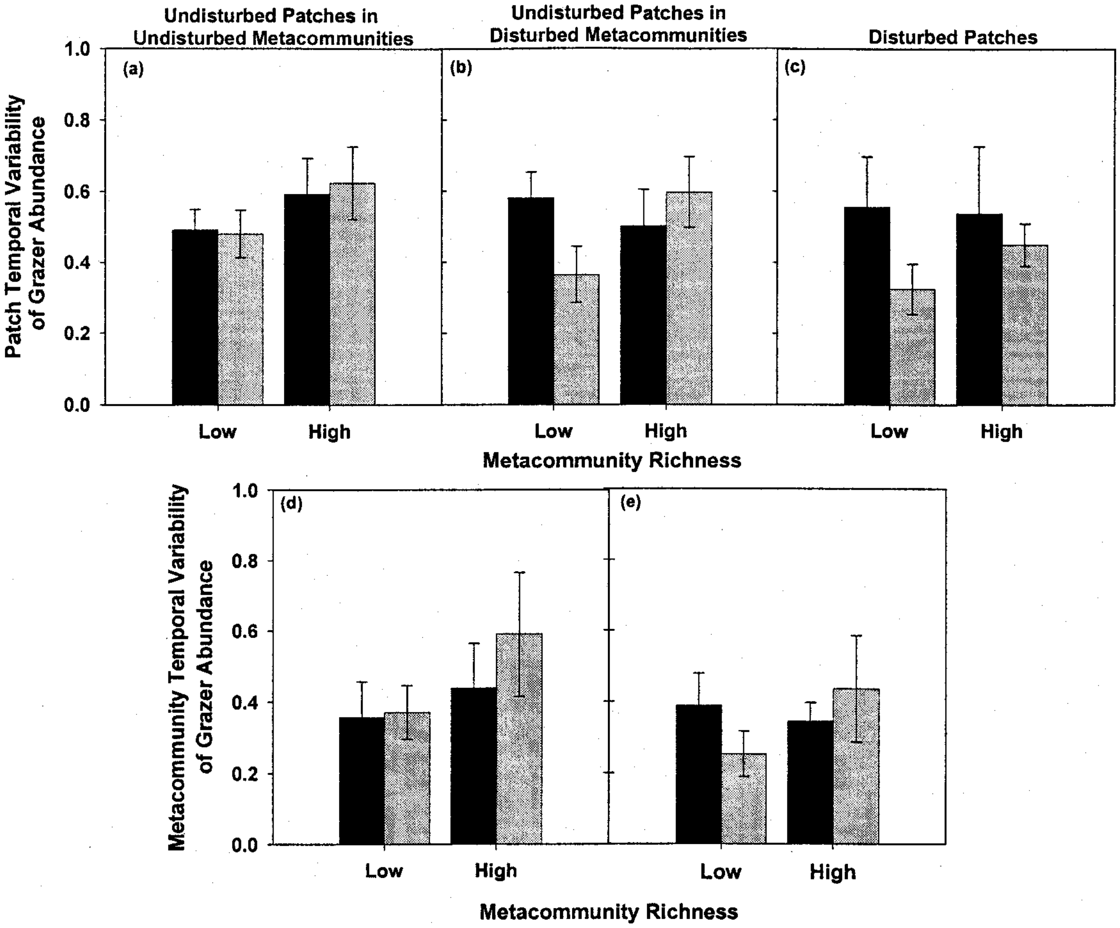

Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
Change in *Zostera* biomass (g)
6
5
4
3
2
1
0
-1
-2
Db ***
Microalgal Mat Biomass (g)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
R *
Final Epiphytic Chlorophyll *a*
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Db **
Wall Chlorophyll *a*
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
R *
3 spp.
8 spp.
3 spp.
8 spp.
3 spp.
8 spp.
Metacommunity Richness

Figure 5



day 16: R ***, Db *
day 22: Db ***, RxDb †
day 30: Db **
day 44: Db **

Figure 6



Undisturbed Patches in Undisturbed Metacommunities
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
(a)
(b)
(c)
Patch Temporal Variability of Grazer Abundance
1.0
0.8
0.6
0.4
0.2
0.0
Low
High
Low
High
Low
High
Metacommunity Richness
(d)
(e)
Metacommunity Temporal Variability of Grazer Abundance
1.0
0.8
0.6
0.4
0.2
0.0
Low
High
Low
High
Metacommunity Richness

Figure 7

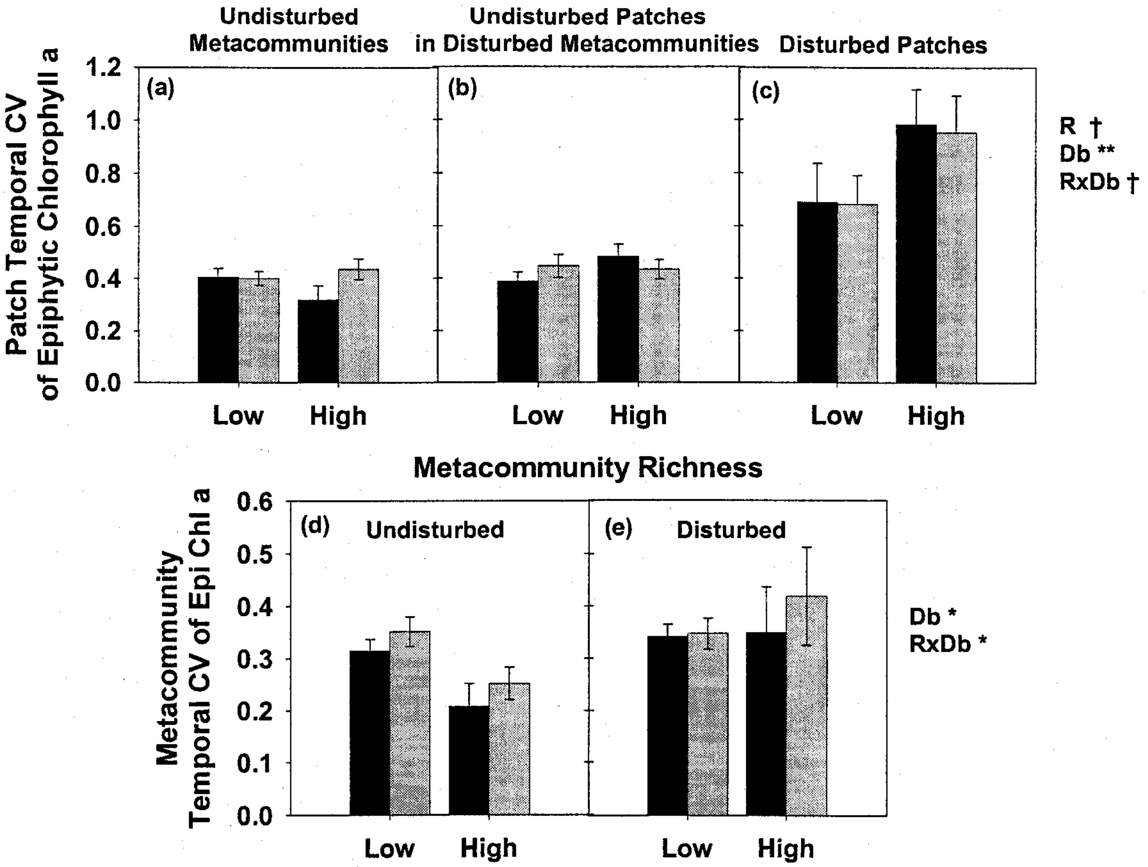
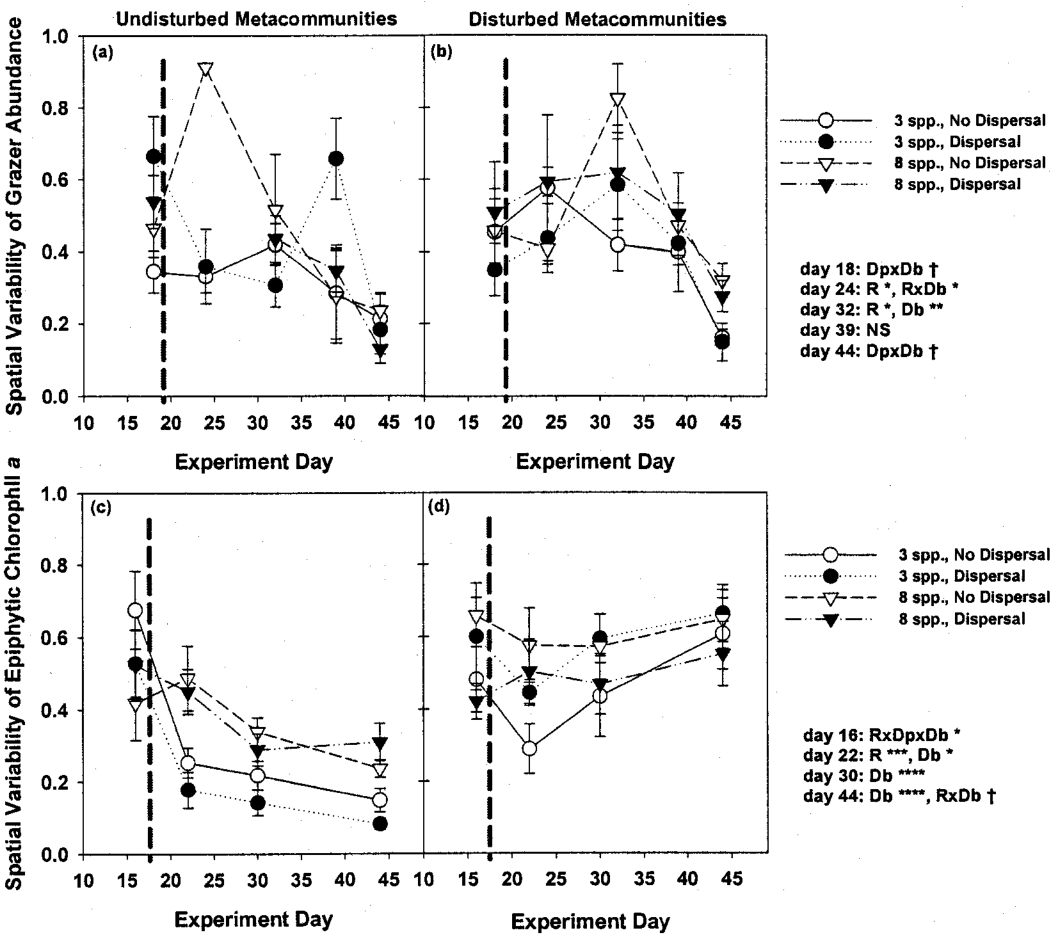

Undisturbed Metacommunities
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
Patch Temporal CV of Epiphytic Chlorophyll a
1.2
1.0
0.8
0.6
0.4
0.2
0.0
(a)
(b)
(c)
Low
High
Low
High
Low
High
R †
Db **
RxDb †
Metacommunity Richness
Metacommunity Temporal CV of Epi Chl a
0.6
0.5
0.4
0.3
0.2
0.1
0.0
(d) Undisturbed
(e) Disturbed
Low
High
Low
High
Db *
RxDb *

