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DIVERSITY PATTERNS IN PEN SHELL (*ATRINA RIGIDA*) COMMUNITIES

By

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Mi trabajo de los ultimos seis años es en memoria a Jorge Matute Remus y Castor, y esta dedicado a mi familia, con cariño.

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ABSTRACT

My dissertation work involves the study of how marine communities develop in the context of local and regional processes. In particular, I am interested in how diversity in a community can be affected through processes such as habitat destruction, community density, and migration, using pen shells and their inhabitants as a model system. In St. Joe Bay, Florida, pen shells (*Atrina rigida*) are the most abundant source of hard substrate, and the shell provides habitat for approximately 70 species. These communities are discrete habitats that differ from the surrounding seagrass beds and sandy areas. Sixty-six percent of the species found on pen shells are not found in the habitat surrounding pen shells. Pen shells provide shelter for many motile species and hard substrate for settling sessile species and egg-laying fishes. I first demonstrate the role of the pen shell community within sea grass ecosystems. Results suggest that a large component of species found on pen shells are only found with pen shells, and those that are found in the surrounding habitat tend to occur at much lower densities. I then carried out an experiment that showed that the age of the community can affect diversity at local and regional scales. Results also showed that more motile species were more sensitive to these spatial scales, and showed changes in the spatial relationship through time; while for sessile species, the local-regional diversity relationship did not change with succession. In 2003 I performed an experiment that tested successional patterns on pen shells that occurred at high and low densities, as well as a pen shell region that suffered habitat destruction. Local community density did affect local diversity as predicted. Further, motile and sessile species had different responses to habitat destruction. What was interesting from this study is the way individual species responded to different regional sizes. It seems that species' changes in abundance and distribution (number of shells occupied) differed between the common species and the rare species. The pattern and probability of successful dispersal among habitats can therefore be crucial in determining whether local populations will become rare or increase in abundance. I studied three amphipod species that disperse at different life stages: *Neomegamphopus hiatus* and *Melita nitida* disperse as adults, while *Bemlos unicornis* disperses as juveniles. The metapopulation dynamics of the three species seems highly dependent on the life history stage involved in dispersal.

INTRODUCTION

Current ecological theory often partitions diversity into two different spatial scales. Species interactions are thought to largely take place within smaller local scale, while dispersal, habitat destruction and habitat heterogeneity become influential at larger regional scales. However, as ecologists are starting to develop hypotheses about ecological processes at different scales, they are finding that performing experiments at such large scales is problematic. Furthermore, it has been hard to determine where local and regional scales start and end (not all communities present discrete boundaries). Because of this, theory is outpacing experiments that attempt to explain patterns in nature. In order to perform experiments to test this theory, natural communities that are easy to manipulate are needed.

My dissertation work involves the study of how marine communities develop in the context of local and regional processes. In particular, I am interested in how diversity at different spatial scales in a community can be affected through processes such as habitat destruction, community density, and migration, using pen shells and their inhabitants as an experimental system. Pen shells (*Atrina rigida*) are large bivalves (average length 19 cm) that live embedded in the sand within sea grass patches. Once the mollusk inside the shell dies, the shell remains embedded in the sand for approximately one year, during which time a large variety of animals and algae colonize the empty shell. Among the 70 species found on or within pen shells are barnacles, oysters, shrimp, fish, crabs and amphipods. I define a shell and the species that assemble on it as a local community, because this is the scale over which many species directly interact through competition and predation. Neighboring shells can be considered part of a region where dispersal, shell destruction and degradation play important roles. The species found on pen shells can be divided into two broad groups. Motile species are defined as those species that have the potential to move among shells as adults. Sessile species on the other hand, are those species that remain attached to the pen shell as adults.

Different species of pen shells are found through out the world. There have been few studies however, that describe pen shell communities, the best known studies were done in Australia and in the Mediterranean. The work presented in this dissertation was

carried out in St. Joe Bay, Florida, in the northern Gulf of Mexico. St. Joe Bay is a shallow, well-protected bay with sandy bottom, large sea grass beds, and little freshwater input. Pen shells generally occur in the sea grass beds, at densities up to 11 shells per m^2. Pen shell mortality commonly occurs by either asphyxiation as sand is stirred during storms, or when they fall prey to large gastropods such as the horse conch. Australian pen shells are estimated to live approximately five years, however the life span of *Atrina rigida* is unknown.

I begin by demonstrating the role of the pen shell community within sea grass ecosystems (*Chapter 1*). Are pen shell communities true discrete communities or are the species present are also part of the larger seagrass matrix? An extensive survey was carried out in 2005 to determine which of the pen shell inhabitants were found in habitats outside of pen shells. Results suggest that a large component of species found on pen shells are only found with pen shells, and those that are found in the surrounding habitat tend to occur at much lower densities.

Given that pen shell communities provide a habitat for a relatively discrete community, and that pen shells are scattered through out St. Joe Bay, the next series of questions that I addressed were (1) how does the diversity on a single shell relate to the diversity of a larger area that encompasses a number of shells? (2) Also, if communities tend to undergo successional changes through time, does the age of a community affect diversity at different spatial scales? And if there are such changes in relationships, are these dependent on the species' natural histories? During the summer and fall of 2001 I carried out an experiment that showed that the age of the community can affect diversity at local and regional scales (*Chapter 2*). Results also showed that more motile species were more sensitive to these spatial scales, and showed changes in the spatial relationship through time; while for sessile species, the local-regional diversity relationship did not change with succession.

If diversity on pen shells depends on the local-regional relationship, then successional changes in diversity could depend on the number of habitats in the region: regions with many local communities could accumulate species faster than in regions with few local communities. If this is true, then we can make predictions of the effects of habitat destruction, as regions change from a high to a low number of local communities.

In the summer of 2003 I performed an experiment that tested successional patterns on pen shells that occurred at high and low densities, as well as a pen shell region that suffered habitat destruction (*Chapter 3*). Local community density did affect local diversity as predicted. Further, motile and sessile species had different responses to habitat destruction.

What was interesting from this study is the way individual species responded to different regional sizes. It seems that species' changes in abundance and distribution (number of shells occupied) differed between the common species and the rare species. Because common and rare species presented different patterns, I decided to test the neutral theory of biodiversity (in which all individuals in a community are considered equal, and only stochastic death and migration give rise to diversity patterns) and determine whether pen shell communities behaved in a "neutral" way or not (*Chapter 4*). The results suggest that with the motile group, rare species seem to drive the diversity patterns suggesting that environmental requirements can help determine changes in species abundance and distribution. With sessile species, both common and rare species have similar changes through time, following the neutral theory. This study showed that both neutral and niche patterns can be observed in the same system, however, by following successional changes, one can identify the mechanisms and conclude whether species follow neutral or niche theories.

Because previous studies suggested that the dispersal patterns of species were particularly critical in the maintenance of pen shell diversity, I decided to focus on a group of amphipods and see how their recruitment strategies influenced population dynamics (*Chapter 5*). The pattern and probability of successful dispersal among habitats may be crucial in determining whether local populations will become rare or increase in abundance. Here we present data on the dispersal strategy and population dynamics of three marine amphipods living in pen shells (*Atrina rigida*) in the Gulf of Mexico. The three amphipod species disperse at different life stages: *Neomegamphopus hiatus* and *Melita nitida* disperse as adults, while *Bemlos unicornis* disperses as juveniles. The two species that disperse as adults have the highest initial population sizes when a new shell becomes available, likely because arriving females of these species release their brood into these recently occupied shells. This dispersal pattern results in initially

higher population growth, but fewer occupied shells as noted by their clumped distribution. In contrast, the species that disperses as juveniles accumulates more slowly and more evenly across habitats. Eventually this species dominates the other two in terms of numerical abundance. The metapopulation dynamics of the three species seems highly dependent on the life history stage involved in dispersal.

While the pen shell system may be an appropriate model system for some questions in community ecology, it also has several unique characteristics, and caution should be exercised when generalizing to other systems. First, the concept of dispersal in pen shell communities is particularly problematic. Given that there are 70 species using pen shells as habitats and the range of dispersal abilities varies greatly among species, understanding the effect of dispersal limitation on diversity is highly problematic. Pen shell density seems to explain little variation in community structure (*Chapter 1*): even though the pen shell community presents discrete boundaries, individual species may operate at different scales, which could obscure community-level patterns. Therefore generalizing the effects of dispersal limitation on diversity and community structure becomes highly context-dependent. Second, the scales at which local and regional processes operate in pen shells may not be the same in larger systems. This becomes particularly important when comparing mechanisms that operate at different spatial scales. For example, the effects of habitat destruction (*Chapter 3*) in the pen shell system generally operate at the scale of a shell (e.g. individual shells degrade with age); however, it is unlikely that at the scale of St. Joe Bay any of the pen shell inhabitants will go extinct with the demise of a single shell. However, in larger ecosystems, habitat destruction may have a greater effect when local communities disappear, given that the area destroyed would be proportionally larger. Finally, the life cycle of organisms relative to the dead pen shell life span may also affect diversity patterns. The number of generations that pen shell inhabitants can undergo before the shell disappears is highly variable, ranging from one generation to several in one season. Therefore, caution must be taken when extrapolating successional patterns at local and regional scales (e.g. *Chapter 2*); the concept of climax and saturation of space may never occur in pen shell communities if the pen shell is destroyed before all of the space is occupied. This can have implications when invoking theories that attempt to explain the mechanisms behind

diversity patterns (*Chapter 4*). It is clear therefore, that temporal and spatial constraints are present in the pen shell system, and a challenge is to scale the effects observed in pen shells to the predicted effects in larger systems.

This dissertation shows the importance of succession in community formation and diversity patterns. By focusing on a group of species, I show how local mechanisms that allow for species coexistence interact with among-community mechanisms (e.g. dispersal) that affect species persistence at regional scales. The temporal and spatial variation that pen shell inhabitants show is the strength of this work: studying all of the inhabitants of a single community highlights the complexity that communities can undergo.

CHAPTER 1

SPATIAL STRUCTURE OF PEN SHELL (*ATRINA RIGIDA*) COMMUNITIES.

ABSTRACT

In St. Joe Bay, Florida, pen shells (*Atrina rigida*) are the most abundant source of hard substrate, and the shell provides habitat for approximately 70 species. These communities are discrete habitats that differ from the surrounding seagrass beds and sandy areas. Sixty-six percent of the species found on pen shells are not found in the habitat surrounding pen shells. Pen shells provide shelter for many motile species and hard substrate for settling sessile species and egg-laying fishes. Community structure (the abundance and identity of pen shell inhabitants) varied across eight regions of St. Joe Bay. The variation in community structure could be related to the surrounding seagrass bed quality either directly (e.g., inhabitants of pen shells directly benefit from the surrounding seagrass) or indirectly (e.g., pen shells and seagrass both benefit from similar factors such as current and nutrients). Even though most pen shell inhabitants occupy pen shells, their distribution across shells is highly variable. Many motile species are randomly distributed across shells, with a few species showing clumped distributions. Most of the sessile species have clumped distributions, such that when found, sessile species tend to be highly abundant. This study demonstrates the need to consider a community as the group of species living in a single habitat, while taking into consideration the differences in species' spatial perception.

INTRODUCTION

Over the last twenty years, spatial ecology has received a large amount of attention (Ricklefs and Schluter 1993). Current theory suggests diversity patterns are driven by the synergistic contribution of mechanisms at the local scale such as competition and disturbance, coupled with mechanisms at broader, regional scales such as dispersal and habitat heterogeneity (Cornell and Lawton 1992). In recent years, theory has addressed not only the relationship between spatial scales affecting diversity, but the

mechanisms that give rise to spatially-structured diversity patterns (Chase et al. 2005). Field research has focused on identifying the mechanisms that regulate diversity in natural systems (Holyoak et al. 2005). However, few systems have been found to have the appropriate requirements needed to test the spatial community ecology theory (Srivastava et al. 2004).

There have been two related obstacles in the study of spatially-structured communities. First, the physical boundaries of communities are often hard to define. Some examples of how ecologists have addressed this problem include devising methods for estimating diversity at the local scale (e.g. Gotelli and Colwell 2001), and the partitioning of communities across environmental gradients (e.g. Shmida and Wilson 1985). Second, an often-overlooked aspect in spatial ecology is the fact that the different species that comprise the community may be regulated by processes that operate on very different spatial scales (Huston 1999). Recognizing the spatial scale at which individual species are regulated may help understand the role of the habitat where populations occur as well as the habitat that connects these populations. In this fashion, the spatial area that would be considered a "community" for one species could in fact be only a part of a larger habitat for another species. The spatial scale at which species operate combined with the physical structure of communities needs to be considered in order to understand diversity patterns.

In marine ecosystems, defining the boundaries for populations and communities is especially problematic. Many marine species have at least two distinct life history stages that operate at very different spatial scales. The first stage is the dispersal stage, which is often composed of larvae or juveniles that are cast into the water column in search for new habitats to colonize (e.g. Roughgarden et al. 1985, Palmer et al. 1996). The second stage is a more sedentary stage, usually made up of adults that are territorial or sessile (e.g. Olson 1985), or even if capable of active transport, move only short distances (e.g. Mora and Sale 2002). These two life history stages have the potential of acting at different spatial scales: an among-habitat (i.e. regional) scale perceived by the disperser stage, and a local scale perceived by the sedentary stage. Therefore, the spatial arrangement of local habitats can be crucial for population dynamics and diversity patterns, where communities are part of a mosaic of different habitats.

The main objective of this study was to determine whether dead pen shells (from *Atrina rigida*) were occupied by a different community than that found in the surrounding sea grass habitat in St. Joe Bay, Florida. I asked the following questions: (1) Do the species occupying pen shells constitute a discrete community, or are they just part of a larger community within sea grass beds? More specifically, what proportion of pen shell inhabitants are also found in the habitat surrounding pen shells? (2) Does pen shell community structure vary with spatial scale, especially across St. Joe Bay? Spatial variation in community structure could occur as a function of environmental conditions including the density of communities in different areas of St. Joe Bay. I also focus on a subset of pen shell inhabitants to compare the distribution of different species. In any given community, species may operate at different spatial scales (Huston 1999), which can be reflected in the distribution of individuals.

METHODS

This study was conducted in St. Joe Bay, FL; a shallow, well-protected bay in the northern Gulf of Mexico. Substrate in the bay is composed of a bare sandy bottom intermixed with patches of sea grass (*Thalassia testudinum* and the less common *Halodoule wrightii*). Live pen shells (*Atrina rigida*) are found within the sea grass beds, anchored in the sand. These large bivalves can also be found in open sandy areas, however, at much lower densities (pers. obs.; Kulhmann 1996). When the mollusk inside the shell dies, the shell becomes occupied by a diverse array of species (Munguia 2004), which use the shell as either refuge, egg laying substrate, or settling habitat. This community persists until the shell breaks down or gets buried in the sand.

The discrete habitat boundaries offered by individual pen shells delimit a community at a local scale. In St. Joe Bay, dead pen shells make up the great majority of the hard substrate available for colonization. The main objective of this study was to quantify the proportion of pen shell inhabitants that can also be found in habitats between pen shells (e.g. seagrass, benthos, and the water column).

Eight sites within the bay were surveyed in the summer of 2005. Each site occurred within a unique sea grass bed, with at least one meter from the edge, however sandy areas within the sea grass patch occurred and were also sampled. Each of the 15 x 15 m sites was mapped with Cartesian coordinates and several sampling techniques were

carried out. First, all of the live and dead pen shells were mapped, and up to ten dead shells were collected by divers. To minimize the loss of inhabitants before sampling, Ziploc bags were carefully placed over the shells in situ, then the bags were sealed and brought to the surface. For these sampled shells, the distance to the nearest neighboring shell was measured in the field. The shells were taken to the laboratory and all species found on or inside were identified and counted. Second, we used ten haphazardly located 1 m^2 quadrats inside the 15 x 15 m perimeter to sample macrofauna. All the animals that are known to occupy pen shells were identified from each quadrat and counted in the field. Next, plankton tows (0.25 mm mesh) were carried on the perimeter of the site on foot, just above the substrate with forceful sweeps in order to dislodge small organisms from seagrass blades. Preliminary testing of methods suggested that this was the best way to obtain both small organisms swimming among seagrass blades as well as those loosely attached to the blades. Samples were sieved in 0.5 mm^2 mesh, identified and counted. This process was aimed at obtaining amphipods, snails, hermit crabs, but disregarded invertebrate larvae, since the identification of pen shell inhabitants involved either juveniles or adults. Finally, seagrass density and blade length were quantified using a 0.15 x 0.15 m quadrat randomly tossed ten times inside the 15 x 15 m perimeter. All of the seagrass blades inside the quadrat were counted, and three of these blades were picked at random and measured from the beginning of the plant to the tip.

Data analysis

All of the species found in either the pen shells or the adjacent habitat were compiled and standardized by unit area sampled. To obtain pen shell area, I used the equation of the line regressing a scanned pen shell area (imageJ, NIH) against the area obtained by the product of the shell length and width for 27 shells. This regression was highly significant ($F = 694.77$, $P<0.0001$) and explained 97% of the variance; therefore Length x width was a good predictor of pen shell area. Data were log transformed and averages for pen shell and adjacent habitat compared. I split the species into two groups to be consistent with previous studies (e.g. Munguia 2004) and because there are two general life history traits of species occurring on pen shells: motile species, defined as those species that were mobile as adults, and sessile species, which were attached to the substrate once they settled onto a pen shell.

I compared community structure on each shell with habitat (variance in seagrass density and blade length), and nearest neighbor distance. Abundance data were standardized by the maximum value for each species (Quinn and Keough 2003). Therefore, abundance was expressed as a percentage which controlled (1) large abundance differences across species as well as (2) comparisons of sessile clonal species and sessile species that produced small individuals. A Canonical Correspondence Analysis (CCA) was performed using the species data. I included the 22 most abundant motile species and the 15 most abundant sessile species (I defined abundant species as those having more than 20 individuals across shells in all plots) as well as the variance in sea grass density and variance in blade length as environmental data. I first tested for a horseshoe effect known to bias CCA analyses (Quinn and Keough 2003): I proceeded with the analysis only after failing to find any such effect. The first four axis scores of the CCA were used to quantify community structure influenced by the environment (how the identity of each species and their abundance in each shell relates among shells). Next, these axis scores were used in a Multivariate Analysis of Variance (MANOVA) as dependent variables, testing for differences between sites and using nearest neighbor distance as a covariate. This approach allowed me to test for similarities at a large spatial scale (among-sites), while taking into account nearest neighbor distance, which tests the hypothesis that communities with similar densities will have similar community structure.

A subset of the most common species, 11 motile and 9 sessile, was selected for analysis of patterns of abundance and distribution. These species were selected based on their overall high abundance, which would allow the variation in their distributions to be quantified. I calculated Morisita's standardized index (Krebs 1999) for each species in each region. I also calculated Morisita's index for dead shells at three different spatial scales within each region: 1x1 m, 3x3 m, and 5x5 m. The standardized version of the index creates an upper and lower boundary from –1 to +1 based on χ^2 distribution values with *n-1* degrees of freedom (*n*= no. of pen shells in each site). An index value of 0 is indicative of a random distribution, while +1 indicates a clumped distribution and –1 corresponds to a uniform distribution. With this standardized index, the 95% confidence intervals have an upper and lower boundary of +0.5 and –0.5 respectively (e.g. values

above 0.5 would correspond to a significantly clumped distribution). This index controls for differences in sample size among sites when calculating dispersion patterns.

RESULTS

Dead pen shells occur in densities ranging between 0.1 and 4 dead pen shells per m^2. In the sites surveyed, live pen shells occurred in densities up to 10 per m^2. Other un-sampled areas of the bay had densities up to 11 per m^2.

Of the species found in pen shell communities, only 33% of the motile and 16% of the sessile species are found in the adjacent habitat (Fig. 1.1). Those motile species that are not exclusive to pen shells tend to occur at much lower densities in the sea grass beds relative to pen shell habitats, except for a hermit crab and toothed gastropods (*Dentalium* sp.) which are frequently found on the sand among the sea grass. Blue crabs (*Callinectes sapidus*) and bay scallops (*Aequipecten irradians*) had been previously found in pen shells, however, in this survey none were found inside pen shells (Fig. 1.1). Of the sessile species, only mussels (*Modiolus demissus*) were found in relatively high abundances among the sea grass; this species is also able to form large beds in St. Joe Bay, however, they are low-lying and do not support pen shell inhabitants.

The CCA revealed that the first four axes explained only 41.2% of the variance in motile species community structure. Variation in sea grass density did not influence community structure ($F = 1.62$, $P=0.07$), therefore it was removed from the full analysis. Variation in blade length did influence community structure ($F = 3.87$, $P = 0.001$), and therefore it was retained, having a 71.6% correlation with the first axis score. Under the MANOVA, site differences explained 95% of the variance, while nearest neighbor distance ($r^2 = 10.3\%$) had a significant effect on community structure (Table 1.1). Communities with similar densities tended to have similar abundance levels and similar composition of species.

For sessile species, the first four axes of the CCA explained 47.4% of the variance in community structure. Environmental variables had a 67.7% correlation with the first axis score and influenced the analysis significantly (variation in sea grass density: $F = 4.77$, $P =0.002$; variation in blade length: $F = 3.10$, $P = 0.001$). Site differences explained 94% of the variation in sessile species community structure (Table 1.1), however, nearest neighbor distance had no significant effect.

The distribution patterns of 11 sessile species were investigated, including 3 crabs, 3 gastropods, 2 amphipods, 1 polychaete, 1 isopod, and 1 shrimp. The distributions of 9 sessile species were studied, including 2 polychaetes, 2 bryozoans, and one of each of the following: an algae, sponge, oyster, barnacle, and ascidian. Dead pen shells had a random distribution within sites, irrespective of quadrat size (Fig. 1.2A), so the habitat distribution itself is neither clumped nor over dispersed. None of the species on pen shells showed an overdispersed distribution. Motile species ranged in their index of dispersion (Fig. 1.2B), with the shrimp *Palaemon floridianus*. and the amphipod *Dulichiella appendiculata* having clumped distributions, and the rest having a random distribution. All but three of the sessile species had strong clumped distributions (Fig. 1.2C). The bryozoan *Schizoporella unicornis,* the polychaete *Neanthes succinea* and the barnacle *Balanus eburneus* had dispersion indices not different from random. Given the large error bars in the dispersion indices, it appears that the patterns of species distributions are site dependent; in some sites a species can be clumped while in others present a more random distribution. However, this study is unable to tease apart the influence of environmental factors on the pen shell density.

DISCUSSION

Pen shell communities are highly diverse, with species representing many different taxonomic groups. Few of the species found on pen shells are found in the surrounding sea grass habitat, and those that do occur there, do so at low densities (Fig. 1.1). However, pen shell community structure tends to vary across different regions of St. Joe Bay. Community structure has significant correlations with variables of seagrass bed quality (e.g. blade length). This suggests that although pen shell inhabitants live mostly in pen shells, factors affecting seagrass variation also affect pen shell community structure. This connection between seagrass beds and pen shell communities may be direct (e.g., inhabitants of pen shells directly benefiting from the surrounding seagrass) or indirect (e.g., pen shells and seagrass both benefiting from similar factors such as current and nutrients). One explanation for this variation is that shell density seems to affect motile but not sessile species community structure (Table 1.1). These differences between motile and sessile species suggest that pen shell inhabitants do not operate on the

same spatial scales, which is a concept often overlooked in community studies (e.g. Ricklefs 1987, Tilman 1994, Chase et al. 2005, but see Munguia 2004).

Pen shells are important habitat for two main reasons. First, shells offer shelter for many species; second, they offer hard substrate for settling sessile species and egg-laying fishes. Many arthropods, including amphipods, crabs and isopods, occur on pen shells at relatively high densities. Their dispersion indices varied from clumped aggregations to random distributions, suggesting that these species operate at different spatial scales. The dispersion index was not correlated with taxons, for example the amphipod *Dulichiella appendiculata* had a clumped distribution, while *Ampithoe longimana* had a random distribution (Fig. 1.2). These differences could be a reflection of different mechanisms: behavioral, competitive ability, or the use of other substrates among sea grass beds. Both species are found on other habitats in different parts of the eastern Atlantic (Bousfield 1973, Sotka and Hay 2002), and *A. longimana* occurs at relatively high densities in the habitat surrounding pen shells (Fig. 1.1). Field experiments have shown that motile species can colonize pen shells within a day of the shell becoming available (Munguia *et al*. submitted; unpubl. data), suggesting that pen shells are a limiting resource in St. Joe Bay. Juveniles of the snail *Fasciolaria hunteria* are also found regularly in pen shells; these individuals may be seeking refuge before obtaining larger sizes. Sessile species tend to crowd shells (Fig. 1.2) with no predictable dominant species. Even though shells accumulate species rapidly, there was always available space in shells (Munguia 2004). The toad fish (*Opsanus beta*), Florida Blennie (*Chasmodes saburrae*), and clingfish (*Gobiesox strumosus*) are the three most common fishes, which use the shell as egg laying substrate (Kuhlmann 1996). During the survey a small juvenile gag grouper (*Mycteroperca microlepis*) was found inside a shell, suggesting that the shells may be important habitats for juvenile individuals of pelagic species as well.

