

# Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA

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**Abstract** Deep-sea corals provide important habitat for many organisms; however, the extent to which fishes and other invertebrates are affiliated with corals or other physical variables is uncertain. The Cape Fear coral mound off North Carolina, USA (366–463 m depth, 33° 34.4'N, 76° 27.8'W) was surveyed using multibeam sonar and the Johnson-Sea-Link submersible. Multibeam bathymetric data (2006) were coupled with in situ video data (2002–2005) to define habitat associations of 14 dominant megafauna at two spatial scales. Results suggested greater habitat specificity of deep-reef fauna than previously documented, with fishes showing greater affinity for certain habitat characteristics than most invertebrates. High vertical profile, degree of coral coverage, and topographic complexity influenced

distributions of several species, including *Beryx decadactylus*, *Conger oceanicus*, and *Novodinia antillensis* on the smaller scale (30 × 30 m). On the broad scale (170 × 170 m), several suspension feeders (e.g., *N. antillensis*, anemones), detritivores (*Echinus* spp.), and mesopelagic feeders (e.g., *Beryx decadactylus*, *Eumunida picta*) were most often found on the south-southwest facing slope near the top of the mound. Transient reef species, including *Laemonema barbatulum* and *Helicolenus dactylopterus*, had limited affiliations to topographic complexity and were most often on the mound slope and base. Megafauna at deep-water reefs behave much like shallow-water reef fauna, with some species strongly associated with certain fine-scale habitat attributes, whereas other species are habitat generalists. Documenting the degree of habitat specialization is important for understanding habitat functionality, predicting faunal distributions, and assessing the impacts of disturbance on deep-reef megafauna.

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## Introduction

Marine species are often predictably affiliated with certain habitats due to a combination of ecological, biological, and environmental factors operating over various temporal and spatial scales. Species-habitat associations are well-studied in shallow-water (<200 m) ecosystems, including seagrass beds (e.g., Orth et al. 1984; Attrill et al. 2000), coral reefs (e.g., Hixon and Beets 1993; Munday et al. 1997), and *Sargassum* spp. mats (e.g., Casazza and Ross 2008). Species-specific assemblages have also been documented using submersibles and ROVs in structurally complex habitats (e.g., deep-sea coral reefs, tubeworm aggregations, and mussel beds) along continental margins (200–4,000 m; see Levin et al. 2010). However, faunal associations with

fine-scale habitat parameters (e.g., vertical profile, topographic complexity) that are often affiliated with shallow-water reef fauna are less well-known in the deep sea (>200 m). Detailed, topographic data produced by multi-beam sonar have facilitated species-habitat association studies, and integrating these data with in situ video provides the opportunity to examine and map the distribution of fauna relative to habitat variables in deep-sea ecosystems (Wilson et al. 2007).

Biogenic habitats, such as deep-sea (cold-water) coral reefs, like shallow-water reefs, concentrate resources and increase local diversity (e.g., Jensen and Frederiksen 1992; Ross and Quattrini 2007). In the deep Atlantic Ocean, *Lophelia pertusa* is the dominant reef-building coral (Roberts et al. 2009), but other scleractinians, antipatharians, octocorals, and sponges attach to existing hardbottoms (e.g., Roberts et al. 2006, 2009) and form deep-reef habitat. Deep-water reefs harbor higher species richness, higher densities of organisms, and different species assemblages compared to surrounding non-reef habitats (e.g., Mortensen et al. 1995; Ross and Quattrini 2007), but the degree to which fauna are closely associated with deep-reef habitat varies by location (Ross and Quattrini 2009; Buhl-Mortensen et al. 2010). Despite increasing studies on the biodiversity of deep-sea reefs (e.g., Cordes et al. 2008; Roberts et al. 2008), little quantitative data exist on how habitat structure, particularly at fine spatial scales, influences the associated megafaunal communities (Roberts et al. 2008). The question remains whether deep-reef megafauna exhibit similar habitat-specific associations to species inhabiting shallow-water coral reefs.

Broadly defined habitat type (i.e., coral, cobble, and rubble) and depth are two important factors influencing abundance, diversity, and distribution of megafaunal species at deep-sea reefs. For example, species richness and abundance of sessile and mobile invertebrates were often comparable between *L. pertusa* and other structured habitats, such as coral rubble or rock, yet differed from mud, sand, and cobbles (Mortensen et al. 1995; Roberts et al. 2008). In addition, different substrates (outcrop, gravel, and boulders) with varying degrees of attached fauna influenced the distribution of the fish assemblages in the Gulf of Maine (Auster 2005). In contrast, depth, not habitat type, influenced the species composition of deep-reef fish assemblages in the northeastern Atlantic (Costello et al. 2005). Both differences in habitat structure and depth likely influenced the distribution of deep-reef fish assemblages of the southeastern US (SEUS; North Carolina through Florida; Ross and Quattrini 2007, 2009). Although these studies provided insight into broad scale distribution patterns at deep-sea reefs and nearby habitats, knowledge concerning fine-scale habitat affiliations is still lacking.

A characteristic fauna (particularly fishes) associated with deep-water reefs appears to distinguish SEUS and Gulf of Mexico (GOM) deep reefs from those in other regions (Ross and Quattrini 2007; Sulak et al. 2007). This unique fauna includes recently discovered species (McCosker and Ross 2007; Fernholm and Quattrini 2008; Nielsen et al. 2009; Mah et al. 2010; Anker and Nizinski 2011) and numerous species not previously known in those regions (Caruso et al. 2007; Ross and Quattrini 2007; Henry et al. 2008). This suggests that megafauna associated with deep reefs may have stronger affiliations with particular habitats within the SEUS compared to other deep reefs, such as those in more northern Atlantic latitudes (Auster 2005; Costello et al. 2005). This is further supported by observations of numerous fish species often in direct contact with coral surfaces, either lying on, burrowing, or sheltering within the coral framework (Ross and Quattrini 2007; Sulak et al. 2007). Such intimate contact seems less common or lacking in similar observations in other areas (e.g., of California, Tissot et al. 2006). Unique faunal associations at deep reefs coupled with a fauna typified by new range records and new species make the SEUS and GOM regions appealing for investigating species-specific, deep-reef habitat associations.

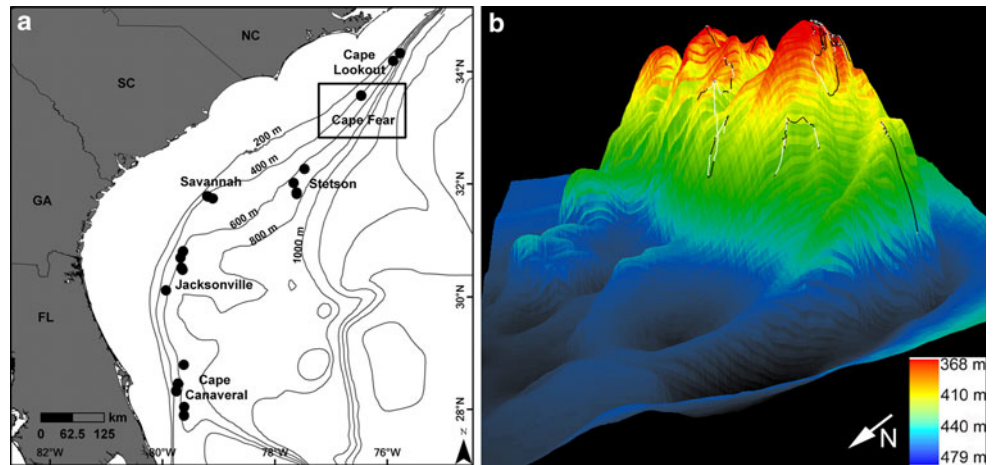
In this study, multibeam sonar and in situ video data were coupled to test whether deep-reef species exhibit affinities to particular habitat types at deep-sea reefs. Megafaunal-habitat associations were, therefore, examined at fine (10 s of m) to broad (100 s of m) spatial scales on a deep-sea coral mound off North Carolina, USA. We focused on the structural characteristics of the habitat rather than variable water mass parameters (e.g., temperature, dissolved oxygen) to facilitate comparisons with shallow-water reef studies. To determine whether megafaunal species associated with deep-sea corals were affiliated with certain habitat types: (1) habitat variables were derived from multibeam and video data, (2) dominant invertebrates and fishes were enumerated using submersible video, (3) megafaunal abundances were mapped with habitat variables, and (4) two statistical techniques were used to examine species' distributions relative to habitat types.

