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Demersal fishes associated with *Lophelia pertusa* coral and hard-substrate biotopes on the continental slope, northern Gulf of Mexico

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Abstract

The demersal fish fauna of *Lophelia pertusa* (Linnaeus, 1758) coral reefs and associated hard-bottom biotopes was investigated at two depth horizons in the northern Gulf of Mexico using a manned submersible and remote sampling. The Viosca Knoll fauna consisted of at least 53 demersal fish species, 37 of which were documented by submersible video. On the 325 m horizon, dominant taxa determined from frame-by-frame video analysis included Stromateidae, Serranidae, Trachichthyidae, Congridae, Scorpaenidae, and Gadiformes. On the 500 m horizon, large mobile visual macrocarnivores of families Stromateidae and Serranidae dropped out, while a zeiform microcarnivore assumed importance on reef "Thicket" biotope, and the open-slope taxa Macrouridae and Squalidae gained in importance. The most consistent faunal groups at both depths included sit-and-wait and hover-and-wait strategists (Scorpaenidae, Congridae, Trachichthyidae), along with generalized mesocarnivores (Gadiformes). The specialized microcarnivore, *Grammicolepis brachiusculus* Poey, 1873, appears to be highly associated with *Lophelia* reefs. The coral "Thicket" biotope was extensively developed on the 500 m site, but fish abundance was low with only 95 fish per hectare. In contrast to *Lophelia* reefs from the eastern North Atlantic, the coral "Rubble" biotope was essentially absent. This study represents the first quantitative analysis of fishes associated with *Lophelia* reefs in the Gulf of Mexico, and generally in the western North Atlantic.

The deep-water matrix-building scleractinian coral, *Lophelia pertusa* (Linnaeus, 1758) (hereafter *Lophelia* in this paper) occurs circumglobally (Rogers, 1999; Costello et al., 2005), including the Gulf of Mexico. This coral species builds large thickets and elevated banks that function as deep-water coral reefs (Rogers, 1999), providing three-dimensional habitat heterogeneity, shelter for invertebrates and fishes, feeding habitat for ambush predators and microvores, and probable spawning grounds for a few demersal fish species (Fosså et al., 2000; Reed et al., 2005). *Lophelia* habitats function as oases of macrofaunal and megafaunal biodiversity (Teichert, 1958; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Fosså and Mortensen, 1998; Husebø et al., 2002; Costello et al., 2005; Reed et al., 2005) amidst the otherwise monotonous open sedimented landscape of the continental slope. *Lophelia* reefs also appear to serve as focal points that concentrate megafaunal organisms otherwise occurring in low abundance on non-coral habitats. Additionally, such reefs may also concentrate particulate food resources, as the

elevated coral matrix intercepts bottom currents, generating eddies that entrain plankton and organic particles. While the demersal fish fauna associated with *Lophelia* reefs has been relatively well investigated in the eastern North Atlantic (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Husebø et al., 2002; Costello et al., 2005), the fish fauna of those in the western North Atlantic remains essentially undocumented. The present investigation reports on the demersal fish fauna of two *Lophelia* reef study sites in the northern Gulf of Mexico.

The occurrence of living *Lophelia* in the Gulf of Mexico was first reported by Moore and Bullis (1960) from a bottom trawl sample taken on the continental slope south of Mississippi (29°05'N, 88°19'W, 420–512 m depth). In attempting to relocate the Moore and Bullis site, subsequent investigators discovered well-developed *Lophelia* colonies inhabiting topographic highs along the continental slope of the northern Gulf of Mexico (Schroeder, 2002). These topographic highs are salt diapirs, partially capped by authigenic calcium carbonate (biologically precipitated in irregular layers and blocks in areas of hydrocarbon seepage). The clean, hard surface of the carbonate rock provides a settlement substrate for the larvae of diverse sessile invertebrates (anemones, sponges, bamboo corals, black corals, gorgonians, scleractinian corals), including *Lophelia*.

The present investigation was undertaken by the U.S. Geological Survey (USGS) to provide a first level community structure analysis of demersal fish species richness, abundance, and biotope affinity on *Lophelia* reefs and comparative biotopes in the Gulf of Mexico. The present fish study complements a parallel submersible study of geology, coral biology, and sessile invertebrate community ecology, targeting the same study sites undertaken by Continental Shelf Associates (CSA) and supported by the Minerals Management Service (MMS). The present study is one component of a broader suite of multi-disciplinary investigations of *Lophelia* coral reefs sponsored by USGS, and a sub-component of ongoing megafaunal community structure investigations of *Lophelia* reefs.

