SPATIAL VARIATION DRIVES PATTERNS OF COMMUNITY COMPOSITION AND TROPHIC INTERACTIONS IN A MARINE SYSTEM

A dissertation submitted to the Temple University Graduate Board

---

In partial fulfillment of the requirements for the degree
DOCTOR OF PHILOSOPHY

By
Elizabeth Wheeler Rielly
July 2015

Examining Committee Members:

Amy L. Freestone, Advisory Chair, Biology
Robert W. Sanders, Dissertation Examining Chair, Biology
Erik E. Cordes, Biology
Michael P. Russell, External Member, Villanova University

ABSTRACT

Examining how ecological processes are influenced by spatial variation can provide valuable insights into how communities are formed and how they may change in dynamic landscapes. In this thesis I address three objectives surrounding the spatial and temporal variation in species' recruitment and predation, the influence of habitat isolation on consumer-resource relationships, and the influence of habitat fragmentation on a multi-trophic system. I used marine invertebrates, specifically crustaceans, bivalves, and sessile species as a model system.

First, I address the spatial and temporal variation in local and regional processes in a multispecies assemblage of marine sessile invertebrates. Using diverse communities of marine sessile invertebrates as a model system I tested the hypothesis that spatial and temporal variation in recruitment and predation would shape local communities, and that both recruitment and predation would have significant effects on the abundance and structure of adult communities. I found that both recruitment and predation vary through time and space leading to the emergence of regional community divergence.

I also address how habitat isolation interacts with top-down and bottom-up processes in seagrass ecosystems. Spatial structure of the habitat may mediate top-down and bottom-up controls of species abundances through decreased habitat connectivity and increased habitat isolation. I manipulated top down and bottom up processes by excluding mesograzers, adding resources, or altering both factors in isolated and contiguous patches of artificial seagrass. I then measured epiphyte recruitment, epiphyte abundances, and macroalgae abundance. I paired this with epiphyte sampling from isolated natural seagrass patches. I found that habitat isolation significantly decreased the abundance of epiphytes settling on seagrass blades due to dispersal

limitation for epiphytic invertebrates. I found that consumers had strong effects on epiphyte biomass in continuous habitats, but not isolated habitats. Resource additions increased macroalgae cover and epiphyte biomass only in isolated habitats. The results suggest that isolated habitats may be nutrient limited and that top-down effects are stronger in continuous habitats, while bottom-up effects may dominate in isolated habitats.

In my third objective, I address how habitat fragmentation may alter marine food webs. I examined whether predation rates, prey, and predator behavior differed between continuous and fragmented seagrass habitat in a multi-trophic context at two sites in Barnegat Bay, NJ. I hypothesized that blue crab predation rates and foraging would decrease in fragmented seascapes, due to a reduction in adult blue crab densities, increasing survival rates of juvenile blue crabs and hard clams. I expected hard clams to exhibit weaker predator avoidance behavior in fragmented habitats because of decreased predation. I found that species' responses to fragmentation were different based on trophic level. Clams experienced higher predation and burrowed deeper in continuous habitats at both sites. Densities of blue crabs, the primary predator of hard clams, were higher in continuous habitats at both sites. Predation on juvenile blue crabs was significantly higher in fragmented seagrass at one site. Our results suggest that in fragmented seascapes, the impact of fragmentation on higher trophic level predators may drive predation rates and prey responses across the seascape, which may lead to trophic cascades in fragmented habitats.

DEDICATION

To PMAC.

ACKNOWLEDGEMENTS

First, I would like to thank Amy Freestone for her guidance, motivation, and mentorship. I have learned so much from her example. I would also like to thank my committee members, Erik Cordes, Mike Russell, and Bob Sanders for useful feedback during the development of the projects and subsequent manuscripts.

I owe many thanks to all of the undergraduate students who assisted me in the field for all of these experiments. I thank Kathleen Bezik, Kathryn Bendon, Chris Carnivale, Chris Clark, Ray Czaja, Cheryl Doughty, Crystal Hines, Ally Kessler, Lien Ly, Sean Kennedy, Bobby Kwait, Jennifer Linnell, Diana Lopez, Rachel Maddeluna, Pat Malezewski, Luis (Dan) Marrero, Mike McQuillan, Veronica Radice, Natasha Remon, and Brian Smith, for laboratory and field assistance. I am also extremely grateful to Kathleen Bezik for her video analyses and data organization. I thank Island Beach State Park, Rutgers University Marine Field Station, Great Bay Marina, All Seasons Marina, Dock Outfitters, JR and Debby Higgins, McGlades Restaurant, and Cape Horn Marina for accommodating our research, as well as Dan Parsons from Parsons Seafood Inc. for generously donating hard clam seed for all of my experiments that required clams.

I thank Katherine Papacostas, Sarah DeVaul, Kim Reuter, and Danielle DeLeo for coffee breaks, brunches, laughter, and moral support. I am so thankful to have gained such wonderful friends throughout this journey. It has been a privilege and joy to work with all of you. I thank all of the staff and faculty in the Temple Biology Department, especially Shohreh Amini, Derrick Love, Sheryl Love, Toni Matthews, Regee Neely, Allen Nicholson, Tania Stephens, Evelyn Vleck, Richard Waring, Demaris Watford, and Steve Widing.

I also want to thank my family, particularly my parents, Michael and Mary Ellen Rielly, whose love, guidance, and encouragement have continually given me the confidence and motivation to continue pursuing my goals.

My most heartfelt appreciation and deepest gratitude goes to Philip Carroll who has endlessly supported me through long days in the field and nights in the lab. I cannot imagine how this would have been possible without his unwavering encouragement, generosity, and patience; and to our son, Philip Michael Atticus, who has expanded my heart and mind in ways I never dreamed possible.

Finally, I would also like to thank my funding sources, which made this work possible in many ways. I thank the Sigma Xi Grants-in-Aid of Research Program, a Temple University Graduate school for a University Fellowship, and the National Science Foundation GK-12 program, and the National Science Foundation Division of Ocean Sciences.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

A longstanding and primary aim in community ecology has been to unravel how variation in spatial structure influences patterns of diversity in natural communities (Agrawal et al. 2007; Chesson 2000; Connolly and Roughgarden 1999). The spatial arrangement of physical and biological ecosystem properties is known to be an important driver of species' interactions such as competition, predation, and reproduction. However, clarifying how spatial variation influences patterns of species' distributions and abundance has been difficult to quantify (Legendre and Fortin 1989). Specifically, diversity patterns are a often the result of multiple ecological processes, which frequently operate at more than one spatial scale (Borcard et al. 1992; Fortin et al. 2002). Further adding to the complexity, an organism's responses to its environment may also vary with scale (Bellier et al. 2007). As a result of this complexity, how spatial variation influences community dynamics and interactions is not always clear.

1.1 Local and Regional Processes

Local species interactions such as predation and competition can have a strong influence on community structure, shaping patterns of species' diversity and composition (Connell 1961; Menge 2000). Large scale variation in recruitment, the supply of new individuals from the regional species pool to local populations, has long been recognized as a major factor affecting species interaction outcomes and community composition, and has the potential to supersede the influence of local interactions (Doherty and Fowler 1994; Hubbell 2001; Lathlean et al. 2010; Leibold et al. 2004; Lewin 1986; Minchinton

and Scheibling 1991). It is largely well accepted that both local and regional scale processes are important to structuring natural communities (Palmer et al. 1996; Ricklefs 1987). The relative importance of local interactions and regional recruitment remains a topic of debate, and to further add to this complexity, both local interactions and recruitment can vary through time in addition to space (Lagos et al. 2005). The spatial and temporal variation in the strength of these processes likely results in interactive effects on community structure.

1.2 Consequences of Habitat Fragmentation

In addition to the natural variation in ecological processes through space and time, the effects of habitat loss on the spatial patterning of habitat has become increasingly crucial to understand. Habitat loss is the primary driver of biodiversity loss, and is accelerating at unprecedented rates (Brooks et al. 2002; Duffy 2003; Krauss et al. 2010; Orth et al. 2006). Habitat loss results in the division of large connected areas of habitat into smaller more isolated patches (Fahrig 2003). The effects of habitat isolation on species distributions can be both direct and indirect (Gustafsson and Salo 2012; Johnson and Heck 2006). Habitat isolation can directly alter the abundances of organisms through dispersal limitation (Prugh et al. 2008). In addition, trophic-relationships may be altered by isolation through changes in the abundances of predators or resources (Chase 2010).

Ecologists have long utilized Island Biogeography Theory (IBT) to make predictions about the impacts of habitat isolation (Ferraz et al. 2007; MacArthur and Wilson 1967; Prugh et al. 2008). A central supposition of IBT is that an island's distance from a source of colonists determines the number of species that will inhabit the island, with isolated islands being less likely to receive immigrants due to decreased connectivity

(Ferraz et al. 2007; Gustafsson and Salo 2012; MacArthur and Wilson 1967; Prugh et al. 2008; Roberts and Poore 2006; Schüepp et al. 2011; Steffan-Dewenter and Tscharntke 1999). However, empirical studies in many ecosystems have shown these affects may be stronger on higher trophic levels (Brückmann et al. 2011; Krauss et al. 2010; Valladares et al. 2006). Subsequently, top-down and bottom-up relationships in isolated habitats may be changed.

Habitat fragmentation, another consequence of habitat loss, may also change species' trophic interactions (Hovel and Lipcius 2002; van Nouhuys 2005). Habitat fragmentation is the breaking apart of one patch of habitat into several smaller patches (Franklin 2002). The behavior of both predator and prey is crucial to their ability to survive and reproduce, emphasizing the importance of understanding how fragmented conditions may alter behavior (Dill et al. 2003; Flynn and Smee 2010; Tigas et al. 2002). In particular, the rate of foraging activity or strength of anti-predator strategies may change with landscape structure and trophic position. However, no studies have explicitly tested the effects of habitat fragmentation on multi-trophic interactions (>two levels) *in situ* in a marine systems (but for a mesocosm exception see Johnson and Heck 2006). Therefore, how habitat fragmentation drives more complex trophic interactions, changes in behavior, and the cascading effects on other trophic levels is not clear.

1.3 Specific Aims

Examining how ecological processes are influenced by spatial variation can provide valuable insights into how communities are formed and how they may change in dynamic landscapes. I therefore address three objectives related to the spatial and temporal variation in species' recruitment and predation, the influence of habitat isolation

on consumer-resource relationships, and the influence of habitat fragmentation on a multi-trophic system. These studies used marine invertebrates as a model system, specifically crustaceans, bivalves, and sessile species. The following chapters outline the three studies designed to address these objectives.

First, I address the spatial and temporal variation in local and regional processes among a multispecies assemblage of marine sessile invertebrates. The relative importance of regional processes such as recruitment and local biotic processes like predation are not well understood, especially for diverse communities. Particularly in marine systems, where most previous empirical efforts to explore the relationship between recruitment, predation, and adult abundances have taken a single species perspective (Caffey 1985; Dethier et al. 2010; Karlson 2006; Lagos et al. 2005; Rilov and Schiel 2011). I determined how the spatial and temporal variation in both recruitment and predation influences community structure across a large region.

Second, I address how habitat isolation may interact with or alter top-down and bottom-up processes in seagrass ecosystems. Effects of habitat isolation on species distributions may differentially affect trophic levels. Alterations in the distributions of higher trophic level organisms or resource availability may alter consumer-resource interactions. Reduced abundances of higher trophic levels may subsequently increase the abundances of lower trophic levels through weakened top-down control (Davies et al. 2000). In addition, there is also recent evidence that habitat isolation may reduce nutrient availability (Haddad et al. 2015). Spatial structure of the habitat may mediate top-down and bottom-up controls of species abundances through decreased habitat connectivity and

increased habitat isolation (Komonen et al. 2000; Simon 1992; Tilman and Kareiva 1997).

Finally, for my third objective, I address how habitat fragmentation may alter predation rates, predator foraging behavior, and prey anti-predator behavior in a multi-trophic *in-situ* system. As noted previously, certain trophic levels may be more influenced by fragmentation due to their behavioral responses (Tigas et al. 2002). In particular, the rate of foraging activity or strength of anti-predator strategies may change with landscape structure and trophic position (Kinlan and Gaines 2003). Like in terrestrial systems, habitat fragmentation has been shown to have negative effects on predator abundances in marine environments (Hovel and Lipcius 2001; Layman et al. 2007; Eierman and Connor 2014); however no multi-trophic *in situ* examples have been performed. How habitat fragmentation drives more complex trophic interactions, changes in behavior, and the cascading effects on other trophic levels is not clear.

CHAPTER 2

SPATIOTEMPORAL VARIABILITY IN RECRUITMENT AND PREDATION SHAPES LOCAL DIVERSITY PATTERNS AND DRIVE REGIONAL COMMUNITY DIVERGENCE

2.1 Abstract

The diversity of ecological communities can be strongly limited by recruitment of individuals, and highly influenced by post-recruitment processes such as predation. Recruitment can also have temporal implications, with early recruits having a persisting impact on patterns of adult abundances. Predation, a key species interaction, has also been shown to affect the diversity of adult communities. Previous theoretical and empirical studies have shown predation can enhance coexistence and diversity by increasing the abundance of less competitive species. Both recruitment and predation are likely important to shaping diversity patterns at different spatial scales, but how spatial and temporal variability in each acts to characterize patterns of regional diversity is less clear. Using diverse communities of marine sessile invertebrates as a model system I tested the hypothesis that spatial and temporal variation in recruitment and predation would shape local communities, and that both recruitment and predation would have significant effects on the abundance and structure of adult communities. I found that both recruitment and predation vary through time and space leading to the emergence of regional divergence in adult communities.

2.2 Introduction

A longstanding and primary aim in community ecology has been to disentangle the underlying mechanisms that maintain patterns of diversity in natural communities (Agrawal et al. 2007; Chesson 2000; Connolly and Roughgarden 1999). From a supply-

side perspective, diversity patterns in mature communities are characterized by fluctuations in the supply of individuals to local populations from the regional species pool (i.e., recruitment) that can override the influence of local interactions (Hubbell 2001; Lathlean et al. 2010; Leibold et al. 2004; Lewin 1986; Minchinton and Scheibling 1991). By contrast, local species interactions also exert strong forcing over community structure and can shape patterns of species' diversity and composition (Connell 1961; Menge 2000). Presently, it is largely well accepted that both regional and local scale processes are important to structuring observed patterns in natural communities (Palmer et al. 1996; Ricklefs 1987). The relative importance of each remains a topic of debate; in particular, few studies have examined the influence of both local and regional processes on multi-species assemblages. To further add to this complexity, both recruitment and local interactions can vary with space and time (Lagos et al. 2005), and the spatial and temporal variation in the strength of these processes likely results in interactive effects on community structure.

Spatial and temporal variation in recruitment of new individuals to the local community can have important impacts on community structure (Caffey 1985; Connell 1985; Karlson 2006; Nathan and Muller-Landau 2000; Sale et al. 1984). Indeed, the diversity of communities can be strongly limited by recruitment (Palardy and Witman 2014), and temporal variation in recruitment can result in temporal niche partitioning, wherein species peak in their recruitment at different time points. Temporal niche partitioning can serve as a mechanism to increase richness by allowing the establishment of rare species (Fernandez et al. 2014; Stachowicz et al. 2002). Colonization and early survival of recruits can also have persisting implications for patterns of adult community

diversity (Palardy and Witman 2014, Sutherland 1981). However, other studies have shown regional recruitment to be highly divergent and decoupled from local community structure and abundances (Caro et al. 2010; Dethier et al. 2012)

A possible mechanism for the decoupling of recruitment and adult community composition may be strong local interactions, such as predation, the effect of which can also vary widely across space and time. Landmark empirical studies have demonstrated the importance of predation in structuring communities (Connell 1961; Menge and Sutherland 1976; Paine 2002). Predation can increase resource availability and the abundance of less competitive species, thereby increasing coexistence, the variation among local communities (i.e., beta diversity), and regional diversity (Shurin and Allen 2001; Chase et al. 2002). Like regional processes, predation can also be spatiotemporally variable. The effect of predation can be context-dependent and vary across spatial gradients such as latitude (Freestone et al. 2011) and seasonal temporal gradients (Hovel and Lipcius 2001; Lass and Spaak 2003; Sih et al. 2000). Variation in predator identity (Bernot and Turner 2001; Grabowski et al. 2008; Turner et al. 1999), density (Crowder and Cooper 1982; Louda 1982; Sih et al. 1998), and predation intensity (Connolly and Roughgarden 1999; Denno et al. 2005; Sutherland 1982) can cause a suite of different outcomes including an increase or decrease in competition (Wootton 1994), an increase or decrease in coexistence (Caswell 1978), or have no observable effect (Chase et al. 2002; Knights et al. 2012). Predation on superior competitors can increase coexistence by preventing competitive exclusion, allowing inferior competitors to become established (Caswell 1978; Weis and Vasseur 2014; Wollrab et al. 2013). Temporal variability in predation can also be important to structuring community composition (Navarrete 1996).

Predation can often be more important at early assembly stages than mature stages (Osman and Whitlatch 2004; Rilov and Schiel 2006; Sams and Keough 2007), and these early stage effects can persist over time (Nydam and Stachowicz 2007). Spatiotemporal variability in predation can therefore have important and lasting effects on community structure.

The interactive importance of recruitment and predation hinges on their relative strengths. High recruit abundances can override predator influence (Sams and Keough 2007a), and likewise, the effect of predation can be dependent on the recruitment rate (Robles 1997). Predation has also been shown to account for more variability in species densities than recruitment (Rilov and Schiel 2011). Importantly, the two are inexorably linked; propagule abundances at the regional scale are determined in part by abundances of reproductive adults, which are in turn affected by species interactions like predation (Connolly and Roughgarden 1999). Despite the inherent linkage between the two processes, few studies have examined them simultaneously on a multi-species assemblage (but see Osman and Whitlatch 2004).

How the interactive influence of recruitment and predation, and the spatiotemporal variability in these processes, shape multi-species assemblages is therefore not clear; particularly in marine systems, where most previous empirical efforts to explore the relationship between recruitment, predation, and adult abundances have taken a single species perspective (Caffey 1985; Dethier et al. 2010; Karlson 2006; Lagos et al. 2005; Rilov and Schiel 2011). This gap in our understanding is partly because descriptions of temporal variability in patterns of richness and structure of recruiting individuals are scarce due to the logistical difficulties of working with multispecies

assemblages of recruits (Fernandez et al. 2014). Existing empirical studies that examine a multispecies assemblage of recruits have found a decoupling of adult communities and recruitment rates (Caro et al. 2010; Fernandez et al. 2014; Forde and Raimondi 2004; Osman and Whitlatch 2004). Local interactions were hypothesized to be important in explaining these differences but were not explicitly considered (but see Osman and Whitlatch 2004).

To assess the interactive influence of recruitment and predation, I examined how spatiotemporal variability in each may drive patterns of community structure in a marine ecosystem. I hypothesized that both recruitment and predation would have significant effects on the abundance and structure of adult communities.

2.3 Methods

To test for effects of spatiotemporal variability in recruitment and predation on community structure I utilized marine sessile invertebrate communities, which occur worldwide in assemblages that vary in diversity (Palardy and Witman 2014; Witman et al. 2004). These communities can be influenced by the regional recruitment pool and local interactions such as predation (Freestone et al. 2001; Freestone et al. 2013; Sams and Keough 2012, 2013; Vieira et al. 2012), but it is unclear how spatiotemporal variation in recruitment and predation may influence community structure. In bays and estuaries, a large proportion of marine invertebrate species are restricted to hard substrate, facilitating collection using artificial settlement substrates (Ruiz et al. 1997; Ruiz et al. 2009). The study region encompassed three bays along a 90 km stretch of coastal New Jersey, protected by barrier islands (Fig. 2.1). From north to south these bays were

Barnegat Bay (39.8517° N), Great Bay (39.5100° N), and Great Egg Harbor Bay (39.3042° N). I established three study sites per bay, for a total of nine sites across the region, although only eight sites were considered due to the loss of all replicates at one site in Little Egg Harbor Bay (see Table 2.1 for site descriptions and abbreviations, Fig 2.1 for map).