## Materials and methods

### Coral-mound surveys

The Cape Fear (CF) coral mound, ~140 km east of Cape Fear, North Carolina (33° 34.4'N, 76° 27.8'W), was surveyed using the Johnson Sea-Link (JSL) submersible and multibeam sonar. The combination of good quality multibeam data and broad coverage of submersible dives (traversing 4.9 km) across this isolated mound made this site

**Fig. 1** **a** General locations of deep-reef study sites along southeastern US coast. Cape Fear coral mound is boxed. **b** Nine JSL tracks (some parts hidden by 3-D view) shown on 3-D topographic image of Cape Fear coral mound generated from multibeam data. Vertical exaggeration =  $\times 5$



one of the best-surveyed deep-coral mounds in the SEUS region (Fig. 1a; for site descriptions see Partyka et al. 2007; Ross and Quattrini 2007, 2009). Nine JSL dives were conducted (2002–2005) across the mound in summer-fall (see Ross and Quattrini 2007 for more dive details). No multibeam data were available to help guide the JSL dives, so details of mound morphology could not be used to guide dives. Our overall dive objectives were to locate the coral mound, survey the habitats and fauna, and collect within *Lophelia pertusa* habitat. Although dives targeted *Lophelia pertusa* thickets, transects over other habitats were also conducted. Transects included all times when the submersible was moving across the bottom. Methods were standardized as much as possible by keeping the sub as close to the bottom as practical, maintaining slow speed, tilting the external camera downward ( $\sim 30$ – $50^\circ$  toward seafloor), and videotaping on wide-angle view. The consistent camera field of view and motion of the JSL maintained consistency among dive videos so that data were comparable. For scale, two laser pointers were mounted (25 cm apart) on the camera. As a back-up, video was also recorded with a handheld camera from the bow compartment of the JSL throughout each dive. Depth, temperature, salinity, date, and time were logged at  $\leq 1$  scan  $s^{-1}$  intervals using a Sea-Bird SBE 25 or 19 plus conductivity–temperature–depth (CTD) logger attached to the submersible. CTD data were overlain on the external videotapes. The submersible’s position was tracked irregularly (every 4 s to 10 min) during all dives from the surface support ship using a Trackpoint II USBL system (1% slant range error, JSL crew, HBOI, pers. comm.). Multibeam data were collected in 2006 using the Kongsberg-Simrad EM1002, a 95 kHz echosounder with 111 beams  $ping^{-1}$  over a maximum coverage sector of  $150^\circ$  (beam spacing was equidistant), mounted on the NOAA vessel *Nancy Foster*. Raw multibeam data were processed using CARIS HIPS and SIPS (v 6.1) to produce a 10-m-resolution bathymetric map.

### Dive track processing

Post-processing of JSL dive tracks was completed to remove erroneous track data following Partyka et al. (2007). We used speed of the JSL and the depth logged by the CTD to guide the removal of erroneous positions. Given a maximum JSL speed of 1 knot (1 knot =  $0.51 \text{ m s}^{-1}$ ) (JSL crew, HBOI, pers. comm.) and a possible 1 knot current from the stern, the JSL could travel at its fastest predicted speed of  $1.11 \text{ m s}^{-1}$ . As a conservative measure, this estimate was doubled, and location points that were more than  $2.22 \text{ m s}^{-1}$  away from previous locations were deleted. The location points were plotted in ArcGIS (v 9.2, ESRI) and further edited by averaging every three points along each track. Remaining dive track positions were then error-checked by viewing the internal and external JSL dive videos to ensure that depths of positions along the dive tracks obtained from the JSL CTD data matched the multibeam bathymetry. Video review also revealed whether the overall direction of travel and small-scale movements (e.g., turns, stops) of the JSL matched the plotted tracks. Although accuracy in position is important in georeferencing the dive track to the multibeam bathymetry and in obtaining habitat variables calculated from the digital terrain model, the smallest scale of terrain analysis ( $30 \times 30 \text{ m}$ , see “Digital terrain model analyses” section) was large enough that potential inaccuracies ( $< 30 \text{ m}$ ) in the positional data would not influence the results.

### Video analyses

Fourteen species of megafaunal fishes and invertebrates consistently associated with SEUS deep-sea reef habitats were selected for analysis. Of the 18 species of reef fishes observed on the CF mound (Ross and Quattrini 2009), eight dominant species of fishes were selected: alfoncino *Beryx decadactylus* (Berycidae), American conger eel *Conger*

*oceanicus* (Congridae), blackbelly rosefish *Helicolenus dactylopterus* (Scorpaenidae), western roughy *Hoplostethus occidentalis* (Trachichthyidae), shortbeard codling *Laemonema barbatulum* (Moridae), coral hake *Laemonema melanurum* (Moridae), roughtip grenadier *Nezumia sclerorhynchus* (Macrouridae), and wreckfish *Polyprion americanus* (Polyprionidae). Mobile invertebrates analyzed included the following: sea urchins *Echinus* spp. (Echiniidae), squat lobster *Eumunida picta* (Eumunididae), and spider crab *Rochinia crassa* (Epialtidae). Sessile invertebrates included the following: brisingid seastar *Novodinia antillensis* (Brisingidae), actinostolid anemones (Actinostolidae), and flytrap anemone *Actinoscyphia saginata* (Actinoscyphiidae). It was difficult to differentiate species of *Echinus* on video, including *E. tyloides* and *E. gracilis*, which have both been collected in the region, so these species were combined and reported as *Echinus* spp. In addition, *A. saginata* was the only species of anemone that could be accurately identified to species on video; all other anemones were identified to family.

Dominant megafaunal species were enumerated and identified to the lowest possible taxonomic level during nine dives when the JSL was transecting (see Ross and Quattrini 2007, 2009). Submersible transects were divided into 10 s segments (~5 m in length) so that variability in JSL movement (stopping to collect specimens or rapid speed) and poor video quality (zoomed or dark views) could be removed from analyses. These segments also accounted for the abrupt, fine-scale habitat changes that occurred along transects. We also deleted data if the JSL crossed its own track during any one dive. Individuals of each species were counted during each segment except actinostolid anemones, which were coded as absent, rare (1–10 individuals), common (10–100 individuals), or abundant (>100 individuals). Our counts were conservative to ensure that no individuals were counted more than once. Megafaunal abundances during each 10-s segment were georeferenced to the corrected dive track and plotted (ArcGIS v 9.2) onto CF bathymetry using time as a correlate.