Materials and Methods

The manned JOHNSON-SEA-LINK (JSL) submersibles were used to conduct two missions in July–August 2004 and September 2005. Both missions investigated the demersal fish faunas of two prominent elevated topographic features on the continental slope of the northern Gulf of Mexico (Fig. 1). Identified by reference to the MMS oil lease blocks in which they lie, these two features have been designated Viosca Knoll 826 (VK-826), and Viosca Knoll 906/907 (VK-906/907)¹ by previous researchers. Viosca Knoll 826 rises to a minimum depth of between 435–480 m; VK-906/907 to a minimum depth of between 305–340 m. The two sites represent two biologically distinct depth horizons centered on depths of 500 m and 325 m, respectively, on the continental slope in terms of resident megafaunal fishes and invertebrates. Together, they provide a distinct three-dimensional hard-substrate, live-bottom continental slope sub-biome, in contrast to the dominant, essentially two-dimensional, soft-substrate, open slope biome.

The 2004 submersible mission was largely devoted to site exploration, specimen collection for taxonomic identification, and video documentation to characterize and differentiate biotopes utilized by demersal fishes (all fishes regularly associated with the benthic boundary layer, whether benthic or benthopelagic). The term *biotope* as used herein specifies a distinct physical (substrate, topography) and biological (sessile invertebrate assemblage) environment inhabited by the resident demersal fish fauna. The initial 2004 mission was also used to establish parameters (lighting, camera settings, submersible logistics) to enable consistent video transect methodology. Only five quantitative transects useful for analysis were accomplished in 2004. However, our portion of the

¹The study area has subsequently been resolved as located more precisely within blocks VK-906/862.

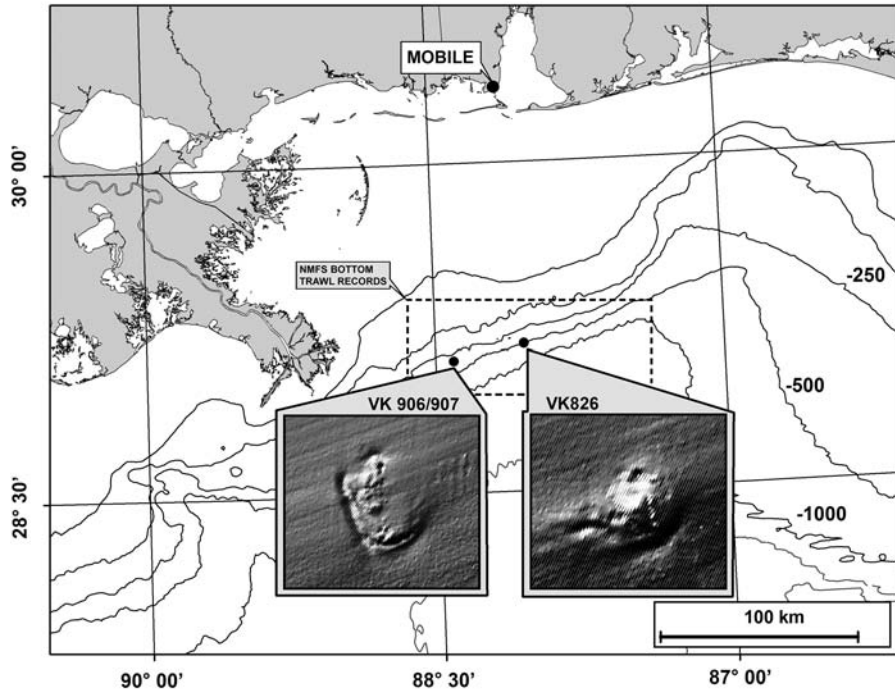


Figure 1. Location of two Viosca Knoll-826 submersible *Lophelia* reef study sites in the northern Gulf of Mexico, and location of comparative NOAA bottom trawl records (open rectangle). Depth contours are in meters.

