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Megafauna community composition associated with *Lophelia pertusa* colonies in the Gulf of Mexico

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ABSTRACT

The deep-water coral *Lophelia pertusa* provides habitat for diverse communities in the Gulf of Mexico. Photomosaics and analyses within a Geographic Information System (GIS) were used as non-destructive sampling tools to examine megafauna community composition associated with *L. pertusa* colonies on authigenic carbonate outcrops in two regions of the Gulf of Mexico. Megafauna communities associated with *L. pertusa* were more similar within a region than between regions. Within regions, the amount of dead coral, number of abiotic and biotic substrata, and percentage of live *L. pertusa* influenced the diversity, composition, and structure of the coral-associated communities. Elevated diversity levels in the communities associated with *L. pertusa* structure indicate that *L. pertusa* provides a distinct, localized habitat source. Outcrops with high proportions of dead *L. pertusa* harbored more higher order consumers than outcrops with primarily live coral framework.

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1. Introduction

Foundation species (sensu Dayton, 1972), such as reef-building corals and the kelp *Macrocystis pyrifera*, provide habitat, colonization opportunities, and increased local and regional habitat complexity. Different types of foundation fauna provide different forms of structure, and these distinct habitats often harbor distinct assemblages of associated organisms (Bruno and Bertness, 2001). Mixed assemblages of structuring organisms, such as those forming coral reefs, provide increased habitat heterogeneity and complexity, which affect the composition of the associated community and typically lead to higher diversity.

The deep-water coral *Lophelia pertusa* (*L. pertusa*) is a foundation species (Jonsson et al., 2004; Cordes et al., 2008) that is found throughout the world's oceans on topographic features, from depths ranging from 40 m (Freiwald and Roberts, 2005) to 2170 m (Cairns, 1979). *L. pertusa* requires a hard substrate such as carbonate rock to settle (Moore and Bullis, 1960). On the Upper Louisiana Slope of the Gulf of Mexico, authigenic carbonate is produced as an indirect byproduct of a coupled reaction between methane oxidation and sulfate reduction carried out by microbial consortia in seep sediments (Aharon and Fu, 2000; Boetius et al., 2000; Thiel et al., 2001). As a result, *L. pertusa* and other

deep-water corals are frequently found near areas of active hydrocarbon seepage in the Gulf of Mexico. However, corals appear to be limited to regions where hydrocarbon concentrations are at most slightly elevated above background levels (Hovland et al., 1998; Cordes et al., 2008) and current speeds are high enough to provide sufficient prey and prevent sedimentation on coral tissues (Frederiksen et al., 1992; Mortensen et al., 2001).

L. pertusa's anastomosing branches provide a large, stable structure, and host communities consisting of both coral-dependent and habitat-generalist fauna, including many other types of corals (e.g., octocorals and other scleractinians), other cnidarians, crustaceans, fishes, and polychaete worms (Reed et al., 2006; Roberts et al., 2006; Mortensen et al., 2008). In the northeast Atlantic, extensive communities of *L. pertusa*-associated fauna have been discovered that have diversity indices as high as those found in shallow-water coral communities (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Rogers, 1999). In the Atlantic and the Gulf of Mexico, these corals have been shown to provide important habitat for commercially important deep-sea fishes (Ross and Quattrini, 2007). Targeted physical sampling using a Bushmaster device to obtain standardized collections of *L. pertusa* colonies on the upper slope of the Gulf of Mexico found 64 species associated with the coral framework, of which at least three had well-identified relationships with the coral (Cordes et al., 2008).

In this study, we investigated the relationship between substrata and associated megafauna to determine which habitat characteristics influence the community composition, diversity, and structure across carbonate outcrops with *L. pertusa* present.

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We used a Geographic Information System (GIS) to analyze photomosaics created from high-resolution imagery obtained from two regions of the Gulf of Mexico. Megafauna were identified and their densities and coverage areas were quantified within each photomosaic. We expected that live and dead *L. pertusa* would host specific communities that differ from other hard-bottom and biogenic substrata.

2. Methods

2.1. Site descriptions

Photomosaics were assembled from nine locations at five sites in two regions in June 2004 and September 2005. Sites are named according to the Bureau of Ocean Energy Management, Regulation and Enforcement (BOEMRE) lease blocks in which they occur. Each site provided at least one photomosaic location. Two of the sites were within the Viosca Knoll (VK) region of the Gulf of Mexico, on the upper DeSoto Slope between 315 and 470 m depths (Table 1). Three sites were in the Green Canyon region on the Upper Central Dome and Basin region, more than 350 km west of Viosca Knoll, at depths of 500 and 535 m (Table 1).

The four photomosaics at the Viosca Knoll lease block 826 site (VK826) were obtained from the top and flanks of a knoll that rises approximately 100 m from the seafloor (Brooke and Schroeder, 2007; Cordes et al., 2008). Extensive *L. pertusa* colonies occur over an area of 600 × 300 m², including living coral growing from a dead coral framework. Aggregations of seep-related *Lamellibrachia luymesii* and *Seepiophila jonesii* tubeworms (Polychaeta: Siboglinidae) occur occasionally near coral colonies in this area (Cordes et al., 2006). Sediment, disarticulated shells, and carbonate rubble surrounded the outcrops selected as study sites. The single photomosaic at the Viosca Knoll 862 site (VK862) is on a topographic high of exposed carbonate rock. Scattered live *L. pertusa* thickets grow on large carbonate boulders with abundant anemones, *Callogorgia americana delta*, bamboo corals (Isididae), antipatharians, and an unidentified species of hexactinellid sponge. This area lacked visible seep megafauna.