Three general habitat types (modified from Partyka et al. 2007) were classified using video data and scientists' observations: (1) soft/rubble = soft substrate with <50% rubble (dead, broken, unattached rock or bio-eroded coral pieces) coverage, (2) rubble = soft substrate with >50% rubble coverage, or (3) hard coral  $\geq 50\%$  coverage of intact branches or thickets of dead or live *L. pertusa*. No conspicuous octocorals were observed on this mound. Hard coral habitat was further differentiated by gradients of vertical profile, live coral coverage, and percent bottom coverage. Profile was characterized by coral height: low  $\leq 0.5$  m, moderate = 0.5–1 m, or high  $\geq 1$  m. Percent live coral classifications were defined as: low  $\geq 0$ –10%, low-moderate  $\geq 10$ –50%, moderate-high = 50–75%, or high  $\geq 75\%$ . Lastly, bottom

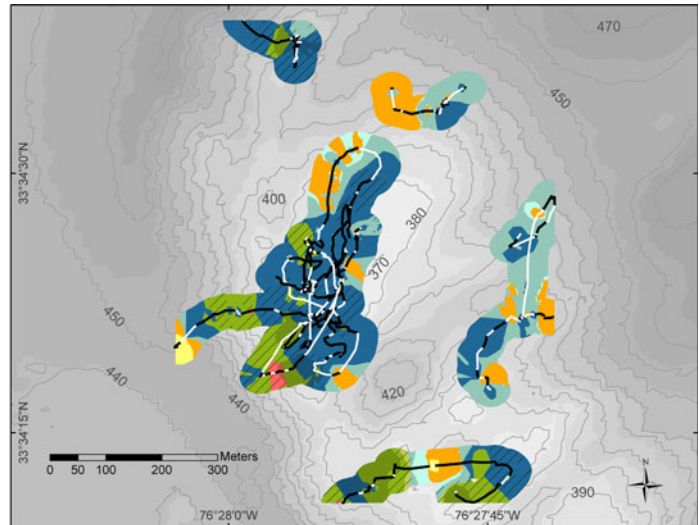
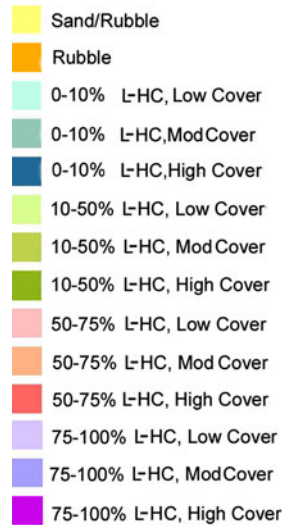
coverage was measured by percent of seafloor covered by hard corals: low  $\leq 50\%$ , moderate = 50–75%, or high  $\geq 75\%$ . Time was recorded when the habitat changed. Using these times as correlates, habitat data were georeferenced to the dive tracks and then mapped (ArcGIS) using the Inverse Distance Weighted interpolation to 30 m on either side of each dive track to facilitate map readability.

#### Digital terrain model analyses

A digital terrain model (DTM) of the CF mound was created (ArcGIS) from the 10-m-resolution multibeam bathymetry (Fig. 2b) and used to calculate habitat variables at two spatial scales. Habitat variables were calculated across the DTM at fine (30  $\times$  30 m) and broad (170  $\times$  170 m) spatial scales using Landserf 2.2 (Wood 2005) and ArcGIS extension Benthic Terrain Modeler (NOAA, Oregon State University) software programs. Habitat variables (Table 1) calculated with these software packages included: aspect, bathymetric position index (BPI), curvature, fractal dimension, rugosity, and slope. Altitude was calculated by subtracting the depth of the JSL recorded by the CTD from average bottom depth at the base of the mound determined using the DTM.

Habitat calculations at two spatial scales were performed using a sliding window analysis. Analysis windows were based on the resolution of the multibeam data (Albani et al. 2004; Hartley et al. 2004; Wilson et al. 2007). Each pixel (10 m) on the DTM became a centroid in the analysis window, and the perimeter surrounding the central pixel consisted of either 3 or 17 pixels in both the x and y directions. The size of each analysis window was determined by multiplying the resolution (10 m) of the multibeam data by the number of pixels (e.g., 3  $\times$  10 m = 30 m and 17  $\times$  10 m = 170 m). Therefore, 30  $\times$  30 m and 170  $\times$  170 m analysis windows were established as fine and broad spatial scales, and habitat variables were then calculated within these areas across the DTM. Because of the multibeam resolution, 30  $\times$  30 m was the smallest possible area in which a habitat variable could be calculated. This was also the smallest practical scale because a 1-pixel analysis window is unsatisfactory as it could capture the elevation errors that can occur within a DTM (Albani et al. 2004). The 170  $\times$  170 m window was determined to be an appropriate measure for broad-scale analysis using measures of fractal dimension (Hartley et al. 2004; Wilson et al. 2007; Dolan et al. 2008). Fractal dimension (surface complexity) values at different spatial scales can denote the boundary between fine- and broad-scale terrain properties (Hartley et al. 2004; Wilson et al. 2007). We calculated fractal dimension in analysis windows of 9, 17, 33, and 65 pixel sizes. At window sizes >17 pixels, fractal dimension values changed little, so 17 pixels were used to denote the break between fine

**Fig. 2** Habitat types mapped to 30 m on each side of each dive track at Cape Fear coral mound (10-m contours). *Black* portions of dive tracks represent useable segments for video analysis; white portions represent unusable segments. Habitat types color coded. Hard coral (HC) habitat types listed in legend by percent live (L) coral coverage followed by low, moderate (mod), or high bottom coverage. Hatching denotes moderate to high vertical profile



**Table 1** Habitat variable definitions calculated at two spatial scales (30 × 30 m and 170 × 170 m)

Habitat variable	Definition	Reference
Altitude	Height above the base of the mound	NA
Aspect	Direction in degrees, converted to relative northness [=sin (aspect in radians)] and eastness [=cosine (aspect in radians)]	Hirzel (2004), Wood (2005)
Slope	Degree of change from the horizontal	Wood (2005)
Terrain complexity	Variation and diversity in terrain	
Rugosity <sup>a, b</sup>	Ratio of surface area to planar area	Jenness (2002)
Fractal dimension <sup>b</sup>	Measure of surface complexity	Mandelbrot (1983), Wood (2005)
Curvature	Measurements for peaks, valleys, and ridges along the terrain	
BPI <sup>a</sup>	Index value for topographic high or low	Lundblad et al. (2006)
Mean curvature	Average of maximum convexity and minimum concavity, based on elevation and aspect	Evans (1980)
Plan Curvature	Rate of change in slope; distinguishing downslope ridges and valleys	Evans (1980), Wood (1996)
Profile curvature	Rate of change in aspect; distinguishing along-slope ridges and valleys	Evans (1980), Wood (1996)

Definitions of each habitat variable and corresponding references listed

<sup>a</sup> Calculated using the ArcGIS benthic terrain modeler. Other variables calculated with Landserf 2.2, except for altitude

<sup>b</sup> Rugosity calculated at the fine spatial scale; fractal dimension calculated at broad scale

and broad-scale terrain properties (Hartley et al. 2004; Wilson et al. 2007).

**Statistical analyses**

Associations between megafaunal species and habitat variables were statistically analyzed using canonical correspondence analysis (CCA, Canoco v 4.5 [see ter Braak 1996; ter Braak and Šmilauer 2002]). CCA explains species distribution patterns by calculating the species centroid, or optimum location, among habitat variables and functions well with datasets that contain numerous zero values (ter Braak 1986, 1996). We considered the 10-s segments per dive as independent samples because fine-scale habitats and/or depth changed from segment to segment. Abundances per segment were square-root transformed to downweight

abundant compared to rare individuals. Altitude and rugosity were log (X + 1) transformed to reduce skewed data distribution. Because negative values occurred in the BPI data, BPI values were standardized by adding a constant to each value to move the minimum value of the distribution to 1.0 before a log (X + 1) transformation was applied. Two CCA tests were performed; one test included habitat data from video and from 30 × 30 m DTM calculations, and the other test only included habitat data from 170 × 170 m DTM calculations. For each test, the biplot scaling option on inter-species distances was selected, and a Monte Carlo permutation tested significance of the first canonical eigenvalue and the sum of all canonical eigenvalues. Simple ordination plots were created (CanoDraw for Windows 4.4), displaying weighted averages of each species along categorical habitat types (as points) and quantitative habitat

variables (as arrows, ter Braak 1986). The length of each arrow is correlated to the ordination axes, in that a longer arrow indicates a stronger correlation and explains more variation in species' distribution patterns (ter Braak 1986). The resulting ordination diagrams combined with the low eigenvalues prompted us to perform two additional CCA tests that were similar to the first two tests except that they included fish abundance data only.

A second multivariate analysis based on eigensystem computation, ecological niche factor analysis (ENFA; Biomapper v 4.0, [Hirzel et al. 2004]), was used to supplement the CCA and obtain additional information on megafaunal-habitat associations. ENFA compares the observed distribution of a species within localities characterized by particular habitat conditions to a reference set of habitat variables describing the whole study area. Although ENFA results cannot infer causality, they can indicate which habitat conditions are highly associated with the observed species distribution (Hirzel et al. 2002). Deep-sea data are often limited, so ENFA is particularly useful because this analysis only requires presence data (Hirzel et al. 2002; Wilson et al. 2007).