2005 submersible mission was devoted largely to definitive video transects to enable a fundamental analysis of fish species composition, diversity, abundance, and habitat associations. All dives were conducted during daylight hours, although complete darkness prevails at the depths of our submersible operations. During both missions a small number of fishes were collected in situ using the JSL suction sampler and manipulator, and small baited traps deployed by the submersible. Additional fishes were collected by bottom trawl on a supplementary remote sampling cruise in 2005.

Sites for submersible dives and for deployment of traps and trawls were determined using a pre-existing three-dimensional topographic map of the VK-906/907 site accomplished by the U.S. Navy submersible NR-1, and a composite map prepared from an oil industry single-beam echosounder transect survey of the VK-826 site (Schroeder, 2002). Additionally, we conducted single-beam acoustic transect surveys between submersible dives, and at night during both USGS submersible missions. Acoustic profiles were obtained using a SIMRAD EQ50 color echosounder at a frequency of 38 kHz, tuned to detect the characteristic acoustic reflection of the hard coral matrix, and a Knudsen 320 B/R oceanographic monochromatic echosounder at a frequency of 3.5 kHz. Pulse interval and gain were adjusted to maximize erratic acoustic reflection from coral structures, contrasting with the continuous strong reflection defining the hard substrate seafloor. Ship's position was determined via differential GPS, accurate to within 5 m. Submersible position on the bottom was estimated via Trackpoint II "Integrated Positioning System" (ORE Offshore) using dual acoustic beacons interpreted topside by HBOI submersible operations personnel. Only returns with signal strength above a pre-determined threshold were accepted in plotting the most probable bottom positions of the submersible.

Quantitative submersible transects.—Bottom transects were accomplished largely opportunistically during bottom exploration or during transits between target coral collection sites. The fundamental method was a "belt transect", conducted with the submersible cruising as slowly

as possible (typically 0.3 kt) into the direction of bottom current to maintain constant speed and consistent course direction. Altitude was held as close above the substrate as possible (i.e., bottom of JSL skimming over the bottom). Color video was obtained using a Sony DX2 3000A 3-chip CCD camera, with 6–48 mm zoom lens, mounted on an extensible arm on the port side of the submersible sphere, 1.37 m above the bottom of the vehicle. The “belt”, or area of substrate being transected, was typically illuminated by two high intensity 400 W, 5600 °K HMI lights affixed to the submersible’s forward upper work bar, and by four additional individually-selectable HMI lights surrounding the video camera. Additionally, a 1000 W, 6000 °K xenon arc light mounted on the starboard side of the JSL upper work bar was used for forward reconnaissance to illuminate the intended transect path ahead of JSL (usually not illuminating the very near field used for fish analysis). Video and audio information was recorded to a mini-DV format tape recorder and an S-digital recorder. The S-digital recorder was used to obtain very high-quality video (with no data overlay) to enable preparation of high-quality frame grabs to facilitate species identification. During video transecting, the extensible support arm supporting the video camera was kept fully retracted and focal length was maintained at 6 mm (i.e., full wide angle). The camera was panned inward (toward the transect centerline) 15°, and tilted downward 45°. Pan, tilt, and zoom were held in this pre-determined configuration throughout designated transects. With the submersible transecting parallel to the bottom, minimum distance between the camera lens and a fish situated on flat substrate directly ahead of camera was 1.94 m. Targeted transect duration was 5.0 min (sometimes truncated by limiting topography, video tape change-out, or JSL operational exigencies). During transecting, data including time (hr:min:sec) and depth (ft) data were continuously overlaid onto the video record.

The areal field of view available for analysis during standardized moving transects was determined by deployment on the substrate of a 1.78 by 1.22 m wire panel (“hogwire”) painted white, with its outer frame painted orange. This panel was subdivided into smaller rectangles of known dimensions, with two rectangular reference grids of 1.0 m by 0.5 m dimensions delineated in black. Additionally, a 0.5 m diameter Secchi disk type signpost (one half of disk painted flat white, the other half neutral gray) was deployed to estimate the distance at which fishes could be recognized from the background, and at which fishes could be viewed well enough to be positively identified. The submersible was backed away from the grid panel until the panel lay within the illuminated field available for fish identification and enumeration. The submersible was similarly backed away from the signpost until the gray, and then the white halves merged into the background from the perspective of the scientist within the sphere. At each of these two points, the submersible’s ranging sonar was used to resolve respective distances to the signpost. The submersible video camera mounting was also equipped with two lasers that projected parallel beams 25 cm apart, used as a reference scale to determine size of objects and fishes.

