EPIFAUNAL ASSEMBLAGES ON DEEP-WATER CORALS IN ROATAN, HONDURAS

A Thesis

by

KATHERINE LAVELLE

Submitted to the Office of Graduate Studies of Texas A&M University
and Texas A&M University–Corpus Christi
in partial fulfillment of the requirements for the joint degree of

MASTER OF SCIENCE

August, 2012

Major Subject: Marine Biology

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Approved as to style and content by:

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ABSTRACT

EPIFAUNAL ASSEMBLAGES ON DEEP-WATER CORALS IN ROATAN, HONDURAS

(August, 2012)

Katherine Lavelle, B.S., State University of New York at Stony Brook

Co-Chairs of Advisory Committee: Dr. Thomas Shirley and Dr. John W. Tunnell, Jr.

Deep-water corals provide complex habitat structure for diverse assemblages of invertebrates and fishes. Similar to shallow coral reefs, oyster reefs, and seagrass beds, these complex biogenic structures serve many ecosystem functions: (a) as prey items; (b) sites for reproduction; (c) feeding stations, elevating suspension feeders above the benthos; and (d) refuges from predation. Because deep-sea corals provide some of the only three-dimensional habitats in the deep-sea, they may host distinct assemblages of epifauna. Non-destructive video surveys of deep-water coral assemblages were made to depths of 700 m at eight sites off Roatan, Honduras in May and December, 2011. Abundance, species richness, and distribution of epifauna were measured for 305 corals. We observed sixteen morphospecies of coral and twenty-six morphospecies of epifauna. Coral and epifaunal abundances were highest in the 335-449 m depth zone. Some epifauna had high fidelity for a single coral species or for a few species of similar morphological complexity. Other coral species had overlapping assemblages of habitat generalists. This is the first research on the biodiversity of deep-sea coral communities in Roatan, Honduras, and provides information on the assemblages, their depth distributions and ecological interactions.

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Introduction

Deep-water corals are biotic habitat structures often inhabited by diverse macrofaunal communities. Similar to shallow coral reefs and seagrass beds, deep-sea corals support more diverse assemblages of macrofauna and megafauna than bare substrate (Bergquist et al., 2003). These complex biotic structures serve many ecosystem functions: (a) prey (Harasewych and Sedberry, 2006; Krieger and Wing, 2002); (b) feeding stations above the benthos (Stone, 2006); (c) predation refuge; and (d) sites for reproduction (Baillon et al., 2012; Etnoyer and Warrenchuk, 2007). Deep-water corals provide some of the only biogenic habitat in the deep-sea and attract a high diversity of specialized and generalist fauna.

Deep-sea corals have a cosmopolitan distribution but require cold temperatures, moderate current flow, and hard substrate. With few sources of primary productivity, deep-water communities are dependent upon inorganic and organic matter, and phytodetritus originating from the surface waters (Roberts et al., 2009). This material is transported by currents and lateral advection. The slope of the continental shelf can influence the rate of delivery and amount of nutrients to these remote habitats. Depth distribution of corals is sometimes reflected in the distribution of associated fauna (chapter 2). Many aspects of the physical environment can affect the depth distribution of deep-sea coral communities.

The branched morphology of corals makes them ideal for capturing particulate matter from the water column. This in turn attracts a variety of epifaunal suspension feeders which use the coral structure to elevate themselves out of the benthic boundary layer, which is a better environment for deposit feeders. Mobile and sessile suspension feeders live on coral to get closer to a food source and to move above benthic predators. Juvenile echinoderms and crustaceans hide in the lattice framework of many coral to avoid predators. Some species attach egg sacs to coral for the same reason. Hundreds of species of epifaunal invertebrates and vertebrates are associated with deep-water corals (Raes and Vanresusel, 2006; Buhl-Mortensen and Mortensen, 2005).

All forms of symbiosis, including parasitism, have been reported for deep-sea corals. Some associations between coral and epifauna are species-specific symbioses while in others the coral provides a suitable habitat (Cho and Shank, 2010). Species-specific association and species distributions can create differences in beta diversity between coral habitats. In mutualistic relationships between coral and epifauna, the coral may benefit from being cleared of sediment and suspended matter. Many obligate symbionts require the coral skeleton as habitat and the coral is unaffected by their presence. Assemblages of species with similar ecological requirements are often consistently found on the same coral species. In addition to utilizing coral as a habitat structure or symbiotic host, epifauna can co-occur for reproductive reasons. Specific communities are also associated with the various stages of coral (i.e., living, dead, rubble). Because of the difficulty of deep-sea research, knowledge of the species associations in deep-sea communities is limited.

Many of the epifauna associated with coral are habitat generalists (Quattrini et al., 2012). In Roatan, we found that bythitid fish, galatheid crabs, and brisingid seastars are among the most conspicuous habitat generalists recorded near coral. Bythitid fish may have sublethal predation on epifauna within coral colonies. Juvenile galatheid crabs are often observed within scleractinian coral framework but adults live on bare substrate and various coral species. Brisingid seastars are deep-sea suspension-feeders recorded in all major ocean basins. As opportunistic suspension-feeders, brisingids probably compete with coral and epifauna for plankton and other suspended material. These large seastars have been observed on boulders, coral rubble and live coral. The co-occurrence of epifauna and corals can be a species-specific association or a function of species having the same resource requirements.

Non-destructive video surveys were made in Roatan, Honduras, a relatively unexplored region of the Caribbean Sea, to document the biodiversity of benthic megafauna and coral. The primary purpose of my research was to compare diversity of epifaunal assemblages from different coral substrates, depth zones and sites. The results of this research are contained within Chapter 2. The distribution, abundance, and habitat selection of the brisingid seastar *Novodinia antillensis* (A. H. Clark, 1934) is analyzed in detail in Chapter 3. This research represents the first analysis of deep-sea biodiversity in Roatan, Honduras.

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EPIFAUNAL ASSEMBLAGES ON DEEP-WATER CORALS IN ROATAN, HONDURAS

Introduction

Biogenic habitats support higher diversity macrofaunal communities than adjacent structurally simple environments (Bergquist et al., 2003). In the deep-sea, cold-water corals fill this role by providing complex habitat structure for diverse assemblages of crustaceans, fishes, echinoderms, and other cnidarians (Grassle et al., 1975; Krieger and Wing, 2002; Lessard-Pilon et al., 2010; McClain, 2007; O'Hara et al., 2011; Probert et al., 1997; Shank, 2010). Deep-sea corals function as biotic, three-dimensional structures which provide several important ecosystem functions: (a) food items for predators (Harasewych and Sedberry, 2006; Krieger and Wing, 2002; Mah and Foltz, 2011); (b) feeding stations, elevating suspension feeders above the benthic boundary layer (Krieger and Wing, 2002; Stone, 2006); (c) refuges from predation; and, (d) reproductive sites (Church and Buffington, 1966; Etnoyer and Warrenchuk, 2007).

The distribution of many deep-sea corals is limited to areas of enhanced current flow, cold temperatures, and hard substrate (Roberts et al., 2009). Reef-building scleractinia, sea fans, and black corals require stable, hard substrate for larvae to settle and grow into large colonies. They are often found in higher abundances in areas with faster currents. Currents deliver oxygen, suspended inorganic matter, and detrital food particles to the benthos and are influenced by topography, bathymetry, and location (Gage, 2003). The relative contribution of each of these physical variables can affect faunal depth zonation (Messing et al., 1990). In addition to creating an optimal physical environment for deep-water corals, currents affect the distribution of the fauna associated with corals. Deep-sea fauna have both planktotrophic and lecithotrophic larva; dispersal distance could in part be determined by currents and availability of settlement habitat. Currents and depth have pronounced effects on the biozonation of fauna on the continental shelf (Grassle et al., 1975; Rowe and Menzies, 1969; Wei et al., 2010).

Deep-water corals are oases for suspension feeders of the deep-sea. Because there is limited primary productivity in the deep-sea, deep-water organisms, including coral, are dependent on the delivery of phytodetritus and other organic matter sedimenting from surface waters (McClain, 2010). Particle flux to the benthos is episodic and subject to scavenging by pelagic organisms. Parts of the continental shelf with a steep slope often receive greater inputs of phytodetritus via downslope processes. Gently sloping areas will be more dependent on the lateral transport and resuspension of sedimented material by currents (Klitgaard et al., 1996). Branched coral structures erect in the water column capture particulate matter sedimenting from the surface waters. Coral also provide a refuge from predators in the benthic boundary layer. Competition between suspension feeders for food increases higher in the water column because plankton and resuspended material is more abundant in the benthic boundary layer (Wishner, 1980). The tradeoff of an accessible food source for a predation refuge could be important in determining which epifauna utilize corals.

Epifaunal distribution is dependent on physical factors, the availability of coral substrate, and biotic interactions. Competitive exclusion over habitat or prey may result in allopatry of competing epifaunal species. In preliminary observations at the study site, two chirostyloid crab species were rarely observed on the same coral colony but both species occurred on a variety of coral species. Predators may also alter the composition of an assemblage. Barnacles, anemones, and small mollusks frequently occur on sections of coral where coral polyps have been removed. This is likely an example of facilitation. These species cannot settle on a coral without another species first damaging the coral, probably through predation, and providing space for settlement. Community dynamics on biotic habitats are complex and vary between coral species, generating beta diversity.

Lophelia pertusa, a deep-water scleractinian with a cosmopolitan distribution, supports an abundance of habitat generalists (Lessard-Pilon et al., 2010; Quattrini et al., 2012). Only a fraction of deep-water scleractinian species are true constructional, framework-forming coral (Roberts et al., 2009). Framework-forming scleractinians may support more diverse assemblages of megafauna than gorgonians because they have greater volume and surface area, providing more microhabitats (Metaxas and Davis, 2005). Living *L. pertusa* grows on top of dead coral (often conspecifics) and is surrounded by rubble. These three microhabitats harbor distinct assemblages of smaller suspension feeders, detritivores and juvenile fauna (Roberts et al., 2009). Nematodes and other meiofauna may feed on the biofilm that grows on dead coral (Roberts et al., 2009). Higher diversity of invertebrates and distinct communities of meiofauna have been reported from dead coral and rubble (Frederiksen et al., 1992; Raes and Vanreusel, 2006). Rubble is a product of bioerosion by sponges and fungi and is very important to deep-water reef development and persistence (Roberts et al., 2009). Dynamic, three-dimensional habitats provided by corals are occupied by a variety of generalist and specialist fauna.

A higher diversity of fauna and a different set of functional groups are found on deep-sea corals compared to on bare substrate (Cordes et al., 2008). Symbiotic relationships between corals and epifauna have been documented for several species of fishes, gastropods, echinoderms, and crustaceans. Many of these species are suspension feeders but others are parasitic or corallivorous (Buhl-Mortensen and Mortensen, 2005; Krieger and Wing, 2002). The copepod, *Gorgonophilus canadensis*, is one of several parasites that specialize on octocorals (Buhl-Mortensen and Mortensen, 2004a). The polychaete *Eunice norvegica* is a non-obligate mutualist which cleans the host coral of sediment particles and strengthens the coral skeleton, but also steals food from polyps. Several ophiuroids have an obligatory symbiosis with deep-water corals at a species-specific level (Emson and Woodley, 1987; Grange, 1991; Mosher and Watling, 2009; Stewart, 1998). These relationships could be mutualistic or commensalistic in that the coral benefits by being 'cleaned' and the ophiuroid gains a predation refuge and elevation into the water column. Juvenile golden king crabs, rockfish, and shrimp utilize a variety of coral species as a habitat or predation refuge in the Gulf of Alaska (Krieger and Wing, 2002; Stone, 2006). The distribution of fauna on deep-water corals indicates that some species have highly specialized relationships while others are less restricted to specific substrates.

The integrity of deep-water coral communities is threatened by anthropogenic activities. Mining for precious metals, manganese, and sulfide could create sediment plumes and damage the endemic species on seamounts and hydrothermal vents (McClain, 2007; Roberts et al., 2009). Oil and gas exploration can disperse drilling muds and fragments across great distances on the seafloor (Roberts et al., 2009). The collapse of several fisheries on the continental shelf has led towards deeper species being targeted. Evidence of trawling and longline gear occurs in all oceans (Fosså et al., 2002; Probert et al., 1997; Stone, 2006). Trawl scars, displacement of coral, seafloor scouring, and coral bycatch are some of the detrimental effects of bottom-trawling. In order to preserve these deep-sea communities, coral conservation must be considered in fisheries management plans.

Deep-water corals are important as biogenic habitat for deep-sea megafauna. Megafauna-coral associations are determined by biological interactions, ecological requirements, and physical conditions. Knowledge of how these remote ecosystems function is improving with advances in ROV and submersible technology. Non-destructive video surveys were made in Roatan, Honduras, an unexplored region of the Caribbean Sea, to gather data on species diversity, abundance, and community composition. We aim to answer the following research questions.

1. What coral and epifaunal species are present in Roatan, Honduras?
2. How does the composition of epifaunal assemblages vary between coral species?
3. Are epifaunal assemblages similar across depth zones and sites?
4. What corals host the most diverse assemblages?
5. Do epifauna show host-specificity?

We expect that patterns in epifaunal assemblages on corals would be similar to what has been reported for the Gulf of Mexico and western Atlantic. These surveys provide baseline data which can be used in long-term monitoring programs for ecosystem health and coral conservation.

Material and Methods

Study Site: Roatan, Honduras

Isla Roatan is part of the Bay Islands archipelago in the southwestern Caribbean Sea. It is approximately 50 km north of mainland Honduras. The island is of volcanic origin and the continental slope is predominantly soft sediment and basalt and limestone boulders. The boulders are heterogeneous in size and distribution. The bottom topography has areas of steep walls, furrows, and low-slope, sediment-covered bottom. Roatan is on the southern edge of the Cayman Trough and surrounded by deep water. Approximately 20 km northeast of Roatan is the Bonacca Deep, a deep feature (5400 m) located at the base of the Cayman Trough escarpment (Banks and Richards, 1969; Pinet, 1976). The Bay Islands themselves lie on top of the Bonacca Ridge (Banks and Richards, 1969). The steep vertical relief surrounding the island permits rapid descent to bathyal depths.

