

Spatial structure of communities on dead pen shells (*Atrina rigida*) in sea grass beds

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Abstract Delimiting communities in marine habitats is difficult because co-occurring species often have different life histories and the life stages experience the environment at different spatial scales. The habitat of a particular community is embedded within a larger habitat or ecosystem with many species shared between the focal community and the larger system. Pen shells (*Atrina rigida*) are large bivalves that, once the mollusk dies, provide shelter for motile species and hard substrate for settling larval invertebrates and egg-laying fishes. In St. Joseph's Bay, Florida (29°45'N, 85°15'W), pen shells are the most abundant source of hard substrate, especially inside sea grass (*Thalassia testudinum*) beds, where they reach densities of 0.1–4.0 m⁻². This study, which was conducted from May to August 2005, measured the overlap in species densities between dead pen shells and the surrounding sea grass communities at eight sites to determine the discreteness of the pen shell communities. Of the 70-epibenthic taxa recorded, 66% were found on the pen shells but not in the surrounding sea grass habitat. Community structure, which

varied among shells within sites and among the eight sites, could be related to sea grass characteristics such as blade density and length either directly (e.g., inhabitants of pen shells directly benefit from the surrounding sea grass) or indirectly (e.g., pen shells and sea grass both benefit from similar factors such as current and nutrients). Pen shells were randomly distributed at several spatial scales within the 15 × 15 m sites as were many motile species. Two exceptions were the shrimp, *Palaemon floridanus* and the amphipod, *Dulichella appendiculata*, whose distributions were clumped. Most of the sessile species had clumped distributions, tending to be very abundant when they were present. These pen shell communities provide an opportunity for experimental studies of factors affecting species diversity on small, discrete, naturally occurring habitats.

Introduction

In marine ecosystems, defining the boundaries for populations and communities has been problematic. Many marine species have at least two distinct life history stages that persist at very different spatial scales. The dispersal stage (a larva or juvenile) is cast into the water column where it is transported to distant settlement habitats (e.g., Roughgarden et al. 1985; Palmer et al. 1996). The more sedentary adult stage may be territorial or sessile (e.g., Olson 1985) or even capable of moving 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 experienced by the disperser stage and a local scale experienced 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.

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Over the last 20 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 ecological communities have been found to have the appropriate attributes for testing spatial 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 are manifested on very different spatial scales (Huston 1999). Species can differ in their mating strategies, competitive and dispersal abilities and whether the dispersal stage (e.g., adults or larvae) can select and discriminate potential habitats for settlement (e.g., Keough 1984; Huston 1999; Jenkins 2005; Munguia 2006). 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 function combined with the physical structure of communities needs to be considered in order to understand diversity patterns.

The main objective of this study was to determine whether dead pen shells (from *Atrina rigida* bivalves) were occupied by a different community than that found in the surrounding sea grass habitat in St. Joseph Bay, Florida. Pen shells (i.e., *Atrina* spp. and *Pinna* spp.) have been found to affect macrofauna diversity in surrounding habitats (e.g., Warwick et al. 1997; Cummings et al. 1998), and even studied as settling habitat for sessile species (e.g., Keough 1984). Pen shell communities have the potential to address questions regarding spatially structured communities (Srivastava et al. 2004), but first their spatial structure and role within the larger sea grass bed community must be described. Therefore, in this study I asked the following