Non-transect video segments.—For all 2004 and 2005 dives, video obtained when the submersible was slowly traversing bottom, but the video camera not standardly configured for transecting (as above), was utilized for a second type of analysis of rank order by species occurrence. Only segments with a wide angle perspective were utilized for this second type of analysis.

Supplementary video.—In addition to analysis of the video records documenting the two USGS submersible missions, video records from the parallel CSA 2004–2005 submersible missions (S. Viada, CSA, pers. comm.) from the Viosca Knoll region (12 of 16 dives on VK-826, VK-862, and VK-906/907, representing approximately 30 hrs total) were also examined. Submersible video records from four additional Viosca Knoll dives were obtained from a NOAA Exploration mission in 2005 (W. Schroeder, Dauphin Island Marine Laboratory, pers. comm.). Examination of supplementary video was undertaken to qualitatively scan for potential additional fish taxa contributing to the demersal fauna, but not recorded during USGS dives.

Video analysis.—In the laboratory, all original mini-DV tapes were copied onto DVD as VOB (Video Object) files (MPEG2 compatible format) at full quality for subsequent preparation of frame grabs and to create a backup video data archive. The entire video record of each dive (ca 2 hrs total bottom time) was then converted from DVD to sequential still frames (0.9 mb each), separated by an interval of approximately one second (0.996 s) using VideoCharge™ 3.0 frame-grab software (which requires DVD input). Analysis of the resulting full-quality images (in uncompressed .tiff format) proceeded as follows:

Analysis I.—Quantitative species abundance and rank order from standardized transects: Step 1) The original mini-DV was initially viewed using a Sony® GV-D9000 DVR linked to a Sony Trinitron commercial-quality high resolution monitor to establish identities of all demersal fish species recorded (identification by senior author), denote time segments for capture as still images to document species identifications, empirically define biotopes encountered, and record the starting and ending times of each quantitative transect. Separate high-quality frame grabs documenting individual fish species were assembled into a taxonomic identification reference library used by project personnel. Step 2) Using the sequential frame grab record, each designated transect was viewed (on monitors with either 1660 × 1200 pixel or 1280 × 1024 pixel resolution, 0.26 mm pixel pitch) advancing frame-by-frame using the Microsoft Windows™ software “Picture and Fax Viewer” utility. Each transect was analyzed by each sequential 1-s still frame, building an Excel spreadsheet file recording dive number, transect number, frame grab file number, date, time, depth, fish occurrence by species, major biotope, and sub-biotope designations. The number of frame grabs was totaled for each transect to yield the total time analyzed (i.e., total number of grabs, multiplied by 0.996 s⁻¹ per grab).

Deployment on the substrate of the wire mesh panel of known dimensions resolved the typical video camera illuminated field of view useful for analysis per frame grab during moving transects as 15.0 m² (range 12.0–16.0 m²). However, at a speed over ground of 0.3 kt (0.15 m s⁻¹), the actual area for scoring demersal fish counts per 1-second frame was approximately 1.0 m². A fish of typical total length (0.25–0.75 m) was in the illuminated field of view (lower two-thirds of the video screen) for a maximum of 15 s, and crossed the video frame margin in < 3 s. However, a fish was only scored when it left the field of view and intersected the video frame margin (bottom, left, or right). Since each fish scored in a 0.996 s⁻¹ frame grab occurred within a scoring area of 1.0 m², the total area analyzed per transect could then be determined. There was a very low probability of counting the same fish in the same scoring area again in sequential frames. The record of frame grab fish scores revealed only one instance where sequential frames with fish of the same species were within 3 s of one another.

To minimize recounts of individual fish swimming along with the submersible, appearing in more than one frame grab, and/or re-entering the field of view, each fish was counted only once, as it left the field of view. Leaving the field of view was defined as exiting the frame by crossing the bottom, left, or right video margin (i.e., fish leaving the video field of view as the submersible advanced forward). Species abundance scores were totaled per transect to determine rank order. Scores for all species were totaled to estimate population density per unit area.