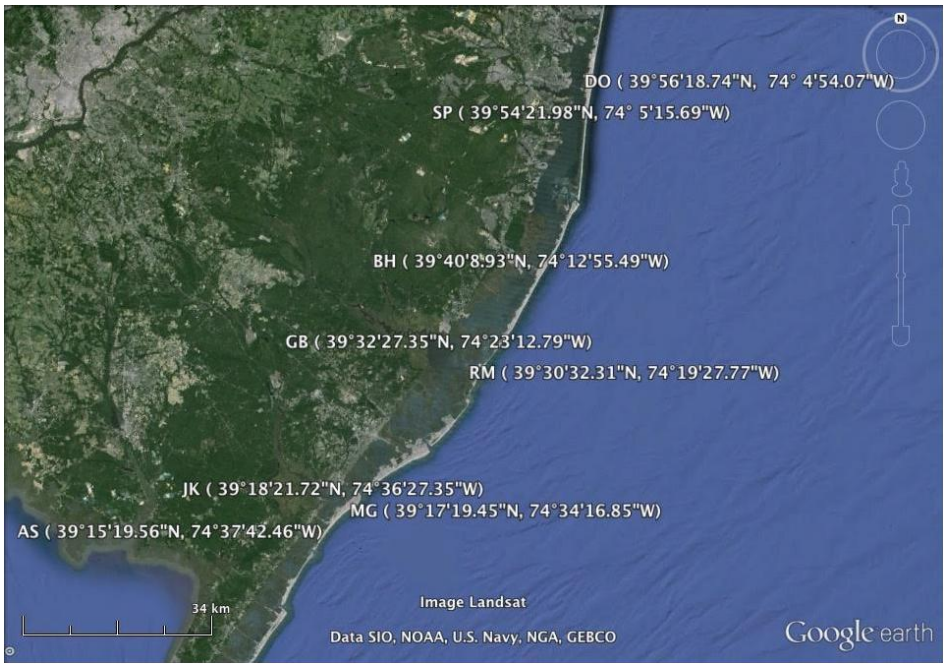

Figure 2.1: *Study Region Map.* Site abbreviations and sampling information can be found in Table 2.1.

Table 2.1: Study site information

Site	Abbreviation	Bay	Collected
Higgins Park	HP	Barnegat Bay	Adults
Island Beach State Park	IBSP	Barnegat Bay	Recruits, Adults
Dock Outfitters	DO	Barnegat Bay	Adults
Rutgers Marine Field Station	RMFS	Great Bay	Adults
Cape Horn Marina	CH	Great Bay	Adults
Great Bay Marina	GBM	Great Bay	Recruits, Adults
Ocean City	OC	Little Egg Harbor Bay	Recruits, Adults
All Seasons Marina	ASM	Little Egg Harbor Bay	Adults
Kennedy Park	KP	Little Egg Harbor Bay	Lost

To examine temporal and spatial variability in recruitment, I measured recruitment rates in the presence and absence of predators at three sites (one per bay), using 10cm x 10cm polyvinyl chloride (PVC) panels beginning in May 2012, when juvenile recruitment begins in the region (Rielly and Freestone unpublished data). At each site, five panels were deployed exposed to predation and five were enclosed in mesh (1.7 × 1.4 mm) fiberglass caging to exclude both macro and micropredators (N=30). Preliminary experiments in the same study region showed no effect of caging or cage controls on recruitment communities (Rielly and Freestone unpublished data), and previous studies indicate that this mesh size is effective at excluding nearly all predators without excluding the settlement of sessile invertebrate larvae (Freestone et al. 2011). Panels were attached in a vertical orientation to a 0.65 cm plastic mesh support with treatments arranged haphazardly on the mesh support, which was secured upright into the sediment with PVC stakes. Panels were attached to the support leaving 10cm of plastic mesh between the bottom of the panels and the sediment to reduce sedimentation while allowing for benthic predator access. After two weeks, the panels were retrieved and

replaced with clean panels. The recruits on the retrieved panels were identified to the lowest taxonomic unit possible (usually species) and enumerated for richness and abundance (i.e., number of individuals/taxonomic group).

To examine the influence of recruitment and predation on adult community structure, I deployed fifteen 10cm x 10cm PVC panels at each of the nine sites in the study region simultaneously with the recruitment experimental deployment in May 2012 (Table 2.1). Within each site, I deployed the following three treatments in replicates of five (15 panels per site, N=135): (1) predation exclusion (panels enclosed in 1.7 x 1.4 mm caging to exclude predators); (2) predation exposure (panels exposed to the full predator community); and (3) predation control (panels partially caged with a top and two sides constructed of 1.7 x 1.4 mm caging). Every two weeks the cages were cleaned and replaced if needed. Panels were deployed for 12 weeks, encompassing the peak recruitment season for the region (Rielly and Freestone, unpublished data). Upon retrieval, all organisms were identified to the lowest taxonomic unit possible (usually species), and communities were enumerated for total richness and percent cover of each species using a 100-point grid.

I first tested for spatial and temporal variability in recruitment across the study region. To analyze how patterns of recruitment may vary both spatially and temporally, and how predation may affect recruitment within the study region, I used a mixed model with factors of site (random effect, 3 levels), time point of collection (fixed effect, 6 levels), predation (fixed effect, 2 levels), and all interaction terms to test for differences in total abundance (of all species) and richness. Post-hoc comparisons on any significant effects were made using Tukeys honest significant difference test (HSD). To detect site

specific differences in the richness and abundance of recruits I performed separate analysis of variance (ANOVA) on recruits at each site with a fixed effect of time. For these analyses only data from unmanipulated panels (no caging) were used to examine observed variability through time. To examine how the community composition of recruits may vary through time and across sites, I used a permutational ANOVA (PERMANOVA) (Anderson 2001) with factors of site (random effect), predation (fixed effect), collection time point (fixed effect), and all interaction terms on community composition. Of particular interest, the interaction between for site and collection time point tested for temporal and spatial variability in recruit community composition. I also used a PERMDISP with a random effect of site to test for homogeneity of dispersion to identify changes in community divergence within groups. PERMDISP compliments PERMANOVA by illustrating how community dissimilarity (divergence) may increase or decrease within a treatment. For all multivariate analyses I used Bray-Curtis similarity matrices to compare communities.

Next, I examined the spatial variability in predation on adult communities. To test for spatial variation in the abundance (percent cover) and richness of adult communities I used a mixed model analysis with factors of site (random effect, 8 levels), nested within bay (random effect, 3 levels), predation treatment (fixed effect, 3 levels), and all interaction terms. Post-hoc analyses on significant fixed effects were made using Tukeys HSD test. To test for spatial variation in the effect of predation on adult community composition, I used a PERMANOVA with site (random effect, 8 levels) nested within bay, bay (random effect, 3 levels), and predation treatment (fixed effect, three levels), and all interaction terms. Post-hoc comparisons were made using

PERMANOVA pairwise tests. I extracted the components of variation from the individual PERMANOVAs at each site and applied a square root transformation to estimate an effect size of treatment. I also used a PERMDISP with predation as a fixed factor to examine the regional effect of predation across all eight sites to identify changes in community divergence within groups. SIMPER analysis was employed to identify the species that are most important in structuring the observed patterns in similarity or dissimilarity.

To compare the recruit community composition to adult community composition at the three sites where I collected both suites of data I used a PERMANOVA with a fixed effect of age (i.e. adult or recruit) and random effect of site (3 levels) to determine if the composition of recruits and adults were similar. For this analysis I omitted the factor of collection time point for recruits because I was interested in the aggregate differences among all recruit communities and adult communities. Post-hoc comparisons were made by using PERMANOVA pairwise tests. I also tested for differences in dispersion between recruits and adults using a PERMDISP with a fixed factor of age. For all analyses where recruit communities were directly compared to adult communities, I transformed recruit abundances to percent cover, calculated by multiplying the number of individuals by the average recruit size settling on a panel divided by the surface area of the panel ($100cm^2$) to ensure that the data were directly comparable to adult communities which were measured as percent cover. Recruit size was measured using ImageJ software to digitize the area of each recruit on photos of two week old recruitment communities. I measured 795 individual recruits from a diversity of taxonomic groups across 55 recruitment panels and averaged all measurements. The average recruit size

across all species was 0.0725±0.059 cm^2. To ensure that the comparison of the recruit data to adult data was robust, I also utilized two other approaches to standardize these data sets: 1) I transformed the recruit data into percentages by using the proportion of the site maximum for each species (Caro et al. 2010) and then analyzed the data as described above using a Bray-Curtis similarity matrix, and 2) used a Jaccard's similarity matrix (presence-absence) in analyses described above to examine patterns of species occurrence between recruit and adult communities. All results were qualitatively similar, and here I present only the results from the recruitment percent cover transformation using a Bray-Curtis similarity matrix.

2.4 Results

My results supported the hypothesis that recruitment is temporally variable, for total abundance, richness, and community structure of the recruit assemblage. The abundance of recruits on the settlement panels changed through space and time at each site (Fig. 2.2).

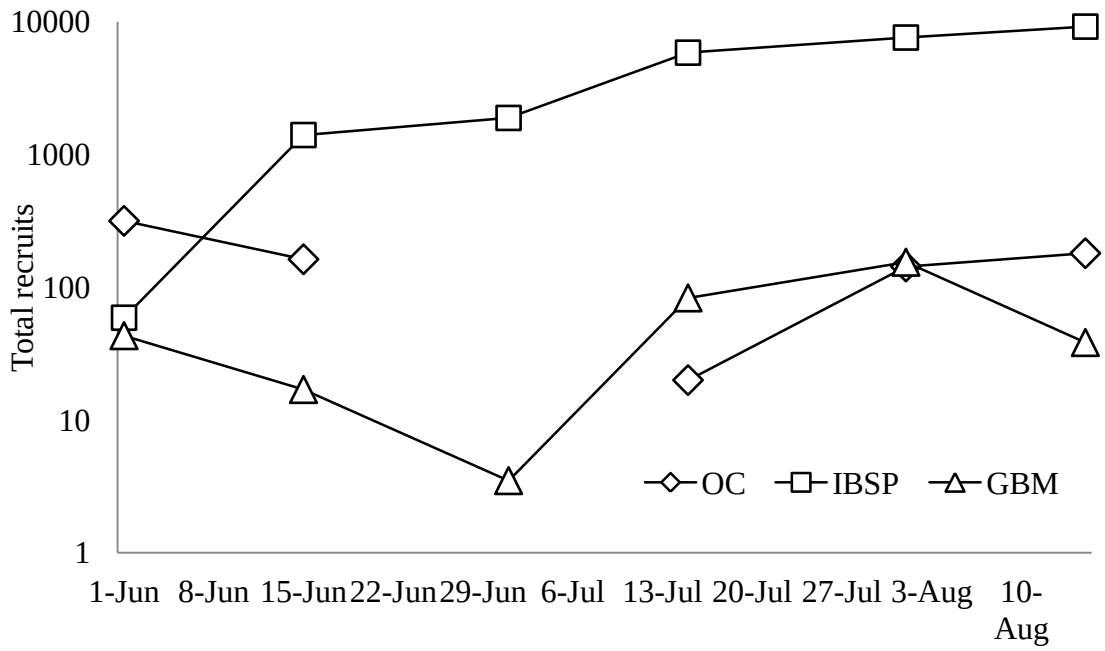

Figure 2.2: *Recruitment rates across three sites are temporally variable.* Site IBSP is open squares, Site OC is open diamonds, and site GBM is opened triangles. Mean values are shown on a log scale.

The most variation in recruit abundance patterns was explained by site (47%). After site, the time point of collection by site interaction term explained 40% of the variation. Time point of collection was not a significant main effect in the model (mixed model: R^2_{adj}=0.874, N=157; time point of collection: $F_{1/9.11}$=0.98, P>0.05; predation treatment: $F_{1/2.18}$=1.39, P>0.05; predation treatment x time point of collection: $F_{1/8.13}$=0.80, P>0.05). The large amount of variation accounted for in the site by time point of collection interaction term combined with the absence of a main effect of collection time point suggests that while the abundance of recruits varies through time, this effect is spatially dependent.

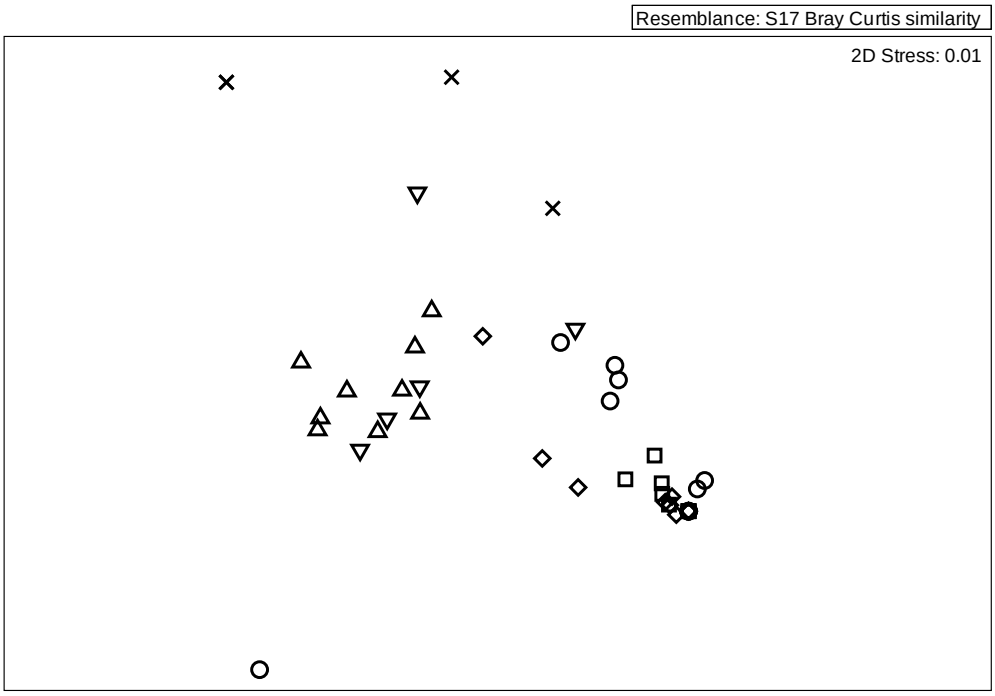

Figure 2.3: *Composition of recruits varies through time.* Non-metric multidimensional scaling ordinations (nMDSs) on the basis of Bray-Curtis dissimilarity measure over time at site GBM [upright triangle: June 1, downward triangle: June 15, x: July 1, square: July 15, diamond: August 1, circle: August 15].

At IBSP, recruitment continued to increase throughout the entire reproductive period (ANOVA: R^2_{adj}=0.75, N=25, $F_{4/20}$=19.43, p<0.0001). Recruit abundances increased from a mean low of 60 individuals to a mean high of nearly 10,000 individuals. Recruitment at OC had two distinct peaks, one in the beginning of the reproductive period and one at the end. Abundances declined by 90% between peaks (ANOVA: R^2_{adj}=0.76, N=25, $F_{4/20}$=19.84, p<0.0001). Site GBM follows a similar trend of increase and decline, but recruitment was low overall, with a maximum that was 50% less than the maximum for OC and 92% less than IBSP, and abundances had only marginally significant changes

across time (P=0.091). I found a similar pattern for recruit species richness. Site was again the most important random effect in the model, accounting for 43.17% of the variation. The interaction between site and time point of collection accounted for 17.09% of the variation (Mixed model: R^2_{adj}=0.615, N=157; time point of collection: $F_{1/9.28}$=01.45, P>0.05; predation treatment: $F_{1/2.11}$=0.0097, P>0.05; treatment x time point of collection: $F_{1/8.44}$=3.37, P>0.05).

In addition to temporal variation for recruit abundance and richness, the community composition of recruits on settlement panels changed through time as well, with distinct recruit communities settling at most time points throughout the sampling period (PERMANOVA: site: Pseudo -$F_{2/123}$=53.541, P(perm)=0.0001; site x predation treatment: Pseudo -$F_{2/123}$=1.547, P(perm)=0.01; site x time point of collection: Pseudo – $F_{9/123}$=13.581, P(perm)=0.0001; site x time point of collection x predation treatment: Pseudo –$F_{8/123}$=1.65, P(perm)=0.0001). At OC and IBSP, community composition of recruiting assemblages at each time point differed from all other recruit communities at that site (PERMANOVA pairwise comparison). At GBM, communities from June 1 and June 15 were not significantly different from each other but all other possible comparisons were different (Fig. 2.3; PERMANOVA pairwise comparison). Predation had an inconsistent small effect on some rounds of recruitment at some sites (PERMANOVA pairwise comparison). Site was also very important to shaping community composition of recruits and similarly will be addressed in greater detail below. The temporal variability in recruit community composition is site specific and spatially dependent. Similar to the pattern observed in recruit abundance and richness,

time is not a significant main effect but rather the interaction between site and time point of collection is important to community composition.

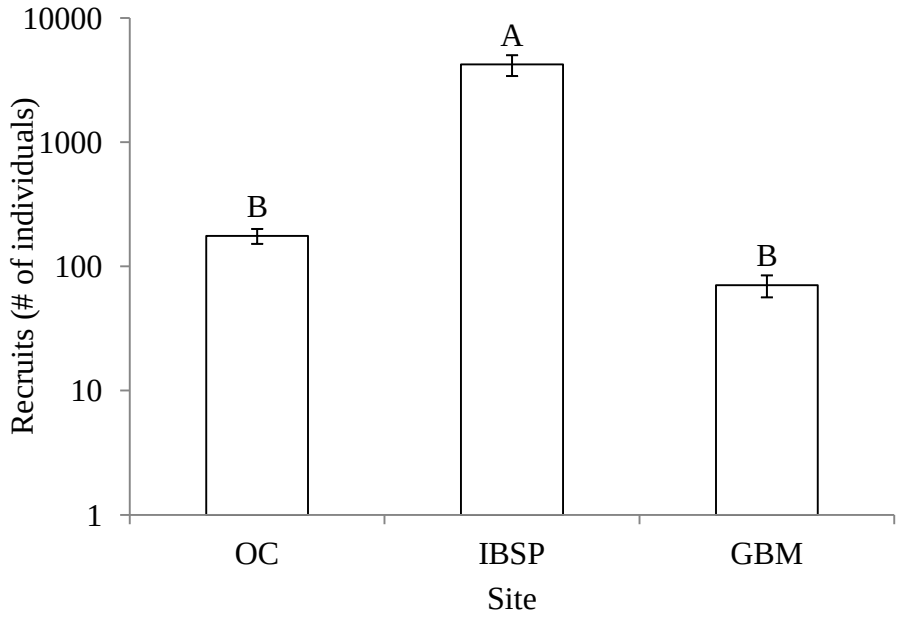

Figure 2.4: *The abundance of recruits is spatially variable*. Mean total recruitment at 3 sites. Natural log transformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

Recruitment was spatially variable; the variation in recruit abundance and richness was 47% and 43% accounted for by site alone, respectively. Recruit abundances were the highest at IBSP (Fig. 2.4). The mean abundance of recruits at IBSP was higher than both site OC and GBM (Tukey HSD). Recruit mean abundance at IBSP was seventy-five times higher than the mean abundance of recruits at GBM, where recruitment was the lowest. Mean recruit abundance at OC was double GBM, however, the two sites were not significantly different from each other. The richness of recruits

also differed among sites (Tukeys HSD). GBM had the lowest abundance of recruits and also had the lowest taxonomic richness. Recruit richness showed patterns similar to recruit abundance. Richness was highest at IBSP, where recruit abundances were also highest, and vice versa, lowest at GBM where recruitment abundance was also lowest. Recruit richness at IBSP was double that of GBM (7.8 and 3.5 species respectively). Each site also had very distinct communities of recruits that differed from both other sites (Fig. 2.5). Recruit communities at each study site not only differed in composition, but also in community dispersion, or within site compositional variability (PERMDISP: pseudo-$F_{3/155}$= 10.58, P(perm)= 0.0002) within and among sampling time points. The high recruit abundances at IBSP were driven by large numbers of spirorbid worm recruits, which resulted in very similar recruit communities that were dominated by these worms. In contrast, within sites OC and GBM, the recruit assemblages were more dissimilar in their composition leading to higher community dispersion. Both OC and GBM were more variable in composition than IBSP (PERMDISP all pairs comparison).

Table 2.2: Components of variation (square root) for the effect of predation on the community composition of adult sessile invertebrates.

Site	Components of Variation (SQRT)
ASM	19.40
IBSP	23.39
OC	30.5
HP	31.98
OC	33.73
DS	41.15
CH	42.79
GBM	45.76

While recruitment varied spatially and temporally, another interesting outcome was that predation had little to no effect on recruitment. Predation had no effect on the abundance or richness of recruits, and had a minimal and inconsistent effect on recruit community composition. Predation resulted in a change in recruit composition at only one or two out of the twelve time points of collection (PERMANOVA pairwise comparisons).