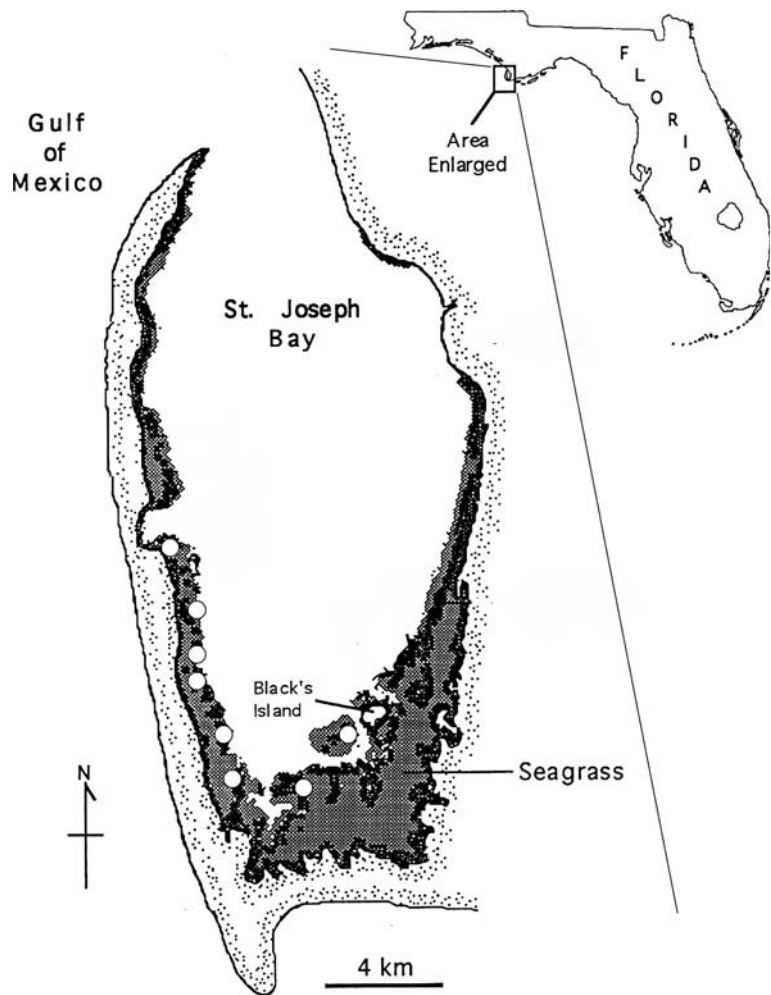
questions: (1) Do the species occupying pen shells constitute a discrete community, or are they just part of a larger community within sea grass beds? More specifically, what proportion of pen shell inhabitants is also found in the habitat surrounding pen shells? If pen shells share a large number of species with the surrounding sea grass habitat, this would suggest that a pen shell “reef” is nested within the larger sea grass habitat. (2) Does pen shell community structure vary with spatial scale, specifically on a scale of 0.1–10 km across St. Joseph Bay? Spatial variation in community structure could occur as a function of environmental conditions including the density of communities in different areas of St. Joseph Bay. I also focus on a subset of pen shell inhabitants to compare the distribution of different species. In any given community, populations may grow and disperse at different spatial scales (Huston 1999), which can be reflected in the distribution of individuals. The difference between the distribution of habitat and species should reflect the way species track habitats: if both habitat and species have the same distribution, then species would tend to follow such habitat, suggesting that habitat may be limiting. Alternatively, if species have a clumped distribution relative to the habitat, this means that a biotic (e.g., habitat selection, competition, dispersal ability) mechanism limits the distribution, reflected in the aggregated individuals. If species have a uniform distribution relative to the habitat, then the above mechanisms are not constraining the distribution.

Methods

Description of natural system

This study was conducted in St. Joseph Bay, Florida (also referred to as St. Joe Bay); a shallow, well-protected bay in the northern Gulf of Mexico (Fig. 1). Substrate in the bay is composed of a bare sandy bottom intermixed with patches of sea grass (*Thalassia testudinum* and the less common *Halodule wrightii*). Sea grass beds occupy approximately 2,560 ha of the bay, mostly on the shallow areas (less than 3 m; Wolfe et al. 1988). 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 (personal observation; Kulhmann 1996). When alive, pen shells have up to 30% of their surface area exposed to the water column, and are not fully available for colonization by other organisms. When the mollusk inside the shell dies, the shell becomes increasingly exposed (until the whole shell is lying on the sand) and is occupied by a diverse array of species (Munguia 2004), which use the shell as either refuge, egg laying substrate, or settling

Fig. 1 Map of St. Joe Bay with the location of the field sites in circles. Shaded area represents sea grass beds. Black areas represent sandy bottom within the sea grass beds. Modified from Kuhlmann (1996)



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., sea grass, benthos, and the water column).