ENFA was conducted on each species, except for *Hopl-ostethus occidentalis* because <10 individuals were observed. Landserf and ArcGIS raster grids of mapped habitat variables and abundance data were first imported into Biomapper. Floating point raster grids were then converted into an Idrisi (Eastman 1997) format using the Biomapper conversion tool and manual modification of document reference files. The Box-Cox function was applied to the quantitative habitat variables derived from the DTM in the Biomapper program to reduced skewed data. Species abundance data were analyzed as a Boolean dataset. Anemones were analyzed using the weighted species presence option in Biomapper because they were qualitatively coded into abundance categories.

ENFA results provide information on the habitat specificity of each species in the form of marginality and specialization output factors (see Hirzel et al. 2002). Marginality, explained by the first output factor, reveals how the distribution of a species differs from the mean habitat conditions of the study area. The higher the absolute value of each habitat coefficient, the further the distribution of a species departs from the mean value of that particular habitat variable. A negative value indicates the species is found in areas with values for habitat variables lower than the mean value. A positive value indicates a species is found in areas where values for habitat variables are higher than the mean value. The first output factor also explains a portion of the specialization (reported as %, Table S1), which describes the specificity of a species to a particular habitat value. The remaining output factors also indicate the degree of specialization of a species toward a particular habitat variable

where higher absolute values of coefficients indicate a species will more likely be found within a particular habitat range. Biomapper also computes global marginality, specialization, and tolerance values. Global marginality values are generally 0–1; a value closer to 1 indicates that a species is found in habitats where conditions differ significantly from the mean of all habitats surveyed. Global specialization ranges from 1 to  $\infty$ ; a higher number indicates greater specialization to a particular habitat within the study area. Finally, global tolerance values range from 0 to 1, with higher values indicating that a species has a more widespread distribution within the study area than expected for habitat specialists.

## Results

### Cape fear mound habitat

The CF coral mound is  $\sim 0.7$  km<sup>2</sup>, exhibiting slopes up to 80° and rising  $\sim 100$  m from the surrounding seafloor. This biogenic mound appears to have been created by the successive growth, collapse, and sediment entrapment of *Lophelia pertusa*. The top of the mound exhibits double peaks with one at 366 m and the other at 374 m depth. The average depth around the base of the mound is 463 m (450–480 m range; Fig. 1b). A tear-drop-shaped trench, seemingly current-scoured, with the narrow end facing northward occurs around the base of the mound. Although habitats were patchy, low profile, dead (90–100%), *L. pertusa* with >75% bottom coverage was the dominant fine-scale habitat type observed on the mound, particularly on the slope and the top (Fig. 2). Most of the moderate-to-high-profile, hard coral habitat was observed at  $\sim 5$ –45 m from the top of the mound and appeared to be concentrated on the south-southwest (up-current) facing slope (Fig. 2). The majority of the live coral was also concentrated in these areas where high-profile coral colonies were observed. Conversely, the north-northeast slope of the mound was covered with mostly soft/rubble, rubble, and low profile, dead (90–100%) hard coral habitats (Fig. 2).

Habitat values calculated at the 30 × 30 m and 170 × 170 m scales revealed fine- to broad-scale habitat changes across the mound (see Figs. S1–3). At the fine scale, the steepest gradient in slope (up to 86°) was observed on the south-southwest side of the mound, whereas the slope on the north-northeast side of the mound was more gradual. Broad-scale (170 × 170 m) slope values showed the same pattern as fine-scale slope values, but were calculated to be much lower (up to 25°). Rugosity and fractal dimension values indicated that the most complex terrain occurred on top of the 374-m peak and along the 420-m contour on the west and south-west sides of the

mound. Finally, measures of curvature and BPI indicated that very few fine-scale crests, ridges, and valleys occurred across the mound; except that along-slope ridges following bathymetric contours (380–420 m) were common near the top on the south-southwest facing slope. At the broad scale, little variability was observed in curvature and BPI; rather these measurements illustrated the topographic highs and lows of the whole mound.

#### Species-habitat data

Fourteen dominant invertebrate and fish species were enumerated during 4 h of transect time (1,453 10-s segments) from the nine JSL dives. Dominant fishes were, in decreasing order of abundance, as follows: *Beryx decadactylus* ( $n = 69$  individuals), *Laemonema barbatulum* ( $n = 23$ ), *Conger oceanicus* ( $n = 18$ ), *Helicolenus dactylopterus* ( $n = 12$ ), *Nezumia sclerorhynchus* ( $n = 12$ ), *Polyprion americanus* ( $n = 11$ ), *Laemonema melanurum* ( $n = 10$ ), and *Hoplostethus occidentalis* ( $n = 8$ ). Dominant mobile invertebrates were, in decreasing order of abundance, as follows: *Eumunida picta* ( $n = 1,517$ ), *Echinus* spp. ( $n = 545$ ), and *Rochinia crassa* ( $n = 13$ ). Actinostolid anemones, *Actinoscyphia saginata* ( $n = 3,350$ ), and *Novodinia antillensis* ( $n = 16$ ) were the most abundant sessile species attached to *L. pertusa* colonies. Although abundances were low for some species, they were included in analyses because little data exist on the majority of these species.

The species-habitat relationships were significant (CCA, Monte-Carlo,  $P = 0.002$ ) in the CCA tests that included all megafaunal species. Also, results were similar between the CCA tests that included either habitat variables calculated at the fine scale or variables calculated at the broad scale. Approximately 60–70% of the variance in species-habitat data was explained by the first two canonical axes (Table 2). However, eigenvalues were small, and correlations were moderate for each canonical axis when all species were included in analyses. Reanalysis of the datasets using only the fish data yielded considerably higher eigenvalues and correlations (Table 2). Thus, the species-habitat relationship was strengthened, suggesting that fishes analyzed in this study showed greater affinity to habitat variables than the invertebrates. In addition, global specialization values for fishes were generally higher than those for most invertebrates, further supporting that fishes were more habitat-specific than the invertebrates observed in this study (ENFA, Table 3).

Both *Beryx decadactylus* and *Conger oceanicus* were most frequently observed on the south-southwest facing slope near the top of the coral mound (reef crest) (Figs. 3, 4a, b). These two species were associated with high-profile, hard coral habitat that had low-moderate to moderate-high percentages of live coral cover (CCA, Figs. 3, 4a, b). CCA

**Table 2** Eigenvalues, species-environment correlation coefficients, and cumulative percent variance of species-environment relationship for first four axes determined by canonical correspondence analysis

Axis	Eigenvalues	Species-environment correlations	Species-environment cum. % variance
(a)			
1	0.08 (0.74)	0.36 (0.87)	31.90 (41.20)
2	0.06 (0.43)	0.42 (0.66)	58.10 (65.10)
3	0.03 (0.32)	0.30 (0.61)	71.90 (83.10)
4	0.03 (0.12)	0.20 (0.36)	82.70 (90.00)
(b)			
1	0.13 (0.67)	0.49 (0.83)	46.00 (49.10)
2	0.07 (0.38)	0.44 (0.64)	69.70 (76.60)
3	0.04 (0.13)	0.27 (0.38)	83.20 (85.90)
4	0.02 (0.12)	0.19 (0.35)	90.30 (94.50)