Submersible Idabel

Video survey transects were completed using the *Idabel* submersible. *Idabel* is owned and operated out of Roatan, Honduras by Karl Stanley’s private company, Stanley Submarines. The submersible measures 3.9 x 2 x 2.1 meters. *Idabel* is equipped with redundant propulsion, manually operated emergency drop weights (350 lbs.), life support for three days, and a 76 cm diameter hemi-spherical viewport for passenger observation. The pilot stands with a 360° view through a series of nine 16 cm diameter portholes surrounding the conning tower. It is depth-rated to 1000 m and can carry two passengers in addition to the pilot. Two Sony HD Handycams (HDR-HC9) were used during each survey. One was mounted on the interior of the viewport mounted on a tripod affixed to the base of the viewport and the other was in an external housing mounted near the bow of the submersible. Lasers mounted 10 cm apart at the base of the housing for the external Handycam were used as a size reference. Still photos were taken from inside *Idabel* with a Canon SLR (Rebel T2i) connected to an external flash. A Seabird Seacat v 19 conductivity-temperature-depth-oxygen (CTD-O) profiler was mounted on the lower starboard side rail. *Idabel* is not equipped with a mechanical arm so a lightweight rod with a dip net was attached to the body in order to collect various invertebrates. The submersible operator had previously been successful with this technique.

Survey Transects

Idabel was towed offshore (~2 km) by a small boat to an approximate location and descended to a target maximum depth of 700 m. On dives nearer to shore, Idabel motored to and from its dock under its own power. Coordinates were recorded before the submersible descended. Video recording began at the seafloor and ended between 50-100 m. Detailed maps of the seafloor were not available so all transects were in the general direction of the launching dock. Ten dives were made but two were excluded from analysis because they were outside of the target depth range. Six dives were made in May 2011 and four dives were made in December 2011. All dives were on the northwestern end of Isla Roatan: Old Loafer’s, Anthony’s Key, Luna Beach, Half Moon Bay, Lawson’s Rock, Sueno del Mar, Sueno del Bahia, Gibson Bight (Figure 1). Sites were named for landmarks visible from the point of descent. Dives were made without replicates.

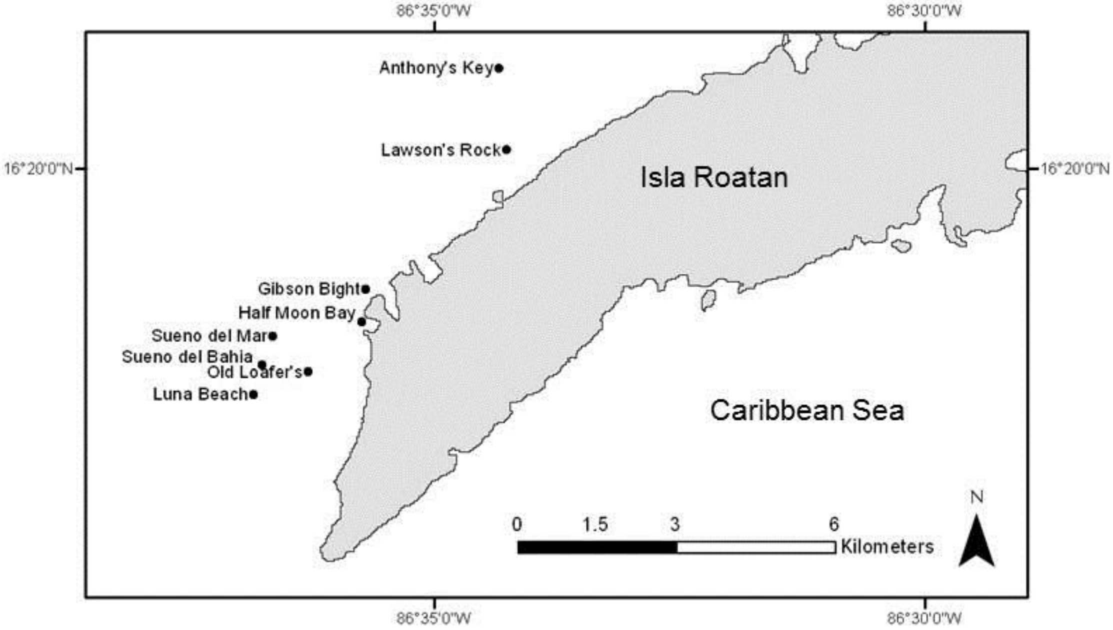


Figure 1. Map of survey sites in Roatan, Honduras.

Every five minutes, depth (m), temperature (°C), and time were recorded along with a landmark from that timecode (e.g., boulder with crab species A) (Etnoyer et al., 2011). Recording was continuous during transects in order to document observations which were not necessarily captured on the video monitor. These data logs were later used to assign depths to observed organisms and assemblages. During transects still images were taken of coral colonies, invertebrate epifauna, and any other interesting organisms happened upon. HD video footage was digitized using FinalCutPro 6.0.6. Frame grabs were made from digitized video to record habitat distribution, depth, abundance, and diversity of species. Few specimens were collected so species identifications were to a morphospecies level and made based on gross morphology and available ecological data. All fauna included in analysis were larger than 2 cm and assemblages were designated to include the host coral and all fauna on or within 1 m of the coral substrate.

Data analysis

Epifaunal assemblages were compared using a one-way incomplete blocking design ANOVA where coral substrate was the main effect and site and depth were the blocks (SAS 9.2). Differences in the following variables were examined with the GLM procedure: total number of species (S), total number of individuals (Tn), Simpson's diversity index ($\lambda = \Sigma P_i^2$), and Hill's diversity index ($N2 = 1/\lambda$). The sampling design was not haphazard or random, but it was limited by the availability of design criteria (i.e., not all corals were found in all depth zones or sites). A major assumption to the model was that there were no interactive effects, because of the limitation of design criteria. There were very few instances of replication. Discontinuities in faunal distributions were used to create four depth zones for analysis (150-334, 335-449, 450-549, 550-700 m).

Biodiversity measures

Species data was pooled for each unique coral assemblage (n=305). The Primer application, DIVERSE, was used to make biodiversity measures on the assemblages on corals (Clarke and Gorley, 2001). Total species (S) is the total number of species in each unique assemblage. N is the total number of individuals. Margalef's species richness (d) is calculated as $d = (s-1)/\log_e N$. Simpson's diversity index emphasizes dominant species: $1-\lambda = 1 - (\Sigma P_i^2)$. Hill's diversity number N2 was also calculated ($N2 = 1/\Sigma P_i^2$). Hill's

N2 represents the number of very abundant species in a sample. We repeated all of these measurements after averaging by sample (n=305).

Non-metric multidimensional scaling

Non-metric multidimensional scaling (MDS) was used because the assemblage data was non-normal. This technique was employed to compare assemblage composition between coral substrates, sites and depth zones. A square-root transformation was used to normalize the data because it is the least extreme. A Bray-Curtis similarity matrix, a measure of ecological distance, was then built from this transformed data. MDS ordination was run on the similarity matrix. MDS ordination represents samples in 2-dimensional space based on rank-order distances calculated from Bray-Curtis coefficients. Points close together on the MDS have similar species composition; points farther apart represent samples with different species composition. With this ordination method the ranked differences in species are preserved. All steps were repeated after averaging by sample. These analyses were used to detect patterns in species zonation, assemblage composition, and any patterns of depth distribution. The ANOSIM procedure was used to determine if there were significant differences in assemblages between coral substrates, sites, and depth zones (9999 permutations). Pairwise tests with an R statistic greater than 0.5 and a significance level (p) less than 5% were considered significant. Pairwise tests failed when both substrates had only 1 sample.

Results

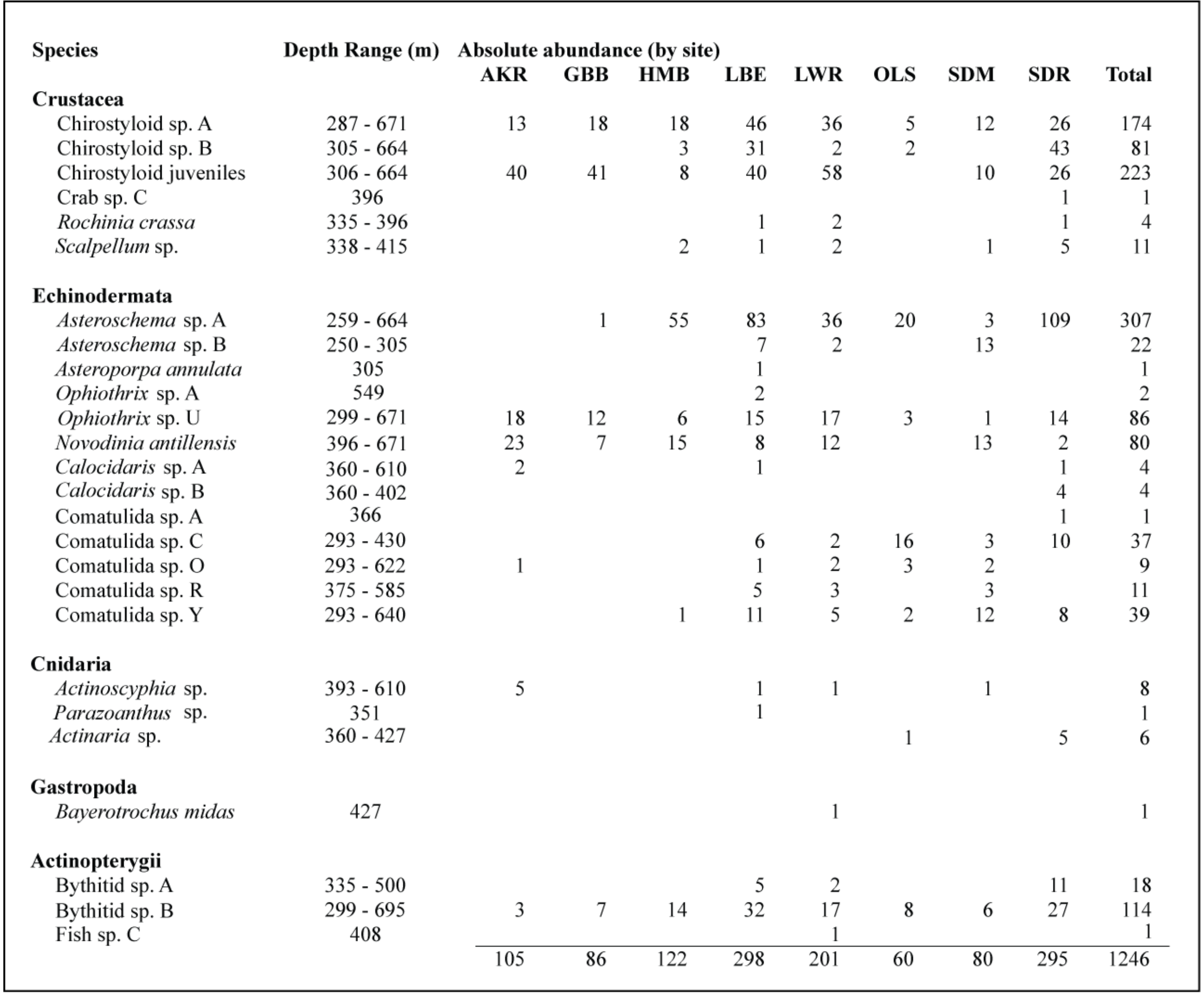
Species abundance and association

Sixteen morphospecies of coral and twenty-six morphospecies of epifauna were included in the analysis of epifaunal assemblages (Table 1 and 2). Many species were only identifiable to order or family level. Crustaceans and echinoderms had the most representatives, with six and fourteen species, respectively. Other groups included in analysis were the cnidarians, gastropods and fishes. Two distinct species of chirostyloid crabs (Superfamily: Chirostyloidea) were abundant, we suspect that the morphospecies referred to as chirostyloid sp. B is *Eumunida picta* (Smith, 1883). Crab sp. C is a decorator crab with a sponge on its carapace. *Rochinia crassa* (A. Milne-Edwards, 1879) is a distinct brachyuran crab found along the Atlantic Coast and in the Caribbean (Perry and Larsen, 2004). Gooseneck barnacles (*Scalpellum* sp.) were observed on the bare stalks of several coral species.

Table 1. Absolute abundance of coral morphospecies at study sites (AKR= Anthony's Key, GBB= Gibson Bight, HMB= Half Moon Bay, LBE= Luna Beach, LWR= Lawson's Rock, OLS= Old Loafer's, SDM= Sueno del Mar, SDR= Sueno del Bahia).

Species	**Depth Range (m)**	**Absolute abundance (by site)**								
Alcyonacea		**AKR**	**GBB**	**HMB**	**LBE**	**LWR**	**OLS**	**SDM**	**SDR**	**Total**
Acanthogorgia sp.	664		1							1
Chrysogorgiidae sp.	622 - 671		1	1		1				3
Corallium sp.	518 - 664	1	3	1	1					6
Isididae sp.	366 - 521		1						1	2
Paramuricea sp. P	305 - 671		2		31	28	2	3	12	78
Paramuricea sp. Y	250 - 664	1	2	16	16	11	3	2	30	81
Primnoidae sp. A	427 - 664	3	1	1	11	9		2		27
Primnoidae sp. B	610 - 671	2	1		2					5
Antipatharia										
Antipatharia sp.	335 - 640	4	1	6	3	1		3	3	21
Antipathes sp.	287 - 372		3		4	2	3	3	8	23
Bathypathes sp.	335 - 695	1	1	3	5		1			11
Plumapathes sp.	381 - 610	1			7	2			4	14
Scleractinia										
Dendrophyllia alternata	366 - 500				4	7		1	12	24
Enallopsamia sp.	664		1							1
Lophelia pertusa	351 - 664		1		1	1		2	2	7
Madrepora sp.	625		1							1
		13	20	28	85	62	9	16	72	305

Table 2. Absolute abundance of epifaunal species at study sites (AKR= Anthony's Key, GBB= Gibson Bight, HMB= Half Moon Bay, LBE= Luna Beach, LWR= Lawson's Rock, OLS= Old Loafer's, SDM= Sueno del Mar, SDR= Sueno del Bahia).