Given the range in dispersion indices and high variation in community structure, the pen shell system shows the same problems associated with other marine communities (Palmer et al 1996, Srivastava et al 2004). Pen shell density seems to explain little variation in community structure, which supports the idea that individual species may operate at different spatial scales. Pen shell communities may experience lower effects of

dispersal limitation relative to terrestrial systems (e.g. Srivastava et al. 2004). This could suggest that recruitment limitation either occurs at much larger spatial scales (e.g. beyond a small area within St. Joe Bay), or it has no effects on diversity because of the significant variation in dispersal ability among individual species. Therefore, only by understanding the spatial extent of individual species can we understand the concept of dispersal limitation and delimit an appropriate regional scale for pen shell communities.

This study demonstrates the need to consider a community as the group of species living in a single habitat, while taking into consideration the differences in species' spatial organization. Pen shell communities are discrete, and different from the surrounding sea grass habitat. While the species found in or on pen shells are not endemic or unique to this substrate, they do not occur at the same densities outside shells. The high species density suggests that pen shells are important habitats within sea grass beds. The changes in diversity in pen shells are probably under different mechanisms than those of sea grass communities. Because pen shells are small and discrete, they are amenable for experiments that test mechanisms affecting diversity (e.g. Keough 1984, Munguia 2004, Srivastava et al. 2004).

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Table 1.1. Results from the MANOVA testing motile species community structure among different sites with nearest neighbor distance (NND) as a covariate. η^2 = proportion of the variance explained by the model.

MOTILE SPECIES	η^2	F	P-value
Wilks' Lambda	0.948	9.72	<0.001
Pillai's Trace		8.68	<0.001
SITE DIFFERENCES			
Wilks' Lambda	0.932	9.54	<0.001
Pillai's Trace		8.48	<0.001
	NND	2.96	0.0421
SESSILE SPECIES			
Wilks' Lambda	0.937	5.69	<0.001
Pillai's Trace		4.64	<0.001
SITE DIFFERENCES			
Wilks' Lambda	0.924	5.95	<0.001
Pillai's Trace		4.74	<0.001
	NND	1.08	0.36

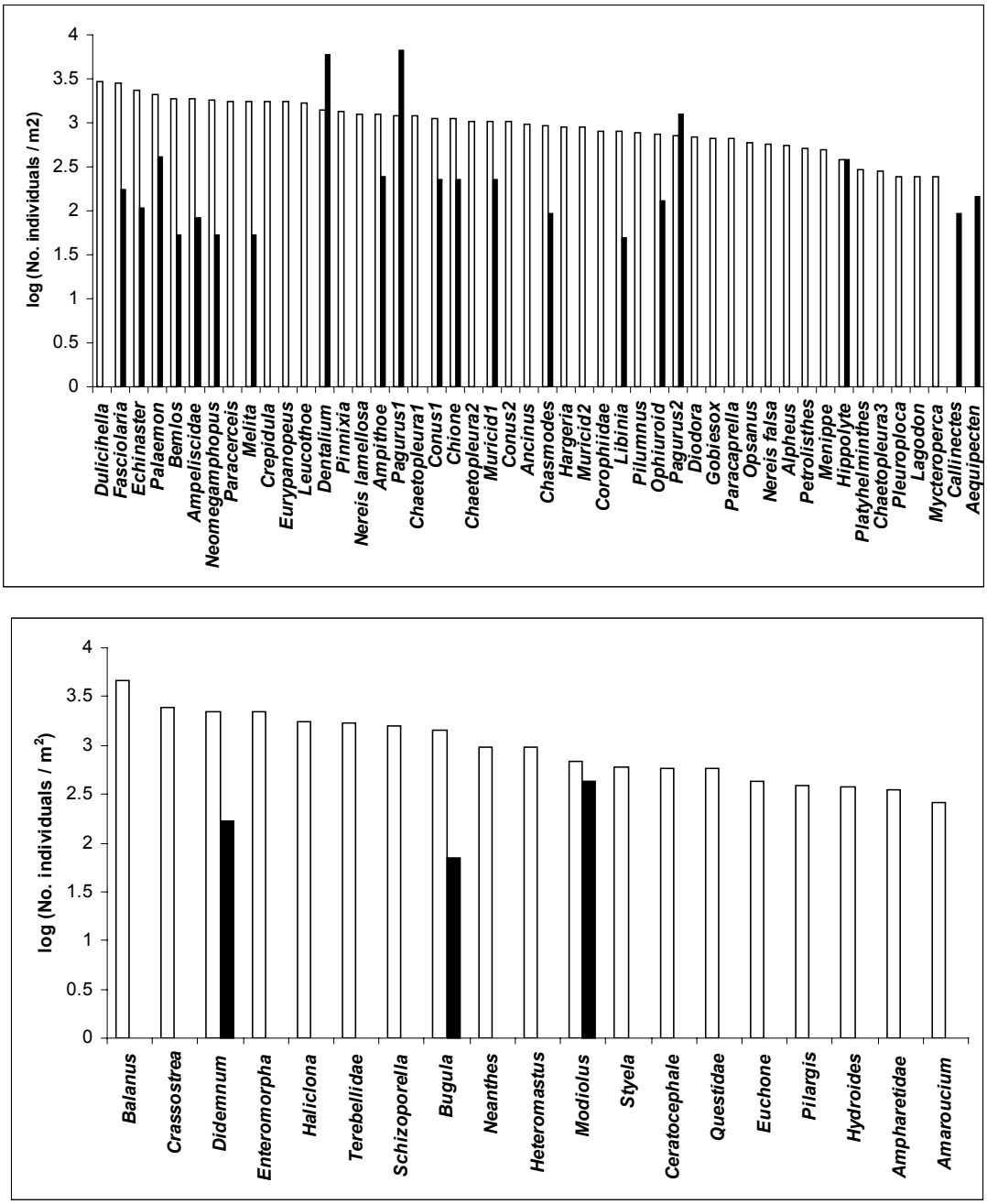

Figure 1.1. Density of organisms found in pen shells (open bars) and the surrounding sea grass habitat (filled bars). The density was standardized by the area sampled (e.g. total area that pen shells offered, and total area of each site). Top panel represents motile species, bottom panel sessile species.

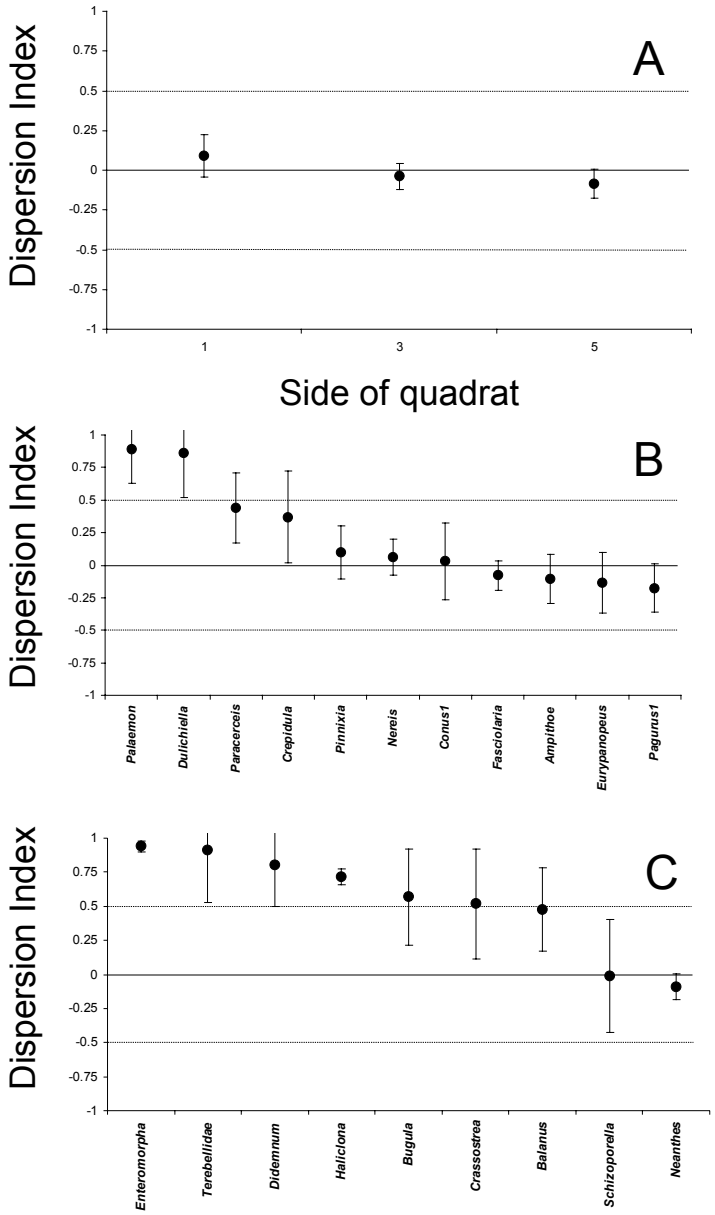

Figure 1.2. Average index of dispersion of (A) pen shell communities at 3 different spatial scales within the surveyed areas: 1x1 m, 3x3 m, and 5x5 m. Motile (B) and sessile (B) indices of dispersion for representative species. Dashed lines represent the 95% confidence interval around zero that delimits a random distribution. Points above 0.5 indicate a clumped distribution, and below –0.5 a uniform distribution. N=8 different sites across St. Joe Bay, error bars represent one standard deviation.

CHAPTER 2

SUCCESSIONAL PATTERNS ON PEN SHELL COMMUNITIES AT LOCAL AND REGIONAL SCALES.

ABSTRACT

I present a successional study of marine organisms on pen shells (*Atrina rigida*) at different regions of St. Joe Bay, Florida. By incorporating measures of relative abundance and assembly time I show how the relationship between local and regional diversity develops through different successional stages. The results showed that, with time, motile species richness increases significantly while evenness indices remain high and constant. Sessile species, on the other hand, increased in both species richness and evenness through time. For the motile species, regions seem to remain different while local saturation is observed. These results suggest that this group is under species sorting: species are mobile enough that recruits and adult dispersal within a region maintain differences among regions, while local communities are saturated. For the sessile species, the local-regional relationship was unsaturated at all sampling dates with both untransformed and rarefied data. Regions are initially similar in community structure, then differ through time to become similar again at the last sampling date. This may reflect a priority effect: propagules that arrive at a shell initially may exert influence on the species composition on a shell, so that at intermediate sampling times regions differ in community structure. However, at the last sampling there were no differences detected among regions, suggesting that dispersal distances might be larger for this group of species. These results suggest: (1) the degree of species saturation will depend on the successional stage of a community. (2) Incorporating species abundances (i.e. through rarefaction or other techniques) demonstrates the role of species commonness or rarity in determining patterns of community diversity at different scales. (3) Depending on the group of species studied, the size of the region will vary and will influence the local-

regional dynamics: the perceived region for sessile species may be larger than for motile species.

INTRODUCTION

Benthic communities present different diversity patterns at different spatial scales (Findley & Findley, 2002; Karlson & Cornell, 1998). It has been suggested that species interactions act at discrete scales, resulting in community patterns at local scales. Alternatively, different local communities may be connected through processes such as migration, creating distinctive community patterns at broader, more regional scales (e.g. Cornell & Lawton, 1992). Scientists have become aware of the relative importance of the processes observed at these two scales and their interaction, but field studies have proven elusive at presenting clear patterns (e.g. Karlson & Cornell, 2002). One of the main problems associated with experiments in benthic systems is selecting the appropriate local and regional scales (Karlson, 2002; see Westoby, 1998; Srivastava, 1999 for general comments) as well as accounting for historical effects such as succession. Here I present a successional study conducted on relatively small benthic communities that have discrete boundaries to elucidate the relative importance of succession at localized and larger regional scales.

Cornell (1985) proposed a graphical representation of the relationship between diversities at two spatial scales, known as a local-regional plot (Cornell & Lawton, 1992). The within-community diversity is referred to as the local scale, and the among-community diversity as the regional scale. Following this model, there are two idealized relationships between local and regional diversities. The first scenario is a linear relationship between the two scales where a constant proportion of species at the regional scale occurs at the local scale. As proposed, this unsaturated curve has a slope less than one, representing dispersal limitation: not all species at the regional scale are found at the local scale. The second relationship is a saturated curve in which diversity at the local scale asymptotes, eventually staying constant regardless of the size of the regional species pool. The degree of saturation is thought to indicate the degree of interaction among species within a local community (Cornell & Lawton, 1992).

Local-regional patterns are relatively easy to quantify and observe, however, the biological mechanisms driving those patterns are elusive (Srivastava, 1999; Winkler &

Kampichler, 2000). The relative importance of mechanisms acting at different scales will vary depending on the species' colonization and competition abilities (Holt, 1993). Both the species-specific traits, as well as the resulting community assemblage, may change through a community's age. Mouquet *et al*. (in press) predicted a change in the local-regional relationship through time: all species are initially rare, causing a saturated relationship; however as the colonization probability increases, the relationship becomes unsaturated until competitive interactions dominate, driving the local-regional relationship to saturation again. This suggests that local-regional experiments must be interpreted in the context of community succession.

Benthic habitats provide interesting systems for testing the effects working at different spatial scales because many species have several different life stages and thus perceive the environment at different scales during each life stage. In some species, individuals are able to disperse over large distances at the larval stage, but are sessile or relatively sedentary as adults. Other species may present sedentary larvae or juveniles while adult stages are relatively motile. Examples of these habitats include communities found on coral reefs, or epifauna growing over rocks or other hard substrates such as shells. The overgrowth on these substrates creates patchy communities that can be studied at discrete spatial scales. Differences in local and regional diversities could vary depending on the interaction between the different spatial perceptions among species (Wiens 1989).

Pen shells (*Atrina rigida* Lightfoot) are relatively large bivalves (mean adult length = 19 cm) that live embedded in sand within sea grass beds (Kulhmann, 1998). These shells represent the most abundant source of hard substrate for many fouling organisms in St. Joe Bay, Florida (for studies on similar molluscs see Keough, 1984; Cummings, *et al.*1998). Pen shell mortality is typically due either to old age, predation by whelks, or environmental disturbance. Once the mollusc dies, the empty shell offers refuge and egg-laying substrate for many invertebrates and fish. The empty shell remains anchored in the sand for a limited period of time (approximately one year, pers. obs.), thus presenting an ephemeral habitat where an associated community assembles and goes extinct when the shell is dislodged or degrades. A shell and the species that assemble on it can be regarded as the local community, because this is the scale at which most of the

competitive and predatory interactions occur. Furthermore, the small size of the community allows for complete sampling of all of the species coexisting at the local scale. Neighbouring shells, then, can be considered part of a region where migration, shell predation and shell degradation play important roles. Pen shell communities present an appropriate system with which to experimentally test the relative importance of within- and among-community processes affecting diversity.

This study quantifies the pen shell community structure at two spatial scales during succession to address the following hypotheses: (1) Migration limitation will cause a positive relationship between local and regional diversity. (2) This relationship will vary with successional stages in a predictable way (Mouquet *et al*. in press). (3) Motile and sessile species groups within the community will show different local-regional diversity relationships. (4) Incorporating species' relative abundances through rarefaction should alter the relationship between local and regional diversities. Incorporating a measure of abundance will highlight the proportion of rare species that are present at the local scale and their contribution to the local-regional relationship.

METHODS

Field methods

This study was conducted at St. Joe Bay, Florida (29º45´ N, 85º15´ W), which is a shallow bay with a sandy bottom and patches of sea grass. In order to provide a relatively uniform settling substrate, I collected live shells in the summer of 2001 and removed the flesh. All of the shells were relatively free of fouling and were photographed for future comparison. The experiment consisted of establishing local communities (individual shells) within regions (plots). "Regions" for this study consisted of ten 5 m by 5 m plots. Each region was separated from the next by at least 60 meters. Regional plots were placed parallel to the coast at a depth of less than two meters along the western (peninsula) side of St. Joe Bay. Four transects were placed within each region using the shoreline as reference. Each transect consisted of a 4.5 m x 0.1 m hard plastic mesh onto which five shells were anchored with cable ties at intervals of 1.2 meters. This density fell within the average natural live pen shell density at St. Joe Bay (range: 0.2 to 2 m^{-2}; Kuhlmann 1996, pers. obs.). The total sample size was 200 shells:

five shells for each of four collection times, which in turn were replicated by 10 regions (10 x 5 x 4 = 200).

The shells were anchored in July of 2001 and collected at four different times: 16, 32, 64, and 128 days post anchoring. At each sampling time, a transect was randomly selected from each plot, and all five shells within a transect were collected. Collection of samples involved placing a plastic bag over a shell, cutting the shell free from the mesh and removing the entire shell. Most of the fish caught in the shells were returned to the water after recording the species and its total length; a few were kept for identification purposes. The shells were taken to the lab and rinsed over a 1 mm mesh to collect all organisms, which were subsequently preserved in 70% ethanol. I divided all of the species into two groups, motile and sessile, based on their known adult dispersal abilities. Sessile species were defined as being fixed to the substrate and primarily sedentary. For example, tube-building amphipods were considered motile because the adults have the ability to move between shells and their tubes are ephemeral. Tube-building polychaetes, on the other hand, were considered sessile because their tubes are fixed to the substrate and worms have not been observed to leave tubes. Sessile organisms were identified, counted (where discrete individuals could be identified) and measured as percent cover. Shell photographs were used to identify new fouling individuals. Motile organisms were identified and counted under a dissecting microscope. Species were identified using keys in Uebelacker & Johnson (1984), Hopkins, Valentine & Lutz (1989), Kensley & Schotte (1989), and Thomas (1993).

Statistical analysis

I first tested for differences in species richness and evenness (J' = H' / log S, where H' is Shannon-Weiner index and S is species richness; Zar 1999) within each sample date for each group. Because shells were destructively sampled, instead of using repeated-measures ANOVA, I first tested for the interaction between collection time and plots. To test for differences among the 10 regions for each sampling time, I performed one-way ANOVAs on richness and evenness. When testing for differences in collection times I used Tukey's HSD test to compare means for each collection time. In these statistical tests I log-transformed species richness to meet assumptions of normality.

To test the similarity of local communities from different regions, I performed a Correspondence Analysis with a scaling on inter-sample distances (bi-plot scaling) and a down weight of rare species, using the most abundant motile and sessile species (21 and 15 species respectively). I performed a multivariate analysis of variance (MANOVA) for the first four principal component axes scores using plot as the independent variable for each time series. Normality of the scores and the correlation among variables was tested before the MANOVA was performed.

I considered each shell to be a local community and each plot to be a region for purposes of analysing local-regional dynamics. The average number of species per shell for each region was plotted against the total number of species for each region. The local-regional plots were determined for each time interval. Community means were used to avoid problems of pseudoreplication when regressing local against regional diversity (see Srivastava 1999). A rarefaction analysis was used for species mean abundance at each time interval with 1000 iterations (Gotelli & Entsminger 2001). I compared local-regional plots between rarefied and untransformed data using ANCOVA. Regression analyses were used to test whether the slopes for either rarefied or untransformed plots were significantly different from zero. I used SAS 8.01 for all statistical analyses (SAS Institute Inc., Cary, NC) and CANOCO (Centre for Biometry Wageningen, Wageningen, The Netherlands) for the correspondence analysis.

RESULTS

Species richness and evenness

There were 70 species (20 sessile and 50 motile) found inhabiting the pen shells. Some shells were destroyed during the course of the study, and two entire regions were destroyed at the first and last sampling dates. In general, the motile group had higher species richness per shell than the sessile species. Motile richness increased with time while evenness seemed to stay constant relative to sessile species (Fig. 2.1). Sessile richness and evenness increased with time (Fig. 2.1).

Pen shell communities had different spatial variation among the ten regions across time (Table 2.1). Motile species richness and evenness per shell did not differ across regions during the first colonizing stage (16 days). As time progressed, species richness diverged among regions (ANOVA, $P<0.05$) even though evenness was not

significantly different among regions (ANOVA, P>0.05). At the end of the season, all regions presented similar richness, and evenness (Table 2.1). Sessile species, on the other hand presented initial differences among the 10 regions, but as time progressed and substrate became saturated, regions converged on similar richness and evenness (Table 2.1).

Community composition

All of the species found during the course of this study appeared in initial pilot studies; therefore I expect that the regional species pool was constant throughout the sampling period. Local species composition clearly changed through time for both motile (Fig. 2.2) and sessile groups (Fig. 2.3). Some species that were rare initially tended to increase in frequency at later sampling times while others remained rare. Common species exhibited a range of patterns, from remaining common across all samples to becoming relatively more rare.

For example, the isopod *Paracerceis caudata* Say (Fig. 2.2) decreased in shell occupancy through time, while the amphipod *Neomegamphopus hiatus* Barnard and Thomas increased its frequency. The polychaetes *Nereis lamellosa* Ehlers and *N. falsa* Qautrefages were rare at the first sampling time, but became quite common at the last sampling time, probably due to the establishment of other polychaete tubes in which they find shelter. Another amphipod, an Ampeliscidae, was always rare throughout the duration of the experiment. Sessile species such as algae (*Enteromorpha* sp.) and barnacles (*Balanus* sp.) were common throughout the sampling period (Fig. 2.3). The polychaete *Neanthes succinea* (Frey and Leuckart) was rare at the first sampling date, however its frequency had increased by the last sampling date.

I used a correspondence analysis (CA) to compare the species composition in each shell across plots for each time interval. This method estimates species pool similarities among all regions. The first four axes of the CA explained over 50% of the variance in all cases but two (Table 2). The lack of correlation among CA axis scores supports the use of Wilk's Lambda in the MANOVA as a statistic (Zar 1999). I also present Pillai's Trace since this statistic tends to be more conservative than Wilk's Lambda. The results of the MANOVA are different for sessile and motile groups (Table 2.2). In the case of motile species, the MANOVA shows that for each time interval, all

of the local communities are different among regions. For sessile species, communities across regions are similar during initial settlement, diverge during intermediate sampling dates, and then converge to become similar by the last sampling date.

Local and regional diversity

I plotted both the rarefied and untransformed local species average against the total number of species found at each plot for each time interval (Figs 2.4 and 2.5). Untransformed data show no significant relationship between motile local diversity and regional diversity at 16 days (Figs 2.4a and 2.6a, Table 2.3). The slope increases at 32 and 64 days, only to decrease while still remaining different from zero at 128 days (Figs 2.4b-d, and 2.6). On the other hand, with rarefied motile diversity the slope decreases with sampling dates; however, the slopes were not found to be statistically different from zero (Figs 2.4e-h, and 2.6). Sessile species present relatively high slopes for both untransformed and rarefied data (Fig. 2.5). Untransformed local sessile species richness is saturated at 16 and 64 days, while rarefied species richness is saturated only at 64 days (Fig. 2.6b, Table 2.3).

When comparing the local-regional slopes between rarefied and untransformed data, motile and sessile species groups have different results through time. Motile species presented differences in the untransformed and rarefied curves only at 64 days (ANCOVA testing for interaction between slopes $df = 3,1$, $F = 22.7$ $P < 0.01$), the other sampling times presented similar curves (Fig. 2.4). Local richness of motile species tended to be rare 16 days, regardless of the regional species pool size (Fig. 2.4a); however, when using the rarefied richness the slope of the line is greater (Fig. 2.4e), but there are no differences between the two (ANCOVA testing for interaction between slopes, $df = 3,1$, $F = 1.15$ $P > 0.05$). Untransformed motile slopes seem to increase with time and then decrease, while rarefied seem to remain statistically similar (Fig. 2.6a). In the case of sessile species, the untransformed and the rarefied curves are not significantly different (ANCOVA testing for interaction between slopes for each sampling time, $P > 0.05$).

DISCUSSION

This study shows that pen shells develop and maintain rich communities of sessile and motile species. The diversity of these communities at local and regional scales varies

with the successional stage at which a community is sampled and will depend on the natural history of the species. Incorporating species relative abundance influences a local-regional relationship, and highlights the proportion of rare species and their contribution to this relationship.

