Habitat utilization, demography, and behavioral observations of the squat lobster, *Eumunida picta* (Crustacea: Anomura: Eumunididae), on western North Atlantic deep-water coral habitats

Martha S. Nizinski[a*], Jennifer P. McClain-Counts[b,c], Steve W. Ross[b]

[*]corresponding author

[a]NOAA, NMFS, National Systematics Laboratory, Smithsonian Institution, PO Box 37012, NHB, WC-57, MRC-153, Washington, DC 20013 USA, 202-633-0671 (phone), 202-633-8848 (fax)
nizinski@si.edu

[b]University of North Carolina at Wilmington, Center for Marine Science, 5600 Marvin Moss Lane, Wilmington, NC 28409 USA
rosss@uncw.edu

[c]present address: U.S. Geological Survey, Wetland and Aquatic Research Center, 7920 NW 71st Street, Gainesville, FL 32653 USA
jmcclaincounts@usgs.gov

Keywords: squat lobster, *Eumunida picta*, deep-water coral associates; cold-water corals; *Lophelia pertusa*; video analysis; feeding behavior

Abstract

Deep-sea coral habitats, comprising mostly *Lophelia pertusa* (Linnaeus 1758), are well developed on the upper and middle continental slope off the southeastern United States (SEUS). These habitats support a diverse and abundant invertebrate fauna, yet ecology and biology of most of these species are poorly known. Ten cruises conducted off the SEUS (Summer–Fall; Cape Lookout, NC–Cape Canaveral, FL) from 2000–2005, and in 2009 provided an opportunity to investigate abundance and distribution of *Eumunida picta* Smith 1883, a large-sized species of squat lobster commonly associated with these deep-water coral habitats. Video analysis from 70 manned-submersible dives documented occurrence, density, location on the coral colony, and behavioral observations for 5,774 individuals of *E. picta*. Individuals collected (n = 178) from coral and adjacent habitats (e.g., rubble, soft sediments) were measured and their sex determined. Males and females were comparable in size (to 53.5 mm carapace length) and exhibited a sex ratio of approximately 1:1. *Eumunida picta* were most frequently observed as solitary individuals on high-profile coral matrix and were noted only infrequently on coral rubble, or rarely on soft substratum. Presence of coral habitat (i.e., live/dead *L. pertusa*), geographic region within the sampling area, and depth significantly influenced abundances of *E. picta*. Additionally, coral habitat (dead versus live coral), vertical position on the coral (upper, middle, or lower zone), as well as horizontal position in relation to the coral matrix (outer surface versus embedded in coral matrix) were significant factors influencing *E. picta* distributions within the coral habitat. More individuals were found on dead versus live coral, and most frequently occurred on the outer surfaces of coral branches located on the upper portion or near the tops of coral colonies. *Eumunida picta* were most often observed with claws extended into the water column. This unique hunting stance provides this squat lobster the opportunity to capture prey from the water

column. An active predator, this species utilizes both pelagic (i.e., fishes, pyrosomes) and benthic (e.g., scavenging and grazing) food resources, and may function as an important trophic link between the water column and the benthos. Although considered a facultative reef associate in the strictest sense of the term, *E. picta* has a complex and intimate relationship with *L. pertusa*. Based on observations from dive videos, *E. picta* is a dominant and ecologically important member of the invertebrate assemblage associated with deep-sea coral habitats off the SEUS. As such, this species figures prominently in the structure and function of this ecosystem.

1. Introduction

Squat lobsters are a diverse group of anomuran crustaceans comprising two superfamilies, seven families, 47 genera, and approximately 1402 species (WoRMS 2022a, 2022b) with additional species identified as new to science. Squat lobsters inhabit broad geographic and bathymetric ranges, occurring circumglobally, primarily in tropical and temperate waters from the surface to abyssal depths (Schnabel et al., 2011). Commonly found in the deep sea at depths greater than 200 m, many species of squat lobsters are associated with hydrothermal vents, seeps, and whale and wood falls (Williams and Turner, 1986; Chevaldonné and Ohu, 1996; Martin and Haney, 2005; Macpherson and Segonzac, 2005; Smith and Baco, 2003). Additionally, squat lobsters, particularly those in the Superfamily Chirostyloidea, are commonly associated with deep-sea corals (e.g., Mortensen et al., 1995; Baba, 2005; Ross and Nizinski, 2007; Le Guilloux et al., 2010; Lessard-Pilon et al., 2010).

Eumunida picta Smith 1883, a medium- to large-sized squat lobster, occurs from Northeast Channel, Canada (Buhl-Mortensen and Mortensen, 2004a; MSN, unpubl. data); Massachusetts to Florida, off the north coast of Cuba, in the Gulf of Mexico (Felder et al., 2009); and provisionally (specimens needed for verification) off Isla Roatán, Honduras (Lavelle, 2012; SWR, pers. obs.) at depths of 200-600 m (Felder et al., 2009). One of several crustaceans new to science that were collected during the early exploratory expeditions conducted in the western North Atlantic, *E. picta* is surprisingly scarce in museum collections. Thus, general knowledge of *E. picta* is limited, being largely taxonomic (e.g., Smith, 1883; Milne-Edwards and Bouvier, 1894, 1900; de Saint Laurent and Macpherson, 1990). Other studies list *E. picta* as a member of the invertebrate faunal assemblage associated with deep-coral habitats (e.g., Wenner and Barans, 2001; Reed et al., 2006; Cordes et al., 2008; Quattrini et al. 2012), or include this species as part of those collected during a faunal survey (Wenner, 1982). A small number of other studies have addressed basic biological and ecological questions involving *E. picta,* such as habitat association (Kilgour and Shirley, 2008a, 2008b), parasitism and reproduction (Wenner, 1982), and visual acuity (Frank et al., 2012).

Considering that much of what is known about *E. picta* is based on trawl-caught individuals collected over a broad geographic area, museum specimens, and only more recently, *in situ* observations, it is not surprising that detailed information on habitat use by this species is lacking. Defining and understanding habitat utilization by *E. picta* at a finer scale have been hindered by small sample sizes, lack of detailed ecological data generally associated with trawl collections, and limited information on habitat associations under natural conditions. Similarly, limited *in situ* observations hamper our overall understanding of how this species utilizes the habitat and interacts with other organisms. For example, details regarding fundamental life-history traits such as feeding are scarce. Previous studies suggest most squat lobsters are scavengers (e.g., Lovrich and Thiel, 2011) and are rarely active predators (Nicol 1932). However, *E. picta* were observed feeding on mesopelagic fauna on the Cape Fear coral mound (Quattrini et al., 2012). More data are needed to fully understand the extent of this feeding behavior and whether its association with the coral habitat may be linked. Expeditions using manned submersibles and remotely operated vehicles (ROVs) have provided opportunities to examine organisms like *E. picta in situ* and therefore gain better understanding of their ecology, biology and behavior.

Deep-sea coral habitats are hotspots of biodiversity (e.g., Jensen and Fredrickson, 1992; Mortensen et al., 1995; Rogers, 1999; Jonsson et al., 2004; Roberts et al., 2006; Ross and Quattrini, 2007; Henry and Roberts, 2007; Cordes et al., 2008; Roberts et al., 2008). Structure-forming deep-sea corals provide a variety of microhabitats (Buhl-Mortensen and Mortensen, 2005; Mortensen and Fosså, 2006; Buhl-Mortensen et al., 2010) which support a diverse faunal assemblage comprising recreationally, commercially, and ecologically important species. Some mega-faunal species are strongly associated with certain fine-scale habitat attributes, while others use these habitats more opportunistically.

Eumunida picta, frequently associated with deep-water corals, can be locally abundant and a numerically dominant member of the mega-invertebrate faunal assemblage (Cordes et al., 2008; Lessard-Pilon et al., 2010; Nizinski and Ames, 2017). Off the southeastern United States (SEUS), deep-sea coral habitats, composed mostly of the scleractinian coral *Lophelia pertusa* (Linnaeus 1758), are extensive and appear to represent some of the best-developed deep-coral habitat in U.S. waters (Ross and Nizinski, 2007; Hourigan et al., 2017). As part of several expeditions off the SEUS, a combination of collecting gears, including manned submersibles and trawls, were used to explore deep-sea coral habitats, yielding a variety of data on *E. picta*. Specific objectives of the present study were to: (1) document and quantify habitat utilization and preference of *E. picta* across a large geographic region; (2) quantify frequency of occurrence, abundance and density of *E. picta* in the different habitats where they were observed; (3) delineate geographic distribution; (4) synthesize life-history information, including size, sex, and reproductive status for collected specimens; and (5) analyze *in situ* behavioral observations, including feeding ecology and individual interactions among conspecifics.

2. Material and Methods

2.1 Site Descriptions

Brief descriptions of the study sites surveyed during this project are presented below. For additional details, see Ross and Nizinski (2007), Partyka et al. (2007), Ross and Quattrini (2007, 2009), and Quattrini et al. (2012) (Fig. 1).

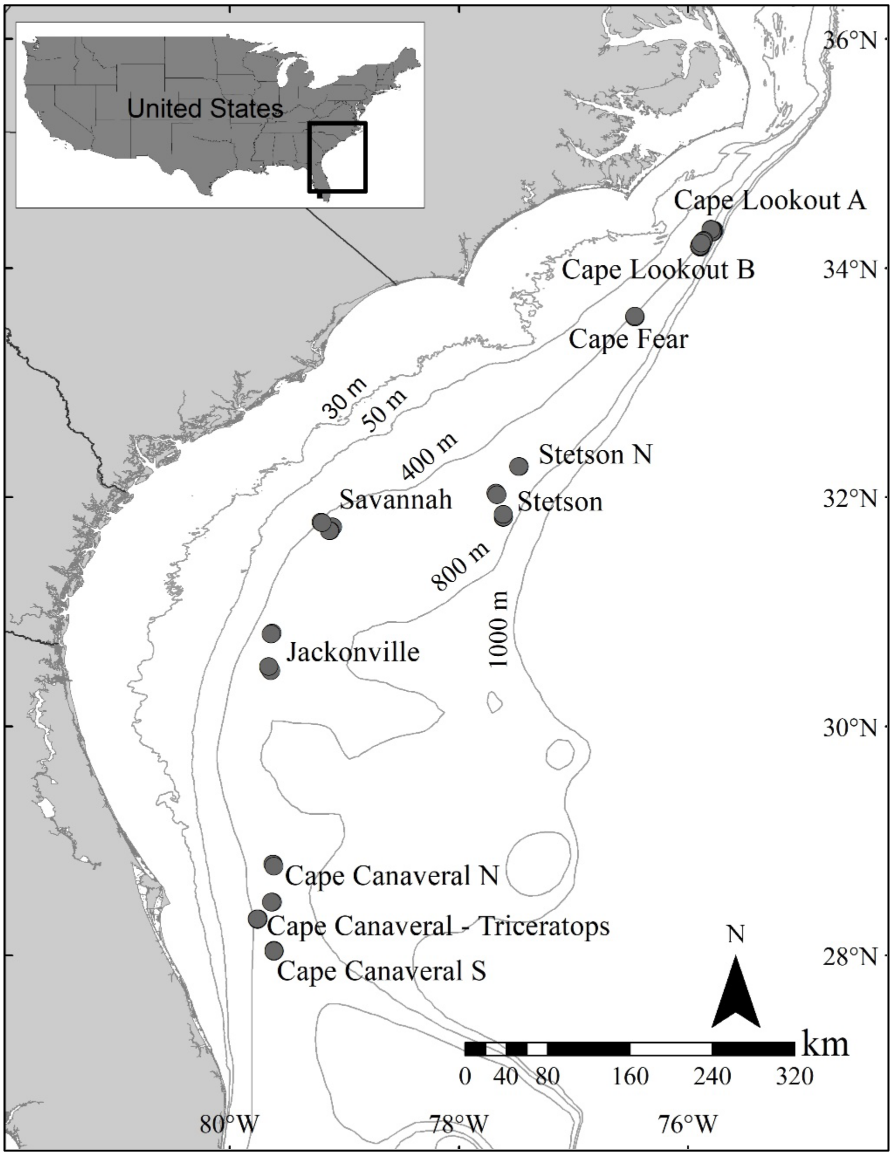

Figure 1. Sampling sites in the western North Atlantic off the southeastern United States.

Cape Lookout A and B: Off North Carolina, *Lophelia pertusa* occurs in mostly monotypic reef-like structures. These reefs are extensive and can extend horizontally for nearly a km and reach a vertical extent of 80–100 m.

Cape Fear: Off North Carolina, this site is characterized by a single large mound (see data in Quattrini et al., 2012). The mound is mostly covered (>75%) with low-profile (≤0.5 m, dead (90–100%) *L. pertusa*, particularly on the slope and top of the mound.

Savannah Banks: *Lophelia pertusa* habitat is less developed here compared with that at all other sites. Colonies of *L. pertusa* are smaller and sparsely scattered over a landscape of soft sediments.

Stetson Banks: Located farthest offshore compared with the other sites, Stetson Banks is characterized by an abundance of hard pavement and rocky structures in the south as well as coral-built mounds similar to the North Carolina sites in the north. *Lophelia pertusa* is scattered over rugged topography and is present in a variety of forms, including smaller, low-profile colonies as well as extensive complex coral matrices. This site supports higher coral diversity, including other scleractinian corals as well as black and bamboo corals.

Jacksonville: Rock ledges with a variety of attached coral species, including *L. pertusa* and mixed soft corals characterize this survey area. See also Paull et al. (2000) and Ross et al. (2015) for additional details.

Cape Canaveral: Coral habitats surveyed in this region occurred in two different depth zones. A highly diverse coral assemblage, including *L. pertusa*, covering tops of mounds surrounded by soft sediments and rubble best characterizes the deeper sites, designated as Cape Canaveral North and Cape Canaveral South, surveyed in this area. In contrast, Triceratops, three adjacent mounds separated from each other by about 500 m, is closer inshore, in shallower water, and located between the deeper sites. The mounds, capped by live *L. pertusa*, support a high diversity of other corals and are surrounded by coral rubble and coarse sand substrata.

Table 1. Station data off the southeastern US, 2000-2009, for Johnson-Sea-Link (JSL) submersible (SUB), otter trawl (OT), benthic sled (BS) and Tucker trawl (TT).

Station	Site	Date	Gear	Latitude Start	Longitude Start	Latitude End	Longitude End	Depth Range (m)	*E. picta* Observed	Sample Time (min)
JSL-04-4681	Cape Canaveral N	06/09/04	SUB	28.79	-79.62	28.79	-79.62	709-783	0	122
JSL-04-4682	Cape Canaveral N	06/09/04	SUB	28.80	-79.62	28.80	-79.62	760-773	0	122
JSL-04-4702	Cape Canaveral N	06/20/04	SUB	28.79	-79.62	28.79	-79.62	712-738	0	124
JSL-04-4703	Cape Canaveral N	06/20/04	SUB	28.78	-79.62	28.78	-79.62	741-755	0	104
JSL-09-3703	Cape Canaveral N	08/08/09	SUB	28.46	-79.63	28.46	-79.63	698-721	1	134
JSL-09-3704	Cape Canaveral N	08/08/09	SUB	28.46	-79.64	28.47	-79.64	714-737	0	118
JSL-04-4704	Cape Canaveral S	06/21/04	SUB	28.04	-79.61	28.04	-79.61	735-745	0	124
JSL-04-4705	Cape Canaveral S	06/21/04	SUB	28.04	-79.61	28.04	-79.61	679-725	2	110
JSL-09-3718	Cape Canaveral S	08/15/09	SUB	28.03	-79.61	28.04	-79.61	681-736	0	135
JSL-09-3719	Cape Canaveral S	08/16/09	SUB	28.04	-79.61	28.04	-79.61	681-722	0	150
JSL-09-3720	Cape Canaveral S	08/16/09	SUB	28.04	-79.61	28.04	-79.62	684-725	7	133
JSL-09-3721	Cape Canaveral S	08/17/09	SUB	28.04	-79.61	28.04	-79.61	681-709	1	150
JSL-09-3700	Cape Canaveral - Triceratops	08/06/09	SUB	28.32	-79.75	28.32	-79.75	396-461	99	168
JSL-09-3708	Cape Canaveral - Triceratops	08/10/09	SUB	28.32	-79.75	28.32	-79.75	391-465	77	169
JSL-09-3709	Cape Canaveral - Triceratops	08/11/09	SUB	28.32	-79.76	28.32	-79.76	401-445	13	149
JSL-09-3711	Cape Canaveral - Triceratops	08/12/09	SUB	28.31	-79.76	28.32	-79.76	401-442	6	149
JSL-09-3712	Cape Canaveral - Triceratops	08/12/09	SUB	28.32	-79.76	28.32	-79.76	399-442	19	131
JSL-02-3308	Cape Fear	08/13/02	SUB	33.57	-76.47	33.57	-76.47	369-449	333	149
JSL-03-3425	Cape Fear	08/21/03	SUB	33.57	-76.47	33.57	-76.46	369-394	404	146
JSL-03-3426	Cape Fear	08/21/03	SUB	33.57	-76.47	33.57	-76.47	368-431	329	147
JSL-03-3427	Cape Fear	08/22/03	SUB	33.57	-76.46	33.57	-76.46	380-434	40	138
JSL-03-3428	Cape Fear	08/22/03	SUB	33.57	-76.47	33.57	-76.46	368-397	384	126
JSL-04-4696	Cape Fear	06/17/04	SUB	33.57	-76.46	33.57	-76.46	389-402	7	114
JSL-04-4697	Cape Fear	06/17/04	SUB	33.58	-76.46	33.58	-76.46	394-411	13	102
JSL-05-4896	Cape Fear	10/20/05	SUB	33.57	-76.46	33.57	-76.46	372-399	267	148
JSL-05-4897	Cape Fear	10/20/05	SUB	33.58	-76.47	33.58	-76.47	404-443	110	126

CH-01-092	Cape Lookout A	08/28/01	OT	34.34	-75.80	34.33	-75.80	397-398	NA	NA
CH-01-094	Cape Lookout A	08/28/01	OT	34.32	-75.80	34.31	-75.79	409-434	NA	NA
CH-01-096	Cape Lookout A	08/28/01	OT	34.33	-75.80	34.32	-75.80	390-420	NA	NA
JSL-00-4206	Cape Lookout A	07/28/00	SUB	34.33	-75.77	34.32	-75.79	385-470	85	114
JSL-00-4207	Cape Lookout A	07/28/00	SUB	34.33	-75.79	34.32	-75.79	388-418	188	109
JSL-01-4361	Cape Lookout A	09/22/01	SUB	34.33	-75.79	34.33	-75.79	381-427	185	159
JSL-01-4362	Cape Lookout A	09/22/01	SUB	34.32	-75.79	34.32	-75.79	367-399	387	135
JSL-01-4363	Cape Lookout A	09/23/01	SUB	34.32	-75.79	34.32	-75.79	370-417	478	165
JSL-01-4364	Cape Lookout A	09/23/01	SUB	34.31	-75.78	34.31	-75.79	398-443	3	171
JSL-02-3304	Cape Lookout A	08/11/02	SUB	34.33	-75.78	34.33	-75.77	384-447	104	148
JSL-02-3305	Cape Lookout A	08/11/02	SUB	34.32	-75.79	34.32	-75.79	381-416	235	149
JSL-02-3306	Cape Lookout A	08/12/02	SUB	34.32	-75.79	34.32	-75.79	382-418	183	147
JSL-02-3307	Cape Lookout A	08/12/02	SUB	34.32	-75.79	34.32	-75.79	367-416	66	47
JSL-03-3430	Cape Lookout A	08/23/03	SUB	34.32	-75.79	34.32	-75.79	384-415	336	155
JSL-03-3431	Cape Lookout A	08/24/03	SUB	34.33	-75.78	34.32	-75.79	382-432	196	136
JSL-03-3432	Cape Lookout A	08/24/03	SUB	34.32	-75.79	34.32	-75.79	381-424	306	130
JSL-04-4692	Cape Lookout A	06/15/04	SUB	34.32	-75.79	34.32	-75.79	380-426	96	124
JSL-04-4693	Cape Lookout A	06/15/04	SUB	34.32	-75.79	34.33	-75.79	392-431	50	127
SJ-02-036	Cape Lookout A	08/10/02	OT	34.32	-75.80	34.32	-75.81	396-405	NA	NA
SJ-02-041	Cape Lookout A	08/11/02	BS	34.31	-75.79	34.31	-75.79	426-430	NA	NA
SJ-04-025	Cape Lookout A	06/15/04	OT	34.33	-75.80	34.32	-75.80	370-407	NA	NA
CH-06-015	Cape Lookout B	09/19/06	OT	34.21	-75.88	34.19	-75.89	423-443	NA	NA
CH-06-016	Cape Lookout B	09/19/06	OT	34.23	-75.87	34.22	-75.87	406-440	NA	NA
CH-06-021	Cape Lookout B	09/19/06	TT	34.19	-75.89	34.18	-75.90	0-431	NA	NA
CH-06-027	Cape Lookout B	09/20/06	OT	34.24	-75.86	34.22	-75.87	419-430	NA	NA
CH-06-028	Cape Lookout B	09/20/06	OT	34.21	-75.88	34.20	-75.88	408-455	NA	NA
CH-06-029	Cape Lookout B	09/20/06	OT	34.20	-75.90	34.18	-75.90	415-431	NA	NA
JSL-01-4365	Cape Lookout B	09/24/01	SUB	34.19	-75.90	34.19	-75.90	412-428	21	153
JSL-01-4366	Cape Lookout B	09/24/01	SUB	34.18	-75.89	34.18	-75.89	438-450	3	74
JSL-03-3429	Cape Lookout B	08/23/03	SUB	34.19	-75.90	34.19	-75.90	412-450	11	136
JSL-04-4694	Cape Lookout B	06/16/04	SUB	34.19	-75.89	34.19	-75.90	387-440	11	132