Species	**Depth Range (m)**	**Absolute abundance (by site)**								
		AKR	**GBB**	**HMB**	**LBE**	**LWR**	**OLS**	**SDM**	**SDR**	**Total**
Crustacea										
Chirostyloid sp. A	287 - 671	13	18	18	46	36	5	12	26	174
Chirostyloid sp. B	305 - 664			3	31	2	2		43	81
Chirostyloid juveniles	306 - 664	40	41	8	40	58		10	26	223
Crab sp. C	396								1	1
Rochinia crassa	335 - 396				1	2			1	4
Scalpellum sp.	338 - 415			2	1	2		1	5	11
Echinodermata										
Asteroschema sp. A	259 - 664		1	55	83	36	20	3	109	307
Asteroschema sp. B	250 - 305				7	2		13		22
Asteroporpa annulata	305				1					1
Ophiothrix sp. A	549				2					2
Ophiothrix sp. U	299 - 671	18	12	6	15	17	3	1	14	86
Novodinia antillensis	396 - 671	23	7	15	8	12		13	2	80
Calocidaris sp. A	360 - 610	2			1				1	4
Calocidaris sp. B	360 - 402								4	4
Comatulida sp. A	366								1	1
Comatulida sp. C	293 - 430				6	2	16	3	10	37
Comatulida sp. O	293 - 622	1			1	2	3	2		9
Comatulida sp. R	375 - 585				5	3		3		11
Comatulida sp. Y	293 - 640			1	11	5	2	12	8	39
Cnidaria										
Actinoscyphia sp.	393 - 610	5			1	1		1		8
Parazoanthus sp.	351				1					1
Actinaria sp.	360 - 427						1		5	6
Gastropoda										
Bayerotrochus midas	427					1				1
Actinopterygii										
Bythitid sp. A	335 - 500				5	2			11	18
Bythitid sp. B	299 - 695	3	7	14	32	17	8	6	27	114
Fish sp. C	408					1				1
		105	86	122	298	201	60	80	295	1246

Two species of *Asteroschema* sp. ophiuroid brittle stars were wrapped around coral colonies. Five morphospecies of comatulid crinoids (unstalked) were observed during survey transects. Two species of urchins and one brisingid seastar were also present. Cnidarians included the Venus-flytrap anemone *Actinoscyphia* sp., the colonial zoanthid *Parazoanthus* sp., and an actinarian anemone *Actinaria* sp. Several slit shells were observed, but only one, *Bayerotrochus midas*, was observed on coral. Three species of fishes were observed amongst coral colonies, two from the family Bythitidae and one unknown species (fish sp. C).

The sixteen coral morphospecies included in analysis represent the orders Alcyonacea, Antipatharia, and Scleractinia. We were able to identify species from the following families: Acanthogorgiidae, Antipathidae, Schizopathidae, Chrysogorgiidae, Corallidae, Dendrophyllidae, Isididae, Caryophyllidae, Oculinidae, Plexauridae and Primnoidae. The zoanthid, *Parazoanthus* sp., was considered an epibiont because it was observed growing on top of other corals. Sixty-six percent of coral substrates with epifaunal assemblages were observed between 335-449 m, and 22 percent were between 550-700 m. The most abundant corals were *Paramuricea* sp. Y, *Paramuricea* sp. P, and Primnoidae sp. A (26.6%, 25.6%, and 8.9%, respectively). The rarest corals were *Acanthogorgia* sp., *Enallopsamia* sp., *Madrepora* sp., Isididae sp., and Chrysogorgiidae sp.

Table 3. Coral species distribution by depth zone.

Coral substrate	**Depth zone (m)**				
	150-334	**335-449**	**450-549**	**550-700**	**Total**
Alcyonacea					
Acanthogorgia sp.				1	1
Chrysogorgiidae sp.				3	3
Corallium sp.			1	5	6
Isididae sp.		1	1		2
Paramuricea sp. P	1	75		2	78
Paramuricea sp. Y	7	67	4	3	81
Primnoidae sp. A		1	7	19	27
Primnoidae sp. B				5	5
Antipatharia					
Antipatharia sp.		5	3	13	21
Antipathes sp.	7	16			23
Bathypathes sp.		1		10	11
Plumapathes sp.		11	1	2	14
Scleractinia					
Dendrophyllia alternata		21	3		24
Enallopsamia sp.				1	1
Lophelia pertusa		3		4	7
Madrepora sp.				1	1
	15	201	20	69	305

The most abundant epifaunal species were *Asteroschema* sp. A, chirostyloid juveniles, chirostyloid sp. A, and bythitid sp. B, respectively. The rarest species included crab sp. C, *Asteroporpa annulata*, comatulid sp. A, *Bayerotrochus midas*, and fish sp. C.

Many species had restricted distributions (Table 4). *Asteroschema* sp. A occurred only on two color morphs of a paramuriceid coral (76.2% on *Paramuricea* sp. Y, 23.8% on *Paramuricea* sp. P, Appendix 1). Chirostyloid juveniles were observed on Primnoidae sp. A and *Lophelia pertusa* (54.3% and 17.5%, respectively). Chirostyloid sp. A was predominantly found on Primnoidae sp. A corals and *Paramuricea* sp. Y (27.6% and 20.1%, respectively). Bythitid sp. B was most often found associated with *Paramuricea* sp. Y, Primnoidae sp. A and *Antipathes* (30.7%, 17.5%, and 14.9%, respectively). Fifty percent of the *Novodinia antillensis* that were associated with corals were with Primnoidae sp. A and 20% were near *Lophelia pertusa*. The brittle star *Ophiothrix* sp. U was most often observed in the branches of *Antipathes* sp. and Primnoidae sp. A (33.7% and 32.6%, respectively). Comatulid sp. C was associated with *Antipathes* sp. and *Paramuricea* sp. Y (56.8% and 24.3%, respectively). Comatulid sp. Y was another abundant crinoid but occurred on various corals. All crinoids were abundant on sponges. Many of the epifauna species we observed were also found on bare substrate; however those individuals were not included in analysis because only the epifaunal assemblages on coral were being analyzed.

Table 4. Relative abundance of epifauna on coral substrates.

Epifauna species	**Coral substrate**					
Crustacea	*Acanthogorgia* sp.	Antipatharia sp.	*Antipathes* sp.	*Bathypathes* sp.	Chrysogorgiidae sp.	*Corallium* sp.
Chirostyloid sp. A		12.6	6.9	5.2	2.3	4
Chirostyloid sp. B		1.2	19.8			
Chirostyloid juveniles	0.4	1.8	0.4			5.8
Crab sp. C						
Rochinia crassa			25			
Scalpellum sp.						
Echinodermata						
Asteroschema sp. A						
Asteroschema sp. B						
Asteroporpa annulata						
Ophiothrix sp. A			100			
Ophiothrix sp. U						
Novodinia antillensis	1.2	9.3	33.7			4.7
Calocidaris sp. A						15
Calocidaris sp. B				25		25
Comatulida sp. A			25			
Comatulida sp. C						
Comatulida sp. O			56.8			
Comatulida sp. R			55.6			
Comatulida sp. Y						45.5
Cnidaria		7.7	43.6			
Actinoscyphia sp.						
Parazoanthus sp.		25				
Actinaria sp.						
Gastropoda						
Bayerotrochus midas						
Actinopterygii						
Bythitid sp. A						
Bythitid sp. B			33.3			
Fish sp. C		7.9	14.9	3.5		1.8

Epifauna species	**Coral substrate**					
Crustacea	*Dendrophyllia alternata*	*Enallopsamia* sp.	Isididae sp.	*Lophelia pertusa*	*Madrepora* sp.	*Paramuricea* sp. P
Chirostyloid sp. A	1.1		1.1		1.7	12.1
Chirostyloid sp. B	14.8			17.3		18.5
Chirostyloid juveniles	8.5			17.5	2.7	0.4
Crab sp. C				100		
Rochinia crassa						25
Scalpellum sp.						36.4
Echinodermata						
Asteroschema sp. A						23.8
Asteroschema sp. B						4.5
Asteroporpa annulata						
Ophiothrix sp. A						
Ophiothrix sp. U			2.3			
Novodinia antillensis		2.5		20		2.5
Calocidaris sp. A						
Calocidaris sp. B				25		
Comatulida sp. A			100			
Comatulida sp. C	5.4			5.4		2.7
Comatulida sp. O	11.1					
Comatulida sp. R	9.1			9.1		
Comatulida sp. Y	7.7			12.8		5.1
Cnidaria						
Actinoscyphia sp.						
Parazoanthus sp.						100
Actinaria sp.						33.3
Gastropoda						
Bayerotrochus midas	100					
Actinopterygii						
Bythitid sp. A	11.1			22.2		22.2
Bythitid sp. B	7.9		2.6	1.8		9.6
Fish sp. C						

Epifauna species	**Coral substrate**			
Crustacea	*Paramuricea* sp. Y	*Plumapathes* sp.	Primnoidae sp. A	Primnoidae sp. B
Chirostyloid sp. A	20.1	5.2	27.6	
Chirostyloid sp. B	18.5	6.2	3.7	
Chirostyloid juveniles	4.9	0.9	54.3	2.2
Crab sp. C				
Rochinia crassa	50			
Scalpellum sp.	63.6			
Echinodermata				
Asteroschema sp. A	76.2			
Asteroschema sp. B	95.5			
Asteroporpa annulata				
Ophiothrix sp. A			100	
Ophiothrix sp. U	5.8	1.2	32.6	9.3
Novodinia antillensis	1.3		50	8.8
Calocidaris sp. A	25		25	
Calocidaris sp. B	50			
Comatulida sp. A				
Comatulida sp. C	24.3	5.4		
Comatulida sp. O	11.1		22.2	
Comatulida sp. R			36.4	
Comatulida sp. Y	2.6	15.4	2.6	2.6
Cnidaria				
Actinoscyphia sp.		12.5	62.5	
Parazoanthus sp.				
Actinaria sp.	33.3	33.3		
Gastropoda				
Bayerotrochus midas				
Actinopterygii				
Bythitid sp. A	5.6	5.6		
Bythitid sp. B	30.7	1.8	17.5	
Fish sp. C	100			

Site and depth distribution

Many species had a depth range exceeding 300 m: *Asteroschema* sp. A, bythitid sp. B, chirostyloid sp. A, *Ophiothrix* sp. U, chirostyloid sp. B, chirostyloid juveniles, comatulid sp. Y, and comatulid sp. O. Differences in depth zonation existed at all sites and most epifauna were observed in the 335-449 m and 550-700 m depth zones (64.8% and 22.8%, respectively; Figure 2). The sites with the most corals and epifauna were Luna Beach, Sueno del Bahia, and Lawson's Rock. In general coral and fauna were distributed randomly across transects but dense assemblages of corals such as *Paramuricea* sp. Y and P and *Dendrophyllia alternata* were observed on the tops and sides of tall boulders. Salinity and temperature data from CTD casts were similar between dives and expeditions (Appendix 1 and 2). Salinity, temperature, and pH all decreased with depth.

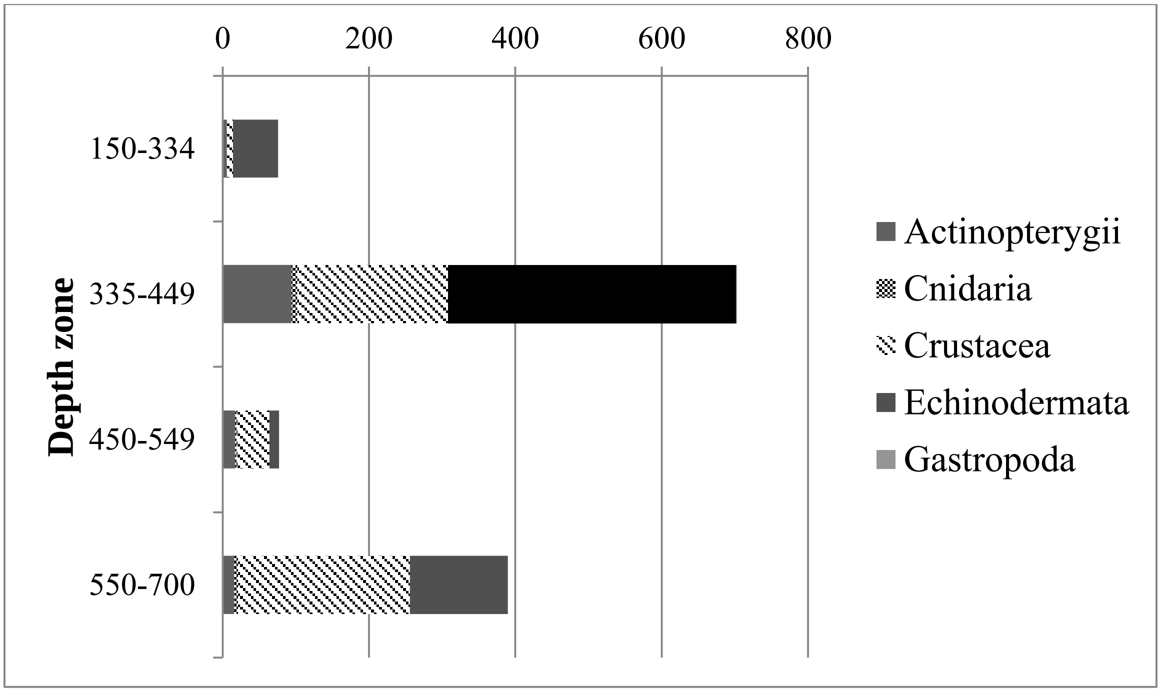
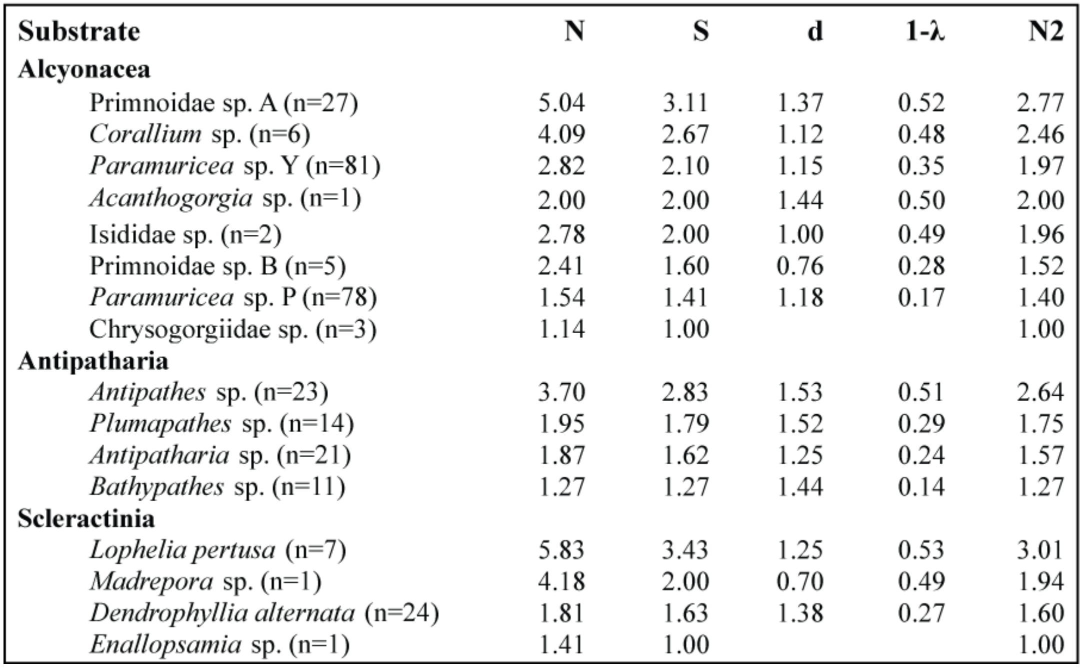


Figure 2. Absolute abundance of epifauna by depth zone.