Many motile species were rare at the initial successional stage relative to subsequent sampling stages (Fig. 2.2). This rarity may allow local diversity to be independent of the regional species pool size (Fig. 2.6a). As succession proceeds (days 32 and 64), there was significant linear relationship between the two scales, suggesting that species were largely migration limited (Fig. 2.6). At the last sampling date after significant succession and growth has occurred, the reduced relationship between scales could have been due to species interactions. Local diversity of motile species seemed to maintain differences among regions through time (Table 2.2). However, when species relative abundance was incorporated a different pattern emerges. Many of the species are rare and did not occur in all regions. Even if species diversity increased through time, the evenness index remained constant (Fig. 2.1). Local communities seemed to be saturated (Fig. 2.6), while maintaining regional differences (Table 2.2), suggesting that species sorting was taking place (MacArthur, 1972). Local-scale dynamics did not necessarily limit the number of coexisting species, but may have limited both the species composition and their abundance found in each community.

In the case of sessile species, both species richness and evenness increased through the sampling dates. Sessile species maintained similar community structure among regions initially, but, at intermediate successional stages the regions began to differ (Table 2.2), and by the end of the experiment, the regions were similar again. The local community maintained a high proportion of the species pool at local scales through time with few of these species being rare (Table 2.3, Fig. 2.6). The lack of a saturated relationship could be due to predation or disturbance opening up space and reducing competition, not allowing enough time for competitive interactions to occur, or not using the appropriate regional scale.

The Sessile species group exhibited regional similarities at the beginning and end of the experiment (Table 2.2); local communities became similar across regions, homogenizing the species pool for St. Joe Bay. This may reflect a priority effect:

propagules that arrive first on newly available substrate may exert influence on the species composition on a shell. Recruitment could occur in pulses through time, maintaining a high proportion of the species on shells, but changing species composition across regions at different sampling dates. This is consistent with the regional similarity hypothesis (Mouquet and Loreau, 2002). Dispersal among local communities is high enough to homogenize local areas increasing diversity (Fig. 2.1), and non-independence between spatial scales will take longer to observe.

That communities were at equilibrium is a critical assumption when looking at diversity patterns across different spatial scales. The temporally distinct species frequencies demonstrated here suggest different patterns depending on when the community was sampled, with the local-regional slope varying from zero to significantly positive (Fig. 2.6). The sampling period of this study, 128 days, is a large fraction of the total life span of the shell as a habitat resource.

In this paper I present untransformed local-regional plots and rarefied plots to demonstrate the effect of incorporating species abundances into these plots. The slope of the relationship between local and regional diversities increased for motile species when using untransformed presence-absence data (Fig. 2.6a). However, the slope decreased when data were rarefied. The increase in slope for untransformed data may have been due to an increase in rare species in a local community or to some artefact (i.e. increase in species pool size through time). But taking relative abundance into account demonstrates that many of the species at the local scale were rare, and rarity increases as community assembly progresses. As the number of rare species in the species pool increases, not all of the same species are found in all regions (Table 2.2). But, within a shell, all species increase in abundance similarly, increasing richness and maintaining a constant evenness. On the other hand, sessile species presented a different local-regional relationship. Local diversity maintained a constant proportion of the species pool through time with both untransformed and rarefied data. At the regional scale, there were few rare species. At the scale of a shell, species composition varied such that regional similarity depended on the age of the community.

Regional size

The first obstacle in local-regional comparisons is defining the appropriate scales. The size of the local community is dependent on the scale at which individuals interact while the size of the region is dependent upon the scale at which individuals from neighbouring communities interact via migration (Holt, 1993; Huston, 1999). The "regional" scale can vary from continents (Caley & Schluter, 1997), to many kilometres (Cornell, 1985; Findley & Findley, 2002; Karlson & Cornell, 1998), to a few meters (Winkler & Kampichler, 2000). The largest regions are appropriate for examining speciation and biogeographical changes in diversity, but may not be useful when addressing species interactions and the dynamics between within- and among-community diversities (Westoby, 1998).

Marine benthic systems frequently occur on discrete patches within which most of the species are interacting. It has been relatively easy to demonstrate how processes acting at the local scale can drive diversity (e.g Keough, 1984). However, defining the regional scale, and unveiling the processes that drive diversity at regional scales, has been problematic (Karlson & Cornell, 2002; Westoby, 1998). Previous studies tend to confound regional scale with area or with regional differences in environmental processes (e.g. Caley & Schluter, 1997; Srivastava, 1999). In this study, the regions were identical in size and were small enough to have the same environmental factors acting upon them.

The small scales of this system are appropriate for addressing the degree of species interaction within a locality and the among-community dynamics via migration across relatively uniform regions. Motile species composition varied among regions at all four sampling intervals (Table 2.2). However, sessile species were similar among regions, and the local-regional dynamics did not change much with time, which leaves open the possibility that the scale was inappropriate. When trying to unveil ecological processes, a region does not have to include the maximum range of a species' propagules, but a relatively homogeneous area in which the species has a probability of being present at all neighbouring local habitats. With pen shells, individuals that are mobile can sort themselves out within a group of pen shells; however, this sorting will vary across the regions because there are relatively few individuals of these species in the water column.

In contrast, it may be that sessile species perceive a much larger region than the 25 m^2 plots and therefore all regions seem homogenous.

Lack of independence among regions can also be a problem when interpreting local-regional patterns. Srivastava (1999; see also Fox, McGrady-Steed & Petchey 2000) proposed that one should use species pools with little overlap in the identities of species and, that the regions should be similar in every other way (i.e. environmentally). However, by using different species when comparing two or more regions, the results will be confounded by the intrinsic properties of those species driving a local-regional curve (e.g. some species being more interactive than others, or having greater dispersal ability) and by the size of the species pool creating saturated or unsaturated communities (Loreau, 2000). The "regions" in my study use the same set of species; therefore the species pool size is not driving the local-regional slope. The distribution of planktonic larvae could be patchy enough to create differing colonizing probabilities depending on the abundance of each species in the water column surrounding the shells (Sale, 1977; 1982).

Potential Mechanisms driving Pen shell Diversity

Local-regional dynamics on pen shell communities vary across time. Considering that the motile species group has (1) many rare species at the local scale, (2) an increase in species and a constant evenness through time, (3) community composition differences among regions, and (4) the local-regional relationship changing through time; there are two potential mechanisms taking place. First, motile species have stochastic recruitment (Sale, 1977), which appears to be taking place throughout the sampling period. However, recruitment is likely to be more important at initial stages of community formation. After 2 or more species have colonized pen shells, species interactions will occur, contributing to community patterns. Second, all regions differed in species composition through time, suggesting that the limit to diversity is not acting at the regional scale, but at the local scale, even when there is an uniform distribution of individuals.

Sessile species dynamics on pen shells seem relatively slower than motile species. Species are dispersal-limited, but their range may be greater than the definition of a region in this study. Sessile species occur on all regions at initial stages of community development. The increase in number of species through time may cause regions to

differ during the intermediate sampling times. However, because the same species that have high competitive ability occur on all regions, the regions become more similar again later in succession. Because the shell habitat is ephemeral, there may be insufficient time for the establishment of a competitive equilibrium.

This study demonstrates that pen shell communities exhibit species successional patterns that affect the relationship between spatial scales. Furthermore, these patterns seem to differ depending on the life history of the group of species. Motile species diversity seems to be driven by species sorting, while sessile species, which may grow colonies and increase significantly in size, seem to be driven by priority effects. These differences are reflected in community comparisons among regions, where differences or similarities arise depending on the type of organisms and on the assembly time of the communities. Pen shell communities reflect how dynamic and complex marine systems can be and highlight the importance of studying the mechanisms that drive diversity patterns across different spatial scales.

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Table 2.1. Series of ANOVAs testing for differences among regions in richness and evenness for both sessile and motile species groups for each sampling date. MS = Mean Squares, S = Species richness, J' = Evenness. * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

TIME		MOTILE		SESSILE	
		S	J'	S	J'
	Df	MS	MS	MS	MS
16 Days	7	0.054	0.003	0.206**	0.222***
Error	32	0.084	0.005	0.059	0.006
32 Days	9	0.372*	0.021	0.067	0.027**
Error	36	0.155	0.023	0.048	0.007
64 Days	9	0.171**	0.023	0.035	0.023*
Error	32	0.056	0.027	0.045	0.009
128 Days	7	0.046	0.006	0.078	0.007
Error	14	0.032	0.004	0.039	0.004

Table 2.2. Correspondence analysis (CA) and MANOVA results on CA scores for sessile and motile diversity with eigenvalues (EIGEN) and cumulative variance (VAR) explained by the first four axes. η^2 represents the proportion of the variance that is explained by the experimental factor (region). 16 and 128 days d.f. =28; 32 and 64 days d.f. = 36. * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

MOTILE								
DAYS		AXIS 1	AXIS 2	AXIS 3	AXIS 4	MANOVA	F	η^2
16	EIGEN	0.341	0.294	0.220	0.196	Wilks' Lambda	3.28***	0.90
	VAR	0.165	0.308	0.414	0.509	Pillai's Trace	2.67***	
32	EIGEN	0.470	0.328	0.270	0.247	Wilks' Lambda	2.58***	0.88
	VAR	0.175	0.299	0.399	0.491	Pillai's Trace	1.99**	
64	EIGEN	0.294	0.283	0.199	0.142	Wilks' Lambda	2.14**	0.87
	VAR	0.148	0.291	0.391	0.463	Pillai's Trace	1.88**	
128	EIGEN	0.338	0.249	0.187	0.147	Wilks' Lambda	4.02***	0.99
	VAR	0.219	0.380	0.501	0.596	Pillai's Trace	2.62***	
SESSILE								
DAYS		AXIS 1	AXIS 2	AXIS 3	AXIS 4	MANOVA	F	η^2
16	EIGEN	0.401	0.043	0.017	0.011	Wilks' Lambda	1.36	0.67
	VAR	0.803	0.889	0.924	0.945	Pillai's Trace	1.26	
32	EIGEN	0.300	0.166	0.027	0.016	Wilks' Lambda	2.13**	0.84
	VAR	0.539	0.838	0.886	0.914	Pillai's Trace	1.64*	
64	EIGEN	0.218	0.155	0.023	0.020	Wilks' Lambda	3.40***	0.94
	VAR	0.459	0.785	0.834	0.877	Pillai's Trace	2.60***	
128	EIGEN	0.218	0.158	0.080	0.053	Wilks' Lambda	1.30	0.89
	VAR	0.344	0.594	0.721	0.805	Pillai's Trace	1.22	

Table 2.3. Regressions for local (L)-regional (R) plots for each collection time. L = Local richness, R = regional richness. * Indicates significance at the P<0.05 level, ** = P<0.01 *** = P<0.001.

	MOTILE – UNTRANSFORMED		MOTILE – RAREFIED	
	MODEL	r^2	MODEL	r^2
16 days	L = 5.23 + 0.15*R	0.18	L = 4.47 + 0.49*R	0.17
32 days	L = -1.4 + 0.55*R	0.54*	L = 9.48 + 0.19*R	0.06
64 days	L = -0.8 + 0.56*R	0.82***	L = 15.59 + -0.06*R	0.06
128 days	L = 8.74 + 0.32*R	0.69*	L = 9.0 + 0.13*R	0.24
	SESSILE – UNTRANSFORMED		SESSILE – RAREFIED	
	MODEL	r^2	MODEL	r^2
16 days	L = 1.15 + 0.34*R	0.24	L = 1.13 + 0.60*R	0.91***
32 days	L = 2.37 + 0.41*R	0.49*	L = 3.9 + 0.38*R	0.53*
64 days	L = 4.33 + 0.30*R	0.38	L = 3.92 + 0.51*R	0.35
128 days	L = 4.0 + 0.39*R	0.82**	L = 2.92 + 0.35*R	0.73**

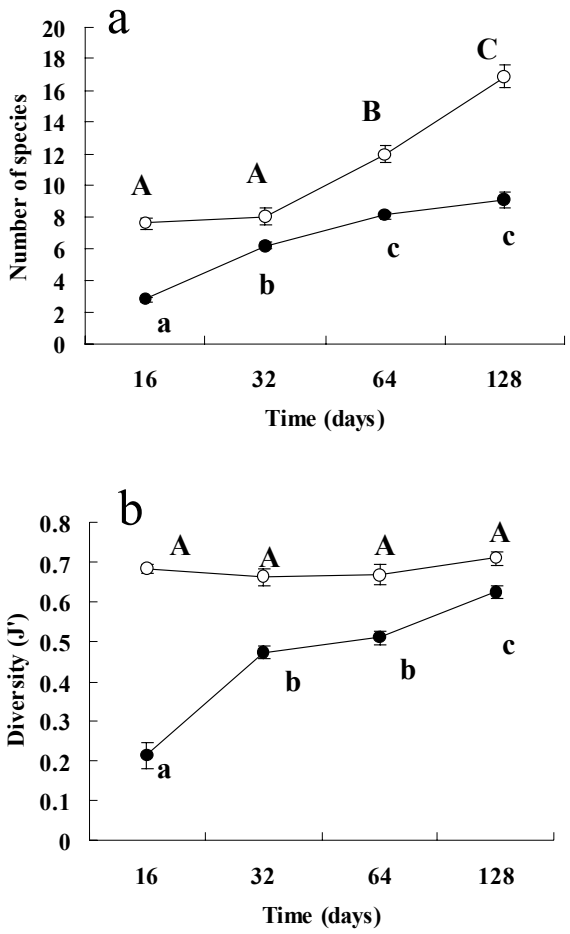

Figure 2.1. Average pen shell species richness (a) and evenness (b) change across time for both sessile and motile species groups. Open circles represent motile species, shaded circles sessile species. Means ±SE. Different letters represent statistically significant differences under a Tukey HSD test ($P < 0.05$).

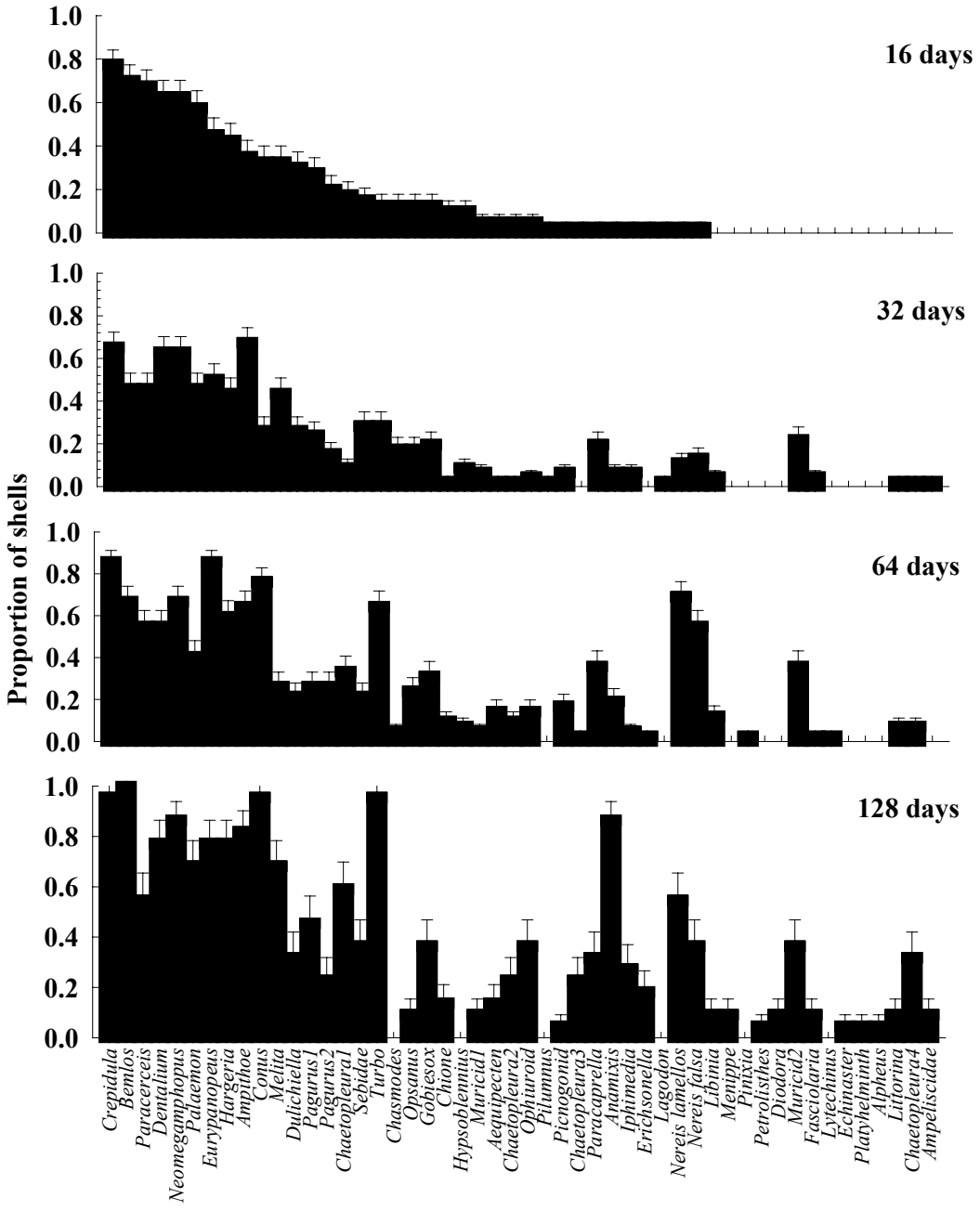

Figure 2.2. Motile species mean pen shell frequency across time. Means +SE. The species are ordered by rank abundance for the first collection time, and the order is kept constant. Most of the species are presented with their genus, however some present only family level.

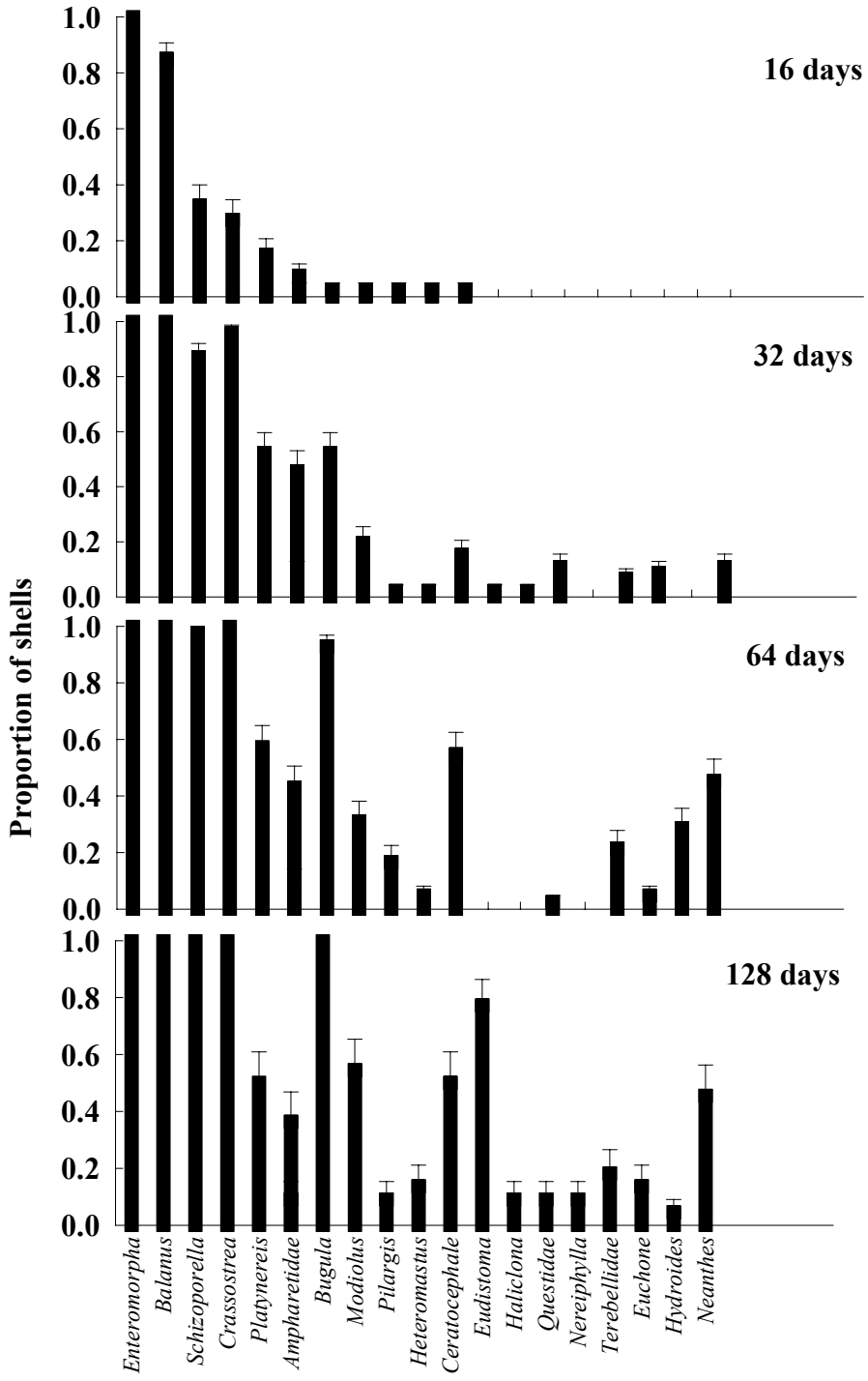

Figure 2.3. Sessile species mean pen shell frequency across time. Means +SE. The species are ordered by rank abundance for the first collection time, and the order is kept constant. Most of the species are presented with their genus, however some present only family level.

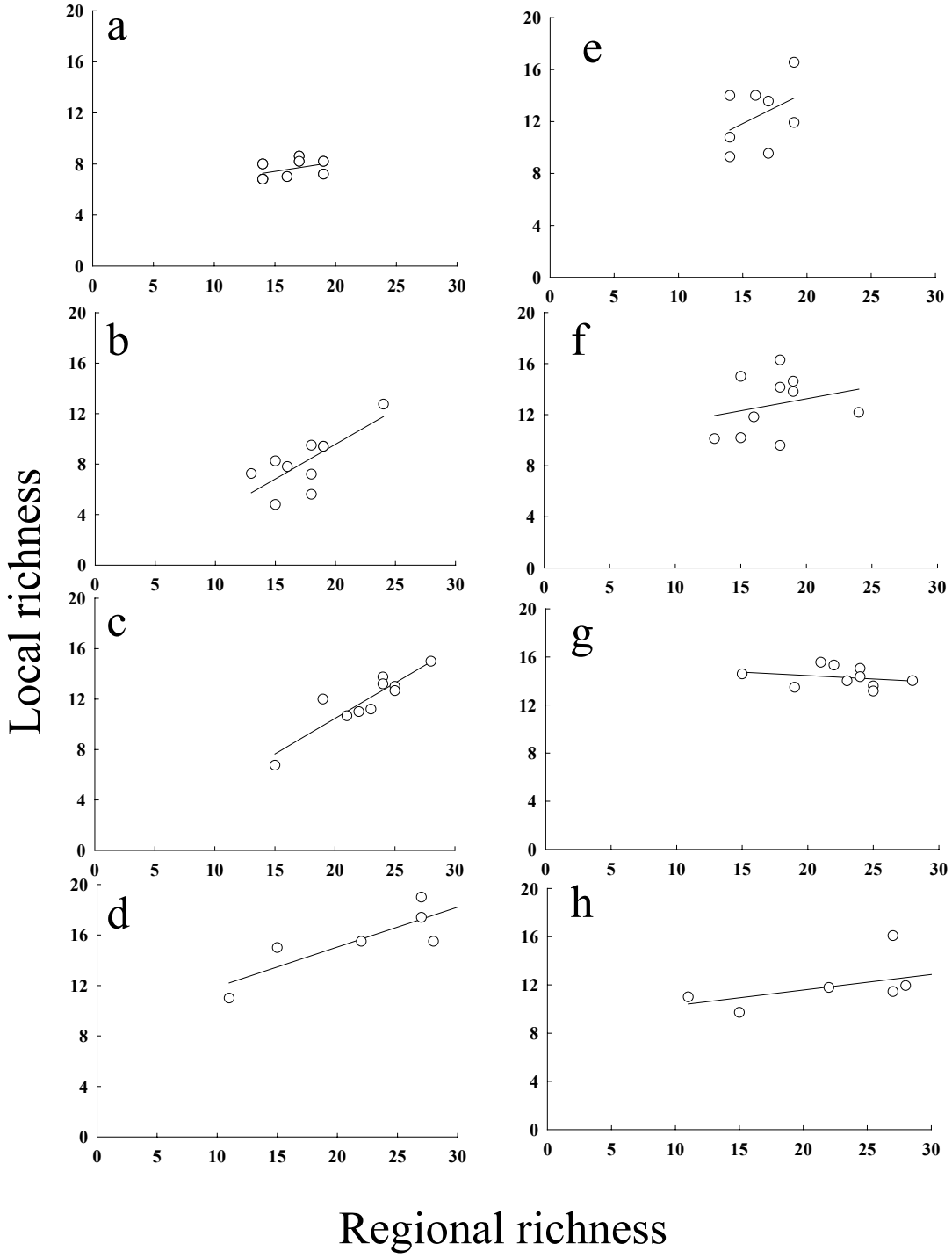

Figure 2.4. Local-regional plot for motile species: average local diversity is plotted against total species diversity for each plot (the species pool). (a-d) untransformed data. (e-h) rarefied data. Even though some regressions present slopes not different from zero (Table 3), the line is drawn to present the relationship.