The photomosaic in the Green Canyon 354 site (GC354) was obtained over a slope that descends from 520 to 560 m. Abundant authigenic carbonate boulders occur, along with occasional *L. pertusa* colonies (between 3–5 m in diameter and 2–3 m height) that consist primarily of dead coral and intermittent live coral branches extending from the framework. As the slope descends, carbonate outcrops support smaller *L. pertusa* colonies. There are also scattered vestimentiferan tubeworms around the periphery of the many carbonate outcrops near the base of the slope (Cordes et al., 2006). The two photomosaics within the Green Canyon 234 site (GC234)

were obtained along a single ridge approximately 100 m long at 500-m depth that contains colonies of *L. pertusa* with predominantly dead coral and live outer branches. Abundant *C. americana delta* gorgonians are also found on authigenic carbonate boulders in this site. A few colonies of scattered vestimentiferan tubeworms occur along the ridge. Corals and abundant chemosynthetic communities, dominated by tubeworms and mussels, occur a few hundred meters east of the ridge (MacDonald et al., 1990, 2003; Sager et al., 1999). Corals at the “Bush Hill” site in Green Canyon 185 (GC185) are located on the western edge of an active seep on an authigenic carbonate hillock approximately 40 m tall. There are several low-relief boulders colonized by *C. americana delta* and small colonies of mostly dead standing *L. pertusa*. Vestimentiferan tubeworms and bathymodiolin mussels with methanotrophic symbionts are abundant along the crest of the hill at approximately 540-m depth (MacDonald et al., 1989).

2.2. Image collection and analysis

All imagery was collected using a Canon PowerShot G2 digital camera encased in a pressure-safe housing and mounted on the side of the *Johnson-Sea-Link I* submersible perpendicular to the sea floor. Light for the images was provided by xenon arc lights. The submersible was maneuvered over haphazardly selected outcrops colonized by *L. pertusa* in a series of overlapping lines, while overlapping pictures were taken of the sea floor. The images within each line and the lines within the photomosaic overlapped one another by approximately 20%. Parallel lasers were spaced 10 cm apart and were visible in most images to provide a scale reference. The images were optimized using Photoshop CS2 autolevel, autocolor, and autocontrast settings to maximize image evenness and clarity. Optimized images were then assembled into photomosaics using a Matlab program (Pizarro and Singh, 2003) that seamlessly blends the overlapping edges of the images together to produce a composite image (Fig. 1A).

A scaling system was created for the photomosaics based on the presence of the parallel lasers in each image. The distance between the laser points in the images was measured using Photoshop CS2's measure tool for at least 10 images per photomosaic, and this distance was averaged and scaled to represent 10 cm. Photomosaics were imported into ArcGIS v 9.1 using the laser-derived scale in an undefined coordinate system. Each of the individual high-resolution images was hyperlinked to the photomosaic. The individual images have resolution sufficient to identify organisms and objects greater than 2 cm in size and were referenced to identify and digitize the fauna and abiotic substrata. Living, standing dead, and mixed live and dead *L. pertusa*, other habitat-forming corals (including bamboo corals, antipatharians, and gorgonians), carbonate rock, rubble

Table 1

Description of areas containing photomosaics. The first two letters of each area represent the region (GC=Green Canyon and VK=Viosca Knoll) and the numbers represent the BOEMRE lease block number. The species richness (number of taxa found in each of the study sites divided by the area of the outcrop in the photomosaic) included all fauna, and the Shannon diversity index (*H'*) and Pielou's evenness index (*J'*) were calculated for all organisms that were enumerated in the images.

Study site	Area (m ²)	Depth (m)	Latitude	Longitude	Area-weighted species richness (# m ⁻²)	Shannon Diversity (<i>H'</i>)	Pielou's Evenness (<i>J'</i>)
GC185	3.3	540	27°35.90'N	91°49.60'W	2.14	0.76	0.47
GC234a	10.2	509	27°44.81'N	91°13.44'W	1.37	0.85	0.35
GC234b	11.6	507	27°44.81'N	91°13.44'W	1.21	1.79	0.75
GC354	26.5	524	27°35.89'N	91°49.60'W	0.49	1.71	0.71
VK826a	45.9	465	29°09.50'N	88°01.07'W	0.33	1.99	0.75
VK826b	11.0	464	29°09.50'N	88°01.07'W	0.91	1.73	0.79
VK826c	9.9	470	29°10.21'N	88°00.72'W	1.01	1.74	0.79
VK826d	11.4	459	29°10.21'N	88°00.72'W	0.79	1.85	0.89
VK862	26.5	313	29°05.80'N	88°23.09'W	0.57	1.09	0.41