Site selection and sampling

Eight sites within the bay were surveyed in the summer of 2005 (Fig. 1), distance between sites was 120 m and the greatest ~ 10 km. Each site occurred within a unique sea grass bed, with at least 1 m from the edge, however sandy areas within the sea grass patch occurred and were also sampled. Each of the 15×15 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, and 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 15×15 m perimeter to sample macrofauna. All organisms occupying roughly 0.25 cm^2 or more of the substrate, which were known to occupy dead pen shells, were identified and counted in each quadrat. 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 sea grass blades and collect individuals suspended in the water column. Preliminary testing of methods suggested that this was the best way to obtain both small organisms swimming among sea grass blades (e.g., amphipods and shrimp) as well as those loosely attached to the blades (e.g., hermit crabs). Samples were sieved over a 0.5 mm mesh, identified and counted. This process was aimed at obtaining amphipods, snails, hermit crabs, but disregarded invertebrate larvae, since pen

shell inhabitants are present in either juvenile or adult stages. Finally, sea grass density and blade length were quantified using a 0.15×0.15 m quadrat randomly tossed ten times inside the 15×15 m perimeter. All of the sea grass blades inside the quadrat were counted, and three of these blades were picked at random and measured from the base 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 30 shells. This regression was highly significant ($df = 29$, $F = 694.77$, $P < 0.0001$) and explained 97% of the variance; therefore length \times width was a good predictor of pen shell area. Data were log transformed and averages for pen shell and adjacent habitat compared. Data from the quadrats were standardized to densities per 1 m^2 . The plankton data was standardized to the approximate volume of water sampled (0.27 m net diameter and 60 m^2 of area sampled giving a total water volume sampled of 3.43 m^3) per site covering an area of 16.2 m^2 . 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. For example, tube-building polychaetes were considered sessile because their tubes are fixed to the substrate and these worms have not been observed to leave tubes, errant polychaetes were considered motile species. Tube-building amphipods were considered motile because the adults have the ability to move between shells and their tubes are ephemeral (Munguia 2006, unpublished data).

I compared community structure on each shell among the different sites using the variance in sea grass density and blade length as habitat variables for each plot, as well as the distance to the nearest pen shell as an estimate of density. Abundance data were standardized by the maximum value for each species (Quinn and Keough 2003). Therefore, abundance was expressed as a percentage which allowed for (1) large abundance differences among species as well as (2) comparisons between sessile clonal species and sessile species with single, small individuals. A partial Canonical Correspondence Analysis (CCA) was performed using the 22 most abundant motile species and the 15 most abundant sessile species (those having more than 20 individuals among shells in all sites). The variance in sea grass density and variance in blade length were used as environmental