JSL-04-4695	Cape Lookout B	06/16/04	SUB	34.19	-75.89	34.19	-75.90	407-442	18	130
JSL-04-4683	Jacksonville	06/10/04	SUB	30.52	-79.66	30.52	-79.66	543-581	90	143
JSL-04-4684	Jacksonville	06/10/04	SUB	30.52	-79.66	30.51	-79.66	548-571	192	126
JSL-04-4685	Jacksonville	06/11/04	SUB	30.81	-79.63	30.81	-79.63	626-652	0	135
JSL-04-4686	Jacksonville	06/11/04	SUB	30.50	-79.65	30.50	-79.65	591-638	76	113
JSL-04-4700	Jacksonville	06/19/04	SUB	30.51	-79.66	30.51	-79.66	558-567	28	90
JSL-04-4701	Jacksonville	06/19/04	SUB	30.48	-79.64	30.48	-79.64	645-674	3	99
JSL-05-4907	Jacksonville	11/01/05	SUB	30.80	-79.64	30.80	-79.64	517-553	24	139
JSL-05-4908	Jacksonville	11/01/05	SUB	30.52	-79.66	30.52	-79.66	568-628	147	137
JSL-04-4687	Savannah Banks	06/12/04	SUB	31.74	-79.10	31.74	-79.09	497-541	2	101
JSL-04-4688	Savannah Banks	06/12/04	SUB	31.77	-79.19	31.78	-79.19	505-532	0	93
JSL-05-4900	Savannah Banks	10/22/05	SUB	31.74	-79.10	31.74	-79.09	500-544	9	134
JSL-05-4901	Savannah Banks	10/23/05	SUB	31.71	-79.12	31.71	-79.12	507-508	0	7
JSL-05-4902	Savannah Banks	10/26/05	SUB	31.70	-79.13	31.71	-79.12	497-519	1	139
JSL-05-4905	Savannah Banks	10/30/05	SUB	31.78	-79.20	31.77	-79.20	505-558	2	143
JSL-05-4906	Savannah Banks	10/30/05	SUB	31.77	-79.19	31.78	-79.19	507-543	0	86
JSL-03-3419	Stetson	08/17/03	SUB	32.03	-77.67	32.03	-77.67	592-622	41	131
JSL-03-3420	Stetson	08/17/03	SUB	32.03	-77.68	32.03	-77.68	624-640	4	126
JSL-04-4689	Stetson	06/13/04	SUB	31.82	-77.61	31.82	-77.60	666-672	2	120
JSL-04-4698	Stetson	06/18/04	SUB	31.82	-77.61	31.83	-77.61	680-703	1	109
JSL-04-4699	Stetson	06/18/04	SUB	31.85	-77.61	31.85	-77.61	658-721	6	130
JSL-05-4903	Stetson	10/27/05	SUB	32.02	-77.67	32.02	-77.67	613-633	0	111
JSL-05-4904	Stetson	10/27/05	SUB	31.85	-77.61	31.85	-77.61	649-705	5	143
JSL-05-4898	Stetson N	10/21/05	SUB	32.27	-77.47	32.27	-77.47	549-646	13	118
JSL-05-4899	Stetson N	10/21/05	SUB	32.26	-77.48	32.26	-77.48	540-603	24	123

2.2 Data Collection

Data were collected during 10 research cruises conducted in late summer to late fall from 2000-2005 and 2009 (Table 1). See Ross and Quattrini (2007, 2009) for station details for the 2000-2005 cruises. An additional cruise was conducted off east-central Florida in August 2009 using the R/V *Seward Johnson* and the manned submersible *Johnson-Sea-Link II* (JSL).

2.2.1 Field methodology

Assessments of habitat type and *in situ* ecological and behavioral observations of individuals of *E. picta* were made using the manned submersibles, *Johnson Sea Link I* and *Johnson Sea Link II* (JSL; Harbor Branch Oceanographic Institution). Submersibles were equipped with: 1) internal and external video cameras; 2) two external laser pointers mounted 25 cm apart for estimating area, size, and densities; and 3) manipulator arm and suction device for collections. Video data were recorded throughout the entire submersible deployment, which typically lasted two to three hours per dive (see Ross and Quattrini 2007 for more details).

Specimens of *E. picta* were collected opportunistically at sampling locations throughout the project's geographic (28° 02.09' N, 79° 36.87' W to 35° 37.30' N, 74° 48.27' W) and bathymetric (301–783 m) ranges. Individuals were collected either directly from the coral substrata itself or from substrata adjacent to coral habitat using the JSL manipulator arm or suction device, various trawls (e.g., otter, Tucker), a benthic sled, and traps (Table 1).

2.2.2 Video analysis

Video from 70 dives conducted in deep-sea coral habitats along the SEUS slope were reviewed to document presence of *E. picta*. When present, video was analyzed to determine abundance, habitat use, and density estimates, as well as document behavior of *E. picta*. Time and depth were usually displayed on the video overlay; however, if absent, time was back-calculated using data from audio logs created by the lead science diver. Individual video frames were examined to estimate abundances as accurately as possible, taking care to count individuals only once. Habitat, broadly defined as the substratum where individual *E. picta* were observed, was categorized as dead coral (dead portions of intact colonies of *L. pertusa*), live coral (live, intact colonies of *L. pertusa*), rubble (low relief, dead pieces of *L. pertusa* lying on the seafloor), soft substratum, or other. The other category referred to a variety of natural and fabricated structures, including, but not limited to, rocks, sponges, black coral, octocorals, anemones, or traps.

Vertical and horizontal position of *E. picta* in relation to the various substrata were also recorded. Substrata exhibiting vertical relief were subjectively divided along the vertical plane into three equal zones: upper, middle and lower (Fig. 2). The zone where each individual squat lobster was observed was recorded. Whether an individual was observed on top of, or at the highest point on, the substratum was also noted. However, for statistical analyses, individuals observed on tops of coral colonies or other features were enumerated with those observed in the upper zone. Rubble and soft substrata did not exhibit vertical relief; therefore, the vertical position of *E. picta* was not assessed for these substrata. Horizontal position in relation to the substrata was also noted only for those individuals observed on coral substrata. Individuals were recorded either as embedded within the coral matrix or on the outer surface of the coral colony (Fig. 2). Individuals were considered embedded when at least the entire abdomen, up to the posterior edge of the carapace, was not visible, but was hidden within the coral matrix. Individuals on the outer surface were completely exposed (i.e., whole animal was visible).

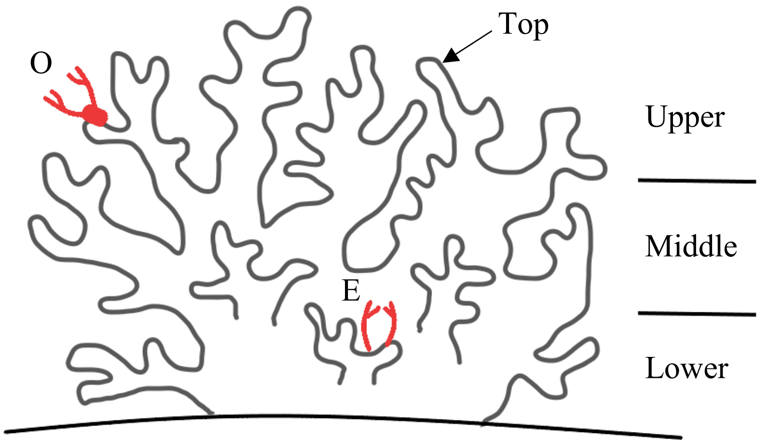

Figure 2. Diagram of a coral colony illustrating the vertical and horizontal placement of individuals of *Eumunida picta*. The colony was subjectively divided into 3 zones (upper, middle, lower) to describe vertical placement of individuals within the coral habitat. "Top" is a subdivision of the Upper zone, and was included with the Upper zone in statistical analyses. Horizontal placement within coral habitat was designated as (O)uter edge or (E)mbedded in the coral framework.

Behavioral observations for each *E. picta* were documented and classified into six broad categories. These categories, defined in Table 2, included 1) claws extended, 2) walking, 3) fighting, 4) feeding, 5) swimming, or 6) other.

Table 2. Summary and definition of behavioral observations documented for individual *E. picta*.

Observed Behavior	Definition
Claws Extended	An individual sitting still on the substratum with both claws raised vertically above the body into the water column.
Walking	An individual observed moving over the substratum or substrata.
Fighting	Any agonistic display such as pushing, pinching, or grabbing between two or more individuals.
Feeding	An individual holding or capturing prey items either from the water column or from the benthos and bringing those items towards the mouthparts.

Swimming	An individual quickly moving its abdomen ventrally toward the body (i.e., “tail flip”), thus propelling itself over the substrata.
Other	Any other recognizable behavior, including, but not limited to, waving claws, not extending claws or extending only one claw, moving legs, sitting still, stretching entire body, grabbing at passing fish, or undetermined.

To determine if substrata influenced the occurrence or frequency of a particular behavior, each behavior was enumerated by type of substrata on which the behavior was observed. In instances where multiple behaviors were recorded for a single individual, each behavior in the observed sequence was counted. Observations of an individual *E. picta* displaying a single behavior while straddling more than one type of substrate (e.g., partially on dead and live coral, or rubble and soft substrata) were excluded. Counts of all behaviors observed were square-root transformed to downweight the contribution of the high number of the claws-extended behavior compared with those of other behaviors.

Still frames that included both the habitat and associated *E. picta* were taken from videos where habitat was clearly visible, in focus, and laser pointers were visible. From these still frames, 2-dimensional area (length x width in m^2) of the habitat where *E. picta* were observed was estimated using laser pointers as a spatial reference. The relative density of *E. picta* (no. ind. observed/m^2 area of habitat) was documented for each still frame where area of coral habitat was estimated to be ≥ 1 m^2. Based on our observations of habitat use and visual resolution of the images, 1 m^2 represents the smallest area that would provide the most realistic estimates of density. Only coral substrata were considered since this was by far the most common habitat sampled, and *E. picta* was most frequently found associated with coral. These are conservative estimates because area calculations do not account for the 3-D nature of the coral nor individuals deeply embedded in the coral colony. Complete dataset compiled from video analyses are available in McClain-Counts et al. (2022)

2.2.3 Laboratory analysis

Eumunida picta specimens were examined (n = 182; Appendix A) and measured (n = 178) following the methodology of de Saint Laurent and Macpherson (1990). Carapace length (CL) and carapace width (CW) for each individual were measured to the nearest 0.01 mm using digital calipers. However, the smallest individuals (< 7 mm CL) were measured with a microscope fitted with an ocular micrometer. Sex was determined based on position of the gonopores and shape of the pleopods (Thiel and Lovrich, 2011). For ovigerous females, a subsample of 15 eggs was measured to the nearest 0.01 mm diameter using an ocular micrometer. All specimens are cataloged and deposited in the invertebrate zoology collection at the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

2.3 Statistical Analysis

Abundance data for *E. picta* were examined as a function of habitat, region, depth, and sampling event. Habitat categories were limited to live and dead *L. pertusa*, since these were the only habitats where sample sizes were sufficient for statistical analysis. To assure sample sizes were adequate, geographic range was divided into three regions based on latitude, overall composition of coral assemblage and habitat characteristics, and number of sampling events. Moving north to south, these regions included the northern region comprising the three North Carolina study locations (Cape Lookout A and B, and Cape Fear), the middle region comprising the Savannah Banks, Stetson Banks, and Jacksonville study locations, and the southern region comprising the three Cape Canaveral study locations. Depth was partitioned based on known bathymetric distribution of *E. picta.* Shallow, defined as 300–600 m depth, refers to the depth range where individuals are more likely to occur based on previously reported occurrences, whereas deep, defined as depths greater than 600 m, refers to depths greater than the reported bathymetric limits of this species. Each sampling event was denoted by cruise year.

A Negative Binomial Hurdle model selection approach was used to address the questions of whether presence of at least one *E. picta* is a function of habitat, region, depth and/or sampling event, and secondly, when *E. picta* is present, is abundance of squat lobsters a function of these same factors (Supplemental Table 1). Hurdle models, a class of models for count data that accommodates excess zeros and over-dispersion, are two-part models that specify one process for zero counts and another process for positive counts (Mullahy, 1986). The first part models whether the observation is positive or not (i.e., presence/absence of a squat lobster). The second part, in this case a negative binomial model, fits only positive counts (i.e., if a squat lobster is present, how many were observed). The negative binomial family of models include an unexplained heterogeneity parameter that allows for the mean and variance to be different making this model the better option because negative binomial models can deal with over- and under-dispersion as well as excessive zeros (Su and He, 2013). As all explanatory variables were categorical, the intercept of the model represents a baseline condition, and all parameter estimates reflect differences from this baseline. For these models, the levels of each variable chosen to represent the baseline conditions included dead coral habitat, the northernmost region (North Carolina), shallow depths, and the first sampling event. The fitted models were explored visually using rootograms (Kleiber and Zeileis, 2016). Analyses were conducted in R, version

4.0.2 (R Core Team, 2020) using RStudio version 1.1.456 (RStudio Team, 2016) with the *countreg* (Zeileis and Kleiber, 2018) and *pscl* (Jackman, 2020) packages.

To determine whether *E. picta* occurred more frequently on a particular substratum or location on that substratum, abundances of *E. picta* were analyzed using log-linear ANOVA. Habitat (dead or live coral), vertical position (upper, middle, lower zones) and horizontal position (embedded within or on outer surface) in relation to the coral colony were the independent variables in this analysis.

3. Results

Seventy submersible dives conducted at deep-sea coral habitats from Cape Lookout, NC to Cape Canaveral, FL (Fig. 1) were analyzed to assess frequency of occurrence, abundance, density estimates, habitat utilization, and behavioral observations of *E. picta*. From the resulting 8925 minutes of videotape, 5744 individuals of *E. picta* were observed during 57 of 70 dives. No *E. picta* were observed in the remaining 13 dives, most of which were conducted at the most southern sites (i.e., 3 dives from Savannah Banks, 1 at Stetson Banks, 1 off Jacksonville, 5 at Cape Canaveral North and 3 dives at Cape Canaveral South).

3.1 Frequency of Occurrence and Abundance

Compared with other regions sampled, this squat lobster occurred in highest abundance off North Carolina, where 84% of the total individuals (n = 4849; Fig. 3) were observed. During all 29 JSL dives made at the three NC sites, Cape Lookout A (n = 15), Cape Lookout B (n = 5), and Cape Fear (n = 9), *E. picta* usually were observed in high abundance (mean = 167 individuals/dive; 1.3 ind/minute bottom-time). However, during seven dives less than 20 individuals were observed (0.08 ind/min bottom-time). Highest abundances (50% of all individuals) were noted at Cape Lookout A. Second highest abundance (33% of total individuals) of *E. picta* was recorded from Cape Fear (n = 1887; Fig. 3). Although Cape Lookout A was sampled most frequently, the Cape Fear site had higher numbers of individuals observed per dive compared with those at Cape Lookout A (mean = 210 ind/dive; 1.6 ind/min bottom-time versus 193 ind/dive; 1.4 ind/min bottom-time, respectively). Cape Lookout B exhibited some of the lowest numbers of individuals observed during any of the JSL dives, with < 20 individuals observed during four of the five dives conducted at this site (0.1 ind/min bottom-time).

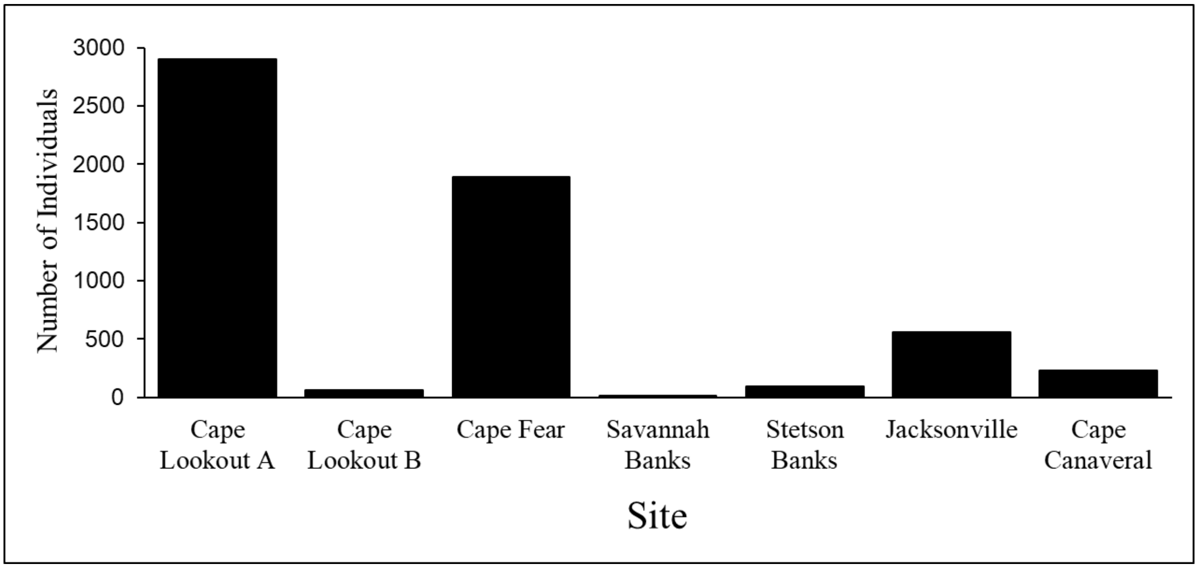

Figure 3. *Eumunida picta* abundance observed at each sampling site.

The fewest number of individuals of *E. picta* were reported from Savannah Banks. Only 14 individuals were observed over four of the seven JSL dives conducted (Fig. 3). Numbers of individuals observed per dive were consistently low (1 or 2 individuals observed during three of the four dives; 0.03 ind/min bottom-time).

Nine JSL dives were conducted in the Stetson region, two of which were located at Stetson North where coral habitat is more extensive than in the southern portion of the region. Individuals of *E. picta* were observed during all but one of these dives. Overall, abundances were low at this site; only 96 total individuals were observed during the nine dives. Numbers of individuals observed per dive ranged from 1–41 ind/dive (0.1 ind/min bottom-time) with over half of dives recording < 10 individuals (0.3 ind/min bottom-time). Although more individuals were observed at the two Stetson North stations (0.2 ind/min bottom-time versus 0.08 ind/min bottom-time at the other Stetson stations), the highest abundance of *E. picta* (41 ind; 0.3 ind/min bottom-time) observed at any one station was recorded at an easternmost, shallower station in the mid-portion of the survey area.

Eight JSL dives were conducted off Jacksonville; individuals of *E. picta* (n = 560; Fig. 3) were observed during seven of these dives. More than 20 individuals were observed per dive for all but one of the dives conducted in this region (range 3–192; mean = 70.0 ind/dive; 0.7 ind/min bottom-time).

Cape Canaveral was the most frequently sampled site in this study; dives were distributed throughout the region with six dives at Cape Canaveral North, five at Triceratops, and six at Cape Canaveral South. However, of 17 JSL dives conducted in this region, *E. picta* (n = 225; range 1–99; mean = 13.2 ind/dive; 0.2 ind/min bottom-time; Fig. 3) were only observed during nine of these dives, most of which were at the shallower, inshore Triceratops mounds. Numbers of individuals observed per dive were low with 11 individuals observed at Cape Canaveral North (one dive; n = 1 ind; 0.01 ind/min bottom-time) and Cape Canaveral South (three dives; n = 10 ind; 0.03 ind/min bottom-time) stations combined. Abundances were usually higher at Triceratops, particularly on the middle mound, the largest of the three. Here, 77 and 99 individuals were recorded (0.5 ind/min bottom-time) during two dives. Fewer individuals (6–19 individuals/dive; 0.09 ind/min bottom-time) were observed at the western-most (i.e., inshore) mound.