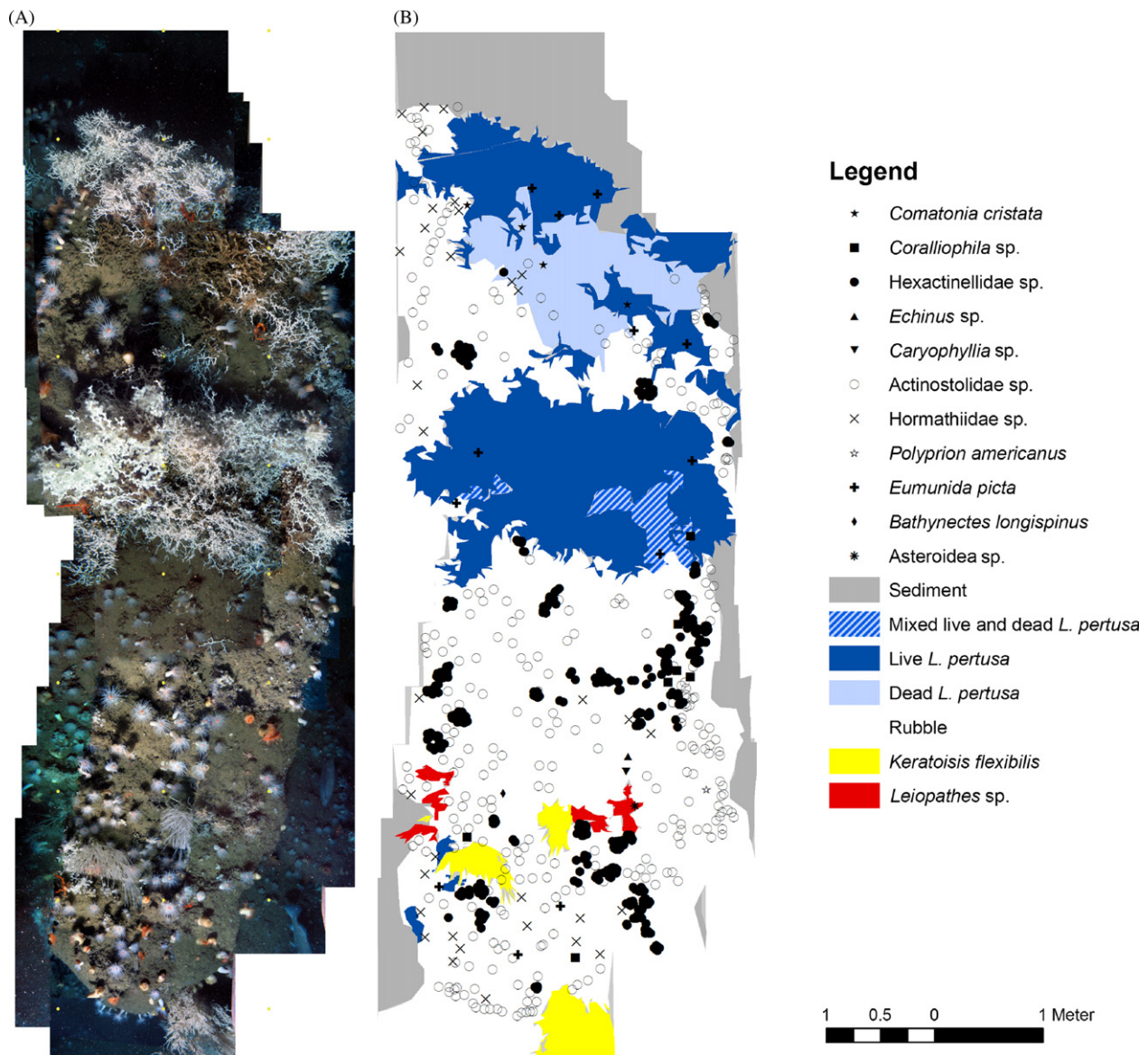


Fig. 1. A photomosaic in the Viosca Knoll 862 site. Fig. 1A is the completed photomosaic and Fig. 1B is a digitized version of the photomosaic.

(consisting of crushed dead coral and isolated small pieces of carbonate rock in sediment), bacterial mats, demospongiae sponges, and tubeworms were digitized as polygons and were analyzed as potential habitat sources (substrata) for mobile or non-colonial organisms. Small, solitary, or mobile fauna, including arthropods, fishes, anemones, solitary corals, sabellid polychaetes, snails, echinoderms, and a small hexactinellid sponge were digitized as points, as these organisms were not considered potential habitat sources (Fig. 1B). All assembled and digitized photomosaics are included as supplementary material, except for the one in the VK862 site, which is included as Fig. 1A and B. All fauna were identified to the lowest possible taxonomic level. Location-based queries were used to determine the distribution of the solitary fauna across each of the substrata.

2.3. Statistical analysis

Diversity was assessed as standardized species richness (calculated as the number of species present within a photo-

mosaic divided by the area of the photomosaic), as well as the Shannon diversity index (natural log scale) and Pielou's evenness index, using all organisms that could be enumerated in the images (excluding hydroids and *L. pertusa*). The Shannon index and Pielou's evenness were calculated using the DIVERSE application in PRIMER v. 5 software (Clarke and Warwick, 2001).