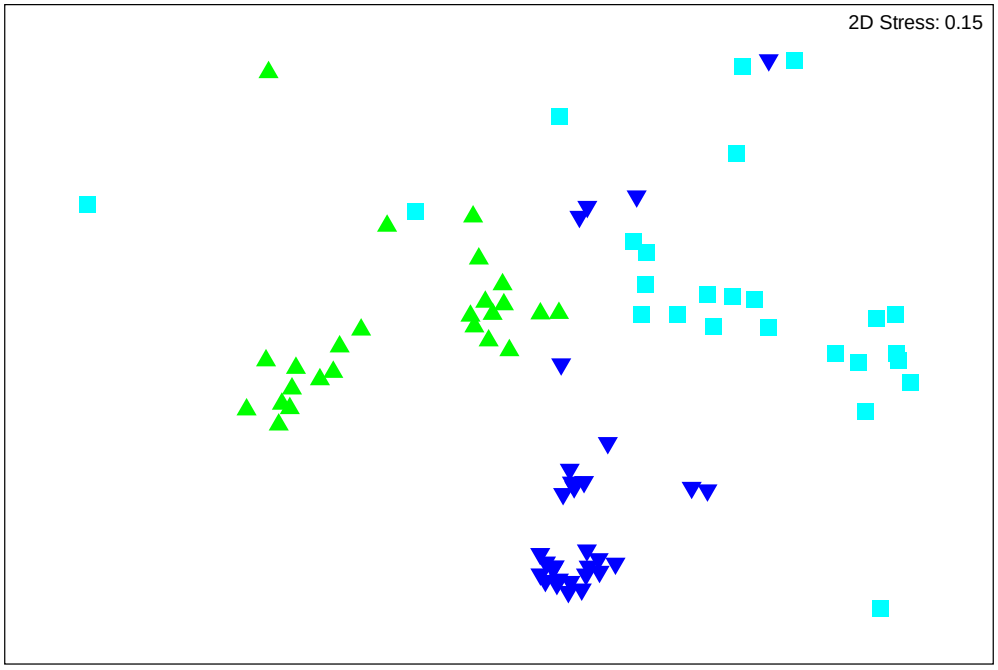

Figure 2.5: *The composition of recruits is spatially variable*. Non-metric multidimensional scaling ordinations (nMDSs) on the basis of Bray-Curtis dissimilarity measure by site [green upright triangle: site OC, teal square: site GBM, blue inverted triangle: site IBSP].

In contrast to the weak effect of predation on recruits, predation shaped adult assemblages at each of the eight sites where I collected adult communities (PERMANOVA: predation treatment: pseudo-$F_{2/94}$=8.201; P(perm)= 0.0001; site[bay]: pseudo-$F_{5/94}$=26.391, P(perm)=0.0001; predation treatment x site[bay] interaction:

pseudo-$F_{10/94}$=3.762, P(perm)=0.0001; bay: P(perm)>0.05; bay x predation treatment interaction: P(perm)>0.05). PERMANOVA pairwise comparisons showed that predation altered community composition at each site. The results suggest that predation may have a weaker effect on earlier life stages, but the aggregate effect over time acts to shape the composition of adult communities.

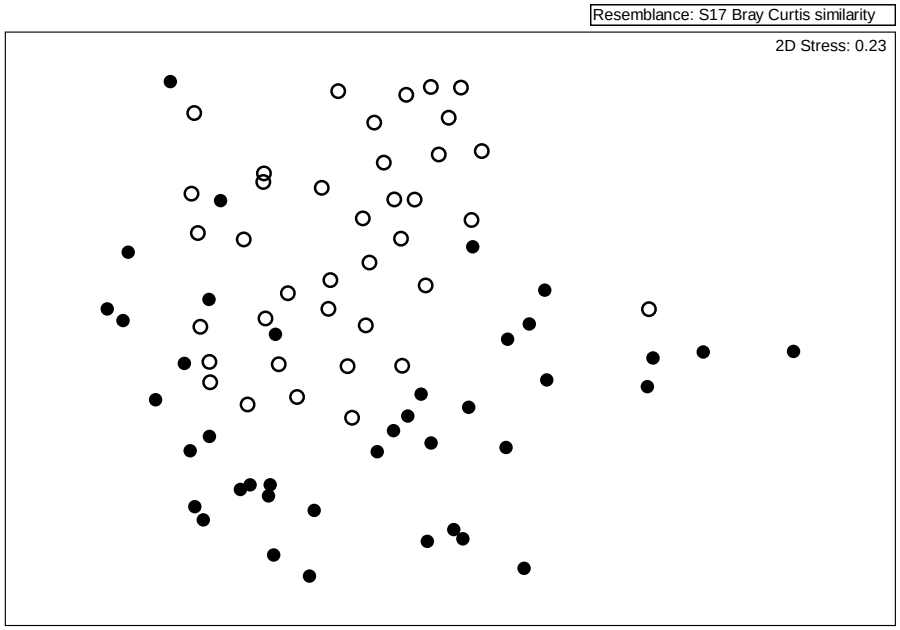

Figure 2.6: *The effect of predation drives regional divergence in adult community composition*. Non-metric multidimensional scaling ordinations (nMDSs) on the basis of Bray-Curtis dissimilarity measures for adult communities across all 8 sites in the study region exposed to (filled circles) and excluded from (open circles) predation.

While the effect of predation on adult communities was consistently significant, the strength of the effect varied by over two fold, as shown in the significant interaction term between site[bay] and predation treatment, and the components of variation, a measure of effect size of predation on community structure (Table 2.2). Interestingly,

among those sites where both recruit and adult communities were measured, the effect size was lowest at the site where recruitment was the highest (IBSP), and in contrast, the effect size of predation was the highest at the site where recruitment was the lowest (GBM).

Adult communities exposed to predation had greater community divergence (i.e., variation in composition) across the region than those which were excluded from predation (Fig. 2.6, PERMDISP predation treatment: pseudo-$F_{1/76}$=14.14, P(perm): 0.001). *Molgula manhattensis*, a solitary tunicate, was the most important species to structuring the observed patterns in dissimilarity between communities exposed to and excluded from predation (SIMPER), experiencing large declines in abundance in the presence of predators, allowing for the settlement of other less dominant species (Fig. 2.7). Interestingly, while predation had a consistent effect on the composition of adult communities, it did not affect total abundance of all species or the taxonomic richness of adults (mixed model: $p>0.05$).

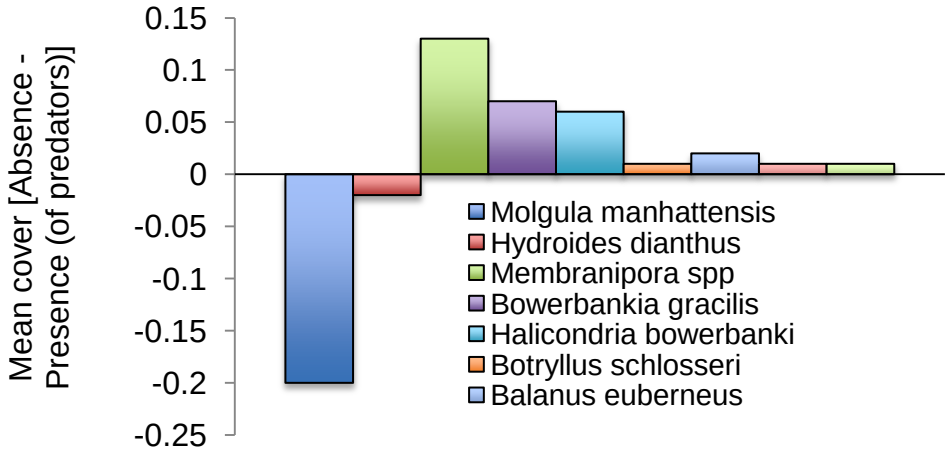

Figure 2.7 *Predation results in a decline of dominate species and increase in a suite of other species.* Change in species' abundances between predation exposure and exclusion.

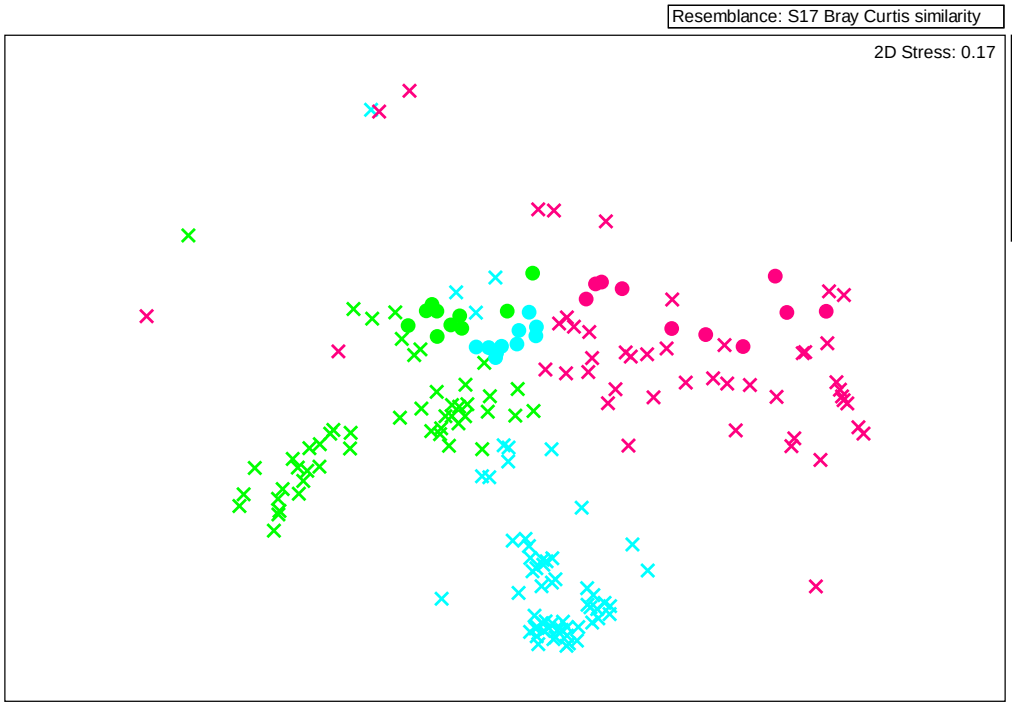

Figure 2.8: *Adult communities are more converged than recruit communities.* Non-metric multidimensional scaling ordinations (nMDSs) on the basis of Bray-Curtis dissimilarity measure for recruits (x) and adult (filled circles) communities at IBSP (teal), GBM (pink), and OC (green).

When examined together, the community composition between recruits and adults is significantly different (Fig. 2.8, PERMANOVA: site: pseudo-$F_{2/180}$=13.54, P(perm)=0.0001; age: pseudo-$F_{1/180}$=1.63, P(perm)>0.05; site x age interaction: $F_{2/180}$=9.40, P(perm)=0.0001). At each site the composition of recruits was significantly different from the adult composition (PERMANOVA all pairs comparison). In addition, community composition of all incoming recruits was significantly more variable than adult community composition (Fig 2.8, PERMDISP: pseudo-$F_{1/184}$=86.82, P(perm): 0.0001), showing that adult communities are more converged in their composition than the incoming composition of recruits.

2.5 Discussion

The results demonstrated repeated and significant variability over space and through time in both the recruit community and the effect of predation on adult communities. These differences can be characterized in two ways: magnitude effects and composition effects. First, for magnitude effects there were significant differences in the abundance of recruits both temporally and spatially. Recruit abundances varied significantly at each time point and between each site on the order of thousands of individuals. I also found that the effect size of predation on adult community composition varied by more than 100% between sites. Second, for composition effects, the community structure of recruits was significantly different at each time point and at each site. Adult communities were significantly different in composition from not only the incoming recruit communities, but each site retained adult communities distinct from all others.

As predicted in my hypothesis, I found significant temporal variation in the abundance of recruits. At all three sites, recruitment experienced increases and decreases in total recruit abundance before beginning to taper off for the season. Interestingly, the recruits varied not only in abundance over time, but also in composition (Fig. 2.2, 2.3). Differing species assemblages recruiting at different times throughout the recruitment season may enhance the development of more diverse adult communities over time (Fernandez et al. 2014). This temporal niche partitioning can be an effective mechanism of coexistence to avoid competition or dominance of a few species (Caffey 1985; Stachowicz and Byrnes 2006).

A high influx of individuals may lead to intense competition for space among these sessile organisms (Bertness 1989). As a result, predation may become an important structuring mechanism by increasing resource (space) availability (Caswell 1978; Chase et al. 2002; Gurevitch et al. 2000). The increased supply from the regional species pool could act to increase the strength and importance of local interactions (Connolly and Roughgarden 1999; Navarrete et al. 2005). However, in contrast to theoretical prediction I found that the effect size of predation on adult community composition at IBSP, the site with the highest recruitment, was 50% lower than both of the other recruitment sites (Table 2.2). Recruitment at IBSP was dominated by high recruitment of two species (both spirorbid worms) and this is reflected in community dispersion where recruits at site IBSP were more converged in composition than the other two sites. Adult communities at this site, however, were not dominated by spirorbid worms, which build calcified tubes as protection against predators, rather a colonial tunicate (*Botryllus schlosser*i), which was also less preferred by local predators. The effect of predators, therefore, may hinge on species-specific effects and predator preference at both the recruit and adult life stages in addition to recruitment rates.

Interestingly, the temporal variability in predation was a difference in the timescale over which an effect of predation was observed. Predation had a minimal effect on the composition or abundance of recruit communities. All adult communities, however, experienced a significant effect of predation on community composition. The lack of a predation effect on recruit communities is in contrast to many studies that have found strong predation on the early life stages of marine sessile invertebrates (Osman and Whitlatch 2004; Sams and Keough 2007). However, the absence of a predation effect on

juvenile life stages does not suggest a lack of predation on recruits but rather that the effect of predation is an aggregate effect which accumulates over time, despite there being no acute effect on recruits at specific time points.

Site to site local variation in the effect of predation led to the emergence of interesting regional patterns. While an effect of predation on adult community composition was consistently observed, effect sizes fluctuated among sites and species. Predation did not affect richness or percent cover of adult communities, but the effect of predation on adult community composition ranged from 19% to 45% across the eight sites. These compositional changes due to predation, however, were primarily driven by a small subset of species from the community (Table 2.2). The results demonstrated this was a result of an increase in less common species and a decrease in common species, including the most common, *Molgula manhattensis*, a soft-bodied solitary tunicate. Across the region, predation acts to decrease the abundance of more dominant species and allow for increases in abundances of less common species.

Despite spatially variable and species-specific effects of predation, strong regional patterns emerged. Adult communities excluded from predators had greater convergence in composition than communities that were exposed to predators across the study region (Fig. 2.6). Stated differently, communities experiencing predation became more compositionally dissimilar to each other across the region. This empirical result supports theoretical predictions and builds on previous examples in other systems where predation led to greater beta diversity and divergent composition across a region (Chase et al. 2002; Chesson and Kuang 2008; Gurevitch et al. 2000; Shurin and Allen 2001). Community divergence increases due to the settlement of different suites of species benefiting from

the increase resource availability (space) and reduced competition in the absence of *M. manhattensis* across the region.

While adult communities exposed to predation were more divergent in their composition than communities excluded from predation, adult communities on the whole were significantly more converged than the recruit communities. Post-recruitment processes have been shown to have significant impact on community development in this and other systems (Johnson 2007; Menge 2000; Sousa et al. 2007; Wright and Steinberg 2001). Despite this community convergence over time, adult communities still maintained differences in composition among all sites. Post-settlement processes in the study region clearly characterized the community composition over time; however, I did not find that patterns of spatial variability initiated in the recruit community were completely superseded by post-settlement processes. While both predation and recruitment varied in space and time, each contributed to the community composition of adults. While recruit communities were significantly different from adult communities due to the convergence of adult communities over time, this does not suggest that recruitment is unimportant to community structure. The strong spatial differences in recruit communities were maintained in adult communities, with adult community composition consistently varying among sites.

These results demonstrate the spatial and temporal variability at play in both recruitment and predation in a coastal marine ecosystem. Each of these ecological processes is an important structuring mechanism for patterns of community composition. The nuanced variability in each through space and time has interesting effects on community composition. The temporal variability in recruitment likely evolved from

temporal niche differentiation of different recruiting species. The spatial variability in recruitment defines sharp boundaries of community composition, and while adult communities tend to converge in comparison to recruit communities, the sharp spatial differences between sites persist from early life stages to adulthood. The temporal variation in predation is a slow cumulative effect, which manifests on community composition at the adult stage. Perhaps most striking is the variation in the site to site response to predation. Predation acts to decrease the abundances of a competitive dominant in adult communities across the region; however, at each local site the suite of species which benefits from increased resource availability is different, increasing the divergence in community composition across the study region. The results demonstrate that while complex, it is important to incorporate the influences of processes that operate at different spatial and temporal scales to understand community assembly and composition.

CHAPTER 3

HABITAT ISOLATION INTERACTS WITH TOP-DOWN AND BOTTOM-UP PROCESSES IN A SEAGRASS ECOSYSTEM

3.1 Abstract

Habitat loss is accelerating at unprecedented rates, leading to the emergence of smaller, more isolated habitat remnants. Habitat isolation has been shown to adversely affect many ecological processes, but little is known about how habitat isolation may influence top-down and bottom-up processes. Understanding the relative importance of consumers (top-down control) and resources (bottom-up control) has been a longstanding primary aim in ecology. Habitat isolation can alter the distribution of both consumers and their resources, but how this may influence the top-down or bottom-up cycling of ecosystems has not been explicitly tested. To investigated the possible interaction between habitat isolation and top-down and bottom-up controls I tested two hypotheses about how habitat isolation, resource availability, and consumer distribution interact to shape the abundance and composition of primary producers (algal epiphytes and benthic macroalgae) and basal prey species (epiphytic sessile invertebrates) in a seagrass ecosystem in Barnegat Bay, NJ. I hypothesized that increased resource availability would interact with habitat isolation and lead to a larger increase in primary producer abundances in isolated habitats due to the absence of consumers. I also hypothesized that epiphytic invertebrate abundances would be either lower in isolated habitats due to dispersal limitation, or higher in isolated habitats due to reduced consumer abundances. I used artificial seagrass to mimic habitat isolation and then manipulated top down and bottom up processes by excluding grazers, adding resources, or a combination of both

treatments. I found that habitat isolation significantly decreases the abundance of epiphytes settling on seagrass blades due to dispersal limitation. I also found that resource additions increased macroalgae cover and epiphytic algae richness only in isolated habitats, suggesting that isolated patches may be nutrient limited and that isolated habitats may experience stronger bottom up control than continuous habitats.

3.2 Introduction

Habitat loss is among the greatest threats to global biodiversity and is a key driver of species' extinctions (Brooks et al. 2002; Carr et al. 2002; Wilcox and Murphy 1985). Habitat loss results in fragmentation, in which large, continuous habitat is divided into smaller habitat patches (Fahrig et al. 1995). As habitat loss progresses, more patches are created which can vary in shape, size, and isolation from other suitable habitat (Franklin 2002; Ranta et al. 1998). Each of these patch characteristics: shape, size, and isolation, have been shown to have deleterious effects on species in fragmented terrestrial landscapes (Fahrig et al. 1995; Hovel and Lipcius 2001; Krauss et al. 2010; Smith et al. 2011). In marine systems, the biological consequences of habitat fragmentation on seascapes are not as well understood, especially in regard to the effects of habitat isolation and how it may interact with ecological processes.

Using Island Biogeography Theory (IBT) to make predictions about the impacts of habitat loss has been a useful tool for ecologists in terrestrial systems. A central prediction of IBT is that an island's distance from a source of colonists (typically the mainland) determines the number of species that will inhabit the island, with isolated islands being less likely to receive immigrants due to decreased connectivity (Ferraz et al.

2007; Gustafsson and Salo 2012; MacArthur and Wilson 1967; Prugh et al. 2008; Roberts and Poore 2006; Schüepp et al. 2011; Steffan-Dewenter and Tscharntke 1999). Despite being a commonly employed metric in terrestrial landscape ecology, a recent review of marine habitat loss described connectivity as the most often overlooked application of landscape ecology to coastal environments (Bostr et al. 2011). We can apply IBT to marine systems to fill gaps in our understanding of how isolation of marine habitats influences species' abundance patterns (Allison et al. 1998; McNeill and Fairweather 1993). The primary mechanism for decreased abundances due to habitat isolation is likely dispersal limitation in marine systems (Borthagaray et al. 2009; Grantham et al. 2003; Shanks 2009). The larval stage of many marine species is often short in length and characterized by a small larval size and poor swimming ability, constraining dispersal potential (Berril 1975, Grantham et al. 2003, Shanks 2009, Young et al. 1988). Here, I focus on how decreased connectivity affects species' colonization of isolated habitat, which has been shown to be essential to population persistence (Cowen and Sponaugle 2009).

Species colonization of habitat is also characterized by the distribution of their consumers and the availability of resources. Alterations in the distributions of higher trophic level organisms or resource availability may change consumer-resource interactions. Under top-down control, an organisms' abundance is controlled by its consumer (Power 1992). Any biological process that may reduce the abundance of higher trophic levels will subsequently increase the abundances of lower trophic levels through weakened top-down control (Davies et al. 2000). When species abundances are constrained by resource availability (bottom-up control) (Hunter and Price 1992), limited

primary producer growth can limit the abundances of organisms at higher trophic levels (Pace et al. 1999; Pauly and Christensen 1995). Under conditions of increased resource availability, primary production can increase thereby alleviating resource limitation for higher trophic levels. The relative importance of top-down and bottom-up effects can be mediated by the physical environment (Hoekman 2010), diet breadth of consumers (Jiang and Morin 2005), and community composition (Bracken et al. 2014).