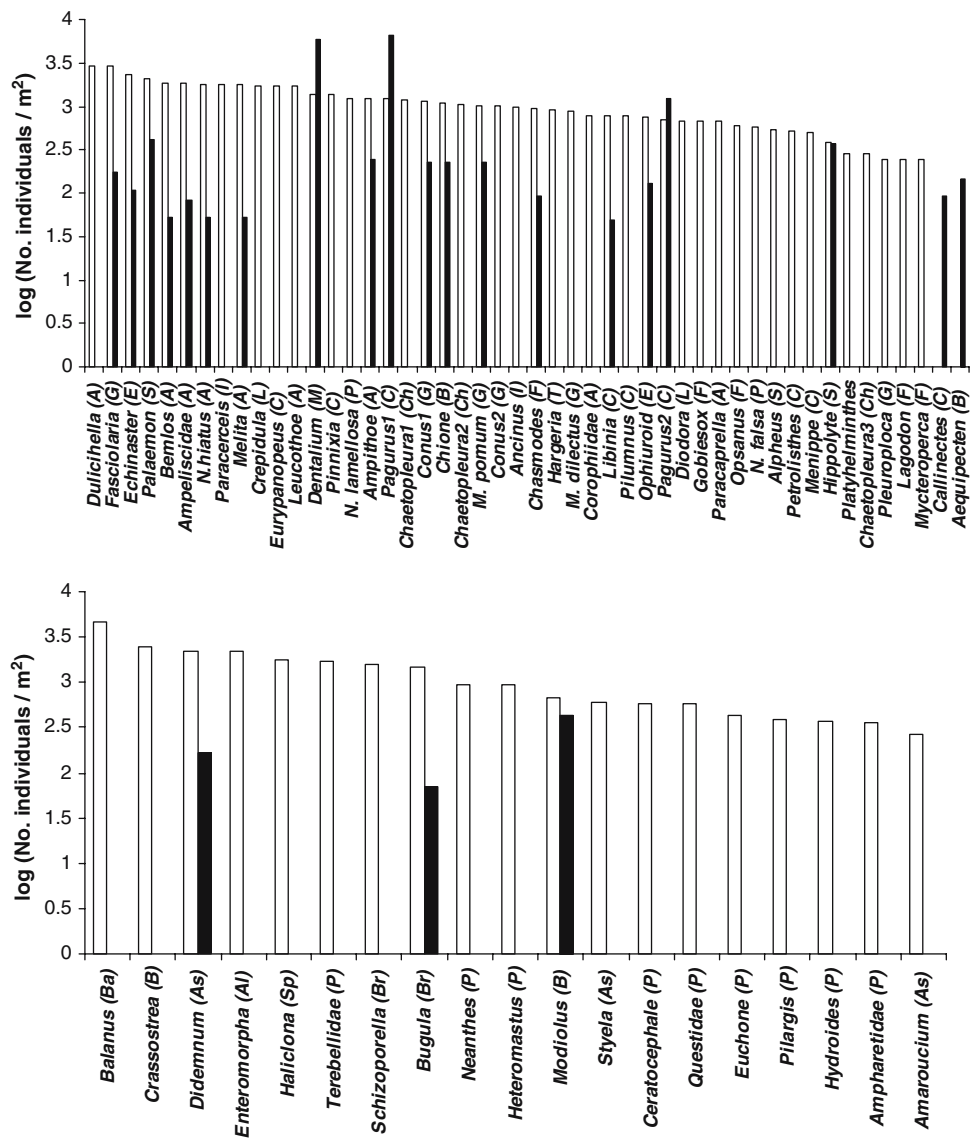
data in the CCA; I tested their explanatory power on the variation in community structure using a Monte Carlo permutation test (with 1,000 iterations). I first tested for a horseshoe effect known to bias CCA analyses (Quinn and Keough 2003) proceeding with the analysis only after failing to find any such effect. The first four axis scores of the CCA were used to represent community structure (how the identity of each species and their abundance in each shell relates among shells) influenced by the environment. Next, these four 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. I used two statistical values from the MANOVA, Wilk's lambda and Pillai's trace, because the former is the most common metric while the latter tends to be more conservative than Wilks' lambda. 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 11 motile and 9 sessile species 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 site. I also calculated Morisita's index for dead shells at three different spatial scales within each site: $1 \times 1 \text{ m}$, $3 \times 3 \text{ m}$, and $5 \times 5 \text{ m}$. Estimating distribution patterns of patchy habitats is required in order to understand spatially structured communities. 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 ($n =$ number 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 occurred in densities ranging between 0.1 and 4.0 dead pen shells m^{-2} . In the sites surveyed, live pen shells occurred in densities up to 10 m^{-2} . Other un-sampled areas of the bay had densities up to 11 m^{-2} . Pen shell area had a positive but weak relationship with species richness for both motile ($N = 56$, $F = 5.08$, $P = 0.03$, $r^2 = 0.08$) and sessile species richness ($N = 56$, $F = 10.32$, $P = 0.002$, $r^2 = 0.16$).

Fig. 2 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. *Letters* represent the following: *A* Amphipod, *G* Gastropod, *E* sea star, *S* Shrimp, *I* Isopod, *L* Limpet, *Sc* Scaphopod, *P* Polychaete, *Ch* Chiton, *F* Fish, *T* Tanaid shrimp, *B* Bivalve, *Ba* Barnacle, *As* Ascidian, *Al* Alga, *Sp* Sponge, *Br* Bryozoan. The full taxonomic names are available in Appendix 1



Of the species found in pen shell communities (Appendix 1), only 33% of the motile and 16% of the sessile species were found in the adjacent habitat (Fig. 2). Those motile species that were not exclusive to pen shells tended 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 were 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 (Munguia 2004, unpublished data), however, in this survey none were found inside pen shells (Fig. 2). Of the sessile species, only mussels (*Modiolus demissus*) were found in relatively high abundances among the sea grass; this species also forms large beds in St. Joe Bay but they are low-lying (i.e., do not protrude more than 4 cm above the substrate) and do not support pen shell inhabitants.