Similarity in community composition among regions and sites was examined using the Bray–Curtis similarity index in PRIMER v. 5 with presence/absence transformations to permit analysis of both solitary and colonial fauna. Multi-dimensional scaling plots and average linkage cluster analyses were used to determine which photomosaics were most similar to one another on the basis of community composition. The ANOSIM procedure in PRIMER was used to determine whether there were significant differences in community composition at sites between regions (Green Canyon versus Viosca Knoll) and among photomosaics within sites. We used the BIO-ENV analyses in PRIMER to test for relationships between community composition and habitat characteristics by comparing a similarity matrix of the community composition data across the photomosaics with similarity

matrices of all combinations of the habitat characteristics data. For all analyses, the percent hard substrata (including live and standing dead *L. pertusa*, carbonate rock, and rubble), percent live *L. pertusa*, percent standing dead *L. pertusa*, ratio of live to dead coral, percent abiotic substrata (including dead corals, rubble, and rock), number of substrata available, and depth and area covered by the photomosaic were considered as habitat characteristics.

Chi-square analyses were used to test whether there were significant associations between the enumerated fauna and substrata within a photomosaic. A general linear model in Minitab v. 12.21 with Tukey pairwise comparisons was used to examine differences in the Shannon diversity index among substrata within photomosaics.

Solitary fauna were divided into one of three trophic levels on the basis of feeding morphology: primary consumers, secondary consumers, and higher order consumers or scavengers. Least-squares regression was used to compare the proportion of primary to secondary and higher order consumers to habitat characteristics.

3. Results

3.1. Diversity and colonization trends

Thirty taxa were distinguished in the photomosaics (based on morphotypes), with each photomosaic containing between seven

and 15 taxa (Table 2). Of these taxa, 28 represent a single species. The exceptions included *Munidopsis* species and hydroids, which could not be differentiated to the species level in the images. Most photomosaic locations hosted the galatheoids *Eumunida picta* and *Munidopsis* spp., as well as *Odontozona edwardsi* shrimp (identified as *Stenopus* sp. in Cordes et al. (2008)), the solitary coral *Caryophyllia* sp., and cerianthid anemones. In the VK862 photomosaic, there were extremely high abundances of anemones, which included one morphotype of *Actinostolidae* and one morphotype of *Hormathiidae* (Table 2). A fish (*Polyprion americanus*) that has not been previously reported at Gulf of Mexico deep coral sites was also observed at the VK862 study site (Fig. 2). Chi-square analyses indicated that many of the fauna associated with coral communities were non-randomly distributed across substrata and identified positive associations between certain organisms and particular substrata (Figs. 3 and 4). In particular, *Munidopsis* spp. and *E. picta* crabs were strongly associated with dead coral and rubble (Figs. 3 and 4). There were also strong associations between the snail *Coralliophila* sp. and live coral (Fig. 4). Crinoids (*Comatonia cristata*) and *Echinus* spp. urchins were found within photomosaics with large amounts of living *L. pertusa*, which occurred primarily at the Viosca Knoll sites. Fishes were associated with various types of vertical relief, including mixed live and dead coral and carbonate rock. *Munidopsis* spp. crabs were associated with tubeworms when tubeworms were present, and were not observed at VK862, which was the only area where there are no tubeworms (Figs. 3 and 4).

Table 2

Distribution of organisms across photomosaics. The letter “p” indicates that an organism was present but not enumerated.

	GC185	GC234a	GC234b	GC354	VK826a	VK826b	VK826c	VK826d	VK862
Arthropoda: Crustacea									
<i>Bathynectes longispinus</i>				4		2			1
<i>Eumunida picta</i>		7	10	13	61	11	13	17	12
<i>Munidopsis</i> spp.	29	18	7	38	20		33	15	
<i>Odontozona edwardsi</i>		19	2	3	4		16	13	
Annelida									
Sabellidae sp.	69	614	31		35	30	10	30	
<i>Lamellibrachia luymesi</i>	p	p	p		p				
Chordata									
<i>Laemonema cf. goodebeanorum</i>	1	2		3	3				
<i>Hoplostethus</i> sp.		23	1						
<i>Urophycis</i> sp.		1							
<i>Polyprion americanus</i>									1
Cnidaria									
<i>Callogorgia americana</i>	1	4	2						
<i>Caryophyllia</i> sp.		50	33	1	1	2			1
<i>Leiopathes</i> spp.					10	3			5
<i>Keratois flexibilis</i>			15	1					4
<i>Lophelia pertusa</i>	p	p	p	p	p	p	p	p	p
<i>Muricides hirta</i>				8					
Cerianthidae sp.		13	2	5	16	2	13	23	
<i>Actinostolidae</i> sp.									284
<i>Hormathiidae</i> sp.					5				31
<i>Hydroidea</i> spp.		p	p						
Echinodermata									
<i>Comatonia cristata</i>					88	20	2		4
<i>Echinus</i> sp.					12	4	2	10	1
<i>Asteroidea</i> sp. 1			2						1
<i>Asteroidea</i> sp. 2							1	1	
<i>Asteroschema</i> sp.		8	1						
<i>Holothuroidea</i> sp.							1		
Mollusca: Gastropoda									
<i>Coralliophila</i> sp.					1			4	7
Porifera									
<i>Demospongiae</i> sp. 1				41	7				
<i>Demospongiae</i> sp. 2				1					
<i>Hexactinellidae</i> spp.	1					6			580

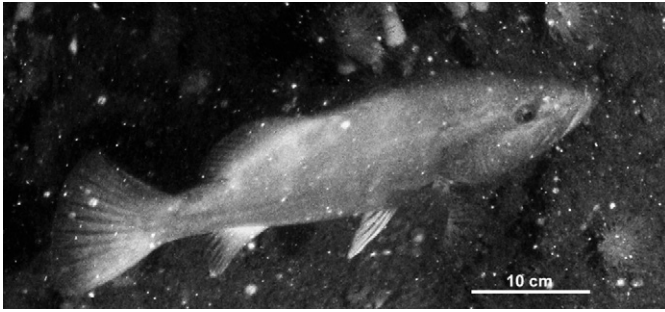


Fig. 2. The fish *Polyprion americanus* was observed at Viosca Knoll 862.