Habitat spatial structure may also mediate top-down and bottom-up controls of species abundances through decreased habitat connectivity and increased habitat isolation (Komonen et al. 2000; Simon 1992; Tilman and Kareiva 1997). Isolation can decrease the ratio of predators to prey, which can weaken the ability of consumers to control primary producer abundances (Shulman and Chase 2007). Declines in consumer abundances due to isolation have been shown to weaken top-down forces in aquatic metacommunities (Chase et al. 2010) and forest fragments (Terborgh et al. 2001). Habitat isolation has been shown to reduce nutrient retention in isolated habitats (Haddad et al. 2015). Changes in nutrient cycling may interact with the effects of habitat isolation on trophic interactions. If consumer abundances are low in isolated habitats due to dispersal limitation, primary producers may experience a release of top-down control and increased growth, or may be constrained by limited nutrient availability. Despite extensive habitat loss in both terrestrial and aquatic ecosystems leading to increased habitat fragmentation across the globe (Brooks et al. 2002; Gallant et al. 2007; Gibbons et al. 2000; Hoekstra et al. 2005; Short and Burdick 1996; Waycott et al. 2009), we have only a rudimentary understanding of how top-down and bottom-up processes may

differentially affect communities in isolated versus continuous habitats (Gripenberg and Roslin 2007).

Marine habitats have been declining at historic rates (Orth et al. 2006). Seagrass habitats are an ideal system with which to examine the interactive effects of habitat isolation, consumer abundances, and resource availability. Seagrass habitats are experiencing global loss and are becoming increasingly fragmented, disappearing at a rate of 110km^2/year since 1980 (Orth et al. 2006; Waycott et al. 2009). This rate of loss is equivalent to losses of mangroves, coral reefs, and rain forests (Waycott et al. 2009), placing seagrass among the most threatened ecosystems. Like many marine foundation species, seagrasses support high species diversity by providing refuge and nursery areas for invertebrates and fish (Heck et al. 2003). The value of seagrass nutrient cycling alone has been estimated at $1.9 trillion annually (Lavelle et al. 2005). Many organisms, primarily mesograzers, also rely on epiphyte communities (algae and invertebrates that grow directly on seagrass blades) and benthic macroalgae as a source of food (Bell 1991; Duffy and Hay 1991; Duffy et al. 2001; Zimmerman et al. 1979). In seagrass ecosystems, consumer-resource interactions between epiphytes, benthic macroalgae, and mesograzers can control epiphyte and macroalgae overgrowth that might otherwise damage the seagrass through photosynthesis inhibition (Verhoeven et al. 2012; Whalen et al. 2013). Yet how these interactions are mediated by resource availability and habitat isolation is not resolved. Mesograzers have been shown to exert enough consumptive pressure on epiphytes and macroalgae to counteract increases in the growth of algal epiphytes and macroalgae when released from resource limitation (Cook et al. 2011; Heck and Valentine 2007; Hemminga and Duarte 2000; Hughes et al. 2004). However,

habitat isolation has been shown to significantly reduce the abundances of several mesograzer taxonomic groups such as isopods, gastropods, and amphipods (Gustafsson and Salo 2012; Kumagai 2006). There are currently no empirical studies examining whether mesograzers will control epiphyte and macroalgae abundances in isolated habitats when resources are not limiting. In addition, there are also no empirical studies that examine how resources may be influenced by fragmentation in marine systems.

I tested two hypotheses about how habitat isolation, resource availability, and consumer distribution interact to shape the abundance and composition of primary producers (algal epiphytes and benthic macroalgae) and basal prey species (epiphytic sessile invertebrates) in a seagrass ecosystem. First, I hypothesized that increased resource availability will interact with habitat isolation and lead to a larger increase in primary producer abundances in isolated than in continuous habitats due to lower abundances of higher trophic levels (grazers) in isolated habitats. Second, I hypothesized that epiphytic invertebrate abundances would be either lower in isolated habitats due to dispersal limitation, or higher in isolated habitats due to reduced consumer abundances. I further predicted that these effects on algal and invertebrate epiphytes would result in compositional differences in epiphytic communities between isolated and continuous habitats.

3.3 Methods

I conducted three field experiments to determine if habitat isolation, resource availability, and consumer abundances interact to alter epiphyte biomass and community structure, and macroalgae abundance. In the Barnegat Bay-Little Egg Harbor Estuary,

New Jersey, 50–88% of seagrass biomass has been lost since the 1980s (Kennish et al. 2007; Kennish et al. 2009), making the area well situated to examine the impacts of habitat isolation. In Island Beach State Park, a preserved area of Barnegat Bay, New Jersey, I selected a large (0.32km^2) continuous meadow of *Zostera marina*, the dominant seagrass species in the outer portions of the estuary, surrounded by both seagrass patches and unvegetated sediment for the study site (39°N 47' 24.8064", 74°W 6' 28.476").

Habitat isolation and consumer-resource relationships

To investigate the possible interaction between habitat isolation and consumer-resource relationships, I ran a field experiment in July 2013. I used artificial seagrass units (ASUs) as my experimental unit to avoid potentially confounding factors such as seagrass density and blade length. ASUs were constructed of green polypropylene ribbon attached to plastic mesh. ASU area (0.6m x 0.6m) and blade length (31 cm) were based on preliminary surveys of patches at the study site. Blade density was determined from the literature (239-466 shoots m^{-2}) and was 308 shoots m^{-2} (ASUs contained 111 seagrass blades) (Kennish et al. 2009). Each blade was 4.7mm wide. Twenty ASUs were placed at three isolation levels relative to the continuous meadow: 1) 10m within the meadow, 2) 10m isolated, and 3) 25m isolated from the continuous meadow (N=60). The 10m and 25m isolation treatments represent the 25th and 75th percentile for the distance of natural patches to the meadow based on preliminary surveys of meadow-patch spatial arrangements at the site. Within isolation levels, ASU patches were spaced 2.5m away from each other.

I manipulated bottom-up and top-down processes through nutrient additions and mesograzer exclusions, respectively. The following four treatments were haphazardly applied to five ASUs within each isolation level: grazer exclusion, nutrient addition, a combination of grazer exclusion and nutrient addition, and no manipulation (N=60). In order to exclude grazers, I incorporated Carbaryl (Sevin SL), an insecticide which inhibits arthropods through neurodisruption, into plaster to form 7.5% carbaryl blocks (Poore et al. 2009). Previous studies have demonstrated the efficacy of carbaryl in reducing herbivorous grazer abundances within a 30cm radius (Poore et al. 2009; Whalen et al. 2013). I attached the blocks to a stake 15cm above the sediment in the center of the ASU patch. As the plaster block dissolves, carbaryl is released into the water column deterring herbivorous grazers. Carbaryl blocks were replaced on a weekly basis, prior to complete dissolution. To manipulate nutrient levels I attached 300g of Scott's™ continuous release plant fertilizer (10-10-10; N:P:K) enclosed in nylon mesh bags to stakes in the ASUs and replaced on a weekly basis (prior to complete dissolution). For the combined grazer exclusion and nutrient addition treatment I added both a carbaryl block and a nutrient bag to the stake in the ASU. The experiment was deployed for eight weeks, accounting for a large portion of the growing season (Kennish et al. 2009).

At the completion of the experiment, ASUs were sampled for epiphytic and benthic macroalgae, epiphytic invertebrates, and herbivorous grazers; data were compared among treatments. Ten blades were clipped from each ASU within the 30cm radius around the center (where the treatment was placed). A subset of three blades from three replicates of each treatment (N=36) was used to determine epiphyte community structure. To estimate community structure, invertebrates and (macroscopic) algae were

identified to the lowest taxonomic group possible (usually species) using a dissecting microscope, and abundances of each group were recorded as the numbers of individuals observed across all three blades per replicate. All of the 10 clipped ASU blades in each replicate (N=60) were scraped of epiphytes using a razor blade, and epiphytes were dried at 60°C for three days and weighed for dry biomass. Epiphytes were then incinerated at 500°C for four hours and reweighed to determine epiphyte ash free dry weight (AFDW). Percent cover of macroalgae (primarily drift algae or algae loosely attached to the ASU) was recorded in the field using a 10-point grid, with points equidistant across the full area of the ASU. Herbivorous grazers were sampled using a small dipnet, and preserved using 70% ethanol in the laboratory for enumeration. The effects of isolation, resource, and consumer manipulations on epiphyte biomass, epiphyte richness and abundance, herbivorous grazer richness and abundance, and macroalgae percent cover were analyzed using analysis of variance (ANOVA, JMP® v.11 2007) with fixed effects of habitat isolation distance, nutrient level, and grazer presence, and all possible interactions among terms. Macroalgae percent cover was arcsin square root transformed prior to analysis. The effects of isolation, resource, and consumer manipulations on epiphyte community composition were analyzed using a permutational multivariate ANOVA (PERMANOVA, Anderson 2001) based on a Bray-Curtis similarity matrix with fixed effects of isolation distance, nutrient level, and grazer presence, and the interactions among factors. I used PERMDISP (Anderson 2004) to identify changes in community divergence (variability in community composition) among habitat isolation, resource availability, or consumer treatments. To identify what species may drive differences in community similarity, I

used a SIMPER analysis to identify the species that are most important in structuring the observed patterns in similarity or dissimilarity.

After the deployment of the experiment, I began to observe an increase in macroalgae associated with the patches that received nutrient additions or excluded mesograzers. To ensure that this phenomenon was a treatment effect and that there were no experimental artifacts associated with the stakes used to support the grazer exclusion and nutrient addition treatments, I conducted a control experiment. Twenty-five ASUs were deployed in June 2014 in the same study area with the following five treatments (five replicates/treatment, N = 25): mesograzer exclusion, nutrient addition, a combination of mesograzer exclusion and nutrient addition, no treatment, and a control which consisted of a plaster block with no carbaryl and a mesh bag of small gravel attached to the same stake used to support the grazer exclusions. The ASUs were placed approximately 10m away from the meadow to represent an intermediate distance from the continuous meadow. The experimental duration was eight weeks, and all treatments were replaced on a weekly basis as in the prior experiment. Sampling of mesograzers, macroalage and epiphytes (composition and AFDW) was completed using the same methods described above, except that a subset of five of the 10 clipped blades from each replicate were used to estimate epiphyte community structure. Effects of the experimental manipulations on macroalgae percent cover (arcsine square root transformed data) were analyzed using planned contrasts to differentiate between treatment effects and potential artifacts from the treatment apparatus.

Natural Seagrass

To compare the results from artificial seagrass to patterns in natural seagrass, I sampled epiphytes from naturally occurring seagrass patches. In August 2013, upon completion of the artificial seagrass experiment, I established five 50 meter transects extending from randomly selected starting points 10m within the continuous seagrass meadow into the surrounding matrix of seagrass patches in the study area. At the start of each transect I collected 10 blades from a 0.3m x 0.3m area in the continuous meadow, I then collected 10 blades from each natural seagrass patch greater than 0.3m x 0.3m in area (N=18) observed along the transects. All of the 10 clipped natural seagrass blades in each replicate were scraped of epiphytes using a razor blade, and epiphytes and seagrass were dried at 60°C for three days and weighed for dry biomass. Epiphytes and seagrass were then incinerated at 500°C for four hours and reweighed to determine epiphyte ash free dry weight (AFDW). I categorized transect samples into three habitat isolation groups that correspond to distances used in the artificial seagrass experiment: meadow, isolated (0-20m separated from the meadow), and very isolated (>20m separated from the meadow). I then tested the effect of habitat isolation (3 groups) on the biomass of epiphytes in natural seagrass patches using a one-way ANOVA, with a fixed factor of habitat isolation.

Recruitment

To determine if dispersal limitation of invertebrates and algae into isolated patches influenced epiphyte abundance on seagrass, I monitored recruitment of epiphytes into experimental patches for eight weeks beginning June 2014. While recruitment

measurements integrate both differences in dispersal as well post-settlement mortality due to predation, prior research suggests very low levels of predation on newly-settled recruits in this area (Chapter 2). I placed five small ASUs (0.15m x 0.15m) which contained 10 blades at each of the three experimental isolation levels (10m into the meadow, 10m isolated, and 25m isolated) for a total of 15 ASUs. Each small, recruitment ASU was set inside a larger 0.6m x 0.6m ASU. Recruitment ASUs were retrieved every two weeks and replaced with new ASUs for eight weeks. Epiphytic invertebrates and algae were identified to the lowest taxonomic group possible (usually species), and abundances of each group were recorded as the numbers of individuals observed across all 10 blades per replicate. I used an ANOVA to test for differences in invertebrate and algae recruit abundance and richness with a fixed factor of habitat isolation and date as a random effect.

3.4 Results

I found that habitat isolation had an effect on the biomass, abundance, and community composition of seagrass epiphytes, and isolation further mediated consumer-resource dynamics. ASUs which were isolated at either 10 or 25m had lower epiphyte biomass (AFDW) than ASUs from the meadow (Fig 3.1. ANOVA full model: R^2_{adj}=0.47, N=60, $F_{11/48}$=3.97, p=0.0005, habitat isolation: $F_{2/57}$ = 15.11, p=<0.0001). Grazers also reduced epiphyte biomass, but this effect occurred in isolated (10 and 25m) patches only (isolation x grazer presence: $F_{2/57}$=3.49, P=0.039; Tukey HSD). Habitat isolation also reduced total epiphyte individuals (ANOVA full model: R^2_{adj}=0.30, N=36, $F_{11/24}$=2.38, p=0.0364, habitat isolation: $F_{2/33}$ = 5.64, p=0.0098), as did nutrient additions (nutrients: $F_{1/34}$ = 6.94, P=0.0145). The community composition of epiphytes was also affected by

habitat isolation (Fig. 3.2, PERMANOVA: Pseudo-$F_{2/24}$ = 2.3547, P(perm) = 0.0461), along with nutrient addition (Psuedo-$F_{1/24}$=4.77, p(Perm)=0.0088) and grazing (Pseudo-$F_{1/24}$=3.69, P(perm)=0.017). Differences in community structure due to isolation were largely due to declines in the abundance of certain invertebrate epiphytes from meadows to more isolated habitats. *Spirorbid spirillum* (tube-building worm), *Spirorbid violaceus* (tube-building worm), and *Botryllus schlosseri* (compound ascidian) account for a combined 84% and 83% of variation between the meadow and 10m or the meadow and 25m isolated patches respectively; (SIMPER analysis). A decline in the total abundance of invertebrates was observed from meadows to both isolated groups (ANOVA: Full model: R^2_{adj}=0.36, N=36, $F_{11/24}$=2.76, habitat isolation: $F_{2/33}$=6.25, p=0.0065).

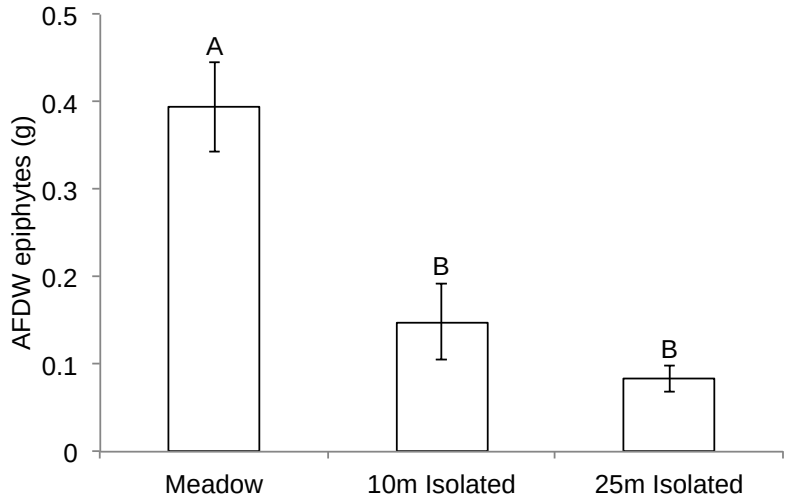

Figure 3.1: Habitat isolation reduced epiphyte biomass in artificial seagrass: Epiphyte biomass expressed as the ash free dry weight of seagrass epiphytes across three habitat isolation treatments. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

Habitat isolation and consumer-resource dynamics also interacted to shape patterns of algal epiphyte richness (Fig 3.3. ANOVA full model: R^2_{adj}=0.36, N=36, $F_{11/24}$=2.82, P=0.0162; grazing: $F_{1/34}$=18.69, P=0.0002; Nutrients x Grazing x Isolation: $F_{2/33}$=3.41, P=0.0497; Tukey HSD). In seagrass meadows, grazers reduced algal epiphyte richness under ambient nutrient levels only; under enriched nutrient levels, there was no observable effect of grazers, and richness remained high. In contrast, in very isolated habitats (25m), grazing reduced algal epiphyte richness only when nutrients were added; consumers did not affect algal richness at ambient nutrient levels. Algal epiphyte richness in these isolated habitats was highest when nutrients were added and grazers were excluded. Therefore at ambient nutrient levels, I observed stronger top-down control in meadows and weaker top-down control in very isolated habitats for algae richness. Bottom-up effects were weak in meadows (no nutrient effect), and strong in isolated habitats (nutrient additions increased epiphytic algae richness).

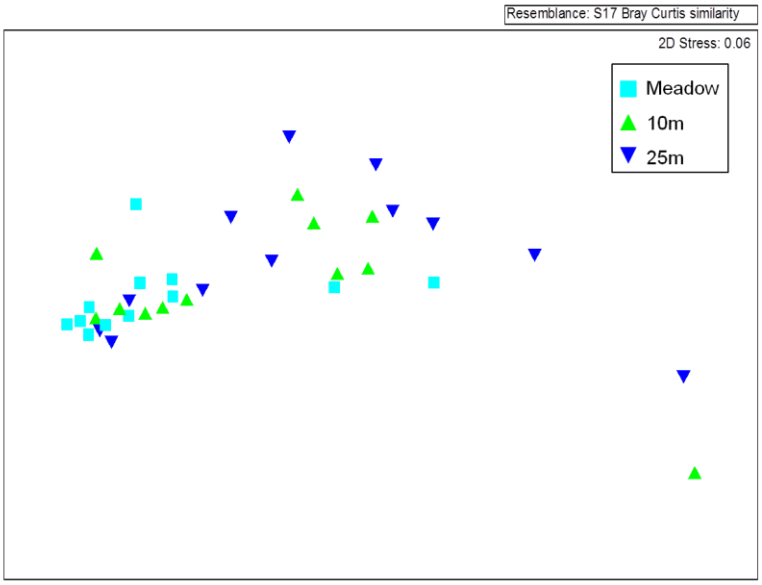

Figure 3.2: Habitat isolation altered epiphyte community composition: Non-metric multidimensional scaling ordinations (nMDSs) on the basis of Bray-Curtis similarity measure for the centroids of epiphyte communities in patches within the meadow (teal squares), 10m isolated (green upright triangles), and 25m isolated (blue downward triangles) patches.

Habitat isolation also mediated the impact of resource additions on patterns of macroalgae abundance (Fig. 3.4. ANOVA: Full model: R^2_{adj}= 0.42, N=57, $F_{11/45}$= 4.75, P<0.0001, nutrients x habitat isolation: $F_{2/54}$ = 3.23, P = 0.0488, nutrients x grazers: $F_{2/54}$=30.42, P<0.0001). Nutrient additions only increased macroalgae percent cover within isolated patches, and did not increase macroalgae percent cover in the seagrass meadow habitat (Tukey HSD). This pattern is similar to the pattern observed in algal epiphyte richness in meadows. The nutrient and grazer interactions showed that grazers only reduced macroalgae abundance under ambient nutrient conditions, unlike epiphytic algae, there was no three-way interaction for macroalgae and the effect of grazers did not depend on isolation level. Differences in macroalgae percent cover were shown to be due to treatment effects rather than artifacts from the treatment application apparatus.

Nutrient and grazer exclusion treatments had more macroalgae than the gravel and plaster control treatment (Planned Comparison: $F_{1/20}$=7.50, P=0.0126), which was not different from unmanipulated patches (P>0.05).