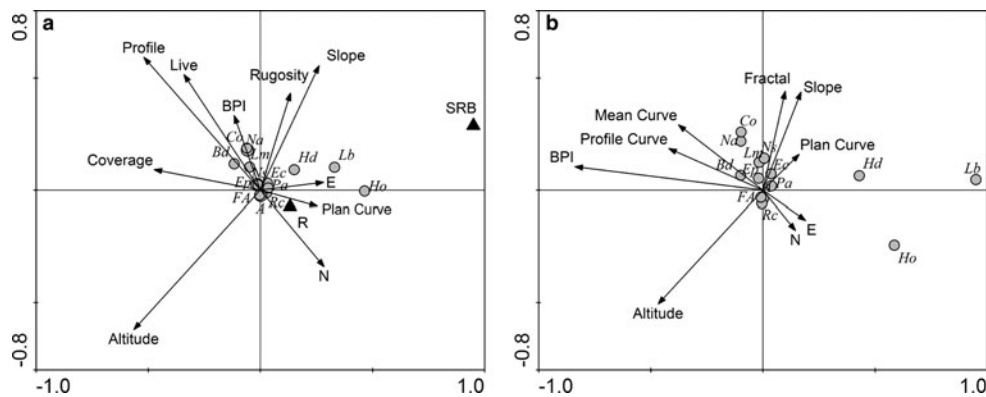
Results from analyses with habitat variables calculated at two spatial scales (a)  $30 \times 30$  m and (b)  $170 \times 170$  m. Results from analyses with fish data only in parentheses

**Table 3** Global marginality, specialization, and tolerance values for each species from ecological niche factor analysis

Species	Marginality	Specialization	Tolerance
Invertebrates			
Actinostolidae	0.54	1.79	0.56
<i>Actinoscyphia saginata</i>	0.20	1.08	0.92
<i>Echinus</i> spp.	0.15	1.06	0.94
<i>Eumunida picta</i>	0.34	1.09	0.92
<i>Novodinia antillensis</i>	0.98	4.50	0.22
<i>Rochinia crassa</i>	0.44	3.78	0.27
Fishes			
<i>Beryx decadactylus</i>	1.04	2.97	0.34
<i>Conger oceanicus</i>	1.27	5.49	0.18
<i>Helicolenus dactylopterus</i>	0.60	5.90	0.17
<i>Laemonema barbatulum</i>	0.90	7.92	0.13
<i>Laemonema melanurum</i>	0.54	6.60	0.15
<i>Nezumia sclerorhynchus</i>	0.46	5.24	0.19
<i>Polyprion americanus</i>	0.50	4.16	0.24

Marginality values close to 1 indicate a species' habitat differs from mean habitat conditions on coral mound. Specialization values from 1 to  $\infty$ : a higher number indicates greater affinity to a particular habitat on coral mound. Tolerance values closer to 1 indicate a more wide-spread distribution on coral mound

also revealed that high values of BPI calculated at the fine scale, and high values of mean and profile curvature calculated at the broad scale were important habitat variables, indicating that these two species were associated with topographic highs (CCA, Fig. 3). ENFA (see Table S1) results were consistent with CCA, except ENFA also indicated that *C. oceanicus* was associated with high values of fractal dimension, suggesting that this species had an affinity for rough terrain. *Conger oceanicus* was frequently observed



**Fig. 3** CCA ordination diagrams with habitat variables at **a** 30 × 30 m and **b** 170 × 170 m spatial scales. Circles denote species distributions. Arrows represent habitat variables. Negligible arrows for mean and profile curvature values deleted from plot (a). Closed triangles represent categorical habitat types (*R* rubble, *SRB* soft substrate-rubble). Hard Coral habitat type deleted from (a) because it occupied centroid of entire plot, overlaying species symbols. Species names abbreviated as follows: *A* = Actinostolid anemones, *Bd* = *Beryx decadactylus* (alfonsino), *Co* = *Conger oceanicus* (American conger eel),

*Ec* = *Echinus* spp. (sea urchin), *Ep* = *Eumunida picta* (squat lobster), *FA* = *Actinoscyphia saginata* (flytrap anemone), *Hd* = *Helicolenus dactylopterus* (blackbelly rosefish), *Ho* = *Hoplostethus occidentalis* (Western roughy), *Lb* = *Laemonema barbatulum* (shortbeard codling), *Lm* = *Laemonema melanurum* (coral hake), *Na* = *Novodinia antillensis* (brisingid seastar), *Ns* = *Nezumia sclerorhynchus* (rougthead grenadier), *Pa* = *Polyprion americanus* (wreckfish), *Rc* = *Rochinia crassa* (spider crab)

on the 374-m peak and along the most northern dive track where complex terrain was more common (Fig. 4b). In addition, *C. oceanicus* was often observed protruding from holes within the coral matrix. Both *B. decadactylus* and *C. oceanicus* had the highest marginality values of all species examined, indicating that these species occurred in habitats that differed most from the mean habitat conditions at the CF mound (Table 3). These preferred habitats of *B. decadactylus* and *C. oceanicus*, topographic highs of high-profile, live hard coral, were not as common as the lower profile, dead hard coral habitat that covered the majority of the mound (Fig. 2).

*Laemonema melanurum* had a similar distribution to *B. decadactylus* and *C. oceanicus*, except *L. melanurum* was often observed in moderate profile habitats and not as often in live coral habitats (CCA, Figs. 3, 4f). ENFA results were consistent with CCA results (Table S1). The global marginality value (0.54) indicated that this species occurred in habitat conditions that differed somewhat from the mean habitat conditions on the mound (ENFA, Table 3). This result is likely due to the association of *L. melanurum* with uncommon moderate-to-high-profile fine-scale habitats, as well as dead (90–100%) hard coral with 90–100% bottom coverage (Fig. 2), a commonly observed fine-scale habitat.

*Hoplostethus occidentalis* and *Laemonema barbatulum* were prevalent on steeper slopes on the north-northeast sides of the coral mound (CCA, Figs. 3, 4d, e). *Hoplostethus occidentalis* was restricted to this side of the mound, whereas *L. barbatulum* was also observed on the top of the mound and at the base of the south-southwest facing slope. These two species were often found in hard coral habitats generally characterized by low to moderate profile with a

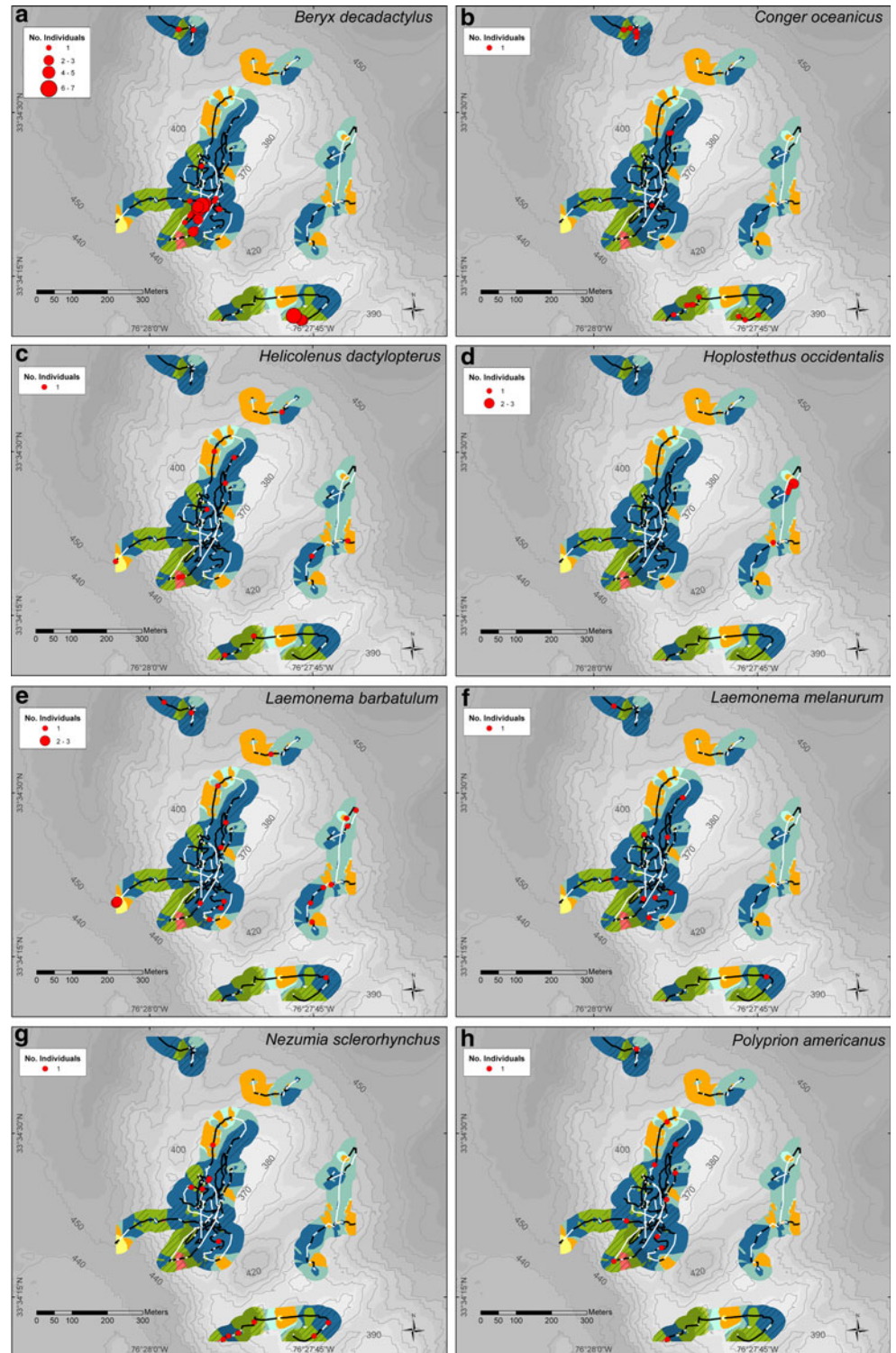
low percentage of bottom coverage near the base of the mound (CCA, Fig. 3). Associations with the base of the mound were indicated by affinities for low values of curvature and BPI calculated on the broad scale (Figs. 3, 4d, e). ENFA results were consistent with CCA (Table S1). A high global marginality value indicated that *L. barbatulum* occurred in a range of habitat conditions that were different from the mean conditions at the mound (ENFA, Table 3). This was most likely due to associations with fine-scale habitats not commonly observed on the mound (Fig. 2), such as a low percentage of hard coral bottom coverage, and rubble and sand/rubble habitats.