Other deep-sea background fauna, such as asteroids and the giant isopod *Bathynomus giganteus*, occasionally occurred in the sediment near the coral communities; however, the densities of these organisms were very low (less than 1 per 10 m squared). A survey of images and video taken from the surrounding sea floor at each photomosaic location showed mostly sediment, with very few visible megafauna.

3.2. Within-region analyses

MDS ordination and average linkage cluster analyses showed a separation of the photomosaics by region (Fig. 5), which was confirmed with an ANOSIM that found significant differences in community composition based on region (global $R=0.609$, $p=0.008$). As a result of this analysis and the presence of several confounded variables, including depth, proximity to actively seeping communities, and different current and nutritional input regimes, each region was further analyzed separately.

At Viosca Knoll, an ANOSIM test showed significant differences in community composition among photomosaics ($r=0.353$, $p=0.01$). All of the VK826 photomosaics were more similar to each other than to the photomosaic at VK862, and the strongest differences separated VK826a ($r=0.625$, $p=0.008$) and VK826b ($r=0.656$, $p=0.008$) from VK862. Community composition was not dependent on substrata within the photomosaics at Viosca Knoll (global $R=0.127$, $p=0.12$). The BIOENV analysis indicated that the percentage of standing dead coral within a study site was the strongest determinant of community composition ($R=0.964$, $p < 0.05$).

At Green Canyon, significant differences in community composition were detected among sites (one-way ANOSIM, global $R=0.335$, $p=0.04$), and there were differences among communities when substrata were considered as a factor (global $R=0.229$, $p=0.055$). The proportion of hard substrata available at a study site best explained the differences in community composition within Green Canyon ($R=0.464$), although this result was not significant ($p > 0.10$).

3.3. Within-site analyses

Shannon diversity indices of the communities of mobile megafauna varied significantly across substrata (General linear model, F statistic=9.01, $p < 0.001$; Fig. 6), with live and standing dead *L. pertusa* and rubble communities exhibiting higher diversity than bacterial mats, sponges, tubeworms, or other corals (including antipatharians, gorgonians, and scleractinians other than *L. pertusa*). Tukey pairwise comparisons demonstrated that both live and dead *L. pertusa* had significantly higher diversity indices than *Demospongiae* sp. ($p=0.001$, $p=0.002$, respectively), bacterial mats ($p=0.017$, $p=0.017$, respectively),

and other corals ($p < 0.001$, $p < 0.001$, respectively). Rubble hosted communities that had significantly higher Shannon diversity indices than sponges ($p=0.006$), tubeworms ($p=0.002$), and other corals ($p < 0.001$). Communities associated with dead corals also had significantly higher diversity indices than tubeworm communities ($p=0.006$).

The proportion of organisms in different trophic levels also varied among photomosaics (Fig. 7). Almost no higher order consumers were present in the VK862 photomosaic, but almost one third of the organisms present were secondary or higher order consumers in some Green Canyon photomosaics. Regression analysis revealed that study sites with greater proportions of dead coral hosted a higher frequency of higher order consumers ($T=12.17$, $p < 0.001$). There was no significant effect of area ($T=2.06$, $p=0.078$), region ($T=-0.68$, $p=0.52$), or percent hard substrata ($T=1.8$, $p=0.12$) on the abundance of fauna of higher trophic levels.

4. Discussion

Large bioherms of living and dead *L. pertusa* framework may persist for thousands of years, providing a long-lasting and stable habitat resource for communities of associated animals (Freiwald and Roberts, 2005). Photomosaics provide an opportunity for non-destructive examination of the distributions and associations among corals, other substrata, and the solitary megafauna in deep-water coral communities (Solan et al., 2002).

The Shannon diversity index was highest in living *L. pertusa*, which was followed by dead *L. pertusa* and rubble and then by carbonate rock across all photomosaics (Fig. 6). Mortensen et al. (1995) also found the highest diversity of organisms associated with dead and living coral, and Cordes et al. (2008) found a weak positive correlation between the proportion of live coral in a physical collection and the Shannon diversity index of that collection. However, the photomosaic at VK862 had the greatest amount of live coral and the highest standardized species richness but a low Shannon diversity index. The large number of rare species and very high abundance of actinostolid anemones found on carbonate rock and rubble resulted in a low Pielou's evenness value and accounted for the low Shannon diversity index. At 315 m this site is also shallower than the VK826 site, which lies between 459 and 470 m depth. In general, the study sites at Viosca Knoll contained higher amounts of live coral than those at Green Canyon, and also had higher species richness.