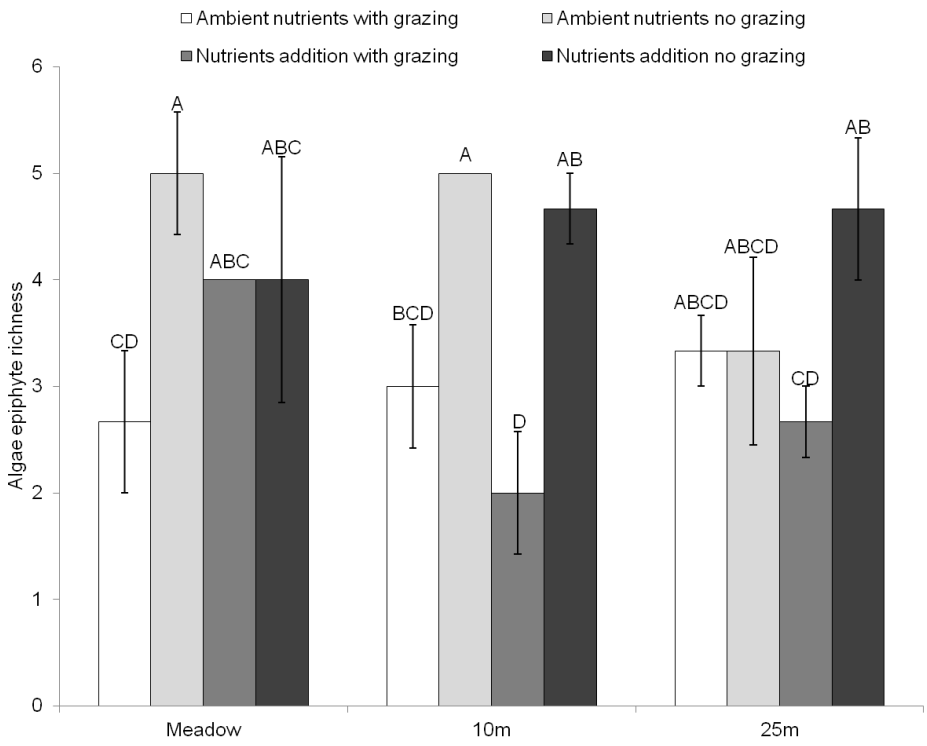

Figure 3.3: Nutrient additions had opposite patterns on algal epiphyte richness in meadows and isolated patches: Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

Habitat isolation also shaped patterns of grazer abundances, yielding insight into the weaker consumer effects observed in isolated habitats under ambient nutrient levels for epiphytic algae richness. Grazer abundances were lower in very isolated patches

(25m) than in the meadow or 10m isolated patches (ANOVA full model: R^2_{adj}=0.28, $F_{11/45}$=3.06, N=57, P=0.0039; habitat isolation: $F_{2/55}$=9.74, P=0.0003; Tukey HSD). In addition, the grazer exclusion treatment was shown to be effective, causing a reduction in the abundance of grazers by 50% (grazing exclusion: $F_{1/56}$=4.96, P=0.031).

Patterns of natural seagrass epiphyte biomass mirrored those found in the artificial seagrass experiments. In natural seagrass patches, isolation had a significant effect on epiphyte biomass. For patches outside the meadow (0-20m and >20m), epiphyte biomass was lower than in meadow patches (Fig. 3.4, Wilcoxon each pair: Meadow:>20m, $Z_{1/7}$=2.76, P=0.0058; Meadow:0-20m, $Z_{1/8}$=2.41, P=0.016). The isolated groups were not significantly different from each other (P>0.05). Habitat isolation also significantly affected the community composition of epiphytes in natural seagrass (PERMANOVA Pseudo-$F_{1/15}$: 2.13, P(perm)=0.0327).

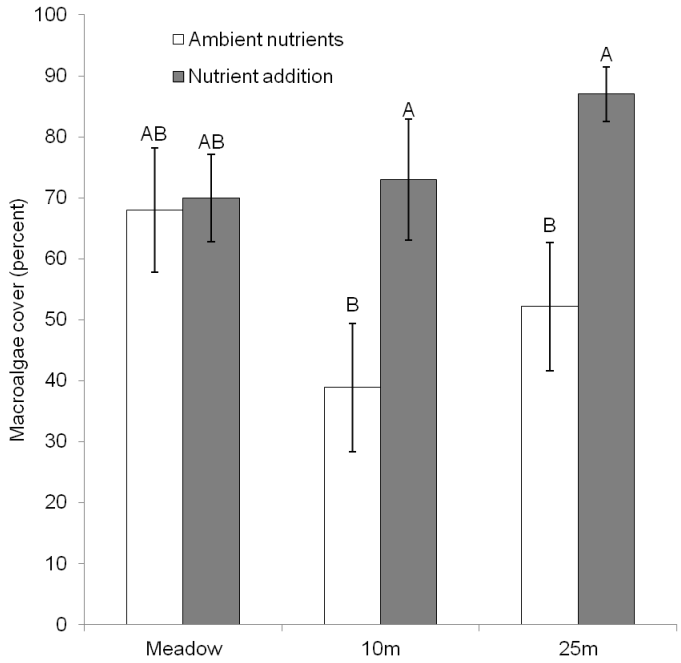

Figure 3.4: Nutrient additions increased macroalgae percent cover in isolated habitats: Macroalgae percent cover for isolation and nutrient treatments. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

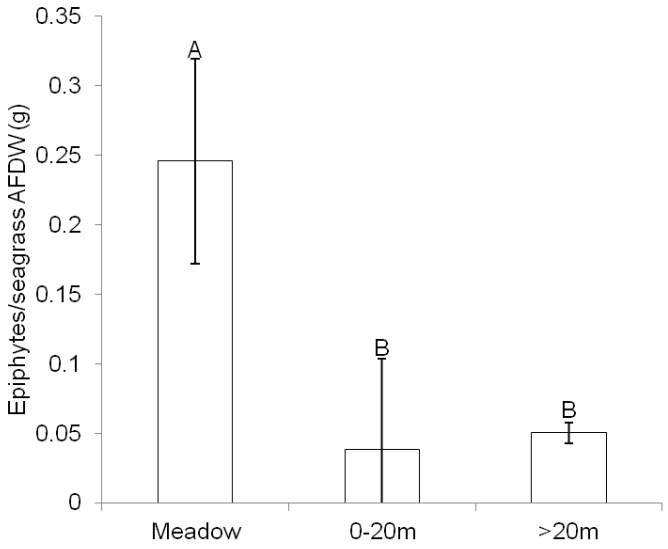

Figure 3.5: Habitat isolation reduced epiphyte biomass in natural seagrass: Epiphytes are expressed as grams of ash free dry weight per gram of ash free dry weight of seagrass across three habitat isolation treatments. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Wilcoxons each pair tests.

Recruitment measurements support the findings that habitat isolation decreases total abundance and richness. I found significantly lower invertebrate recruit abundances and richness in the isolated patches (both 10 and 25m) than the meadow patches across the experimental duration (Fig. 3.6, ANOVA full model abundance: $R^2_{adj} = 0.86$, $F_{11/46}=33.32$, $P<0.0001$; ANOVA full model richness: $R^2_{adj}=0.42$, $N=58$, $F_{11/46}=4.71$, $P=<0.0001$). The abundance and richness of algae recruits was not significantly affected by isolation ($P>0.05$).

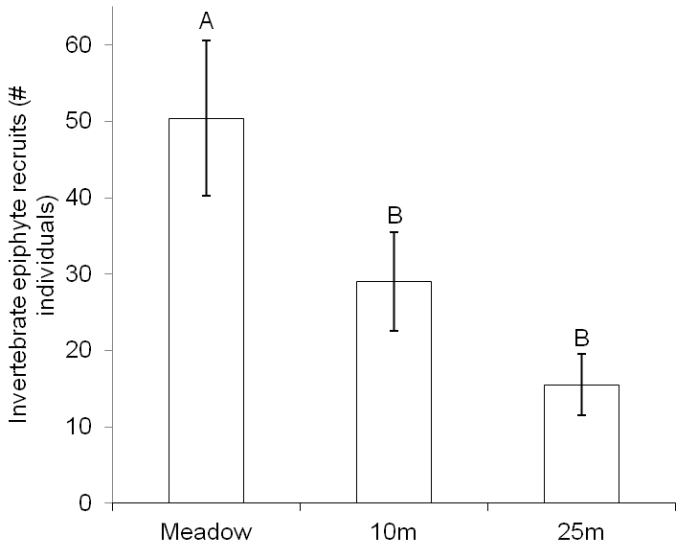

Figure 3.6: Habitat isolation reduced the abundance of invertebrate epiphyte recruits: Recruits are expressed as the mean number of individuals recruiting to each habitat type per two-week period across the 8 week experimental timeframe. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using Wilcoxons each pair tests.

3.5 Discussion

Habitat isolation changed the abundance and structure of epiphytes, and consumer-resource dynamics may change in isolated habitats. I found that habitat isolation had a significant impact on epiphyte biomass, abundance, and community structure, demonstrating that small scale changes in habitat structure can have strong ecological effects in this marine ecosystem. Both artificial and natural seagrass patches isolated from meadow patches had significantly lower epiphyte biomass and different community composition than patches from the continuous meadow. Any separation of a patch from a continuous meadow and thus a population "source" impacts the abundance of individuals that are able to disperse through the matrix. Habitat isolation had

particularly strong effects on invertebrate epiphytes, with decreases in invertebrate epiphytes driving the changes in community composition and biomass. The recruitment results support the assertion that dispersal limitation is a likely mechanism for declines in epiphyte abundances. Patterns of epiphyte recruitment revealed that the number of individuals settling in seagrass patches declines as distance from the meadow increases. Again, this pattern was driven by invertebrate recruits, likely due to their short pelagic stage and weak swimming ability.

The results match the findings of a recent review of pelagic larval duration in marine systems (Shanks 2009); which found that many species of sessile invertebrate groups such as cnidarians, bryozoans, ascidians, and sponges often settle within 10m of their source (Ayling 1980; Bergquist and Sinclair 1968; Berril 1975; Bingham and Young 1991; Collin et al. 2013; Uriz et al. 1998; Young et al. 1988). In particular, ascidians tend to have the shortest dispersal potential, as many are limited by their larval yolk sac as a nutrient source, and compound ascidians often settle within minutes (Collin et al. 2013; Svane and Young 1989). I saw that declines in *B. schlosseri*, a compound ascidian in the system, accounted for a large portion of the dissimilarity in community structure between meadow and isolated habitats. While many marine organisms such as fish, algae, and mollusks may have dispersal potentials on the order of 100s of meters (Grantham et al. 2003; Shanks 2009), the results show that this is not true for all taxonomic groups. Small isolation distances in marine systems can be a barrier to dispersal for many sessile invertebrates, and these barriers can have important community-level consequences.

My results further demonstrate that habitat isolation can mediate consumer-resource dynamics. While the primary producers in this system, algal epiphytes and benthic macroalgae, were not sensitive to habitat isolation alone, the responses of algal epiphytes and benthic macroalgae to changes in resource availability or consumer presence was spatially dependent. Grazers had strong effects on the richness of epiphytic algae. Interestingly, this effect was dependent on both habitat isolation and resource availability. In meadows, under ambient nutrient conditions, consumer effects on epiphytic algal richness are strong. When nutrients are added, no consumer effects are observed. In very isolated patches under ambient nutrient conditions there is no effect of consumers on algae richness. The results suggest that at ambient resource availability, top-down processes are strong in meadows, and weak in isolated habitats for algae richness. This supports theoretical predictions and previous empirical results in aquatic and terrestrial systems that top-down forces may be weakened by habitat isolation due to lower consumer abundances (Chase et al. 2010; Terborgh et al. 2001). Indeed, grazer abundances declined in very isolated habitats (25m).

In isolated patches, nutrient additions increased macroalgae cover. In the meadow, macroalgae percent cover was unaffected by resource availability. A possible mechanism for nutrient limitation in isolated habitats may be decreased decomposition rates and decreased organic material. Existing research in this area is sparse, particularly in marine habitats, but it has been shown that litter-fall can decrease in terrestrial systems with fragmentation (Sizer 2000) and isolation (Carvalho and Vasconselos 1999), and that habitat isolation decreases nutrient retention (Haddad et al. 2015). In addition, isopods and amphipods have been shown to be the primary consumers of dead seagrass material

(Robert and Mann 1980). I found that the abundances of these organisms decline in isolated habitats, which may decrease decomposition rates and nutrient availability.

My results demonstrate that habitat isolation in marine ecosystems can affect community structure, richness, biomass, and abundance over very short distances. I also show that the relative importance of top-down and bottom-up processes to primary producer abundance is spatially dependent. For both algal epiphytes and macroalgae, top-down processes are stronger and bottom-up processes are weak in meadow habitats, while the opposite pattern was observed in isolated habitats. I provide evidence that the likely mechanism is a combination of both declines in resource availability and consumer abundances in isolated habitats. Habitat isolation may change food web directions from top-down to bottom-up controlled. My results emphasize the need for a greater understanding of how fundamental ecological processes may vary spatially in marine systems, especially as marine habitat loss continues to accelerate.

.

Chapter 4

HABITAT FRAGMENTATION ALTERS PREDATION RATES AND BEHAVIOR OF BOTH PREDATORS AND PREY IN A MULTI-TROPHIC MARINE SYSTEM

4.1 Abstract

Habitat fragmentation has been shown to alter predation rates, predator behavior, and prey behavior. Most research on the effect of habitat fragmentation is limited to terrestrial landscapes, and examples in marine systems are often restricted to one trophic level. Seagrass is being lost at a rate of 110 km^2/yr, leading to the emergence of fragmented seagrass seascapes. Habitat fragmentation is expected to affect trophic levels differently, with higher trophic levels being more sensitive to fragmentation, stressing the importance of a multi-trophic perspective. Utilizing the trophic relationship between the blue crab (*Callinectes sapidus*) and hard clam (*Mercenaria mercenaria*), where adult blue crabs prey on juvenile blue crabs, and both adult and juvenile blue crabs prey on hard clams, I examined whether predation rates, prey, and predator behavior differed between continuous and fragmented seagrass habitat in a multi-trophic context at two sites in Barnegat Bay, NJ. I hypothesized that blue crab predation rates and foraging will decrease in fragmented seascapes, due to a reduction in adult blue crab densities, increasing survival rates of juvenile blue crabs and hard clams. I expected hard clams to exhibit weaker predator avoidance behavior in fragmented habitat because of decreased predation. I found that species' responses to fragmentation were different based on trophic level. Clams experienced higher predation and burrowed deeper in continuous

habitats at both sites. Densities of blue crabs, the primary predator of hard clams, were higher in continuous habitats at both sites. Predation on juvenile blue crabs was higher in the fragmented seagrass at one site. My results suggest that the impact of fragmentation on higher trophic-level predators may drive predation rates and prey responses across the seascape.

4.2 Introduction

The effects of habitat fragmentation on biodiversity have been well studied (Andren 1994; Ewers and Didham 2006; Fahrig 2003; Krauss et al. 2010; Ranta et al. 1998), but less is known about how habitat fragmentation may affect interactions between species, particularly multi-species interactions and behavioral changes of both predators and prey that may occur as a result of altered trophic relationships (Fahrig 2003). Habitat fragmentation, where large continuous habitat is broken into smaller and more isolated habitat patches, has been shown to alter species relationships including trophic interactions, but often this has been in one or two trophic-level relationships (Crist et al. 2006; Fahrig 2003; Martinson et al. 2012). This approach may overlook important variation in trophic-dependent responses to fragmentation as not all trophic levels are predicted to respond similarly to fragmentation (van Nouhuys 2005). For example, species at higher trophic levels tend to have larger habitat requirements, and may experience greater population declines due to fragmentation (Davies et al. 2000). The dispersal and demography of a particular species, which may also be linked to trophic level, may be an underlying mechanism responsible for trophic-dependent responses to fragmentation (Kareiva 1987). Additionally, certain trophic levels may be more influenced by fragmentation due to their behavioral responses (Tigas et al. 2002).

In particular, the rate of foraging activity or utilization of anti-predator defenses may change with landscape structure and trophic position. How habitat fragmentation drives more complex trophic interactions, changes in behavior, and the cascading effects on other trophic levels is not clear.

Most of the empirical examples examining the effects of fragmentation on species interactions in a multi-trophic context are in terrestrial insect systems, where fragmentation has been shown to lead to declines in predation, herbivory, and parasitism (Tscharntke and Brandl 2004; Valladares et al. 2006; Wimp et al. 2011). The effects of habitat fragmentation on multi-trophic interactions (>two levels) in marine systems are rare (but for a mesocosm exception see Johnson and Heck 2006). Fragmented habitats in marine systems may differ in conditions such as flow (Martinson et al. 2012), sedimentation (Scoffin 1970), and prey refuge, which may differentially affect species' responses in marine ecosystems.

Species losses due to fragmentation have been shown to vary based on trophic position (Krauss et al. 2010; Zabel and Tscharntke 1998). Specifically in terrestrial systems, habitat fragmentation has been shown to disproportionately affect higher trophic levels (Didham et al. 1998; Roslin et al. 2014). An underlying mechanism for the disproportionate effect on higher trophic positions may be larger space requirements and smaller population size (Brückmann et al. 2011; Cohen et al. 2003; Greenleaf et al. 2007; van Nouhuys 2005). The effects of habitat fragmentation on higher trophic levels may be especially strong in marine systems where predation is a particularly important biotic interaction; predators strongly influence population sizes, community structures, and ecosystem function (Casini et al. 2012; Emmett Duffy et al. 2003; Paine 2002; Shurin et

al. 2002). In marine systems, however, higher trophic level species may disperse farther, perhaps providing some buffering capability to the effects of fragmentation (Kinlan and Gaines 2003). Like in terrestrial systems, habitat fragmentation has been shown to have negative effects on predator abundances in marine environments (Hovel and Lipcius 2001; Layman et al. 2007; Eierman and Connor 2014); however no multi-trophic *in situ* examples have been performed. It is therefore unclear whether habitat fragmentation differentially affects trophic levels in marine systems.

Since the majority of studies examining how habitat fragmentation affects consumer distribution patterns are restricted to one or two trophic levels, it also unclear if effects on basal prey are direct or the result of a trophic cascade. Prey survival ultimately depends on the distribution of predators, which can vary with habitat fragmentation, and on the level of refuge the habitat provides, which may decrease in fragmented habitats (Hovel and Lipcius 2001). In marine mesocosms, effects of habitat patch size on prey survival and behavior varied with the number of trophic levels present (Johnson and Heck 2006). However, multi-trophic systems have not been examined *in-situ*, therefore, it is not well known whether the effects of habitat fragmentation cascade to lower trophic levels in marine systems.

Fragmentation may also lead to behavioral changes. Predator foraging behavior and predator avoidance behavior of prey may be altered in fragmented habitats (Bach and Kelly 2004; Tscharntke et al. 2002). The behavior of both predator and prey is crucial to their ability to survive and reproduce, emphasizing the importance of understanding how fragmented conditions may alter behavior. In marine systems, habitat fragmentation has been shown to alter predator behavior (Bernot and Turner 2001; Ljungberg et al. 2013;

Werner and Peacor 2003). Fragmentation produces edge effects which can result in enhanced encounter frequencies between predators and prey (Fagan et al. 1999; Ries et al. 2004), further driving increases in predator foraging rates in fragmented habitats (Andren 1994; Hovel and Regan 2008). Top marine predators have been shown to increase foraging at microhabitat boundaries despite being relatively uncommon in these areas in comparison to other habitats (Eierman and Connor 2014). If marine predators decline in fragmented habitats, the cascading effects are not limited to shifts in population sizes at different trophic levels, but changes in the behavior of prey as well (Burkholder et al. 2013; Dill et al. 2003; Heithaus et al. 2008).

If habitat fragmentation results in increased foraging or declines in predator abundances, it is not known whether prey may subsequently also experience changes in abundance or anti-predator responses. In marine systems, only a handful of studies have examined prey behavior in response to fragmentation. Juvenile blue crabs decreased their foraging as patchiness increases, due to an increased threat of predation (Macreadie et al. 2012). In mesocosms, grass shrimp alter their habitat preference in fragmented habitats (Ljungberg et al. 2013). In terrestrial systems, prey have been shown to alter their movement patterns (Anderson and Boutin 2002), and prey that rely on coverage dependent anti-predator defenses experience higher predation in fragmented habitats (Takakura and Yamazaki 2007).

Many marine habitats are severely fragmented, including seagrass. Seagrass has been disappearing at a rate of 110/km per year since 1980 (Waycott et al. 2009). While seagrass naturally occurs in a variety of spatial configurations (Boström et al. 2006), current rates of fragmentation are unprecedented and fragmentation is increasing beyond

historical levels (Orth et al. 2006), making seagrass an ideal habitat to examine questions regarding the effects of habitat fragmentation. Seagrass is particularly useful for examining how habitat fragmentation may affect patterns of species distributions, behavior, and trophic relationships as it supports a wide variety of flora and fauna, and seagrass associated food webs are complex and both commercially and ecologically important (Christian and Luczkovich 1999; Costanza et al. 1997; Hemminga and Duarte 2000).