Figure 8



day 18: DpxDb †
day 24: R *, RxDb *
day 32: R *, Db **
day 39: NS
day 44: DpxDb †

day 16: RxDpxDb *
day 22: R ***, Db *
day 30: Db ****
day 44: Db ****, RxDb †

Figure 9

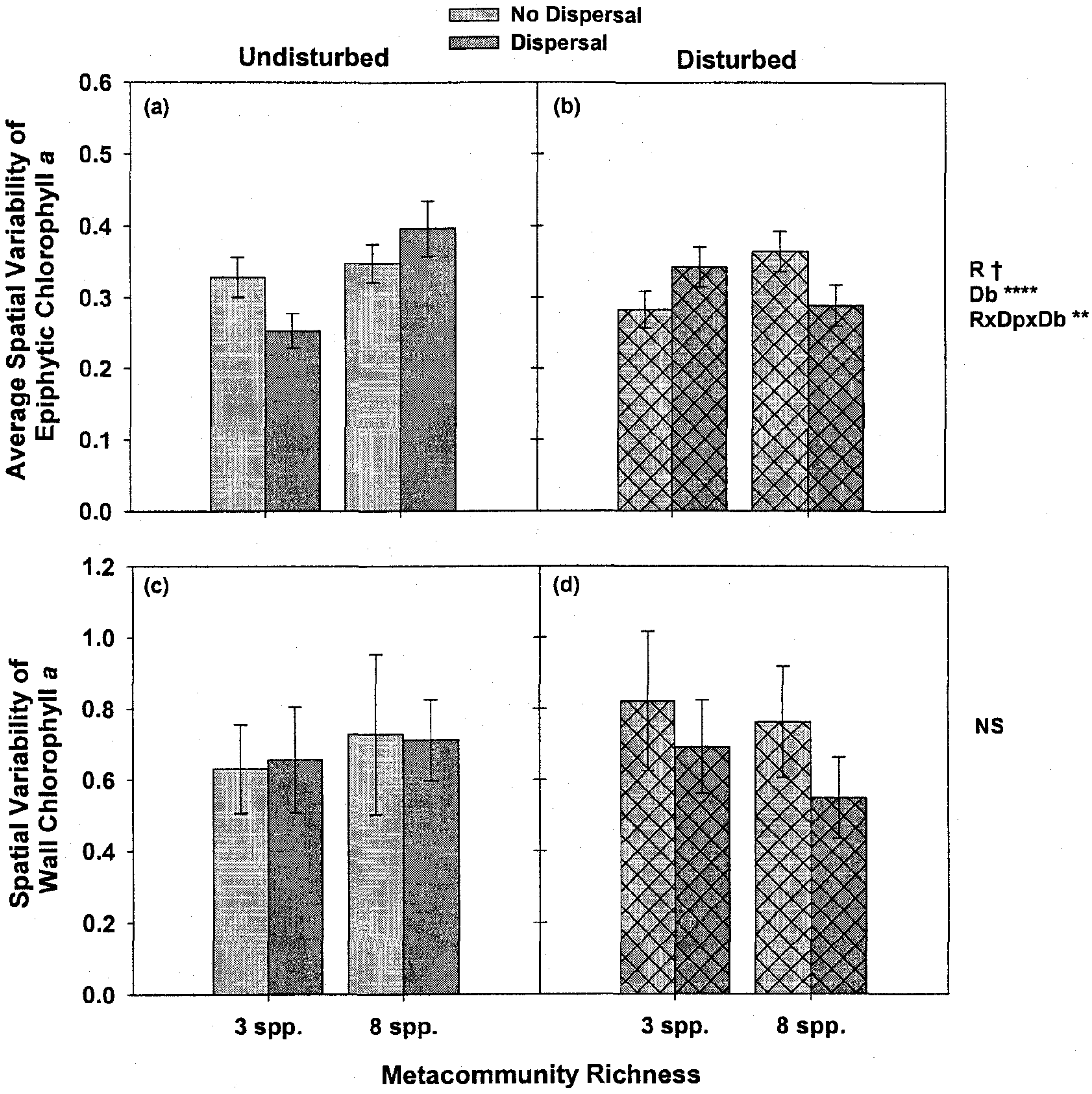

No Dispersal
Dispersal
Undisturbed
Disturbed
(a)
(b)
(c)
(d)
Average Spatial Variability of Epiphytic Chlorophyll *a*
Spatial Variability of Wall Chlorophyll *a*
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.0
0.2
0.4
0.6
0.8
1.0
1.2
R †
Db ****
RxDpxDb **
NS
3 spp.
8 spp.
3 spp.
8 spp.
Metacommunity Richness

Figure 10

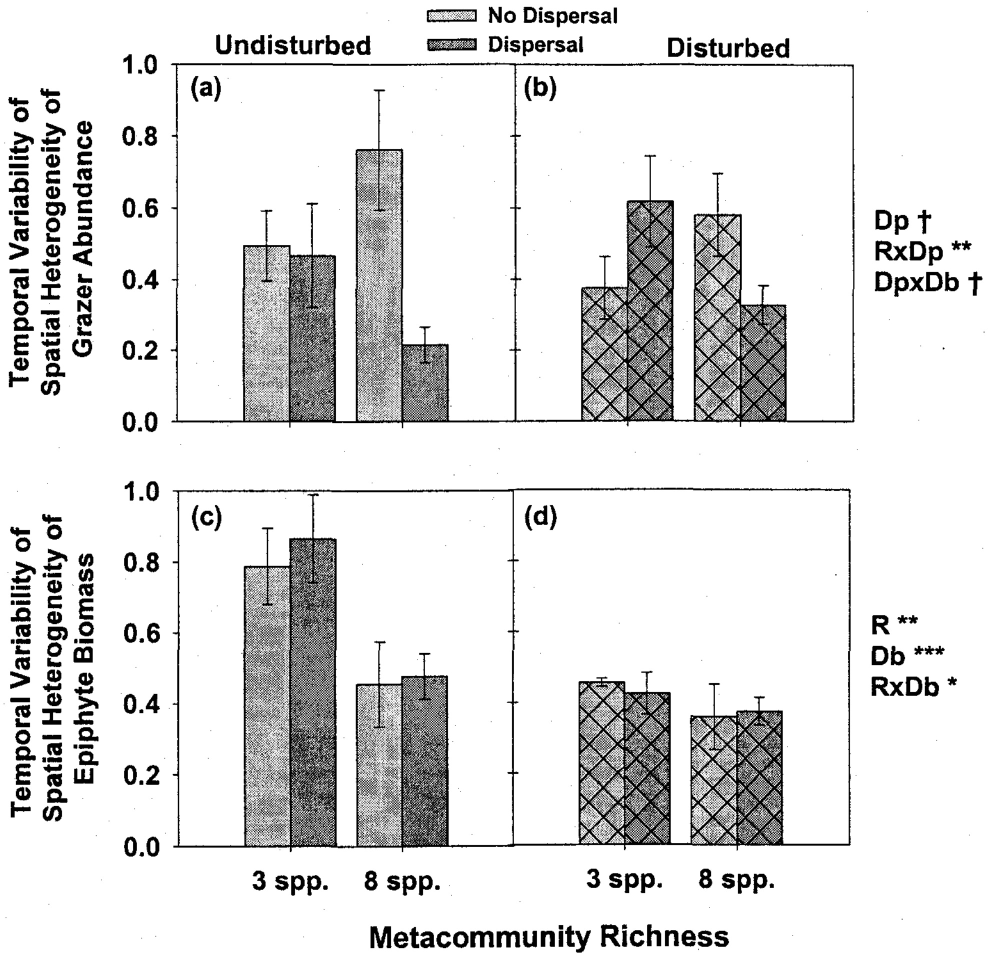

No Dispersal
Dispersal
Undisturbed
Disturbed
Temporal Variability of Spatial Heterogeneity of Grazer Abundance
(a)
(b)
1.0
0.8
0.6
0.4
0.2
0.0
Dp †
RxDp **
DpxDb †
Temporal Variability of Spatial Heterogeneity of Epiphyte Biomass
(c)
(d)
R **
Db ***
RxDb *
3 spp.
8 spp.
3 spp.
8 spp.
Metacommunity Richness

Figure 11

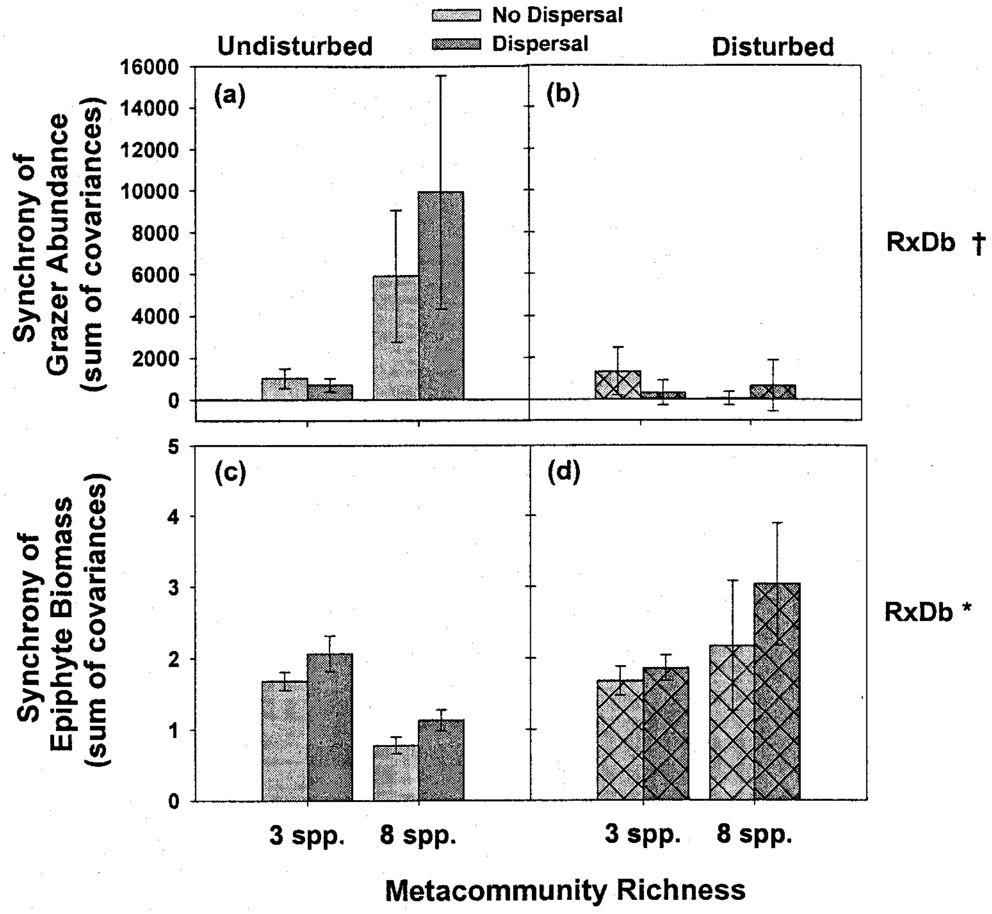

No Dispersal
Dispersal
Undisturbed
Disturbed
Synchrony of Grazer Abundance (sum of covariances)
16000
14000
12000
10000
8000
6000
4000
2000
0
(a)
(b)
RxDb †
Synchrony of Epiphyte Biomass (sum of covariances)
5
4
3
2
1
0
(c)
(d)
RxDb *
3 spp.
8 spp.
3 spp.
8 spp.
Metacommunity Richness