Diversity trends

Species richness (S) was highest in *Lophelia pertusa* (3.43), Primnoidae sp. A (3.11), *Corallium* sp. (2.67) and *Antipathes* sp. (2.83) **(**Table 5). Substrates which hosted the greatest number of individuals (N) were *Lophelia pertusa* (Appendix 3), Primnoidae sp. A (Appendix 4), *Corallium* sp. (Appendix 5), and *Madrepora* sp. Margalef's species richness index (d) was highest for *Plumapathes* sp., *Antipathes* sp., *Acanthogorgia* sp., and *Bathypathes* sp. Simpson's diversity values (1-λ) were highest in *Lophelia pertusa* (0.53), Primnoidae sp. A (0.52), and *Antipathes* sp. (0.51). Hill's diversity number two (N2) was highest for *Lophelia pertusa* (3.01), Primnoidae sp. A (2.77), *Antipathes* sp. (2.64) and *Corallium* sp. (2.46).

Table 5. Averaged biodiversity measures for coral morphospecies (N=total individuals, S=species richness, d=Margalef's species richness, 1- λ = Simpson's diversity, N2=Hill's number 2).



Substrate	**N**	**S**	**d**	**1-λ**	**N2**
Alcyonacea					
Primnoidae sp. A (n=27)	5.04	3.11	1.37	0.52	2.77
Corallium sp. (n=6)	4.09	2.67	1.12	0.48	2.46
Paramuricea sp. Y (n=81)	2.82	2.10	1.15	0.35	1.97
Acanthogorgia sp. (n=1)	2.00	2.00	1.44	0.50	2.00
Isididae sp. (n=2)	2.78	2.00	1.00	0.49	1.96
Primnoidae sp. B (n=5)	2.41	1.60	0.76	0.28	1.52
Paramuricea sp. P (n=78)	1.54	1.41	1.18	0.17	1.40
Chrysogorgiidae sp. (n=3)	1.14	1.00			1.00
Antipatharia					
Antipathes sp. (n=23)	3.70	2.83	1.53	0.51	2.64
Plumapathes sp. (n=14)	1.95	1.79	1.52	0.29	1.75
Antipatharia sp. (n=21)	1.87	1.62	1.25	0.24	1.57
Bathypathes sp. (n=11)	1.27	1.27	1.44	0.14	1.27
Scleractinia					
Lophelia pertusa (n=7)	5.83	3.43	1.25	0.53	3.01
Madrepora sp. (n=1)	4.18	2.00	0.70	0.49	1.94
Dendrophyllia alternata (n=24)	1.81	1.63	1.38	0.27	1.60
Enallopsamia sp. (n=1)	1.41	1.00			1.00

One-way ANOVA

Species richness differed between coral substrates and depth zones (p=0.0001, p=0.0472, Table 6). The total number of individuals also varied significantly between substrates. Species diversity (Simpson's Index, Hill's N2) also varied between substrate and depth. Hill's diversity was also significantly different between coral substrates and depth zones. Significantly different sources were not detected using the Tukey post-hoc test. There were no localized regions of extremely high or low diversity.

Table 6. Results from a one-way ANOVA (y = Substrate Site Depth).

Source	Coral substrate		Site		Depth	
Variable	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*
Species Richness	6.74	0.0001	1.57	0.1429	2.68	0.0472
Total Individuals	6.34	0.0001	1.58	0.1425	1.07	0.3622
Simpson's Diversity Index	4.02	0.0001	0.64	0.7238	2.88	0.0364
Hill's N2	4.06	0.0001	1.08	0.3743	3.62	0.0136

Non-metric multidimensional scaling

Epifaunal assemblages did not vary among the sites (Figure 3, Appendix 7, global R=0.038, p=0.2), but did vary with depth. The assemblages occurring in the depth zone of 335-449 m had little overlap with the assemblages occurring from 550-700 m (Figure 4, Appendix 8, global R=0.207, p=0.01). The assemblages found in the zone at 450-549 m included species from both the deepest zone and the shallower zone. Some assemblages were affiliated with coral substrates (Figure 5). Primnoidae sp. A, Primnoidae sp. B, and *Paramuricea* sp. Y had the most distinct assemblages. Other coral substrates, e.g., *Dendrophyllia alternata*, did not have a distinct assemblage associated with it. *Antipathes* sp. coral had mixed assemblages with species also found in *Dendrophyllia alternata*, Primnoidae sp. A, *Plumapathes* sp., and *Paramuricea* sp. Y. Substrates had overlapping assemblages and some had very different assemblages

(ANOSIM; Appendix 9, global R=0.364, p=0.01). The following pairs of substrates had very different assemblages (R>0.7): *Bathypathes* sp. – *Lophelia pertusa* (R=0.797, p=0.01); *Bathypathes* sp. – Primnoidae sp. B (R=0.818, p=0.03); Chrysogogiidae sp. – *Lophelia pertusa* (R=0.792, p=0.8); *Enallopsamia* sp. – *Paramuricea* sp. Y (R=0.789, p=1.3); *Enallopsamia* sp. – Primnoidae sp. A (R=0.728, p=3.6); *Lophelia pertusa* – *Paramuricea* sp. Y (R=0.716, p=0.01); and Paramuricea sp. Y – Primnoidae sp. B (R=0.744, p=0.01).

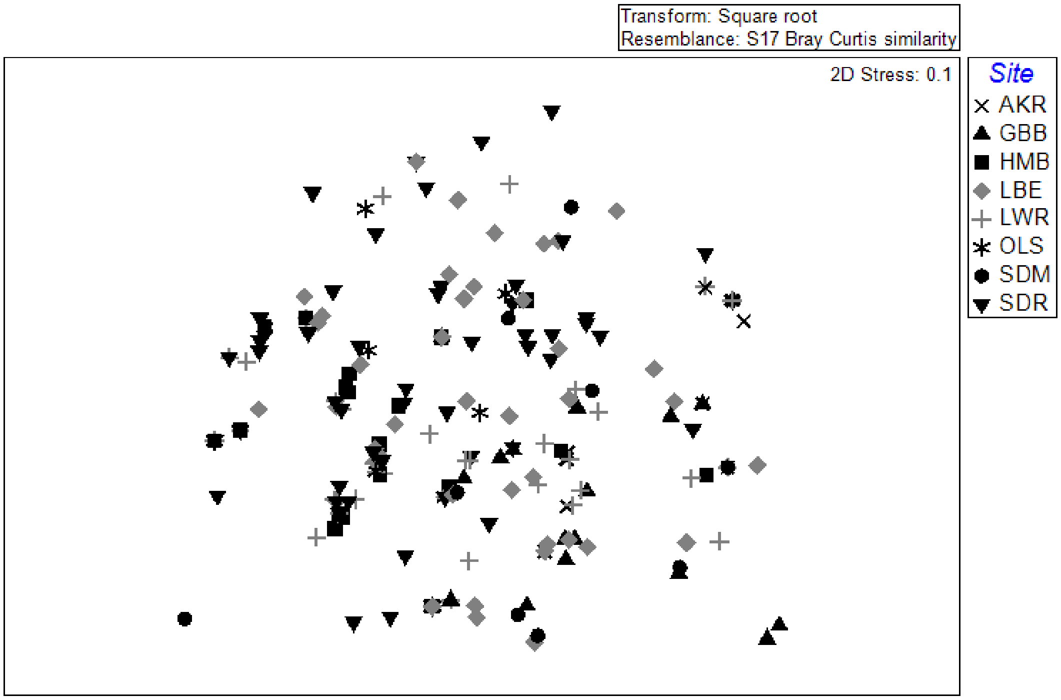


Figure 3. MDS plot of epifaunal assemblages by site (AKR= Anthony's Key, GBB= Gibson Bight, HMB= Half Moon Bay, LBE= Luna Beach, LWR= Lawson's Rock, OLS= Old Loafer's, SDM= Sueno del Mar, SDR= Sueno del Bahia).

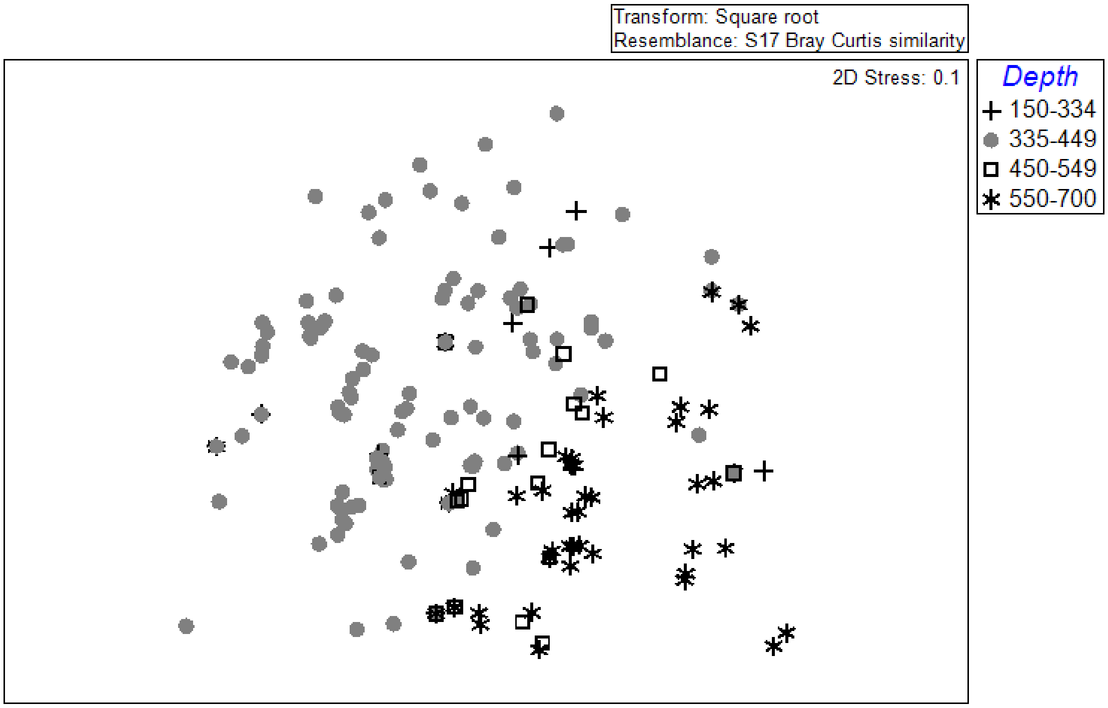


Figure 4. MDS plot of epifaunal assemblages by depth zone (m).

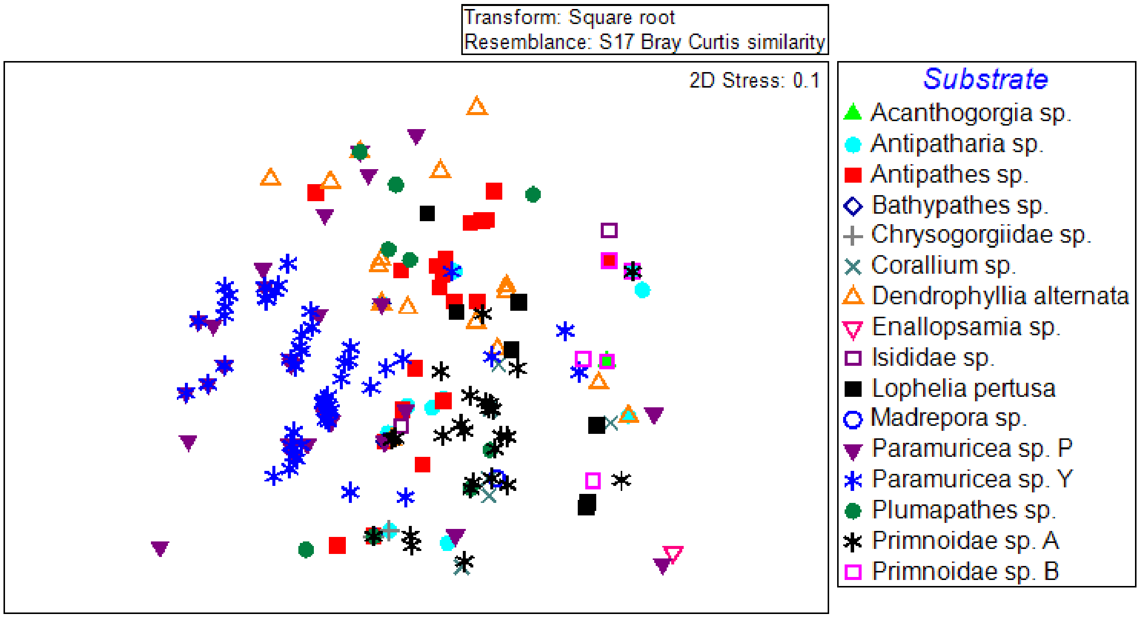


Figure 5. MDS plot of epifaunal assemblages by coral substrate.