*Helicolenus dactylopterus* exhibited a distribution similar to *H. occidentalis* and *L. barbatulum*; however, *H. dactylopterus* was also frequently observed on the southwest facing slope (Figs. 3, 4c). ENFA results were similar to CCA results (Table S1), and further supported associations of *H. dactylopterus* with high slope values. A moderate global marginality value indicated that *H. dactylopterus* was often associated with habitat that was fairly common on the mound (ENFA, Table 3), such as low profile, dead (90–100%) hard coral habitat. However, this species was also observed in rubble habitat that was not as common as hard coral habitat.

*Polyprion americanus* and *Nezumia sclerorhynchus* were observed in numerous habitat types (Figs. 3, 4g, h). Of all fishes observed in this study, these two species exhibited the least affinities for a particular habitat type (CCA, Figs. 3, 4g, h). ENFA results, however, revealed that *P. americanus* and *N. sclerorhynchus* were associated with the south-southwest side of the mound (Table S1). This association can be seen in the abundance maps (Fig. 4g, h),



**Fig. 4** Abundance data by species overlain on habitat map (Fig. 2)

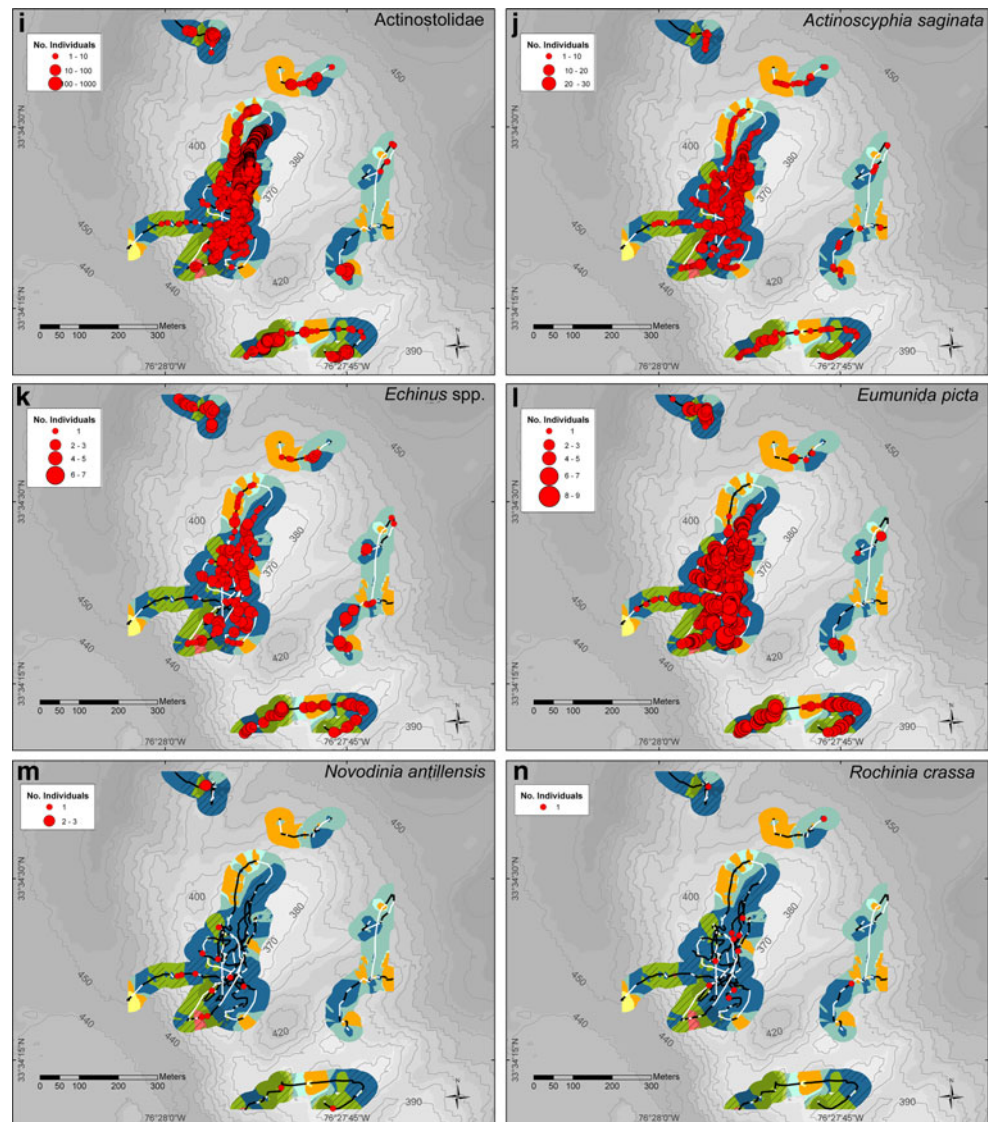


but was not revealed in the CCA analysis (Fig. 3). Overall, global marginality values were the lowest of all fishes analyzed in this study, indicating that these two species were associated with habitat types that were common on the coral mound (ENFA, Table 3).

In general, invertebrates showed less affinity to particular habitat variables than fishes. The brisingid seastar,

*Novodinia antillensis*, was the only exception, sharing a distribution similar to *Beryx decadactylus* and *Conger oceanicus* on the south-southwest facing slope near the top of the mound in high-profile, hard coral habitat with moderate-to-high live coral coverage (CCA, Figs. 3, 4m). Furthermore, individuals were notably absent from rubble and soft substrate habitats and were more frequently observed on

Fig. 4 continued



branches of live coral compared to other invertebrates. ENFA results were consistent with CCA (ENFA, Table S1). *Novodinia antillensis* had the highest marginality and specialization values of all invertebrates analyzed in this study (ENFA, Table 3). These high values indicated that this species was found in particular habitat types that were not commonly observed on the coral mound: topographic highs of high-profile live hard coral.