Figure 12

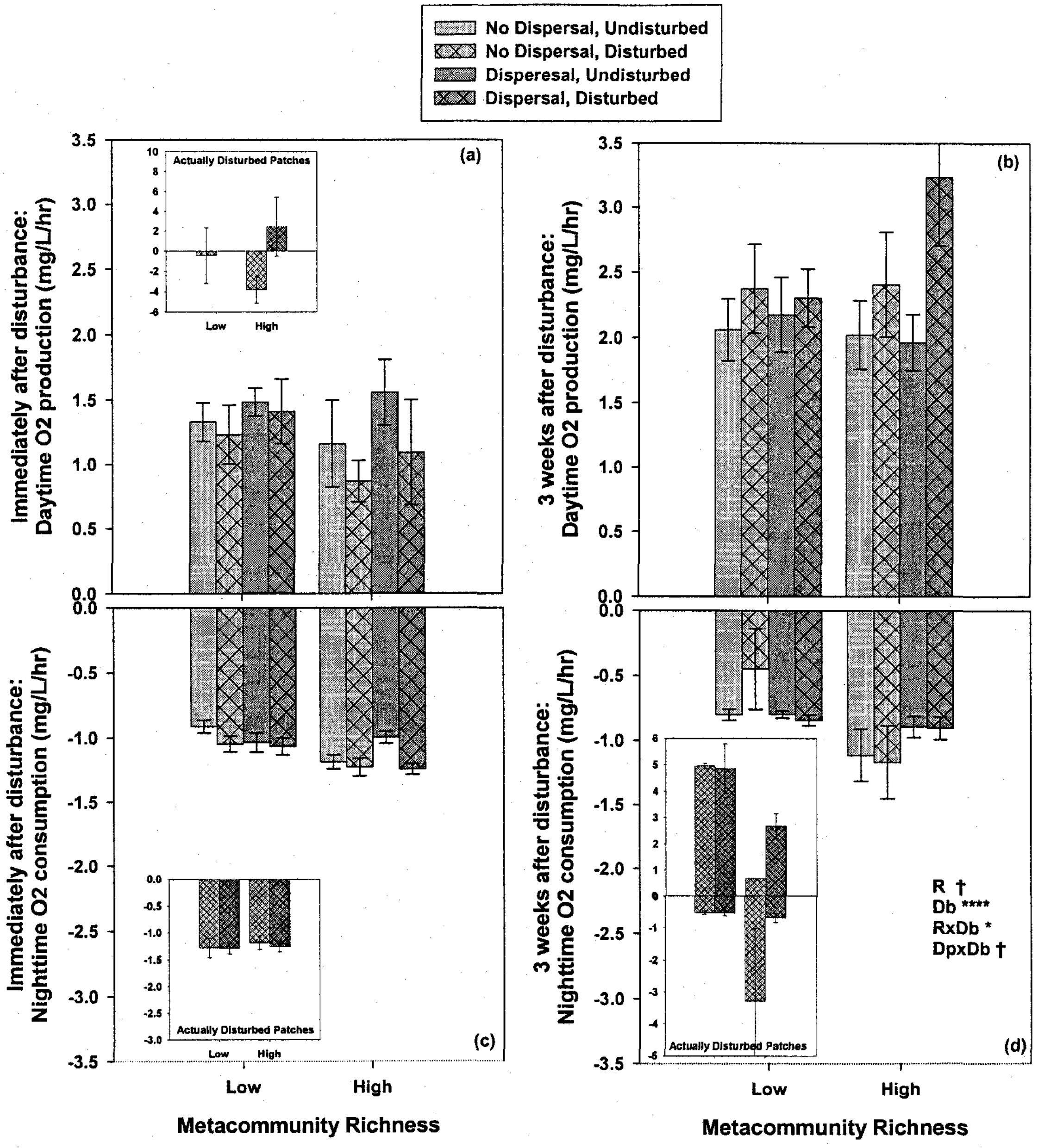
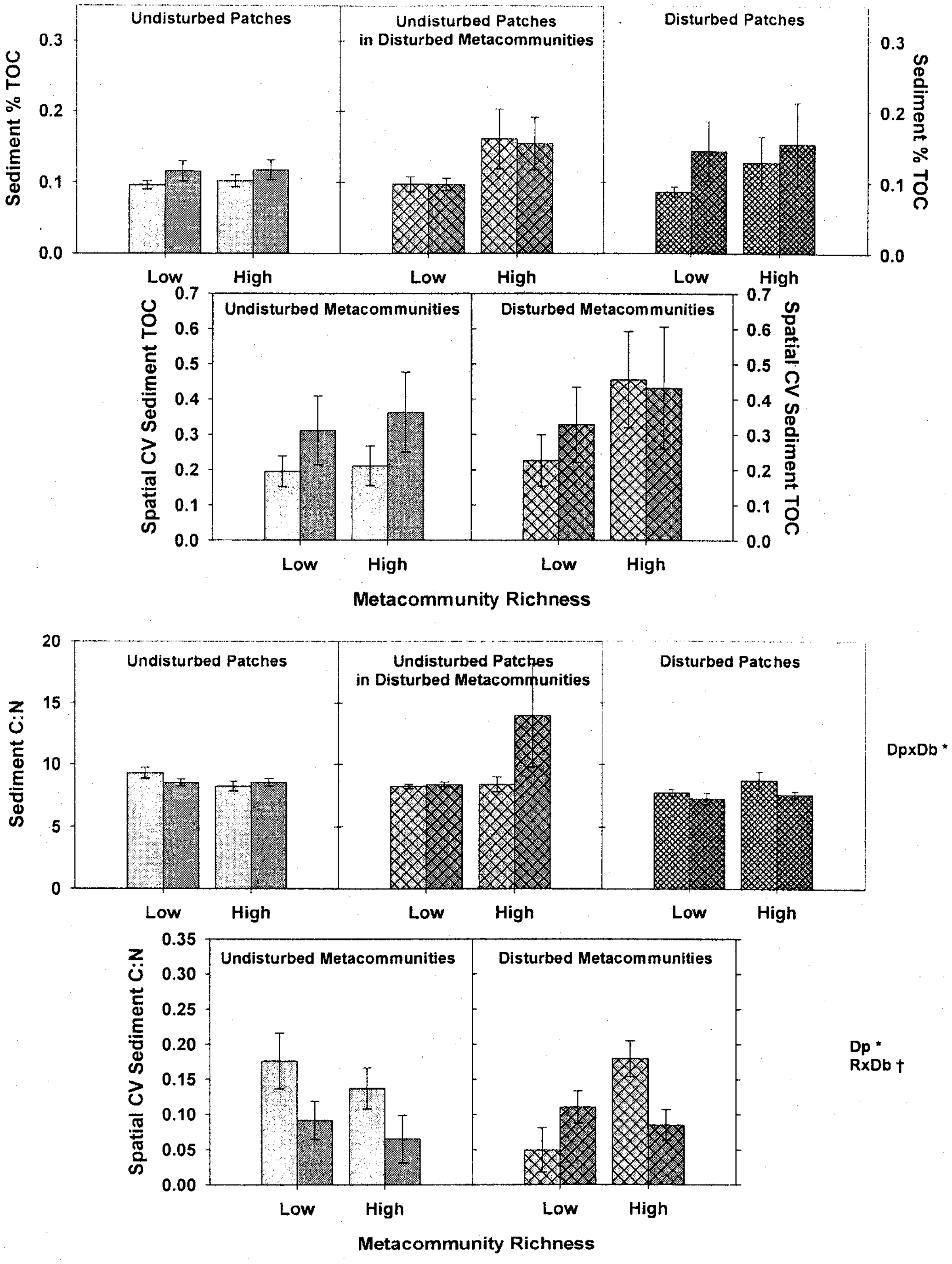

No Dispersal, Undisturbed
No Dispersal, Disturbed
Disperesal, Undisturbed
Dispersal, Disturbed
Immediately after disturbance: Daytime O2 production (mg/L/hr)
3 weeks after disturbance: Daytime O2 production (mg/L/hr)
Immediately after disturbance: Nighttime O2 consumption (mg/L/hr)
3 weeks after disturbance: Nighttime O2 consumption (mg/L/hr)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
-3.5
(a)
(b)
(c)
(d)
Actually Disturbed Patches
Low
High
R †
Db ****
RxDb *
DpxDb †
Metacommunity Richness

Figure 13


Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
Sediment % TOC
0.0
0.1
0.2
0.3
Low
High
Undisturbed Metacommunities
Disturbed Metacommunities
Spatial CV Sediment TOC
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Metacommunity Richness
Sediment C:N
0
5
10
15
20
DpxDb *
Spatial CV Sediment C:N
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Dp *
RxDb †

LIST OF APPENDICES

Appendix 4-1

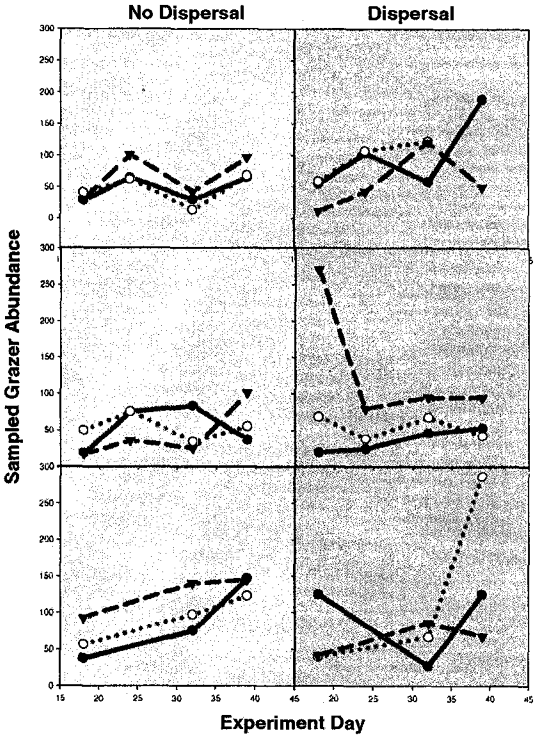
Metacommunity ID	Patch ID	# of species in pool	Dispersal?	*C. compta*	*D. appendiculata*	*E. attenuata*	*G. mucronatus*	*I. baltica*	*E. levis*	*M. nitida*	*A. valida*	# of species	SUM
1	1	8	No	4	0	2	0	12	4	4	4	6	30
1	2	8	No	2	2	2	8	0	6	6	4	7	30
1	3	8	No	6	6	8	2	6	2	0	0	6	30
2	4	3	No	12	0	0	10	8	0	0	0	3	30
2	5	3	No	12	0	0	6	12	0	0	0	3	30
2	6	3	No	12	0	0	8	10	0	0	0	3	30
3	7	3	Yes	10	0	0	12	8	0	0	0	3	30
3	8	3	Yes	10	0	0	12	8	0	0	0	3	30
3	9	3	Yes	4	0	0	18	8	0	0	0	3	30
4	10	8	No	4	2	2	2	10	4	6	0	7	30
4	11	8	No	0	8	6	6	0	4	4	2	6	30
4	12	8	No	6	2	2	2	8	6	2	2	8	30
5	13	8	Yes	4	4	8	0	6	2	4	2	7	30
5	14	8	Yes	2	6	6	2	6	0	0	8	6	30
5	15	8	Yes	4	2	8	2	4	0	8	2	7	30
6	16	8	Yes	0	2	4	0	8	4	2	10	6	30
6	17	8	Yes	2	6	6	2	10	2	0	2	7	30
6	18	8	Yes	2	0	8	4	4	6	0	6	6	30
7	19	8	No	2	2	8	0	10	2	4	2	7	30
7	20	8	No	4	4	4	4	4	4	4	2	8	30
7	21	8	No	4	2	4	8	6	2	4	0	7	30
8	22	3	Yes	14	0	0	12	4	0	0	0	3	30
8	23	3	Yes	4	0	0	12	14	0	0	0	3	30
8	24	3	Yes	18	0	0	6	6	0	0	0	3	30
9	25	8	Yes	4	4	2	2	6	2	2	8	8	30
9	26	8	Yes	6	4	8	0	0	6	2	4	6	30
9	27	8	Yes	4	4	2	4	4	4	6	2	8	30
10	28	3	No	8	0	0	8	14	0	0	0	3	30
10	29	3	No	8	0	0	16	6	0	0	0	3	30
10	30	3	No	12	0	0	10	8	0	0	0	3	30
11	31	3	Yes	10	0	0	14	6	0	0	0	3	30
11	32	3	Yes	8	0	0	10	12	0	0	0	3	30
11	33	3	Yes	14	0	0	10	6	0	0	0	3	30
12	34	8	No	4	2	2	0	4	2	6	10	7	30
12	35	8	No	0	0	12	10	4	4	0	0	4	30
12	36	8	No	0	0	6	8	0	6	8	2	5	30
13	37	3	No	12	0	0	8	10	0	0	0	3	30
13	38	3	No	14	0	0	4	12	0	0	0	3	30
13	39	3	No	10	0	0	6	14	0	0	0	3	30
14	40	8	Yes	2	2	4	6	2	6	2	6	8	30
14	41	8	Yes	4	2	6	2	6	0	10	0	6	30
14	42	8	Yes	8	8	4	0	0	6	0	4	5	30
15	43	8	No	4	2	4	6	2	4	0	8	7	30
15	44	8	No	2	4	0	2	4	8	8	2	7	30
15	45	8	No	2	6	4	6	4	2	0	6	7	30
16	46	3	No	12	0	0	6	12	0	0	0	3	30
16	47	3	No	6	0	0	18	6	0	0	0	3	30
16	48	3	No	6	0	0	8	16	0	0	0	3	30
17	49	3	Yes	10	0	0	12	8	0	0	0	3	30
17	50	3	Yes	8	0	0	10	12	0	0	0	3	30
17	51	3	Yes	10	0	0	8	12	0	0	0	3	30
18	52	3	Yes	8	0	0	14	8	0	0	0	3	30
18	53	3	Yes	14	0	0	4	12	0	0	0	3	30
18	54	3	Yes	6	0	0	12	12	0	0	0	3	30
19	55	3	No	10	0	0	8	12	0	0	0	3	30
19	56	3	No	14	0	0	12	4	0	0	0	3	30
19	57	3	No	12	0	0	8	10	0	0	0	3	30