Discussion

Epifaunal assemblages on deep-water corals of Roatan, Honduras were highly diverse. Most epifaunal species were rare (defined as 1-11 individuals total) but several were abundant (Table 2). A number of corals without visible epifauna were excluded from analysis, including *Parazoanthus* sp., *Madracis* sp., *Oculina* sp., bamboo coral (Isididae), and several unidentified scleractinians and antipatharians. These corals probably were habitat to many small crustaceans, mollusks, polychaetes, and foraminifera. The proportional abundances and taxonomic composition of epifauna species varied between coral morphospecies. Recurring assemblages and patterns are reported for several coral morphospecies (Table 4).

The differences in species diversity and richness between depth zones may be driven by a number of variables including local currents, bathymetry, or bottom topography combined with the effects of species interactions (e.g., interspecific competition for food or habitat). Side-scan sonar and bottom-mapping might allow determination of whether bathymetry and the distribution of boulders influenced the distribution of corals and epifauna. Water masses affect the disposition of sediments, the distribution of organic matter, and the location of the fauna dependent on that organic matter, including coral (Arantes et al., 2009; Rowe and Menzies, 1969). Additionally, currents affect larval recruitment and retention, generating bands of greater species abundance and richness such as those in the 335-449 and 550-700 m depth zones. Strong currents were not observed during our submersible surveys, so in Roatan currents may be less important than the angle of the continental slope and the rate of organic input in determining faunal distribution. However, the differences in current speed which influence faunal distribution might be subtle. The 450-549 m depth zone might be flat, leaving fauna in this zone dependent on resuspension of benthic material. On the continental slope of North Carolina, epibenthic invertebrates had distinct depth distributions, particularly in the 200-1000 m range (Rowe and Menzies, 1969). High coral density was reported from 200-300 m in Alaska (Stone, 2006) and Norway (Fosså et al., 2002). Discontinuities in species distributions were marked by changes in sediment type and current direction and strength. Benthic sampling and oceanographic studies might confirm if these processes are related to species distribution at the study site.

Chirostyloid squat lobsters were some of the most abundant and widespread epifauna. Unlike *Eumunida picta* (conservatively labeled chirostyloid sp. B), chirostyloid sp. A was rarely seen except on a living coral. There were twice as many chirostyloid sp. A as B observed on corals, indicating that chirostyloid sp. A required a biotic three-dimensional habitat. Chirostyloid sp. A was predominantly observed on Primnoidae sp. A amongst juvenile chirostyloids and on *Paramuricea* sp. Y with *Asteroschema* sp. A. Co-occurrence of chirostyloid sp. A and *Asteroschema* sp. A suggests that these species must interact because they have the same resource requirements. Juvenile chirostyloids were another abundant group observed between coral branches and on the fringe of coral colonies. They had high fidelity to Primnoidae sp. A, but many more individuals likely were hidden amongst coral rubble, *Lophelia pertusa*, and *Dendrophyllia alternata*. Coral functions as an important habitat refuge for a number of invertebrates, including juvenile chirostyloids (Buhl-Mortensen and Mortensen, 2004b; Buhl-Mortensen and Mortensen, 2005; Metaxas and Davis, 2005).

Paramuricea sp. Y and Primnoidae sp. A colonies had the highest constancy of assemblage fidelity. This is mostly likely what drives the grouping of these coral species

(Figure 5). The ANOSIM test provides additional evidence that the assemblages on these corals were significantly different from each other (R=0.554, p=0.01). Absolute abundance of epifauna was highest on these coral species (Table 2 and 4). *Asteroschema* sp. A was exclusively observed on *Paramuricea* sp. color morphs (which might represent different species of *Paramuricea*). Individual *Asteroschema* were on either side of a colony with most arms wound around coral branches and the other arms sweeping the colony. Suspension-feeding epifauna such as this ophiuroid may be utilizing the same food source as its host coral. Many ophiuroids have commensal relationships with corals (Cho and Shank, 2010; Fujita and Ohta, 1988; Mosher and Watling, 2009). Some ophiuroids and coral are mutualistic; the coral benefits by being ‘cleaned’ and the ophiuroid gains a predation refuge and elevation into the water column (Grange, 1991; Stewart, 1998). Almost all *Asteroschema* sp. A had regenerating arm tips, suggesting that they rely on the coral as a refuge from predators. Alternately, the regenerating arm tips may be evidence of non-lethal agonistic interactions with the chirostyloid sp. A., bythitid sp. A, or more mobile predators. Non-lethal predation on an organism capable of regeneration indicates that this species may be a renewable food source (Brooks et al., 2007). *Paramuricea* sp. colonies with ophiuroids rarely had evidence of predation or damage, indicating that the relationship was not detrimental to the host. Paramuriceids damaged from predation rarely had *Asteroschema* sp. A, but they did host urchins suspected to be corallivores. Urchins were observed on several species of coral and may have detrimental effects on their host (Table 4). *Paramuricea* sp. Y colonies had similar assemblages with high fidelity and low diversity.

Primnoidae sp. A had taxonomically rich and abundant assemblages. These large sea-fans are upright but flexible in the water column and have layers of branches, providing ample space for epifauna. Unlike *Paramuricea* sp., these colonies were occupied by significantly larger individuals of chirostyloid sp. A and had the highest proportion of juvenile chirostyloids. Two large colonies hosted 21 and 31 chirostyloid individuals. Tall Primnoidae sp. A provide an optimum habitat for juvenile crustaceans avoiding benthic predators. Primnoidae sp. A was the primary coral habitat for *Novodinia antillensis* and the Venus flytrap anemone *Actinoscyphia* sp. Three comatulid crinoids were predominantly found on *Antipathes* sp. colonies (comatulid sp. C, O, and Y). *Ophiothrix* sp. U had equal preference for Primnoidae sp. A and *Antipathes* sp.

Coral species with the most diverse assemblages of epifauna were *Lophelia pertusa*, Primnoidae sp. A, and *Antipathes* sp. These corals also had high numbers of average individuals and high Hill's N2 values (Table 6). There was overlap in assemblage composition between these three corals (Table 4, Figure 5). These species were among the largest and most structurally complex of the corals observed. *Lophelia pertusa* is a rugose scleractinian which can anastomose its branches and grow into a stable and intricate habitat (CSA International, 2007). *Lophelia pertusa* thickets have an outer layer of live coral growing over and around rubble, providing various microhabitats to hundreds of deep-sea fauna (Costello et al., 2005; Rogers, 1999). Live coral is more important habitat than rubble because there was not much rubble at the Roatan sites. *Antipathes* sp. also has a complex morphology; layers of thin branches and small crevices were occupied by galatheoids, ophiuroids, and comatulids. Physical samples would undoubtedly reveal many more cryptic epifauna within the coral branches. *Lophelia* *pertusa*, Primnoidae sp. A, and *Antipathes* sp. supported diverse assemblages of fauna with similar habitat and feeding requirements.

Recurring epifaunal assemblages were observed on some but not all coral morphospecies. Coral structure alone cannot be the determinant because complex corals such as *Dendrophyllia alternata*, Antipatharia sp., and *Plumapathes* sp. had lower diversity. However, differences in diversity measures could be related to the non-invasive sampling design, which may have prevented observation of epifauna hidden within coral. Coral is an excellent refuge from predation for juveniles and yet only a small percentage of the 1246 individuals we observed were juveniles. Juvenile fauna must be hidden in corals, on alternative substrates, occur infrequently, or have rapid growth into the adult stage.

Some epifaunal species were observed on rock or sand bottom, or among coral rubble (*Bayerotrochus midas*, *Novodinia antillensis*, *Eumunida picta*,). *Bayerotrochus midas* was observed on a damaged Chrysogorgiidae coral in preliminary dives. This species, like other deep-sea mollusks, is probably a mobile corallivore (Harasewych and Sedberry, 2006; Taviani et al., 2009). The majority of the *Novodinia antillensis* were observed on boulders but 22 % were at the base of Primnoidae sp. A (see chapter 3). This opportunistic suspension feeder selects its habitat based on food availability and currents (Emson and Young, 1994). The galatheid crab *Eumunida picta* has been reported on shipwrecks, living and dead *Lophelia pertusa*, bare sediment, and other coral species (Cordes *et al.*, 2008; Kilgour and Shirley, 2008; Lessard-Pilon et al., 2010). This species lacked fidelity to specific coral species or substrates and can be considered a habitat generalist.

Additional assessments are necessary to understand what ecological interactions are most important in structuring epifaunal assemblages on deep-sea corals. Do epibionts compete for the best habitat or are they restricted to specific corals based on habitat availability or physical location? On some corals the majority of associated epifauna are suspension feeders using the coral for elevation into the water current (Buhl-Mortensen and Mortensen, 2005; Frederiksen et al., 1992). Epifauna may be deterred from or enticed to inhabit a coral based on the composition of the mucus. *Lophelia pertusa* will exude mucus to thicken the epitheca when polychaetes and foraminifera settle on its branches (Freiwald and Wilson, 1998). Other species may rely on the mucus as a food source. We observed few instances of predation on coral, but asteroids, nudibranchs and snails are known to feed on coral polyps (Krieger and Wing, 2002). Some epibionts of coral are categorized as commensalistic or parasitic (e.g., *Epizoanthus* sp. anemones ingest coral tissue) (Buhl-Mortensen and Mortensen, 2005). Gooseneck barnacles were rare at the study site and we suspect that this group can only settle on a coral through facilitation (e.g., polyps must be cleared by corallivores before the barnacles settle). Competition for resources including predation refuge, food, and reproduction grounds may also contribute to assemblage structure.

Implications

Deep-sea coral communities are threatened by many anthropogenic activities such as oil and gas exploration, pollution, mining, trawling, and ocean acidification. Trawling for commercially important species can inadvertently result in the destruction of their juvenile habitat (Stone, 2006). In addition to removing coral, sediment resuspension by trawling could have a negative effect on suspension-feeding communities in the deep-sea.

Mining for manganese and other metal nodules has grown as an industry with advances in technology and increases in the value of metals. Hydrothermal vents and seamounts have many endemic species and are being targeted for their sulfide deposits (McClain, 2007; Roberts et al., 2009). Drilling for oil and gas disperses rock fragments, cuttings, and drilling muds and fluids, which have been found on corals four kilometers from the drilling site. The effects of drilling fluids on deep-water corals and megafauna are unknown (Roberts et al., 2009). Ocean acidification may affect calcium carbonate test formation in foraminifera and coccolithophores (Guinotte et al., 2006). These plankton are important in pelagic productivity and may influence the functioning of the coral communities which depend on them for nutrition (Johnson et al., 2007). Although salinity, currents, and temperature could also be influenced by ocean acidification, no experiments have been done to determine how these changes could affect deep-water corals (Guinotte et al., 2006).

The epifauna associated with deep-water corals in Roatan, Honduras were taxonomically diverse and abundant. Some species of epifauna and coral were always observed together, signifying that there are species-specific relationships. Higher abundances of all species in specific depth zones may ultimately be determined by physiographic factors and hydrodynamics. This study provides important biodiversity information that can be used in baseline assessments. Our non-destructive sampling proved successful in collecting biodiversity data. Many of the coral morphospecies and invertebrate epifauna we observed have previously been reported from the Gulf of Mexico and other parts of the Caribbean (Cordes et al., 2008; Emson and Woodley, 1987;

Etnoyer, 2009; Felder et al., 2009; Hourigan et al., 2007; Lessard-Pilon et al., 2010; Lutz and Ginsburg, 2007; Messing et al., 2008; Rice and Miller, 1991)

Some of the epifauna we observed may be represented by congeners or ecological equivalents in other ocean basins (Cho and Shank, 2010; Tissot et al., 2006). The information on range and distribution of deep-sea fauna is useful for studies on island biogeography, endemicity, evolution, and symbiosis. Deep-sea coral communities are unique in that they exist with a biotic substrate and depend on surface productivity for many resources. Future research should focus on species interactions in order to learn more about how these communities are structured.

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ECOLOGY AND DISTRIBUTION OF A BRISINGID SEASTAR IN THE DEEP WATERS OF ROATAN, HONDURAS

Introduction

Asteroids of the order Brisingida are distinctive deep-sea megafauna, but their distribution, ecology, and life history are poorly understood. Most of the available information is from taxonomic studies and deep-sea benthic surveys. Brisingida is monophyletic and includes three families: Brisingidae, Freyellidae, and the recently constructed, Novodiniidae (Mah and Foltz, 2011). A taxonomic key including Novodiniidae is not yet available so we use the descriptions for brisingids outlined in Clark and Downey (1992).

Brisingida includes more than 70 species and the two families Brisingidae and Freyellidae are separated by several morphological and ecological differences (Clark and Downey, 1992; Mah, 1998; Appeltans et al., 2012). Freyellids are generally found in deeper water and softer substrate than brisingids, which are found on hard substrate. Most freyellids cannot raise their arms above the disc, but some behavioral observations suggest a few species may be suspension feeding. Species in Brisingidae typically keep their arms extended into the water current. Direct observations and gut content analysis indicate that species in the order Brisingida use various feeding methods (Emson and Young, 1994). Because primary production in the deep-sea is limited, deep-sea organisms are dependent on sedimentation of production in surface waters (Duineveld et al., 2004; McClain, 2010). The morphology of brisingid seastars allows them to sieve the particulate matter sedimenting from the surface waters.

Based on its morphological description and distributional range, we believe that the brisingid species we observed was *Novodinia antillensis* (A. H. Clark, 1934). *N.*

antillensis has 10-17 arms, a depth range of 366-2700 m, and has been reported from Puerto Rico, West Indies, Gulf of Mexico, Brazil (Campos Basin), Lau Basin and the Bahamas (Campos et al., 2009; Clark and Downey, 1992; Craddock, 2005; Emson and Young, 1994). We plan to collect specimens in the future to verify species identification. Although reports of brisingids date to 1880, little is known of their ecology, because of the difficulties of conducting experiments and making observations in the deep-sea. We observed brisingids in high abundances during preliminary submersible dives in Roatan, Honduras. This study is intended to provide new information on the habitat distribution, depth range and abundance of brisingids.