To determine how habitat fragmentation influences multi-trophic food web relationships, predator and prey behavior, and predator distributions in marine systems, I utilized the trophic relationship between the adult blue crab (*Callinectes sapidus*), juvenile blue crabs, and the hard clam (*Mercenaria mercenaria*). In this tri-trophic system, adult blue crabs consume juvenile blue crabs, and both adult and juvenile blue crabs prey upon the hard clam. Seagrass is an important nursery area for both juvenile blue crabs and hard clams (Heck et al. 2003). Blue crabs have been shown to be more abundant in continuous seagrass habitats than in fragmented habitats (Hovel and Lipcius 2001); however it is unknown if juvenile and adult blue crabs share the same pattern of distribution. Juvenile blue crab survival may be inversely related to patch size in fragmented habitats (Hovel and Lipcius 2001), while the effect on basal prey bivalves such as the hard clam has been variable and may be related to predator distributions (Irlandi 1994, 1997). To my knowledge, the influence of top and intermediate predator distributions on prey survival in patches has not been explicitly tested. I tested the hypothesis that fragmented habitats would differentially affect trophic levels within a tri-trophic system. I predicted that the adult blue crabs would be less abundant and change

their behavior by increasing foraging rates in fragmented habitats due to increased encounter rates. I also predicted that juvenile blue crabs and hard clams would experience reduced predation rates in fragmented habitats driven by lower densities of adult blue crabs. In response to reduced predation rates, I hypothesized that hard clams would employ weaker anti-predator responses in fragmented habitats.

4.3 Methods

In Barnegat Bay-Little Egg Harbor Estuary, New Jersey, 50–88% of seagrass biomass has been lost since the 1980s (Kennish et al. 2007; Kennish et al. 2009), making the area well situated to examine the impacts of seagrass habitat fragmentation. I selected two sites in Island Beach State Park, a preserved area of Barnegat Bay, New Jersey. At site one, "Seining" (39°51'17.84"N, 74° 5'27.69"W); the study area consisted of a 0.60km^2 continuous meadow of *Zostera marina* and *Rupia maritima*, the two dominant seagrass species in the estuary. At site two, "Sedge" (39° 47' 24.8064"N, 74° 6' 28.476"W), the study area consisted of a 0.32km^2 continuous meadow of *Z. marina*. A matrix of fragmented seagrass patches and unvegetated sediment surround each meadow. Patch size in the fragmented seascape ranged from 0.5m^2 to 9.9m^2 with a mean of 3.02m^2 (Rielly, unpublished data). Seagrass shoot density did not vary between fragmented and continuous habitats in this system, and averaged 108.58 ± 42.97 shoots/m^2 at Seining and 46 ± 8.3 shoots/m^2 at Sedge (Rielly, unpublished data). I conducted four field experiments to determine if habitat fragmentation differentially affects predation rates, predator and prey abundances, and prey behavior among three trophic levels.

Predation Rates

To test for effects of fragmentation on juvenile blue crab survival I employed a tethering experiment. Tethering is widely used to measure survival rates among treatments and provides an experimental method of assessing predation (Butler et al. 2014; Heck and Thoman 1981; Hovel and Lipcius 2001, 2002). Tethering has been used in a variety of marine habitats including seagrass (Bologna and Heck 1999; Hovel and Lipcius 2001; Peterson et al. 2001). Juvenile blue crabs were collected by seining along 10m transects with a 1.75m seine net, in both continuous and fragmented habitats. Crabs were tethered the day of collection. Only intermolt crabs with no missing periopeds between 45 and 75 mm were selected for tethering. The tethering harness was looped under each lateral spine and secured with a drop of cyanoacrylate glue. The harnessed crab was attached to a 30.5 cm stainless steel 15 kg test fishing leader (AUSLINE) which was then affixed to a stake. Harnessed crabs were then staked directly in the sediment in either continuous seagrass or a seagrass patch within the fragmented seagrass habitat. Selected seagrass patches within the fragmented habitat were between 10 and 15m from the continuous seagrass habitat and were between $0.5m^2$ and $2m^2$. Half of all crabs in both habitats were tethered inside plastic 2.5 cm mesh cages (one crab/cage) that eliminated predator access to serve as a control for the effectiveness of the tether apparatus. At Seining, I tethered seven crabs per treatment (N=28). At Seining, I tethered five crabs per treatment (N=20). I assessed juvenile blue crab survival after 72 hours by categorizing crabs as alive or missing. Missing crabs were assumed to be lost to predation as no crabs were lost or separated from their tethers in the control treatments. I used a nominal logistic regression to test for differences in survival rate at each site with factors of habitat type (fixed effect), treatment (fixed effect), and a habitat type by

treatment interaction term. Data for this analysis and all subsequent analyses were collected between late July and early September 2014.

To test for the effects of habitat fragmentation on hard clam predation I used a mark and recapture predator exposure experiment. At Seining, I established eleven 0.3m^2 circular plots for each of four treatments (N=44) by lowering landscape edging completely (14cm depth) into the sediment around the plot. The treatments were (1) fragmented seagrass predator exposure, (2) fragmented seagrass control, (3) continuous seagrass predator exposure, and (4) continuous seagrass control. Ten clams were added to each plot. Clams were between 8 and 12mm and marked with a small dab of white paint to facilitate recapture. Control treatments were covered with plastic 0.65cm mesh to exclude predators. At Seining I utilized the same experimental design, however each treatment had 9 replicates instead of 11 (N=36). After 10 days I hand dug the plots and sieved all material (500 micron sieve) to collect remaining clams and recorded seagrass shoot density. Whole live clams were categorized as surviving. Any unburied clams were assumed to be dead and were excluded from analysis. Missing or fragments of clams were categorized as consumed. I used an analysis of variance (ANOVA) with factors of treatment (fixed factor), habitat type (fixed factor), and the interaction term to test for the effect of habitat type and predation on the proportion of clams surviving at each site. Because the data was proportional, I applied an arcsine square root transformation to the data prior to analysis.

Predator distribution

To test for differences in the distribution of adult and juvenile blue crabs I performed standardized 10m length seines with a 1.75m wide seine net in continuous and fragmented habitats (N=56). The number and carapace width (a proxy for crab age) of captured crabs were recorded. I used a t-test to test for differences in number of crabs caught per seining effort and a Welches test to test for differences in carapace width in continuous and fragmented habitats due to unequal variances in the data.

Behavior

I used tethering experiments to test for differences in hard clam anti-predator behavior (burrowing) across fragmented and continuous habitats using a block design. Juvenile hard clams between 10 and 12mm were tethered to metal landscaping staples (22cm in length) with 20cm long monofilament fishing line (13.6 kg test). One end of the line was glued to the valve of the shell using a drop of cyanoacrylate glue. The other end of the line was secured to the landscaping staple. Clams were deployed into paired plots approximately 1m apart which were each 0.5m x 0.5m in area. Each plot received nine clams by securing the metal staple into the sediment; clams were placed on top of the sediment hinge up (living position). All plots were covered in plastic 0.65cm mesh to prevent predator access. A blue crab actively foraging on hard clams, which I provided as a resource, was placed within a plastic 0.65cm mesh cage over one plot in each pair to serve as a control. The actively foraging blue crab sends chemical cues signaling the presence of a predator inducing predator avoidance behavior in the hard clams (burrowing). Hard clams exposed to actively foraging predators have been shown to

burrow significantly deeper than clams excluded from predators (Flynn and Smee 2010). Each block consisted of a set of paired plots in the continuous habitat and a nearby set of paired plots in the fragmented habitat. Within each block, 15-20m separated paired plots in continuous habitat and fragmented habitat; 25-30m separated each block. At Seining, I established 3 blocks (N=108 clams) and at Sedge I established two blocks (N=72 clams). After 10 days I measured the distance on the 20cm monofilament line that remained exposed above the sediment on each clam after it had burrowed and subtracted it from the total length of the line to determine how far each clam had burrowed. Any missing or dead clams were excluded from analysis. I used a mixed model with factors of site (random effect), block (random effect), treatment (fixed effect), habitat type (fixed effect), and all interaction terms to test for differences in clam burial depth among continuous and fragmented habitats. Preliminary analyses showed that the effect of "site" accounted for a negligible amount of variation in the model, therefore "site" was removed, and "block" was retained as the only random effect in the model.

I used underwater video to test for differences in predator behavior between continuous and fragmented habitats. In both continuous and fragmented seagrass habitats I provided a bait resource (*Brevoortia tyrannus*) in a plastic 2.5cm mesh envelope staked into the sediment. This allowed active foraging but prevented predators from completely removing the bait. I placed an underwater video camera (GoPro Hero3) approximately 0.25m away from the bait. Each filming event was 1-2.5 hours, and I recorded nearly 18 hours of video. Recording session replicates were deployed on different days but on each day both a continuous and fragmented video were filmed simultaneously (N=14). The video footage was processed in the laboratory and I recorded the number of blue crab

visits to the bait resource per hour, duration of each foraging event, and length of time to first visit. I performed t-tests to test for differences in number of visits per hour, and length of time to first visit for fragmented and continuous habitats. I used a Welches test to test for differences in duration of foraging events due to unequal variances in the data. All video data was square root transformed prior to analysis.

4.4 Results

I found that the effect of habitat fragmentation on predation rates was dependent on the trophic level of the predator. The results showed that predation on juvenile blue crabs was higher in fragmented habitats at Seining (Fig. 4.1, Nominal logistic regression: DF = 3, R^2 = 0.580, N=21, ChiSquare=16.18, P = 0.001; Treatment (tethering effectiveness): ChiSquare=11.32, P=0.0008; Habitat Type x Treatment: ChiSquare=5.91 , P=0.015). At Sedge however, predation on juvenile blue crabs was high in both habitat types and I found no difference in loss of crabs between the two treatments (Nominal logistic regression: DF=3, ChiSquare=21.15, P<0.0001; Tethering treatment: ChiSquare=21.09, P<0.0001, habitat type x tethering treatment: ChiSquare=1.47, P > 0.05). No crabs were lost from control tethers at either site, demonstrating the effectiveness of the tethering method.

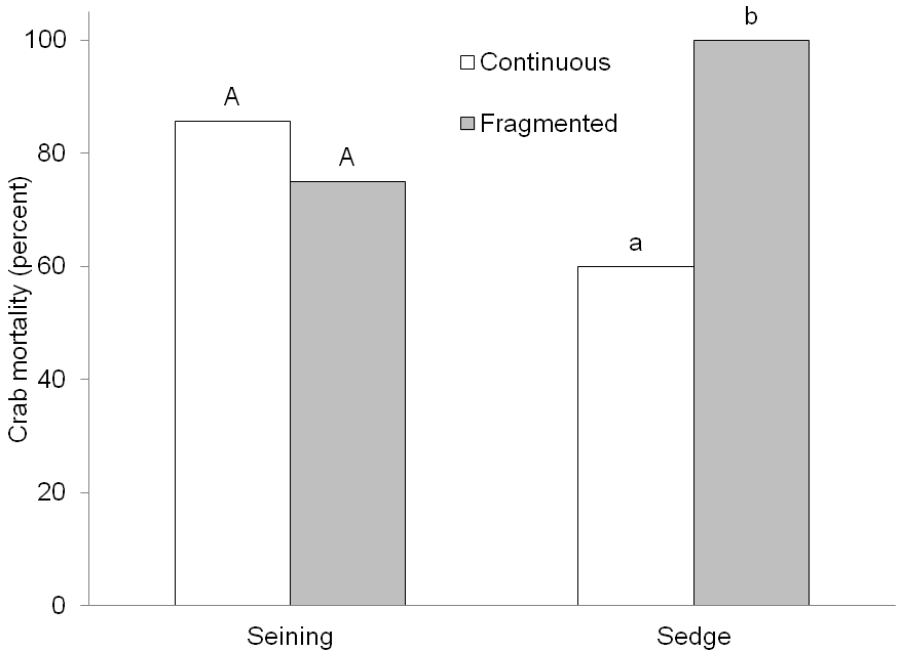

Figure 4.1: Juvenile blue crab mortality was higher in fragmented habitats at one site. Proportion of mortality among tethered juvenile blue crabs in continuous habitats (white bars) and fragmented habitats (gray bars). Untransformed data are shown. Letters indicate significant differences between treatments, as determined using Nominal Logistic Regression.

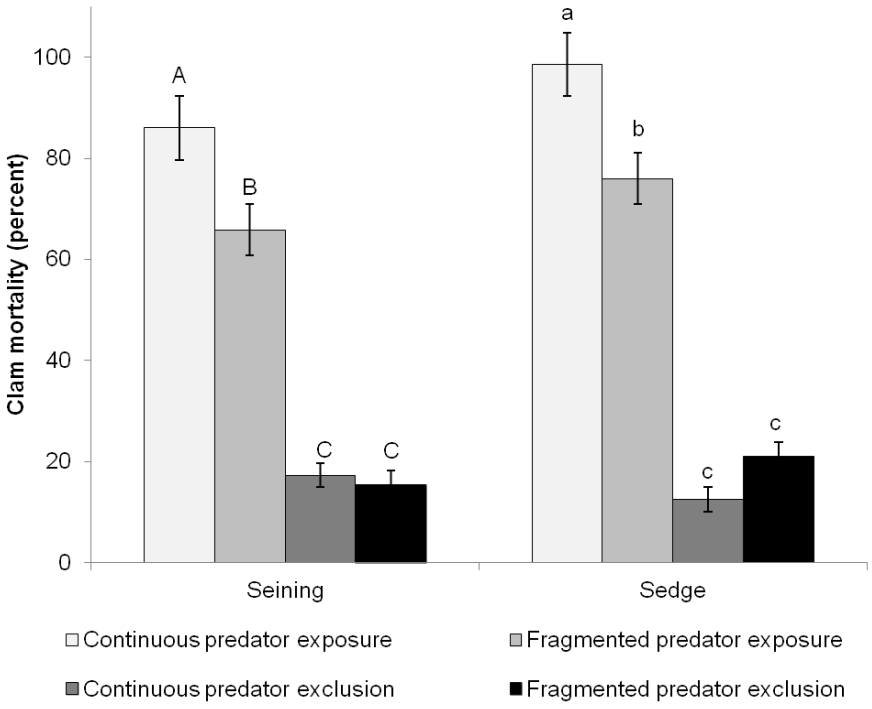

Figure 4.2: Hard clam mortality is higher in continuous habitats (white bars) than in fragmented habitats (light gray bars) when exposed to ambient predation. The continuous and fragmented controls (predator exclusion) are indicated by the dark gray and black bars, respectively. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

I found significantly higher predation on hard clams in continuous habitats than in fragmented habitats (Fig. 4.2, Seining, ANOVA: R^2_{adj}=0.76, N=40, $F_{3/36}$=37.57, P<0.0001; habitat type: $F_{1/38}$=6.10, P=0.0184; treatment: $F_{1/38}$=101.673, P<0.0001; habitat type x treatment interaction: $F_{1/38}$=4.681, P=0.0372; Seining, ANOVA: R^2_{adj}=0.86, N=34, $F_{3/30}$=62.07, p<0.0001; habitat type: P.0.05; treatment: $F_{1/32}$=183.98, P<0.0001; habitat type x treatment interaction: $F_{1/32}$=9.003, P=0.0054). Clams in both

the fragmented and continuous habitats exposed to predators experience much higher mortality than the predator exclusion controls. However, when clams are exposed to predators in the continuous habitat they experience higher clam mortality than clams exposed to predators in fragmented habitats.

Habitat fragmentation also affected predator abundance and the size structure of the population. Blue crabs were more abundant in continuous habitats than in fragmented habitats at both sites (Seining, Welches test: N=35, $F_{1/22.38}$=4.360, P=0.00484; Seining, ANOVA: R^2_{adj}=0.15, N=31, $F_{1/29}$=5.235, p<0.0296). Crabs in fragmented habitats, however, were larger in carapace width than crabs captured in continuous habitats (Fig. 4.3, Seining, Welches test: N=13, $F_{1/20.86}$=23.435, P=0.0005; Seining, Welches test: N=18, $F_{1/4.328}$=10.549, P=0.028).

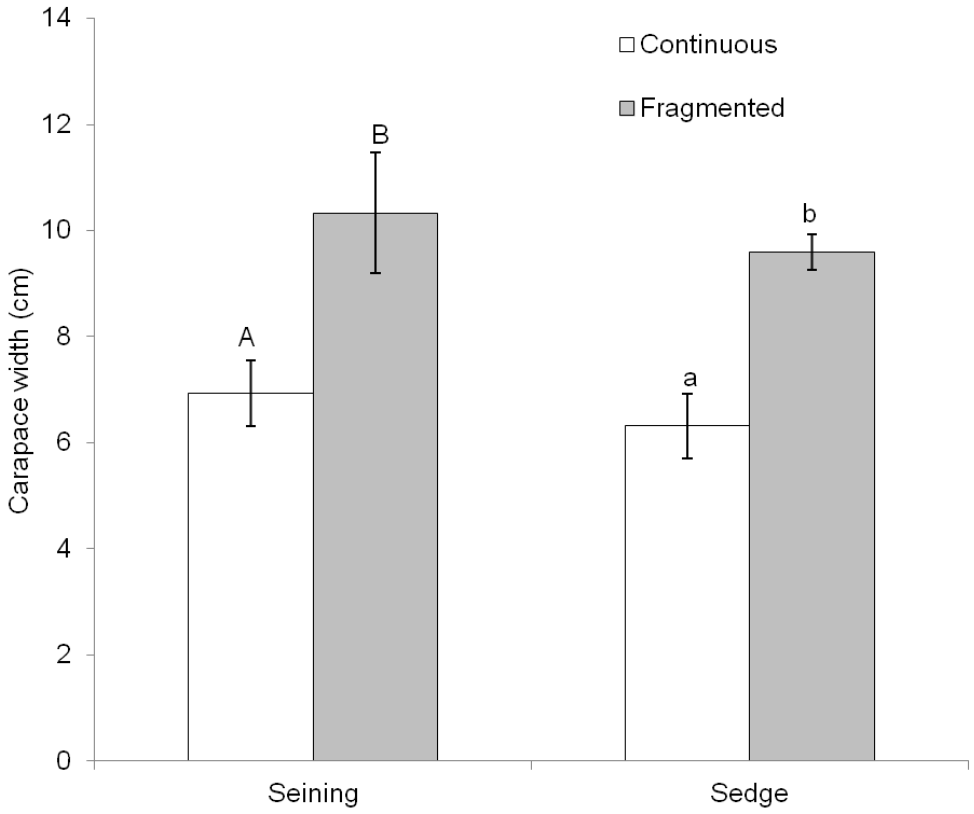

Figure 4.3: Mean blue crab carapace width is larger in fragmented habitats than continuous habitats. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Welches test.

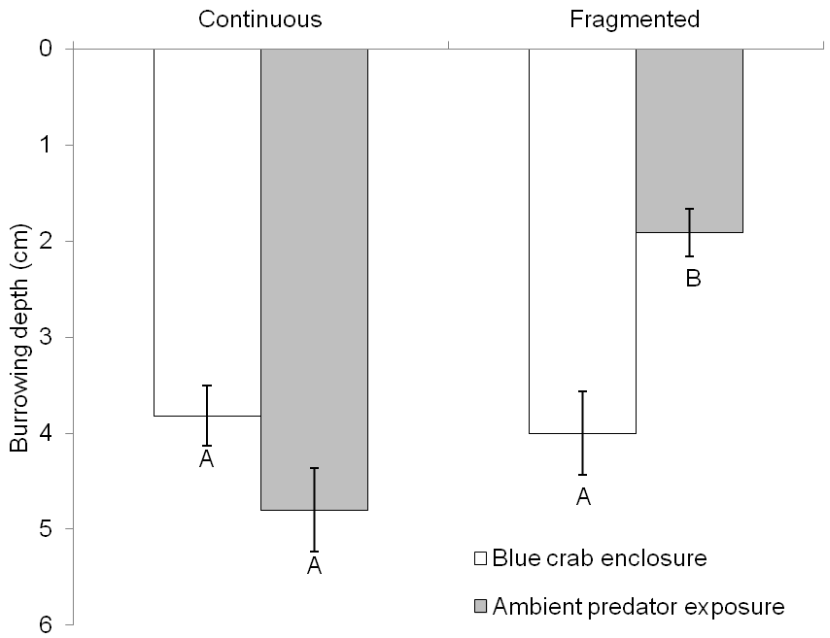

Figure 4.4: Clams exposed to ambient predation burrowed deeper in continuous habitats than in fragmented habitats (pooled data from both sites). Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

Habitat fragmentation influenced both prey and predator behavior. Clams burrowed deeper in continuous habitats than fragmented habitat (Fig. 4.4, Mixed model: R^2_{adj}=0.65, N=98; habitat type: $F_{1/4.297}$=2.84, P=0.1623; treatment: $F_{1/3.617}$=0.7928, P=0.4285; habitat type x treatment: $F_{1/3.433}$=29.31, P=0.0086). The continuous habitat predation exposure treatment was not different from either of the treatments with actively foraging blue crabs (experimental control). Clams in the fragmented habitat predation exposure, however, burrowed to a shallower depth than all other treatments. Predator behavior was also significantly affected by habitat fragmentation. The video observation of predator foraging showed that blue crabs took more time to find the offered prey item

in continuous habitats than in fragmented habitats (Fig. 4.5, Seining, t-test: R^2_{adj}=0.49, N=6, $F_{1/4}$=5.903, P=0.0360; Seining, t-test: R^2_{adj}=0.74, N=8, $F_{1/6}$=17.89, P=0.0055). Blue crabs also actively foraged longer in continuous habitats than in fragmented habitats (Fig 4.6, Seining, Welches test: N=68, $F_{1/24.622}$=5.384, P=0.0289; Seining, Welches test, N=155, $F_{1/53.467}$=8.865, P<0.0044). By contrast, blue crabs had higher number of visits per hour in fragmented habitats (Fig. 4.7, Seining, t-test: R^2_{adj}=0.74, N=6, $F_{1/4}$=15.36, P=0.0173; Seining, t-test: R^2_{adj}=0.51, N=8, $F_{1/6}$=6.25, P=0.0465).