3.2 Habitat Utilization

Eumunida picta, most frequently observed as solitary individuals, were found almost exclusively on some type of structure (Fig. 4). Only about 2% of all individuals (139 of 5744) occurred on soft substrata. Among substrata utilized by *E. picta*, approximately 54% of individuals (n = 3114) were observed on dead *L. pertusa*, 25% on live *L. pertusa*, 17% on rubble, and 1% on other types of substrata, such as rock or other organisms, including sponges, anemones, octocorals or black corals.

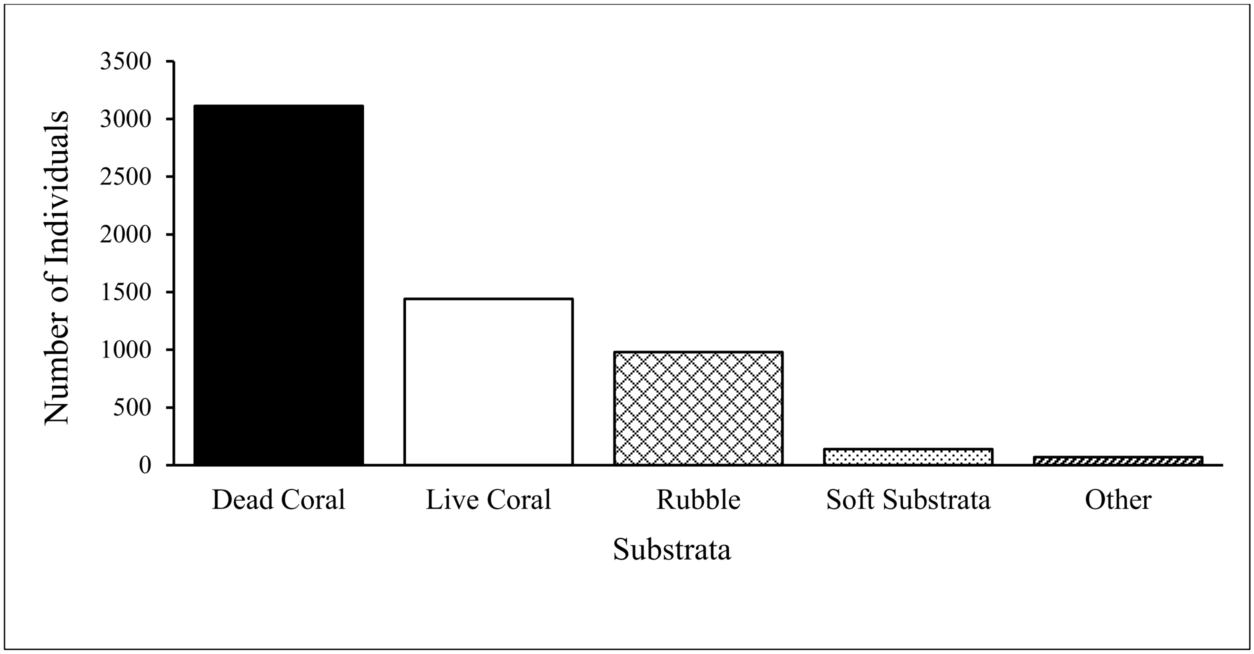

Figure 4. *Eumunida picta* abundance observed on each type of substrata.

Habitat use was similar among all sites (Fig. 5). Individuals of *E. picta* were most frequently observed on dead *L. pertusa* at five (Cape Lookout A, Cape Fear, Stetson Banks, Jacksonville, and Cape Canaveral) of the seven sites and observed on live *L. pertusa* at all sites, except Savannah Banks. Live coral was the most frequently utilized substratum at Cape Lookout B and the second most utilized substratum (after dead coral) at Cape Lookout A and Cape Canaveral.

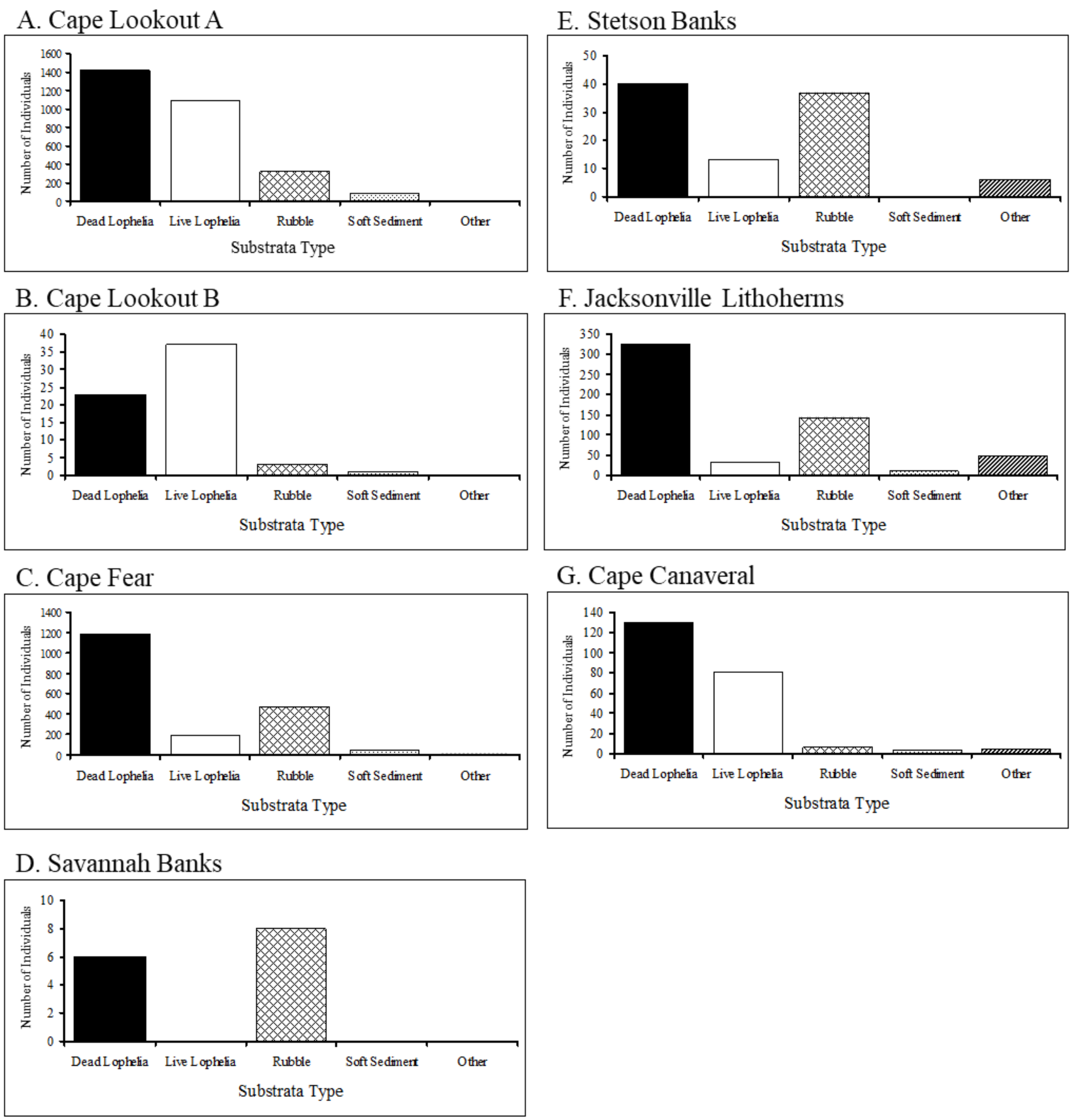

Figure 5. *Eumunida picta* abundance observed on each type of substrata at each sampling site.

Abundances of *E. picta* were further examined as a function of habitat, region, depth and/or sampling event (i.e., cruise). The Negative Binomial Hurdle Model fit the observed frequencies relatively well. Results of the model selection revealed two models had the most support (accounting for ~97% of the model weights): one with additive effects of coral habitat, region, and depth, and one that also included the sampling event variable. However, sampling event parameters were not significant in either part of the hurdle model. Given this result and the fact that including a 'time' parameter in the model was of questionable utility due to the frequency of sampling, we only discuss results from the model that excluded sampling event. Coral habitat, depth and region significantly influenced presence and/or abundance of this squat lobster (Fig. 6). Presence of *E. picta* was driven primarily by the region in which the survey was conducted (Table 3). These squat lobsters were more likely to be observed at study locations off North Carolina than at the other regions surveyed.

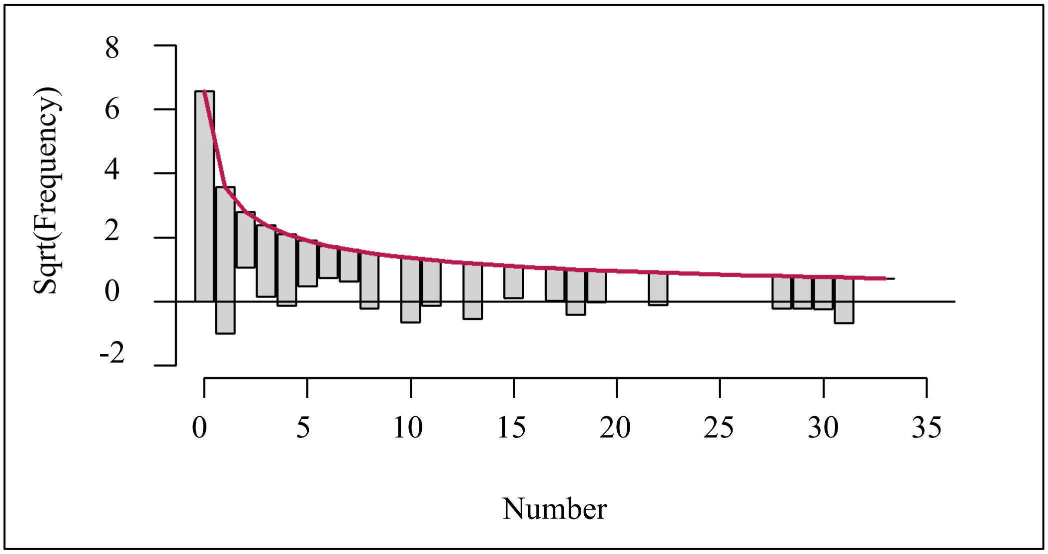

Figure 6. Rootogram of the two-part Negative Binomial Hurdle Model, with number of squat lobsters as a function of habitat, region and depth. Rootograms are used to visually compare observed frequencies (bars) with model-predicted frequencies (line) to indicate where the model is over- and underfitting (Kleiber and Zeileis 2016).

Table 3. Results of the two-part Negative Binomial Hurdle Model: A) the zero hurdle model, using a binomial with logit link; and B) count model, using a truncated negative binomial with log link. Number of squat lobsters was a function of habitat (Dead *Lophelia* = 0; Live *Lophelia* = 1), region (North Carolina = 0, Georgia/Stetson/northern Florida = 1, and Cape Canaveral = 2), and depth (< 600 m = 0, > 600 m = 1).

A.

Parameter	Estimate	Standard Error	p-value
Intercept	3.71	0.78	< 0.001
Habitat = 1	-0.66	0.44	0.132
Region = 1	-2.74	0.82	< 0.001
Region = 2	-3.23	0.87	< 0.001
Depth = 1	-0.75	0.47	0.115

B.

Parameter	Estimate	Standard Error	p-value
Intercept	4.49	0.30	< 0.001
Habitat = 1	-0.98	0.34	0.004
Region = 1	-1.06	0.57	0.065
Region = 2	-1.56	0.47	0.001
Depth = 1	-1.97	0.60	0.001

Contingent on presence, the abundance of *E. picta* was influenced by all three factors (Table 3). When at least one squat lobster was present, *E. picta* were observed more frequently on dead *Lophelia* and in shallower water (< 600 m). By region, again, contingent on presence of at least one *E. picta*, the abundance was not significantly different between the northern (North Carolina) and the middle (Georgia/northern Florida) regions, but was significantly lower in the southern region (Cape Canaveral) relative to North Carolina (Table 3).

To investigate the relationships between *E. picta* abundances and these variables further, potential interactions between the region and depth variables were explored. However, deep coral habitats were not found/surveyed in the North Carolina region making it impossible to produce a straightforward matrix of interaction effects. Thus, the Hurdle Negative Binomial models were rerun using a single, 5-level factor representing each region/depth combination (e.g., North Carolina Shallow). The results were qualitatively similar (Supplemental Table 2). The most supported model, with 64% of the weight, included the region and habitat variables (Table 4). The second-most supported model, with 34% of the weight, included the same two variables plus the interaction effect, but no parameter estimates of the interaction effects were significant. Based on results of the most supported model, the likelihood of at least one squat lobster being present was significantly lower at three of the region levels (Georgia/Stetson/northern Florida Shallow, Georgia/Stetson/northern Florida Deep, Cape Canaveral Deep) relative to the North Carolina Shallow, dead coral habitat condition. Cape Canaveral Shallow (i.e., Triceratops) was not significantly different from North Carolina Shallow. When at least one individual was present, habitat and all four region levels significantly and negatively affect *E. picta* abundance, relative to the North Carolina Shallow, dead coral habitat condition. Squat lobster individuals were observed on rubble at all sites (Fig. 5). This type of substratum was most frequently utilized at Savannah Banks, where that habitat type was abundant. Although more individuals were observed on dead *L. pertusa* at Stetson Banks, similar numbers of individuals were observed on rubble as were observed on dead coral (40 versus 37 individuals, respectively) at this site. Rubble was the second most utilized substratum at both Jacksonville and Cape Fear.

Table 4. Results of the two-part Negative Binomial Hurdle Model: A) the zero hurdle model, using a binomial with logit link; and B) count model, using a truncated negative binomial with

log link. The number of squat lobster was a function of habitat (Dead *Lophelia* = 0; Live *Lophelia* = 1) and region (a five-level factor that incorporated both region, with North Carolina = 0, Georgia/Stetson/northern Florida = 1, and Cape Canaveral = 2 and depth, with < 600 m = 0, > 600 m = 1).

A.

Parameter	Estimate	Standard Error	p-value
Intercept	3.79	0.79	< 0.001
Habitat = 1	-0.78	0.48	0.106
Region = 1, Depth = 0	-3.40	0.84	< 0.001
Region = 1, Depth = 1	-2.87	0.84	0.001
Region = 2, Depth = 0	-1.14	1.28	0.372
Region = 2, Depth = 1	-4.78	0.89	< 0.001

B.

Parameter	Estimate	Standard Error	p-value
Intercept	4.58	0.30	< 0.001
Habitat = 1	-1.11	0.35	0.002
Region = 1, Depth = 0	-1.52	0.52	0.004
Region = 1, Depth = 1	-2.83	0.46	< 0.001
Region = 2, Depth = 0	-1.18	0.57	0.037
Region = 2, Depth = 1	-4.85	0.80	< 0.001

Individuals of *E. picta* were observed infrequently (1.2 % of total individuals) on other substrata at five of the seven sites (Fig. 5). No individuals were observed on other substrata at Cape Lookout B and Savannah Banks. Utilization of other types of substrata was most common at Jacksonville, where approximately half of individuals (24 of 45 individuals) observed on these types of substrata were found on rock. This is not surprising given that the habitat at many of the Jacksonville stations is composed typically of rock ledges with attached fauna. Half of the individuals on other substrata at Stetson Banks were also observed on rock; Stetson Banks is the only other site where rock ledges were observed. Sponges were the second most utilized other substratum. Again, *E. picta* were most commonly observed on sponges at Jacksonville (21 of 23 total individuals observed on sponges). One of the other two individuals was observed at Cape Canaveral, the other at Cape Fear. Rarely were *E. picta* present on anemones, octocorals, and black corals.

3.3 Position

Given that live and dead colonies of *L. pertusa* were the most frequently utilized substrata and the dominant substrata that provided 3-D structure with considerable vertical relief, position of squat lobsters was examined only on *L. pertusa* colonies. The majority of *E. picta* were observed on the upper zone of the coral (including the highest point on the colony; Fig. 7) with 45% of individuals found in this zone. Only 15% of these individuals (305/2038) were found on the distal tops of the coral colonies. More individuals of *E. picta* were observed in the middle zone than occurred in the lower zone of the colonies, with 33% and 22% of individuals observed in these zones, respectively.

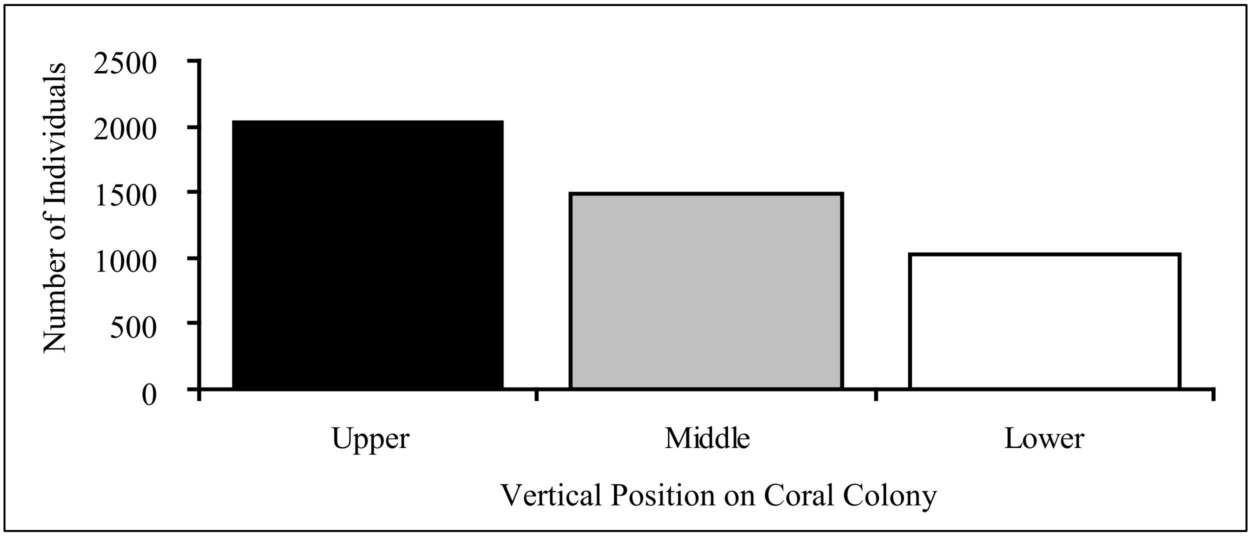

Figure 7. *Eumunida picta* abundance expressed in terms of an individual's vertical position in relation to the coral colony. Coral colonies were subjectively divided into three parts: upper, middle and lower zones (see Fig. 2 for clarification).

When examining the position of squat lobsters relative to the coral matrix, significantly more individuals were observed on the outer surfaces of the coral than were embedded within the coral matrix (Fig. 8; 86% versus 14%). For those individuals observed on the outer surface, frequency of occurrence increased with increasing elevation off the bottom. More individuals were observed in the upper zone and tops of colonies than occurred in the middle or lower zones (45%, 31%, and 24%, respectively). In contrast, individuals of *E. picta* embedded in the coral matrix were most frequently observed in the middle zone (44% of embedded individuals). Although the number of individuals observed embedded in the upper zone was comparable to that of the middle zone (n = 253 versus 269), fewer (n = 93, 15%) individuals were observed embedded in the matrix in the lower zone. Very few individuals (n = 6) were observed embedded on the distal tops of colonies.

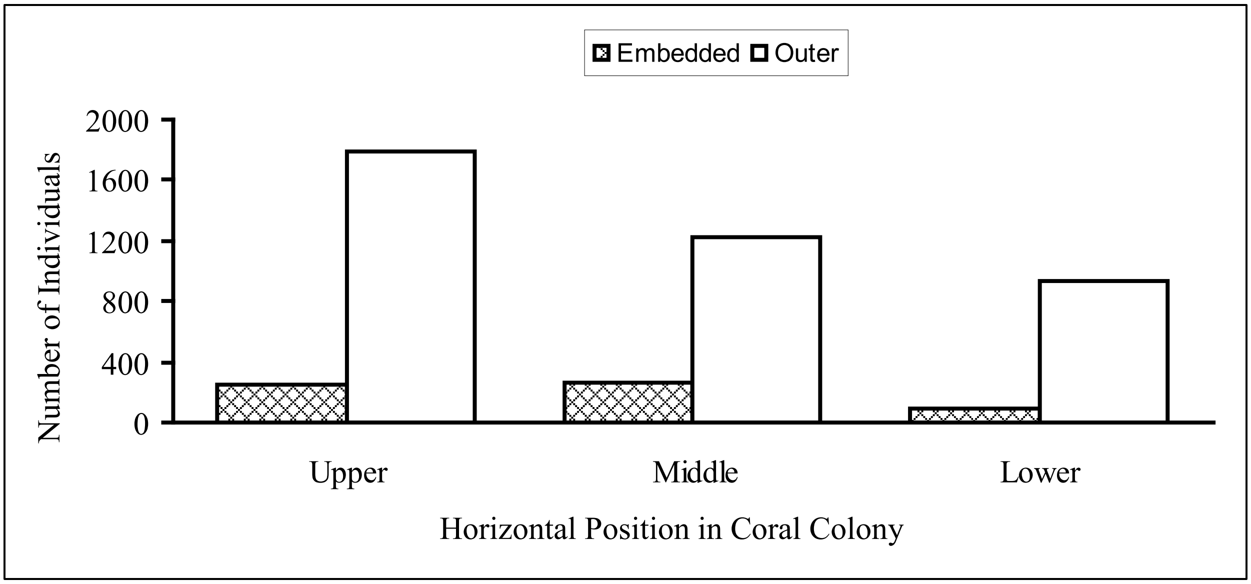

Figure 8. *Eumunida picta* abundance expressed in terms of an individual's horizontal position in relation to the coral colony. Individuals were either exposed and on the outer surface of the coral colony (white bars) or embedded within the coral matrix (hatched bars).