Material and Methods

Study Site: Roatan, Honduras

Isla Roatan is part of the Bay Islands archipelago in the southwestern Caribbean Sea. It is approximately 50 km north of mainland Honduras. The island is of volcanic origin and the continental slope is predominantly soft sediment and basalt and limestone boulders. The boulders are heterogeneous in size and distribution. The bottom topography has areas of steep walls, furrows, and low-slope, sediment-covered bottom. Roatan is on the southern edge of the Cayman Trough and surrounded by deep water. Approximately 20 km northeast of Roatan is the Bonacca Deep, a deep feature (5400 m) located at the base of the Cayman Trough escarpment (Banks and Richards, 1969; Pinet, 1976). The Bay Islands themselves lie on top of the Bonacca Ridge (Banks and Richards, 1969). The strong vertical relief surrounding the island permits rapid descent to bathyal depths.

Submersible Idabel

Video survey transects were completed using the *Idabel* submersible (Etnoyer et al., 2011). *Idabel* is owned and operated out of Roatan, Honduras by Karl Stanley's private company, Stanley Submarines. The submersible measures 3.9 x 2 x 2.1 meters. *Idabel* is equipped with redundant propulsion, manually operated emergency drop weights (158 kg.), life support for 3 days, and a 76 cm diameter hemi-spherical viewport for passenger observation. The pilot stands with a 360° view through a series of 9-16 cm diameter portholes surrounding the conning tower. It is depth-rated to 1000 m and can carry two passengers in addition to the pilot. Two Sony HD Handycams (HDR-HC9) were used during each survey. One was mounted on the interior of the viewport and the other was in an external housing above the parallel lasers. Externally mounted lasers 10 cm apart were used as a size reference. Still photos were taken from inside *Idabel* with a Canon SLR (EOS1) connected to an external flash. A Seabird Seacat v 19 conductivity-temperature-depth-oxygen (CTD-O) profiler was mounted on the lower starboard side rail.

Survey Transects

Idabel was towed offshore (~2 km) to an approximate location and descended to a target maximum depth of 700 m. Coordinates were recorded before the submersible descended. Video recording began at the seafloor and ended between 50-100 m. Detailed maps of the seafloor were not available so all transects were in the general direction of the launching dock. Ten dives were made but two were excluded from analysis because they were outside of the target depth range (Figure 1.). Preliminary dives from August

2010 were excluded from analysis because they did not follow the same protocol. Six dives were made in May 2011 and four dives were made in December 2011. All dives were on the northwestern end of Isla Roatan: Anthony's Key, Gibson Bight, Half Moon Bay, Lawson's Rock, Luna Beach, Old Loafer's, Sueno del Bahia, and Sueno del Mar. Sites were named for landmarks visible from the point of descent. Dives were made without replicates.

Every five minutes depth (m), temperature (°C), and time was recorded along with a landmark from that timecode (e.g. boulder with crab species A) (Etnoyer *et al.*, 2011). Recording was continuous during transects in order to document observations which were not necessarily captured on the video monitor. These data logs were later used to assign depths to observed organisms and assemblages. During transects still images were taken of coral colonies, invertebrate epifauna, and any other interesting organisms happened upon. HD video footage was digitized using FinalCutPro 6.0.6. Frame grabs were made from digitized video to record habitat distribution, depth, abundance, and diversity of species. Discontinuities in faunal distributions were used to create four depth zones for analysis. Few specimens were collected so most species identifications were to a morphospecies level and made based on gross morphology and available ecological data. We considered all brisingids to be the same species because of their similar morphology but it is possible that more than one species was present. No brisingid seastars were collected during the DeepCAST II or III expeditions.

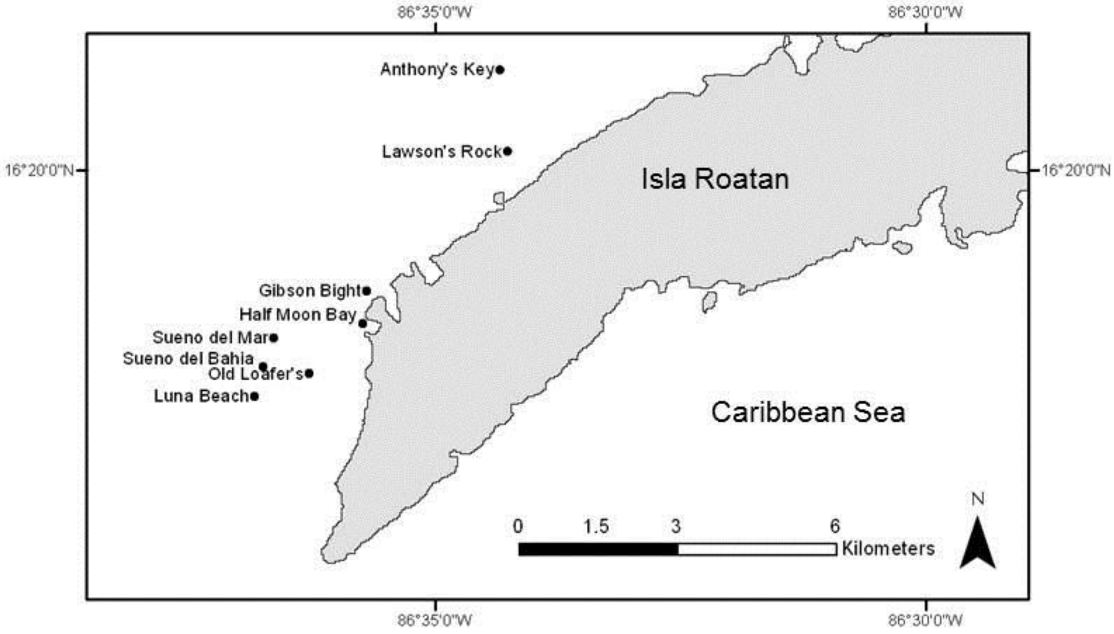

Figure 1. Map of survey sites in Roatan, Honduras.

Results

We observed a total of 229 brisingids from seven sites. Sueno del Mar, Anthony's Key, and Half Moon Bay were the sites where *N. antillensis* was most abundant (Figure 2). *Novodinia antillensis* was the largest sessile epifaunal species observed. Individuals were often observed in groups and each unique occurrence included all individuals within 0.5 m of another. The average density for each unique occurrence was three individuals, but there were four occasions when there were more than 10 brisingids. *N. antillensis* were observed on boulders, sponges, coral rubble, and several morphospecies of deep-sea coral (Table 1.). We observed 25 unique coral morphospecies but brisingids were only associated with 8 coral species. Few coral specimens were collected; therefore all identifications of biotic substrates were based on observations of morphology. Sixty-two percent of *N. antillensis* were on boulder substrate and 17 percent were observed at the base of primnoid sea fans. No brisingids were observed on bare sediment. Brisingids were rarely, if ever, in direct contact with other epifaunal species.

Our sampling was limited by the availability of design criteria and the lack of replication, so a 1-way incomplete blocking design was used, where substrate was the main effect and site and depth were the blocks (SAS 9.2). *Novodinia antillensis* abundance was not significantly different between substrates, sites or depth zones (one-way ANOVA, p>0.7828, p>0.2248, and p>0.0758, respectively). Although abundance was not significantly different between depth zones, 95 percent of *N. antillensis* were observed between 550-695 m, the maximum depth surveyed (Figure 2).

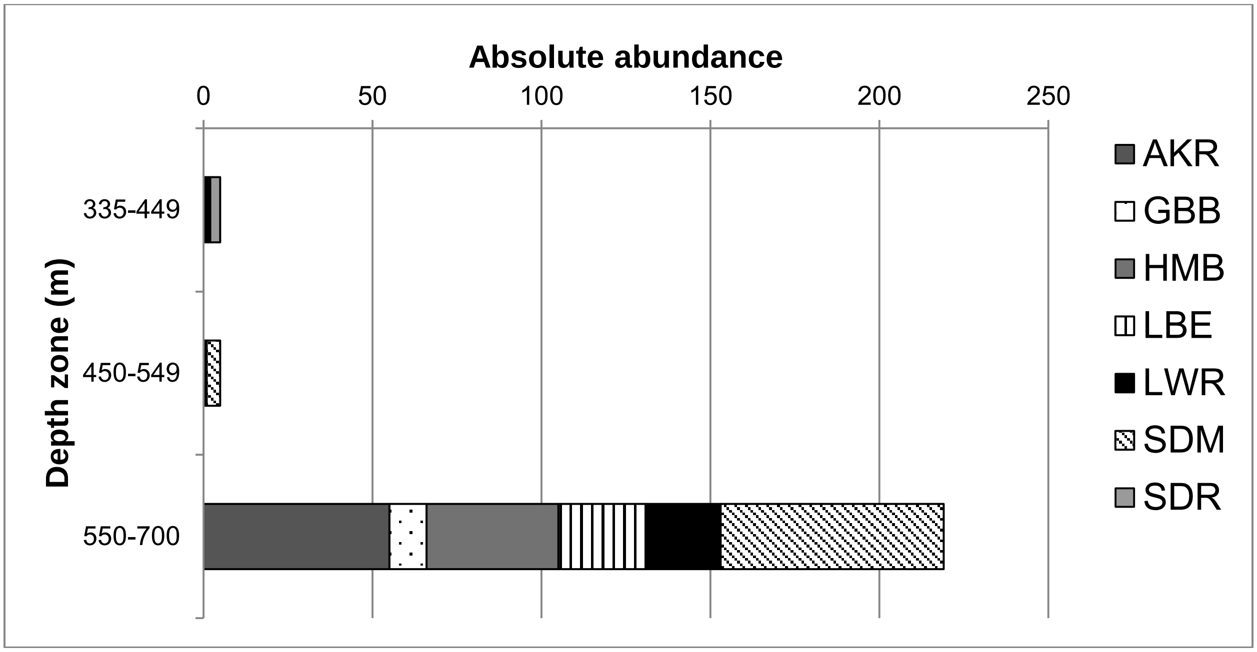

Figure 6. Abundance of *Novodinia antillensis* by site and depth (AKR= Anthony's Key, GBB= Gibson Bight, HMB= Half Moon Bay, LBE= Luna Beach, LWR= Lawson's Rock, SDM= Sueno del Mar, SDR= Sueno del Bahia).

Table 7. *Novodinia antillensis* abundance on different substrates.

Substrate (n)	**Total abundance**	**Mean**	**STD**
boulder (50)	143	3	3.077
coral rubble (1)	1	1	
sponge (2)	2	1	0
Primnoidae (7)	40	6	4.716
Primnoidae B (1)	7	7	
Lophelia pertusa (4)	16	4	3.162
Enallopsamia sp. (1)	2	2	0
Corallium sp. (2)	12	6	7.071
Paramuricea sp. P (2)	2	1	0
Paramuricea sp. Y (1)	1	1	
Unidentified coral b (1)	3	3	0

Almost all brisingids were observed with their arms bent upwards with the tip curved in towards the disc. This basket-like orientation is similar to observations by Emson and Young (1994). An alternative posture was the brisingids keeping a few arms on the substrate and raising the rest into the water column. Based on relative size, we observed 11 juvenile brisingids. It was not possible to record average arm lengths for the majority of individuals because the lasers were not always in the frame. Average arm length for those we could measure was 25±5 cm (n=4). The angle of the camera and arm posture limited our ability to count the number of arms, but we were able to count the number of arms for 60 individuals (avg= 15, std= 2.5). Ten individuals were in the process of regenerating arms. Many of the arms were almost fully regenerated, but other individuals had numerous small segments extending from the disc (Figure 3). Most brisingids were regenerating a few arms at a time, but one individual was regenerating 13 arms.

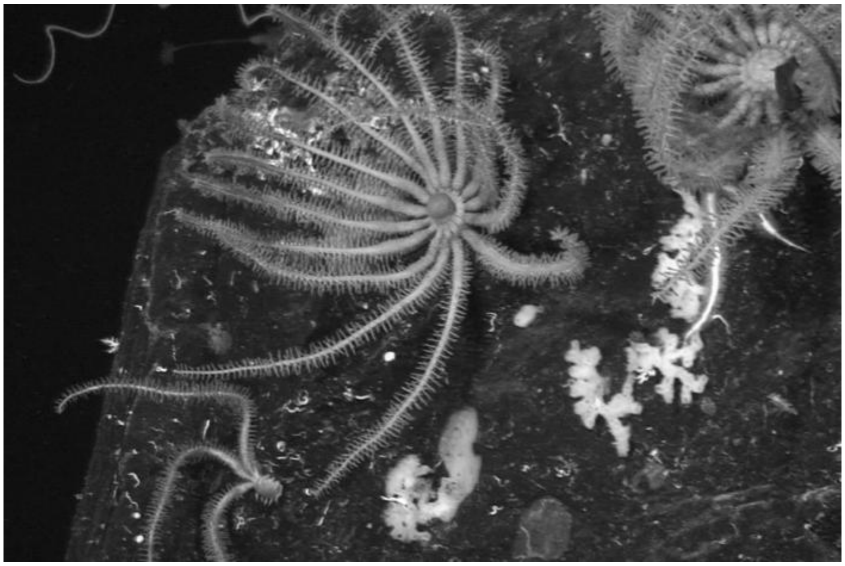

Figure 7. *Novodinia antillensis* on a boulder at Anthony's Key, 591 m.

Discussion

Novodinia antillensis was abundant and widespread across the survey sites. Brisingids occurred on boulders, corals, and sponges, consistent with previous observations (Emson and Young, 1994). Large aggregations of individuals were occasionally on boulder faces, but most frequently in pairs or as single individuals. In our study areas 95% of individuals were found below 550 m, suggesting a preference for deeper depths. The observed depth range is probably not a function of habitat distribution because the most common habitat (boulders) occurred in all depth zones. Boulders contribute to the complexity of ridges and furrows, making the habitat heterogeneous and accelerating flow. Enhanced flow transports oxygen, suspended inorganic matter, and detrital food particles downslope and to the benthos, which in turn attracts a diversity of epifaunal organisms (Frederiksen et al., 1992). Higher availability of benthopelagic plankton within 10 m of the bottom also contributes to this enriched benthic environment (Wishner, 1980). Regions with faster flow have higher biomass of macrobenthic suspension feeders (Flach and Thomsen, 1998).