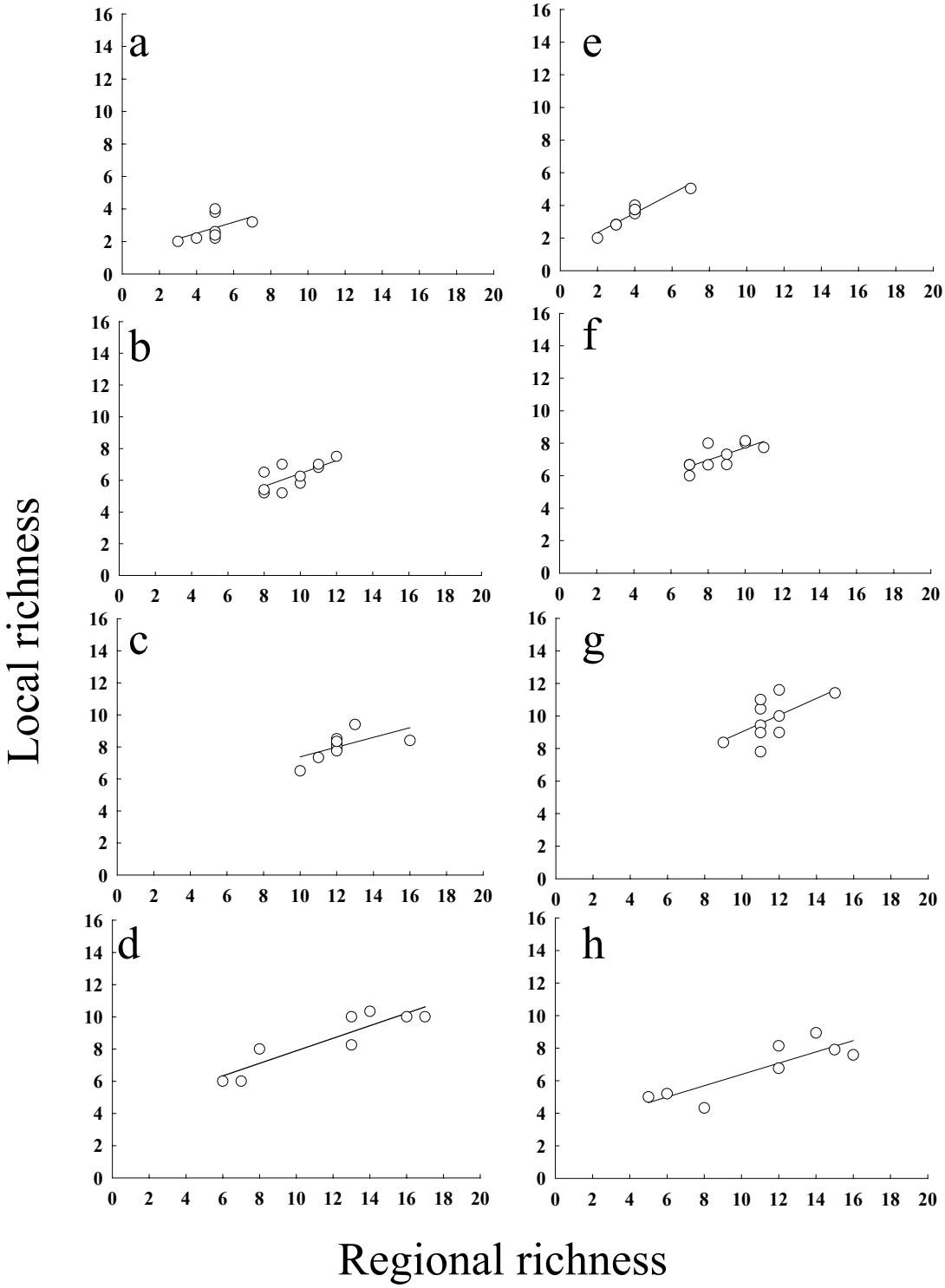

Figure 2.5. Local-regional plot for sessile species: average local diversity is plotted against total species diversity for each plot (the species pool). (a-d) untransformed data. (e-h) rarefied data. Even though some regressions present slopes not different from zero (Table 3), the line is drawn to present the relationship.

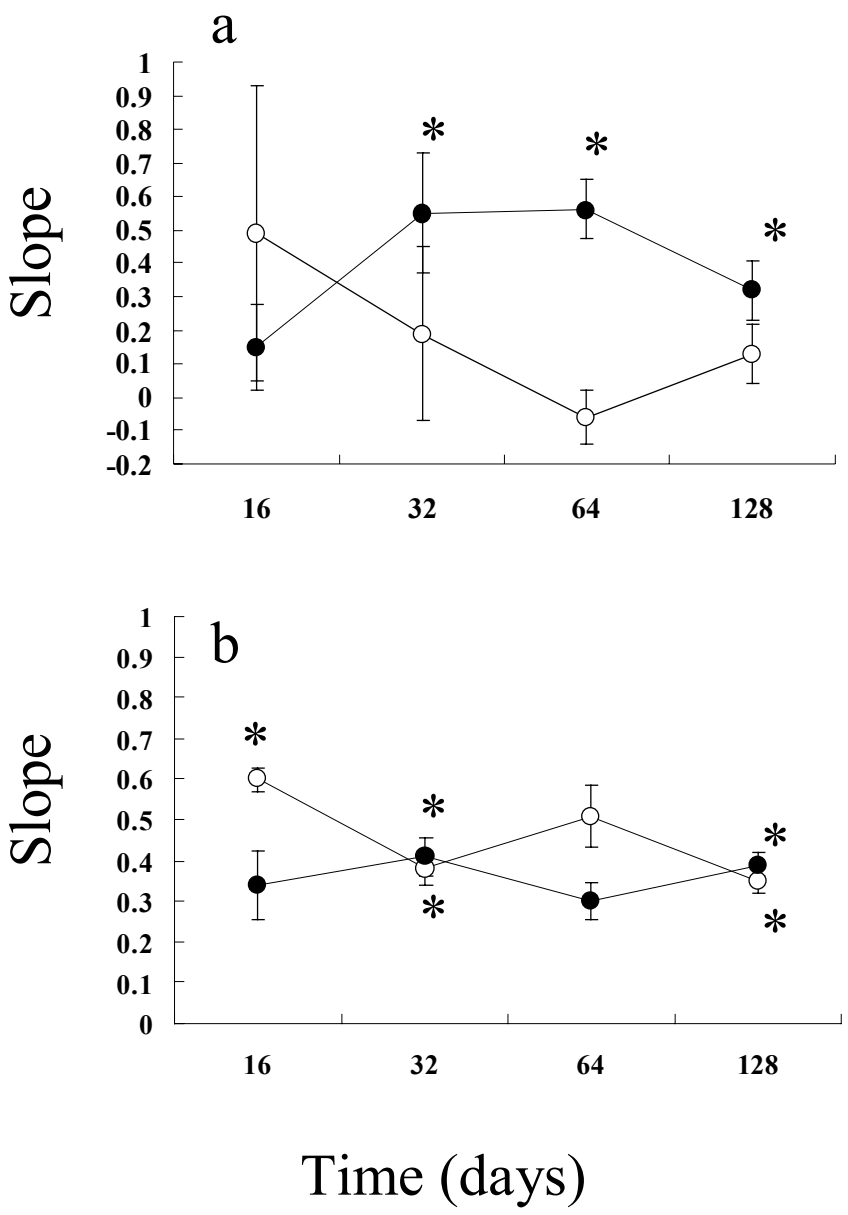

Figure2. 6. Slopes of the local and regional diversity relationships across sampling dates (slope ±SE). Shaded circles represent untransformed data, open circles rarefied data for motile (a) and sessile (b) species respectively. Bars represent standard errors. Asterisks denote slopes significantly different from zero ($P < 0.05$).

CHAPTER 3

HABITAT DESTRUCTION AND METACOMMUNITY SIZE IN PEN SHELL REEFS

ABSTRACT

The rate of habitat destruction in both terrestrial and marine habitats has continued to increase in the last several decades, generally because of human activities. Most research stimulated by this destruction has consisted, by necessity, of uncontrolled post-hoc studies. Our study involved the experimental destruction of entire local communities within larger regions in natural marine microcosms. Large and small arrays of dead pen shells were created in a shallow bay in north Florida, and the colonization by both encrusting and motile species were followed through time. After most species had become established, half of the large arrays were converted to small arrays by removal of half the shells. After 48 days of further community development, comparisons of the large arrays, converted small arrays, and original small arrays suggested that the mechanisms by which habitat destruction affects diversity can depend on the size of the region affected and that the effects of habitat destruction can depend on the natural history of the species being studied.

INTRODUCTION

Habitat destruction is the primary explanation for the rapid loss of biodiversity in many habitats over the last century—for example, coral reefs have declined by an estimated 27% because of pollution and human exploitation, and over 78 million acres of tropical forest are estimated to be lost each year to deforestation (Stone 1995; Gardner et al. 2003)—but we still do not know the mechanisms by which habitat destruction affects diversity (Debinski and Holt 2000). It may act directly by reducing available area: the relationship between habitat area and the number of species in a habitat is well established (MacArthur and Wilson 1967; Brown and Lomolino 1998). However, destruction may also have significant secondary effects by changing the spatial structure of populations and communities (Tilman et al. 1994; Gonzalez et al. 1998).

Habitat destruction can occur at different spatial scales, with consequences for the resulting community patterns (e.g., Miller 1982). A common ecological scenario is the effect of localized disturbances creating smaller patches of destruction within a larger matrix of an established community (e.g. by Connell 1978; Paine and Levin 1981). When destruction occurs on a larger scale (i.e., larger or more frequent), it can result in a large community being broken down into smaller units (fragments; Collinge 2000; Gonzalez 2000; Fahrig 2003). If the habitat is already spatially structured, (or has been fragmented) such that established smaller "local" communities occur as patches, then large-scale destruction can eliminate entire local communities, affecting both the density and distance among local patches.

Habitat destruction thus has two effects; first, a direct effect that occurs because of the loss of area in a habitat, and a secondary effect due to the disruption of a continuous habitat into "fragments" (Fahrig 2003), changing the spatial arrangement of communities. This indirect effect will be most important in systems where migration strongly affects diversity (Callum 1997). In communities undergoing habitat fragmentation, the movement of individuals from one patch to another has been considered an important mechanism controlling populations and diversity (Debinski and Holt 2001).

Metapopulation theory has been used to explain how sources and sinks allow species persistence in habitat fragments (Mouquet and Loreau 2003). Similarly, habitat destruction involves the removal of a local community (or fragment, if the community is already fragmented) from the environment and may be particularly important when local communities are linked to one another through migration (i.e. form a metacommunity; Leibold and Miller 2004). One of the proposed outcomes of habitat destruction is the extinction debt (Tilman et al. 1994), which suggests that a reduction in diversity will be observed some time after habitat destruction took place because of the asynchronous population dynamics in sources and sinks.

We can understand the effects of habitat destruction on diversity by considering how local diversity changes with succession, habitat area, and fragmentation (Mouquet et al. 2003). New communities will gain species through time to some asymptote, with larger metacommunities (i.e., those with more local communities) supporting more

species than smaller ones (Fig. 3.1). The reduction in the number of local habitats through habitat destruction might therefore have one of three effects on diversity. First, diversity might simply decrease to a level appropriate to the new metacommunity size (Fig. 3.1). Second, the effects of a small metacommunity and some effect of the destruction itself might combine to produce a diversity lower than that expected from the new metacommunity size (we call this an negative residual effect). Third, an effect of the diversity of the original larger metacommunity might persist, resulting in a new diversity level somewhat higher than that expected from the new metacommunity size (a positive residual effect).

Destruction of local communities can also affect the patterns of species' relative abundance. Studies have demonstrated a positive relationship between local abundance and regional distribution (Brown 1984; Gaston et al. 1997), so most species are believed either to be locally rare and to have narrow distributions or to be locally abundant and to have broad distributions. This abundance-distribution relationship may change, however, with successional patterns as well as with communitywide mechanisms such as habitat destruction. Following habitat destruction, some species may increase their distribution or local abundance, while others will decline, depending on species specific responses to disturbance (Mouquet and Loreau 2003; Shurin et al. 2004).

Here, we use the natural communities of small marine invertebrates found living in empty pen shells as experimental microcosms (see, e.g., Srivastava et al. 2004) to test the effects of metacommunity size and habitat destruction on local diversity and species commonness and rarity. We compare changes in each individual species' habitat occupancy and local abundance through successional time to determine whether species responded similarly to habitat destruction.

METHODS

Our study was carried out in the summer of 2003 in St. Joe Bay, Florida, a shallow, well-protected bay on the northern Gulf of Mexico. The substrate is composed of patches of sea-grass beds intermixed with sandy areas; very few natural hard-bottom surfaces are available other than the empty shells of dead *Atrina rigida* (pen shells). Pen shells are relatively large bivalves (~19 cm length) that live embedded in the sand within sea-grass beds. The shells remain in the sand once the mollusk dies, providing habitat for

a large number of invertebrates and fish (Munguia 2004). Species occurring on pen shells experience three discrete changes in spatial scale: within a individual shell where species interactions such as competition and predation generally occur, among neighboring shells where individuals may move during their lifetimes (which we will operationally define as within the pen-shell metacommunity), and a much larger spatial scale at which reproductive propagules may disperse (including the entire bay and possibly parts of the Gulf of Mexico). For analyses, we divided species found on pen shells into two groups based on their ability to move among shells within a metacommunity. Motile species, such as crustaceans and fishes, can move among communities as adults, whereas sessile species, such as barnacles and bryozoans, have limited motility and move among communities only as propagules (see Munguia 2004 for more details).

Replicate plots of three types of arrays of anchored pen shells were established within 2.25 m^2 areas: two large square arrays consisting of 16 evenly spaced shells and one small square array consisting of 4 shells. All of the shells that were anchored were empty and fouling-free, allowing us to follow natural succession patterns. After 21 days, 12 shells were removed from one of the two large arrays on each plot, leaving an array of 4 neighboring shells: two shells that were on the outside of the original array and two on the inside, in order to account for potential edge effects. Within each plot, the large array represented the "large metacommunity" treatment, the small array the "small metacommunity" treatment, and the reduced array the "habitat destruction" treatment.

We established these arrays in eight areas chosen randomly within St. Joe Bay. Four of these areas contained three arrays of each treatment type, one for each collection time; and four of these areas contained only one array of each type, which was collected at the last sampling time. At 21, 42, and 63 days after deployment of the arrays, one array of each treatment was collected for censusing of species present (N = 4 for 21 and 42 days, N = 8 for 63 days). We chose this range of dates because that is when we see the most turnover in species diversity on pen shells (Munguia 2004; *unpubl. data*). Four shells from each of the large arrays that had the same position within their array as the habitat destruction treatment were used for statistical comparisons with the other two treatments so that sample sizes and positions would be equal. Species richnesses of the

three treatments were compared at each collection time by analysis of variance, treating plots as a blocking effect to account for variance due to spatial location.

We tested the mechanism by which habitat destruction affects species richness by testing two potential sources: the reduction of habitat area and the reduction of the species pool in that particular region. If destruction is just a change in number of communities, then local diversity should vary as a function of the number of communities present in a region. We compared the average local richness from the large array treatment (all 16 shells), a simulated large array treatment (4 sub sampled shells), and the destruction treatment (4 shells). Because of differences in sample size, and because the values in the sub sample were nested within the large array treatment we tested these differences by bootstrapping local richness (1000 iterations of 16 shells per treatment) and interpreting the 95% confidence intervals. Our *a priori* hypothesis is that local diversities would vary in the following fashion: large array ≠ large array (simulated) = destruction, if habitat destruction just reduces the number of habitats. Alternatively, if the large array = large array (simulated) ≠ Destruction, then habitat destruction has an additional effect from just a change in number of communities within an array.

Changes in commonness and rarity

For each colonizing species, the mean number of shells (habitats) occupied in each plot for each treatment was compared with the maximum abundance level (individuals per shell including only those shells occupied) for that species. This comparison has previously been conducted at a single sampling time (Brown 1984; Gaston et al. 1997). In our analysis, we plotted the abundance and distribution for each species for the first and last sampling dates, creating a vector between the two dates. We then standardized all of the species vectors by setting the first collection point to zero; the vectors therefore reflected the direction and magnitude of change in local abundance and the number of shells occupied. Changes in both abundance and proportion of shells occupied were subjected to angular transformation, and we compared all possible pairs of the average vectors for the three treatments using a two-sample second-order analysis of angles (Zar 1999).

RESULTS

Habitat destruction was implemented at mid-succession, when all species in the species pool were present on at least some shells in the array (ANOVA on regional species pools across time, df = 2,15, $P_{motile} > 0.31$; df = 2,15, $P_{sessile} > 0.22$). This timing allowed the effects of both habitat destruction and community age (Mouquet et al. 2003) to occur in our experiment.

Changes in local species richness

Motile-species richness increased with time for local communities in both large and small metacommunities: at 21 days, richness was not significantly different among the three treatments ($F = 1.49$, $P > 0.23$; Fig. 3.2A). At later dates, the treatments diverged in species richness (42 days, $F = 11.07$, $P < 0.0001$; 63 days, $F = 7.09$, $P < 0.0001$); richness in local communities in the large and small metacommunities continued to increase, whereas that of the reduced metacommunity leveled off.

Similarly, sessile-species richness increased with time; all metacommunities showed similar local richness at 21 days ($F = 1.07$, $P > 0.31$). In contrast to that of motile species, however, species diversity in all three treatments continued to increase from day 21 to day 42, after the implementation of habitat destruction (Fig. 3.2B). Treatments were found to differ significantly in species richness at both 42 ($F = 5.65$, $P = 0.005$) and 63 ($F = 5.37$, $P = 0.0085$) days. Richness in both the undisturbed large treatments and the habitat-destruction treatments appears to continue to increase through 63 days, whereas that in the small arrays leveled off after 42 days.

Reduction in habitat area effects

Inspection of the 95% confidence intervals from the bootstrapped values across the large array (16 shells), simulated large array (4 shells) and destruction (4 shells) treatments showed that changes in diversity are not only due to changes in the number of local communities. Diversity in pen shells seems to drop due both to changes in species pool size and in the number of habitats. Three weeks after the destruction was implemented (42 days), for both sessile and motile species there was an overlap in confidence intervals among all three treatments, where the destruction treatment was the lowest. However, at the last sampling date, both the large (L) and the simulated high (Ls) treatments were higher than the destruction (D) treatment, suggesting that habitat

destruction is more than just a shift in habitat density (sessile species richness limits: L=10.91-10.17, Ls=11.56-10.19, D=10.02-9.14; motile species richness limits: L=14.67-12.49, Ls=15.16-12.09, D=11.98-10.91).

Changes in species commonness and rarity

In large metacommunities, over time, motile species tended to increase in proportion of habitats occupied as well as in local abundance (Fig. 3.3A). In small metacommunities, the proportion of habitats occupied by each motile species decreased over time, but local population abundances actually increased. Local diversity in small arrays can therefore reach levels expected for larger arrays (Fig. 3.1). Habitat destruction generally caused populations to experience lower population growth than did those in the large and small metacommunities and therefore little change in the relationship between abundance and habitat occupancy (Fig. 3.3A). Each of the treatment vectors was significantly different from the others (two-sample analysis of vectors: large and small arrays, df = 43,46, $U^2 = 0.46$, $P < 0.01$; large and habitat-destruction arrays, df = 43,50, $U^2 = 0.75$, $P < 0.01$; small and habitat-destruction arrays, df = 46, 50 $U^2 = 0.60$, $P < 0.01$).

Sessile species increased in both local abundance and number of habitats occupied over time in all three treatments (Fig. 3.3B), but the magnitudes of increase differed; increases were greatest in large arrays and smallest in small arrays (Two-sample analysis of vectors: large and small arrays, df = 19,20, $U^2 = 0.44$, $P < 0.01$; large and habitat-destruction arrays, df = 19,21, $U^2 = 0.78$, $P < 0.01$; small and habitat-destruction arrays, df = 20,21, $U^2 = 0.45$, $P < 0.01$). As with sessile species, the habitat destruction appears to have led to lower rates of growth and habitat spread (Fig. 3.3B).

DISCUSSION

Results from our study suggest that habitat destruction can have both direct and secondary effects on local community structure. Destruction does reduce available area, leading to a decrease in richness as described by species-area relationships, but successional history or the deleterious effects of destruction itself may affect the response of a community to habitat destruction. Furthermore, the effects of these two mechanisms will vary depending on whether species involved are motile or sessile.

Local richness of motile species in large arrays increased as the community underwent succession, reaching an asymptote at about 63 days (Fig. 3.2A). Contrary to our expectations, smaller metacommunities reached the same level of richness but more slowly. In metacommunities that suffered habitat destruction during succession, however, richness appeared to stabilize at a relatively low level. These results show that habitat destruction had a secondary, negative, effect on the number of motile species, suggesting that the species that assemble in large metacommunities dominate or otherwise influence the species that occur in the small metacommunities after habitat destruction.

Sessile species in both small and large metacommunities also reached an asymptotic richness by 63 days, with a significantly lower local richness in small arrays (Fig. 3.2B). This result is consistent with our expectation that the initial metacommunity size should influence species richness (Fig. 3.1). Arrays subjected to habitat destruction achieved richness levels that were intermediate between those of the original small and large metacommunities. The initial, pre-destruction richness appears to have had a positive secondary effect on the sessile species richness after destruction. Because sessile species cannot disperse as adults, they may not respond to significant shifts in metacommunity size later in succession. Initial metacommunity size may be important for allowing individuals to select appropriate habitats before they settle (Mouquet and Loreau 2003). Once individuals have had time to grow within habitats, their presence affects the number of incoming recruits, suggesting that priority effects are important for this species group, as has been demonstrated in other studies (e.g., Tilman et al. 1997; Almany 2003; Fukami 2004).

Abundance-distribution relationship

In our experiment, habitat destruction generally caused populations of motile species to experience lower population growth than in the undisturbed large and small metacommunities. Destruction caused a reduction of potential sources for motile species, which may in turn reduce the likelihood that a local population would serve as a source. Changes in species distribution differed among the three treatments. In large metacommunities motile species increased in distribution, while in small metacommunities there was a reduction in the number of occupied shells. In the habitat

destruction treatment there was no change in species distribution. These results highlight the importance of habitat limitation, which affect species distribution, and in turn local diversity in motile species. The reduction of habitats forced motile species to interact more, which kept local diversity from increasing. This suggest that motile species sort themselves among habitats depending on the species composition in each community (Sale 1977), and a reduction of habitats increases the likelihood of a species from being excluded from the group of habitats.

Changes over time in sessile species distribution and abundance suggest that short-distance dispersal is important for some of these species (Olson 1985; Bingham and Young 1991) and that communities at high densities therefore showed high species richness (Fig. 3.2B). Sessile species were not affected by metacommunity size or habitat destruction because the adults could not disperse: they had similar population-growth patterns and distributions in all arrays. Successional changes in sessile species were independent of the size of the metacommunity once the initial colonization pattern had occurred. What is interesting to note is that the initial assembly or colonization pattern, (Belyea and Lancaster 1999), can affect local diversity but not the increase in abundance or distribution of individual species.