The other mobile, megafaunal invertebrates were present in various areas across the mound and rarely showed affinities to particular habitat types. These invertebrates exhibited no particular associations with either high or low values of habitat variables in the CCA plot (Fig. 3). ENFA results and the distribution maps, however, indicated that a few habitat variables may influence the distribution of invertebrates. Higher altitude appeared to be important for invertebrates, as invertebrates were most

abundant near the top of the coral mound (ENFA, Table S1). Most invertebrates examined here were generally absent or rare at the base of the mound and rarely observed on coral rubble or soft substrate (Figs. 3, 4i–n). Additionally, actinostolid anemones and *A. saginata* were concentrated on the south-southwest-facing slopes. *Echinus* spp. and *E. picta* were associated with higher percent coverage of coral and higher values of BPI and curvature, indicating associations with topographic highs (ENFA, Table S1). ENFA indicated that the north-northeast side of the mound was an important habitat variable for *Rochinia crassa*; however, the distributional maps indicated that this species was observed in all areas of the mound. Global ENFA values were similar among invertebrates and also revealed associations with habitat conditions that were most similar to the common habitat conditions on the mound (Table 3).

## Discussion

Knowledge of species' relationships to habitat variables and the degrees to which species depend on fine-scale habitat features are important for understanding habitat functionality, predicting faunal distribution and abundance patterns, and for assessing the impacts of habitat disturbance (Wilson et al. 2008). Habitat affiliations of fishes and mobile, megafaunal invertebrates on deep-sea coral reefs have been documented at fairly broad scales, such as reef versus non-reef or coral versus non-coral (e.g., Mortensen et al. 1995; Auster 2005; Ross and Quattrini 2007). Linking broad habitat classifications to species' distributions has provided insight into occurrence and biodiversity patterns of species inhabiting different deep-reef substrates (rock or coral) and nearby habitats; however, a gap in our understanding of fine-scale habitat functionality remains (Roberts et al. 2008). This is in stark contrast to shallow-water reef ecosystems, where faunal affiliations with fine-scale habitat features, such as topographic complexity, proportion of live coral, and vertical profile, are well studied. This study shows that deep-reef megafauna are affiliated with particular fine-scale habitats, and that certain reef-associated species appear to be habitat specialists, whereas others are habitat generalists.

### Species-habitat associations

At the broad scale, most species, including the majority of live *Lophelia pertusa* colonies, were often distributed within a particular reef zone: near the top of the CF mound on the south-southwest facing slope. This area of the mound, the reef crest, represents the up-current side directly impacted by the northward flowing Gulf Stream. Although there are no long-term oceanographic data from the CF mound, physical data from nearby moorings (~400 m depth) indicate that the predominant current direction on the bottom is northward, but that reversing currents and upwellings also impact these depths due to Gulf Stream meanders (Brooks and Bane 1983; J. Bane, pers. comm.). Also, the teardrop-shaped scoured trench around the base of the mound suggests a predominant northward bottom current. In addition to facing the current, the south-southwest slope near the top of the mound experiences accelerated current speeds as the current flows over the mound (pers. observ.). The interaction of topographic highs with accelerated currents, internal waves, and tidal signals enhances food supply to cold-water corals (Genin et al. 1986; Frederiksen et al. 1992; Thiem et al. 2006; Davies et al. 2009). We propose that the preferential occupation of the elevated up-current side of the CF mound is related to enhanced feeding opportunities.

The Gulf Stream likely influences the broad-scale distributions of benthic suspension feeders (e.g., *L. pertusa*, *Novodinia antillensis*, anemones) and species that actively prey in the water column. The interplay between currents and elevated topography is complex, enhancing feeding in different ways depending on feeding mode. Mobile megafauna that aggregated near the top of the coral mound are likely exploiting both the enhanced food supply delivered by the Gulf Stream as well as the vertically migrating, mesopelagic fauna that impinge on the bottom during the day (Gartner et al. 2008). *Eumunida picta* (as well as other species of squat lobsters, Wilson et al. 2007) prefers the tops of coral mounds and coral colonies. This species actively feeds on mesopelagic fauna when those organisms are near the bottom (pers. observ.). *Beryx decadactylus* also feeds mostly in the water column on mesopelagic fishes, pelagic shrimp, squid, and pelagic tunicates (Goldman and Sedberry 2011). This species may even follow mesopelagic fauna up into the water column at night (Gomes et al. 1998). *Echinus* spp. could be exploiting the phytodetrital material (Campos-Creasey et al. 1994) delivered by currents to the top of the mound.

Current speed and direction and elevated topography may be less important to species that do not require these factors for enhanced feeding opportunities. For example, the transient reef species, *Laemonema barbatulum*, was not particularly associated with the top of the coral mound, and was commonly found off-reef over soft substrate along the upper slope in the region (Quattrini and Ross 2006; Ross and Quattrini 2007). The distribution of this species relative to broad-scale habitat features, such as reef slope and flat, may be driven by a diet consisting of infaunal and benthic invertebrates (Gartner et al. 1997; Weaver and Sedberry 2001). *Rochinia crassa* was also not highly associated with a particular reef zone or other habitat characteristics. Like other species of *Rochinia* (Cordes et al. 2005), *R. crassa* is a likely scavenger; thus, this species would not be constrained to elevated topography or high-current areas.

Certain species were also predictably associated with fine-scale habitat features. For example, the distributions of *Beryx decadactylus*, *Conger oceanicus*, and *Novodinia antillensis* were influenced by vertical profile, high proportion of live coral, high percentage of coral coverage, and topographic complexity. These habitat variables are interrelated, and most commonly found at the top of the mound where live coral growth is enhanced. Species' associations with these fine-scale habitat types are not an artifact of location because these species were not observed in low-profile coral areas that also occurred on the top of the mound (and on other coral mounds off the SEUS, pers. observ.). *Beryx decadactylus* was predictably associated with high-profile coral and often observed under rock ledges and coral thickets throughout deep-water habitats in

the region (pers. observ.). Ledges, undercuts, and holes that are often associated with high vertical profile provide refugia from strong currents and predators as well as sites for reproduction and feeding (e.g., Hixon 1991; Menard et al. 2007). *Conger oceanicus* is also known to forage at night and utilize refugia during the day (Levy et al. 1988). In addition to burrowing in thickets of *L. pertusa*, *C. oceanicus* inhabits tilefish burrows, “pueblo habitats” in the walls of submarine canyons (Levy et al. 1988), and shipwreck components (pers. observ.). Ross and Quattrini (2009) noted that the high-relief profile provided by the *Republic* shipwreck, at ~490 m depth off Georgia, attracted both *C. oceanicus* and *B. decadactylus*. The high-relief structure was hypothesized to be the most important factor driving the fish assemblage similarity between North Carolina *L. pertusa* reefs and the *Republic* shipwreck. Finally, *N. antillensis* was predictably associated with high-profile habitat and often observed perched on the tops of live coral colonies. Occupying the highest profile habitats near the top of the mound in areas of the strongest currents would promote optimal feeding opportunities for this suspension feeder (Emson and Young 1994). Thus, the availability of extensive, complex, high-relief *L. pertusa* thickets or other similar structures appears to influence the distribution of *C. oceanicus*, *B. decadactylus*, and *N. antillensis*.

#### Shallow-water comparisons

The abundance and/or species richness of shallow-water (<200 m) reef megafauna are often highly correlated with various physical habitat parameters. Parameters that influence shallow-water fish and invertebrate species include habitat complexity (e.g., Luckhurst and Luckhurst 1978), vertical structure (e.g., Gratwicke and Speight 2005), reef size and type (e.g., Abele and Patton 1976; Ault and Johnson 1998a; Alexander et al. 2009), reef zone (e.g., Wilson 2001), proportion of live coral (e.g., Bell and Galzin 1984), and/or depth (e.g., Ault and Johnson 1998b; Friedlander and Parrish 1998). The distribution of mobile invertebrates is also often related to the type and size of sessile invertebrates as numerous species, many symbiotic, seek refuge in sponges (Henkel and Pawlik 2005), anemones (Nizinski 1989), and sea fans (Kissling and Taylor 1977). Moreover, abundances and distributions of species can vary due to the level of specialization that a species has to a certain habitat variable (Munday et al. 1997), highlighting the importance of documenting habitat associations at the species level. Although fine-scale habitat associations are lacking for the majority of deep-reef species, a few recent studies have indicated that certain mobile megafaunal invertebrates are closely tied to fine-scale, deep-reef habitat types such as coral species type and vertical relief (Mosher and Watling 2009; Lessard-Pilon et al. 2010). Our results also indicate

that some deep-sea species are similarly influenced by habitat variables as shallow-water reef fauna, at least within the SEUS region.