An in-situ study on the brisingid *Novodinia antillensis* found that it is a suspension-feeder, specializing in macroscopic organisms (Emson and Young, 1994). The species captures benthopelagic and planktonic crustaceans from the water column by raising its arms into the water column and using pedicellariae to capture and tube feet to transfer items to the mouth. We observed species with the same posture in the field. This feeding method is highly efficient because there is more prey available above the sediment surface (Wishner, 1980). The high abundance of *Novodinia antillensis* indicates that this species has developed a successful method for exploiting its food source.

Few individuals were in the process of regenerating arms, arms were either fully grown or in the early or latest stages of regeneration. Any arms that were regenerating were in the same stage of growth. This indicates that predators are consuming whole individuals, several arms during each feeding event, that regeneration of arms is rapid, or that predation is infrequent. No predation events were observed, but a variety of potential predators, including large crabs, lobsters, fish, seastars, and sea urchins, occurred commonly in the transects. Evidence of predation was abundant in another conspicuous macrofaunal species, the brittle star *Asteroschema* sp. In this large ophiuroid species, most arms of most individuals were in the process of regenerating the arm tips.

Most *Novodinia antillensis* individuals were the same size, or at least there were no distinct size classes. This suggests that successful reproduction (larval recruitment) does not occur frequently. If reproduction does occur more often, then growth must be rapid, or early life history stages are cryptic or live in habitats different than the adults. Our observations of *Novodinia antillensis* are in agreement with the depth distribution from other reports. The distribution range of *N. antillensis* should be expanded to include the western Caribbean Sea and the Cayman Trench. The sites where *N. antillensis* was observed were relatively close to shore. It would be useful to compare how bottom topography is related to brisingid abundance and input of suspended matter to sites further offshore. Although our surveys were conducted during different seasons, there was no evidence of seasonal differences. There were no significant differences in depth distribution, abundance or size of individuals between our two sampling expeditions.

Brisingid seastars are conspicuous and abundant on the deep seafloor and yet little is known of their ecology. This paucity of knowledge applies to many deep-sea fauna which remain misunderstood because of the difficulty and limitations of deep-sea research. Although we have compiled information on the depth range and distribution of *Novodinia antillensis*, we can only speculate on what variables limit its range and substrate selection. This species was among the most abundant epifauna in Roatan and surely it has an important role in deep-sea community ecology. Future research should focus on studying aspects of the ecology of *Novodinia antillensis*, including variables affecting depth and latitudinal distributions, growth rates and regeneration, and reproductive biology.

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Summary

Deep-water corals in Roatan, Honduras have diverse epifaunal assemblages. Taxonomic composition and abundance of epifauna varied among coral species. Some coral morphospecies had consistently recurring assemblages, but many had assemblages of similar taxonomic composition. Some epifauna were predominantly abundant but most were rare. Epifauna had a range of habitat preferences; some were found only on specific corals and others were habitat generalists.

Echinoderms and crustaceans were the taxa with the highest number of species and total abundance, respectively. The most abundant echinoderms were an unbranched basket star, *Asteroschema* sp. A, an ophiuroid, *Ophiothrix* sp. U, and the brisingid seastar, *Novodinia antillensis*. Adult and juvenile chirostyloid crabs were observed on many coral species and other habitat types. Paramuriceid, primnoid, and antipatharian corals were the most common coral groups. The density of epifauna was variable among and between coral morphospecies, but was not a function of the colony size. Epifauna and coral were most abundant in the 334-449 and 549-700 m depth zones.

Epifaunal diversity and assemblage constancy varied between coral species. Primnoidae sp. A and *Paramuricea* sp. Y had the highest absolute abundance of epifauna. *Lophelia pertusa*, Primnoidae sp. A, and *Antipathes* sp. had the most diverse assemblages of epifauna. Coral species with the highest number of individuals were *Lophelia pertusa*, Primnoidae sp. A, *Corallium* sp., and *Madrepora* sp., respectively. Similar epifaunal assemblages were observed on *Lophelia pertusa*, *Antipathes* sp., and Primnoidae sp. A. We attribute this to the corals being some of the largest and structurally complex from the study site. An analysis of the infaunal assemblages might reveal different diversity patterns.

Assemblage fidelity was most prominent on *Paramuricea* sp. Y and Primnoidae sp. A colonies. *Asteroschema* sp. A was exclusively observed on *Paramuricea* sp. color morphs. *Asteroschema* sp. A and chirostyloid sp. A were often observed together on *Paramuricea* sp. Y, suggesting that these species use the same resources and possibly interact with each other. Juvenile chirostyloids were predominantly found within Primnoidae sp. A colonies. Bythitid fishes, crinoids, and the chirostyloid *Eumunida picta* were associated with numerous corals and are habitat generalists. These species may not have specific requirements for substrate or other resources.

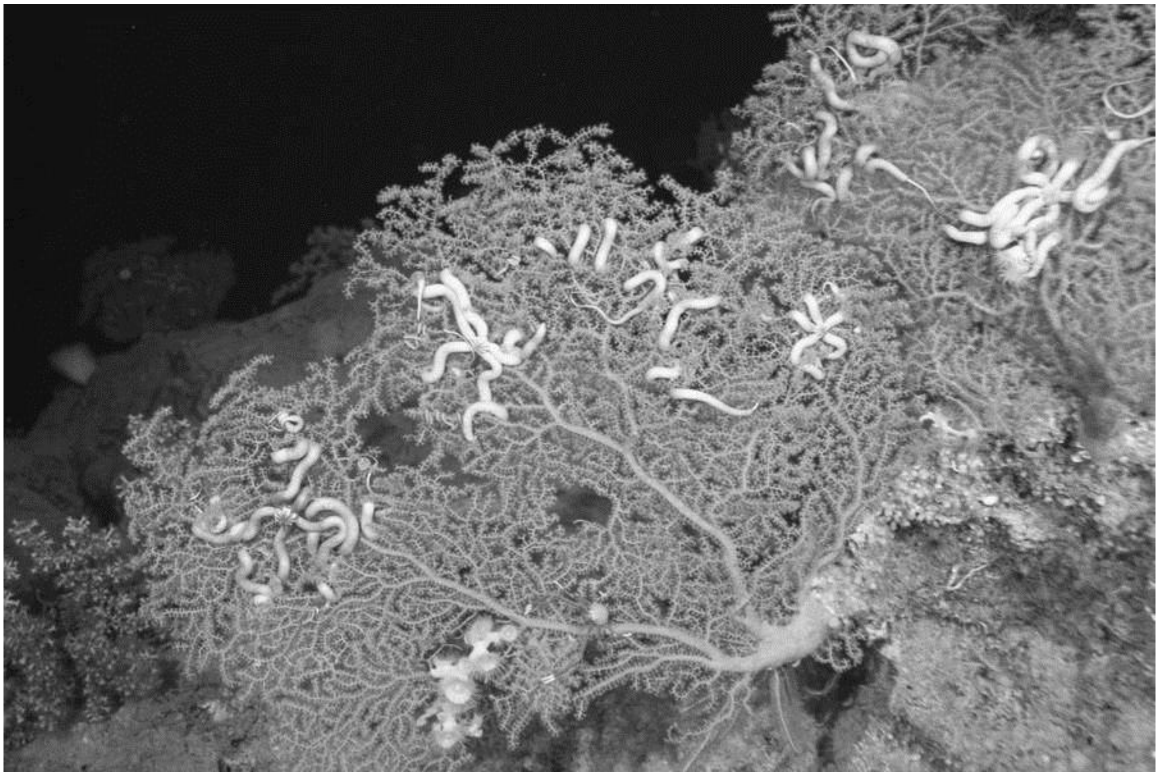
The brisingid *Novodinia antillensis* was abundant and widespread across our study site. *N. antillensis* occurred on boulders, corals, and sponges. The majority was on boulders but they were also on eight different coral morphospecies. Occasionally large aggregations of individuals were near Primnoidae sp. A and B corals. Individuals were predominantly below 550 m. The distribution of these suspension feeders is probably influenced by currents and food availability. There were few instances of arm regeneration which indicates that this species may have few predators. *Novodinia antillensis* was a conspicuous and abundant megafaunal species in Roatan, Honduras. The distribution of *Novodinia antillensis* should be expanded to include the Western Caribbean Sea.

Biotic interactions, the physical environment, and resource availability are all important in structuring deep-sea coral communities. Water masses, currents, and topography affect the depth distribution of coral and epifauna. Megafauna probably compete to occupy coral habitat in areas with optimal current flow and food availability. The concentration of coral and fauna in the 335-449 m depth zone could be driven by bathymetry and the rate of organic input. Interspecific competition for habitat and food is probably an important determinant for the co-occurrence of epifaunal species. Additional assessments are needed to understand what ecological interactions and physical parameters are most important in structuring epifaunal assemblages on deep-sea corals.

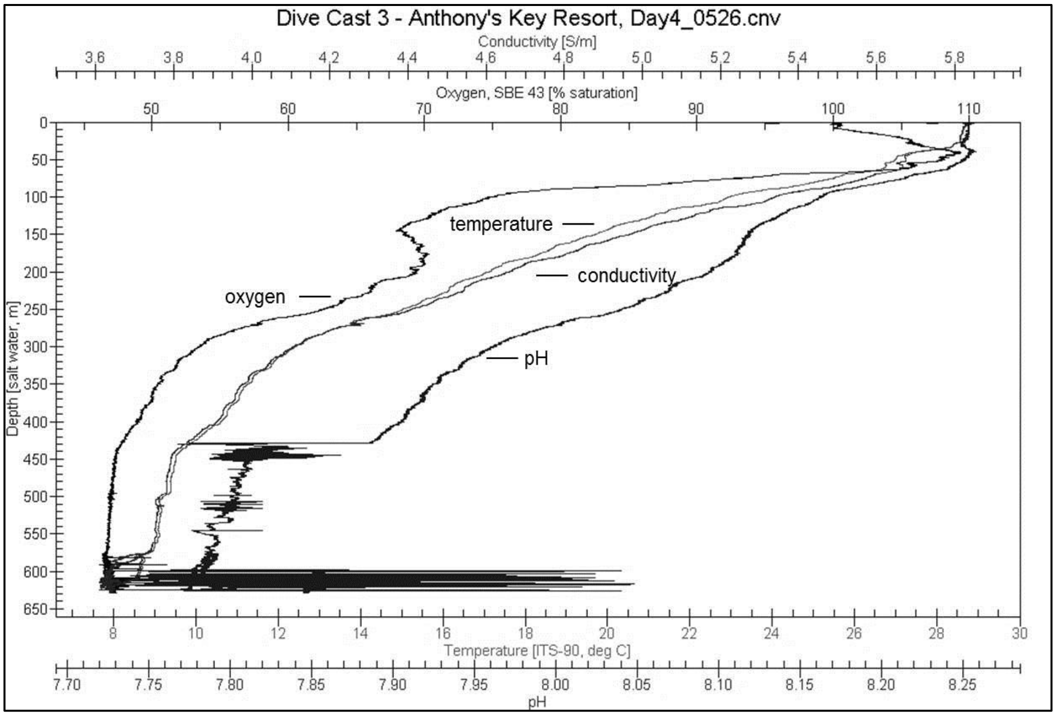
Deep-sea corals are long-lived, habitat forming species which support diverse communities of sessile and mobile fauna. Anthropogenic activities that threaten deep-sea coral communities include trawling, long-line fishing, oil and gas exploration, the jewelry trade, and mining. All of these activities can remove and alter coral habitat, displacing associated communities. Seafloor scouring and coral bycatch are some of the more severe impacts caused by trawls (Probert et al., 1997). Resuspension of sediment from drilling and mining can smother coral habitat. Drill cuttings and oil have been observed on coral polyps. Ocean acidification could alter the aragonite saturation horizon, and thus the distribution of scleractinian corals. Local threats in Roatan include fishing activity and pollution. Trash and fishing gear were observed during several survey transects. The Roatan Marine Park should be extended to include habitat in the 700 m isobath based upon coral presence, vulnerability, and associated biodiversity.

Future research on the deep-water corals of Roatan, Honduras should include specimen collection, genetic analysis, gut content analysis of epifauna, stable isotope research, sediment trap deployment, and bottom mapping with multibeam echosounders and side-scan sonar. Additional observations at the study site would contribute to our understanding of deep-sea community ecology and biodiversity. Deep-sea biodiversity studies continue to provide fascinating information about how these remote ecosystems function. The information from this study can be used for baseline surveys in a previously unexplored region of the Caribbean Sea.

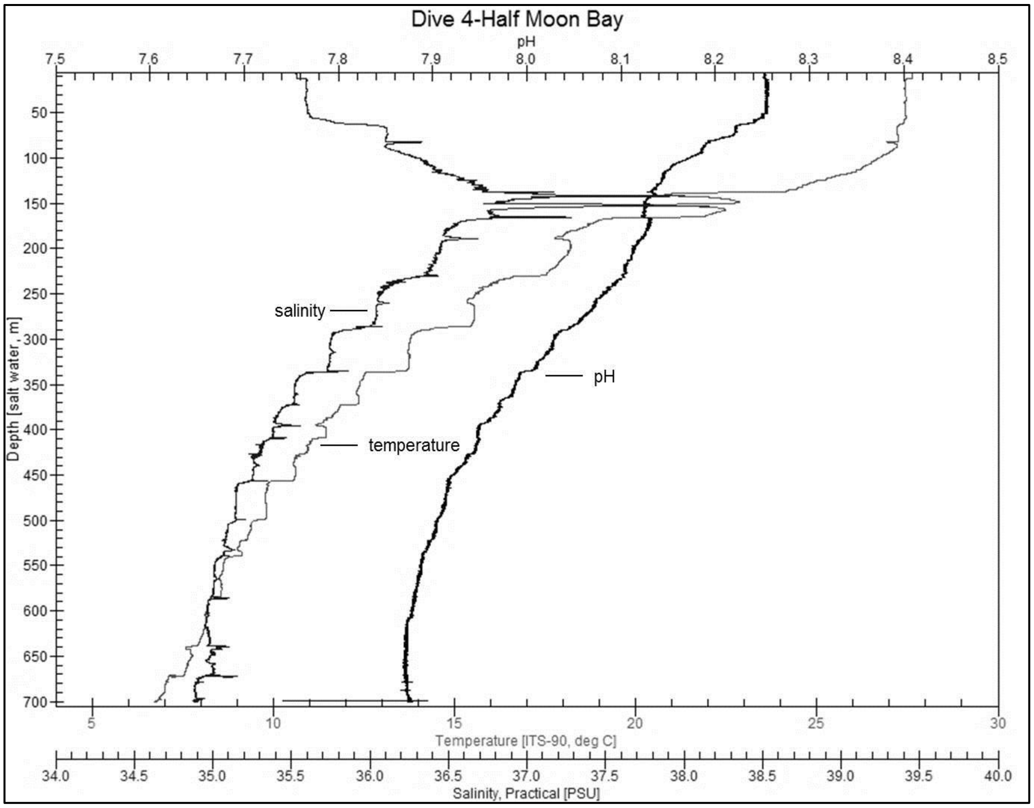
Appendix 1. *Paramuricea* sp. Y at Luna Beach, 338 m.