The metacommunity concept is particularly unique in this study, and it can serve as an example for many other marine communities. Pen shells are discrete communities that occur in limited supply within St. Joe Bay. Pen shell metacommunities are composed of two different regional scales. The first is at the scale of a few meters, represented by the size of the arrays in this study. The second is at a much larger scale, probably at the scale of kilometers. As with other studies that attempt to relate local processes to regional mechanisms, delimiting the scales has been more problematic in natural systems than in theoretical studies (Srivastava 1999, Munguia 2004). The possibility of very long distance dispersal in pen shell metacommunities means they are not a regionally closed system, as is assumed in most metacommunity theory (Leibold et al. 2004). It is likely that no natural metacommunity is completely enclosed within its region, at least at the scale that regional processes (such as dispersal and habitat heterogeneity) are thought to operate. In pen shells, species respond to our manipulations of metacommunity size, which suggests regional scales of neighboring shells are

important up to meters away. However, there is probably a low propagule input from larger scales, which could be crucial for establishing the first colonizers in pen shell metacommunities. An important question that would need to be addressed with natural systems is the changes in influence of processes at different spatial scales as communities undergo succession.

Our study supports recent theoretical studies showing that the interaction between dispersal limitation, species interactions, and habitat heterogeneity can structure diversity (Tilman et al. 1997; Amarasekare et al. 2004). Clearly, habitat destruction can have both direct (through species-area relationships) and secondary effects (positive or negative effects) on community diversity. Species have different dispersal rates, growth rates, and competitive abilities, which contributed to differences in abundance across treatments. The observed community patterns result from the different responses of and interactions among component species. Most biogeographic studies have demonstrated a positive correlation between local abundance and habitat distribution (Gaston et al. 1997), although the pattern may also change with successional stage (Mouquet et al. 2003; Munguia 2004). In general, species that are locally rare also occupy few habitats (Brown 1984; Gaston et al. 1997) and may therefore also be more susceptible to the effects of habitat destruction.

The response of natural communities to habitat destruction clearly depends on scale and the species involved. The metacommunity perspective allows us to partition diversity at different scales: populations in local communities interact through dispersal and share a common regional species pool (Leibold et al. 2004). In pen-shell communities, habitat destruction affects the number of local communities within a region, or metacommunity size, which in turn changes the distribution of sources and sinks for various species. Investigating patterns of species' commonness and rarity (Magurran and Henderson 2003) provides insight into changes in species abundances, in particular suggesting that they are (a) dispersal limited, (b) resource limited, or (c) limited by species interactions (e.g., competition and predation). Habitat destruction can affect any of these parameters, but their combined effects can only be understood in the larger, metacommunity context. Manipulating whole communities has allowed us to study the

interaction between regional size, habitat destruction and their combined effects on diversity.

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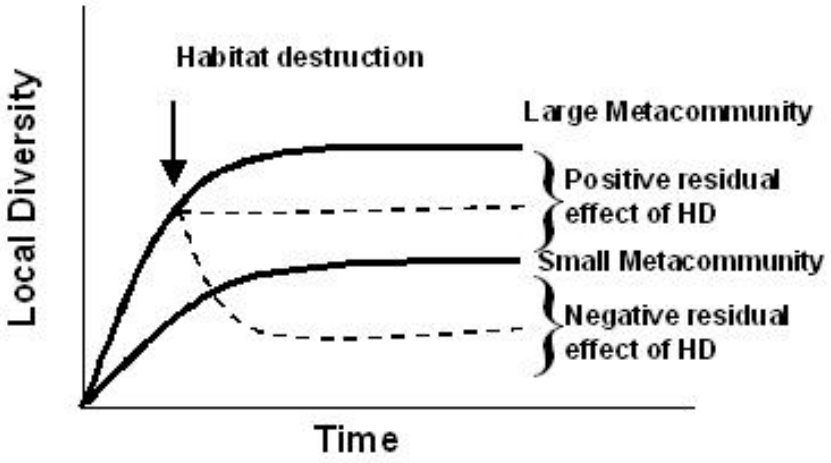

Figure 3.1. Hypothetical representation of the effects of habitat succession and metacommunity size on local diversity undergoing succession. Habitat destruction (HD) can simply shift metacommunity size, it can combine with the effects of original small metacommunity size to produce a greater, negative residual effect, or the effects of original larger metacommunity size can have a positive residual effect, reducing the effects of habitat destruction.

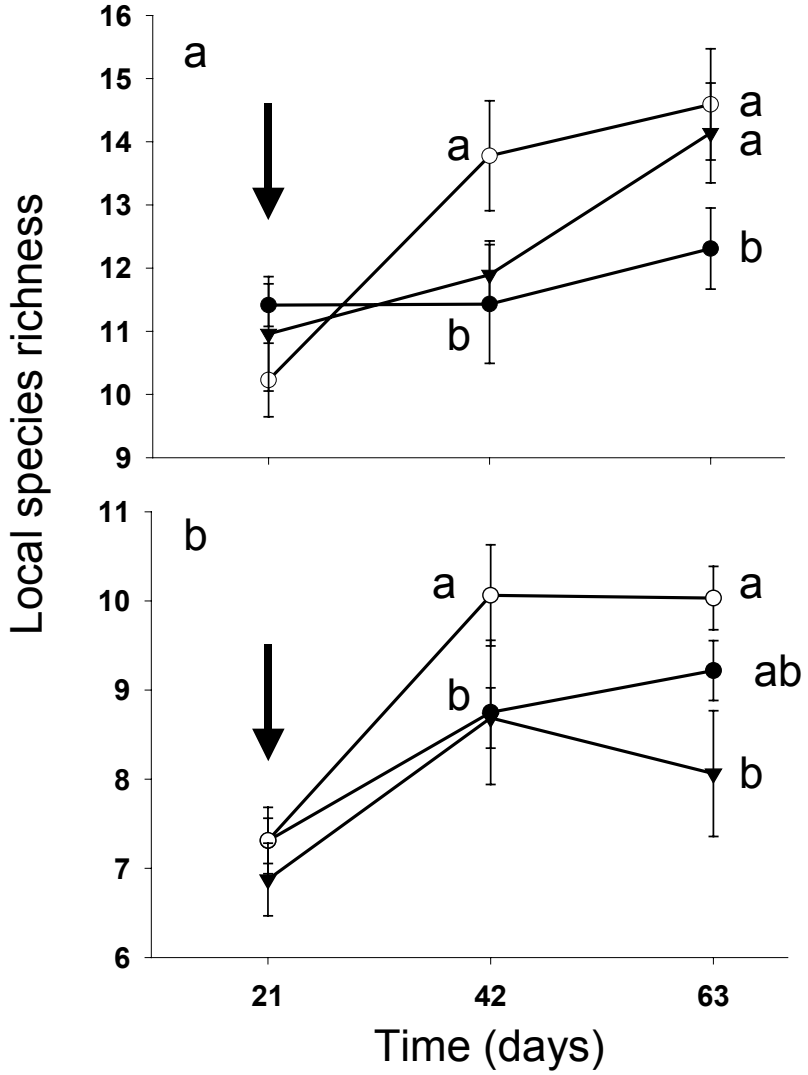

Figure 3.2. Changes in species diversity under habitat destruction. Results from a field experiment on a marine benthic community showing the effects on diversity of motile (A) and sessile (B) species. Open circles represent large arrays of local communities (empty pen shells available for colonization), triangles small arrays, and closed circles arrays reduced from large to small by experimental "habitat destruction" at the point marked by the arrow. Arrays marked by different letters differed significantly ($P < 0.05$; Tukey HSD test). Bars represent one standard error.

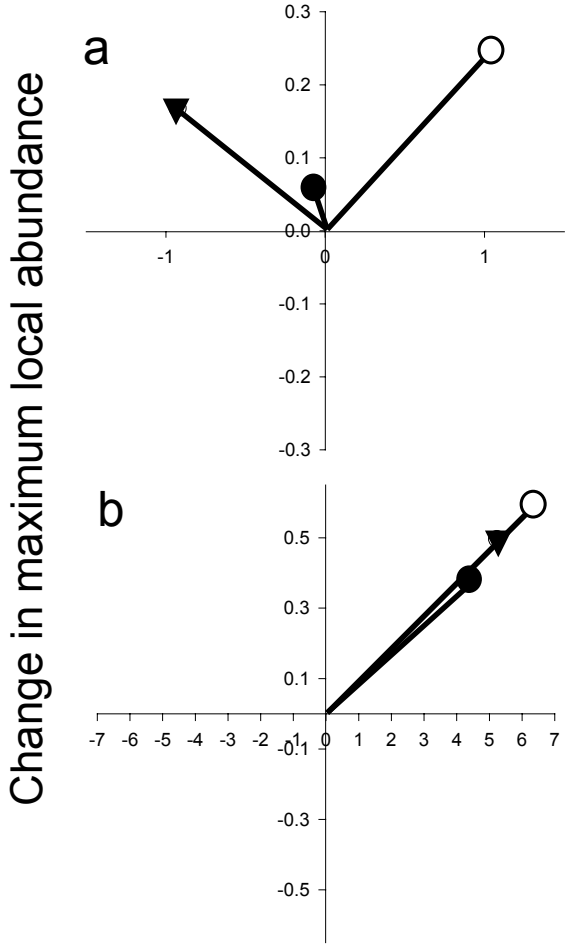

Figure 3.3. Species abundance-distribution trajectories under succession from the field experiment for (A) motile and (B) sessile species. Open circles represent large arrays, triangles small arrays, and closed circles arrays subjected to "habitat destruction."

CHAPTER 4

RECONCILING NEUTRAL AND NICHE THEORIES IN PEN SHELL METACOMMUNITIES.

ABSTRACT

Niche theory and the neutral theory are considered opposing theories that attempt to explain diversity patterns and species coexistence. Identifying the mechanisms behind the observed patterns has been difficult, and most tests of neutral or niche diversity patterns overlook changes through community development. Here, I suggest that following common and rare species through succession can help identify the mechanisms driving diversity patterns. I first used a simulation model to create predictions of common and rare species through time under both neutral and niche scenarios. In a neutral scenario, common and rare species should follow similar changes through time, while in a niche scenario common and rare species would differ in abundance and distribution through time. Next, I carried out a field experiment with the marine benthic inhabitants of pen shells (*Atrina rigida*) to test these predictions. I followed community development through time and partitioned species into sessile and motile based on their natural history. Results suggest that with the motile group, rare species seem to drive the diversity patterns suggesting that environmental requirements can help determine changes in species abundance and distribution. With sessile species, both common and rare species have similar changes through time, following the neutral theory. This study shows that both neutral and niche patterns can be observed in the same system, however, by following successional changes, one can identify the mechanisms and conclude whether species follow neutral or niche theories.

INTRODUCTION

Virtually all communities have a similar pattern of species' relative abundance (Preston 1962), where a few species are abundant, while the majority of the species are less common or rare. This pattern is noted over a wide range of taxon and habitats (Brown 1984) and has implications for larger regional scales; common species within a particular community tend to be the most widespread across a range of similar

communities in a region (e.g. Gaston et al. 1997). Therefore, it is assumed that most species are either locally rare with relatively small ranges, or locally abundant and widely distributed. Deviations from these patterns can occur, but are not common in nature (Rabinowitz 1981).

While these patterns are ubiquitous, identifying the underlying mechanisms has been difficult (e.g. Shmida and Wilson 1985). The classic theory describes mechanisms of coexistence and patterns of species abundance based on the environmental requirements of each species, or niches (MacArthur 1972, Chase and Leibold 2003). Briefly, the niche theory predicts that a number of environmental conditions and resources must be met for a species to exhibit positive or stable population growth. Because different species have different requirements, those groups of species that are able to partition the resources are more likely to coexist in a given habitat. Under this view, species abundances are determined by the amount of niche space utilized by each species.

However, a recent theory suggests that individuals of all species can be considered to be ecologically equivalent, and that stochastic colonization and extinction are the primary mechanisms that determine community diversity (Hubbell 1997, 2001, Bell 2000). This concept, called the neutral theory, is currently challenging the classic view that species have defined niches and that differences among communities are primarily driven by species interactions and environmental conditions (Chase and Leibold 2003, but see Dornelas et al. 2006).

The neutral theory and niche theory appear to be discrete alternative explanations; it is generally thought that both cannot hold true for any given community (Leibold et al. 2004; however, see Chave 2004). Neutral theory requires that species be ecologically equivalent, yet it provides an elegant explanation for community patterns. Alternatively, niche theory, which does incorporate known biological differences among species, has been tested, but with no general conclusion achieved (e.g. Chase et al. 2005, Miller et al. 2005, Dornelas et al. 2006).

Although it has not been discussed previously, it would appear that these two theories make different predictions about changes in community structure through time. Species abundances change through time, usually due to succession following

disturbance or changes in migration rates from other populations (Mouquet et al. 2003). Niche theory suggests that species will persist in habitats as long as their requirements are met, and the competitive abilities of the coexisting species for limiting resources are lower (Chase and Leibold 2003). This leads to a predictable progression of species invading and being replaced in a given habitat until a stable community is established. Alternatively, the neutral theory predicts that every established individual has an equal extinction probability, while incoming individuals have a recruiting probability proportional to their species abundance in their region (Chave 2004); therefore, the progression to any stable state is not generally predictable. In both models, migration from surrounding communities (i.e. within the metacommunity) is required for new species to contribute to community changes.

Here, I first develop a model to compare successional dynamics of common and rare species under neutral and niche scenarios. I then use the species that assemble on large bivalves (*Atrina rigida*) to quantify how common and rare species change in abundance and distribution patterns through succession. Further, I address whether differences or similarities between common and rare trajectories are due to species' natural histories or metacommunity properties. I compare two groups of species to show that differences in their natural history can produce different responses to succession. In particular, sessile species should show little effect of metacommunity size, relative to motile species, which should show a greater response to the number of neighboring habitats (*Chapter 3*). I use metacommunity size (number of local communities in a region) to test the effects of high and low-dispersal rates, which were generated in the model. I assume that dispersal rate will be higher in metacommunities with more interconnected local communities, relative to small metacommunities. The predictions from the model will be compared to the results from the field study to suggest what species groups are under neutral or niche scenarios.

METHODS

A model of neutral and niche succession

A simulation model was used to predict community patterns during succession under two scenarios: species were either neutral (equal per capita birth and dispersal parameters) or were assigned simple niche-related differences (species differ in their

ability to occupy habitats). A network of local communities was colonized by fifteen species. These species had equal per capita birth (set at 0.2) and dispersal parameters, and suffered density dependence through a shared carrying capacity K (set at 1,000) defined for the local community, (equivalent to the term J in Hubbell, 2001). For each species i in community j, a transition matrix T_{ij} was created and incorporated into a population growth model:

$$dN_{ij} / dt = N_{ij} + T_{ij} (K_j - N_j) / K_j \qquad (1)$$

where N_{ij} is the abundance of species i in community j, and N_j is the sum of species abundances in community j. The transition matrix T_{ij} is a species by community matrix where each cell is defined as the birth rate of species i minus the dispersal rate weighted by the distance between community j and every other community (e.g. distance between j and $j = 1$). Each cell is multiplied by α_i, to create variation among species in the same community. In the neutral scenario, α_i is equal to one, while in the niche scenario each species has a different α_i value (randomly distributed between –0.5 and +0.5). There is a stochastic death probability for each species in each community (set at 10%), which has the potential of reducing the local population without extinguishing it. Therefore under neutral conditions, stochastic death and colonization from the surrounding communities drive population and community patterns, with species potentially going extinct from the metacommunity when their abundances are low (e.g. rare). Under the simplest niche conditions I maintained equal birth rates, but assigned random values to α_i in order to create differences in species identities, that are constant across communities (i.e. no habitat heterogeneity). Each run of the model started with abundances set at 5 individuals per species in each local community (the sum of all species within each community totaling 7.5% of the local carrying capacity). Simulations were followed for 100 time steps, which was enough time to observe changes in community composition but not enough for any single species to achieve dominance.

We can graph the average local abundance against the number of habitats occupied (Brown 1984). If a species' local abundance is correlated with the number of individuals present in the larger region (or metacommunity), then rare species will fall in the lower, left-hand area of the graph, while common species are on the upper right-hand area (Fig. 4.1A). However, this approach neglects changes through succession; in order

to understand whether a species was common and became rare or vice versa, we can create trajectories of how a species changes in local abundance and distribution. Using the simulation model, I first divided species into common and rare; common species had a regional abundance level greater than the median +10%, while rare species had abundance levels lower than the median –10%. Then, I plotted the change in abundance against the change in distribution for each species (standardized by the final abundance and distribution) and generated a slope for common and rare species. The model was run 200 times for each of four scenarios: high and low dispersal for niche and neutral scenarios.

Field site and experimental design

Pen shells (*Atrina rigida*) are relatively large bivalves (~19 cm long) that live embedded in the sand within sea grass beds of St. Joe Bay. When the mollusk inside the shell dies, the shell remains anchored in the sand, providing habitat and shelter for up to 70 species of invertebrates and fishes. The shells tend to remain anchored for about one year (*pers. obs*.), making these habitats ephemeral. There is very little other hard substrate in seagrass beds, so most of these species are found only on pen shells (see Chapter 1). There are three spatial scales to consider in pen shell communities. First, the shell and its inhabitants are defined as a local community; competition is likely to occur for shell space and other resources. At a slightly larger scale, there can be movement of juvenile and adult individuals among neighboring shells, which is what I refer to as the regional scale (Munguia 2004). There is an even larger scale of all St. Joe Bay and parts of the northern Gulf of Mexico over which long distance dispersal of reproductive propagules may occur. Here, I focus on the local and regional scales that contribute to the pen shell metacommunity dynamics.

In the summer of 2003, I created pen shell arrays of two different sizes. Large arrays of 16 shells and small arrays of 4 shells were anchored to the bottom of sea grass beds, each shell spaced 40 cm from each other. Each array was considered to be an independent metacommunity. Arrays were collected at one of two time intervals, 21 and 63 days after placement. Shells were collected with a plastic bag and brought to the surface. In the laboratory, all motile animals were filtered through a 1 mm mesh, and

then counted and identified using a dissecting scope. Sessile animals, such as barnacles, sponges and oysters, were counted on the shell as number of individuals.

I established 8 plots within St. Joe Bay. Four plots contained two arrays of each density treatment, one for each collection time; and four plots contained only one array of each density, which was collected at the last sampling time. At 21 and 63 days after deployment of the arrays, appropriate arrays of each density were collected (N = 4 arrays for 21, N = 8 arrays for 63 days).

Data analysis

For each species, I quantified both the local abundance and the number of occupied shells for each array for each collection time. Following Brown (1984), I first plotted local abundance against the proportion of occupied shells for each sampling date (e.g. Fig. 4.1A). I then quantified how this relationship changed with time by calculating the percent of change in abundance and distribution from the initial sampling date to the final sampling date ([final – initial] / final). In this fashion, I was able to tell whether a species increased or decreased in either its abundance or its distribution within each metacommunity array over the 63 days of the experiment.

I plotted changes in abundance against changes in distribution for motile and sessile species and tested for differences between common and rare species in small and large metacommunities. I defined common species as those with a total abundance greater than the median + 10% and rare species as those with a total abundance smaller than the median – 10%. Common and rare species changes in abundance were compared using an ANCOVA using change in distribution as the covariate.

I also compared changes in "rare species" status between the start and end of the experiment. Species could change their "rare" status in two ways, they could increase in abundance, or they could disappear from the metacommunity. I calculated the proportion of species that changed their "rare" status between initial and final sampling dates for each metacommunity size. A low proportion of species that maintained their rare status throughout the succession would indicate that accumulation of individuals was the simple process defining rarity at the local scale. Alternatively, a high proportion of rare species that maintained their rare status would allude to either (1) dispersal limitation or (2) constraints imposed by the community in keeping these species at low abundances.

Finally, I quantified the total amount of bare space in each shell for both collection times and compared it between treatments using a t-test. I correlated bare space against three diversity metrics in both large and small metacommunities: species richness for both motile and sessile species as well as motile abundance. The correlations must be viewed in light of the total amount of space available. If space is limiting, then competition for space may drive species richness down as species are outcompeted; a positive correlation between bare space and the diversity metrics would suggest competition, while a negative correlation would suggest that other forces such as disturbance driving diversity down (e.g. Connell 1978). Alternatively, with large amounts of bare space available on pen shells, positive correlations between bare space and the diversity metrics would suggest that competition is not an important mechanism limiting diversity, while negative correlations would suggest that adverse conditions at the scale of the shell (e.g. recruitment limitation) could be affecting shell occupancy.

RESULTS

Predictions from simulation model

Under a neutral theory scenario, any species, either common or rare, may increase in both abundance and distribution, or decrease in both, with equal probability (Hubbell 1978, Chase et al. 2005), such that the overall slope of local abundance against the proportion of occupied shells for species in a given community does not significantly change. Furthermore, if all species have equal death and birth rates (as in the neutral model), then the changes through time in average abundance and distribution for both common and rare species should be the same (i.e. have the same slope when plotting change in abundance against change in distribution). Thus, the neutral model predicts that common and rare species would have trajectories with similar slopes (Fig. 4.1B). Alternatively, if commonality or rarity were actually attributed to species identity (given life history traits or environmental effects on the focal species) then the trajectories of common and rare species would differ (e.g. rare species might show a reduction in habitats initially occupied relative to common species).

Field results

In both large and small metacommunities, the relationship between local abundance and distribution was positive (Fig. 4.2) when using the data from the last

sampling date (63 days). There were no statistical differences in species richness between large and small metacommunities for motile (ANCOVA, d.f. = 3,127, P = 0.75) or sessile species (ANCOVA, d.f. = 3,25, P = 0.71). A static representation of pen shell communities follows Brown (1984) regardless of the size of the array or species group.

When plotting the trajectories for each species between the first and last sampling date, common and rare species behave differently in small and large arrays. Common and rare motile species in small arrays present similar changes in abundance and distribution, however rare species present a higher intercept (Fig 4.3A; Table 4.1). In large arrays, common and rare species had different changes in abundance and distribution (Fig 4.3B; Table 4.1). The significant interaction coefficient in this comparison is due to common species having a positive relationship between changes in abundance and changes in distribution ($F = 30.7$, $P < 0.001$), while rare species show no relationship ($F = 0.84$, $P = 0.37$). I also compared the trajectories between array sizes. Common species did not have different slopes between large and small metacommunities (t-test, d.f. = 47, t = 0.18, P = 0.85), but rare species did have different slopes between large and small arrays (t-test, d.f. = 36, t = 2.99, P =0.005). Therefore, rare motile species are affected by metacommunity size, and seem to be the species group that drives a neutral or niche pattern.

Sessile species showed no differences between common and rare species in both small (Fig. 4.4A) and large (Fig. 4.4B) metacommunities. Sessile species did have changes in abundance related to changes in distribution, but common and rare species responded the same way through succession (Table 4.1). When comparing slopes between metacommunity sizes, both common (t-test, d.f. = 13, t = 0.61, P = 0.56) and rare (t-test, d.f. = 16, t = 0.50, P = 0.62) species did not show effects of metacommunity size. Because of the very sedentary nature of sessile species, this group does not seem to be affected by between-community pen shell dynamics, only by local dynamics.

In small metacommunities, only 45% of the motile species that were initially rare (from a total of 49 species) maintained a rare status at the final sampling date. In the same metacommunities, 60% of the initially rare sessile species remained rare at the end of the experiment (of a total of 18). In large metacommunities, 61% of motile species tended to maintain rare status, while 69% of sessile species did so. The number of

species that went extinct from the shell arrays was relatively low. With motile species, 10% and 2% species went extinct in small and large metacommunities, while 5% and 0% sessile species went extinct in small and large metacommunities respectively.

Bare space decreased from an average of 82.8% (SD = 16.3%) at the first sampling date to 35.1% (SD = 20.2%) at the last sampling date. However, there were no differences in bare space between large and small metacommunities (t-test, $t = 0.638$, DF = 143, $P = 0.52$). While bare space did not correlate with any of the diversity metrics at the first sampling date, it did present a relationship at 63 days. In large metacommunities bare space had negative correlations with sessile richness ($r = -0.19$, $P = 0.03$), motile richness ($r = -0.41$, $P < 0.001$), and motile abundance ($r = -0.34$, $P < 0.001$). In small metacommunities, bare space was not correlated with sessile richness ($r = -0.08$, $P = 0.68$), motile richness ($r = -0.37$, $P = 0.06$), or motile abundance ($r = -0.16$, $P = 0.43$).