Analysis II.—Species occurrence and relative rank order from non-transect video segments: Step (1) Individual occurrences of each species (regardless of number of individuals of that species simultaneously in the field of view) were recorded per each 1-s frame over the entire frame grab record for that dive, excluding transects, but including time intervals when the submersible was stationary, and when the camera was panning or zoomed in upon the substrate and/or on sessile invertebrate assemblages. The occurrence of a species was positively scored if that species was present within the analyzed field of view (lower two-thirds of the total field of view). Step (2) Scores were summed by species to determine rank order by frequency of occurrence for the total pool of analyzed frames. For both abundance and occurrence analyses, each data entry included scoring of major biotope category, and the presence or absence of *Lophelia* coral. Taxon abun-

dance and occurrence data were analyzed for all dives per each of the two Viosca Knoll depth horizons (325 m and 500 m).

Remote sampling.—In addition to taxonomic voucher fish specimens collected with the JSL, others were obtained during the 2004 submersible mission using small bottom trawls (3-m and 4-m footrope otter trawls) and 1.0 m mouth-opening benthic sled deployed remotely from the submersible mothership. Remote sampling was also conducted using the R/V TOMMY MUNRO (Gulf Coast Research Laboratory) in June 2005, sampling soft-substrate open-slope areas immediately adjacent to the two USGS Viosca Knoll study sites. Specimens were obtained both to help validate taxonomic identifications of fishes obtained by the JSL, and to document the comparative fauna of the open slope away from *Lophelia* coral biotopes. During the same mission, baited commercial fisheries Caribbean “Z” traps (also known as Antillean “Z” traps and “Chevron” traps) (FAO Corporate Document Repository) were also deployed over structured substrate to capture reef-associated fishes. Traps were 1.5 m long with two funnels, a time-release escape panel, and covered with plastic-coated 4 cm wire mesh).

Taxonomic Validation.—Opportunistically during both submersible dives (but not during quantitative transects), the submersible was stopped and high-quality close-up images of individual fish specimens were obtained using the JSL digital still camera and videocamera (employing the zoom function). The digital still camera was mounted atop the forward collection basket, with illumination provided by one fixed HMI light and/or an accessory strobe light. Close-up images were used to assist in validating species identifications. Additional voucher specimens for taxonomic reference were obtained from both JSL in situ collections, and from surface-deployed traps, bottom trawls, and a benthic sled. High quality voucher specimens were prepared and photographed at sea to accompany underwater images and physical specimens documenting the fauna. Specimens were examined in the laboratory to yield definitive species identifications (J.H.C. and K.J.S.). The senior author is responsible for all taxonomic identifications from videotapes and DVDs, except for elasmobranch identifications provided by J. Castro (Mote Marine Laboratory), and Cynoglossidae identifications provided by T. Munroe (NOAA Fisheries Systematics Laboratory). Voucher specimens documenting this investigation are currently maintained at Florida Integrated Science Center, Gainesville, Florida. These specimens will ultimately be curated in the cataloged fish collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and in the fish collection of the U.S. National Museum of Natural History, Smithsonian Institution.

Species recorded during the USGS 2004 and 2005 Viosca Knoll submersible missions were contrasted with demersal fish species reported from historical National Marine Fisheries Service (NOAA) trawl surveys (Springer and Bullis, 1956; Bullis and Thompson, 1965) and the NOAA SEAMAP bottom trawl database (NOAA Fisheries Mississippi Laboratories, Pascagoula, Mississippi, data received 2004). To confine the comparison to the immediate area of the Viosca Knoll study sites, we included only species recorded between 300–550 m depth, and within a rectangle bounded by lat. 28°55′–29°20′N, longitude 87°29′–88°40′W (Fig. 1) ($n = 265$ NOAA trawl stations).

Biotope affinities of the overall Viosca Knoll demersal fish fauna were documented by taxon for both depth horizons combined, expressed as frequency of occurrence of each taxon among the various biotope categories. The null hypothesis that key numerically dominant fish species were randomly distributed, regardless of biotope, was tested by a χ^2 goodness of fit test of observed vs expected frequencies of occurrence from video data analysis.