20	**58**	**8**	Yes	4	6	2	4	0	6	4	4	7	30
20	**59**	**8**	Yes	0	0	6	2	8	2	6	6	6	30
20	**60**	**8**	Yes	2	6	2	4	0	8	4	4	7	30
21	**61**	**3**	Yes	8	0	0	12	10	0	0	0	3	30
21	**62**	**3**	Yes	4	0	0	8	18	0	0	0	3	30
21	**63**	**3**	Yes	14	0	0	8	8	0	0	0	3	30
22	**64**	**8**	No	0	6	0	2	2	2	6	12	6	30
22	**65**	**8**	No	0	6	8	2	2	4	4	4	7	30
22	**66**	**8**	No	4	0	6	4	2	4	4	6	7	30
23	**67**	**8**	Yes	2	6	4	2	2	4	4	6	8	30
23	**68**	**8**	Yes	8	2	6	0	4	2	4	4	7	30
23	**69**	**8**	Yes	4	2	8	2	0	2	2	10	7	30
24	**70**	**3**	Yes	6	0	0	14	10	0	0	0	3	30
24	**71**	**3**	Yes	8	0	0	14	8	0	0	0	3	30
24	**72**	**3**	Yes	6	0	0	14	10	0	0	0	3	30
25	**73**	**3**	No	8	0	0	14	8	0	0	0	3	30
25	**74**	**3**	No	14	0	0	14	2	0	0	0	3	30
25	**75**	**3**	No	10	0	0	10	10	0	0	0	3	30
26	**76**	**3**	Yes	14	0	0	12	4	0	0	0	3	30
26	**77**	**3**	Yes	8	0	0	10	12	0	0	0	3	30
26	**78**	**3**	Yes	8	0	0	14	8	0	0	0	3	30
27	**79**	**3**	No	12	0	0	10	8	0	0	0	3	30
27	**80**	**3**	No	4	0	0	16	10	0	0	0	3	30
27	**81**	**3**	No	10	0	0	10	10	0	0	0	3	30
28	**82**	**3**	No	12	0	0	8	10	0	0	0	3	30
28	**83**	**3**	No	6	0	0	12	12	0	0	0	3	30
28	**84**	**3**	No	10	0	0	10	10	0	0	0	3	30
29	**85**	**8**	Yes	2	2	4	6	2	8	4	2	8	30
29	**86**	**8**	Yes	4	4	0	0	4	0	8	10	5	30
29	**87**	**8**	Yes	2	0	6	6	10	4	2	0	6	30
30	**88**	**3**	No	6	0	0	16	8	0	0	0	3	30
30	**89**	**3**	No	14	0	0	10	6	0	0	0	3	30
30	**90**	**3**	No	10	0	0	10	10	0	0	0	3	30
31	**91**	**8**	Yes	6	2	4	10	0	6	2	0	6	30
31	**92**	**8**	Yes	4	4	2	2	2	4	8	4	8	30
31	**93**	**8**	Yes	4	4	4	4	2	6	6	0	7	30
32	**94**	**3**	Yes	14	0	0	6	10	0	0	0	3	30
32	**95**	**3**	Yes	14	0	0	10	6	0	0	0	3	30
32	**96**	**3**	Yes	14	0	0	4	12	0	0	0	3	30
33	**97**	**3**	Yes	12	0	0	8	10	0	0	0	3	30
33	**98**	**3**	Yes	14	0	0	8	8	0	0	0	3	30
33	**99**	**3**	Yes	10	0	0	16	4	0	0	0	3	30
34	**100**	**8**	No	2	2	0	8	4	4	4	6	7	30
34	**101**	**8**	No	2	4	4	2	6	6	4	2	8	30
34	**102**	**8**	No	2	2	2	4	8	4	4	4	8	30
35	**103**	**8**	No	2	4	6	2	4	6	2	4	8	30
35	**104**	**8**	No	4	6	6	2	2	2	4	4	8	30
35	**105**	**8**	No	2	2	0	4	6	10	2	4	7	30
36	**106**	**8**	No	4	0	4	0	6	6	6	4	6	30
36	**107**	**8**	No	4	8	6	4	4	2	2	0	7	30
36	**108**	**8**	No	4	2	2	2	2	10	4	4	8	30
37	**109**	**3**	No	10	0	0	10	10	0	0	0	3	30
37	**110**	**3**	No	8	0	0	16	6	0	0	0	3	30
37	**111**	**3**	No	14	0	0	4	12	0	0	0	3	30
38	**112**	**3**	Yes	6	0	0	16	8	0	0	0	3	30
38	**113**	**3**	Yes	16	0	0	6	8	0	0	0	3	30
38	**114**	**3**	Yes	6	0	0	16	8	0	0	0	3	30
39	**115**	**3**	No	10	0	0	6	14	0	0	0	3	30
39	**116**	**3**	No	6	0	0	12	12	0	0	0	3	30
39	**117**	**3**	No	8	0	0	8	14	0	0	0	3	30
40	**118**	**8**	No	6	4	2	4	6	6	0	2	7	30
40	**119**	**8**	No	6	2	8	0	4	4	4	2	7	30
40	**120**	**8**	No	2	4	4	6	6	2	4	2	8	30
41	**121**	**8**	Yes	0	0	4	6	2	6	4	8	6	30
41	**122**	**8**	Yes	6	2	4	2	0	6	6	4	7	30
41	**123**	**8**	Yes	4	0	2	10	4	4	0	6	6	30
42	**124**	**8**	No	0	10	0	4	4	4	2	6	6	30
42	**125**	**8**	No	6	6	0	4	0	6	4	4	6	30
42	**126a**	**8**	No	6	4	6	4	0	2	6	2	7	30
43	**126b**	**3**	Yes	4	0	0	18	8	0	0	0	3	30

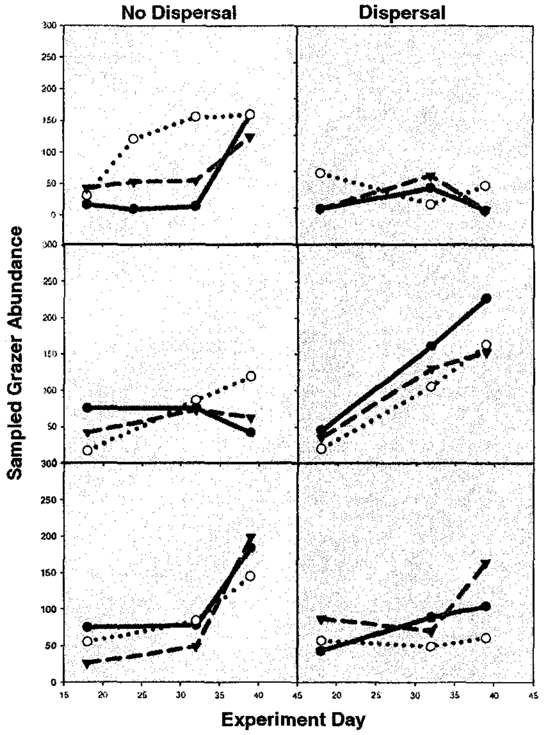
43	**127**	**3**	Yes	8	0	0	18	4	0	0	0	3	30
43	**128**	**3**	Yes	10	0	0	16	4	0	0	0	3	30
44	**129**	**3**	Yes	10	0	0	12	8	0	0	0	3	30
44	**130**	**3**	Yes	6	0	0	12	12	0	0	0	3	30
44	**131**	**3**	Yes	6	0	0	16	8	0	0	0	3	30
45	**132**	**3**	No	12	0	0	10	8	0	0	0	3	30
45	**133**	**3**	No	18	0	0	6	6	0	0	0	3	30
45	**134**	**3**	No	8	0	0	8	14	0	0	0	3	30
46	**135**	**8**	No	2	8	0	0	10	2	4	4	6	30
46	**136**	**8**	No	0	6	4	4	2	2	2	10	7	30
46	**137**	**8**	No	4	4	4	0	6	6	4	2	7	30
47	**138**	**8**	Yes	4	4	2	4	4	6	2	4	8	30
47	**139**	**8**	Yes	8	0	6	0	2	4	8	2	6	30
47	**140**	**8**	Yes	6	2	2	2	2	4	8	4	8	30
48	**141**	**8**	Yes	4	4	4	4	6	0	2	6	7	30
48	**142**	**8**	Yes	4	6	6	2	0	4	6	2	7	30
48	**143**	**8**	Yes	0	6	4	0	6	2	6	6	6	30
49	**144**	**8**	Yes	6	4	10	2	4	0	0	4	6	30
49	**145**	**8**	Yes	2	2	0	12	2	2	4	6	7	30
49	**146**	**8**	Yes	8	2	2	4	4	2	6	2	8	30
50	**147**	**8**	No	6	2	4	6	0	8	2	2	7	30
50	**148**	**8**	No	2	6	4	4	0	4	6	4	7	30
50	**149**	**8**	No	2	2	6	4	8	6	0	2	7	30
51	**150**	**8**	Yes	4	4	2	4	4	4	4	4	8	30
51	**151**	**8**	Yes	10	4	0	6	2	4	2	2	7	30
51	**152**	**8**	Yes	6	2	2	4	4	2	4	6	8	30
52	**153**	**3**	No	6	0	0	12	12	0	0	0	3	30
52	**154**	**3**	No	12	0	0	8	10	0	0	0	3	30
52	**155**	**3**	No	6	0	0	16	8	0	0	0	3	30
53	**156**	**3**	No	4	0	0	16	10	0	0	0	3	30
53	**157**	**3**	No	8	0	0	10	12	0	0	0	3	30
53	**158**	**3**	No	4	0	0	10	16	0	0	0	3	30
54	**159**	**3**	Yes	14	0	0	4	12	0	0	0	3	30
54	**160**	**3**	Yes	8	0	0	10	12	0	0	0	3	30
54	**161**	**3**	Yes	10	0	0	8	12	0	0	0	3	30
55	**162**	**8**	Yes	6	6	4	2	4	0	4	4	7	30
55	**163**	**8**	Yes	0	10	4	6	2	2	6	0	6	30
55	**164**	**8**	Yes	2	6	4	4	4	4	2	4	8	30
56	**165**	**8**	No	2	4	2	4	14	2	0	2	7	30
56	**166**	**8**	No	2	4	2	2	4	10	2	4	8	30
56	**167**	**8**	No	4	2	8	0	4	0	8	4	6	30