DISCUSSION

The neutral model predicts that common and rare species will have similar changes in abundance and distribution through time, while the niche model predicts that common and rare species will behave differently (Fig. 4.1B). The field study showed that motile and sessile pen shell epifauna have the same abundance-distribution pattern, regardless of metacommunity size (Fig. 4.2). However, motile and sessile species respond differently to metacommunity size, and these differences are driven by the rare species. While common motile species have the same pattern in large and small metacommunities, rare species have different slopes in the two metacommunity sizes (Fig. 4.3). Sessile species on the other hand have the same patterns for common and rare species in both metacommunity sizes (Fig. 4.4). This pattern suggests that there are significant differences among rare motile species consistent with the niche concept. The previous notion that only one of the two theories, neutral and niche, could explain community dynamics (e.g. Dornelas et al. 2006) in a single system does not apply to pen shell communities, given that rare and common species are changing in abundance differently during community development.

Mechanistic interpretation of community patterns

Diversity patterns have been attributed to either regional mechanisms such as recruitment limitation, or local mechanisms such as competition for resources (e.g. MacArthur 1972, Schmida and Wilson 1985). In pen shell communities, available space for colonization can be regarded as a limiting resource. At 63 days after colonization, two thirds of the shells are occupied. It is important to consider the orientation of the shell: shells tend to be on their side, creating spatial heterogeneity within a single pen shell. For example, the bottom side facing the substrate does not receive much sunlight and suffers from being in direct contact with sediment, affecting filter feeders in particular. Because of adverse conditions at the scale of a shell, it seems that space will always be available, in particular those areas where species are not able to settle. The negative correlations observed between bare space and the diversity metrics are probably due to adverse conditions in the environment or recruitment limitation. In large metacommunities, as bare space increases, there are fewer motile and sessile species present as well as fewer motile individuals, suggesting that space has not become limiting. In small metacommunities, bare space has no correlation with any of the diversity metrics, suggesting that space is becoming limiting. In either small or large metacommunities however, the amount of space available could be related to the successional stage of the community, therefore, changes in individual species abundances through time need to be considered.

Common motile species have similar patterns in both small (Fig. 4.3A) and large (Fig. 4.3B) metacommunities. However, on average, common species have reduced abundance even if they have an increase in the number of patches they occupied (see also Hubbell 2001). In a metacommunity with few local communities many of the common species at early successional states lose individuals; this suggests that species are sorting themselves among the limited number of habitats (Leibold et al. 2004).

Rare motile species have different dynamics in small and large metacommunities. During initial community formation, motile species in small metacommunities are generally rare, but through time 55% of these species lose their "rare" status by increasing their relative abundance (see also Munguia 2004). However, in large metacommunities there are fewer motile species that lose their initial rare status (39%).

Rare species show no relationship between changes in local abundance and changes in regional distribution in large metacommunities. The lack of a relationship can be attributed to the concave-up relationship between the initial patches occupied and the probability of patch occupancy at the next time step (p*[1-p] where p is the proportion of patches occupied; Levins and Culver [1971]). If a species is initially rare, it will probably increase in patch occupancy if migration rate is high (e.g. large metacommunities), while common species will tend to decrease in patch occupancy. This suggests that because of the large number of interacting communities, many rare species are able to persist, even if they do not have significant increases in abundance. The results from pen shell communities show that what seems to drive community structure is the original abundance level of the species; as Hubbell (2001) showed, a regional rank abundance curve can be generated by chance, and local habitats will have similar patterns of species abundances.

Sessile species on the other hand, do not respond to the regional habitat (i.e. the number of nearby communities) once they attach to the substrate. Some rare species lose their "rare" status over succession (40% and 31% in small and large metacommunities, respectively). Because of this very sessile component in their biology, both common and rare species do not show an effect of metacommunity size (Fig. 4.4). Common - numerically dominant- species can out-compete coexisting species locally, and while they present increases in local abundance, many species present a reduction in the number of habitats they initially occupied.

The patterns shown by sessile species are similar to those generated by the neutral simulation model. There are at least two explanations as to why sessile species patterns may be consistent with the neutral theory. First, it could be that as with Hubbell's (2001) study of tropical forest trees, sessile species are only influenced by dispersal and local extinction. Because sessile species in this system have a large dispersal range (Munguia 2004), the size of the metacommunity has no effect. Alternatively, the order of arrival to a community could be the mechanism that determines which species disappears from the local habitat and which species increases in abundance (e.g. Sale 1977). Dispersal patterns may be decoupled from local population dynamics; however, there is high turnover in local dominance, either rare species become common, or common species

become rare. Those individuals that arrive first, regardless of species, may be able to establish themselves and not be outcompeted from that particular habitat. These patterns suggest that sessile species show priority effects (Leibold et al. 2004, Munguia 2004).

Both neutral and niche theories assume competition among individuals at the local scale. The neutral theory assumes that local communities are near some carrying capacity: the loss of an individual is quickly replaced by a recruit from the metacommunity (Hubbell 2001). Niche theory assumes that species will compete for limiting resources, and the fate of a species at the local scale is determined by its environmental requirements (Chase and Leibold 2003). In this study, pen shells still had bare substrate at the end of the experiment. It seems that successional changes are occurring at different rates: faster in small metacommunities relative to large metacommunities, since it appears that species are still colonizing bare space in large metacommunities. One potential limitation of this system is the stochastic disappearance of the pen shell habitat (a shell lasts approximately one year, *pers. obs*.), which may be faster than a one-generation time of some of the species inhabiting pen shells. This may have implications on the effects of succession on common and rare species.

Very few other studies have explicitly discussed differences in the responses of rare and common species. From a long-term study, Magurran and Henderson (2003) showed that fish species abundance was correlated with the number of years fish occurred in their study site, and that both common and rare species had different distribution curves. Magurran and Henderson explained these patterns based on the biology of common and rare species. This suggests that species within communities may be experiencing different concepts of a "community." Combining all species in a diversity metric tends to dampen the temporal changes of individual species across time.

As with previous studies (Brown 1984, Gaston et al. 1997), when looking at the full complement of either motile or sessile species (Fig. 4.2), we obtain the same patterns observed in other species and systems (*sensu* Brown 1984, Gaston et al. 1997). However, once each species group is partitioned into common and rare species and we follow population dynamics through time, different patterns emerge. Furthermore, some pen shell inhabitants respond differently to metacommunity size. Not only were there differences seen between species groups that differ in their natural history (Figs 4.3 and

4.4), but there were also differences between species that have different abundance levels within the network of communities that they inhabit. It seems that increasing the number of communities in the species pool decreases the chances that species will become rare.

Species living on pen shells respond differently to metacommunity size and this response can vary depending on their natural history, yet, it is unclear whether the neutral theory can be invoked or not. Chave (2004) points out that along a continuum of species richness, mechanistic explanations for coexistence can occur with assemblages of few species, while in speciose systems, species tend to behave neutrally, and death and migration become the determinants of coexistence. However as shown here, niche and neutral concepts can also operate within a system, depending on the life history of the species, the properties of the system (e.g. metacommunity size), and species relative abundance.

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Table 4.1. Analysis of covariance results for motile and sessile species under high and low metacommunity density. C / R = common vs. rare treatment effect, SS = sum of squares.

MOTILE							
LOW COMMUNITY DENSITY				HIGH COMMUNITY DENSITY			
SOURCE	SS	F-Ratio	P-Value	SOURCE	SS	F-Ratio	P-Value
C / R	1.64	9.14	0.004	C / R	0.64	4.68	0.04
Distribution	4.56	25.4	<.0001	Distribution	1.99	14.6	<0.001
Interaction	0.05	0.28	0.6	Interaction	1.36	9.98	<0.01
SESSILE							
SOURCE	SS	F-Ratio	P-Value	SOURCE	SS	F-Ratio	P-Value
C / R	0.07	0.86	0.38	C / R	0.29	2.29	0.15
Distribution	0.69	7.89	0.02	Distribution	0.74	5.77	0.03
Interaction	0.01	0.02	0.9	Interaction	0.1	0.76	0.39

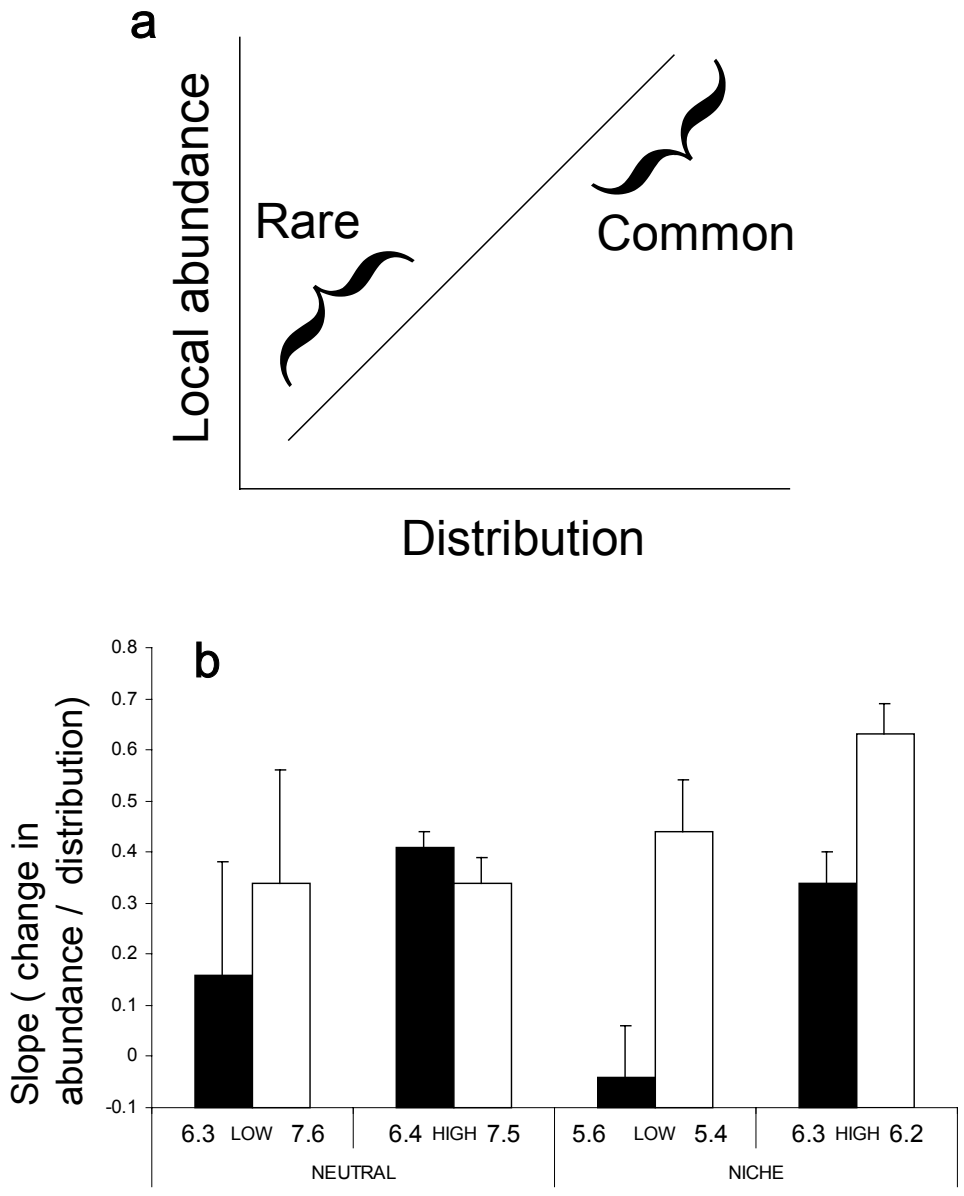

Figure 4.1. (a) The Abundance – distribution relationship is positive (Brown 1984); this curve can be partitioned into common and rare species. (b) Predictions under generated by a simulation model for neutral and niche scenarios. Average slope of the change in abundance over the change in distribution for common (black bars) and rare (open bars) species. Low = low dispersal ability (d = 2); high = high dispersal ability (d =2.5). Error bars represent one standard error of 200 simulations. Numbers under bars are mean number of species for each category.

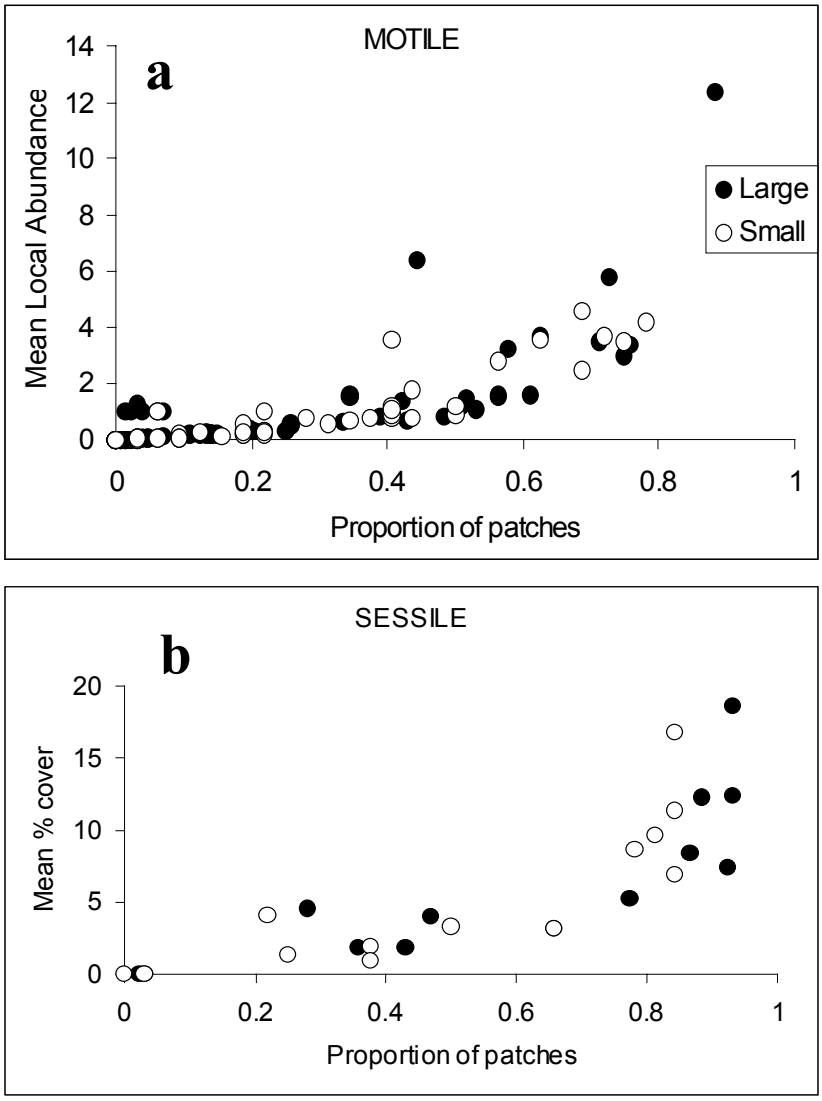

Figure 4.2. Pen shell species abundance – distribution relationship for (a) motile (b) sessile species. Filled circles represent large metacommunities, open circles small metacommunities.

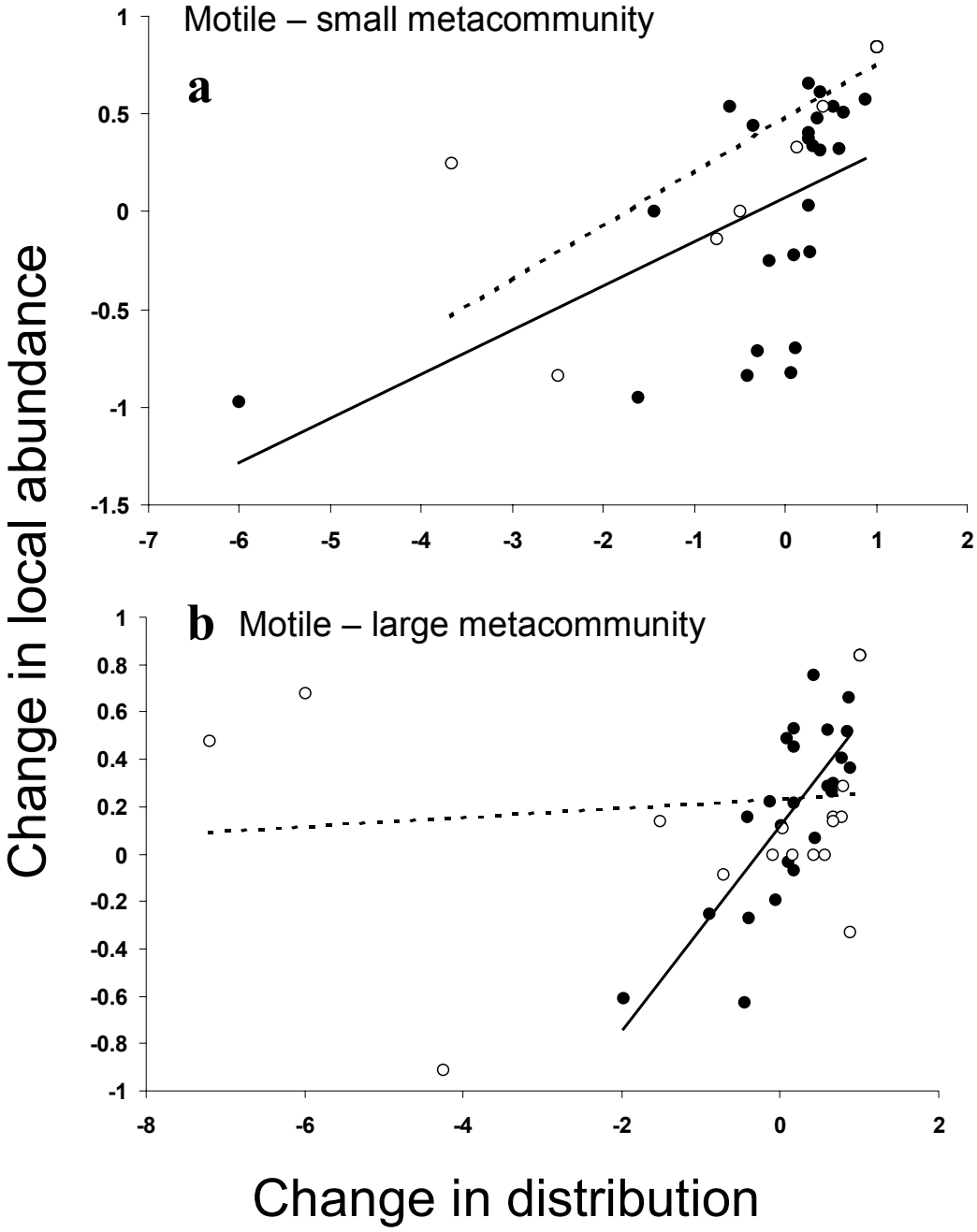

Figure 4.3. Average motile species trajectories (±SE) when plotting changes in local abundance and patch occupancy for (a) small metacommunities and (b) large metacommunities. Dark circles represent common species, open circles rare species. Data are back-transformed.

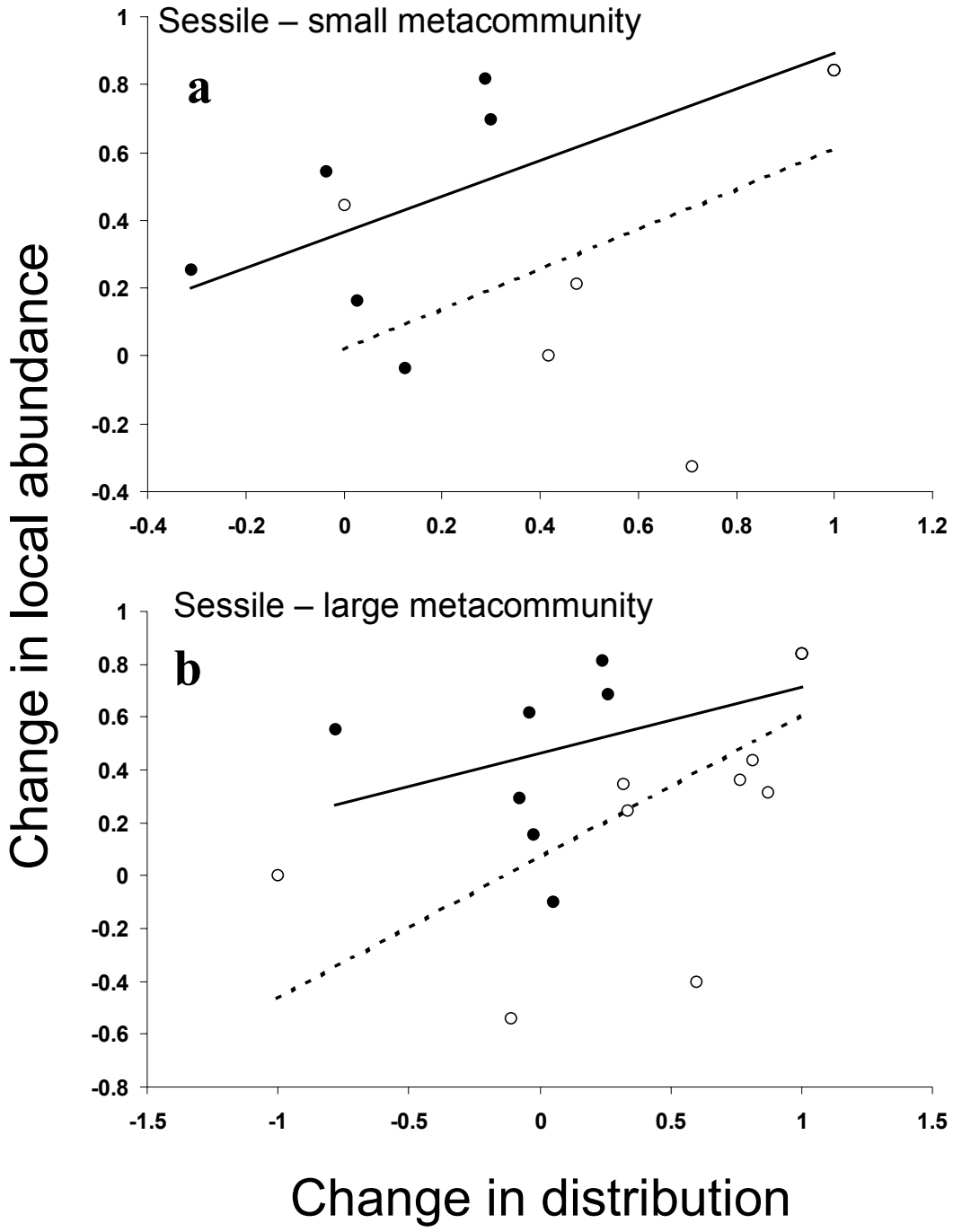

Figure 4.4. Average sessile species trajectories (±SE) when plotting changes in local abundance and patch occupancy for (a) small metacommunities and (b) large metacommunities. Dark circles represent common species, open circles rare species.

CHAPTER 5

THE INFLUENCE OF STAGE-DEPENDENT DISPERSAL ON THE POPULATION DYNAMICS OF THREE AMPHIPOD SPECIES

ABSTRACT

In metapopulations, the maintenance of local populations can depend on source-sink dynamics, where populations with positive growth rate seed populations with negative growth rate. The pattern and probability of successful dispersal among habitats can therefore be crucial in determining whether local populations will become rare or increase in abundance. Here we present data on the dispersal strategy and population dynamics of three marine amphipods living in pen shells (*Atrina rigida*) in the Gulf of Mexico. The three amphipod species in this study disperse at different life stages. *Neomegamphopus hiatus* and *Melita nitida* disperse as adults, while *Bemlos unicornis* disperses as juveniles. The two species that disperse as adults have the highest initial population sizes when a new shell becomes available, likely caused by the arriving females releasing their brood into these recently occupied shells. This dispersal pattern results in initially higher population growth, but fewer occupied shells as noted by their clumped distribution. In contrast, the species that disperses as juveniles accumulates more slowly and more evenly across habitats. Eventually this species dominates the other two in terms of numerical abundance. The metapopulation dynamics of the three species seems highly dependent on the life history stage involved in dispersal.

INTRODUCTION

In spatially structured populations, or metapopulations, source-sink dynamics can sustain local populations that are unable to maintain themselves with their own reproductive output (Pulliam 1988, Amarasekare 2004). Areas with positive population growth are regarded as sources, from which individuals emigrate; conversely, areas with negative population growth are sinks, where populations can only persist through the input of immigrants. Two major theoretical advances have been made with regards to dispersal in metapopulations. The first is the role of density dependent dispersal, where the number of dispersers is dependent on the density of the source population, allowing

species to either increase when rare at the local scale (negative density-dependent dispersal), or reduce a population size if dispersal increases with density (e.g. Pulliam 1988, Fonseca and Hart 1996, Witman et al. 2003, Amarasekare 2004). Second, the cost of dispersal from sources can cause population growth rates to become negative (Gundersen et al. 2001) or even cause local populations to go extinct (Holt 1993). Here we present data on three marine amphipod species that suggest that the life history stage that carries out dispersal can influence population dynamics and cause species to become rare or common.