The results from the ordination analysis suggest that motile species abundance was highly variable among shells and among sites, and this variability correlated with variation in the surrounding sea grass habitat. Furthermore, motile species composition and abundance seemed to be weakly influenced by pen shell density. 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 relate with community structure ($F = 3.87, P = 0.001$), and therefore it was retained, having a 71.6% positive correlation with the first axis score. Under the MANOVA, site differences explained 95% of the variance; while nearest neighboring pen shell distance ($r^2 = 10.3\%$) had a significant effect on community structure (Table 1). Communities with similar densities

Table 1 Results from the MANOVA testing motile and sessile species community structure among different sites with nearest pen shell neighbor distance (NND) as a covariate

	η^2	<i>F</i>	<i>P</i> value
Motile species			
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

η^2 = proportion of the variance explained by the model. I present Pillai's trace as this statistic tends to be more conservative than Wilks' lambda

tended to have similar abundances and species compositions.

Sessile species abundance was also highly variable among pen shells and among sites; further, conditions in the surrounding sea grass beds (i.e., variance in sea grass density and blade length) did correlate with community structure patterns, but pen shell density did not influence community structure. The first four axes of the CCA explained 47.4% of the variance in sessile species abundance patterns. Environmental variables had a positive correlation (67.7%) 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); however, nearest neighbor distance had no significant effect.

The distribution patterns of both pen shell habitat and their sessile and motile epibionts varied considerably. Dead pen shells had a random distribution within sites, irrespective of quadrat size (Fig. 3a), so the habitat distribution itself was neither clumped nor over dispersed. None of the species on pen shells showed an over-dispersed distribution. The distribution patterns of 11 motile species were investigated, including 3 crabs, 3 gastropods, 2 amphipods, 1 polychaete, 1 isopod, and 1 shrimp (Fig. 3b). Motile species ranged in their index of dispersion, with the shrimp *Palaemon floridianus* and the amphipod *Dulichella appendiculata* having clumped distributions, and the rest having a random distribution. The distributions of nine sessile species were studied, including two polychaetes, two bryozoans,

and one of each of the following: an algae, sponge, oyster, barnacle, and ascidian (Fig. 3c). All but three of the sessile species had strong clumped distributions. 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 were site dependent; in some sites a species was clumped while in others it was randomly dispersed.

Discussion

Pen shell communities are highly diverse (per unit area) relative to the surrounding sea grass habitats, 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. However, pen shell community structure tends to vary among different sites of St. Joe Bay. Community structure has significant correlations with variables of sea grass bed quality (e.g., blade length). This suggests that although pen shell inhabitants live mostly in or on pen shells, factors affecting sea grass variation also affect pen shell community structure. This connection between sea grass beds and pen shell communities may be direct (e.g., inhabitants of pen shells directly benefiting from the surrounding sea grass) or indirect (e.g., pen shells and sea grass both benefiting from similar factors such as current and nutrients). St. Joe Bay's *T. testudinum* meadows can reduce water turbulence (Koch and Gust 1999), which would enhance propagule settlement on to pen shells. One explanation for this variation is that shell density seems to affect motile but not sessile species community structure.

While the effect of water flow on pen shell inhabitants is unclear, studies have shown the effect of pen shell densities on water flow, which in turn affects the surrounding macrofauna (e.g., Hewitt et al. 2002; Norkko et al. 2006). Hewitt et al. (2002) showed that macrofauna inhabiting muddy and sandy areas surrounding *Atrina zelandica* patches had a negative ($r^2 = 0.23$) relationship with pen shell densities in New Zealand. In these sites, *A. zelandica* densities are an order of magnitude greater than the densities found in St. Joe Bay; these high densities may be the reason behind the modification of water flow by pen shells and their influence on settling organisms in nearby areas (Norkko et al. 2006). The New Zealand sites have water velocities ranging from 0.05 to 0.35 m s⁻¹ (Hewitt et al. 2002) while in St. Joe Bay water flows much slower, at 0.027–0.045 m s⁻¹ (Koch and Gust 1999), which would also help explain the influence of *A. zelandica* density on the surrounding macrofauna diversity in New Zealand. However, these studies focused on