Results

Twenty submersible dives were accomplished on target *Lophelia* sites; 10 in 2004, and 10 in 2005, with 12 on the VK-826 site, and eight on the VK-906/907 site (Fig. 1). Dive tracks on each site, largely targeting known or suspected *Lophelia* coral areas, intersect-

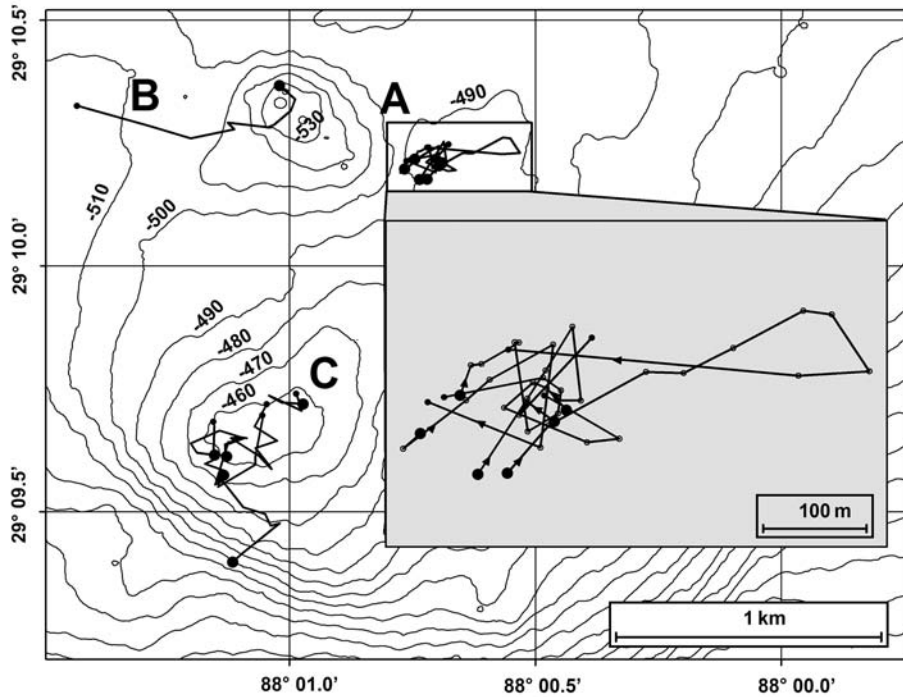


Figure 2. Bathymetric chart (10-m isobaths) of Viosca Knoll-826 *Lophelia* reef study site, showing tracks of 12 USGS submersible dives undertaken in 2004–2005: A = “Big Blue Reef” on northeastern sector of overall feature; B = 100 m deep depression; C = main knoll on southwestern sector of feature (with *Lophelia*). Inset shows detail of eight dives conducted on “Big Blue Reef”. Key: Large dots = beginning of bottom time; small dots = Trackpoint II navigation fixes during the course of a dive, including final fix at end of bottom time; arrowheads indicate direction of submersible movement.

ed multiple times (Figs. 2, 3), the intersection matrix essentially pin-pointing the areas populated by *Lophelia* and other colonial particulate-feeding invertebrates (anemones, sponges, bamboo corals, black corals, gorgonians). Only relatively limited portions of the flanks and crests of selected ridges were found to be colonized by extensive *Lophelia* reef (Fig. 4). Remote deployments to sample fishes included four fish traps, four bottom trawl stations and two benthic sled stations (Table 1). Additional fish specimens were selectively captured on 12 occasions using the submersible manipulator/suction sampler. Total submersible bottom time was 44 hrs, 45.4 min, all of which was used to document demersal fish species identifications. However, due to division of bottom time activities among multi-disciplinary tasks, only a limited portion of that time was available for dedicated moving video transects. Thirty-two transects from seven dives were accomplished to support Analysis I; total transect time was 141 min (Table 1). Additional non-transect segments used for Analysis II totaled an additional 115 min of video.