Marine organisms can disperse at a variety of life history stages. These include the dispersal of broadcast spawned gametes (Scheltema 1986, Grosberg 1991, Swearer et al. 1999, Gilg and Hilbish 2003), the release of brooded larvae from maternal adults (Olson 1985, Sotka et al. 2004), as well as the movement of both juveniles (Martel and Chia 1991, Oliver et al. 1996) and adults (Junkins et al. 2006). The consequence of stage-specific dispersal is stage-specific colonization. Population dynamics at a local habitat will be affected by the life history stage of the founding individuals and subsequent recruits. These differences include size-dependent survivorship, the likelihood of producing offspring and the genetic structure of the founding population (e.g. Highsmith, 1982, Todd et al. 1998).

Variation in the stage of dispersal may also affect the distributional pattern of recruits and adults. Recruitment can be patchy in time and space (e.g. Caffey 1985) and this patchiness is likely to be reduced or magnified by the dispersal stage. Direct developers with limited dispersal ability can clump around benthic egg capsules (Gosselin and Chia 1995) or parental females (Gerrodette 1981). The dispersal of adults could result in an over-dispersed distribution if territorial, or a highly clumped distribution if, for example, they bring a brood of juveniles into the new habitat. Unfortunately, however, most studies on dispersal tend to focus on juvenile or larval propagules as the dispersing agent (Palmer et al. 1996). The combination of qualitative differences in the stage of recruits (e.g. adults vs. juveniles) and the distribution of these recruits is likely to exert an influence on the local and regional population dynamics of these organisms.

The linkage between dispersal stage and local population dynamics is particularly evident in marine systems where fecundity and juvenile mortality are often very high. Flooding the environment with large numbers of highly dispersed offspring will potentially reduce the variance in recruitment to a wide variety of local habitats. In contrast, the dispersal of adults ready to reproduce can have a large influence on the dynamics of the few local habitats that they successfully colonize. In the extreme, the dispersal of brooding females can rapidly found a new local habitat with a population of siblings. Understanding the consequences of these different dispersal strategies to population dynamics can be problematic because they often involve widely disparate taxa, potentially confounding phylogenetic considerations; or different habitats where studies focus on the effects of different environmental conditions (e.g. patch size, resource availability) on the recruiting ability of species.

Here, we explore the population consequences of different dispersal strategies in three co-occurring amphipod species that inhabit pen shell communities in the Gulf of Mexico. In particular, we asked the following questions: (1) what is the life history stage in which these species arrive to shells? (2) Is recruitment dependent on the age of the community (i.e. the successional stage or the time since the shell became available) or is it dependent on temporal patterns (i.e. the conditions when the shell became available)? (3) How does the dispersal mode of these species affect short- and long-term local population dynamics and distribution?

METHODS

Our study was conducted during the springs and summers of 2003-2005 in St. Joe Bay, Florida; a shallow, well-protected bay with patches of sea grass beds. Within the sea grass beds, pen shells (*Atrina rigida*; bivalves with average length of 19 cm length) live anchored to the bottom with byssus threads (Kulhmann 1996, Munguia 2004). These shells offer settling substrate for many invertebrates when the mollusk dies. Pen shells are the most abundant source of hard substrate, in essence becoming "islands" of habitat within the grass beds and sandy substratum for many species found in St. Joe Bay (Munguia 2004).

Among the inhabitants of pen shells are a ten amphipod species, including *Melita nitida, Bemlos unicornis,* and *Neomegamphopus hiatus*. Amphipods are direct

developers where females carry their brood in a marsupium, and release their offspring during molting events (Borowski 1990). Males tend to latch onto the backs of females before a female molts, guarding her from other males attempting to mate. The three amphipods in this study were selected because they were relatively common in pen shell communities. All three amphipod species display sexually dimorphic characters; males have a large secondary gnathopod relative to females, and reproductively active females have a brood pouch, therefore sexes in adult individuals are relatively easy to distinguish. In St. Joe Bay, these three amphipod species are most abundant on pen shells and very rare in sea grass beds where pen shells are not present, probably because they require or prefer the combination of hard substrate and protection these bivalves provide (Kuhlmann 1996, P. Munguia, unpubl. Data,). *M. nitida* is a relatively common amphipod that occurs subtidally along the northwestern Atlantic coast (Bousfield 1973). *B. unicornis*, has been reported for the Gulf of Mexico (Thomas 1993). *N. hiatus* is a tube-dwelling amphipod that can occur in large aggregations of individuals (Thomas 1993, P. Munguia *unpubl. data*).

In order to measure the stage at which individuals arrive to shells (settlement stage), we anchored shells and collected them one day after placement. Anchoring of the shells was synchronized with either the full or new moon to determine if dispersal was linked to a lunar cycle. Next, we decoupled temporal effects and shell age by setting up an array of shells anchored for the same amount of time but placed and collected at different times of the month. Finally, we looked at longer term population dynamics in a series of studies of manipulated and naturally occurring pen shell communities. These studies included an examination of the distribution of the three amphipods at the time of arrival and among naturally occurring pen shell communities. Different experiments were performed in different times of year, and in some cases we used artificial pen shells made out of PVC (Appendix 5.1). Preliminary studies showed that diversity in artificial shells is not different from the diversity found in *Atrina rigida* communities (P. Munguia unpubl. data).

Amphipod Settlement to Shells

In order to measure colonization rates, we anchored empty and unfouled shells in the field and collected them one day after placement. We assumed that all individuals

present after one day had arrived without having grown significantly in size at the new habitat. The anchoring of these shells coincided with either full or new moons in order to test the lunar effect on amphipod recruitment to pen shells (the strongest recruitment contrast is between new and full moons; P. Munguia, unpubl. data). We performed 9 one-day surveys, four at new moon and five at full moon. Each survey consisted of 10 anchored shells.

Collection consisted of placing a zip lock bag over the shell; releasing the anchor and bringing the bag and its contents back to the surface. This provided minimum disturbance to the individuals within shells and allowed us to collect all organisms living in the shells. These samples were brought back to the lab where the contents were flushed with fresh water and collected in a 0.5 mm mesh. Amphipods were then identified, sorted and preserved in 70% ETOH.

Shell age and short-term population patterns

A second experiment tested the effect of shell age and temporal effects on the colonization rates and population dynamics of the three amphipod species. We set out shells and collected them at 1, 4, 8, 12, and 16 days after placement. We retrieved 8 shells each collection time. Shells were 2 meters apart; a distance which preliminary studies suggested that shells are spatially independent from one another (P. Mungiua unpublished data). Subsequent shell arrays were placed on the 4^{th}, 8^{th} and 12^{th} collection dates, each array being collected in sequence, four days after (e.g. shells placed on the 4^{th} day were collected on the 8^{th}, 12^{th} and 16^{th} collection days). This allowed us to test both the effect of shell age (the amount of time the shell spent in the water) as well as temporal effects (when the shell was placed in the water).

Long-term population patterns

We used data from three pen shell community succession experiments carried out in St. Joe Bay (summers of 2001, 2003 and spring of 2004) to compare populations in shells that had been in the water 20 (N = 119 total shells), 40 (N = 89), 60 (N = 133) and 128 days (N = 66). We also examined populations in naturally occurring pen shells from the summer of 2005 to compare the natural distribution and abundance patterns with our experimental data (N = 56 shells collected during 8 sampling periods from May to July). The ages of these naturally occurring pen shell communities were not known.

Abundance-distribution relationship

In order to understand the effect of dispersal stage on the regional distribution pattern, we tested for the degree of aggregation of individuals upon arrival (t = 1 day) and in established shell communities using a standardized Morisita's dispersion index (Krebs 1999). The standardized version of the index creates an upper and lower boundary from –1 to +1 based on a χ^2 distribution values (Appendix 5.2). An index value of 0 is indicative of a random distribution, while +1 indicates a clumped distribution and –1 corresponds to a uniform distribution. With this standardized index, the 95% confidence intervals have an upper and lower boundary of +0.5 and –0.5 respectively (e.g. values above 0.5 would correspond to a clumped distribution). First we calculated the dispersion index using data from natural populations. We then compared the three species by bootstrapping the data (1000 iterations) and calculating 95% confidence intervals around the indices. We also calculated dispersion indices for both males and females in those shells that were anchored for one day (n=9 events) to understand sex-specific distribution patterns at the time of colonization. We then used a log-likelihood ratio contingency test (Zar 1999) to compare the nine one-day distributions among the three species. To compare dispersion indices between sexes for each species, we used a t-test comparing the unstandardized Morisita's index of males and females.

RESULTS

Amphipod Settlement to Shells

The three amphipod species have different dispersal modes; *M. nitida* tends to disperse as adults; 97% of all recruits were adults and almost 50% of the females were brooding (Table 5.1). *N. hiatus* also recruited as adults (95% of all arriving individuals) with nearly 40% of females brooding offspring. *B. unicornis* on the other hand, arrived at shells as juveniles (60%) or juvenile-sized adults (40%). The size of *B. unicornis* juveniles and "adults" did not differ at day one (juvenile head size = 0.33mm ± 0.07 mm, head size of adults at day one = 0.37 ± 0.11 mm; t-test, d.f. = 25, t= 0.726, P = 0.47). These small *B. unicornis* adults were much smaller during recruitment at day one relative to adults found in older, established shells (head size in older shells = .61 ± 0.12 mm; t-test, d.f.=53 t=7.769, P < 0.0001), suggesting that these small adults recently attained a

sexually dimorphic stage, perhaps just prior to immediately after arrival to these pen shells.

The moon phase significantly influenced recruitment patterns in two of the three species. One of the two species that recruits as adults, *M. nitida,* mostly recruited as brooding females during the new moon (81% of females brooding, Appendix 5.3). During the full moon, only 23% of females carried a brood (t-test, d.f. =62, t = 5.851, P <0.0001). The species that recruited as juveniles, *B. unicornis,* had a 16-fold increase in juvenile recruitment during the full moon (t-test, d.f. =50, t = 2.771, P=0.007).

Shell age and short-term population patterns

After 16 days of habitat establishment, *N. hiatus* and *M. nitida* had more juveniles compared to *B. unicornis* (ANOVA at 16 days, d.f. =2,32, F=3.77, P =0.03; Fig. 5.1A). *N. hiatus* had the most adults at this 16 day period compared with the other two species (ANOVA at 16 days, , d.f. =2,32, F=17.49, P < 0.001; Fig. 5.1B) and overall, there were significant differences in total abundances among all three species with *N. hiatus* being most abundant, followed by *M. nitida* and *B. unicornis* (ANOVA at 16 days, , d.f. =2,32, F=14.08, P < 0.001; Fig. 5.1C).

Rates of population growth were tested with an ANCOVA using shell age as the covariate testing the main effects of species (Table 5.2). There was a significant interaction between shell age and species, indicating that these species have different rates of population growth. We then conducted independent regression analyses of each species and noted a significant polynomial term in *N. hiatus* and *M. nitida* indicating that population growth decreased over this interval. In contrast, *B. unicornis* had a linear relationship (no significant polynomial term) indicating a constant increase in numbers over this 16-day interval (Table 5.2). These patterns are consistent with the species arriving as adults having an initial increase in local abundance as their broods are released, while the juvenile disperser has an initially smaller population size, but more constant accumulation of individuals that grow to adulthood.

Over this 16-day time interval, all three species had local populations dominated by females (Fig. 5.1D). An analysis of covariance indicated that all three species had a reduction in the proportion of adults that were male over this 16 day interval, and there was also a significant main effect of species, with *N. hiatus* having the highest proportion

of males, followed by *B. unicornis* and *M. nitida* (ANCOVA, d.f. = 5, 346, F =9.79, P < 0.0001; species effect, F = 20.46, P <0.0001; collection time, F =8.36, P =0.004; interaction, F = 0.027, P =0.97).

Recruitment was dependent on the date of initiating the experiment for two of the three species (Fig. 5.2). *N. hiatus* did not show differences in abundance at day 4 for any of the collection times, suggesting no effect of date on colonization ability (ANOVA, d.f. = 3,35, F=1.07, P=0.37). *M. nitida* had a significantly higher abundance at the four day census for shells placed on the new moon (ANOVA, d.f. = 3,35, F=4.63, P=0.008), despite a non-significant lower rate of adult arrival at day one for this census (t-test, d.f.=49, t = 1.587, P = 0.11; Appendix 5.3). This indicates that this high abundance was driven by the release of juveniles from the high proportion of arriving females that were brooding. In contrast to the other two species, *B. unicornis* had a gradual increase in recruitment noted over a four-day period at these four dates of shell establishment (Fig. 5.2; ANOVA, d.f. = 3, 35, F=5.95, P=0.002).

Long-term population dynamics

Results from longer-term experimental studies of colonization and natural surveys of established pen shell communities exhibited patterns consistent with the short-term dynamics. Experimental studies showed that consistent with the short-term dynamics, *N. hiatus* and *M. nitida,* which had a decreasing population growth over 16 days, had a slightly negative population growth on individual shells over several months (Table 5.4). In contrast *B. unicornis,* which had linear positive population growth over 16 days, continued to increase in abundance on each shell over several months (Table 5.4). These differences in population growth resulted in *B. unicornis* being the most abundant amphipod species after 128 days; with an average of 18.3 individuals per shell compared to 14.8 and 2.27 for *N. hiatus* and *M. nitida* respectively (ANOVA d.f. =2,63, F = 13.61, P <0.0001, see Fig. 5.3).

Consistent with these experimental data, these patterns of abundance at 128 days were similar with a survey of naturally occurring shells (Fig. 5.3). In natural shell communities, *B. unicornis* had the largest populations (mean = 6.38 ± 1.12 SE), followed

by *N. hiatus* (1.91±6.66) and *M. nitida* (0.437±0.88). In addition, there was a significant seasonal pattern in these surveys. Over the period from late spring to summer, *B. unicornis* had a positive increase in abundance (slope = 0.17, F = 13.35, P < 0.001), while *N. hiatus* showed no change in abundance (slope =0.03, F = 0.34, P = 0.54) and *M. nitida* had a significant decrease in abundance (slope = -0.14, F = 9.69, P = 0.003).

Overall, species recruiting as adults showed a rapid initial increase in numbers, while the species recruiting as juveniles showed a slow but constant increase in numbers until it became the most abundant species occupying these pen shell communities. The temporal increase in recruitment noted in *B. unicornis* in the short-term study was also reflected in both the longer-term experimental periods and the natural survey. The polynomial response indicated in the adult dispersers in the short-term study reflected the leveling off or reduction in abundances noted at longer intervals and natural populations collected later in the season.

Abundance-distribution relationship.

These three amphipod species have different patterns of distribution. In naturally occurring pen shells, both *M. nitida* and *N. hiatus* (the adult dispersers) have significantly clumped distributions (mean ±C.I.; Id = 0.53±0.008 and Id=0.52±0.009, respectively). *B. unicornis* (the juvenile disperser) on the other hand, is distributed randomly (Id=0.45±0.003). A similar distribution pattern emerges during colonization; *M. nitida* and *N. hiatus* have clumped distributions, while *B. unicornis* has a random distribution of individuals (χ^2 = 68.95, d.f. = 4, P < 0 .001). Overall, the two species that recruit as adults and brooding females have a more clumped distribution compared to the juvenile dispersing species that has a random distribution. The clumped distribution in the species that disperse as adults may reflect the release of juveniles from brooding females. The persistence of these patterns of clumping in naturally occurring shells indicates the important link between the stage of dispersal and patterns of distribution. It is interesting to note that in the tube-building species, *N. hiatus,* males clump more than females (t-test, d.f. = 9, t = 2.28, P =0.04).

DISCUSSION

Consequences of variation in dispersal stage among amphipod species

This study presents three examples of population consequences of dispersal in marine invertebrates. The three amphipod species disperse at different life stages (Table 5.1). *N. hiatus* and *M. nitida* disperse as adults, while *B. unicornis* disperses as juveniles. The two species that disperse as adults have the highest initial population sizes, likely caused by the arriving females releasing their brood into these recently occupied shells. This dispersal pattern results in initially higher population growth, but fewer occupied shells as noted by their clumped distribution. In contrast, the species that disperses as juveniles accumulates more slowly and more evenly across habitats. Eventually this species dominates the other two in terms of numerical abundance (Fig. 5.3).

Neomegamphopus hiatus arrives to shells as adults (Table 5.1). It has a rapid population growth that asymptotes around 16 days (Fig. 5.1, Table 5.2) and thereafter abundance remains constant in shells that are several months old (Fig. 5.3). *N. hiatus* colonizes shells irrespective of lunar phase or date during the seasons of study. This species presents a clumped distribution in natural pen shell communities because adults are dispersing and because 40% of the arriving females carry broods. While this species is a tube-dweller, they are not constrained to these tubes, as they disperse as adults. In some amphipod species, males pair with females in a single tube prior to and during copulation (Borowsky 1983). After copulation these males depart the tube in search of other receptive females. It may be that in this species, both sexes disperse to new habitats after mating.

Melita nitida also disperses as adults and arrives in relatively large numbers to shells (Table 1). As with the other adult disperser, *M. nitida* has a clumped distribution, both during colonization events and in natural populations of St. Joe Bay. There is no lunar pattern in the numbers of adults recruiting to new shells. However, the status of the arriving females to shells is dependent on a lunar cue: during the new moon the vast majority of the females arrive with brood (Table 5.3). This strategy allows for a periodic rapid population growth when these brooding females arrive and release their offspring, increasing local abundance (Fig. 5.1C). Population growth rate tends to slow within the first 16 days of colonizing new habitats (Table 5.2) and becomes negative in shells that are several months old (Fig. 5.3). Adult abundance starts declining after 12 days (Fig. 5.1B), but in the short term is replaced by the growth of the juvenile cohort in these

localized populations (Fig. 5.1A). These results suggest that *M. nitida* is limited by the availability of new habitat. Adults colonize new habitats and the populations they establish slowly diminish. It is not clear if this species is outcompeted by other species or if they are obligate nomads and disperse as adults to new habitats. Regardless, these populations are the most ephemeral and result in this being the rarest of the three amphipods in the study.

Bemlos unicornis arrives as juveniles to pen shells (Table 5.1), and slowly but constantly increases in abundance over both the successional stage and season from spring through summer (Figs. 5.1 and 5.3). The linear increase of abundance over time (Table 5.2) results in a continuous accumulation of individuals making this species the most common in natural populations (Fig. 5.3). Arrival of individuals to shells is also highly linked to the full moon (Table 5.3). This species presents a random distribution both during initial colonization as well as in naturally occurring shells. Widespread dispersal of juveniles could explain the more random distribution of this species. Unlike the other two species, population growth may be less dependent on the local adult population and the dynamics would be more open, with abundances reflecting overall contributions from the metapopulation rather than local production of offspring.

The two adult dispersers may be nomadic, quickly colonizing new shells and reproducing, but then as their offspring mature, they disperse to new shells. Because recruitment occurs as adults, we were unable to distinguish between stable or slowly declining turnover of individuals and more stable and gradual mortality of initial colonizers. It could be that *M. nitida* adults move on after releasing their brood, which could explain why their populations decline in older shells. *N. hiatus* adults on the other hand, may be less prone to moving on to new habitats because of the investment in tube building. Perhaps dispersal of *N. hiatus* adults is density dependent (e.g. Amarasekare 2004); as tubes accumulate, excess adults move to new habitats. This is a possible explanation for the relatively stable population size after the initial burst in abundance.

Stage-dependent dispersal and metapopulation dynamics

Dispersal can potentially be risky, which could be why many organisms disperse large numbers of relatively inexpensive propagules (Palmer et al. 1996). The trade-off between dispersing as an adult compared to a juvenile or larvae is likely to depend on the

size or stage dependent risks associated with dispersal. If mortality is less dependent on size or stage, then releasing large numbers of small stages may bet hedge against local mortality to a particular habitat. However, if adults face a reduced risk and if upon arrival to a new shell they can release offspring in the relative safety of a protected habitat (e.g. a pen shell), then adult dispersal may be favored.

Regardless of the mechanism driving differences in stage-dependent dispersal, the persistence of amphipod metapopulations in pen shell communities could be influenced by their dispersal strategy. Pen shells are ephemeral hard substrate (they persist approximately one year after the death of the bivalve, *pers. obs*.), forcing species that occupy shells to colonize and reproduce rapidly. Therefore the dispersal phase, as shown in this study, can be an important component in affecting local population growth and distribution. Competition at the local scale may be important but there was no obvious distributional signature of competition (P. Munguia unpubl. data). Theoretical studies tend to focus on the competitive environment that structures species distribution and enables coexistence (e.g. Leibold et al. 2004, Amarasekare et al. 2004). For example, Amarasekare et al. (2004) suggest that in source-sink dynamics where dispersal is the key mechanism for species persistence, competitive ability is crucial in determining population growth or extinction. Our study shows not only how dispersal is important in the maintenance of spatially structured populations, but how dispersal mode can be a key mechanism that leads to population growth and species distribution. Theoretical studies should consider variation in the dispersal stage and its population benefits and consequences.

An important aspect of metapopulation theory is the connectivity among populations. With complete dispersal limitation, subpopulations are isolated from one another, suggesting a "closed" system; however, as dispersal ability increases, populations become more open allowing individuals to reach more habitats (Loreau and Mouquet 1999, Mouquet and Loreau, 2003). Typically, the mechanisms invoked to explain dispersal limitation include high propagule mortality and the ability to invade or colonize habitats. We suggest that another mechanism that can promote or diminish the connectivity among habitats include the stage of the disperser. Late stage dispersers can seed local habitats quickly, but seem to be limited in the number of habitats that are

invaded. In contrast, early stage dispersers can flood a larger range of habitats, but these populations grow slower because increases in abundance are dependent on continued recruitment from other populations.

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Table 5.1. Species abundances and proportions of recruits after one day of recruitment. Means (SE). Letters represent statistically different abundances between species under a Tukey post-hoc test ($P<0.01$, $n=90$). Asterisks represent significant departures from random proportions (Heterogeneity test, $P<0.05$).

	Number of Individuals		Proportions	
SPECIES	Adults	Juveniles	Males : adults	Pregnant: females
N. hiatus	6.24 (1.13)[a]	0.30 (0.16)	0.42 (0.04)	0.37 (0.04)
M. nitida	7.57 (0.59)[a]	0.22 (0.14)	0.24 (0.02)	0.47 (0.04)
B. unicornis	0.27 (0.09)[b]	0.41 (0.1)	0.30 (0.09)	0.07 (0.08)*

Table 5.2. Among-species comparison of abundance levels for short-term population dynamics and polynomial regression values for each species abundance over a 16-day period.

ANCOVA on all three species				
ANCOVA	D.F.	F-ratio	P	
SPECIES	2	82.8683	<.0001	
TIME	1	35.9409	<.0001	
SPECIESxTIME	2	4.7643	0.0092	
REGRESSIONS ON EACH SPECIES				
N. hiatus				
Term	Estimate	SE	t Ratio	P
Intercept	1.374	0.11	12.32	<.0001
TIME	0.348	0.028	12.22	<.0001
(TIME)^2	-0.02	0.004	-4.64	<.0001
M. nitida				
Term	Estimate	SE	t Ratio	P
Intercept	2.072	0.088	23.53	<.0001
TIME	0.229	0.024	9.25	<.0001
(TIME)^2	-0.02	0.0036	-5.31	<.0001
B. unicornis				
Term	Estimate	SE	t Ratio	P
Intercept	0.246	0.0717	3.44	0.0008
TIME	0.116	0.01838	6.32	<.0001
(TIME)^2	0.000	0.0026	0.14	0.8856

Table 5.3. Among-species comparison of amphipod abundance levels from long-term population dynamics in experimental pen shells. Because the interaction term in the ANCOVA was significant, *B. unicornis* data were taken out and regressed independently, and the ANCOVA was performed again for *N. hiatus* and *M. nitida*.