Reef zone is one parameter often associated with shallow-water faunal distributions as successful feeding, recruitment, and/or competitive interactions often result in organisms occurring within a particular zone (e.g., reef crest, slope, flat [Robertson and Gaines 1986; Munday et al. 1997; Friedlander and Parrish 1998; Wilson 2001]). For example, detritivores were more abundant on shallow-water reef crests compared to other reef zones because of the higher quality and availability of particulate organic matter on the reef crest (Wilson 2001). Food resource availability may similarly drive the observed distribution patterns within particular zones at the CF mound. As noted above, several suspension feeders, detritivores, and mesopelagic feeders were found on the south-southwest facing slope near the top of the mound (or the reef crest). In contrast, most transient (not limited to primary reef occupancy) reef species (*Laemonema barbatulum*, *Nezumia sclerorhynchus*, *Helicolenus dactylopterus*, *Rochinia crassa*, and *Polyprion americanus*) were either associated with reef slope, reef flat, or lacked strong association with any particular zone. Transient shallow-water fishes are common in these zones, presumably for foraging, and often have limited affinities with topographic complexity (Friedlander and Parrish 1998). Further work is needed to understand the trophic dynamics of deep-reef megafauna, but our results suggest that local distributions of deep-reef species may change across reef zones according to their trophic guild as has been suggested in shallow-water reef studies (Friedlander and Parrish 1998; Wilson 2001).

Several species were affiliated with increased topographic complexity and high vertical profile, two reef parameters that create refugia for shallow-water species (Hixon 1991; Friedlander and Parrish 1998; Menard et al. 2007). Predation pressure is the primary factor driving refugium use on shallow-water reefs (Hixon and Beets 1993; Beck 1995; Friedlander and Parrish 1998). Likewise, invertebrates may seek refuge in complex structures on deep reefs to escape predation, particularly when molting or reproducing (Beck 1995). Both adult and juvenile squat lobsters have been collected from deep within coral thickets and coral rubble matrices along SEUS deep reefs (pers. observ.) and are often a common prey item of deep-reef associated fishes (e.g., Goldman and Sedberry 2011). For fishes, it is interesting to note that both shallow- and deep-water species utilizing refugia belong to the same orders (e.g., anguilliforms and beryciforms), and this appears to be a common trait in these taxonomic groups. Alternatively, these species may use refugia to maintain position in an optimal feeding location. Occupying refugia would lessen

the metabolic costs of actively swimming in strong currents between feeding periods.

Proportion of live coral and percent cover of coral, rock, or rubble are two additional habitat variables that often influence reef species' distributions. On shallow-water reefs, there are numerous highly specialized species that have obligate relationships with live corals (symbionts), including species that feed on corals. Live coral specialists appear to be less common on deep compared to shallow-water reefs, although a few occurrences have been reported: the corallivorous gastropod *Coralliophila* sp. (Cordes et al. 2008), corallivorous hippasterine seastars (Mah et al. 2010), the reef-aggregating polychaete *Eunice norvegica* (Roberts 2005), and the coral-specific resident ophiuroid *Ophiocreas oedipus* (Mosher and Watling 2009). At the CF mound, megafauna were strongly associated with the proportion of seafloor covered with coral, whether live or dead. Other observations of deep-water slope megafauna also suggested that the proportion of live coral may not be as important as the reef structure itself (Auster 2005). In fact, higher proportions of dead coral are often positively correlated with high diversity of macrofauna (Cordes et al. 2008) and megafauna (e.g., Roberts et al. 2008), although species assemblages associated with dead coral rubble and primary coral framework often differ (Jonsson et al. 2004; Ross and Quattrini 2007). While living coral is often considered a sign of a healthy ecosystem, it does not necessarily predict the biodiversity and abundance at deep reefs. Seafloor covered with a high proportion of dead hard coral thickets provides the necessary structure to support primary reef occupants (Harter et al. 2009). Furthermore, dead coral rubble around the reef is an important component of the deep-reef ecosystem that provides habitat for a diverse, yet different faunal assemblage.

Within the North Atlantic Ocean, the degree to which fishes are specifically associated with habitats might be similar between shelf and slope environments. The characteristic deep-reef ichthyofauna along the continental slopes of the SEUS and GOM (Ross and Quattrini 2007, 2009; Sulak et al. 2007) appears to mirror the habitat affinities of the sub-tropical hardbottom fauna along the shelf and shelf-edge in these regions (e.g., Quattrini and Ross 2006; Kendall et al. 2009). Conversely, many fish species in the higher, colder latitudes of the North Atlantic Ocean appear to exhibit less affinity for microhabitat reef structure at shelf depths (Auster et al. 1995) and also on deep reefs (Auster 2005; Costello et al. 2005). The degree of habitat specialization might decrease with increasing latitude regardless of depth (at least <1,000 m). Further work using similar methodology is needed to test whether this change in habitat specialization among deep-reef fauna corresponds to changes with latitude, as noted for several different faunal groups ranging from terrestrial to shallow-water marine environments (see Stevens 1989).

## Further considerations

Understanding faunal habitat affiliations on coral reefs requires examination at multiple spatial scales because different ecological, biological, and physical processes influence the distributions of species (e.g., Albani et al. 2004; Wilson et al. 2007). Environmental variables such as temperature, surface water productivity, and dissolved oxygen could affect the distribution of fauna at broad spatial scales. Such data should be explored in future work, but it should be recognized that frequently measured long-term data are needed to fully capture the oceanographic conditions and their variability at deep coral mounds (Davies et al. 2009, 2010).

This study excluded microscale analyses of habitat associations, and our scale choices may have been too broad to determine invertebrate habitat affiliations, although they were appropriate in depicting fish distributions. Species-specific associations between mega-invertebrates (e.g., ophiuroids, shrimp) and substrates, such as anemones, sponges, octocorals, and antipatharians, are common and sometimes obligate (e.g., Nizinski 1989; Henkel and Pawlik 2005; Mosher and Watling 2009), emphasizing the importance of examining the relationships between these invertebrates and their preferred substrate type. Although video methodology worked well for quantifying the larger, mobile species, the smaller, more cryptic species deep within the reef matrix, such as ophidiiform fishes (Nielsen et al. 2009), ophiuroids (Brooks et al. 2007), and several species of squat lobsters (M. Nizinski, unpubl data) were not well documented. These smaller-scale associations may be better documented with zoomed-in video data and digital still imagery.

This study indicates greater habitat specificity of deep-reef megafauna than previously documented, supporting and expanding the work by Ross and Quattrini (2007, 2009). Some species are habitat generalists, while several deep-reef, mobile megafaunal species are habitat specialists. Our detailed examination of faunal-habitat associations at the CF coral mound in the SEUS region provides a basis for testing hypotheses concerning faunal-habitat relationships and community assembly processes at deep-sea reefs in other locations. Habitat usage at deep-water reefs likely changes within a region, depending upon such factors as habitat diversity, food availability, predator occurrence, depth of coral mound, competition, migration patterns, recruitment dynamics, and evolutionary history. Within the SEUS, we hypothesize that at broad spatial scales, distributions of deep-reef megafauna are governed by food availability and depth of coral mound. These distributions, however, will be influenced on the fine-scale by topographic complexity, vertical relief, and coral coverage. Future work should concentrate on multi-scale, multi-species

analyses on other reef habitats along the continental slope to determine processes that influence the formation, stability, and connectivity of deep reef communities.

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