Coral habitat (dead versus live coral), vertical position on the coral (upper, middle, or lower zone), as well as horizontal position in relation to the coral matrix (outer surface versus embedded in coral matrix) were significant factors influencing small-scale squat lobster distributions (Table 5). The model was saturated (likelihood ratio, df = 0) and fit the data since the three-way interaction term was not significant. All two-way interaction terms were significant suggesting mutual dependence among the three variables.

Patterns of frequency of occurrence were similar for numbers of *E. picta* found on dead versus live *L. pertusa* substrata (Fig. 9). However, *E. picta* were more likely to be observed on dead coral (Chi-Square, 119.07, $p < 0.0001$) than on live coral. Position of individual squat lobsters in relation to the coral colony was also significant (Chi-Square, 216.95, $p < 0.0001$) with more individuals likely observed in the upper and middle zones of the coral than in the lower zone ($p < 0.0001$). *Eumunida picta* were observed most frequently on the outer surface of the upper zone of the coral regardless of whether the coral was live or dead. Numbers of individuals observed on dead coral substrata were more similar between the different vertical zones (41%, 32%, and 27% at upper, middle and lower zones, respectively; Fig. 9a). In contrast, on live coral substrata, frequency of individuals decreased more dramatically along the vertical gradient from the upper to lower zones (54%, 34%, and 12% of individuals at upper, middle and lower zones, respectively; Fig. 9b). Additionally, horizontal position in relation to the coral matrix was also significant (Chi-Square, 1242.83, $p < 0.0001$) with more individuals observed on the outer surface of the coral than embedded in the coral matrix.

Table 5. Maximum Likelihood (Loglinear) Analysis of Variance for *E. picta* abundance data. Habitat refers only to coral substrata (live or dead). Position refers to the vertical position of individuals in relation to the coral mound (upper, middle, lower). Bed refers to the horizontal position of individuals in relation to the coral mound (outer surface, embedded in coral matrix).

Source	DF	Chi-Square	Pr > Chi-Square
Habitat	1	119.07	< 0.001
Position	2	216.95	< 0.001
Habitat*Position	2	50.17	< 0.001
Bed	1	1242.83	< 0.001
Habitat*Bed	1	116.53	< 0.001
Position*Bed	2	32.04	< 0.001
Habitat*Position*Bed	2	4.18	0.1240
Likelihood Ratio	0		

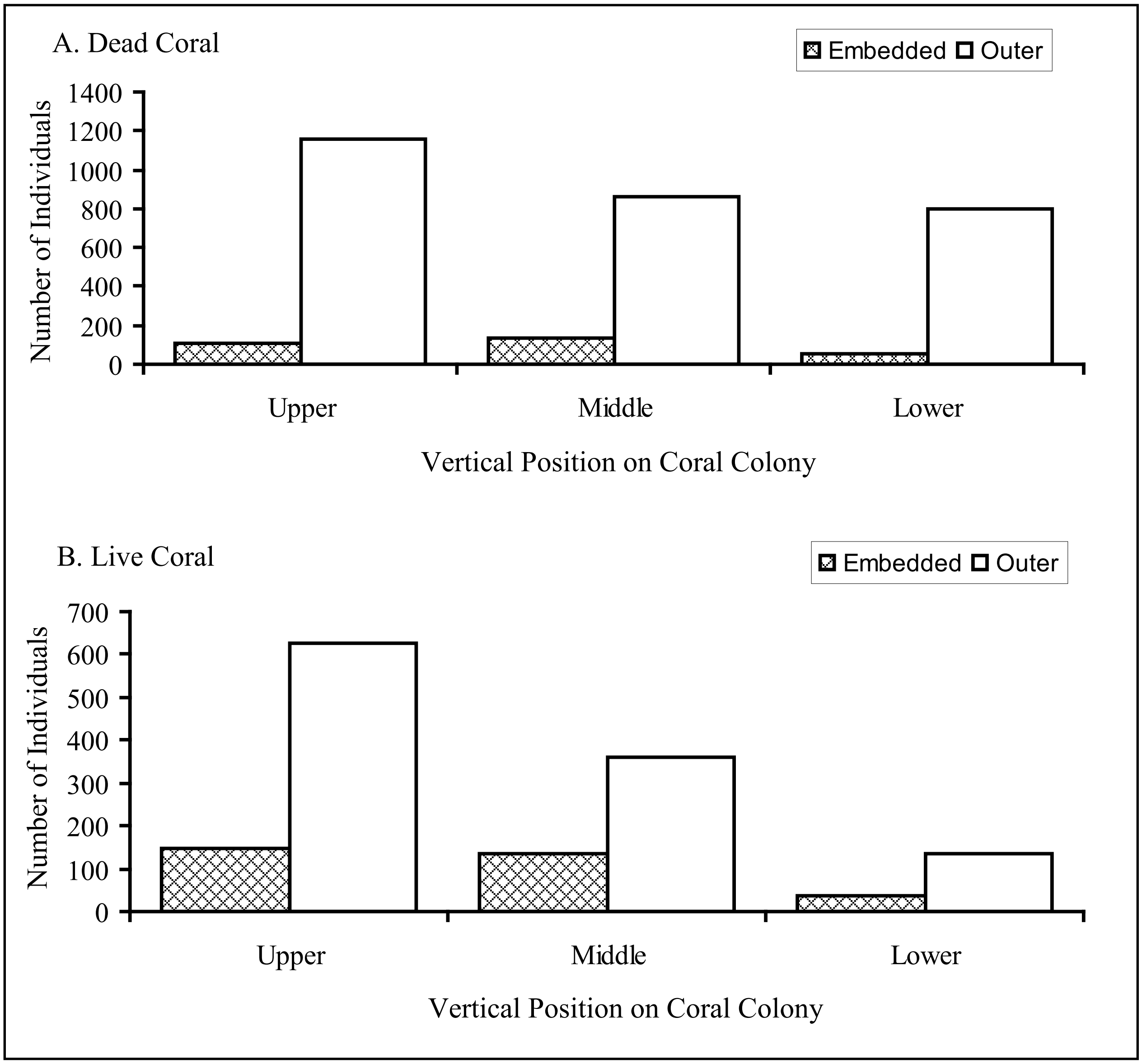

Figure 9. *Eumunida picta* abundance expressed in terms of an individual's vertical and horizontal position in relation to (A) dead and (B) live coral. Individuals were either exposed and observed on the outer surface of the coral colony (white bars) or embedded within the coral matrix (hatched bars).

3.4 Density

Density estimates (based on 98 instances where at least one individual was observed in an area ≥ 1 m^2) of *E. picta* were calculated based on number of individuals observed on coral substratum. Squat lobsters appear to be distributed over the available habitat and not aggregated into relatively small amounts of space within these habitats. Area of coral substratum analyzed per frame ranged from 1.0 to 18.3 m^2 (2.3 ± 0.02 (mean ± SE); median = 1.8 m^2). Density estimates of individuals on coral substrata ranged from 0.2 to 6.8 ind/m^2 (1.3 ± 0.1 ind/m^2); median 0.7 ind/m^2).

Since differences in habitat use by *E. picta* were observed, density estimates were calculated for dead and live coral substrata separately. The amount of dead coral substratum analyzed per frame ranged from 1.0 to 15.8 m^2; density estimates ranged between 0 and 7.1 ind/m^2 (1.0 ± 0.1; median 0.6 ind/m^2). In general, areas of live coral substratum observed were smaller (range of 1.0–6.8 m^2) than areas of dead coral appearing in the frame. However, individuals observed per unit area (0–6.8 ind/m^2; 1.3 ± 0.3; median = 0.4 ind/m^2) were comparable to those observed on dead coral.

Density estimates also differed by geographic region. Highest densities of squat lobsters were observed at the study sites off North Carolina where coral densities were also highest. Cape Lookout A had the highest mean density estimate (2.4 ind/m^2), followed by that for Cape Fear (1.4 ind/m^2). Mean densities were lower at more southern sites with Cape Canaveral Triceratops averaging 1.0 and Jacksonville only 0.5 ind/m^2.

3.5 Behavioral Observations

Eumunida picta is a dynamic species as evidenced by the variety of behaviors (Table 2) observed *in situ* during analysis of approximately 150 hrs of video (Plate 1).

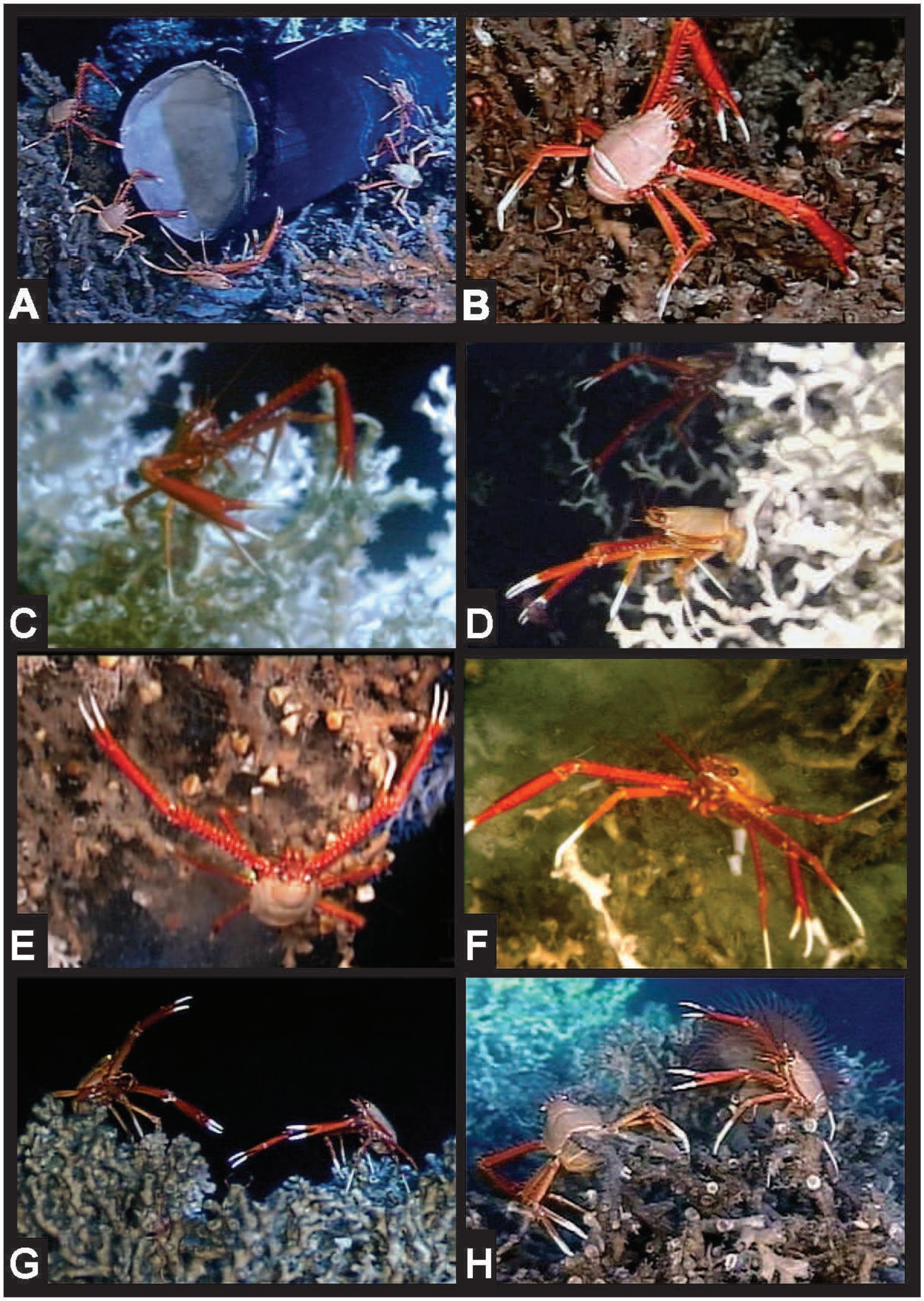

Plate 1. Various behaviors of *Eumunida picta* observed at habitats of *Lophelia pertusa* located off the southeastern coast of the United States (Cape Lookout, NC to Cape Canaveral, FL) at 279–725 m depth. Images produced from videos taken during dives using manned submersibles *Johnson-Sea-Link* I and II. A) Several individuals of *E. picta* attracted to baited fish trap. 365 m. B) Grazing on epifauna growing on *L. pertusa* branches. 364 m. C) Defensive display. 405 m. D) Claws-extended display. One individual with recently caught Lanternfish (Myctophidae). 405 m. E, F) Claws-extended display. 394 m and 405 m. G) Fighting Display. Larger individual (left) backed down and swam away. 363 m. H) Two individuals in close proximity on dead coral. Although usually solitary, multiple individuals were occasionally observed together without antagonistic interactions. 368 m.

Individuals were usually observed demonstrating one behavior per observation (n = 5569; 97% of total). However, 175 individuals were observed demonstrating a sequence of multiple behaviors: 165 (94%) displayed two behaviors in sequence, nine individuals three behaviors, and one individual four behaviors in sequence (Table 6).

Table 6. Counts of behavioral observations documented for individuals of *Eumunida picta* during video analysis, where C = claws extended, W = walking, F = feeding, G = fighting, S = swimming and O = other. Other behaviors are defined in Table 2. Grey highlighted cells indicate only a single behavior was observed for an individual.

Initial Behavior	**Sequence of Additional Behaviors Observed**											
	C	**F**	**G**	**S**	**W**	**O**	**CO**	**FW**	**GS**	**WC**	**WF**	**WOW**
C	4968	27	1	1	95[a]	10	0	1	0	0	3	1
F	1	96	0	2	3	1	0	0	1	2	0	0

G	0	0	7	0	0	0	0	0	0	0	0	0
S	1	0	0	4	1	0	0	0	0	0	0	0
W	10	3[c]	5[d]	1	358[b]	0	0	1	0	0	0	0
O	0	1	0	1	3	134	1	0	0	0	0	0

[a] Most individuals (90%) walked after the claws-extended behavior

[b] For those *E. picta* observed on coral, the majority of individuals were walking away from the upper portion of the coral colony not walking towards the top of the colony. Additionally, squat lobsters usually moved away from other squat lobsters, except when food was available. In this case, the individual was more likely to walk towards the stationary individual that was eating.

[c] The observed individual either moved to a new location after feeding, or walked to a location and began to feed or was observed grazing (or browsing) along the way.

[d] These interactions usually occurred when individuals were in close proximity to one another. In one instance, the first individual encountered another that was eating a fish and the two squat lobsters then fought over the prey item. In only one instance did it appear that the fight was an unprovoked attack.

These behaviors were observed across all study sites, but not all behaviors were performed on all types of substrata (Fig. 10). Interestingly, the frequency of observed behaviors appeared similar across habitat types, but squat lobsters on soft and other substrata exhibited fewer behaviors, most likely because squat lobsters on soft or other substrata were usually solitary individuals, and the overall extent of these habitat types was smaller. Conversely, *E. picta* occurring on rubble habitat were more frequently observed in groups. For example, 91 instances of multiple individuals, ranging from 2–5 individuals per group, were noted on rubble substrata (Plate 1h). Individuals were observed fighting and swimming only on or over coral substrata (i.e., live and dead coral and rubble). Additionally, individuals were rarely recorded feeding while on soft substrata compared with the other habitat types.

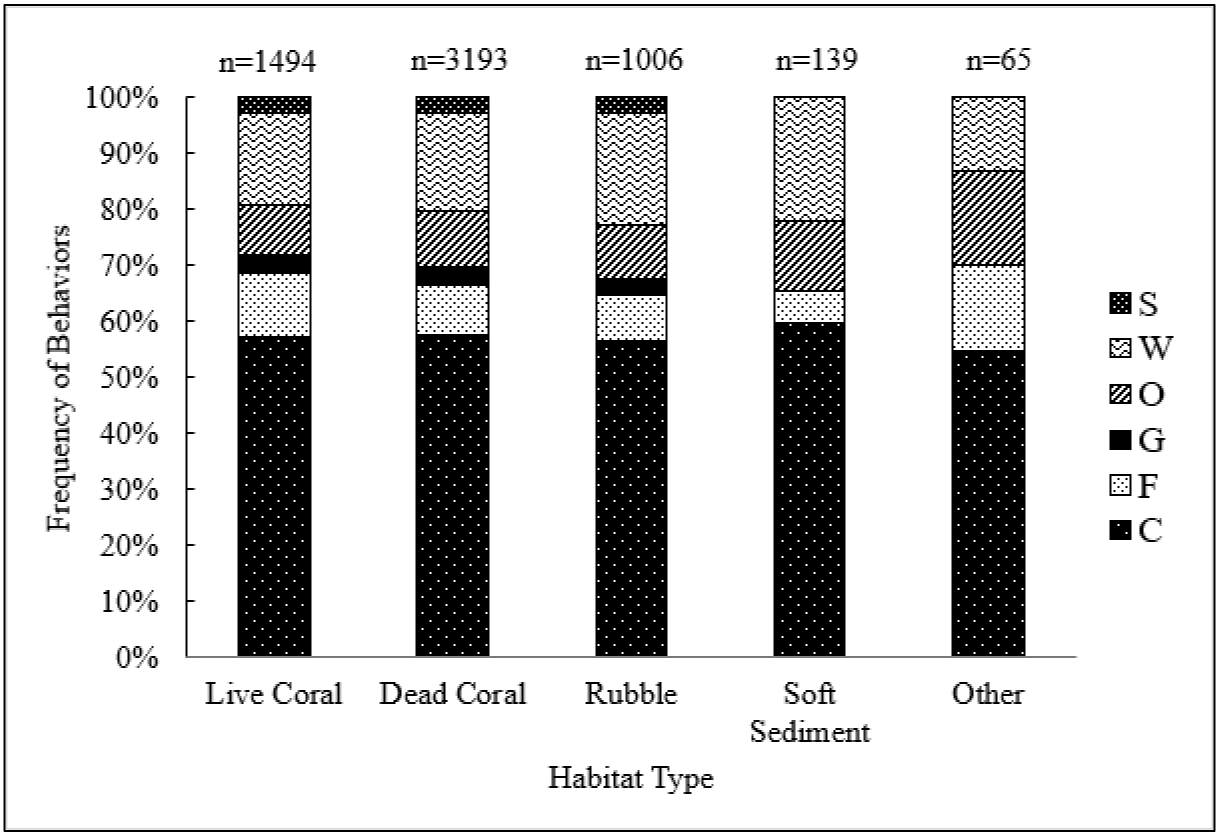

Figure 10. Frequency of behaviors recorded for individual *Eumunida picta* on different habitat types. Count data were square root transformed due to the high frequency of observations of claws extended. Behaviors recorded included claws extended (C), feeding (F), fighting (G), walking (W), swimming (S) and other behaviors (O). Observations were excluded when an individual occupied multiple habitat types while performing the observed behavior.

For those *E. picta* observed on coral substrata, the likelihood of observing a particular behavioral display did not appear to be influenced by whether the coral was dead or live. However, position on the coral colony did influence observed behaviors. For example, individuals observed on the outer surface of both dead and live coral, displayed the claws-extended behavior more frequently when on the upper portion (1048 and 561; dead and live, respectively), compared with those on the middle (783 and 324, respectively) and lower (704 and 123, respectively) portions of the coral colony.

Behavioral trends for embedded individuals were similar regardless of whether they occupied dead or live coral, with claws extended being the most common behavior observed among these individuals. Slightly more individuals embedded in the middle vertical zone of the matrix were observed displaying this behavior (117 and 115, respectively) than in the upper vertical zone (93 and 95, respectively); fewer embedded individuals (45 and 33, respectively) were observed exhibiting the claws-extended behavior in the lower vertical zone.

Although a variety of behaviors were noted for this species (see Table 2), three behaviors in particular, claws extended, feeding, and agonistic behavior, are of particular interest and provide significant insights into the ecology of this species. *Eumunida picta* were observed most frequently with their claws extended into the water column, perpendicular to the substratum (Plate 1d-f). Usually the outstretched claws were in the same vertical plane as the rest of the body. Thus, by holding the claws in this raised position, both the perceived size of the squat lobster and the vertical extent of the squat lobster into the water column were increased.