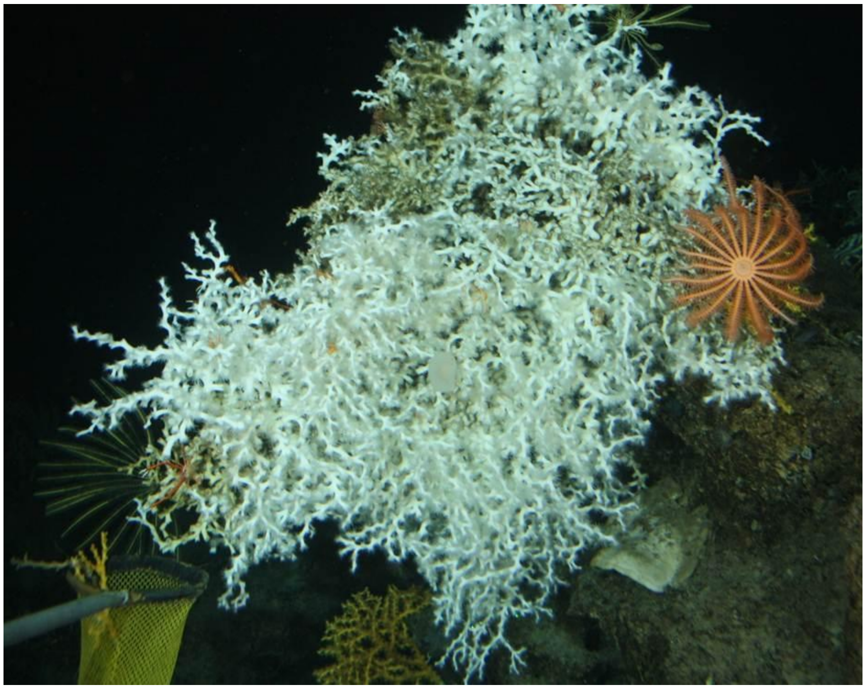
Appendix 1. CTD cast at Anthony's Key.



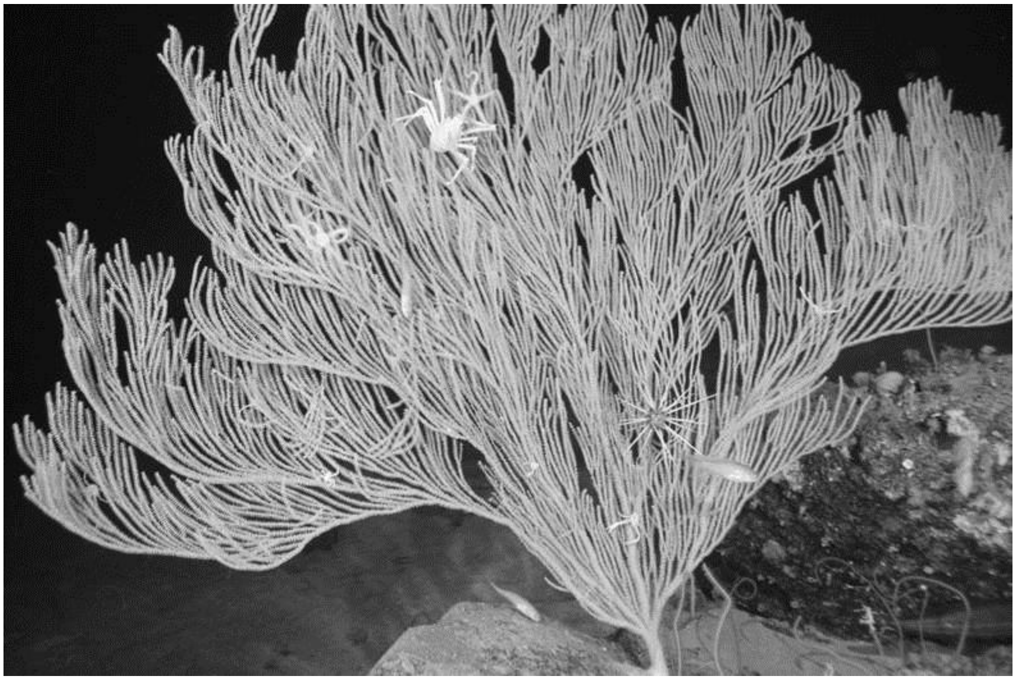
Appendix 3. CTD cast at Half Moon Bay.



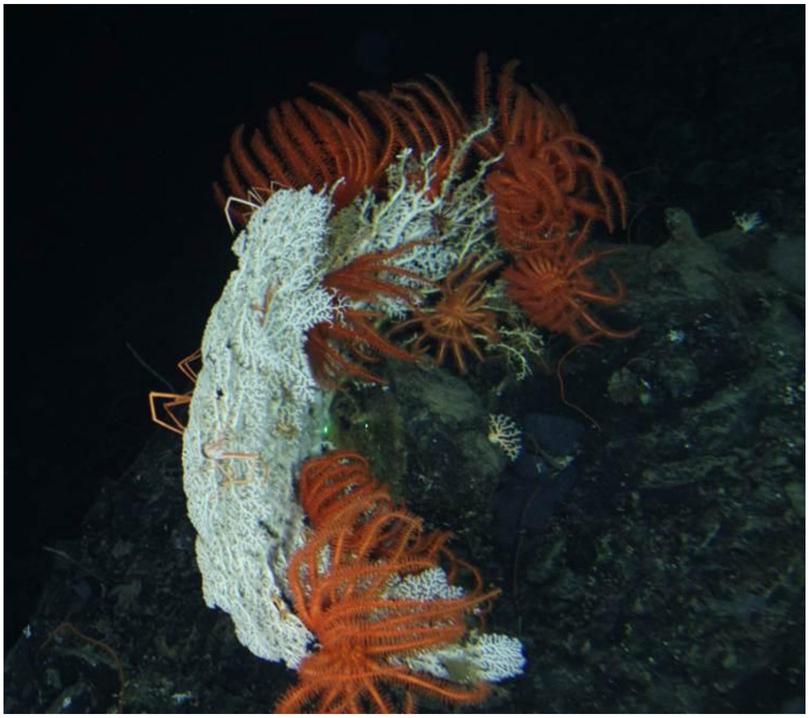
Appendix 4. *Lophelia pertusa* at Sueno del Bahia, 365 m.



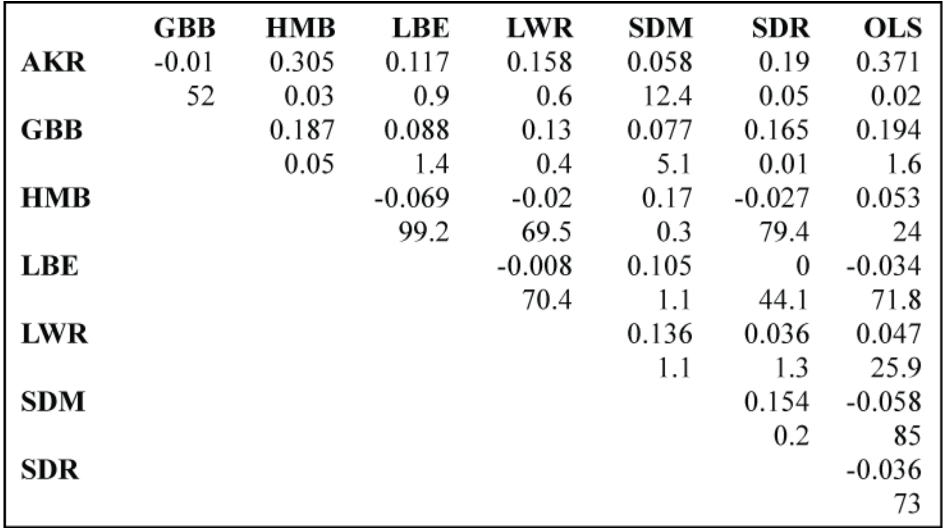
Appendix 5. Primnoidae sp. A colony at Luna Beach, 549 m.



Appendix 6. *Corallium* sp. at Anthony’s Key, 610 m.

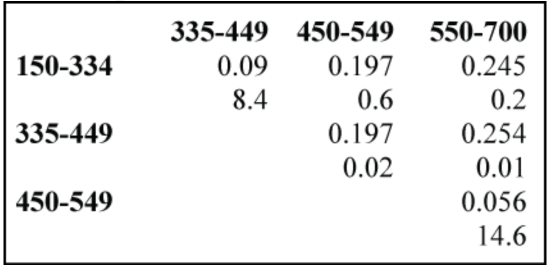


Appendix 7. ANOSIM results for comparing assemblage composition between sites (top value is R statistic, bottom value is significance level as percent).



	GBB	HMB	LBE	LWR	SDM	SDR	OLS
AKR	-0.01	0.305	0.117	0.158	0.058	0.19	0.371
	52	0.03	0.9	0.6	12.4	0.05	0.02
GBB		0.187	0.088	0.13	0.077	0.165	0.194
		0.05	1.4	0.4	5.1	0.01	1.6
HMB			-0.069	-0.02	0.17	-0.027	0.053
			99.2	69.5	0.3	79.4	24
LBE				-0.008	0.105	0	-0.034
				70.4	1.1	44.1	71.8
LWR					0.136	0.036	0.047
					1.1	1.3	25.9
SDM						0.154	-0.058
						0.2	85
SDR							-0.036
							73

Appendix 8. ANOSIM results for comparing assemblage composition between depth zones (top value is R statistic, bottom value is significance level as percent).



	335-449	450-549	550-700
150-334	0.09	0.197	0.245
	8.4	0.6	0.2
335-449		0.197	0.254
		0.02	0.01
450-549			0.056
			14.6

Appendix 9. ANOSIM results for comparing assemblage composition between coral substrate (top value is R statistic, bottom value is significance level as percent).

	Antipatharia sp.	***Antipathes* sp.**	***Bathypathes* sp.**	**Chrysogorgiidae sp.**	***Corallium* sp.**	***Dendrophyllia alternata***	***Enallopsamia* sp.**	**Isididae sp.**	***Lophelia pertusa***	***Madrepora* sp.**	***Paramuricea* sp. P**	***Paramuricea* sp. Y**	***Plumapathes* sp.**	**Primnoidae sp. B**	**Primnoidae sp. A**
***Acanthogorgia* sp.**	0.24	0.208	0.867	1	-0.011	-0.01		-0.5	0.306		0.552	0.714	0.349	-0.4	0.206
	31.8	12.5	9.1	25	42.9	45.8		100	37.5		2.6	5.1	20	100	25
Antipatharia sp.		0.107	-0.107	-0.24	0.148	0.324	0.605	0.165	0.493	0.082	0.39	0.479	0.019	0.391	0.143
		1.3	94.8	92.3	10.3	0.01	4.5	18.6	0.01	31.8	0.01	0.01	26.9	0.2	0.2
***Antipathes* sp.**			0.061	0.036	0.256	0.258	0.593	0.019	0.355	0.246	0.417	0.535	0.08	0.234	0.273
			15.2	31.7	0.2	0.01	4.2	41.3	0.03	8.3	0.01	0.01	5.4	1.1	0.01
***Bathypathes* sp.**				-0.05	0.636	0.395	0.867	0.635	0.797	0.747	0.323	0.368	-0.001	0.818	0.215
				51	0.05	0.01	9.1	3	0.01	18.2	0.03	0.01	37.7	0.03	1.4
Chrysogorgiidae sp.					0.318	0.419	1	0.625	0.792	1	0.311	0.407	-0.221	0.692	0.116
					9.5	0.04	25	10	0.8	25	3.6	1.5	91.8	1.8	24.2
***Corallium* sp.**						0.056	0.6	0.469	0.182	-0.467	0.45	0.603	0.163	0.379	0.022
						23.8	28.6	10.7	6.4	85.7	0.01	0.01	9	1.1	40.3
Dendrophyllia alternata							0.462	0.34	0.068	0.086	0.463	0.631	0.233	0.282	0.368
							4.2	1.3	19.6	29.2	0.01	0.01	0.05	0.6	0.01
***Enallopsamia* sp.**								0	0.218		0.536	0.789	0.484	0.4	0.728
								100	37.5		2.6	1.3	6.7	33.3	3.6
Isididae sp.									0.656	-0.5	0.461	0.549	0.213	0.227	0.318
									2.8	100	1.7	1.8	14.2	14.3	7.4
Lophelia pertusa										-0.02	0.5	0.716	0.369	0.366	0.404
										50	0.01	0.01	0.2	1.8	0.2
***Madrepora* sp.**											0.435	0.596	0.059	0.32	-0.327
											10.4	6.4	40	33.3	92.9
***Paramuricea* sp. P**												0.048	0.369	0.554	0.444
												0.07	0.01	0.01	0.01
***Paramuricea* sp. Y**													0.513	0.744	0.554
													0.01	0.01	0.01
***Plumapathes* sp.**														0.403	0.283
														0.08	0.04
Primnoidae sp. B															0.415
															0.2