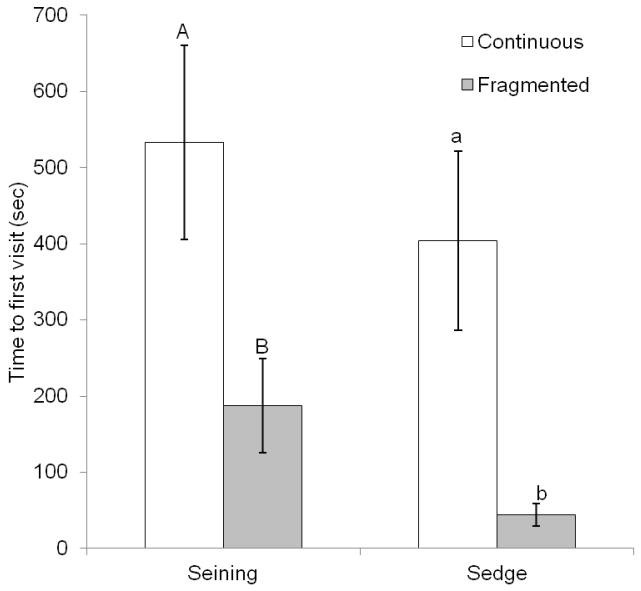

Figure 4.5: Blue crabs took longer to find offered resource in continuous habitats. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a t-test.

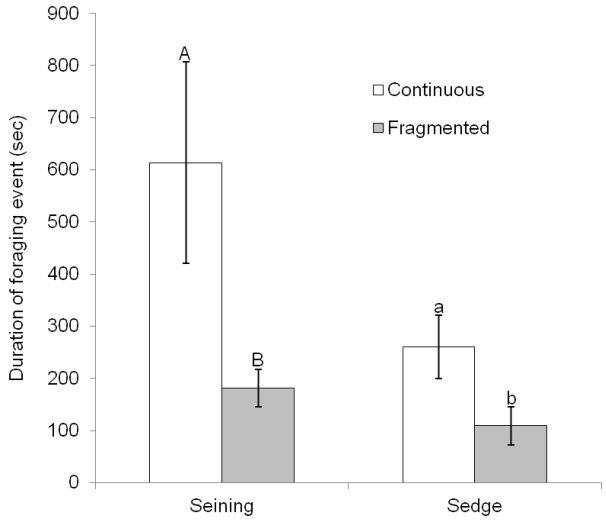

Figure 4.6: Blue crabs foraged longer in continuous habitats. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Welches test.

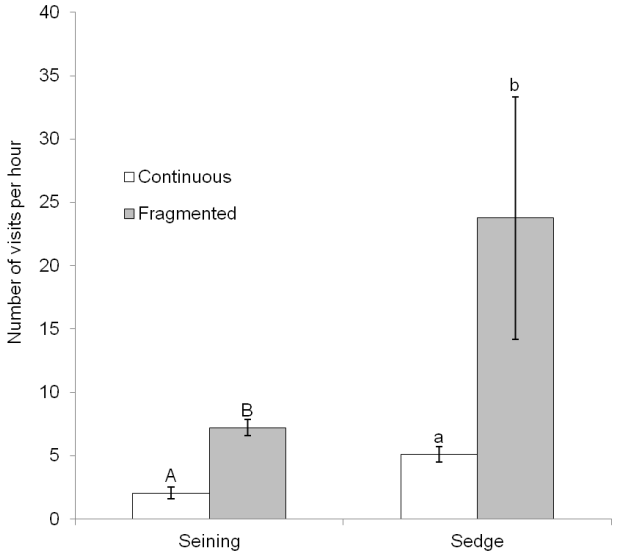

Figure 4.7: *Blue crabs visited resource more frequently in fragmented habitats than in continuous habitats.* Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a t-test.

4.5 Discussion

The results demonstrate that different trophic levels are differentially affected by habitat fragmentation. As I hypothesized, juvenile blue crabs can experience higher predation in fragmented habitats, likely driven by the presence of larger adult blue crabs in fragmented habitats. The abundance of large blue crabs in fragmented habitats could be due to a low refuge value of fragmented habitats for juvenile blue crabs. Juvenile blue crabs have been shown to decrease their own foraging in fragmented habitats due to an increased risk of predation (Macreadie et al. 2012). If fragmented habitats do not serve has a useful prey refuge for juvenile blue crabs, large blue crabs are more easily able to capture prey. While larger adult blue crabs were present in the fragmented habitats, I found the total abundance of blue crabs of all sizes is higher in continuous habitats. This may explain why hard clams experience more predation in continuous habitats, as the large numbers of blue crabs in continuous habitats are likely responsible for heavy predation rates on these prey items. In contrast to juvenile blue crabs, hard clams in fragmented habitats do not experience greater predation in fragmented habitats. This result is in contrast to the hypothesis but emphasizes that responses to fragmentation are specific to trophic level. In addition, the results suggest that the distribution of the top predator in this multi-trophic relationship is likely to be the underlying driver of patterns of abundance of lower trophic levels across continuous and fragmented habitats.

Habitat fragmentation also resulted in changed behavioral responses in both predators and prey. Hard clams, experiencing greater predation in continuous habitats, employed stronger anti-predator avoidance strategies in continuous habitats by burrowing deeper than in fragmented habitats. Results from the video analysis support this result as

well; blue crabs actively foraged longer in continuous habitats. Blue crabs in fragmented habitats find prey items more quickly, have more frequent visits to prey items, but forage for less time. These changes in blue crab behavior support the prediction that fragmented habitats lead to enhanced encounter rates between predators and prey, and increased predator movement, a probable result of edge effects from habitat fragmentation. The effect of fragmentation on the abundance and distributions of consumers clearly manifested not only in changes in predation rates among fragmented and continuous habitats, but also in behavioral responses of both predators and prey.

Taken together, these results demonstrate the importance of examining the effects of habitat fragmentation on species distributions and behavior in a multi-trophic context. Habitat fragmentation did not affect all trophic levels similarly, and the effect on a particular trophic level was determined by the distribution and behavior of the predator in the seascape. Higher predation rates on intermediate predators (juvenile blue crabs) by top predators (adult blue crabs) in fragmented habitats and lower utilization of fragmented habitats by juvenile blue crabs translated to lower predation on the basal prey (hard clam). Lower predation rates on basal prey led to weaker predator-avoidance behaviors in fragmented habitats. These results support previous studies that suggest the effect of fragmentation on lower trophic levels is determined by the effect of fragmentation on higher trophic levels (Krauss et al. 2010; Roslin et al. 2014; van Nouhuys 2005). In marine systems where predation is a critical biotic interaction changes in the abundance of predators may have implications for food web stability in fragmented habitats and the potential for trophic cascades.

As habitat and biodiversity loss accelerate, we expect that the abundance and diversity of higher-level consumers will be more affected than lower trophic levels (Estes et al. 2011). However, a decline in top consumers presents a number of potential cascading effects that may alter other trophic levels. Changes in diversity at one trophic level can produce changes in diversity at other trophic levels (Dyer and Letourneau 2003), potentially influencing ecosystem function (Duffy 2003; Tilman et al. 2001). Here, I have shown that a decline in top consumers from a system due to habitat fragmentation can result in changes in predation intensity and behavior of lower trophic levels, suggesting the potential for strong effects of habitat fragmentation not just on higher trophic levels but ecosystem wide.

Chapter 5

CONCLUSIONS

In this dissertation, I have shown how variation in spatial structure influences recruitment patterns, consumer distributions, resource availability, and food web structure. First, I demonstrated the high variability in recruitment and predation both spatially and temporally. Spatial variation in biological processes is an important structuring mechanism for community composition patterns. My results support the notion that both local and regional processes are important to community composition (Ricklefs 1987). Predation acts to decrease the abundances of a competitive dominant in adult communities across the region, and at each local site the suite of species which benefits from increased resource availability is different, increasing the divergence in community composition across the study region. This result demonstrates the importance of incorporating the influences of processes that operate at different spatial and temporal scales to understand community assembly and composition.

I then demonstrated how habitat isolation in marine ecosystems can affect species' composition, richness, and abundance over very short distances, and that the relative importance of top-down and bottom-up processes to primary producer abundance is spatially dependent. I also show that the likely mechanism is a combination of resource declines and consumer declines in isolated habitats. In addition, I found that isolated patches may be resource limited, further exacerbating changes in top-down and bottom-up control among isolated habitats. The results emphasize the need for a greater understanding of how fundamental ecological processes may vary spatially in marine systems.

Finally, I showed the importance of examining the effects of habitat fragmentation on species distributions and behavior in a multi-trophic context. The effects of habitat fragmentation do not affect all trophic levels similarly. Indeed, I found opposing responses of predators and prey given the habitat arrangement and trophic level of interest. This result suggests that the overall effect of fragmentation on a particular trophic level is determined by the distribution of predators in the seascape. My results support previous studies that suggest the effect of fragmentation on lower trophic levels is determined by the effect of fragmentation on higher trophic levels (Krauss et al. 2010; Roslin et al. 2014; van Nouhuys 2005). Here, I have shown that the changes in consumer abundances due to habitat fragmentation can result in changes in predation intensity and behavior of lower trophic levels, suggesting the potential for strong effects of habitat fragmentation not just on higher trophic levels but ecosystem wide.

In this thesis, I have demonstrated that spatial structure has important ecosystem implications for patterns of species' diversity and trophic relationships. As habitat and biodiversity loss accelerate, we expect that the abundance and diversity of higher-level consumers will be more affected than lower trophic levels (Estes et al. 2011). Changes in diversity at one trophic level can produce changes in diversity at other trophic levels (Dyer and Letourneau 2003), and subsequently changing biodiversity also influences ecosystem function (Duffy 2003; Tilman et al. 2001). Understanding how spatial variation influences species' distributions and interactions can provide valuable insight into how local and regional processes interact, and how ecosystems may respond to changing landscapes.

References Cited

Agrawal, Anurag A., et al. (2007), 'Filling Key Gaps in Population and Community Ecology', *Frontiers in Ecology and the Environment,* 5 (3), 145-52.

Allison, Gary W, Lubchenco, Jane, and Carr, Mark H (1998), 'Marine reserves are necessary but not sufficient for marine conservation', *Ecological Applications,* 8 (sp1), S79-S92.

Anderson, Elizabeth M. and Boutin, Stan (2002), 'Edge effects on survival and behaviour of juvenile red squirrels (Tamiasciurus hudsonicus)', *Canadian Journal of Zoology*, 80 (6), 1038-46.

Anderson, Marti J. (2001), 'A new method for non-parametric multivariate analysis of variance', *Austral Ecology,* 26 (1), 32-46.

Andren, Henrik (1994), 'Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review', *Oikos*, 355-66.

Ayling, Avril L. (1980), 'Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae', *The Biological Bulletin,* 158 (3), 271-82.

Bach, Catherine E. and Kelly, Dave (2004), 'Effects of forest edges on herbivory in a New Zealand mistletoe, Alepis flavida', *New Zealand Journal of Ecology,* 28 (2), 195-205.

Bell, Susan S. (1991), 'Amphipods as insect equivalents? An alternative view', *Ecology*, 350-54.

Bellier, Edwige, et al. (2007), 'Identifying spatial relationships at multiple scales: principal coordinates of neighbour matrices (PCNM) and geostatistical approaches', *Ecography,* 30 (3), 385-99.

Bergquist, Patricia R. and Sinclair, Mary E. (1968), 'The morphology and behaviour of larvae of some intertidal sponges', *New Zealand Journal of Marine and Freshwater Research,* 2 (3), 426-37.

Bernot, Randall J. and Turner, Andrew M. (2001), 'Predator identity and trait-mediated indirect effects in a littoral food web', *Oecologia,* 129 (1), 139-46.

Berril, NJ (1975), 'Chordata: Tunicata', in and J.S. Pearse Geise A.C (ed.), *Reproduction of Marine Invertebrates* (II; New York: Academic Press), 241-82.

Bertness, Mark D. (1989), 'Intraspecific Competition and Facilitation in a Northern Acorn Barnacle Population', *Ecology,* 70 (1), 257-68.

Bingham, Brian L. and Young, Craig M. (1991), 'Larval behavior of the ascidian Ecteinascidia turbinata Herdman; an in situ experimental study of the effects of swimming on dispersal', *Journal of Experimental Marine Biology and Ecology,* 145 (2), 189-204.

Bologna, Paul A. X. and Heck, Kenneth L. (1999), 'Differential predation and growth rates of bay scallops within a seagrass habitat', *Journal of Experimental Marine Biology and Ecology,* 239 (2), 299-314.

Borcard, Daniel, Legendre, Pierre, and Drapeau, Pierre (1992), 'Partialling out the Spatial Component of Ecological Variation', *Ecology,* 73 (3), 1045-55.

Borthagaray, A. I., Brazeiro, A., and Gimenez, L. (2009), 'Connectivity and patch area in a coastal marine landscape: Disentangling their influence on local species richness and composition', *Austral Ecology,* 34 (6), 641-52.

Bostr, MC, et al. (2011), 'Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges', *Marine Ecology Progress Series,* 427, 191-217.

Boström, Christoffer, Jackson, Emma L., and Simenstad, Charles A. (2006), 'Seagrass landscapes and their effects on associated fauna: A review', *Estuarine, Coastal and Shelf Science,* 68 (3–4), 383-403.

Bracken, Matthew E. S., Dolecal, Renee E., and Long, Jeremy D. (2014), 'Community context mediates the top-down vs. bottom-up effects of grazers on rocky shores', *Ecology,* 95 (6), 1458-63.

Brooks, Thomas M., et al. (2002), 'Habitat Loss and Extinction in the Hotspots of Biodiversity

Pérdida de Hábitat y Extinciones en Áreas Críticas para la Biodiversidad', *Conservation Biology,* 16 (4), 909-23.

Brückmann, Sabrina V, et al. (2011), 'The impact of habitat fragmentation on trophic interactions of the monophagous butterfly Polyommatus coridon', *Journal of Insect Conservation,* 15 (5), 707-14.

Burkholder, Derek A, et al. (2013), 'Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade?', *Journal of animal ecology,* 82 (6), 1192-202.

Butler, MJ, et al. (2014), 'Effects of the parasitic dinoflagellate Hematodinium perezi on blue crab (Callinectes sapidus) behavior and predation', *Journal of Experimental Marine Biology and Ecology,* 461 (0), 381-88.

Caffey, Hugh M. (1985), 'Spatial and Temporal Variation in Settlement and Recruitment of Intertidal Barnacles', *Ecological Monographs,* 55 (3), 313-32.

Caro, A. U., Navarrete Sa Fau - Castilla, Juan Carlos, and Castilla, J. C. (2010), 'Ecological convergence in a rocky intertidal shore metacommunity despite high spatial variability in recruitment regimes', (1091-6490 (Electronic)).

Carr, Laurie W, Fahrig, Lenore, and Pope, ShealaghE (2002), 'Impacts of Landscape Transformation by Roads', in KevinJ Gutzwiller (ed.), *Applying Landscape Ecology in Biological Conservation* (Springer New York), 225-43.

Casini, Michele, et al. (2012), 'Predator transitory spillover induces trophic cascades in ecological sinks', *Proceedings of the National Academy of Sciences*, 109 (21), 8185-89.

Caswell, Hal (1978), 'Predator-mediated coexistence: a nonequilibrium model', *American Naturalist*, 127-54.

Chase, Jonathan M., Burgett, Amber A., and Biro, Elizabeth G. (2010), 'Habitat isolation moderates the strength of top-down control in experimental pond food webs', *Ecology*, 91 (3), 637-43.

Chase, Jonathan M., et al. (2002), 'The interaction between predation and competition: a review and synthesis', *Ecology Letters*, 5 (2), 302-15.

Chesson, Peter (2000), 'Mechanisms of maintenance of species diversity', *Annual review of Ecology and Systematics*, 343-66.

Chesson, Peter and Kuang, Jessica J (2008), 'The interaction between predation and competition', *Nature*, 456 (7219), 235-38.

Christian, Robert R and Luczkovich, Joseph J (1999), 'Organizing and understanding a winter's seagrass foodweb network through effective trophic levels', *Ecological Modelling*, 117 (1), 99-124.

Cohen, Joel E., Jonsson, Tomas, and Carpenter, Stephen R. (2003), 'Ecological community description using the food web, species abundance, and body size', *Proceedings of the National Academy of Sciences,* 100 (4), 1781-86.

Collin, Samuel B, et al. (2013), 'Optimizing early detection of non-indigenous species: estimating the scale of dispersal of a nascent population of the invasive tunicate Ciona intestinalis (L.)', *Marine pollution bulletin,* 73 (1), 64-69.

Connell, Joseph H. (1961), 'Effects of Competition, Predation by Thais lapillus, and Other Factors on Natural Populations of the Barnacle Balanus balanoides', *Ecological Monographs,* 31 (1), 61-104.

Connell, Joseph H. (1985), 'The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities', *Journal of Experimental Marine Biology and Ecology,* 93 (1–2), 11-45.

Connolly, Sean R. and Roughgarden, Joan (1999), 'Theory of Marine Communities: Competition, Predation, and Recruitment-Dependent Interaction Strength', *Ecological Monographs,* 69 (3), 277-96.

Cook, K, Vanderklift, MA, and Poore, AGB (2011), 'Strong effects of herbivorous amphipods on epiphyte biomass in a temperate seagrass meadow', *Marine Ecology Progress Series,* 442, 263-69.

Costanza, Robert, et al. (1997), 'The value of the world's ecosystem services and natural capital', *Nature,* 387 (6630), 253-60.

Cowen, Robert K. and Sponaugle, Su (2009), 'Larval Dispersal and Marine Population Connectivity', *Annual Review of Marine Science,* 1 (1), 443-66.

Crist, ThomasO, Pradhan-Devare, SharmilaV, and Summerville, KeithS (2006), 'Spatial variation in insect community and species responses to habitat loss and plant community composition', *Oecologia*, 147 (3), 510-21.

Crowder, Larry B and Cooper, William E (1982), 'Habitat structural complexity and the interaction between bluegills and their prey', *Ecology*, 63 (6), 1802-13.

Davies, Kendi F., Margules, Chris R., and Lawrence, John F. (2000), 'Which traits of species predict population declines in experimental forest fragments', *Ecology*, 81 (5), 1450-61.

Denno, Robert F, Lewis, Danny, and Gratton, Claudio (2005), 'Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations', *Annales Zoologici Fennici* (JSTOR), 295-311.

Dethier, Megan N., et al. (2012), 'Decoupling of recruitment from adult clam assemblages along an estuarine shoreline', *Journal of Experimental Marine Biology and Ecology*, 422–423 (0), 48-54.

Didham, RK, et al. (1998), 'Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments', *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353 (1367), 437-51.

Dill, Lawrence M., Heithaus, Michael R., and Walters, Carl J. (2003), 'Behaviorally mediated indirect interactions in marine communities and their conservation implications', *Ecology*, 84 (5), 1151-57.

Doherty, Peter and Fowler, Tony (1994), 'An Empirical Test of Recruitment Limitation in a Coral Reef Fish', *Science*, 263 (5149), 935-39.

Duffy, J Emmett (2003), 'Biodiversity loss, trophic skew and ecosystem functioning', *Ecology Letters,* 6 (8), 680-87.

Duffy, J Emmett and Hay, Mark E (1991), 'Amphipods are not all created equal: a reply to Bell', *Ecology,* 354-58.

Duffy, J Emmett, et al. (2001), 'Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test', *Ecology,* 82 (9), 2417-34.

Dyer, Lee A and Letourneau, Deborah (2003), 'Top-down and bottom-up diversity cascades in detrital vs. living food webs', *Ecology Letters,* 6 (1), 60-68.

Eierman, LE and Connor, RC (2014), 'Foraging behavior, prey distribution, and microhabitat use by bottlenose dolphins Tursiopstruncatus in a tropical atoll', *Marine Ecology Progress Series,* 503, 279-88.