ANCOVA on all three species from long-term experiments				
ANCOVA	D.F.	F-ratio	P	
SPECIES	2	0.46	0.4969	
TIME	1	28.98	<.0001	
SPECIESxTIME	2	19.52	<.0001	
REGRESSION on B. unicornis				
	D.F.	F-Ratio	P	SLOPE
TIME	1	39.24	<0.001	0.28
ANCOVA on N. hiatus and M. nitida				
	D.F.	F-Ratio	P	SLOPE
SPECIES	1	48.1	<0.001	
TIME	1	8.25	0.0042	-0.06
SPECIESxTIME	1	0.29	0.586	

SUPPLEMENTS

Table A1. List of the different experiments and their setups.

EXPERIMENT	YEAR	MONTHS	SHELL TYPE	TOTAL NUMBER OF SHELLS USED
One-day experiments	2004	March	Natural	20
	2005	May-July	Natural	70
Short-term experiment	2004	March-April	Natural	40
Temporal effect experiment	2004	March-April	Artificial	40
Long-term experiment	2001	June-October	Natural	150
	2003	June-July	Artificial	257
Natural Survey	2005	May-July	Natural	56
			TOTAL	633

Table A2. Morisita's Standardized Index of Dispersion (Krebs 1999).

First, calculate Morisita's dispersion index:

$$Id = n\,[(\Sigma x^2 - \Sigma x) / ((\Sigma x)^2 - \Sigma x)]$$

Where Id = Morisita's dispersion index, n= sample size, x = the number of amphipods per shell

Second, calculate the two critical values used in the standardized index,

For a Uniform distribution,

$$Mu = [\chi^2_{0.975} - n + \Sigma x_i] / [(\Sigma x_i) - 1]$$

Where $\chi^2_{0.975}$ = value of Chi-square with (n-1) degrees of freedom at $\alpha = 0.975$, x_i = number of individuals per shell.

For a Clumped distribution,

$$Mc = [\chi^2_{0.025} - n + \Sigma x_i] / [(\Sigma x_i) - 1]$$

Using Id, Mu and Mc, we can calculate a standardized index depending on the relationship of these three variables (see Krebs 1999 for more information).

Table A3. Effects of moon phase on the number of individuals for each species. Means (SE). T-test comparing new vs. full moons: * = P < 0.05, ** = P <0.01, *** = P< 0.001.

	Juveniles	Adults	Females	Mean prop. Females with brood	Mean prop. males
	N. hiatus				
NEW	0.30(0.35)	3.45(2.59)	2.15(1.81)	0.46(0.08)	0.45(0.08)
FULL	0.42(0.22)	8.83(2.11)	5.67(1.49)	0.26(0.07)	0.46(0.08)
	M. nitida				
NEW	0.60(0.23)	6.05(0.89)	5.00(0.75)	0.81(0.04)***	0.18(0.04)
FULL	0.50(0.19)	7.23(0.73)	5.33(0.61)	0.23(0.04)	0.27(0.03)
	B. unicornis				
NEW	0.05(0.20)**	0.35(0.19)	0.20(0.11)	0.25(0.12)	0.26(0.19)
FULL	0.83(0.16)	0.45(0.12)	0.21(0.06)	0.25(0.14)	0.33(0.13)

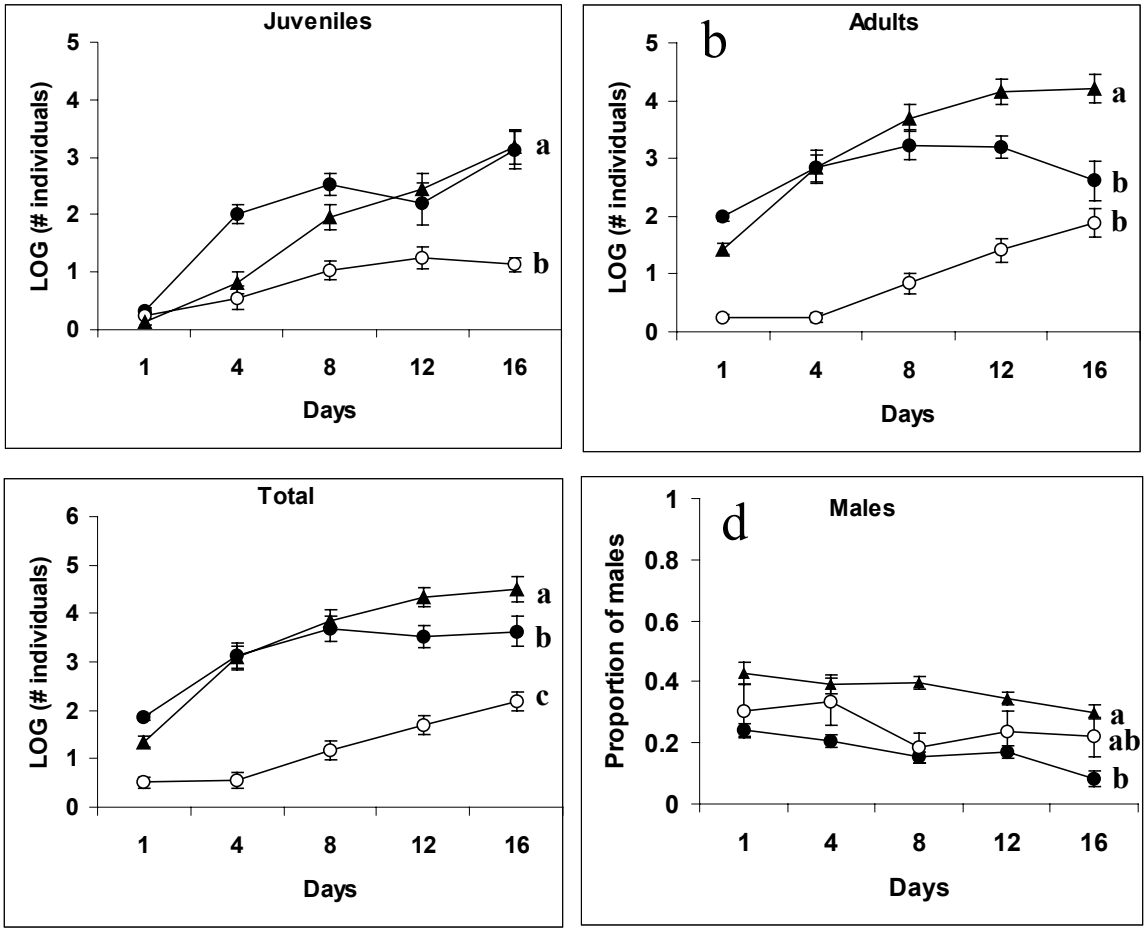

Figure 5.1. Number of (a) juveniles, (b) adults, (c) total individuals and (d) the proportion of males from the total number of adults for the three amphipod species as a function of shell age. Dark circles represent *M. nitida*, open circes *B. unicornis*, dark triangles *N. hiatus*. Means ±SE; different letters represent statistically different ($P<0.05$) values using a Tukey HSD test.

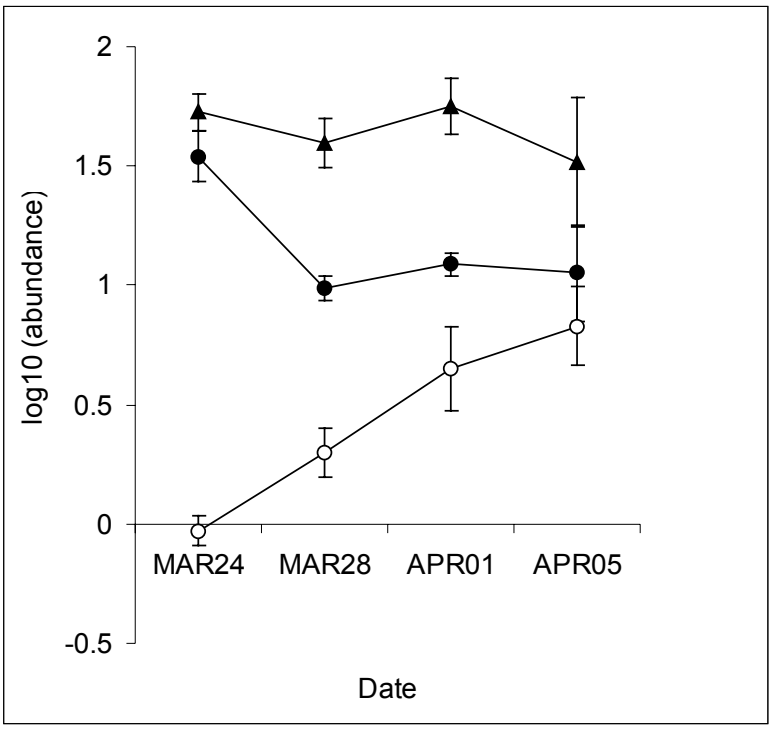

Figure 5.2. Number of individuals for *M. nitida* (dark circles) and *B. unicornis* (open circles) and *N. hiatus* (dark triangles) as a function of date of collection. All of the shells were in the water for four days before collected; they had the same time interval for accumulation. Log transformed data with means ±SE.

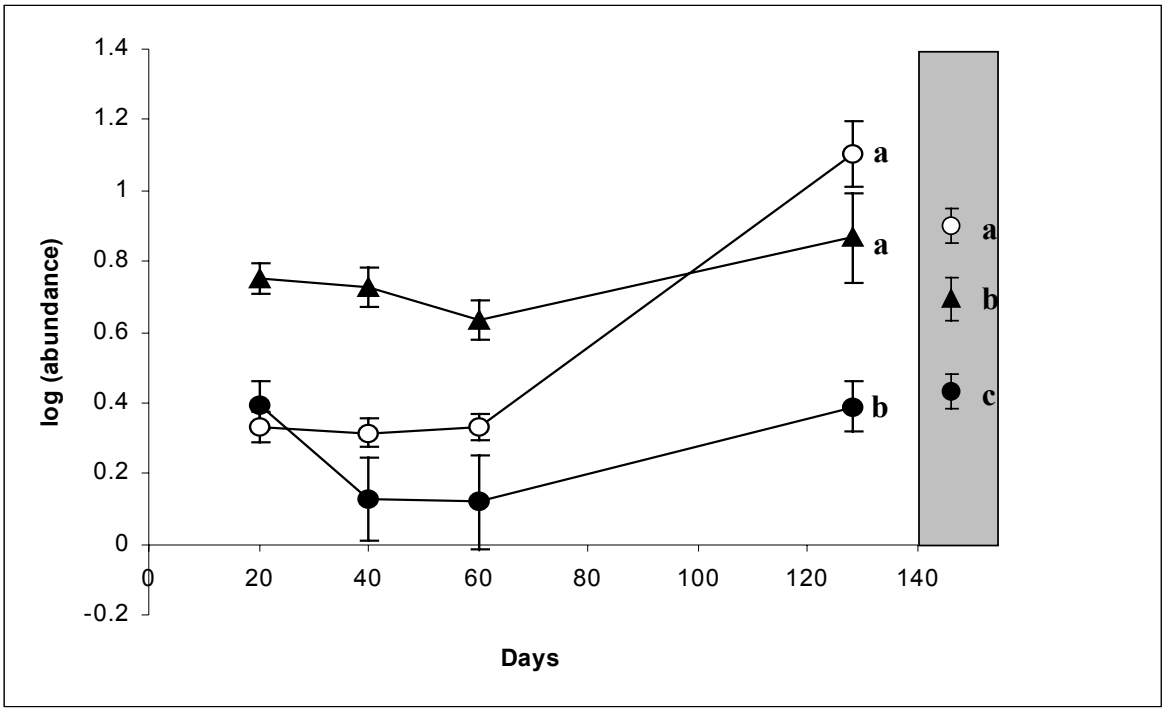

Figure 5.3. Number of individuals on shells that were in the water for long periods of time (16-128 days). Different letters represent statistically different ($P<0.05$) abundances at 128 days using a Tukey HSD test. Shaded area on the right presents data collected from surveys of naturally occurring shells of random ages. Dark circles represent *M. nitida*, open circes *B. unicornis*, dark triangles *N. hiatus*. Log transformed data with means ±SE.

CONCLUSIONS

The work I presented here was aimed at generating a better understanding of spatial processes that may affect communities. Current theory has made great advances, but field studies are lagging behind. Using naturally occuring pen shell communities, I was able to address some important questions in community ecology based on successional processes. First, I showed how local and regional diversity relationships are not "fixed" as biogeographers tend to argue, but are dynamic depending on successional stages and the influence of rare species. Second, in a study with Tom Miller, I showed how habitat destruction –disturbance at larger spatial scales – could affect diversity in marine systems, based on the species' response to changes in distribution and abundance. Based on this same idea of changes in abundance and distribution, I compared common and rare species to test the neutral theory of biodiversity. Finally, I focused on three amphipod species population dynamics (in collaboration with Coleman Mackie and Don Levitan) in order to understand how dispersal mode can influence population dynamics and species distribution.

During the course of these projects, I realized that a number of major questions remain to be addressed with the pen shell system. I will describe some future directions for the research that I started six years ago, while discussing some of the issues that should receive attention in the next few years.

Undesrtanding diversity for different groups of species

The data set on pen shell communities was divided into two broad categories based on the motility of adult individuals, namely sessile and motile species. However, there are other ways to subdivide the species found on pen shells, which may give further insight into processes that structure these communities. For example, one approach that could give insight is to generate an index of pen shell utilization, using a ratio of the abundance of a species in pen shells divided by its abundance in the surrounding habitat. The species could then be divided into groups based on their specialization, providing great insight when their abundance and distribution patterns are compared. This comparison could help explain the role of pen shells as hard substrate on the population dynamics of their inhabiting species.

The importance of larger scale migration in pen shell communities

The dynamics of pen shell communities, as with any natural microcosm (Srivastava et al. 2004), occur at relatively small scales. Their relatively small size and ease of sampling allows for complicated experimental designs while allowing for testing the complexity experienced in larger communities or at larger scales. However, there are limitations as to the type of questions that can be addressed with pen shell communities, because of their relatively small scale. Hypotheses concerning spatial structure of diversity need to be carefully considered. The first question that has arisen is the validity of pen shell communities. What would happen if the pen shells were not present in St. Joe Bay? Pen shell inhabitants are not endemic to pen shells, however there is no other substrate that would support the same composition in St. Joe Bay. None of the hard substrate-producing mollusks in St. Joe offer an analogous habitat to pen shells. This suggests that many of the species found on pen shells would either not occur or occur at drastically reduced abundances if pen shells were not found in St. Joe Bay. However, it would be interesting to sample other benthic, hard substrate communities (such as oyster reefs) in the northern Gulf of Mexico to determine other possible habitats that occur for these species at even larger scales. This would be the first step in addressing problems with spatial scale that arise with marine systems. In the pen shell system, the physical boundary of the community is discrete, and the differences in species composition between pen shells and the surrounding habitat are clear. The suites of species that inhabit pen shells operate on a continuum of spatial scales, which makes understanding the role of dispersal and regional processes difficult.

The role of rare species in community ecology

In any given local habitat, only a few species are abundant, while the remainder are less common or rare. This uneven distribution of abundances is noted over a wide range of taxons and habitats; therefore, research involving rare species is fundamental for understanding diversity patterns. There are two different avenues that rare species research might take. The first involves studying whole communities in order to understand the relative importance of mechanisms that affect rare species in general. The second avenue focuses on individual rare species in order to understand the constraints

imposed by their natural history (such as growth and reproductive behavior, and dispersal ability), and interactions with other species.

At a local scale, rare species form the bulk of diversity, however one of the questions that remains to be addressed is whether these species are also rare at larger spatial scales, such as the network formed by a metacommunity. There are several scenarios for rare species that can be envisioned in a network of communities. First, if niche theory prevails among a homogeneous environments, then the same species should be abundant (or rare) everywhere. Second, niche theory could take place in heterogeneous environments, in which case the dominant local species will vary regionally. Finally, neutral theory predicts essentially the same thing as niche theory with heterogeneity, since colonization and local death are the primary mechanisms. When successional stages are incorporated, then species can change in their rare status: rare species may become common or vice versa. The view that species are either common or rare without more information is too rigid, for it does not incorporate temporal and spatial changes, which are required in order to make predictions.

Given that species composition can change among local communities, the diversity metric of importance is beta diversity. Beta diversity is the change in species composition across habitats. While alpha diversity is a within-habitat measure and gamma diversity is across all local habitats, beta diversity is a very different measure that measures variability in local diversity, rather than diversity itself. Unfortunately, because it is hard to quantify, current research uses different indirect measures of variation in species composition, which is just variance in local diversity, disregarding species identity.

Therefore, a good method is required that can actually calculate variation in species identity when there are more than two communities. The best approach may incorporate ordination techniques, where the sum of the species identities and their abundances for each community are summarized in multidimensional space. However, the use of this approach does not allow for direct comparison with the other two scales of diversity (alpha and gamma). Creating a methodology that allows for true quantification of beta diversity and relating it to local diversity and the species pool is an important goal for community ecology and the understanding of rare species.

Incorporate patterns of individual species

In order to understand the mechanisms behind rare species' abundance and distribution patterns, research needs to focus on individual species. In particular, we need to understand whether rare species are rare because of some intrinsic species characteristic or whether rarity is conveyed because of environmental and community (e.g. species interactions) factors. Life history traits such as number of offspring produced and individual growth rate can constrain population growth and distribution. Behavioral patterns expressed during reproduction, as well as sexually selected traits can also influence a species ability to increase in abundance and distribution. Clearly, just quantifying number of individuals and the locations at which they are found is not enough to understand the causes of rarity. Here, I advocate the inclusion of behavioral studies. It is likely that not all rare species are under the same constraints, therefore studying several rare species that coexist in the same community may be the next step at understanding diversity patterns.

APPENDIX A

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EDUCATION

Postdoctoral Associate, Smithsonian Environmental Research Center, Edgewater, MD 2006-2008

Ph.D. Candidate in Biological Science at Florida State University, Tallahassee, FL 2000-2006 (Advisors: Don Levitan and Thomas Miller)

B.Sc. in Biology (Licenciado en Biologia) Universidad de Guadalajara,Guadalajara, Mexico. 1995-2000

Graduated with honors. (GPA 9.3 of 10)

Exchange Program with the University of Calgary, Canada. 1997-1998

*courses in Kananaskis Field Stations and Bamfield Marine Station

MAIN RESEARCH PROJECTS

Diversity patterns in pen shell (*Atrina rigida*) communities 2000-ongoing

Fugal community structure in temperate and tropical Mexican forests (3 of 4 papers published) 2000

Shorebird diversity in the Laguna de Sayula, Mexico (1 paper published) 2000

**Other research interests*

-Sexual selection in amphipod metapopulations.

-Spatial ecology and scaling of diversity.

-Behavioral ecology of fiddler crabs.

GRANTS AND AWARDS

Magaret Menzel Endowed Award (for outstanding graduate student), Florida State University 2005

Dissertation Improvement Award, Florida State University 2005

Latin American and Caribbean Fellowship, Florida State University (1,000 USD) 2005, 2006

Jack Winn Gramling Research Award, Florida State University (4,000 USD) 2004, 2005

Brenda W. Bennison Memorial Scholarship, Florida State University (1,000 USD) 2003

Robert B. Short Scholarship in Zoology, Florida State University (1,000 USD) 2003

Honorable mention, poster presentation, Benthic Ecology Meeting 2003

COFRS Grant, Florida State University (8,000 USD) in collaboration with Thomas Miller 2003

Institute of International Education Travel Grant (500 USD) 2002

Fulbright Fellowship 2000-2002

Consejo Nacional de Ciencia y Tecnologia Fellowship, Mexico 2000-2002

Idea Wild grant (1,300 USD) 2000

E. Alexander Bergstrom Memorial Research Award, Association of Field Ornithologists (1,500 USD) 2000

University of Calgary-Universidad de Guadalajara Exchange Scholarship 1997-1998

Outstanding Student Scholarship, Universidad de Guadalajara 1996-1997

RELATED WORK EXPERIENCE

Guest Lecturer: for the Scientific Diving course at Florida State University. 2001-2003

Teaching Assistant at Florida State University (2000-2006): Biology for Non-majors; Biology I for majors; Ecology; Evolution; Marine Biology; Experimental Biology: Foraging Ecology; Pollination Biology; Marine Field Ecology.

Teaching Assistant at the Universidad de Guadalajara (1999): Ecology.

* Research Assistant to Tom Miller, Evolution of competitive ability in pitcher plant protozoa 2004
* SeaGrant Research Assistanship, (PI: Felicia Coleman, FSU) 2001
* Visiting researcher, Instituto de Ecología, Xalapa, Veracruz. 2000
* Co-Founder and Vice-president of the Instituto de Biologia, Ecologia y Conservacion, A.C. A non-profit research institute based in Guadalajara, Mexico 2000
* Internship at the Ecophysiology Lab, Department of Ecology, Universidad de Guadalajara 1999-2000
* Research Assistant at the Marine Ecosystems Laboratory, Universidad de Guadalajara

1998-1999

COMMUNITY SERVICE AND VOLUNTEER WORK (since 2000)

* Reviewer for the following Journals: *Ecology Letters(5), Journal of Field Ornithology(1) Marine Ecology Progress Series(3), Oecologia(7).*

* Field Guide, 5th Annual Florida Panhandle Birding and Wildflower Festival, Department of Environmental Protection, Florida 2005
* Advisory Committee, North American Colonial Waterbird Conservation Plan 2000-present
* Advisor for undergraduate Directed Individual Study (8 students) 2002-2006
* Advisor for the Young Scholar's Program, Florida State University 2002
* Judge at the High school regional Science Fair, Tallahassee, FL 2002-2006

TALKS PRESENTED AT MEETINGS ***** *denotes poster presentations*

Invited speaker:

Munguia, P. Instituto de Ecologia, Universidad Autonoma de Mexico, Mexico D.F. August 2005.

Munguia, P. 88th Annual Meeting of the Ecological Society of America, Savannah GA. August 2003.

Munguia, P. Tri-Beta National Honor Society Colloquium, Florida State University, November 2003.

Regular presentations:

Munguia, P. 91rst Annual Meeting of the Ecological Society of America, Memphis, TN. August 2006.

Munguia, P. and D.R. Levitan. 35th Annual Benthic Ecology Meeting, Quebec, Canada. March 2006.

Munguia, P. 86th Annual Meeting Western Society of Naturalists, Seaside, CA, November 2005.

TerHorst, C. and P. Munguia. 86th Annual Meeting Western Society of Naturalists, Seaside, CA, November 2005.

Munguia, P. 34th Annual Benthic Ecology Meeting, Williamsburg, VA. April 2005.

Munguia, P. Ecology and Evolution Seminar Series, Dept. of Biological Science, Florida State University. February 2005.

Munguia, P. Annual Meeting of the British Ecological Society, Lancaster, England, September 2004.

Munguia, P. 33rd Annual Benthic Ecology Meeting, Mobile, AL. March 2004.

Munguia, P. 1rst Southeastern Ecology and Evolution Conference, Atlanta, GA. March 2004.

*****Munguia, P. 32nd Annual Benthic Ecology Meeting, Mystic, CT. March 2003 – ***Honorable mention award***

Munguia, P. Natural History Seminar Series, Dept. of Biological Science, Florida State University. November 2002.

Munguia, P. 87th Annual Meeting of the Ecological Society of America, Tucson AZ. August 2002.

Munguia, P. Florida Ecology and Evolution Symposium, Archibald Research Station, Lake Placid FL, April 2002.

Munguia, P. 31rst Annual Benthic Ecology Meeting, Orlando, FL. March 2002.

Guzman, G., P. Munguia, and F. Ramirez-Gillen. VII Congreso Nacional de Micologia, Queretaro, Mexico, September, 2000.

Munguia, P., G. Guzman, and F. Ramirez-Guillen. VII Congreso Nacional de Micologia, Queretaro, Mexico, September, 2000.

Munguia, P., L. Guzman-Davalos, G. Guzman, F. Ramirez-Guillen, and O. Rodriguez. VII Congreso Nacional de Micologia, Queretaro, Mexico, September, 2000.

*****Munguia, P., L. Guzman-Davalos, and O. Rodriguez. VII Congreso Nacional de Micologia, Queretaro, Mexico, September 2000.

PUBLISHED PAPERS

Munguia, P. 2006. Book Review - Biodiversity of Fungi: Inventory and Monitoring Methods. ***Inoculum*** **57**:8-9.

Munguia, P., G. Guzman, F. Ramirez. 2006. Seasonal community structure of macromycetes in Veracruz, Mexico. ***Ecography*** **29**:57-65.

Munguia, P., P. Lopez, I. Fortes. 2005. Seasonal changes in habitat characteristics for migrant waterbirds in Sayula, Western Mexico. ***Southwestern Naturalist*** **50**:318-322.

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