Cordes et al. (2008) suggested that the snail *Coralliophila* sp. and the shrimp *O. edwardsi* may be tightly associated with *L. pertusa* coral communities, because both are closely related to taxa that play important roles in shallow-water coral reefs. *Coralliophila* sp. was strongly associated with the presence of live *L. pertusa*, although one individual was found on carbonate rubble. This finding supports the suggestion that this snail, which is a known corallivore, may be consuming live coral and may be an obligate associate of live *L. pertusa*. *O. edwardsi* may play a similar role to that of other shrimps in the family Stenopodidae, which are common cleaner shrimp on reefs (Jonasson, 1987). These shrimp were found to be associated with carbonate rock, sponges, and dead or live corals, suggesting that if they are performing a cleaning function in deep-water coral communities, they may be attracted to species found within the three-dimensional structure, and may not be specifically associated with live corals.

Within each region, the amount of dead coral or hard substrata within the study sites were the variables that best explained the similarity among the communities of coral-associated fauna. In addition, at Green Canyon, the number of substrata (a measure of habitat heterogeneity) also had a strong impact on similarity of

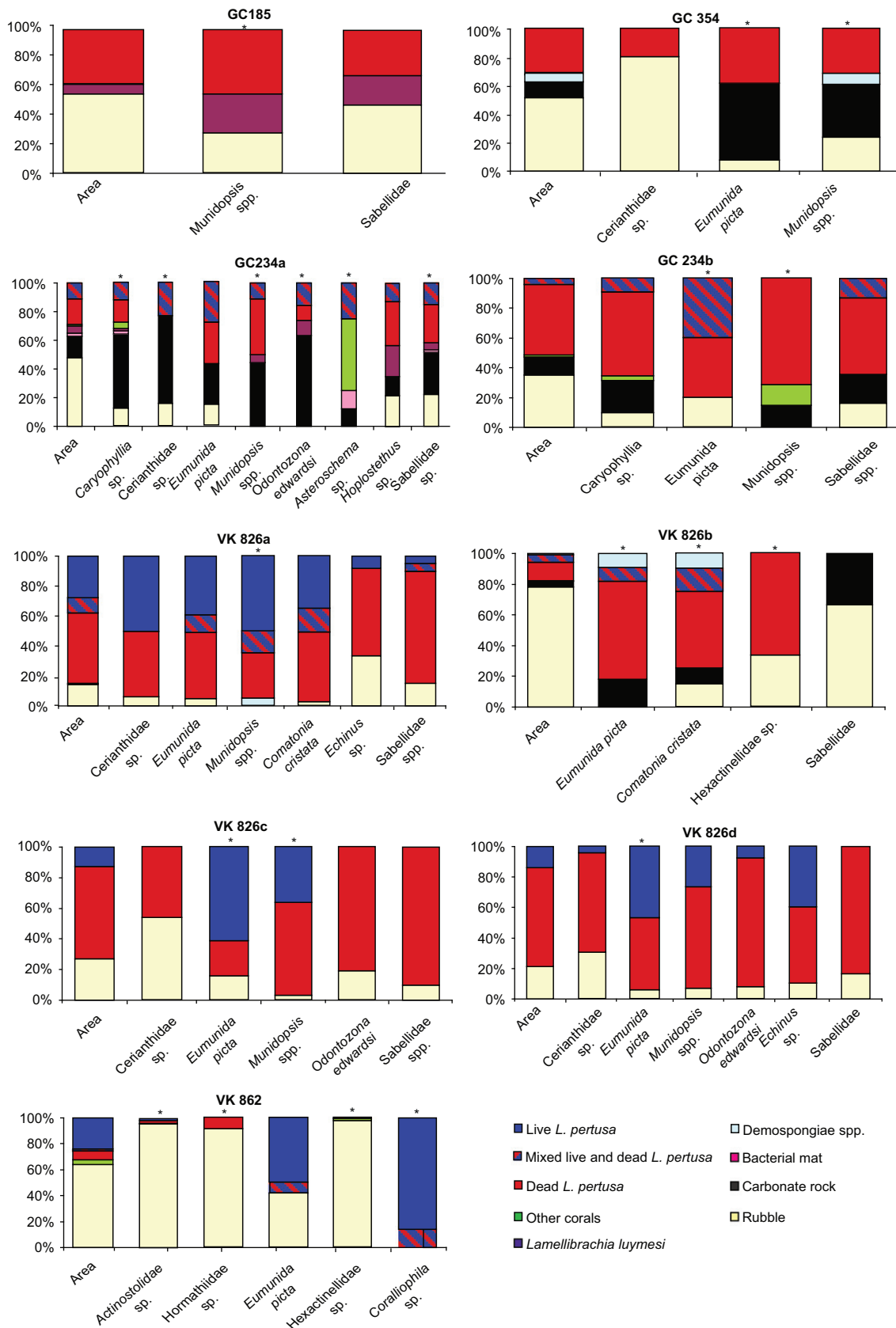


Fig. 3. Barcharts of the distribution of organisms across different substrata for each photomosaic. The first bar in each graph represents the percent area covered by each substratum, and the remaining bars indicate the percent distribution of solitary fauna across available substrata within a photomosaic location. Asterisks above the bars indicate significant non-random distributions across available substrata ($p < 0.05$). Only fauna that were found in numbers greater than six were included on the figure.