Appendix 4-2

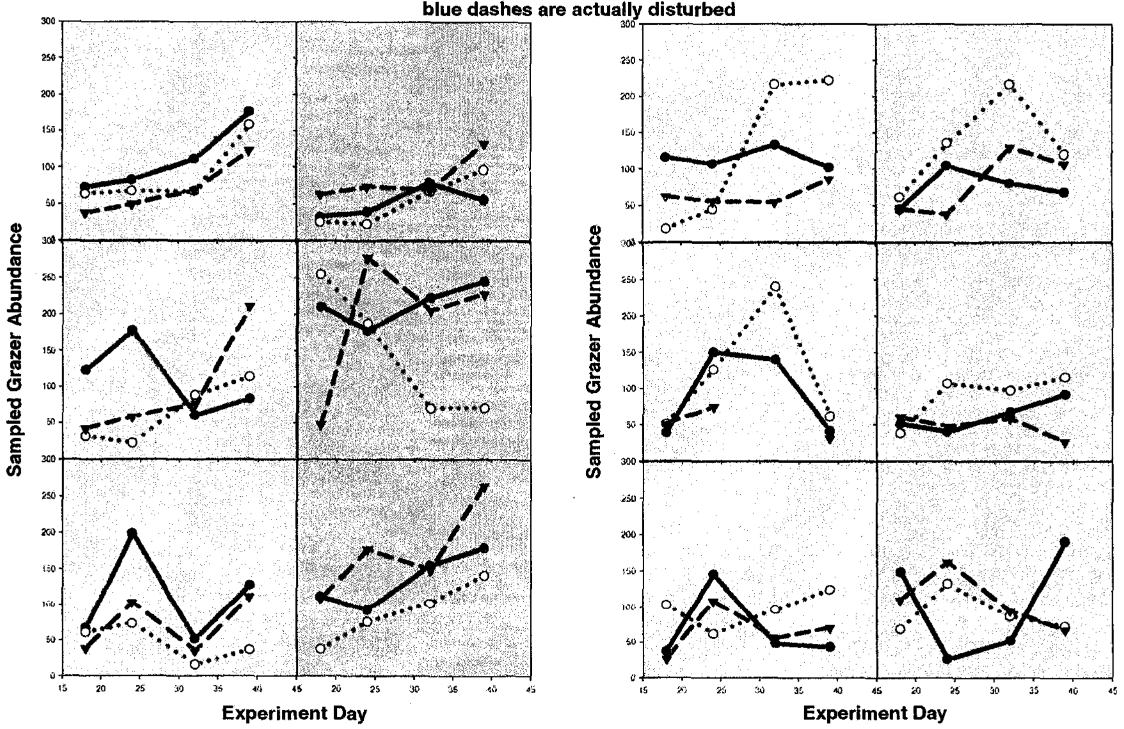
3 spp. Metacommunities



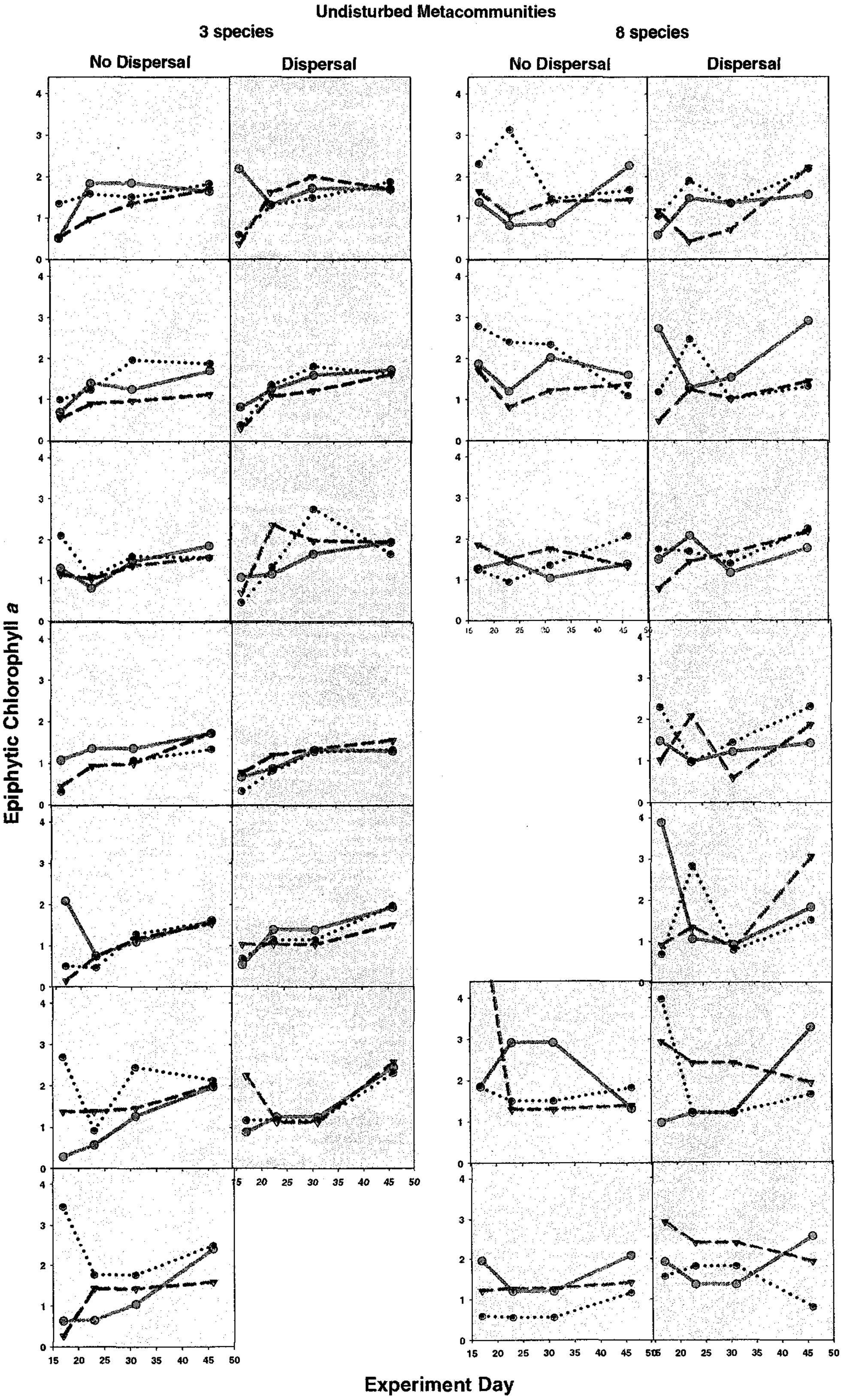
8 spp. Metacommunities



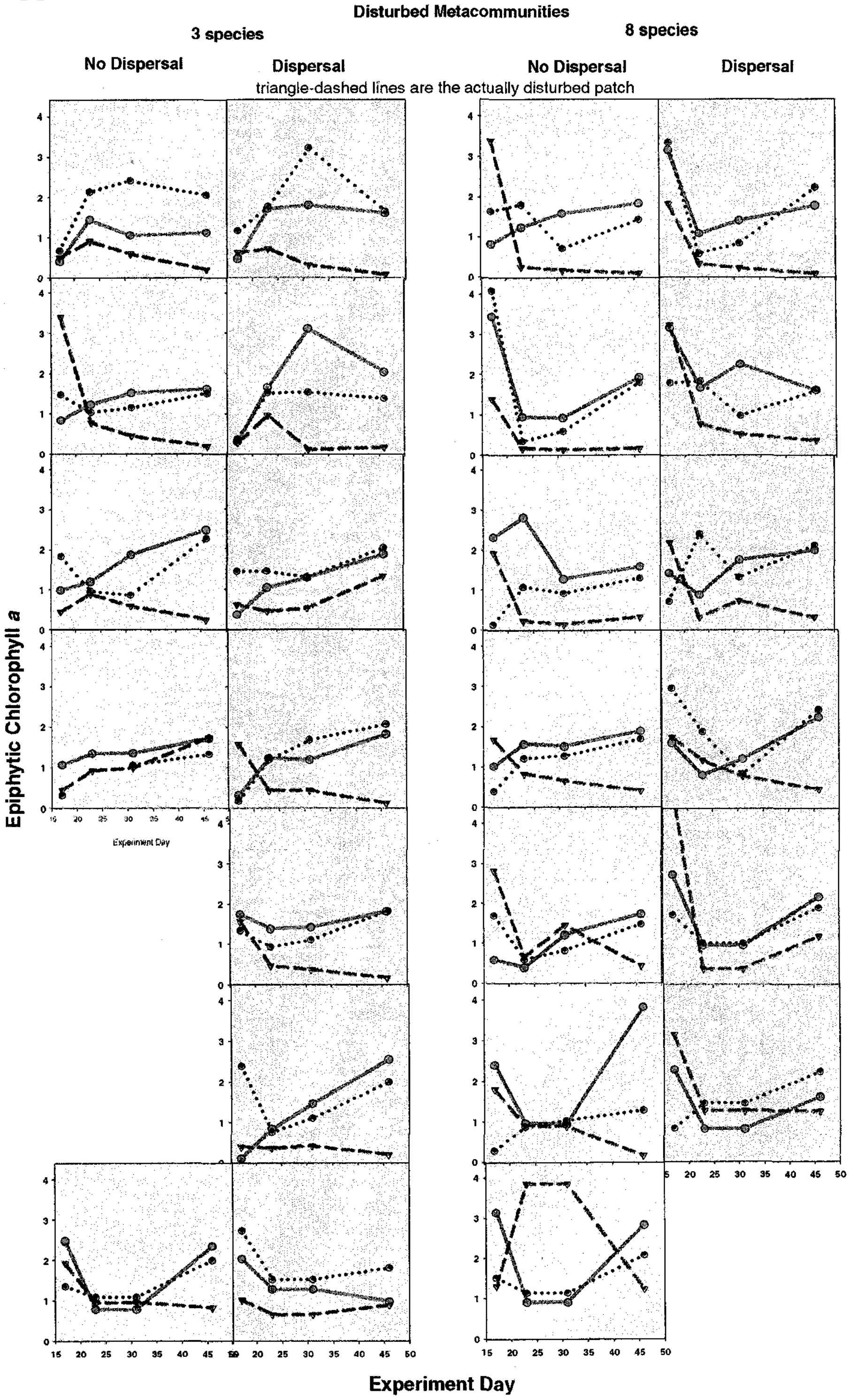
Disturbed Metacommunities
blue dashes are actually disturbed



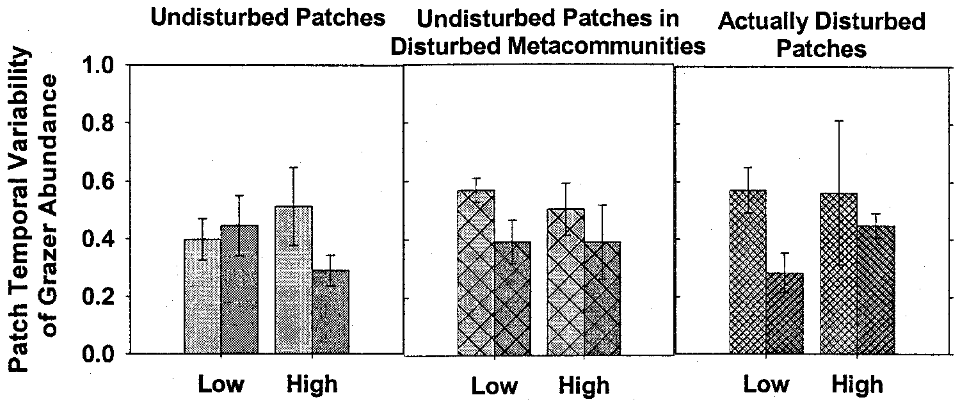
Appendix 4-3-Undisturbed Metacommunities

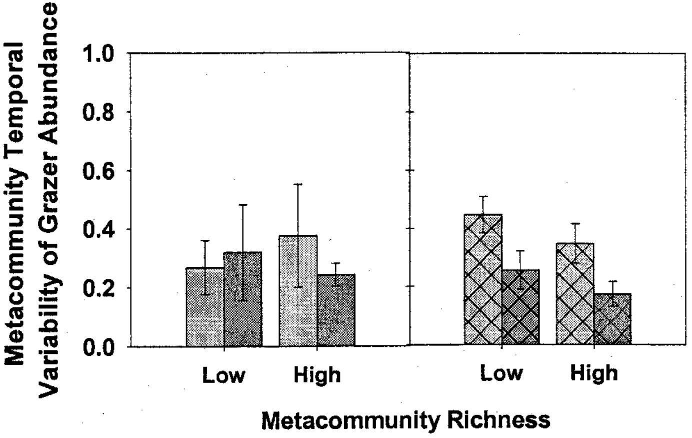


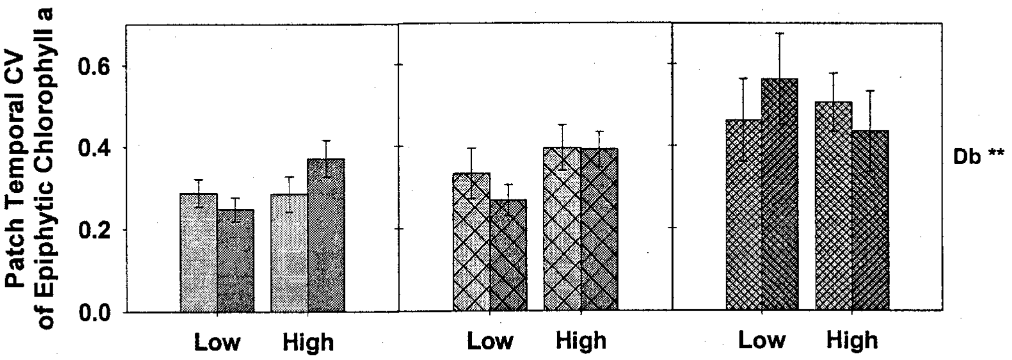
Appendix 4-3 (continued, Disturbed Metacommunities)