Initial video analysis enabled an empirical differentiation of the overall demersal environment of the Viosca Knoll study area into two depth horizons by fish species occurrence, one centered on 325 m, another on 500 m depth. Video analysis yielded four major empirically-defined biotope categories based on terrain, relief, and development of *Lophelia* coral (Table 2), “Open”—open sedimented soft substrate (Figs. 5A,B); “Plate”—flat, low-relief hard substrate biotope (Figs. 5C,D); “Rock”—sculpted, fragmented, and/or eroded high-relief biotope (Fig. 6A,B); and “Thicket”—soft or hard

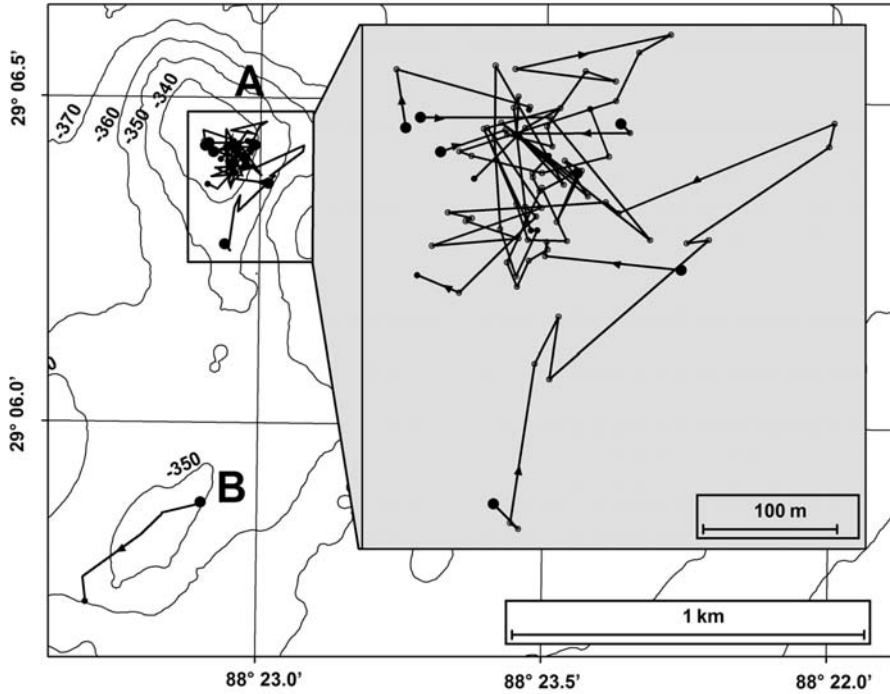


Figure 3. Bathymetric chart (10-m isobaths) of Viosca Knoll-906/907 *Lophelia* reef study site, showing tracks of eight USGS submersible dives undertaken in 2004–2005: A = area of live-bottom development, including *Lophelia* coral; B = area visited on one exploratory dive. Key: Large dots = beginning of bottom time; small dots = Trackpoint II navigation fixes during the course of a dive; arrowheads indicate direction of submersible movement.

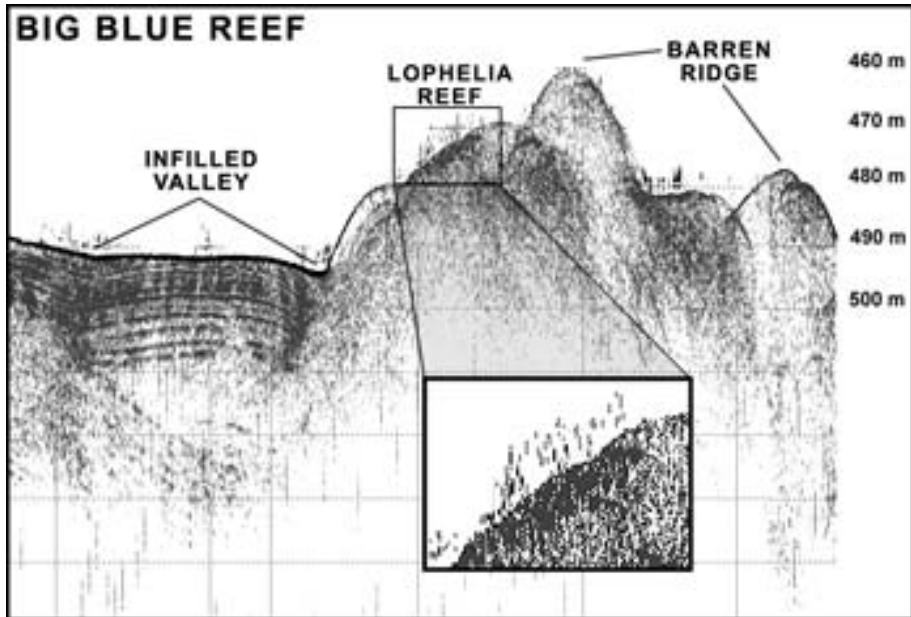


Figure 4. Knudsen echosounder single beam acoustic (3.5 kHz) profile of *Lophelia pertusa* coral reef, Big Blue Reef, on flank of a ridge, northeastern sector of VK-826 study site.