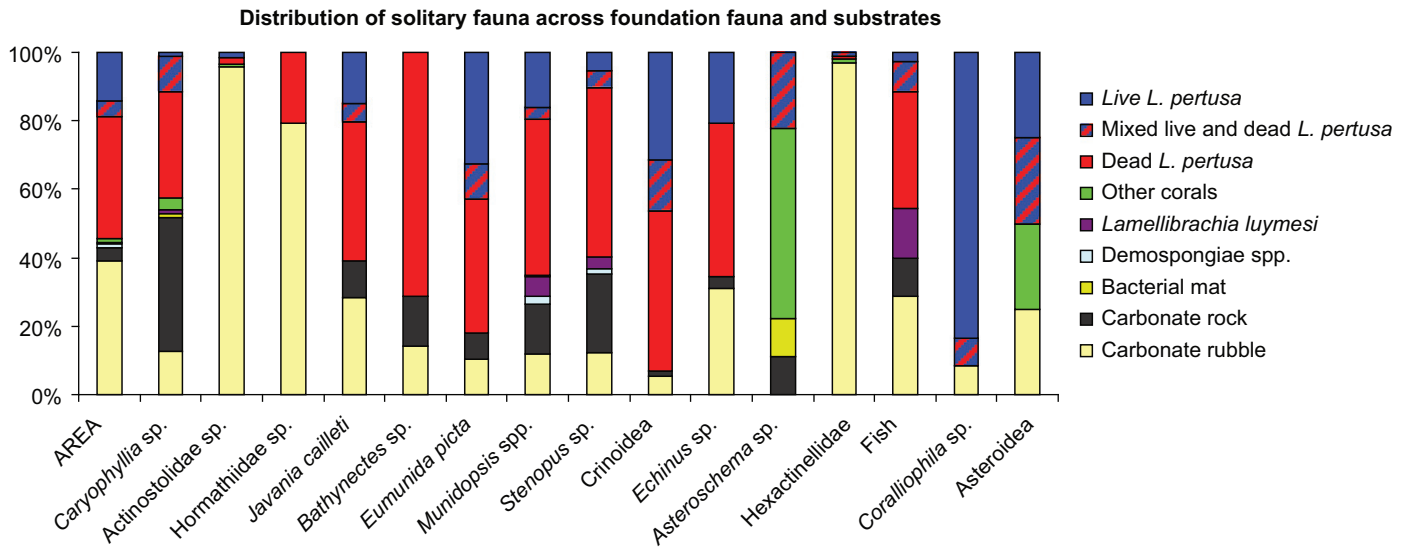


Fig. 4. Cumulative area covered by all substrata across all photomosaics and the cumulative distribution of solitary organisms across all photomosaics and substrata. Only solitary fauna that were found in numbers greater than six were included on the figure.

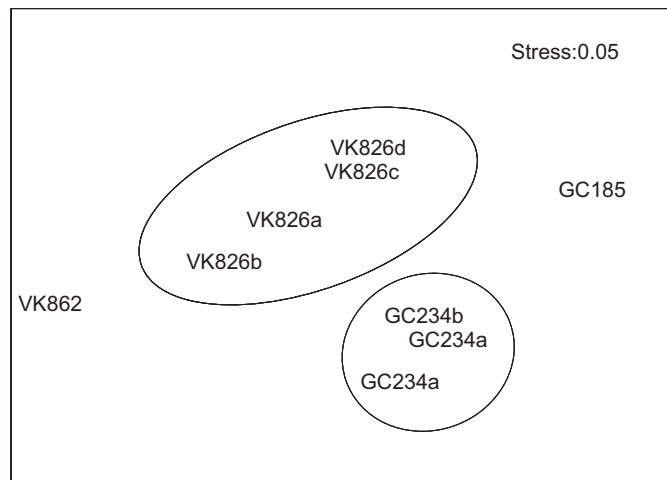


Fig. 5. Multi-dimensional scaling diagram of photomosaics based on the presence/absence of solitary and colonial fauna. Circled groups contain fauna that are at least 60% similar to one another.

community composition among photomosaics. Viosca Knoll is located near the Mississippi River outfall, and may receive different nutrient inputs than Green Canyon, which lies farther west. In addition, the depth differences across these regions coincide with the steepest gradients in chlorophyll *a* abundance (Baguley et al., 2006). Baguley et al. (2006) also report that the resulting higher nutrient input caused by this depth gradient and river input is reflected in the meiofaunal biomass in these regions, and the presence of some of the fauna at Viosca Knoll but not at Green Canyon may reflect this higher nutrient input.

At both Green Canyon and Viosca Knoll, the presence of hard, complex substrata in the form of live or standing dead *L. pertusa* within photomosaics led to a higher standardized species diversity and richness (Fig. 5). Increased habitat complexity has been shown to result in higher species richness and abundance of organisms in many systems (Bartholomew, 2000), including on continental slopes (Cordes et al., in press) by providing increased niche availability (O'Connor, 1991), increased surface area for settlement (Heck and Wetstone, 1977), and decreased competition among organisms

(Diehl, 1988). However, the effect of the structural complexity itself cannot be confounded with the effect of the identity of the particular substratum that is providing the complexity (McCoy and Bell, 1991). In this case, the positive relationship between the abundance of primary consumers and the proportion of live corals within photomosaics indicates that the substrata (here, live *L. pertusa* as opposed to dead *L. pertusa*) is correlated with community structure on these outcrops. This finding indicates that species richness is affected by not only the presence of hard substrata but specifically the identity of those substrata.