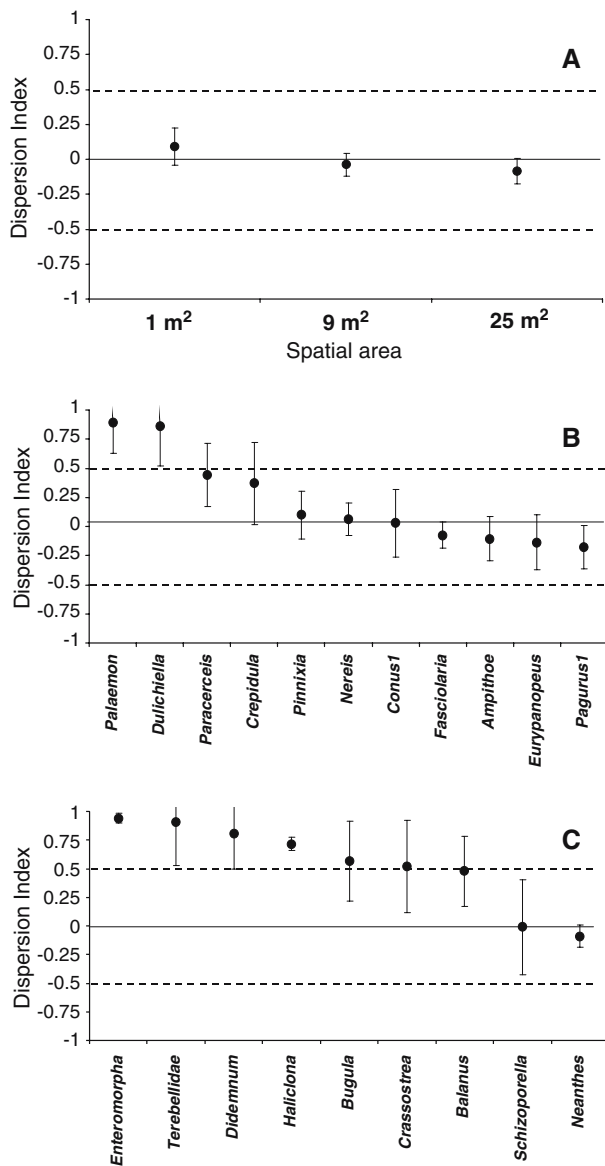


Fig. 3 Average index of dispersion of a pen shell habitats at three different spatial scales within the surveyed areas: 1, 9, and 25 m². Motile (b) and sessile (c) indices of dispersion for representative species. Dashed lines represent the 95% confidence interval around zero that delimits a random distribution. Points above 0.5 indicate a clumped distribution, and below -0.5 a uniform distribution. $N = 8$ different sites among St. Joe Bay, error bars represent one standard deviation. The full taxonomic names are available in Appendix 1

species living in the substrate adjacent to pen shells and not on dead pen shell inhabitants. If fauna not directly associated with pen shells are influenced by water flow, then it can be hypothesized that pen shell inhabitants are also affected, and this is reflected in the differences between motile and sessile species relationships with pen shell density. These differences between motile and sessile species suggest that pen shell inhabitants do not grow and disperse on the same spatial scales, which is a concept often over-

looked in community studies (e.g., Tilman 1994; Chase et al. 2005).

Pen shells represent an 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 grow and disperse at different spatial scales. The dispersion index was not correlated with taxon. For example one amphipod *Dulichella appendiculata* had a clumped distribution while another, *Ampithoe longimana*, had a random distribution. 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 in other habitats in different parts of the western Atlantic (Bousfield 1973; Sotka and Hay 2002), and *A. longimana* occurs at relatively high densities in the habitat surrounding pen shells. Field experiments have shown that motile species can colonize pen shells within a day of the shell becoming available (Munguia 2006; unpublished data), suggesting that pen shells are a limiting resource in St. Joe Bay. Juvenile snails, *Fasciolaria hunteria*, were found regularly in pen shells, which may provide them with a refuge from predation until they grow large enough to reach a size refuge. Sessile species tended to be crowded on shells but with no predictable dominant species, suggesting that pen shell habitat is limiting. However, even though shells accumulate species rapidly (Munguia 2004), there was always available space in shells. The toadfish (*Opsanus beta*), Florida Blenny (*Chasmodes saburrae*), and clingfish (*Gobiosox strumosus*) were 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 spatial variability 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 persist 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 and the results can be generalized to other systems (e.g., Keough 1984; Munguia 2004; Srivastava et al. 2004).

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