This unique behavior could be an avoidance response to the submersible. However, this seems unlikely. Claws-extended behavior was displayed by squat lobsters on all types of substrata, at all positions on the coral colony, and by individuals, both on the outer surface of the coral as well as those embedded in the coral matrix. In total, 87% of individuals were observed displaying only this behavior, whereas 89% of individuals displaying one or more behaviors were observed with claws extended. Claws-extended behavior was most frequently followed by walking (n = 98 individuals). These individuals might be moving to avoid the submersible or, alternatively, better their position on the coral colony. Submersible avoidance again seems unlikely, as the vast majority of individuals observed did not move abnormally (e.g., rapid walking or swimming away) when approached by the submersible. On several occasions, individuals moved their claws to the horizontal plane and spread their chelae in what appeared to be a defensive posture. On 10 occasions, the reverse behavioral sequence was observed with individuals walking over the substratum, stopping, and then extending their claws into the water column.

Our observations document that *E. picta* are active predators "fishing" in the water column. The claws-extended posture is a predatory stance, both intriguing and ecologically significant for this species and for energy flow in the habitat where it is found. In 26 instances, feeding followed the claws-extended behavior, and a few individuals were observed catching prey items from the water column. When a prey item was captured, the individual began consuming the prey immediately. If the predation attempt was unsuccessful, the individual usually brought the chelae to the mouth following the attempt. It is unclear whether small prey items were captured incidentally or whether the individual was grooming (sensu Garm and Hoeg, 2000). Additionally, on three different occasions a series of behaviors, claws extended, followed by walking, and then feeding, was observed. This behavioral sequence may correspond to an individual moving to a less prominent location to consume a recently captured prey item. On three other occasions, the claws-extended stance followed feeding. Once, an individual observed feeding immediately extended its claws into the water column when finished. On two other occasions, the individual finished feeding, walked to a new location, and upon arrival extended its claws into the water column.

Squat lobsters were observed on 12 different occasions either capturing pelagic fishes directly out of the water column or consuming live fishes they had captured (Plate 2). At least three taxa of fishes (Myctophidae, probably *Ceratoscopelus* sp.; Macrouridae, probably *Nezumia* sp.; Sternoptychidae, *Polyipnus sp.*) were captured and consumed. After capture, and while the fish was still alive, the squat lobster held the fish with both chelae while attempting to quickly consume the fish. Fishes were usually consumed tail first (Plate 2d, e, g, h), although less frequently fish were also taken headfirst (Plate 2f). Individual *E. picta* were also observed attempting to grab fishes much larger than themselves, including a black-bellied rose fish (*Helicolenus dactylopterus*), an alphonsino (*Beryx decadactylus*) and a blotched cat shark (*Scyliorhinus meadi*), likely as a defensive mechanism rather than an effort to capture such a large prey item. Successful capture of live fishes was not restricted to the top or upper portion of the coral colony. In fact, of the 12 successful prey captures observed, only five occurred on the upper portion of the coral, whereas three individuals were positioned on the middle portion, and two individuals on the lower portion. Two additional individuals hunted successfully while on the rubble substratum.

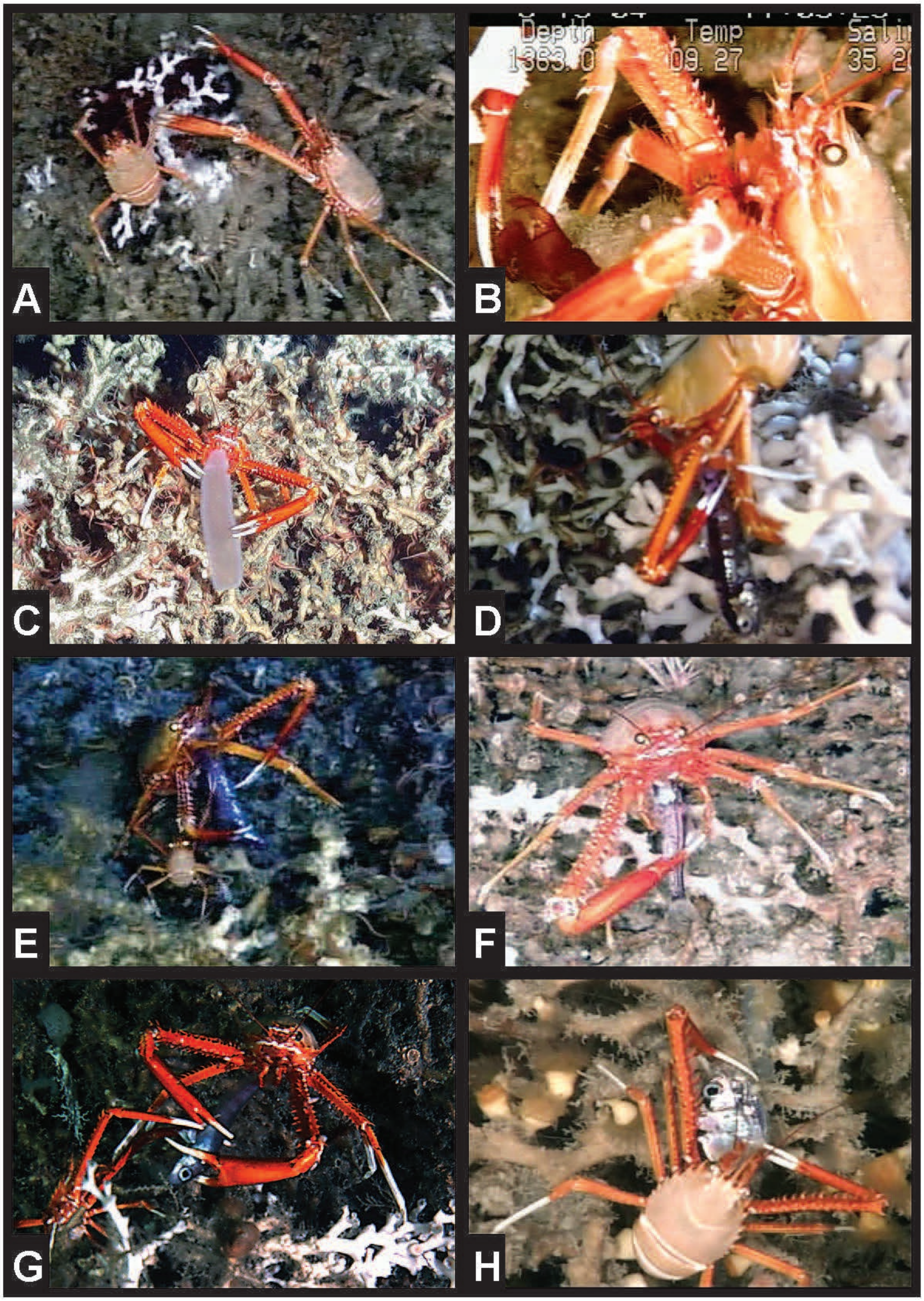

Plate 2. *Eumunida picta* feeding on various invertebrate and fish taxa. Observations made at habitats of *Lophelia pertusa* located off the southeastern coast of the USA (Cape Lookout, NC to

Cape Canaveral, FL) at 279–725 m depth. Images produced from videos taken during dives using manned submersibles *Johnson-Sea-Link* I and II. A) Coronate schyphozoan medusa (cf. *Atolla sp.*). Individual presumably drifted in the water column and became entangled in the coral branches. 408 m. B) Close up of same coronate medusa. 408 m. C) Pelagic tunicate (*Pyrosoma atlanticum*). Depth unknown. D) Lanternfish (Myctophidae, probably *Ceratoscopelus* sp.). 405 m. E) Lanternfish (Myctophidae). Smaller individual grabs at prey. 402 m. F) Lanternfish (Myctophidae, probably *Ceratoscopelus* sp.). 387 m. G) Rattail (Macrouridae, probably *Nezumia* sp.). Smaller individual (bottom left) grabs at prey. 517-535 m. H) Hatchetfish (Sternoptychidae, *Polyipnus sp.*). 417 m.

In addition to preying on fishes, *E. picta* were also observed on three occasions eating large midwater invertebrates. Capture of these pelagic invertebrates was not observed, therefore it is not possible to determine whether *E. picta* extracted these midwater invertebrates from the water column or found them opportunistically. For example, two individuals were observed eating a large, red, gelatinous mass, likely the remnants of a midwater jellyfish (c.f. *Atolla* sp.), that was draped over live *L. pertusa* (Plate 2a, b). One individual eating this mass had no chelae and fed by placing its mouthparts close to the mass and tearing pieces off with its maxillipeds. This observation illustrates how squat lobsters that have lost their chelae can obtain nourishment during the regeneration process. A second, larger individual, arrived at the scene, did not disturb the first individual, and began feeding at the other end of the mass. This individual used its claws to tear off large portions of the mass and subsequently brought these to its mouth. Both individuals continued to feed without any agonistic interactions. Another individual in close proximity to the prey item did not approach the jelly nor did it appear interested in the feeding activities of the other squat lobsters.

Twice, *E. picta* were observed feeding on pyrosomes (*Pyrosoma atlanticum*; Plate 2c). Once, a solitary individual was observed holding the pyrosome in both chelae while ingesting it, while on another occasion, three *E. picta* were observed feeding on the same large pyrosome. These individuals were located in a small sand patch surrounded by dead coral. The squat lobsters were spaced around the pyrosome with one individual at each end, and the third individual feeding on the middle of the pyrosome. Again, no agonistic behaviors were observed between these squat lobsters; individuals fed without incident.

Of the137 individuals observed feeding, 96 were only observed feeding, while the remaining individuals were observed feeding as part of a sequence including other behaviors (Table 6). Although feeding events were observed on all types of substrata (Figure 10), the majority of feeding events (83%) were observed on coral substrata, with more individuals observed associated with dead rather than live coral substrata. The majority of individuals feeding were present on the outer surfaces of the coral, rather than embedded in the coral matrix. This pertained to individuals both on dead (n = 60; 88%) and live coral (n = 34; 71%) substrata. Placement of the squat lobster on the coral during feeding, however, differed between those on dead and live coral substrata. Placement of those individuals observed feeding while on dead coral was more evenly distributed over all portions of the coral, with 25 individuals (37%) observed on the upper portion of the coral, including 8 squat lobsters on the top of the colony; 22 individuals on the middle portion; and 21 individuals on the lower portion. The majority of individuals feeding while associated with live coral substrata (n = 27, 56%) were on the upper portion of the coral, including four individuals on the top of the colony; 16 other squat lobsters were observed in the middle portion, while only five individuals were associated with the lower portion. Other feeding events were occasionally observed for individuals associated with rubble and other substrata and rarely for individuals on soft sediments.

Eumunida picta also engage in a variety of other feeding behaviors, including grazing, scavenging, and stealing food from other predators. Individual *E. picta* were observed grazing (Plate 1b) on attached fauna as they moved along the coral substrata, as well as picking at the surfaces of larger stationary organisms, including the underside of a brisingid sea star, *Novodinia antillensis*, the spines of a sea urchin (*Echinus tylodes*) and what appeared to be the column of an anemone. Additionally, some *E. picta* were seen picking items among the marine snow drifting in the water column. As opportunistic feeders and scavengers, *E. picta* were observed on several occasions moving directly towards larger dead prey items or prey subdued by other squat lobsters. For example, squat lobsters, many coming from several meters away, moved quickly towards a baited trap presumably attracted by the odor of the bait (Plate 1a). Individuals located outside the trap opening as well as on top of the trap were observed feeding, likely picking up pieces of bait that fell through the mesh of the trap. On another occasion, one individual stole a fish from a sea anemone. The squat lobster approached the anemone, grabbed the fish with both chelae, extracted it from the anemone, and then immediately started to consume the fish.

Fighting among squat lobsters was rarely observed (Plate 1g). Only 14 individuals (0.2%) were observed displaying any type of agonistic behavior. Clashes were short, usually lasting only a few seconds with maximum duration of less than a minute. One individual was usually observed chasing its opponent. These squat lobsters usually pushed or probed another individual instead of grabbing or pinching the opponent with their chelipeds. Many of the skirmishes began with one individual approaching another and ended with individuals moving in different directions away from the point of contact.

Seven ‘major’ skirmishes (i.e., longer duration, more aggressive behaviors) were observed. All seven of these events appeared to be an attempt of one individual to move to a higher position on the coral colony; four of these were direct attacks. Twice, a larger squat lobster was observed attacking a smaller individual. Size of the individual seemed to influence the outcome in these battles, as the larger individuals successfully chased the smaller individuals away from the contested position, with the loser retreating to a lower position on the coral colony. The other two direct attacks involved individuals of similar size. In one instance, the aggressor walked across the coral toward another squat lobster. During the struggle, both squat lobsters presumably tried to better their position on the coral colony. The aggressor was the loser in this instance and retreated to a lower position on the coral. In the second instance, two similar-sized squat lobsters were positioned near the top of the coral substratum. The aggressor approached the other individual that did not concede its position. During the struggle that ensued, both squat lobsters moved to a lower position on the coral. When the struggle ended, the squat lobsters separated and moved away from each other in opposite directions. Neither individual returned to their former location on the upper portion of the coral colony.

Two other skirmishes occurred when two individuals encountered each other unexpectedly. In the first instance, both squat lobsters were moving over the coral substrata when they walked into each other resulting in the larger individual chasing the smaller individual for a short distance away from that location. During the second encounter, one individual was swimming and landed on another individual. The resulting struggle was likely a startle response and ended with the swimming individual returning to its original location and position on the coral and the other staying in its original location.

Presence of prey does not consistently trigger agonistic behavior or result in one individual attempting to steal food from another. Individuals in close proximity to a squat lobster that was feeding rarely antagonized that individual. In fact, on several occasions individuals shared a food item (see above). However, during these food-sharing events, we noted that individual squat lobsters were spaced around the prey item in such a way that individuals were as far from each other as possible without losing contact with the food. On several occasions, individuals near a feeding individual did not approach the squat lobster that was feeding. These individuals were either not attracted to the prey item, not hungry, or were unaware that a food item was present. Conversely, in a few instances smaller squat lobsters would sneak bits of food, apparently unnoticed by the larger individual holding the prey item. Still other feeding events involved larger squat lobsters pushing smaller individuals away from the food source. However, no further agonistic behavior was observed between these two individuals, and in at least a few instances, the smaller squat lobster subsequently returned to feed on the prey item along with the larger individual. Only once did a food item incite a ‘major’ contest. In this case, the aggressor launched a direct attack by approaching (walked over the coral) an individual that was eating a fish. The individual that was consuming the prey item kept the aggressor away while guarding the food item. After a short scuffle, the individual with the fish escaped the aggressor by swimming a short distance away. The aggressor followed and then another brief skirmish ensued (outcome unknown).

3.6 Size and sex

Of the 182 individuals examined, 173 were measured, ranging in size from 4.9 mm to 53.5 mm CL. Overall, approximately 60% (n = 101) measured 30 mm CL or larger; but only 2% (n = 3) exceeded 50 mm CL. Approximately 50% (n = 86) measured 30–45 mm CL; 22% were 10 mm or less. Of the specimens where sex could be determined, males (n = 84) ranged in size from 5.0–53.5 mm CL; females (n = 76) attained similar sizes (4.9–50.9 mm CL) to those of males (Fig. 11). Despite similar size ranges between males and females, length-frequency curves were slightly offset with more males reaching larger sizes. Males constituted 72% of all individuals ≥ 40 mm CL. Females were more prevalent in the 30–40 mm CL range and represented 68% of individuals in this size class.

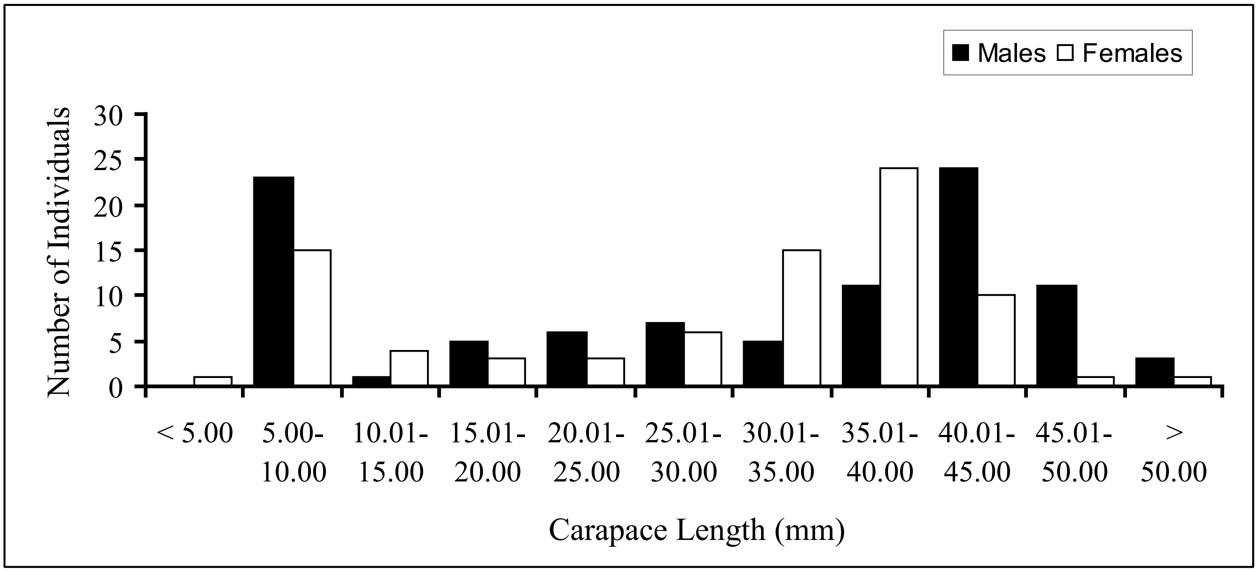

Figure 11. Size frequency distributions of males (black bars) and females (white bars) of *Eumunida picta* collected during this study.

Using various gear types permitted capture of a broad size range of individuals occurring on multiple types of substrata. The benthic sled only captured small individuals (5.0–9.9 mm CL and 5.3–8.9 mm CL, respectively), and generally these samples were collected off the main reef, often in rubble zones. Traps, usually deployed on the main reef, successfully captured medium- to larger-sized individuals (crab trap: 12.5–39.6 mm CL; eel trap: 29.7–40.0 mm CL), while each of the other gear types (e.g., tucker trawl, otter trawl, submersible) collected individuals throughout the size range reported here. The smallest (4.9 mm CL) and largest individuals (53.5 mm CL) were collected by submersible. Based on our collections, juveniles occur in the same general habitat as adults.

Sex ratio was close to unity (1:0.9, males:females). No sexual dimorphism with respect to carapace shape or growth was observed; males and females had the same straight-line size trajectory (Fig. 12). No color variation was observed between sexes or with size of the individual. Smallest individuals had the same appearance as larger adults.

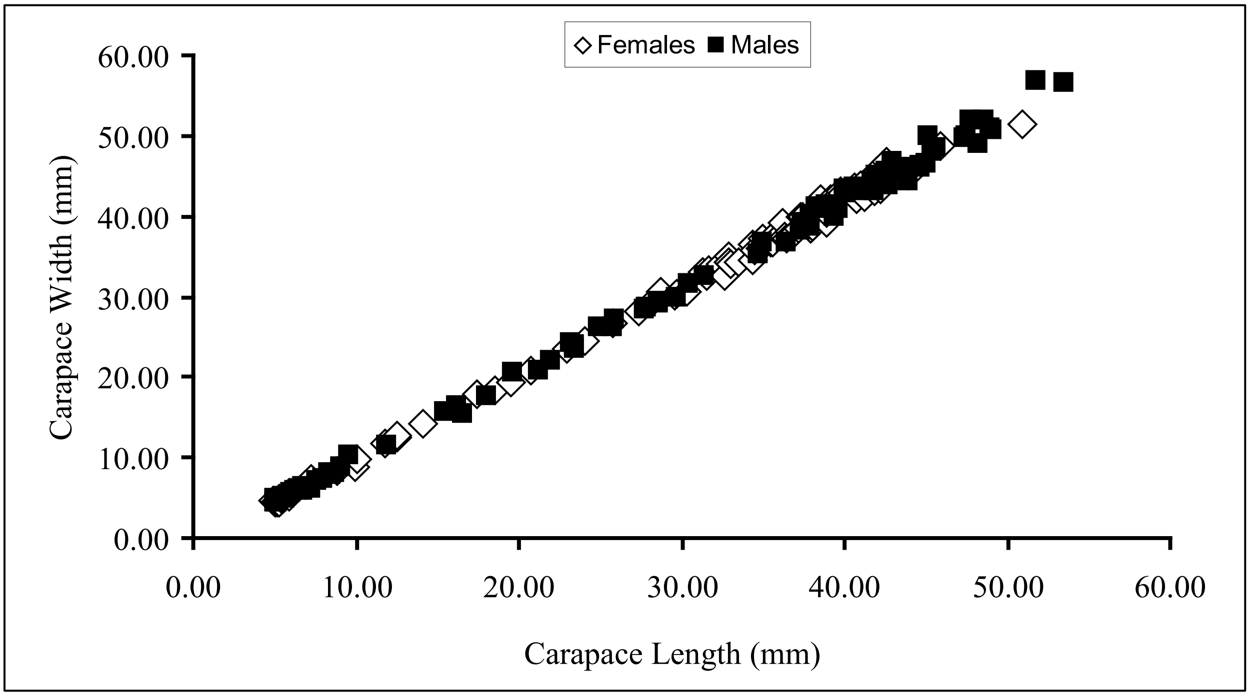

Figure 12. Comparison of carapace width versus carapace length for males (dark squares) and females (open diamonds) of *Eumunida picta*.