Emmett Duffy, J., Paul Richardson, J., and Canuel, Elizabeth A. (2003), 'Grazer diversity effects on ecosystem functioning in seagrass beds', *Ecology Letters,* 6 (7), 637-45.

Estes, James A, et al. (2011), 'Trophic downgrading of planet Earth', *Science,* 333 (6040), 301-06.

Ewers, Robert M and Didham, Raphael K (2006), 'Confounding factors in the detection of species responses to habitat fragmentation', *Biological Reviews,* 81 (01), 117-42.

Fagan, William F, Cantrell, Robert Stephen, and Cosner, Chris (1999), 'How habitat edges change species interactions', *The American Naturalist,* 153 (2), 165-82.

Fahrig, Lenore (2003), 'Effects of habitat fragmentation on biodiversity', *Annual Review of Ecology, Evolution, and Systematics,* 34 (1), 487-515.

Fahrig, Lenore, et al. (1995), 'Effect of road traffic on amphibian density', *Biological Conservation*, 73 (3), 177-82.

Fernandez, Marina O., Navarrete, Sergio A., and Marques, Antonio C. (2014), 'Temporal variation in richness and composition of recruits in a diverse cnidarian assemblage of subtropical Brazil', *Journal of Experimental Marine Biology and Ecology*, 460 (0), 144-52.

Ferraz, Gonçalo, et al. (2007), 'A Large-Scale Deforestation Experiment: Effects of Patch Area and Isolation on Amazon Birds', *Science*, 315 (5809), 238-41.

Flynn, A. M. and Smee, D. L. (2010), 'Behavioral plasticity of the soft-shell clam, Mya arenaria (L.), in the presence of predators increases survival in the field', *Journal of Experimental Marine Biology and Ecology*, 383 (1), 32-38.

Forde, Samantha E. and Raimondi, Peter T. (2004), 'An experimental test of the effects of variation in recruitment intensity on intertidal community composition', *Journal of Experimental Marine Biology and Ecology*, 301 (1), 1-14.

Fortin, Marie-josée, Dale, Mark RT, and Ver Hoef, Jay M (2002), 'Spatial analysis in ecology', *Encyclopedia of environmetrics*.

Franklin, A. B., B. R. Noon, and T. L. George. (2002), 'What is habitat fragmentation?', in T. L. George and D. Dobkin (ed.), *Studies in Avian Biology* (25), 20-29.

Freestone, Amy L, et al. (2011), 'Stronger predation in the tropics shapes species richness patterns in marine communities', *Ecology*, 92 (4), 983-93.

Gallant, Alisa L, et al. (2007), 'Global rates of habitat loss and implications for amphibian conservation', *Copeia*, 2007 (4), 967-79.

Gibbons, J Whitfield, et al. (2000), 'The Global Decline of Reptiles, Déjà Vu Amphibians Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change', *BioScience*, 50 (8), 653-66.

Grabowski, Jonathan H., Hughes, A. Randall, and Kimbro, David L. (2008), 'Habitat complexity influences cascading effects of multiple predators', *Ecology*, 89 (12), 3413-22.

Grantham, Brian A., Eckert, Ginny L., and Shanks, Alan L. (2003), 'Dispersal Potential of Marine Invertebrates in Diverse Habitats', *Ecological Applications*, 13 (1), S108-S16.

Greenleaf, Sarah S, et al. (2007), 'Bee foraging ranges and their relationship to body size', *Oecologia*, 153 (3), 589-96.

Gripenberg, Sofia and Roslin, Tomas (2007), 'Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology', *Oikos*, 116 (2), 181-88.

Gurevitch, Jessica, Morrison, Janet A, and Hedges, Larry V (2000), 'The interaction between competition and predation: a meta-analysis of field experiments', *The American Naturalist*, 155 (4), 435-53.

Gustafsson, Camilla and Salo, Tiina (2012), 'The effect of patch isolation on epifaunal colonization in two different seagrass ecosystems', *Marine Biology*, 159 (7), 1497-507.

Haddad, Nick M, et al. (2015), 'Habitat fragmentation and its lasting impact on Earth's ecosystems', *Science Advances*, 1 (2), e1500052.

Heck, KL and Thoman, TA (1981), 'Experiments on predator-prey interactions in vegetated aquatic habitats', *Journal of Experimental Marine Biology and Ecology*, 53 (2–3), 125-34.

Heck, KL and Valentine, JF (2007), 'The primacy of top-down effects in shallow benthic ecosystems', *Estuaries and Coasts*, 30 (3), 371-81.

Heck, KL, Hays, G, and Orth, RJ (2003), 'Critical evaluation of the nursery role hypothesis for seagrass meadows', *Marine Ecology Progress Series*, 253, 123-36.

Heithaus, Michael R, et al. (2008), 'Predicting ecological consequences of marine top predator declines', *Trends in Ecology & Evolution*, 23 (4), 202-10.

Hemminga, Marten A and Duarte, Carlos M (2000), *Seagrass ecology* (Cambridge University Press).

Hoekman, David (2010), 'Turning up the heat: Temperature influences the relative importance of top-down and bottom-up effects', *Ecology*, 91 (10), 2819-25.

Hoekstra, Jonathan M, et al. (2005), 'Confronting a biome crisis: global disparities of habitat loss and protection', *Ecology Letters*, 8 (1), 23-29.

Hovel, KA and Lipcius, RN (2001), 'Habitat Fragmentation in a Seagrass Landscape: Patch Size and Complexity Control Blue Crab Survival', *Ecology*, 82 (7), 1814-29.

Hovel, KA and Lipcius, RN (2002), 'Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance', *Journal of Experimental Marine Biology and Ecology*, 271 (1), 75-98.

Hovel, KA and Regan, HM (2008), 'Using an individual-based model to examine the roles of habitat fragmentation and behavior on predator–prey relationships in seagrass landscapes', *Landscape Ecology*, 23 (1), 75-89.

Hubbell, Stephen P. (2001), *The unified neutral theory of biodiversity and biogeography* (Princeton [u.a.]: Princeton Univ. Press).

Hughes, Randall A, et al. (2004), 'Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach', (INTER-RESEARCH).

Hunter, Mark D and Price, Peter W (1992), 'Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities', *Ecology*, 73 (3), 723-32.

Jiang, Lin and Morin, Peter J (2005), 'Predator diet breadth influences the relative importance of bottom-up and top-down control of prey biomass and diversity', *The American Naturalist*, 165 (3), 350-63.

Johnson, Darren W. (2007), 'Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish', *Ecology*, 88 (7), 1716-25.

Johnson, Matthew W. and Heck, Kenneth L. (2006), 'Seagrass Patch Characteristics Alter Direct and Indirect Interactions in a Tritrophic Estuarine Food Web', *Estuaries and Coasts*, 29 (3), 499-510.

Kareiva, P. (1987), 'Habitat fragmentation and the stability of predator-prey interactions', *Nature*, 326 (6111), 388-90.

Karlson, RH (2006), 'Metapopulation dynamics and community ecology of marine systems', in JP Krizer and PF Sale (eds.), *Marine Metapopulations* (Academic Press).

Kennish, Michael J., et al. (2009), *Assessment of Eutrophication in the Barnegat Bay-Little Egg Harbor System: Use of SAV Biotic Indicators of Estuarine Condition* (N.J. Department of Environmental Protection, Office of Science).

Kennish, Michael J., et al. (2007), 'Barnegat Bay-Little Egg Harbor Estuary: Case study of a highly eutrophic coastal bay system', *Ecological Applications*, 17 (sp5), S3-S16.

Kinlan, Brian P and Gaines, Steven D (2003), 'Propagule dispersal in marine and terrestrial environments: a community perspective', *Ecology,* 84 (8), 2007-20.

Knights, A. M., Firth, L. B., and Walters, K. (2012), 'Interactions between multiple recruitment drivers: post-settlement predation mortality and flow-mediated recruitment', *PLoS One,* 7 (4), e35096.

Komonen, Atte, et al. (2000), 'Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus', *Oikos,* 90 (1), 119-26.

Krauss, Jochen, et al. (2010), 'Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels', *Ecology Letters,* 13 (5), 597-605.

Kumagai, Naoki H. (2006), 'Distance effects on patterns and processes of dispersal in an octocoral-associated amphipod', *Marine Ecology Progress Series,* 321, 203-14.

Lagos, Nelson A, et al. (2005), 'Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile', *Marine Ecology Progress Series*, 290, 165-78.

Lass, Sandra and Spaak, Piet (2003), 'Chemically induced anti-predator defences in plankton: a review', *Hydrobiologia,* 491 (1-3), 221-39.

Lathlean, JA, Ayre, DJ, and Minchinton, TE (2010), 'Supply-side biogeography: geographic patterns of settlement and early mortality for a barnacle approaching its range limit', *Marine Ecology Progress Series*, 412, 141-50.

Layman, Craig A, et al. (2007), 'Niche width collapse in a resilient top predator following ecosystem fragmentation', *Ecology Letters*, 10 (10), 937-44.

Legendre, Pierre and Fortin, Marie Josée (1989), 'Spatial pattern and ecological analysis', *Vegetatio*, 80 (2), 107-38.

Leibold, M. A., et al. (2004), 'The metacommunity concept: a framework for multi-scale community ecology', *Ecology Letters*, 7 (7), 601-13.

Lewin, R (1986), 'Supply-Side Ecology', *Science*, 234 (4772), 25-27.

Ljungberg, Peter, et al. (2013), 'Effects of small-scale habitat fragmentation on predator–prey interactions in a temperate sea grass system', *Marine Biology*, 160 (3), 667-75.

Louda, Svata M (1982), 'Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation', *Ecological monographs*, 52 (1), 25-41.

MacArthur, R.H. and Wilson, E.O. (1967), *The Theory of Island Biogeography* (Princeton University Press).

Macreadie, Peter I, Geraldi, Nathan R, and Peterson, Charles H (2012), 'Preference for feeding at habitat edges declines among juvenile blue crabs as oyster reef patchiness increases and predation risk grows', *Marine Ecology Progress Series*, 466, 145.

Martinson, Holly M., Fagan, William F., and Denno, Robert F. (2012), 'Critical patch sizes for food-web modules', *Ecology*, 93 (8), 1779-86.

McNeill, SE and Fairweather, Peter George (1993), 'Single large or several small marine reserves? An experimental approach with seagrass fauna', *Journal of Biogeography*, 429-40.

Menge, BA (2000), 'Recruitment vs. postrecruitment processes as determinants of barnacle population abundance', *Ecological monographs*, 70 (2), 265-88.

Menge, BA and Sutherland, JP (1976), 'Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity', *The American Naturalist*, 110 (973), 351-69.

Minchinton, Todd E. and Scheibling, Robert E. (1991), 'The Influence of Larval Supply and Settlement on the Population Structure of Barnacles', *Ecology*, 72 (5), 1867-79.

Nathan, Ran and Muller-Landau, Helene C (2000), 'Spatial patterns of seed dispersal, their determinants and consequences for recruitment', *Trends in ecology & evolution*, 15 (7), 278-85.

Navarrete, Sergio A, et al. (2005), 'Scales of benthic–pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control', *Proceedings of the National Academy of Sciences of the United States of America*, 102 (50), 18046-51.

Nydam, Marie and Stachowicz, John J. (2007), 'Predator effects on fouling community development', *Marine Ecology Progress Series*, 337, 93-101.

Orth, Robert J, et al. (2006), 'A global crisis for seagrass ecosystems', *BioScience*, 56 (12), 987-96.

Osman, Richard W. and Whitlatch, Robert B. (2004), 'The control of the development of a marine benthic community by predation on recruits', *Journal of Experimental Marine Biology and Ecology*, 311 (1), 117-45.

Pace, Michael L, et al. (1999), 'Trophic cascades revealed in diverse ecosystems', *Trends in Ecology & Evolution*, 14 (12), 483-88.

Paine, Robert T. (2002), 'Trophic Control of Production in a Rocky Intertidal Community', *Science*, 296 (5568), 736-39.

Palardy, James E. and Witman, Jon D. (2014), 'Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities', *Ecology*, 95 (2), 286-97.

Palmer, Margaret A., Allan, J. David, and Butman, Cheryl Ann (1996), 'Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates', *Trends in Ecology & Evolution*, 11 (8), 322-26.

Pauly, Daniel and Christensen, Villy (1995), 'Primary production required to sustain global fisheries', *Nature*, 374 (6519), 255-57.

Peterson, Bradley J, et al. (2001), 'Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering', *Marine Ecology Progress Series*, 224, 77-85.

Poore, Alistair G. B., Campbell, Alexandra H., and Steinberg, Peter D. (2009), 'Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed', *Journal of Ecology*, 97 (1), 164-75.

Power, Mary E (1992), 'Top-down and bottom-up forces in food webs: do plants have primacy', *Ecology*, 73 (3), 733-46.

Prugh, Laura R., et al. (2008), 'Effect of habitat area and isolation on fragmented animal populations', *Proceedings of the National Academy of Sciences*, 105 (52), 20770-75.

Ranta, Pertti, et al. (1998), 'The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments', *Biodiversity & Conservation*, 7 (3), 385-403.

Ricklefs, Robert E (1987), 'Community Diversity: Relative Roles of Local and Regional Processes', *Science*, 235 (4785), 167-71.

Ries, Leslie, et al. (2004), 'Ecological responses to habitat edges: mechanisms, models, and variability explained', *Annual Review of Ecology, Evolution, and Systematics*, 491-522.

Roberts, David A. and Poore, Alistair G. B. (2006), 'Habitat configuration affects colonisation of epifauna in a marine algal bed', *Biological Conservation*, 127 (1), 18-26.

Robles, Carlos D. (1997), 'Changing recruitment in constant species assemblages: Implications for predation theory in intertidal communities', *Ecology*, 78 (5), 1400-14.

Roslin, Tomas, et al. (2014), 'Species–area relationships across four trophic levels–decreasing island size truncates food chains', *Ecography*, 37 (5), 443-53.

Sale, PF, et al. (1984), 'Large scale spatial and temporal variation in recruitment to fish populations on coral reefs', *Oecologia*, 64 (2), 191-98.

Schüepp, Christof, et al. (2011), 'Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies', *Oecologia,* 165 (3), 713-21.

Scoffin, Terence P. (1970), 'The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini lagoon, Bahamas', *Journal of Sedimentary Research,* 40 (1), 249-73.

Shanks, Alan L. (2009), 'Pelagic Larval Duration and Dispersal Distance Revisited', *The Biological Bulletin,* 216 (3), 373-85.

Short, Frederick T and Burdick, David M (1996), 'Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts', *Estuaries,* 19 (3), 730-39.

Shulman, Rachel S and Chase, Jonathan M (2007), 'Increasing isolation reduces predator: prey species richness ratios in aquatic food webs', *Oikos,* 116 (9), 1581-87.

Shurin, Jonathan B. and Allen, Emily G. (2001), 'Effects of Competition, Predation, and Dispersal on Species Richness at Local and Regional Scales', *The American Naturalist,* 158 (6), 624-37.

Shurin, Jonathan B., et al. (2002), 'A cross-ecosystem comparison of the strength of trophic cascades', *Ecology Letters,* 5 (6), 785-91.

Sih, Andrew, Englund, Goran, and Wooster, David (1998), 'Emergent impacts of multiple predators on prey', *Trends in Ecology & Evolution,* 13 (9), 350-55.

Sih, Andrew, Ziemba, Robert, and Harding, Karin C (2000), 'New insights on how temporal variation in predation risk shapes prey behavior', *Trends in ecology & evolution,* 15 (1), 3-4.

Simon, A. Levin (1992), 'The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture', *Ecology*, 73 (6), 1943-67.

Smith, Adam C., Fahrig, Lenore, and Francis, Charles M. (2011), 'Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds', *Ecography*, 34 (1), 103-13.

Sousa, Wayne P, et al. (2007), 'Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure?', *Ecological monographs*, 77 (1), 53-76.

Stachowicz, John J and Byrnes, Jarrett E (2006), 'Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors', *Marine Ecology Progress Series*, 311, 251-62.

Stachowicz, John J, et al. (2002), 'Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process', *Ecology*, 83 (9), 2575-90.

Steffan-Dewenter, I. and Tscharntke, Teja (1999), 'Effects of habitat isolation on pollinator communities and seed set', *Oecologia*, 121 (3), 432-40.

Sutherland, William J (1982), 'Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality', *The Journal of Animal Ecology*, 491-500.

Svane, I and Young, Craig M (1989), 'The ecology and behaviour of ascidian larvae', *Oceanogr Mar Biol*, 27, 45-90.

Takakura, KI and Yamazaki, K (2007), 'Cover dependence of predation avoidance alters the effect of habitat fragmentation on two cicadas (Hemiptera: Cicadidae)', *Annals of the Entomological Society of America*, 100 (5), 729-35.

Terborgh, John, et al. (2001), 'Ecological meltdown in predator-free forest fragments', *Science,* 294 (5548), 1923-26.

Tigas, Lourraine A., Van Vuren, Dirk H., and Sauvajot, Raymond M. (2002), 'Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment', *Biological Conservation,* 108 (3), 299-306.

Tilman, David and Kareiva, Peter M (1997), *Spatial ecology: the role of space in population dynamics and interspecific interactions* (30: Princeton University Press).

Tilman, David, et al. (2001), 'Diversity and productivity in a long-term grassland experiment', *Science,* 294 (5543), 843-45.

Tscharntke, Teja and Brandl, Roland (2004), 'Plant-insect interactions in fragmented landscapes', *Annual Reviews in Entomology,* 49 (1), 405-30.

Tscharntke, Teja, et al. (2002), 'Characteristics of insect populations on habitat fragments: A mini review', *Ecological Research,* 17 (2), 229-39.

Turner, Andrew M, Fetterolf, Shelley A, and Bernot, Randall J (1999), 'Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail', *Oecologia,* 118 (2), 242-47.

Uriz, María Jesús, et al. (1998), 'How do reproductive output, larval behaviour, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges?', *Marine Ecology Progress Series,* 167, 137-48.1998.

Valladares, Graciela, Salvo, Adriana, and Cagnolo, Luciano (2006), 'Habitat Fragmentation Effects on Trophic Processes of Insect-Plant Food Webs', *Conservation Biology,* 20 (1), 212-17.

Efectos de la Fragmentación del Hábitat Sobre Procesos Tróficos de Redes Alimenticias Insecto-Planta', *Conservation Biology,* 20 (1), 212-17.

van Nouhuys, Saskya (2005), 'Effects of habitat fragmentation at different trophic levels in insect communities', *Annales Zoologici Fennici,* 42 (4), 15.

Verhoeven, Mirella P. C., et al. (2012), 'Epiphyte grazing enhances productivity of remnant seagrass patches', *Austral Ecology,* 37 (8), 885-92.

Waycott, Michelle, et al. (2009), 'Accelerating loss of seagrasses across the globe threatens coastal ecosystems', *Proceedings of the National Academy of Sciences,* 106 (30), 12377-81.

Weis, Jerome J and Vasseur, David A (2014), 'Differential predation drives overyielding of prey species in a patchy environment', *Oikos,* 123 (1), 79-88.

Werner, Earl E. and Peacor, Scott D. (2003), 'A review of trait-mediated indirect interactions in ecological communities', *Ecology,* 84 (5), 1083-100.

Whalen, M. A., Duffy, J. E., and Grace, J. B. (2013), 'Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem', *Ecology,* 94 (2), 510-20.

Wilcox, Bruce A. and Murphy, Dennis D. (1985), 'Conservation Strategy: The Effects of Fragmentation on Extinction', *The American Naturalist,* 125 (6), 879-87.

Wimp, Gina M., et al. (2011), 'Do edge responses cascade up or down a multi-trophic food web?', *Ecology Letters,* 14 (9), 863-70.

Witman, Jon D, Etter, Ron J, and Smith, Franz (2004), 'The relationship between regional and local species diversity in marine benthic communities: a global perspective',

Proceedings of the National Academy of Sciences of the United States of America, 101 (44), 15664-69.

Wollrab, Sabine, de Roos, André M, and Diehl, Sebastian (2013), 'Ontogenetic diet shifts promote predator-mediated coexistence', *Ecology*, 94 (12), 2886-97.

Wootton, J Timothy (1994), 'The nature and consequences of indirect effects in ecological communities', *Annual Review of Ecology and Systematics*, 443-66.

Wright, Jeffrey T and Steinberg, Peter D (2001), 'Effect of variable recruitment and post-recruitment herbivory on local abundance of a marine alga', *Ecology*, 82 (8), 2200-15.

Young, Craig M., et al. (1988), 'Distributional Consequences of Adhesive Eggs and Anural Development in the Ascidian Molgula pacifica (Huntsman, 1912)', *The Biological Bulletin*, 174 (1), 39-46.

Zabel, Jörg and Tscharntke, Teja (1998), 'Does fragmentation of Urtica habitats affect phytophagous and predatory insects differentially?', *Oecologia*, 116 (3), 419-25.

Zimmerman, R, Gibson, R, and Harrington, J (1979), 'Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community', *Marine Biology*, 54 (1), 41-47.