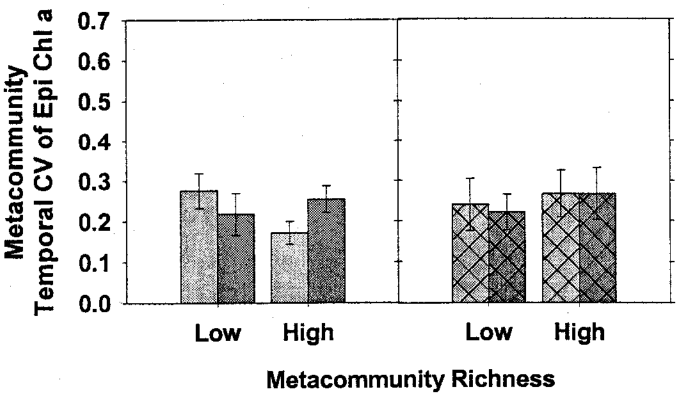


Appendix 4-4

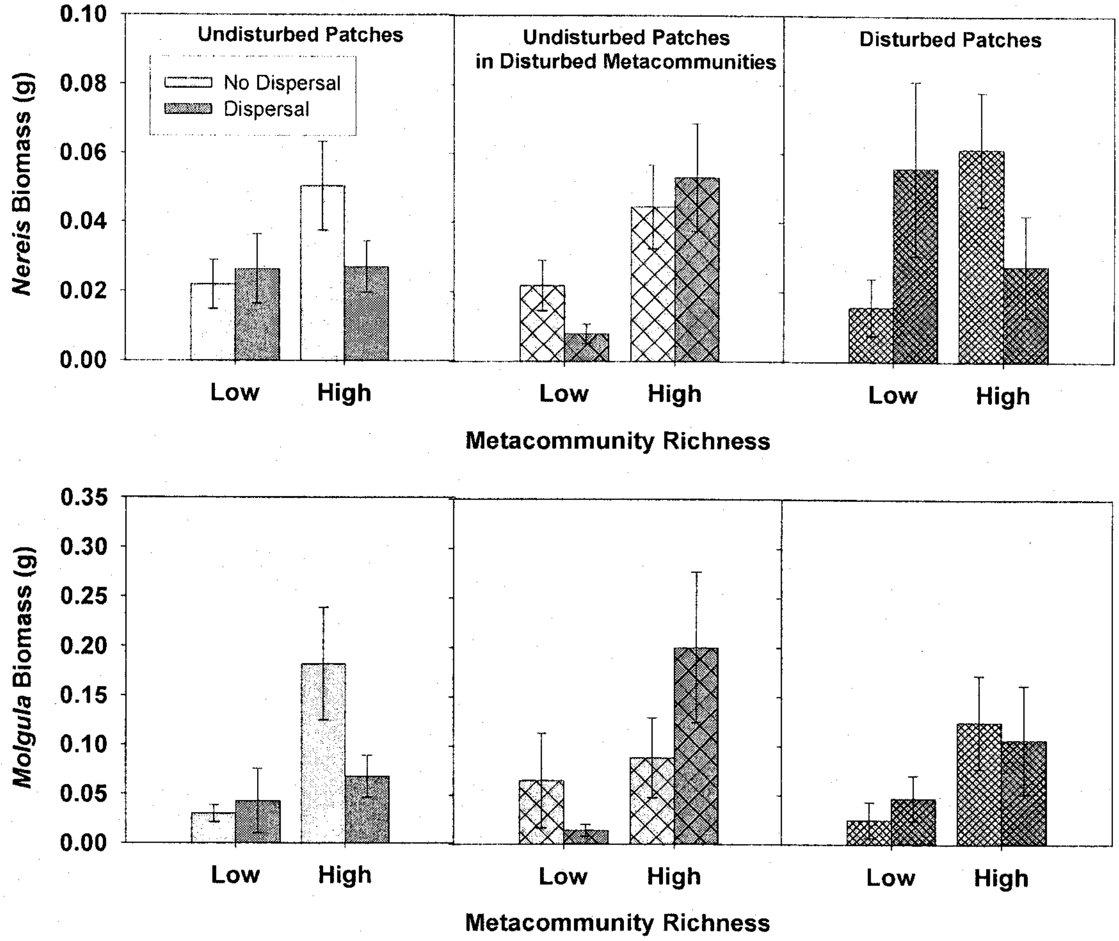

Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Actually Disturbed Patches
Patch Temporal Variability of Grazer Abundance
1.0
0.8
0.6
0.4
0.2
0.0
Low
High
Low
High
Low
High


Metacommunity Temporal Variability of Grazer Abundance
1.0
0.8
0.6
0.4
0.2
0.0
Low
High
Low
High
Metacommunity Richness

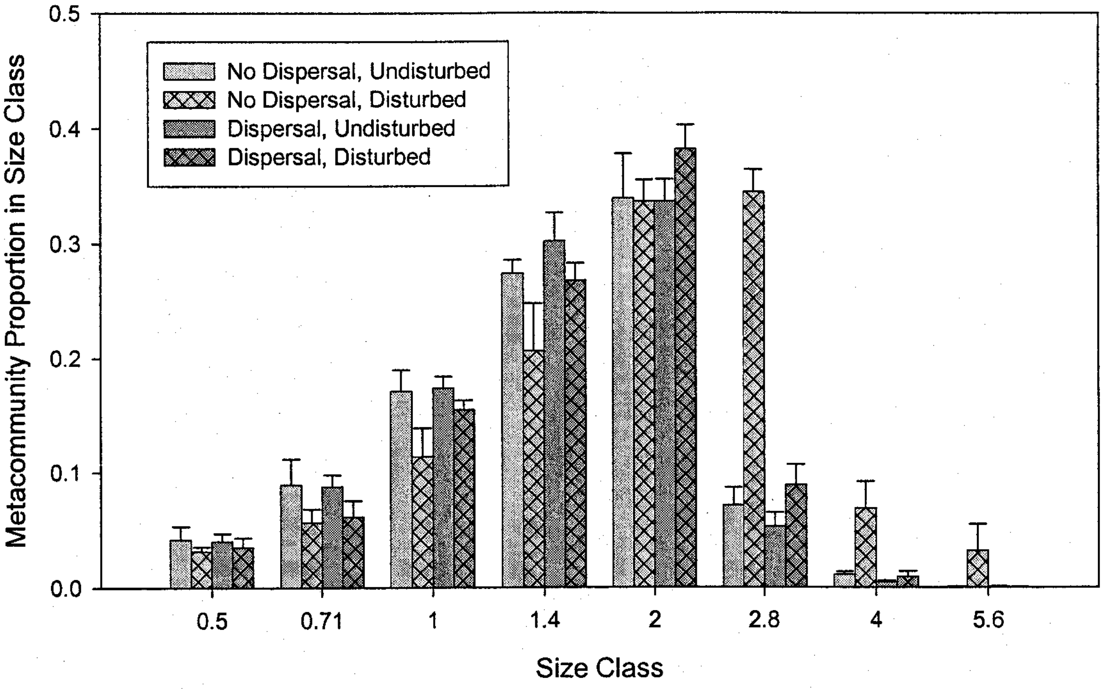

Patch Temporal CV of Epiphytic Chlorophyll a
0.6
0.4
0.2
0.0
Low
High
Low
High
Low
High
Db **


Metacommunity Temporal CV of Epi Chl a
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Low
High
Low
High
Metacommunity Richness

Appendix 4-5


Undisturbed Patches
Undisturbed Patches in Disturbed Metacommunities
Disturbed Patches
No Dispersal
Dispersal
Nereis Biomass (g)
0.10
0.08
0.06
0.04
0.02
0.00
Low
High
Metacommunity Richness
Molgula Biomass (g)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Low
High
Metacommunity Richness

Appendix 4-6


0.5
0.4
0.3
0.2
0.1
0.0
Metacommunity Proportion in Size Class
No Dispersal, Undisturbed
No Dispersal, Disturbed
Dispersal, Undisturbed
Dispersal, Disturbed
0.5
0.71
1
1.4
2
2.8
4
5.6
Size Class

Appendix 4-7: Main and interactive effects of metacommunity richness, dispersal and disturbance on the magnitude and variability of ecosystem properties. Significant ($p < 0.05$) values are **bolded** and highlighted in red. Marginally significant ($0.05 < p < 0.10$) effects are in *italics*. Data were analyzed using a fully-crossed 3-way GLM with all factors fixed. MS are Type III.

			Metacommunity Richness		Dispersal		Disturbance		Richness * Dispersal		Richness * Disturbance		Dispersal * Disturbance		Richness * Dispersal * Disturbance	
Response Variable	**Model d.o.f., Error d.o.f.**	**R2**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**	**MS**	**p-value**
Patch (subsampled 1 patch from each metacommunity Type III sum of squares																
Grazer richness	7, 30	.856	160.1	[illegible]	0	1.000	.053	.8117	.094	.7509	.288	.5791	.094	.7509	0	1.000
Grazer S-W diversity	7, 32	.548	.350	[illegible]	.013	.4118	.098	[illegible]	.010	.4604	.019	.3166	.092	[illegible]	.043	.1355
Grazer abundance (day 18)	7, 32	.053	437	.5115	757	.3889	74.8	.7854	399	.5306	54.7	.8160	33.9	.8546	33.87	.8546
Grazer abundance (day 32)	7, 32	.078	562	.6399	808	.5750	1733	.4128	2158	.3614	103	.8406	186	.7876	1555	.4377
Grazer abundance (FINAL)	7, 31	.123	1974	.9040	19582	.7045	169634	.2685	277963	.1593	22362	.6853	84796	.4318	6880	.8220
Grazer biomass	7, 33	.167	7706	.7442	11396	.6916	93844	.2591	20173	.5980	108933	.2248	237607	*.0767*	53.6	.9783
Grazer resistance (day 32-day 18)	7, 48	.165	2682 7	[illegible]	2.92	.9796	3.97	.9763	697	.6937	1466	.5683	2760	.4346	7092	.2130
Epiphytic chl *a* (day 16)	7, 48	.343	13.2	[illegible]	0	.9790	5.48	[illegible]	.631	.3991	.103	.7325	.057	.7988	1.21	.2437
Epiphytic chl a (day 22)	7, 48	.352	*.969*	.1157	*.814*	.1477	*4.73*	[illegible]	.481	.2636	*1.46*	*.0548*	*.006*	.8982	*.042*	.7412
Epiphytic chl a (day 30)	7, 48	.234	.434	.2502	.171	.4682	3.77	[illegible]	.116	.5507	.034	.7459	.012	.8500	.006	.8811
Epiphytic chl *a* (day 42)	7, 48	.255	.178	.5238	.333	.3839	5.13	[illegible]	.279	.4250	0	.9792	.027	.8016	.194	.5056
Wall chlorophyll *a*	7, 48	.111	.009	[illegible]	0	.7656	0	.9791	0	.6679	.001	.4626	0	.7428	0	.7947
Microalgal mat biomass (mainly cyanobacteria)	7, 48	.145	.011	[illegible]	0	.9439	0	.5195	0	.6008	0	.7560	.004	.1784	.003	.2605
Change in Z. marina biomass	7, 48	.301	5.42	.2571	.085	.8864	. 68.9	[illegible]	.679	.6868	3.11	.3887	.809	.6598	2.80	.4140
Day O2 production (d 24)	7, 22	.193	2.97	.2104	.726	.5302	.075	.8390	.102	.8129	.286	.6926	1.19	.4234	2.64	.2367
Night O2 production (d 20)	7, 12	.306	.005	.7285	.005	.7403	.117	.1093	.033	.3746	.011	.5992	.0002	.9423	.045	.3032
Day O2 production (d ??)	7, 22	.626	5.33	*.0869*	.726	.5153	42.3	[illegible]	.082	.8261	7.41	[illegible]	6.28	*.0649*	1.55	.3442
Night O2 production (d ??)	7, 21	.183	5.79	.3813	4.17	.4567	.535	.7885	4.013	.4652	2.04	.6010	1.88	.6164	2.04	.601
Sediment total organic carbon (%)	7, 22	.157	.0003	.7709	.006	.1564	.004	.2788	.0008	.6133	0	.9395	0	.9085	.0006	.6553
Sediment C:N	7, 22	.362	.001	.9728	.362	.5851	1.35	.297	0	.9924	2.47	.1634	7.27	[illegible]	2.79	.1393
Temporal CV of grazer abundance-all sampling points	7, 32	.188	.015	.7067	.003	.8588	.413	*.0519*	.003	.8736	.228	.1438	.037	.5514	.002	.8775
Temporal CV of grazer abundance-post-disturbance only	7,16	.310	.147	.1007	.018	.5467	.051	.3181	0	.9852	.026	.4756	.060	.2830	.046	.3444
Temporal CV of epi. chl *a*-all sampling points	7, 48	.308	.267	*.0958*	.001	.9121	1.10	[illegible]	.013	.7079	.329	*.0656*	.004	.8412	.067	.3995
Temporal CV of epi. chl *a*-post disturbance only	7, 48	.265	.102	.156*	.030	.4394	.453	[illegible]	.012	.6203	.051	.3129	.010	.6585	.063	.2650
Metacommunity																
Grazer richness																
Grazer S-W diversity	7,33	.507	.602	[illegible]	.012	.4728	.019	.3725	0.0000	.9641	.093	*.0520*	.001	.8051	.064	.1048
Grazer pres-abs beta-diversity	7,33	.188	.009	.2550	.017	.1140	.003	.4946	.011	.2016	.002	.6148	.002	.5887	0	.9441
Grazer abundance beta-diversity	7,33	.447	.080	[illegible]	.0008	.6312	.005	.2402	.0004	.7181	.007	.1541	.0005	.6913	0.000	.9467
Final grazer abundance (d45)	7,33	.224	8634 6	.6578	5809	.9084	1762710	*.0516*	179162	.5241	522781	.2793	1496145	*.0717*	2598	.9387
Final grazer biomass (d 45)	7, 33	.135	2186 2	.8034	411371	.2842	42090	.7299	1917	.9412	232094	.4194	758880	.1487	296086	.3624
Grazer abundance (d 18)	7,47	.216	3970 5	[illegible]	859	.6517	3034	.3974	201	.8269	3161	.3878	629	.6991	2308	.4601
Grazer abundance (d 24)	6,10	.245	2.333	.9853	1428	.6505	15133	.1594	14.1	.9639	603	.7676	290	.8374	--	--
Grazer abundance (d 32)	7,48	.132	4301 6	.1127	13372	.3722	8924	.4654	18134	.2994	1522	.7625	4942	.5865	17700	.3052
Grazer abundance (d 39)	7,16	.144	368	.8958	150	.9334	620	.8651	322	.9025	48780	.1453	416	.8892	5400	.6174
Spatial CV of grazers (d 18)	7,48	.164	.003	*.8181*	*.157*	*.1149*	*.020*	*.5726*	*0.000*	.9892	*.057*	*.3392*	*.242*	*.0519*	.080	.2573
Spatial CV of grazers (d 24)	6,10	.475	.183	[illegible]	.050	.2523	.091	.1329	.079	.1589	.260	[illegible]	.064	.2016	---	----
Spatial CV of grazers (d 32)	7,48	.301	.368	[illegible]	.045	.4171	.486	[illegible]	.095	.2401	.039	.4534	.020	.5906	.137	.1612
Spatial CV of grazers (d 39)	7,16	.401	.011	.5704	.094	.1021	.020	.4365	.033	.3202	.084	.1208	.057	.1968	.037	.2934
Spatial CV of grazers (d 45)	7,48	.266	.034	.1178	.028	.1591	.017	.2723	.005	.5425	.054	[illegible]	.002	.6808	.002	.6723
Avg spatial CV of grazer *abundance*	7,48	.268	.117	[illegible]	.039	.2185	.146	[illegible]	.003	.7300	.045	.1865	.026	.3079	.004	.7075