Only two females were ovigerous. The larger ovigerous female (38.93 mm CL) was captured in June at Cape Lookout A between 392 and 431 m depth. The pleopods of this female were laden with many small eggs ranging in diameter from 0.56 to 0.69 mm (mean = 0.62 mm). Eggs, pinkish in color, were well developed; eyes of developing embryos were visible. The other ovigerous female (34.45 mm CL) was collected in October at Cape Lookout B between 366 and 420 m depth. Eggs of this female were slightly smaller, ranging from 0.38 to 0.50 mm in diameter (mean = 0.45 mm). Fewer eggs were visible on the pleopods; no internal structures of developing larvae were discernible.

4. Discussion

Results presented here represent the largest and most comprehensive data set to date documenting occurrence and densities within specific habitats as well as increasing our knowledge regarding the behavior and ecology of *Eumunida picta*. Our data indicate that *E. picta* abundance is significantly influenced by region, habitat, and depth. Although no interaction effects were statistically significant, the relationships between these three variables and the resulting impacts on the distribution and ecology of *E. picta* need further consideration. Additionally, our data document *in situ* behavioral observations, including a unique behavioral stance that provides *E. picta* the opportunity to actively fish for prey items in the water column.

Many aspects of the distribution and ecology of *E. picta* are influenced by the complex and intimate association between this species and the scleractinian coral, *Lophelia pertusa*. Our data demonstrate that variations in frequency of occurrence, abundance, and density of *E. picta* among sites examined were directly related to abundance and distribution of *L. pertusa*. We observed and/or collected most individuals off North Carolina, where *L. pertusa* is most abundant and habitat created by this coral most extensive among the study sites surveyed. Quattrini et al. (2012) reported that *E. picta* observed on the Cape Fear mound off NC prefer the tops of coral mounds and coral colonies. Additionally, the presence of a steep slope, dominated by medium-sized colonies of *L. pertusa*, explained the significantly higher abundance of *E. picta* observed during one dive at Stetson Banks compared to the other dives in the region. Similarly, *E. picta* occurred in high abundances at Triceratops, where extensive fields of living *L. pertusa* cover the tops of the three coral mounds. In contrast, the deeper, offshore stations in the Cape Canaveral region, characterized by significantly less *L. pertusa* habitat, had the highest frequency of dives where *E. picta* were absent. Likewise, this species was rarely observed at Savannah Banks, a location characterized by soft substrata with lesser amounts of hard substrata, including that formed by *L. pertusa*.

This close association between *E. picta* and *L. pertusa* has been noted previously (e.g., Buhl-Mortensen and Mortensen, 2004b; Kilgour and Shirley, 2008a); however, the extent of this relationship was not fully appreciated until observations reported herein. Our results and those in other published studies strongly suggest that *L. pertusa* is the preferred habitat of *E. picta*, at least off the SEUS and Gulf of Mexico. For example, the majority of individuals observed near the World War II shipwreck *Gulf Penn* in the north-central Gulf of Mexico were associated with *L. pertusa* growing on its hull (Kilgour and Shirley, 2008a), and *E. picta* were reported as relatively common in natural habitats formed by *L. pertusa* in the same area (Cordes et al., 2008; Lessard-Pilon et al., 2010; Nizinski and Ames, 2017). *Eumunida picta* were present, ranging in abundance from dominant to incidental members of the mobile fauna, at the majority (83%) of deep-reef sites surveyed off the southeastern United States, Straits of Florida, and eastern Gulf of Mexico (Reed et al., 2006). Additionally, this species was the dominant member of the benthic megafauna at Stetson reefs, described as an extensive region of bioherms and lithotherms composed of *Lophelia* (Reed et al., 2006), as well as on a shallow (215–248 m) reef system of *L. pertusa* discovered off Jacksonville, FL (Ross et al., 2015). Near the Charleston Bump, *E. picta* were common on moderate-relief coral mounds comprising mostly dead coral, although some mounds were thickly encrusted with live *L. pertusa* and *Enallopsammia profunda* (Wenner and Barans, 2001).

Although we observed *E. picta* most frequently (and usually in high abundance) on *L. pertusa*, this association is not exclusive. This squat lobster has also been observed in the present study on coral rubble, various types of sponges, anemones, black corals, bamboo corals, and rocks. Other studies record this species associated with a variety of organisms and habitats, including the deep-water alcyonaceans, *Primnoa resedaeformis* and *Paragorgia arborea*, in the Northeast Channel off Nova Scotia (Buhl-Mortensen and Mortensen, 2004a), with bubblegum corals (i.e., *Paragorgia* sp.) and on steep canyon walls in mid-Atlantic canyons (SWR, unpubl. data), on shipwrecks and wreck debris in the Gulf of Mexico (Kilgour and Shirley, 2008b), and on low relief outcrops of pebbles and slab-like rocks in the region southeast of Charleston, SC (Wenner and Barans, 2001). *Eumunida picta* is also one of the few squat lobsters identified as inhabiting cold seep environments, both in the Gulf of Mexico (Carney, 1994; Martin and Haney, 2005) and near Baltimore Canyon (Cleland et al., 2021). These results support the hypothesis that most crustaceans found in association with deep-water corals are facultative commensal symbionts (Buhl-Mortensen and Mortensen, 2004b). While *E. picta* may not be an obligate associate of *L. pertusa* in the true sense of the term, this squat lobster appears to prefer complex, high-profile habitats such as colonies, mounds, and reefs of *L. pertusa*.

Associations between squat lobsters and deep-sea corals are not unusual. Various other chirostyloid species, including other species of *Eumunida*, are reported to be associated with deep-sea corals. For example, the western Pacific species *Eumunida annulosa* and *E. capillata* occur on hydrocorals (Stylasteridae; Guerao et al., 2006), and the East Atlantic *E. squamifera*, has been collected off southwestern Africa in areas where bottom substrata consist of coral and rock (de Saint Laurent and Macpherson, 1990). Adult *Sternostylus formosus* (formally *Gastroptychus formosus*) were observed with deep-sea gorgonian and antipatharian corals in the northeastern Atlantic off Ireland (Le Guilloux et al., 2010). In the western North Atlantic, *S. salvadori* (formally *G. salvadori*) has been observed on the echinoderm *Novodinia antillensis* (Rice and Miller, 1991) and a variety of corals, including *L. pertusa*, *M. oculata*, antipatharians (*Leiopathes* sp.), and bamboo corals (Keratoisididae; MSN, unpubl. data). Furthermore, members of *Uroptychus* are usually found in association with gorgonians and sea pens in deep waters (Baba, 2005), although in-depth studies examining the complexity of these chirostylid-coral relationships have not yet been published.

Galatheoids, also commonly associated with deep-sea coral habitats, are usually found within the coral matrix or on coral rubble. Species of *Munidopsis*, *Munida*, and/or *Galathea* have been observed on shipwrecks and associated debris (Gulf of Mexico; Kilgour and Shirley, 2008b); coral rubble, rock, and coral framework macrohabitats (Northeast Atlantic; Roberts et al., 2008); and deep-reef areas (off Sweden and Norway; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Jonsson et al., 2004). As was discovered for *E. picta*, in all of these other studies, galatheoid abundances were highest on, or adjacent to, the coral habitat.

Several researchers (e.g., Auster, 2005; Mortensen and Fosså, 2006; Ross and Quattrini, 2009) hypothesize that the physical structure provided by the coral is the more important factor driving the association between faunal associates and deep-sea corals (see above also). In fact, biomass and diversity of the associated fauna are often higher on dead than live coral (e.g., Mortensen et al., 1995; Buhl-Mortensen and Mortensen, 2005; Cordes et al., 2008; Roberts et al., 2008; Buhl-Mortensen et al., 2010). In general, our results also show that *E. picta* appear to prefer structure with some vertical relief, thus placing individuals higher off the sea floor. Recent work in Norfolk and Baltimore canyons, where *L. pertusa* occurs mostly as small aggregations (Brooke and Ross, 2014; SWR, pers. obs. and unpubl. data), revealed that *E. picta* are more likely attracted to the high profile, vertical relief provided by the coral than to the coral itself.

Furthermore, although some species of squat lobsters prefer specific species of corals (e.g., *Sternostylus formosa* and *Leiopathes* sp. (Le Guilloux et al., 2010); *Uroptychus* sp. and *Parantipathes* sp. (Quattrini et al., 2015), in the majority of cases with sufficient data, the type of structure occupied by squat lobsters is not usually restricted to specific species of deep-water corals or for that matter even to a particular type of hard substrata. For example, *Munida sarsi*, in the northeastern Atlantic, occur at highest frequencies and greatest densities on mounds of *L. pertusa* rubble compared to other types of substrata (Mortensen et al., 1995).

Habitat parameters, such as coral abundance, species composition (i.e., presence of primarily *L. pertusa* versus other coral species), or the overall architecture (i.e., general complexity, height off the bottom) of coral habitat, influence population size of *E. picta* throughout its geographic range. Regions and/or dive locations with rugged terrain, tall mounds, and dense coral cover typically support higher abundances of *E. picta*. In addition, habitat use by this squat lobster was similar among all regions, again suggesting that habitat is more important than the geographic or bathymetric regions where the coral habitat is located. Physical variables likely differ between sites and regions and may help explain why more versus fewer individuals are observed in particular areas. Our data suggest that *E. picta* is more successful in some areas due to a particular suite of environmental conditions in combination with the amount of available coral structure. However, this hypothesis remains speculative until additional supporting physical data, such as current speed and direction, are collected.

Habitat use by small-sized individuals (i.e., ≤10 mm CL) of *E. picta* has not been addressed previously in the literature. Sizes of individuals observed in video or photographs presented in other studies (e.g., Reed et al., 2006; Kilgour and Shirley, 2008b; Lessard-Pilon et al., 2010) are not reported, although these observations are more likely those for the larger, most obvious individuals. Based on our collections and observations, juveniles occur in the same general broad-scale habitats as adults, although smaller individuals may use the habitat differently. For example, the smallest individuals were not observed perched atop coral colonies, rather they were found most frequently within the coral matrix, on or within coral rubble, or under dead coral branches; areas not easily accessed by our sampling gears or easily observed in video. These habitats may offer more protection and food resources to the smaller individuals that likely feed primarily on different prey items (detritus versus larger prey items) than that consumed by larger individuals. More work is needed to evaluate whether size of individuals influences habitat utilization.

Depth also may influence the observed and reported distributions of *E. picta*. In general, *Eumunida* species are restricted to depths shallower than 1000 m (Schnabel et al., 2011) with an average depth around 500 m. *Eumunida picta* occurs consistently between 200 to 600 m depth throughout its geographic range (Smith, 1883; Chace, 1942; Wenner, 1982; de Saint Laurent and

Macpherson, 1990; Wenner and Barans, 2001; Buhl-Mortensen and Mortensen, 2004a; Reed et al., 2006; Cordes et al., 2008; Kilgour and Shirley, 2008a; Felder et al., 2009; Lessard-Pilon et al., 2010; Ross et al., 2015). During this study, we observed and collected *E. picta* over a wide range of depths (366–725 m) with the majority of individuals observed within the previously reported depth range of 200–600 m (Felder et al., 2009). A few *E. picta* were present at deeper depths with eight individuals collected during this study between 684–725 m, representing the deepest captures yet reported for this species. Only one other study (Reed et al., 2006) has recorded this species at depths deeper than 600 m with a maximum depth of 714 m reported therein. *Eumunida picta* were either absent or observed in extremely low abundances at the deepest stations (709–783 m depth range) included in our study. All of these deep stations were located off Cape Canaveral, an area characterized by a diverse coral assemblage, including *L. pertusa*, albeit with more dead coral present in the southern compared to the northern stations. Lower frequencies of occurrence of this species at depths in excess of 600 m suggest that the bathymetric center of abundance for *E. picta* occurs between 200–600 m, with bathymetric limits of distribution located at approximately 725 m depth.

Depth alone is not a reliable predictor of where *E. picta* occurs. For example, no *E. picta* were observed at three stations (505–543 m) at Savannah Banks located within the suitable depth range for this species, but these stations lacked coral habitat or other high relief structures (see above). Additionally, presence or absence of *E. picta* at deeper stations at Stetson Banks were associated with the presence of *L. pertusa*. The highest numbers of individuals observed at Stetson Banks were at depths approaching the lower limit of the reported depth distribution (500–600 m) for *E. picta.* However, at these stations, *L. pertusa* was present. In other locations on Stetson Banks, abundances of *E. picta* were consistently low at both deeper and shallower depths even where hard pavement and rocky structures were prevalent. Similarly, off Jacksonville, three individuals were observed at the deepest (645–674 m) station, whereas no individuals were observed at the slightly shallower (626–652 m) station. Here, rock ledges and coral rubble, with lesser amounts of hard coral present were more characteristic of the habitat suggesting that *E. picta* presence/abundance at this site is related to the amount and type of habitat available.

Thus, both depth and habitat appear to be important factors influencing the distribution of this species. Nearly all individuals observed in the present study occurred at 301–725 m depth with most individuals inhabiting depths between 300–400 m. Occurrences and abundances of *L. pertusa* were also highest at these depths. At the deeper depths of our survey area, large coral features were uncommon; and when present, coral colonies were smaller and more broadly scattered over the seafloor. In contrast, an extensive *L. pertusa* reef habitat recently discovered off South Carolina at 700 m depth supported few if any *E. picta* (A. Quattrini, Smithsonian Institution, oral comm., 2022). Thus, based on our observations, there appears to be a depth/habitat combination that is most favorable to this species. When habitat conditions are favorable (i.e., coral structure is available) the center of bathymetric distribution and abundance for *E. picta* off the SEUS is around 300–400 m.

Data extracted from material examined in this study (Appendix A) greatly increase our knowledge of size frequency and population structure of *E. picta*. Historically, little data on size of individuals are available in the literature. The few published records reporting sizes of individuals are limited to those appearing in taxonomic studies (Smith, 1883; de Saint Laurent and Macpherson, 1990) and a trawl survey (Wenner, 1982). Individuals reported herein represent the smallest and largest known specimens of *E. picta* reported thus far. Comparable to the results reported here, males and females were of similar sizes in these other studies.

Size at maturity data are also minimal for *E. picta*. Wenner (1982) reported that all ovigerous females sampled were ≥ 37 mm (range 37–42 mm CL); de Saint Laurent and Macpherson (1990) examined an additional ovigerous female of 43 mm CL. One mature specimen examined in the present study was slightly smaller (34.5 mm CL) than the previously reported minimum size at maturity, thus decreasing the known minimum size at maturity for *E. picta* to about 34 mm CL. Size at maturity (physiological maturity sensu Comeau and Conan (1992)) was not assessed for males in this study; however, males of *E. picta* had no visible gonad at sizes < 34 mm (Wenner, 1982). Additional sampling is needed to better determine size at maturity for this species.

The majority of previous studies have focused only on larger individuals and adults. This is not surprising given that larger individuals are more likely to be captured and retained by trawls or are more easily observed in videos. As such, biological and ecological information regarding smaller-sized individuals of this species are not formally documented. Based on our observations and collections, all individuals of *E. picta* regardless of sex or size have a similar appearance. Significant changes in morphology or coloration were not observed in specimens examined suggesting little change in appearance with ontogeny.

Few studies have collected adequate amounts of material to determine sex ratios within populations of squat lobsters and assess spawning seasonality. Results presented here (1:0.9; M:F) concur with results of a previous study (Wenner, 1982) where the reported sex ratio of *E. picta* (1:1.2; M:F) was not significantly different from unity.

Another largely unknown aspect of the life cycle of most species of squat lobsters, and in particular for *E. picta*, is the seasonal spawning cycle (if present). Based on capture of six ovigerous females, Wenner (1982) suggested that *E. picta* demonstrated reproductive seasonality in the mid-Atlantic Bight since all ovigerous females were taken in November despite sampling year-round (January, June, September and November). Collection of two ovigerous females off Cape Lookout (present study), one in June and the other in October, increases the length of the presumed spawning season by several months. Since individuals of *E. picta* were sampled opportunistically, it is also possible that the majority of ovigerous females utilize habitats that have not been sampled frequently. Alternatively, the spawning season may differ between the SEUS and the mid-Atlantic Bight regions due to differences in oceanographic and environmental conditions.

Whether *E. picta* spawns throughout the year or has a synchronized spawn during autumn remains to be determined. The ability of a species to synchronize reproductive cycles and larval development with food availability has been hypothesized as an adaptation to planktotrophy (Thorson, 1950; Tapella et al., 2002). Given that *E. picta* has numerous, small eggs and carries its eggs through the winter, and that other species of *Eumunida* do not show abbreviated development (Guerao et al., 2006), but have multiple larval stages, suggest that *E. picta* has planktotrophic larval development. Thus, *E. picta* likely has a seasonal and annual reproductive cycle perhaps coinciding with periods of increased plankton production. Additional sampling throughout the year is needed to address these questions.

The majority of squat lobsters are considered omninvorous and like most other large crustaceans are thought to be scavengers. Squat lobsters appear to play an important role as shredders of large debris (Lovrich and Thiel, 2011). However, few studies have examined feeding and associated behaviors of squat lobsters. Most previous studies report deposit feeding and opportunistic scavenging as the primary modes of feeding (Nicol, 1932; Berrill, 1970; Cartes, 1993; Garm and Høeg, 2000; Romero et al., 2004). Stomach contents often consist of fine sorted particles, detritus, and organic remains resulting from larger prey items being torn into smaller pieces. Many species are considered generalists given that gut contents reflect the composition and abundance of available prey items by location, depth, and season (Cartes, 1993; Romero et al., 2004). Nicol (1932) suggested that predatory activities resulting in carnivory were lost or reduced in importance in the Anomura (Infraorder including squat lobsters) as compared to the Decapoda as a whole. Our results, however, demonstrate that *E. picta* is an active predator capable of hunting and capturing live prey items across a broad size range. Prey items of sizes similar to that of the predator (several species of mid-water fishes) were captured successfully.

In addition to behavioral adaptations, *E. picta* has visual physiological adaptations that may enhance feeding. Presence of dual visual pigments might facilitate feeding on bioluminescent organisms in the water column and improve visual contrast between the substrata and the prey (Frank et al., 2012). This could help explain why *E. picta* is successful at capturing mobile fauna, such as myctophids or sternoptychids, which are highly bioluminescent and gelatinous zooplankton that emit a bluish light spectrum.

The observed behavioral adaptations for hunting (claws-extended; positioning on upper, outer surface of coral colonies) are specific to *E. picta* and are not representative of other chirostyloids associated with deep-sea coral habitats. Other species of chirostyloid, including *Sternostylus salvadori* (western Atlantic, MSN, pers. obs.) and *S. formosus* (eastern Atlantic, Le Guilloux et al. 2010) have been observed prominently perched on deep-sea corals, but these species are most often associated with octocorals and antipatharians, rather than *L. pertusa*.

Similar to *E. picta*, *S. salvadori* and *S. formosus* are also long-armed species. However, the pinchers are proportionally smaller and chelipeds much less robust than those of *E. picta*, suggesting that the claws may not be as strong as those of *E. picta*. In contrast to the commonly observed posture of *E. picta*, stationary individuals of these species of *Sternostylus* are usually flattened against the coral structure with their outstretched legs, including the claws, oriented in the same plane parallel to the coral. Thus, these species are more streamlined with the coral colony and have not been observed with their claws extended into the water column perpendicular to the coral structure. Additionally, diets of *E. picta* and *Sternostylus* spp. differ significantly, with *Sternostylus* spp. feeding mainly off the surface of the coral directly. The inner edges of the chelipeds of *S. formosus* are densely covered with stiff bushy setae used to brush food particles from mucus found on coral branches (Le Guilloux et al., 2010). Bushy setae are absent on the inner edges of the chelipeds of *E. picta*.

Some evidence indicates that a few galatheoid species also prey on pelagic organisms. The relative abundance of pelagic organisms in the diet of *Munida tenuimana* suggests that pelagic resources are obtained by both predation and deposit feeding (Cartes, 1993). Although active predation was not observed, the size and appearance (whole remains instead of torn pieces) of organisms in gut contents indicate that *M. tenuimana* preyed upon pelagic prey (Cartes, 1993). In addition to the present study, only one other study (Hudson and Wigham, 2003) reports squat lobsters actively feeding on pelagic prey. In that study, one individual *Munida sarsi*, surrounded by a swarm of krill, was observed attempting to catch individual krill swimming in the water column. Although the result (capture of live pelagic prey items from the water column) may be the same, *M. sarsi* appears to be employing this feeding behavior opportunistically when prey items occur in large abundance, whereas *E. picta* observed in this study displayed behaviors more similar to those of a sit-and-wait predator.