Previous studies of shallow-water corals have shown that declining live coral coverage is accompanied by a trophic shift (Johnson et al., 1995), which was attributed to fauna using the dead coral as a source of shelter for nearby foraging. Live and dead *L. pertusa* provide very similar habitat types: both are three-dimensional structures with smooth surfaces and interstitial spaces that may be used as a resource for both predators and prey. Henry and Roberts (2007) found higher proportions of filter/suspension feeders than higher order consumers on deep-water coral mounds in the NE Atlantic, which they attributed to the presence of the coral framework and the extensive vertical habitat heterogeneity. *L. pertusa* corals generally occur in areas with fast current speeds where particle encounter rates are very high (Thiem et al., 2006), providing an excellent environment for primary consumers including the filter and suspension feeders that were commonly associated with the presence of live coral in this study. Jonsson et al. (2004) also noted a higher abundance of filter/suspension feeders than predators on coral mounds, with higher order consumers and scavengers found on coral rubble nearby. This study lends additional support for the finding that dead corals and rubble on coral outcrops provide habitat for assemblages that are distinct from those found on live coral within the same outcrop, as higher abundances of predators may be using the structure as a shelter from which to hunt or forage.

L. pertusa acts as a foundation species in the Gulf of Mexico. Bruno and Bertness (2001) modify Dayton's (1972) definition of a foundation species as one that is influential, large, and has a positive effect on community inhabitants through its presence and not through its actions. *L. pertusa* fits this description through its provision of habitat to assemblages of large megafauna associated with the presence of living coral and the three-dimensional structure provided by dead coral or coral rubble.

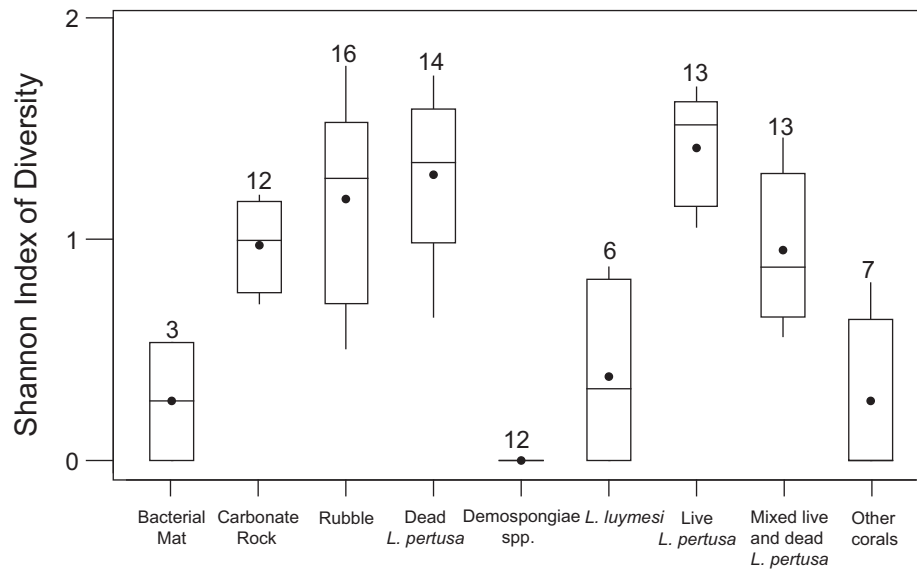


Fig. 6. Shannon diversity index across all of the substrata found within the photomosaics. Within each boxplot, the horizontal lines indicate the median of the data, the points indicate the mean, the box represents the interquartile range, and the whiskers indicate the maximum and minimum values of the data. The number of taxa observed on each substratum is listed above the boxplots.

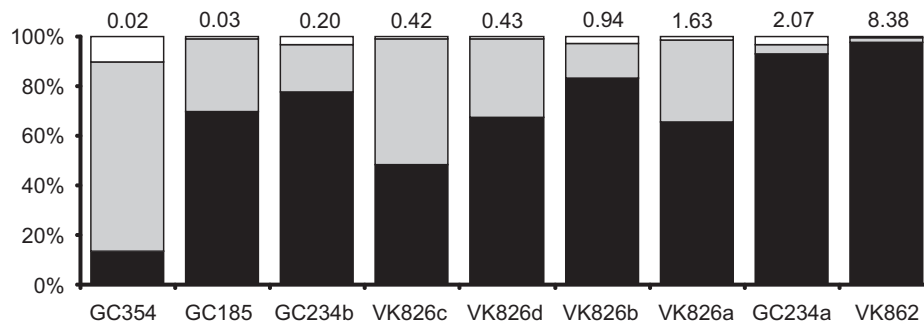


Fig. 7. Frequency of organisms within trophic levels at each photomosaic. Black represents primary consumers, gray indicates secondary consumers, and white represents higher order consumers. Photomosaics are listed in order of increasing live:dead coral ratio (the value listed above each column). GC354 has the lowest live:dead coral ratio and VK862 has the highest ratio.

The association of higher order consumers (i.e., predators and scavengers) with dead corals and coral rubble indicates that the effect of the coral reef goes beyond the presence of the reef itself and also may affect the community of organisms in the soft sediment or rubble surrounding the coral beds.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2010.05.013.

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