Temporal CV of spatial CV of grazer abundance	7,48	.253	.004	.8388	.285	*.0749*	.001	.9109	.852	[illegible]	.008	.7587	.263	*.0864*	0	.9428
Epi. chlorophyll a (d 16)	7, 48	.413	73.5	[illegible]	2.13	.4057	9.14	*.0888*	3.88	.2633	.313	.7489	7.07	.1330	6.31	.1551
Epi. chlorophyll a (d 22)	7, 48	.345	7.39	[illegible]	2.79	.1070	10.52	.0025	.275	.6084	3.79	*.0616*	1.38	.2545	0	.9866
Epi. chlorophyll a (d 30)	7, 48	.270	.827	.3318	.003	.9521	12.83	[illegible]	1.09	.2658	.009	.9159	.159	.6696	.648	.3898
Epi. chlorophyll a (d 42)	7, 48	.482	.218	.5456	1.96	*.0743*	15.9	[illegible]	2.76	[illegible]	.443	.3897	1.39	.1307	.122	.6503
Spatial CV of sediment TOC	7, 22	.221	.074	.1908	.055	.2582	.060	.2371	.004	.7643	.329	.3784	.017	.5286	.012	.5923
Spatial CV of sediment C:N	7, 22	.455	.0007	.6566	.0165	[illegible]	.0009	.6016	.009	.1103	.013	*.0596*	.007	.1661	.013	*.0631*
Spatial CV of epi chl *a* (d 16)	7, 48	.122	.057	.3752	.021	.5865	0	.9589	.009	.7256	.056	.3827	.005	.7989	.305	[illegible]
Spatial CV of epi chl a (d 22)	7, 48	.357	.600	[illegible]	0	.8903	.162	[illegible]	.030	.3668	.022	.4419	.032	.3524	.059	.2078
Spatial CV of epi chl *a* (d 30)	7. 48	.468	.065	.1671	.004	.7322	.964	[illegible]	.047	.2411	.055	.2058	.027	.3708	.069	.1553
Spatial CV of epi chl *a* (day 42)	7, 48	.655	.049	.2135*	0	.8703	2.38	[illegible]	0	.9470*	.124	*.0515*	.002	.8064	.071	.1377
Avg Spatial CV of epiphytic chl *a*	7, 48	.586	.037	*.0818*	.002	.6486	.540	[illegible]	.009	.3956	.011	.3288	0	.9964	.101	[illegible]
Spatial CV of wall chlorophyll *a*	7, 48	.043	.027	.6754	.033	.6439	.043	.6009	0	.9934	.041	.6101	.192	.2708	.025	.6890
Temporal CV of Spatial CV of epi chl a	7, 48	.409	.622	[illegible]	.006	.7438	.782	[illegible]	0	.9722	.274	[illegible]	.011	.6561	.009	.6937
Temporal CV of grazer abundance-including before disturbance	7, 47	.257	.168	*.0829*	.020	.5475	.054	.3187	.116	.1472	.009	.6829	.282	[illegible]	.060	.2930
Temporal CV of grazer abundance-post disturbance only	7,16	.239	.008	.6094	.075	.1390	0	.9631	.010	.5694	.017	.4703	.030	.3416	.015	.4922
Temporal CV of epi. chl *a* – including before disturbance	7, 48	.149	.036	.1972	.005	.6305	.002	.7425*	0	.9514	.021	.3247*	.002	.7814	.003	.7259
Temporal CV of epi. chl *a*-post disturbance only	7, 48	.058	0	.9787	0	.9676	.005	.6158	.021	.2806	.016	.3465	.002	.7663	.012	.4073
Synchrony (sum of covar) epiphytic chl a	7, 48	.153	.046	.7282	.616	.2069	.307	.3711	.123	.5700	1.72	[illegible]	.179	.4942	.522	.2448

CONCLUSION

This dissertation demonstrates the importance of examining biodiversity-ecosystem function relationships in dynamic systems, where diversity is influenced by the history of community assembly and spatial processes. First, the history of community assembly is clearly important in this system. Chapter I demonstrated that priority effects, or the sequence of species colonization, could influence the outcome of competition. Being there first confers an advantage. Similarly, in the two experiments discussed in Chapters II-IV, patches retained their original composition signatures to a large degree, even after six weeks of population growth, as well as colonization through the dispersal corridors. These experiments, along with others (Fukami and Morin 2003, Cardinale et al. 2004, Matthiessen and Hillebrand 2006), illustrate the importance of studying the effects of *dynamic* diversity on ecosystem function. Species are being both lost from and added to systems, and the order and spatial pattern of these processes are likely to be important for diversity and ecosystem function (Cassey et al. 2006).

Second, this work suggests that biodiversity-ecosystem function relationships may scale-up to metacommunities, but that biodiversity-stability relationships might not. We found that diverse communities of mobile consumers contained more individuals, better resisted invasion by organisms at multiple trophic levels, and reduced producer biomass to lower levels than species-poor communities. These results mirror those from the large number of studies on plants and microbes, confirming the generality of biodiversity-ecosystem function relationships and the mechanisms that create them. We also found evidence that biodiversity-ecosystem function relationships can scale-up to metacommunities: the size of the species pool used to assemble metacommunities explained even more variance in ecosystem properties like consumer and producer abundance than patch diversity did. Despite finding prevalent positive effects of biodiversity on ecosystem properties, we did not find many positive effects of biodiversity on predictability of those properties. Though diverse patches had higher resistance to invasion (Chapter I), they had lower resistance to the macroalgae disturbance (Chapter IV). Patches with high diversity grazer communities also had higher temporal variability of grazers and epiphytes (Chapters II-IV), potentially making them more susceptible to population crashes or invasions. Finally, metacommunities assembled from large species pools had high beta-diversity, which made ecosystem properties less predictable in space. These results suggest that biodiversity-stability theory needs to consider both consumer-resource dynamics and spatial processes. Also, posited benefits of diversity for temporal and spatial predictability may not apply to fragmented landscapes.

Furthermore, dispersal of mobile organisms can have a variety of important indirect effects on ecosystem function. Although connecting patches had surprisingly small effects on diversity within patches, it reduced beta-diversity, homogenizing patch composition and other ecosystem properties (Chapters II and IV). Dispersal also homogenized the distribution of individuals throughout the metacommunity, decreasing intraspecific aggregation and reducing average patch density (Chapter III). Despite increasing the performance of already high-performing species, though, dispersal actually reduced grazer abundance, eliminating the positive effects of diversity on grazer abundance (Chapter II). Allowing grazers to move among patches also de-stabilized grazer and epiphyte abundance at both patch and metacommunity scales (Chapters II and IV). Although many dispersal effects were small and marginally significant, they were pervasive. Dispersal modified a large percentage of the relationships between diversity and ecosystem properties (Chapter III). Since this experimental system, with minimal initial patch heterogeneity, limited the scope for metacommunity dynamics, dispersal effects on ecosystem function are likely to be even more important in other systems.

Many of the results presented in this dissertation were not predicted by existing metacommunity theory or biodiversity-ecosystem function theory. For instance, increasing the size of the species pool used to assemble metacommunities:

(1) increased spatial heterogeneity of ecosystem properties (Chapters II and IV),

(2) increased temporal variability of grazer and epiphyte abundance at the patch scale, but not at the metacommunity scale (Chapters II and IV), and

(3) decreased metacommunity resistance to disturbance (Chapter IV).

All of these outcomes were unexpected, since diversity is hypothesized to increase predictability in space and time and provide insurance against disturbance. These deviations from diversity-stability predictions were even more surprising given the strength and prevalence of positive diversity-ecosystem function relationships we found at both patch and metacommunity scales. Allowing grazers to move between patches also had effects not anticipated by biodiversity-ecosystem function theory. Dispersal:

(4) reduced grazer populations in diverse metacommunities without affecting metacommunity diversity (Chapters II and III),

(5) amplified temporal variability of grazer and epiphyte abundance within patches and metacommunities (Chapters II and IV), and

(6) eliminated the few stabilizing effects of diversity (Chapters II and IV).

I suspect that a large proportion of these deviations are because we studied **a)** effects of species pool size, rather than patch diversity, of **b)** actively mobile consumers that **c)** feed on a very dynamic resource. In combination, these three elements created a highly dynamic landscape, where patch heterogeneity was far from fixed. Grazers clearly affected patch heterogeneity of ecosystem properties in this system, as spatial variability of most properties mirrored patterns of beta-diversity. This dynamism in space and time contributed to many of the surprising results. For example, in our experiments, the number of possible interactions and resultant variety in community structures was greatly amplified, compared to previous microcosm experiments (McGrady-Steed et al. 1997, Naeem and Li 1997, Fukami et al. 2001, Morin and McGrady-Steed 2004), by allowing grazer composition to vary between patches, and having those grazers interact with temporally and spatially dynamic food resources. These differences explain why diversity increased, rather than decreased, spatial variability of ecosystem properties in our experiment **(1)**. The scope of interactions made possible by diverse grazer communities, which can compete through behavior as well as simple resource acquisition, feeding on dynamic food resources, might also explain why diversity increased, rather than decreased, temporal variability. Competitive outcomes could have shifted over the course of the experiment, inflating temporal variability of aggregate abundance **(2)** (Tilman 1996, Ives et al. 1999, Tilman 1999, Hughes and Roughgarden 2000, Ives et al. 2000, Ives and Hughes 2002). As another example, the interplay between selective grazer foraging in connected metacommunities and the continually recruiting microalgal community led to accumulations of less edible food sources, which limited grazer populations **(4)**. Similarly, when mobile consumers can actively select habitat patches, connecting patches may allow both rapid recruitment to an optimal habitat and emigration after resource depletion, inflating temporal variability within a given patch **(5)**. Finally, spatial heterogeneity created by grazers led to a wide variety of time courses of epiphytes and grazers among patches within the same metacommunity (Appendices 3-1, 4-2 and 4-3). This variety actually stabilized metacommunity-wide grazer and epiphyte abundance through time in unconnected metacommunities (Chapters II and IV). But, time courses became more synchronous with dispersal, just as patch compositions became more homogenized **(6)**. While these effects are complex, the common theme is that the combination of mobile animals feeding on a dynamic resource in multi-patch landscapes produced the effects.

Actively mobile consumers feeding on dynamic resources is a common scenario in nature, but little theory in the biodiversity-ecosystem function or even the metacommunity and metapopulation realms explores it. This combination of elements is probably the rule, rather than the exception, in aquatic systems. Patch heterogeneity in resource supply is highly variable through time in many aquatic systems, and the striking effects of consumers on primary producers in these systems is legendary (Hairston et al. 1960, Strong 1992). Dynamic patch heterogeneity is fairly common in terrestrial systems too (Levin et al. 1993), due to succession, localized disturbances like pest and disease outbreaks or treefalls, and, importantly, grazing (Sommer 2000, Adler et al. 2001, Flecker and Taylor 2004, Fryxell et al. 2005). However, most biodiversity-ecosystem function theory ignores both patch heterogeneity and temporal variability. Recent multi-trophic biodiversity-ecosystem function theory has predicted that generalist consumers could be de-stabilizing (Thébault and Loreau 2003, 2005, 2006), but has not included dynamic and diverse resources, or allowed consumers to disperse. Metacommunity theory, of course, considers patch heterogeneity and dispersal, but often assumes that patch heterogeneity is fixed, and that consumers cannot generate it. Metapopulation ecologists have tackled dynamic patch heterogeneity (Allen et al. 1993, Gyllenberg and Hanski 1997, Amarasekare and Possingham 2001, Johst et al. 2002), including predator-prey dynamics, but this work has not quite been placed within a metacommunity context yet. These gaps in theory may partly explain why virtually no empirical research has been conducted under these conditions. Hopefully this dissertation, along with recent papers and books focusing attention on these gaps (Srivastava 2002, Giller et al. 2004, Srivastava and Vellend 2005, Duffy et al. in press), the field of metacommunity ecology (Holyoak et al. 2005), and unifying food web theory with landscape ecology (Polis et al. 2004), will help spur theory development and more field and experimental studies that will challenge theory.