Feeding plasticity allows squat lobsters the opportunity to consume resources from a variety of origins (ranging from primary producers to dead organic material) and to play an important role as recyclers in most ecosystems where they occur (Lovrich and Thiel, 2011). Since *E. picta* (and *M. sarsi*) were observed utilizing a variety of feeding modes, the predatory hunting behavior is likely an additional feeding strategy and not a replacement for other more commonly observed feeding strategies. Use of multiple feeding strategies by these species of squat lobsters has the potential to enhance the quality of the diet (Hudson and Wigham, 2003) as well as the quantity of food. Utilizing a variety of feeding modes provides *E. picta* the ability to optimize its foraging; as availability of one prey item decreases or prey capture efficiency declines, the squat lobster can then switch between complementary feeding modes rather than changing its feeding habits completely (Romero et al., 2004). Having this flexibility in feeding habits also allows *E. picta* to remain in the area and not have to relocate to another feeding location if one type of prey becomes scarce or more difficult to capture.

Associations with hard-bottom structural habitats may confer some advantages to squat lobsters. By associating with such structures, squat lobsters gain protection from predators by color matching the underlying structure, hiding in the coral matrix, or elevating themselves beyond the range of strictly soft-bottom, benthic predators. Food acquisition is likely enhanced, both directly through ingesting mucus, detritus, fouling, or dead organisms and indirectly by providing a vantage point for suspension feeders (Baeza, 2011) or prey capture (this study). Additionally, by occupying coral substrata squat lobsters may increase the likelihood of finding a mate since conspecifics are more likely found associated with these habitats than surrounding soft substrata. Association with deep-sea corals and other complex, hard-bottom habitats has been hypothesized to confer similar benefits for fishes (Auster, 2005; Ross and Quattrini, 2007).

Of all the benefits derived from association with *L. pertusa*, taking advantage of currents for feeding may be an important factor influencing this organism-substrata relationship. Deep-sea corals occur in areas overlain with high-speed currents with little to no penetration of sunlight (Rogers, 1999). Currents accelerate around structures elevated off the bottom thus enhancing food supply to deep-sea corals and their associated fauna (Genin et al., 1986; Fredricksen et al., 1992; Thiem et al., 2006; Davies et al., 2009; Buhl-Mortensen et al., 2010). By perching high atop coral structures, squat lobsters place themselves in locations where they are more likely to encounter prey items from a variety of sources. These include increased food supply delivered by strong currents (e.g., the Gulf Stream), mesopelagic resources commonly found in close proximity to the bottom (i.e., vertical migrators, aggregations of mesopelagics found close to the bottom), as well as sinking marine snow from shallower depths (Gartner et al., 2008, and references therein). Similarly, individuals of the oreosomatid fish species, *Neocyttus helgae*, have been observed “holding station” perhaps in an effort to gain refuge from the currents as well as increase encounters with passing zooplankton (Auster et al., 2005). Several species of demersal fishes also were observed to be stationary and inactive in deep-water canyons off Georges Bank, suggesting that these fishes are either sit-and-wait predators, are avoiding predators, or conserving energy, all of which should be successful strategies for life in highly structured benthic habitats (Uiblein et al., 2005). Individuals of *E. picta* appear to have adopted similar strategies by remaining stationary at a fixed location on the corals where they function as sit-and-wait predators ready to capture prey from the ever-changing water column moved by high-speed currents while conserving their energy reserves.

Flexibility in behavioral adaptations (e.g., the stationary hunting strategy) required to exploit multiple food resources, in combination with adequate benthic and pelagic prey items, allow some squat lobsters to be numerically dominant in these habitats. *Munida sarsi* is able to consume a variety of different food resources (Garm and Høeg, 2000), as well as actively capturing live prey using their chelipeds (Hudson and Wigham, 2003). Likewise, *E. picta* is not restricted to feeding solely on benthic prey items but is able to take advantage of the ever-changing spectrum of pelagic and benthic resources available in deep-coral habitats. These adaptations may explain why these squat lobsters are abundant and successful in coral habitats over a large bathymetric and geographic range.

Although many species associated with deep-sea corals also occur in other habitats, Buhl-Mortensen and Mortensen (2004b) suggested that the majority of these species display adaptations to living in association with the corals. These adaptations include, but are not limited to, behavioral postures, placement of individuals on the reef, or coloration. The placement of *E. picta* on the coral and its hunting posture demonstrate the adaptations of this squat lobster to living in association with deep-sea coral habitats. The coral, in particular, and the overall structure of the coral colony, in general, strongly influence the occurrence and distribution of *E. picta* in the western North Atlantic. In fact, the claws-extended predatory stance may represent one example of habitat mimicry in the deep sea. Habitat mimicry, defined as an organism resembling, in size, shape, color and behavior, a particular structural component of the habitat, has been described for other crustaceans (Hacker and Madin, 1991). This posture, in combination with color pattern, of *E. picta* (red body, white-tipped claws) resembles that of the architecture and color of a live *L. pertusa* colony and may influence habitat choice. Being inconspicuous in the coral habitat may not only benefit *E. picta* by avoiding recognition as prey, but also through evading detection by potential prey items.

Eumunida picta has a complex and intimate relationship with *Lophelia pertusa*. Although considered a facultative reef associate in the strict sense of the term, *E. picta* abundance and population density are positively correlated with abundances of live and dead *L. pertusa*. *Eumunida picta* is a dominant and ecologically important member of the invertebrate assemblage associated with deep-sea coral habitats off the SEUS. As such, this species figures prominently in the structure and function of the ecosystem. By utilizing a variety of feeding modes (scavenging, grazing, deposit feeding, and active predation), this species provides an important trophic link in the transfer of energy between the benthos and water column. Because of the intimate relationship between this squat lobster and *L. pertusa*, populations of *E. picta* would be sensitive to changes in the extent and health of the substrata. Destruction and decrease of *L. pertusa* habitats would likely negatively affect populations of *E. picta* in this region.

CRediT authorship contribution statement

Martha S. Nizinski: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. Jennifer P. McClain-Counts: Methodology, Formal analysis, Investigation, Writing – review & editing. Steve W. Ross: Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition.

5. Acknowledgments

We thank the scientific crews of our various cruises for assistance with collection of video and specimens. The pilots and crews of the DSV *Johnson-Sea-Link I, II*, R/V *Seward Johnson* and the R/V *Cape Hatteras* are gratefully acknowledged for cruise support, logistics, and collecting expertise. C. Ames provided technical assistance, translated relevant literature, and produced Plates 1 and 2. A. Villeneuve and W. Keel assisted with curation of specimens. G. Ralph and R. Diaz provided statistical consultations and assisted with analyses. T. Munroe read earlier drafts of the manuscript and provided helpful comments. This work was supported in part by NOAA Office of Ocean Exploration (Grants NA16RP2696, NA030AR4600090, NA040AR4600056, NA050AR4601065 to S.W. Ross, lead PI), Deep Sea Coral Research and Technology Program, and the University of North Carolina at Wilmington. The 2001 and 2006 R/V *Cape Hatteras* cruises were sponsored by the Duke/University of North Carolina Oceanographic Consortium (to S.W. Ross). We thank the U.S. Geological Survey (through the State Partnership Program), particularly G. Brewer, and the Bureau of Ocean Energy Management, particularly G. Boland, for support during many of these cruises. The U.S. Geological Survey Florida Integrated Science Center (now Wetland and Aquatic Research Center, through K.J. Sulak) provided a variety of personnel and logistics support for field operations. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

6. References

Auster, P.J., 2005. Are deep-water corals important habitats for fishes? In: Freiwald, A., Roberts, J.M. (Eds.), Cold-water corals and ecosystems, Springer-Verlag, Berlin, Heidelberg, pp. 747–760. https://doi.org/10.1007/3-540-27673-4_39

Auster, P.J., Moore, J., Heinonen, K.B., Watling, L., 2005. A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-water corals and ecosystems, Springer-Verlag, Berlin, Heidelberg, pp. 761–769. https://doi.org/10.1007/3-540-27673-4_40

Baba, K., 2005. Deep-sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-West Pacific, with a list of species. Galathea Reports 20, 1–317.

Baeza, J.A., 2011. Squat lobsters as symbionts and in chemo-autotrophic environments. In: Poore, G.C.B., Ahyong, S.T., Taylor, J. (Eds.), The biology of squat lobsters, CSIRO Publishing, Victoria, Australia, pp. 249–270.

Berrill, M., 1970. The aggressive behavior of *Munida sarsi* (Crustacea: Galatheidae). Sarsia 43, 1–11. https://doi.org/10.1080/00364827.1970.10411166

Brooke, S., Ross, S.W., 2014. First observations of the cold-water coral *Lophelia pertusa* in mid-Atlantic canyons of the USA. Deep-Sea Research II 104, 245–251. https://doi.org/10.1016/j.dsr2.2013.06.011

Buhl-Mortensen, L., Mortensen, P.B., 2004a. Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). Journal of Natural History 38, 1233–1247. https://doi.org/10.1080/0022293031000155205

Buhl-Mortensen, L., Mortensen, P.B., 2004b. Symbiosis in deep-water corals. Symbiosis 37, 33–41.

Buhl-Mortensen, L., Mortensen, P.B., 2005. Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-water corals and ecosystems, Springer-Verlag, Berlin Heidelberg, pp. 849–879. https://doi.org/10.1007/3-540-27673-4_44

Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, G., King, N.J., Raes, M., 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31, 21–50. https://doi.org/10.1111/j.1439-0485.2010.00359.x

Carney R.S., 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. Geo-Marine Letters 14, 149–159. https://doi.org/10.1007/BF01203726

Cartes, J.E., 1993. Diets of two deep-sea decapods: *Nematocarcinus exilis* (Caridea: Nematocarcinidae) and *Munida tenuimana* (Anomura: Galatheidae) on the western Mediterranean Slope. Ophelia 37, 213–229. https://doi.org/10.1080/00785326.1993.10429919

Chace, F.A., 1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galtheidea. Torreia 11, 1–106.

Chevaldonné, P., Olu, K., 1996. Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold seep communities: a review: Proceedings of the Biological Society of Washington 109, 286–298.

Cleland, J., Kazanidis, G., Roberts, J.M., Ross, S.W., 2021. Distribution of megabenthic communities under contrasting settings in deep-sea cold seeps near Northwest Atlantic canyons. Frontiers in Marine Science 8, 692851. https://doi.org/10.3389/fmars.2021.692851

Comeau, M., Conan, G.Y., 1992. Morphology and gonad maturity of male snow crab, *Chionoecetes opilio*. Canadian Journal of Fisheries and Aquatic Sciences 49, 2460–2468. https://doi.org/10.1139/f92-271

Cordes, E.E., McGinley, M.P., Podowski, E.L., Becker, E.L., Lessard-Pilon, S., Viada, S.T., Fisher, C.R., 2008. Coral communities of the deep Gulf of Mexico. Deep-Sea Research I 55, 777–787. https://doi.org/10.1016/j.dsr.2008.03.005

Davies, A.J., Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., Van Haren, H., Roberts, J.M., 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef Complex. Limnology and Oceanography 54, 620–629. https://doi.org/10.4319/lo.2009.54.2.0620

Felder, D.L, Álvarez, F., Goy, J.W., Lemaitre, R., 2009. Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea, *in* Felder, D.L., and Camp, D.K., (eds.), Gulf of Mexico Origin, Waters, and Biota, v. 1, Biodiversity: College Station, Tex., Texas A&M University Press, p. 1019–1104.

Frank, T.M., Johnsen, S., Cronin, T.W., 2012. Light and vision in the deep-sea benthos: II. Vision in deep-sea crustaceans. Journal of Experimental Biology 19, 3344–3353. https://doi.org/10.1242/jeb.072033

Fredricksen, R., Jensen, A., Westerberg, H., 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe islands and the relation to internal tidal mixing. Sarsia 77, 157–171. https://doi.org/10.1080/00364827.1992.10413502

Garm, A., Høeg, J.T., 2000. Functional mouthpart morphology of the squat lobster *Munida sarsi*, with comparisons to other anomurans. Marine Biology 137, 123–138. https://doi.org/10.1007/s002270000318

Gartner, J.V., Sulak, K.J., Ross, S.W., Necaise, A.M., 2008. Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes. Marine Biology 153, 825–841. https://doi.org/10.1007/s00227-007-0855-1

Genin A.P., Dayton, P.K., Lonsdale, P.F., Speiss, F.N., 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322, 59–61. https://doi.org/10.1038/322059a0

Guerao, G., Macpherson, E., Samadi, S., Richer de Forges, B., Boisselier, M.-C., 2006. First stage zoeal descriptions of five Galatheoidea species from Western Pacific (Crustacea: Decapoda: Anomura). Zootaxa 1227, 1–29. https://doi.org/10.11646/zootaxa.1227.1.1

Hacker, S.D., Madin, L.P., 1991. Why habitat architecture and color are important to shrimps living in pelagic Sargassum: use of camouflage and plant-part mimicry. Marine Ecology Progress Series 70(2), 143–155. https://doi.org/10.3354/meps070143

Henry, L.-A., Roberts, J.M., 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Research I 54, 654–672. https://doi.org/10.1016/j.dsr.2007.01.005

Hourigan, T.F., Reed, J., Pomponi, S., Ross, S.W., David, A.W., Harter, S., 2017. State of deep-sea coral and sponge ecosystems of the southeast United States. In: Hourigan, T.F., Etnoyer, P.J., Cairns, S.D. (Eds.) The state of deep-sea coral and sponge ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4. Silver Spring, MD. 60 p.

Hudson, I.R., Wigham, B.D., 2003. *In situ* observations of predatory feeding behaviour of the galatheid squat lobster *Munida sarsi* using a remotely operated vehicle. Journal of the Marine Biological Association of the United Kingdom 83, 463–464. https://doi.org/10.1017/S0025315403007343h

Jackman, S., 2020. Package: pscl. Classes and Methods for R Developed in the Political Science Computational Laboratory. United States Studies Centre, University of Sydney, Sydney, New South Wales, Australia. R package version 1.5.5. https://github.com/atahk/pscl/

Jensen, A., Frederiksen, R., 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. Sarsia 77, 53–69. https://doi.org/10.1080/00364827.1992.10413492

Jonsson, L.G., Nilsson, P.G., Floruta, F., Lundälv, 2004, Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. Marine Ecology Progress Series 284, 163–171. https://doi.org/10.3354/meps284163

Kilgour, M.J., Shirley, T.C., 2008a. *Eumunida picta* S.I. Smith, 1883, and *Lophelia pertusa* (Linnaeus, 1758): a relationship or just good friends? Crustaceana 81(5), 587–593. https://doi.org/10.1163/156854008784092166

Kilgour, M.J., Shirley, T.C., 2008b. Bathymetric and spatial distribution of decapod crustaceans on deep-water shipwrecks in the Gulf of Mexico. Bulletin of Marine Science 82(3), 333–344.

Kleiber, C., Zeileis, A., 2016. Visualizing count data regressions using rootograms. The American Statistician, 70(3), 296–303. https://doi.org/10.1080/00031305.2016.1173590

Lavelle, K.A., 2012. Epifaunal assemblages on deep-water corals in Roatan, Honduras. Master's thesis: Texas A&M University–Corpus Christi, 68 pp.

Le Guilloux, E., Hall-Spencer, J.M., Söffker, M.K., Olu, K., 2010. Association between the squat lobster *Gastroptychus formosus* and cold-water corals in the North Atlantic. Journal of the Marine Biological Association of the United Kingdom 90(7), 1363–1369. https://doi.org/10.1017/S0025315410000524

Lessard-Pilon, S.A., Podowski, E.L., Cordes, E.E., Fisher, C.R., 2010. Megafauna community composition associated with *Lophelia pertusa* colonies in the Gulf of Mexico. Deep-sea Research II 57, 1882–1890. https://doi.org/10.1016/j.dsr2.2010.05.013

Lovrich, G.A., Thiel, M., 2011. Ecology, physiology, feeding and trophic role of squat lobsters. In: Poore, G.C.B., Ahyong, S.T., Taylor, J. (Eds.), The biology of squat lobsters, CSIRO Publishing, Victoria, Australia, pp. 183–222.

Macpherson, E., Segonzac, M., 2005. Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheidae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. Zootaxa 1095, 1–60. https://doi.org/10.11646/zootaxa.1095.1.1

Martin, J.W., Haney, T.A., 2005. Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. Zoological Journal of the Linnean Society 145, 445–522. https://doi.org/10.1111/j.1096-3642.2005.00178.x

McClain-Counts, J.P., Nizinski, M.S., Ross, S.W., 2022. Abundance, density, habitat placement and behaviors of Eumunida picta in the western Atlantic off the southeastern U.S. coastline from 2000-2009. U.S. Geological Survey data release. doi.org/10.5066/P9SYJUJN.

Milne-Edwards, A., Bouvier, E.L., 1894. Considérations générales sur la famille des Galathéidés. Annales des Sciences Naturelles, Zoologie, 7e série, 16, 191–327. https://doi.org/10.5962/bhl.title.10042

Milne-Edwards, A., Bouvier, E.L., 1900. Crustacés décapodes. Première partie. Brachyures et Anomoures. In: Milne-Edwards, A. (Ed.), Expéditions seientifiques du *Travailleur* et du *Talisman* pendant les années 1880, 1881, 1882, 1883. Masson, Paris, pp. 1–396.

Mortensen, P.B., Fosså, J.H., 2006. Species diversity and spatial distribution of invertebrates on *Lophelia* reefs in Norway. Proceedings of the 10th International Coral Reef Symposium, Okinawa, 1849–1868.

Mortensen, P.B., Hovland, M., Brattegard, T., Farestveit, R., 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian shelf: structure and associated megafauna. Sarsia 80, 145–158. https://doi.org/10.1080/00364827.1995.10413586

Mullahy. J., 1986. Specification and testing of some modified count data models. Journal of Econometrics 33, 341–364. https://doi.org/10.1016/0304-4076(86)90002-3

Nicol, E.A.T., 1932. The feeding habits of the Galatheidea. Journal of the Marine Biological Association of the United Kingdom 18, 87–106. https://doi.org/10.1017/S0025315400051316

Nizinski, M.S., Ames, C.L., 2017. Distribution, abundance, and species composition of the megafaunal invertebrate assemblage associated with deep-sea coral habitats in the Gulf of Mexico. In: Demopoulos, A.W.J., Ross, S.W., Kellogg, C.A., Morrison, C.L., Nizinski, M., Prouty, N.G., Bourque, J.R., Galkiewicz, J.P., Gray, M.A., Springmann, M.J., Coykendall, D.K., Miller, A., Rhode, M., Quattrini, A., Ames, C.L., Brooke, S., McClain-Counts, J., Roark, E.B., Buster, N.A., Phillips, R.M., and Frometa, J., 2017. Deepwater Program: Lophelia II, continuing ecological research on deep-sea corals and deep-reef habitats in the Gulf of Mexico: U.S. Geological Survey Open-File Report 2017–1139, pp. 185–228. https://doi.org/10.3133/ofr20171139

Partyka, M.L., Ross, S.W., Quattrini, A.M., Sedberry, G.R., Birdsong, T.W., Potter, J., Gottfried, S., 2007. Southeastern United States deep-sea corals (SEADESC) initiative: a collaboration to characterize areas of habitat forming deep-sea corals. NOAA Technical Memorandum OAR OER 1. Silver Spring, MD, 176 pp.

Paull, C.K., Neumann, A.C., am Ende, B.A., Ussler III, W., Rodriguez, N.M., 2000. Lithoherms on the Florida-Hatteras Slope. Marine Geology 166, 83–101. https://doi.org/10.1016/S0025-3227(00)00003-7

Quattrini, A.M, Ross, S.W., Carlson, M.C.T., Nizinski, M.S., 2012. Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. Marine Biology 159, 1079–1094. https://doi.org/10.1007/s00227-012-1888-7

Quattrini, A.M., Nizinski, M.S., Chaytor, J.D., Demopoulos, A.W.J., Roark, E.B., France, S.C., Moore, J.A., Heyl, T., Auster, P.J., Kinlan, B., Ruppel, C., Elliott, K.P., Kennedy, B.R.C., Lobecker, E., Skarke, A., Shank, T.M., 2015. Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic habitats and diverse communities. PLoS ONE 10(10): e0139904. https://doi.org/10.1371/journal.pone.0139904

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. R 4.0. 2. https://www.R-project.org/

RStudio Team, 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Version 1.1. 456. http://www.rstudio.com/

Reed, J.K., Weaver, D.C., Pomponi, S.A., 2006. Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the southeastern U.S.: Blake Plateau, Straits of Florida, and the Gulf of Mexico. Bulletin of Marine Science 78, 343–375.