Also, more theory on how diversity might interact with spatial processes is needed. There is some evidence in this dissertation that diverse communities may resist colonizations. As shown in Chapter I, diverse grazer assemblages better resist "invasion" of new individuals because they utilize resources more fully. There is, essentially, less room for new individuals. In Chapter I, we viewed this through the lens of "invasion dynamics." But the same principle probably applies to colonizations in a broader sense, encompassing immigration of species already present in the patch as well as other species. Perhaps, then, diverse communities will be less affected by dispersal. Chapter IV presents slight evidence for this, in that diverse metacommunities may have better resisted synchronization by dispersal. I think that this idea merits exploring, particularly within plant communities. However, most ecosystem properties examined in Chapters II and IV were affected *more* by dispersal in diverse metacommunities than in species poor metacommunities. This apparent contradiction is intriguing, and it will be interesting to see whether or not other studies find that diverse metacommunities are more or less resistant to the effects of dispersal. Clearly, more work is needed to understand interactive effects of connectivity and diversity on ecosystem functions across landscapes.

Finally, I want to highlight the potential relationship between diversity and asynchrony of ecosystem function among patches suggested by this work (Chapters II and III). Asynchrony of aggregate abundance within diverse patches is a long recognized mechanism for generating stability (Tilman 1996, Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, Tilman 1999, Hughes and Roughgarden 2000, Ives et al. 2000, Ives and Hughes 2002). Likewise, metapopulation ecologists have studied the effects of dispersal on asynchrony of populations in patchy landscapes (Hastings 1993, Ranta et al. 1995, Ranta et al. 1997, 1998, Ruxton and Rohani 1998, Blasius et al. 1999, Shimada and Ishihama 2000). However, the idea that diversity at a coarser scale might generate patch heterogeneity sufficient to cause asynchrony among patches is fairly new. Evidence for asynchrony among patches in diverse metacommunities in my experiment was largely deductive: in order for patterns of temporal variability of grazer abundance within patches to differ from patterns of grazer abundance summed across patches within a metacommunity, as they did in Chapter II, patches simply *must* have asynchronous dynamics. This was slightly borne out by measures of asynchrony (Chapter III), but not to the extent I expected.[4] Too, temporal variability of grazers and epiphytes was *not* stabilized by diversity at the metacommunity scale in the second metacommunity experiment (Chapter IV); diversity was de-stabilizing at both scales. I strongly suspect that this was because there were only three patches in those metacommunities, rather than five, restricting the scope for asynchrony. So, again, the evidence for relationships between diversity and asynchrony among patches in this dissertation is not overwhelming. But the hints are sufficiently intriguing to merit further study, particularly because it has important implications for conservation.

For instance, if the number and heterogeneity of patches in a metacommunity is important for stabilizing metacommunity-wide ecosystem function, just as diversity within patches can stabilize patch function, habitat loss will have consequences for ecosystem function in addition to consequences for species persistence. Second, there might be tradeoffs between the levels of connectivity necessary for maximizing diversity, target population survival, and stabilizing ecosystem function. Third, although metapopulation ecologists have been concerned about dispersal-induced synchronization of population dynamics, synchronization of ecosystem function might occur at lower dispersal frequencies than synchronization of individual population dynamics. It will be

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[4] I think new measures of synchrony, designed to capture both phase angle and amplitude, rather than simple linear correlations, might be important for examining synchronization of ecosystem functions.

important to determine if dispersal can synchronize ecosystem function in other systems and in real landscapes, and whether or not it occurs coordinately, before, or after synchronization of population dynamics.

Overall, this dissertation takes steps towards addressing three of the major challenges to making biodiversity-ecosystem function research relevant to conservation: 1) scaling up to landscapes, 2) understanding diversity-function relationships within foodwebs, rather than simply within trophic levels, and 3) separating the direct effects of habitat fragmentation and dispersal on ecosystem function from its indirect effects, mediated by its effects on diversity (Giller et al. 2004, Srivastava and Vellend 2005). It is encouraging that many of the metacommunity-scale results presented here mirror previous patch-scale diversity-function research, especially since I/we allowed diversity to be dynamic, rather than static. However, connecting patches did often completely reverse effects of diversity on ecosystem function, and often rendered effects less predictable. Such interactive effects of connectivity and diversity on ecosystem function seem likely in other systems, given increasing habitat fragmentation in most ecosystems. More work is clearly needed to understand how connectivity and diversity might interactively affect ecosystem function, particularly since patches and ecosystems can be connected, and those connections disrupted, in such an amazing variety of ways. Some examples for future study include: passive vs. active dispersal, spatial configuration of patches and dispersal vectors, bi-directional vs. uni-directional dispersal (i.e. streams), which trophic levels systems are connected at, the degree of spatial or temporal overlap in the dispersal kernels of organisms within and between trophic levels, and whether dispersal vectors also bring or remove nutrients (i.e. most aquatic systems). Since connectivity plays an extremely important role in all of the major drivers of diversity change, particularly habitat fragmentation, species introductions, and climate change, it is essential that we understand how it affects diversity and ecosystem functions. This information is critical for conserving diversity and managing ecosystem services in light of the ongoing and projected changes to regional species pools caused by anthropogenic disturbance.

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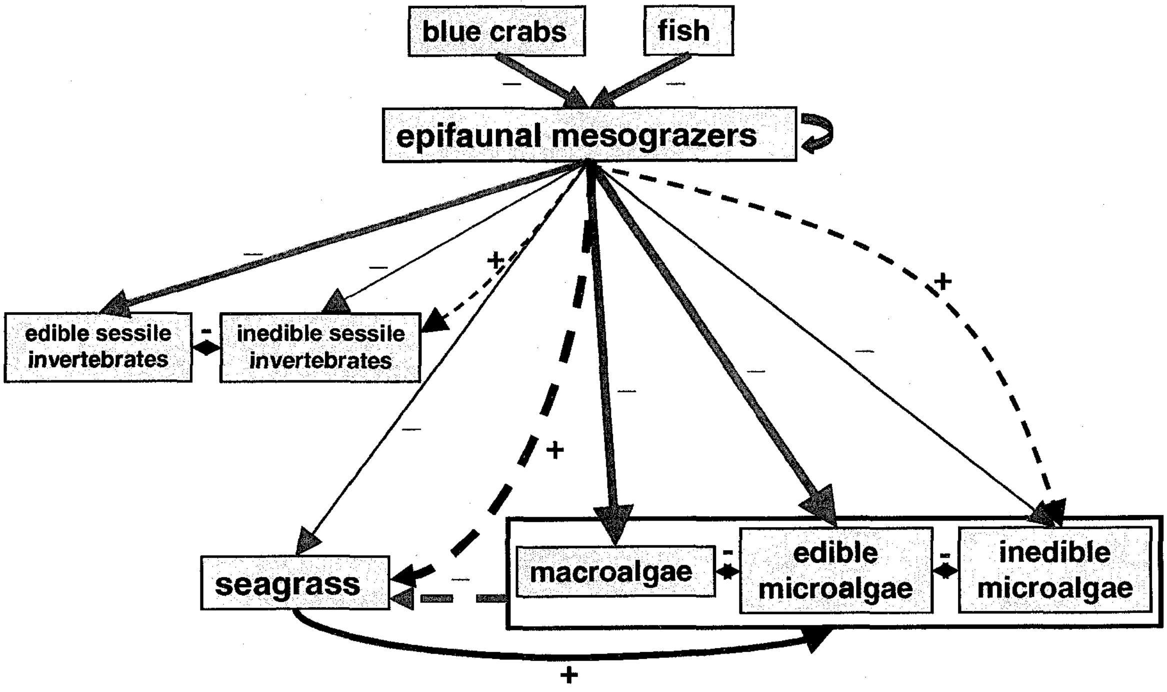
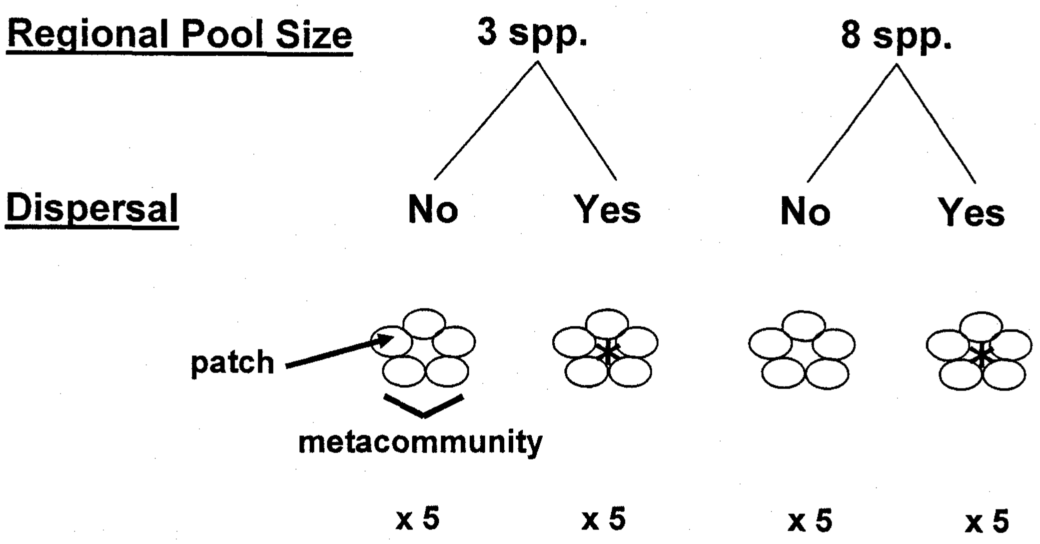
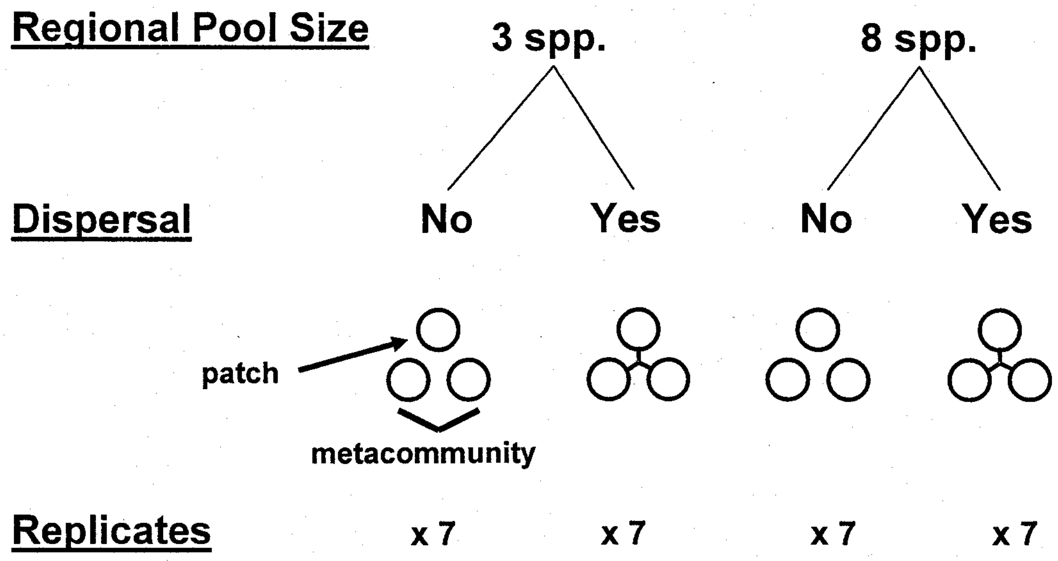


Appendix 5-1. Simplified seagrass food web diagram. Solid lines=direct interactions; dashed lines=indirect interactions. Red arrows indicate negative interactions; black arrows indicate positive interactions. Thickness of the arrows approximates relative interaction strength. Epifaunal grazers compete for resources and/or facilitate each other, depending on the species pair and environmental context. Some grazer species can consume juvenile grazers.



Appendix 5-2. Experimental design for Chapters II and III.



Appendix 5-3. Experimental design for Chapter IV.

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