Rice, A.L., Miller, J.E., 1991. Chirostylid and galatheid crustacean associates of coelenterates and echinoderms collected from the *Johnson-Sea-Link* submersible, including a new species of *Gastroptychus*. Proceedings of the Biological Society of Washington 104, 299–308.

Roberts, J.M., Henry, L.-A., Long, D., Hartley, J.P., 2008. Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic. Facies 54, 297–316. https://doi.org/10.1007/s10347-008-0140-x

Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water ecosystems. Science 312, 543–547. https://doi.org/10.1126/science.1119861

Rogers, A.D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. International Review of Hydrobiology 84(4), 315–406. https://doi.org/10.1002/iroh.199900032

Romero, M.C., Lovrich, G.A., Tapella, F., Thatje, S., 2004. Feeding ecology of the crab *Munida subrugosa* (Decapoda: Anomura: Galatheidae) in the Beagle Channel, Argentina. Journal of Marine Biological Association of the United Kingdom 84, 359–365. https://doi.org/10.1017/S0025315404009282h

Ross, S.W., Brooke, S., Quattrini, A.M., Rhode, M., Watterson, J.C., 2015. A deep-sea community, including *Lophelia pertusa*, at unusually shallow depths in the Western North Atlantic Ocean off northeastern Florida. Marine Biology 162, 635–648. https://doi.org/10.1007/s00227-015-2611-2

Ross, S.W., Nizinski, M.S., 2007. State of deep coral ecosystems in the U.S. southeast region: Cape Hatteras to southeastern Florida. In: Lumsden, S.E., Hourigan, T.F., Bruckner, A.W., Dorr, G. (Eds.) The state of deep coral ecosystems of the United States. NOAA Technical Memorandum CRCP-3. Silver Spring, MD, pp. 233–269.

Ross, S.W., Quattrini, A.M., 2007. The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Research I 54, 975–1007. https://doi.org/10.1016/j.dsr.2007.03.010

Ross, S.W., Quattrini, A.M., 2009. Deep-sea reef fish assemblage patterns on the Blake Plateau (western North Atlantic Ocean). Marine Ecology 30, 74–92. https://doi.org/10.1111/j.1439-0485.2008.00260.x

de Saint Laurent, M., Macpherson, E., 1990. Les espèces atlantiques du genre *Eumunida* Smith, 1883 (Crustacea: Decapoda: Chirostylidae). Journal of Natural History 24, 647–666. https://doi.org/10.1080/00222939000770441

Schnabel, K.E., Cabezas, P., McCallum, A., Macpherson, E., Ahyong, S.T., Baba, K., 2011. Worldwide distribution patterns of squat lobsters. In: Poore, G.C.B., Ahyong, S.T., Taylor, J. (Eds.), The biology of squat lobsters, CSIRO Publishing, Victoria, Australia, pp. 149–182.

Smith, S.I., 1883. Preliminary report on the Brachyura and Anomura dredged in deep water off the south coast of New England by the United States Fish Commission in 1880, 1881, and 1882. Proceedings of the United States National Museum 6, 1–57. https://doi.org/10.5479/si.00963801.6-343.1

Smith, C.R., Baco, A.R., 2003. Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology Annual Review 41, 311–354. https://doi.org/10.1201/9780203180594.ch6

Su, Z., He, J.X., 2013. Analysis of Lake Huron recreational fisheries data using models dealing with excessive zeros. Fisheries Research 148, 81–89. https://doi.org/10.1016/j.fishres.2013.08.012

Tapella, F., Lovrich, G.A., Romero, M.C., Thatje, S., 2002. Reproductive biology of the crab *Munida subrugosa* (Decapoda: Anomura: Galatheidae) in the Beagle Channel, Argentina. Journal of the Marine Biological Association of the United Kingdom 82, 589–595. https://doi.org/10.1017/S0025315402005921

Thiel, M., Lovrich, G.A., 2011. Agonistic behaviour and reproductive biology of squat lobsters. In: Poore, G.C.B., Ahyong, S.T., Taylor, J. (Eds.), The biology of squat lobsters, CSIRO Publishing, Victoria, Australia, pp. 223–247.

Thiem, Ø., Ravagnan, E., Fosså, J.H., Berntsen, J., 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. Journal of Marine Systems 60, 207–219. https://doi.org/10.1016/j.jmarsys.2005.12.004

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates, Biological Reviews 25, 1–45. https://doi.org/10.1111/j.1469-185X.1950.tb00585.x

Uiblein, F., Youngbluth, M., Jacoby, C., Pagès, F., Picheral, M., Gorsky, G., 2005. *In situ* observations of deep-water fishes in four canyons off the Georges Bank, NW Atlantic. In: Shotton, R., (Ed.), Deep Sea 2003: Conference on the governance and management of deep-sea fisheries. Part 1. Conference Reports. FAO Fisheries Proceedings 3/1, pp. 98–106.

Wenner, E.L., 1982. Notes on the distribution and biology of Galatheidae and Chirostylidae (Decapoda: Anomura) from the middle Atlantic Bight. Journal of Crustacean Biology 2, 360–377. https://doi.org/10.2307/1548053

Wenner, E.L., Barans, C.A., 2001. Benthic habitats and associated fauna of the upper- and middle-continental slope near the Charleston Bump. In: Sedberry, G.R. (Ed.), Island in the stream: oceanography and fisheries of the Charleston Bump, American Fisheries Society, Symposium 25, Bethesda, MD, pp. 161–176.

Williams, A.W., Turner, R.D., 1986. Squat lobsters (Galatheidae: *Munidopsis*) associated with mesh-enclosed wood panels submerged in the deep sea. Journal of Crustacean Biology 6, 617–624. https://doi.org/10.1163/193724086X00415

WoRMS (2022a). Galatheoidea Samouelle, 1819. Accessed at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=106685 on 2022-04-22.

WoRMS (2022b). Chirostyloidea Ortmann, 1892. Accessed at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=562583 on 2022-04-22.

Zeileis, A., Kleiber, C., 2018. countreg: Count Data Regression. R package version 0.2-1. http://R-Forge.R-project.org/projects/countreg/

Appendix A. Material Examined.

Cape Lookout A: USNM 1143569; 1(8 mm CL); 34.33° N 75.79° W; 427–384 m; Sept 22 2001. USNM 1143570; 1(43.25 mm CL); 34.33° N 75.79° W; 427–384 m; Sept 22 2001. USNM 1143571; 1(31.58 mm CL); 34.33° N 75.79° W; 427–384 m; Sept 22 2001. USNM 1143572; 2(5.25–5.5 mm CL); 34.33° N 75.79° W; 427–384 m; Sept 22 2001. USNM 1143573; 2(22.91–37.97 mm CL); 34.32° N 75.79° W; 399–370 m; Sept 22 2001. USNM 1143574; 3(29.68–40.04 mm CL); 34.32° N 75.79° W; 417–371 m; Sept 23 2001. USNM 1143575; 1(34.8 mm CL); 34.32° N 75.79° W; 399–370 m; Sept 22 2001. USNM 1143576; 3(37.41–43.96 mm CL); 34.32° N 75.79° W; 418–384 m; Aug 12 2002. USNM 1143577; 1(14.13 mm CL); 34.32° N 75.79° W; 418–384 m; Aug 12 2002. USNM 1143578; 1(5.13 mm CL); 34.32° N 75.79° W; 418–384 m; Aug 12 2002. USNM 1143579; 1; 34.32° N; 75.79° W; 416–385 m; Aug 11 2002. USNM 1143580; 3(7.25–11.75 mm CL); 34.32° N 75.80° W; 405–396 m; Aug 10 2002. USNM 1143581; 12(28.65–43.88 mm CL); 34.32° N 75.80° W; 405–396 m; Aug 10 2002. USNM 1143582; 6(5.25–8.88 mm CL); 34.31° N 75.79° W; 426–430 m; Aug 11 2002. USNM 1143589; 1(38.8 mm CL); 34.32° N 75.79° W; 432–389 m; Aug 24 2003. USNM 1143593; 1(31.42 mm CL); 34.32° N 75.79° W; 424–385 m; Aug 24 2003. USNM 1143610; 3(5.88–6.63 mm CL); 34.33° N 75.80° W; 370–407 m; Jun 15 2004. USNM 1143611; 2(38.93–39.14 mm CL); 34.33° N 75.80° W; 370–407 m; Jun 15 2004. USNM 1143617; 1(19.67 mm CL); 34.32° N 75.79° W; 425–384 m; Jun 15 2004. USNM 1143618; 1(42.4 mm CL); 34.32° N 75.79° W; 425–384 m; Jun 15 2004. USNM 1143619; 1(5.5 mm CL); 34.32° N; 75.79° W; 431–392 m; Jun 15 2004. USNM 1143620; 2(37.96–47.52 mm CL); 34.32° N 75.79° W; 431–392 m; Jun 15 2004. USNM 1143621; 2(40.58–41.8 mm CL); 34.32° N 75.79° W; 431–392 m; Jun 15 2004. USNM 1143622; 1(38.93 mm CL); 34.32° N 75.79° W; 431–392 m; Jun 15 2004. USNM 1143627;

1(5.38 mm CL); 34.33° N 75.79° W; 420–389 m; Oct 17 2005. USNM 1143628; 1(45.1 mm CL); 34.33° N 75.79° W; 420–389 m; Oct 17 2005. USNM 1143629; 1(20.79 mm CL); 34.32° N 75.79° W; 433–380 m; Oct 17 2005. USNM 1143630; 1(35.51 mm CL); 34.32° N 75.79° W; 433–380 m; Oct 17 2005. USNM 1143651; 1(6.63 mm CL); 34.32° N 75.79° W; 433–380 m; Oct 17 2005. USNM 1143652; 2(5.25–12.5 mm CL); 34.32° N 75.79° W; 433–380 m; Oct 17 2005. USNM 1143656; 3(5.0–5.13 mm CL); 34.32° N 75.79° W; 378 m; Dec 4 2009. USNM 1143657; 1(5.25 mm CL); 34.32° N 75.79° W; 381 m; Dec 4 2009. USNM 1143658; 1(5 mm CL); 34.32° N 75.79° W; 381 m; Dec 4 2009. USNM 1143659; 1(9.88 mm CL); 34.33° N 75.80° W; 361 m; Dec 4 2009. USNM 1143663; 1(16.56 mm CL); 34.33° N 75.80° W; 398–397 m; Aug 28 2001. USNM 1143664; 1(41.95 mm CL); 34.32° N 75.79° W; 434–409 m; Aug 28 2001. USNM 1143665; 2(36.39–42.23 mm CL); 34.32° N 75.79° W; 434–409 m; Aug 28 2001. USNM 1143666; 2(18.54–40.96 mm CL); 34.32° N 75.80° W; 420–390 m; Aug 28 2001. USNM 1143667; 1(39.21 mm CL); 34.32° N 75.80° W; 420–390 m; Aug 28 2001. USNM 1146141; 1(5.3 mm CL); 34.33° N 75.78° W; 447–386 m; Aug 11 2002. USNM 1146142; 1; 34.32° N 75.79° W; 416–385 m; Aug 11 2002. USNM 1150204; 1; 34.32° N 75.79° W; 418–384 m; Aug 12 2002. USNM 1150205; 3(6.25–7.63 mm CL); 34.33° N 75.79° W; 427–384 m; Sep 22 2001. **Cape Lookout B:** USNM 1143631; 1(6.88 mm CL); 34.23° N 75.87° W; 411–375 m; Oct 18 2005. USNM 1143632; 1(8.5 mm CL); 34.23° N 75.87° W; 411–375 m; Oct 18 2005. USNM 1143633; 1(28.19 mm CL); 34.23° N 75.87° W; 411–375 m; Oct 18 2005. USNM 1143634; 1(23.46 mm CL); 34.23° N 75.87° W; 419–371 m; Oct 18 2005. USNM 1143635; 5(12.5–39.61 mm CL); 34.23° N 75.87° W; 419–371 m; Oct 18 2005. USNM 1143636; 1(25.73 mm CL); 34.22° N 75.88° W; 413–395 m; Oct 19 2005. USNM 1143668; 2(42.52–48.16 mm CL); 34.20° N 75.88° W; 443–423 m; Sept 19 2006. USNM 1143669; 1(37.94 mm CL); 34.23°

N 75.87° W; 440–406 m; Sept 19 2006. USNM 1143670; 3(5.0–11.88 mm CL); 34.19° N 75.90° W; 431–279 m; Sept 19 2006. USNM 1143671; 1(47.74 mm CL); 34.23° N 75.87° W; 430–419 m; Sept 20 2006. USNM 1143672; 1(7.25 mm CL); 34.20° N 75.89° W; 455–408 m; Sept 20 2006. USNM 1143673; 14(10.0–51.06 mm CL); 34.21° N 75.88° W; 455–408 m; Sept 20 2006. USNM 1143674; 2(16.15–32.97 mm CL); 34.19° N 75.90° W; 431–415 m; Sept 20 2006. USNM 1146137; 1; 34.22° N 75.88° W; 413–395 m; Oct 19 2005. **Cape Fear:** USNM 1143583; 1(38.27 mm CL); 33.57° N 76.47° W; 377–371 m; Aug 22 2003. USNM 1143585; 1(27.69 mm CL); 33.57° N 76.47° W; 377–371 m; Aug 22 2003. USNM 1143586; 1(30.14 mm CL); 33.57° N 76.47° W; 377–371 m; Aug 22 2003. USNM 1143587; 6(19.53–41.79 mm CL); 33.57° N 76.47° W; 377–371 m; Aug 22 2003. USNM 1143588; 3(31.29–45.44 mm CL); 33.57° N 76.47° W; 377–371 m; Aug 22 2003. USNM 1143590; 3(30.27–36.37 mm CL); 33.57° N 76.46° W; 381–418 m; Aug 22 2003. USNM 1143591; 1(30.46 mm CL); 33.57° N 76.46° W; 381–418 m; Aug 22 2003. USNM 1143594; 2(24.04–39.23 mm CL); 33.57° N 76.47° W; 386–379 m; Aug 21 2003. USNM 1143623; 1(21.17 mm CL); 33.57° N 76.46° W; 390–402 m; Jun 17 2004. USNM 1143624; 1(4.88 mm CL); 33.57° N 76.46° W; 390–402 m; Jun 17 2004. USNM 1143637; 1(29.66 mm CL); 33.57° N 76.46° W; 397–374.89 m; Oct 20 2005. USNM 1143638; 1(28.63 mm CL); 33.57° N 76.46° W; 397–375 m; Oct 20 2005. USNM 1143639; 1(8.75 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1143640; 1(32.34 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1143641; 1(41.97 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1143642; 2(34.91–43.93 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1143643; 1(32.65 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1143644; 1(32.89 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. USNM 1146138; 1(29.49 mm CL); 33.57° N 76.46° W; 397–375 m; Oct 20 2005. USNM 1146139;

2(5.38–9.63 mm CL); 33.58° N 76.47° W; 443–408 m; Oct 20 2005. **Stetson North:** USNM 1143645; 1(44.97 mm CL); 32.27° N 77.47° W; 642–550 m; Oct 21 2005. USNM 1143646; 2(31.62–42.24 mm CL); 32.26° N 77.48° W; 603–587 m; Oct 21 2005. USNM 1143647; 1(23.43 mm CL); 32.26° N 77.48° W; 603–587 m; Oct 21 2005. USNM 1143648; 1(40.09 mm CL); 32.26° N 77.48° W; 603–587 m; Oct 21 2005. **Stetson:** USNM 1143592; 1(44.63 mm CL); 32.03° N 77.67° W; 622–597 m; Aug 17 2003. USNM 1143625; 1(15.41 mm CL); 31.83° N 77.61° W; 703–664 m; Jun 18 2004. USNM 1143626; 1(41.28 mm CL); 31.85° N 77.61° W; 696–660 m; Jun 18 2004. **Savannah Banks:** USNM 1143649; 1(39.9 mm CL); 31.71° N 79.13° W; 516–514 m; Oct 26 2005. **Jacksonville Lithoherms:** USNM 1143612; 1(44.7 mm CL); 30.52° N 79.66° W; 568–544 m; Jun 10 2004. USNM 1143613; 2(42.91–49.07 mm CL); 30.51° N 79.66° W; 569–554 m; Jun 10 2004. USNM 1143614; 1(25.95 mm CL); 30.50° N 79.65° W; 638–593 m; Jun 11 2004. USNM 1143615; 1(43.29 mm CL); 30.50° N 79.65° W; 638–593 m; Jun 11 2004. USNM 1143650; 1(40.61 mm CL); 30.52° N 79.66° W; 585–625 m; Nov 1 2005. USNM 1146140; 1(39.71 mm CL); 30.51° N 79.66° W; 564–558 m; Jun 19 2004. **Cape Canaveral:** USNM 1143777; 1(36.19 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143778; 1(24.86 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143779; 1(21.98 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143780; 1(53.46 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143781; 1(23.24 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143782; 1(48.54 mm CL); 28.32° N 79.75° W; 450–424 m; Aug 6 2009. USNM 1143783; 1(27.9 mm CL); 28.32° N 79.75° W; 453–398 m; Aug 10 2009. USNM 1143784; 1(45.86 mm CL); 28.32° N 79.75° W; 453–398 m; Aug 10 2009. USNM 1143785; 1(38.24 mm CL); 28.32° N 79.75° W; 453–398 m; Aug 10 2009. USNM 1143786; 1(50.89 mm CL); 28.32° N 79.75° W; 439–408 m; Aug 12 2009. USNM

1143787; 1(36.4 mm CL); 28.46° N 79.72° W; 532–499 m; Aug 13 2009. USNM 1143800; 1(38.88 mm CL); 28.39° N 79.77° W; 446–407 m; Aug 14 2009. USNM 1143801; 1(43.54 mm CL); 28.39° N 79.77° W; 446–407 m; Aug 14 2009. USNM 1143802; 1(48.93 mm CL); 28.39° N 79.77° W; 446–407 m; Aug 14 2009. USNM 1143803; 1(40.72 mm CL); 28.39° N 79.77° W; 446–407 m; Aug 14 2009. USNM 1150202; 4(25.78–42.47 mm CL); 30.52° N 79.66° W; 625–585 m; Nov 1 2005. USNM 1150203; 1(44.65 mm CL); 30.52° N 79.66° W; 625–585 m; Nov 1 2005.

Supplemental Table 1. The full set of candidate models, with AIC results, for the two-part Negative Binomial Hurdle models. The number of squat lobster was a function of habitat (dead and live *Lophelia*), region (North Carolina, Georgia/Stetson/northern Florida, and Cape Canaveral), depth (< 600 m and > 600 m), and cruise (10 research cruises conducted in late summer to late fall from 2000-2005 and 2009).

Model	Equation			k	AIC	Δ	w
hnb_1	Individuals	~	Habitat	6	1040.27	66.27	< 0.001
hnb_2	Individuals	~	Region	8	989.13	15.12	< 0.001
hnb_3	Individuals	~	Depth	6	999.53	25.53	< 0.001
hnb_4	Individuals	~	Cruise	16	1012.41	38.41	< 0.001
hnb_5	Individuals	~	Habitat * Region	14	980.90	6.89	0.016
hnb_6	Individuals	~	Habitat * Depth	10	994.14	20.13	< 0.001
hnb_7	Individuals	~	Habitat * Year	30	1016.61	42.60	< 0.001
hnb_8	Individuals	~	Habitat + Region + Depth	12	974.01	0.00	0.508
hnb_9	Individuals	~	Habitat + Region + Depth + Cruise	24	974.14	0.13	0.476

Supplemental Table 2. The full set of candidate models, with AIC results, for the two-part Negative Binomial Hurdle models. The number of squat lobster was a function of habitat (dead and live *Lophelia*), region (a five-level factor that incorporated region and depth, with North Carolina Shallow = 01, Georgia/Stetson/northern Florida Shallow = 10, Georgia/Stetson/northern Florida Deep = 11, Cape Canaveral Shallow = 20, and Cape Canaveral Deep = 21), and cruise (10 research cruises conducted in late summer to late fall from 2000-2005 and 2009).

Model	Equation			k	AIC	Δ	w
hnb$_1$	Individuals	~	Habitat	6	1040.27	80.03	< 0.001
hnb$_2$	Individuals	~	Region	12	968.52	8.28	0.010
hnb$_3$	Individuals	~	Cruise	16	1012.41	52.17	< 0.001
hnb$_4$	Individuals	~	Habitat + Region	14	960.24	0.00	0.636
hnb$_5$	Individuals	~	Habitat * Cruise	30	1016.61	56.37	< 0.001
hnb$_6$	Individuals	~	Region + Cruise	24	978.52	18.28	< 0.001
hnb$_7$	Individuals	~	Habitat * Region	22	961.49	1.25	0.341
hnb$_8$	Individuals	~	Habitat + Region + Cruise	26	968.02	7.78	0.013