Table 1. Submersible dives and surface vessel bottom sampling stations conducted by USGS during three Viosca Knoll cruises, 2004–2005. Key: BS = benthic sled, BT = bottom trawl, FC = submersible fish collection, FT = baited fish trap, V = submersible video documentation.

USGS Cruise number	Station number	Study site	Depth (m)	Sample type	Video bottom time (hh:mm:ss)	Number of video transects	Transect time (hh:mm:ss)
2004-03	JSL-4744	VK-906/907	315	V and FC	2:44:46	0	0:00:00
2004-03	JSL-4745	VK-906/907	336	V and FC	0:58:01	0	0:00:00
2004-03	JSL-4746	VK-906/907	345	V and FC	2:01:58	0	0:00:00
2004-03	JSL-4747	VK-906/907	316	V and FC	2:58:00	0	0:00:00
2004-03	JSL-4748	VK-826	446	V and FC	2:24:17	0	0:00:00
2004-03	JSL-4749	VK-826	511	V	2:29:23	0	0:00:00
2004-03	JSL-4750	VK-826	528	V and FC	2:32:01	4	0:19:09
2004-03	JSL-4751	VK-826	462	V and FC	2:46:07	0	0:00:00
2004-03	JSL-4752	VK-826	469	V	2:40:44	0	0:00:00
2004-03	JSL-4753	VK-826	475	V	2:37:41	1	0:05:08
2004-03	USGS-9004	VK-906/907	327	BT	NA	NA	NA
2004-03	USGS-9007	VK-826	536	BT	NA	NA	NA
2004-03	USGS-9013	VK-826	457	BS	NA	NA	NA
2004-03	USGS-9014	VK-826	382	BS	NA	NA	NA
2004-03	USGS-9017	VK-826	308	BT	NA	NA	NA
2004-03	USGS-9018	VK-826	325	BT	NA	NA	NA
2005-03	USGS-0017/0073	VK-906/907	360	FT	NA	NA	NA
2005-03	USGS-0018/0074	VK-906/907	360	FT	NA	NA	NA
2005-03	USGS-0025/0075	VK-826	486	FT	NA	NA	NA
2005-03	USGS-0027/0076	VK-826	486	FT	NA	NA	NA
2005-04	JSL-4873	VK-906/907	315	V	1:49:18	0	0:00:00
2005-04	JSL-4874	VK-906/907	315	V	1:43:31	6	0:25:18
2005-04	JSL-4875	VK-906/907	337	V	2:19:49	5	0:22:23
2005-04	JSL-4876	VK-906/907	312	V	2:47:16	6	0:27:00
2005-04	JSL-4877	VK-826	479	V	2:28:35	0	0:00:00
2005-04	JSL-4878	VK-826	465	V	1:02:06	0	0:00:00
2005-04	JSL-4879	VK-826	454	V and FC	2:29:28	4	0:12:00
2005-04	JSL-4880	VK-826	455	V	2:25:50	6	0:29:56
2005-04	JSL-4881	VK-826	451	V	2:31:18	0	0:00:00
2005-04	JSL-4882	VK-826	478	V	0:55:17	0	0:00:00
Totals			315–536		44:45:26	32	2:20:54

substrate extensively covered with *Lophelia* coral (Fig. 6C). A fifth biotope category, “Rubble” (Fig. 6D), occurred only rarely on Viosca Knoll, but was included to provide comparability with major *Lophelia* biotopes identified in investigations from other geographic regions (e.g., Mortensen et al., 1995; Freiwald et al., 2002). “Rubble” was defined as: live and/or dead coral branches and fragments lying on the substrate. To score each frame grab according to a specific category, > 50% of the analyzed field of view (lower two-thirds of the total field of view) had to correspond to one of the five categories.

Video analysis yielded 37 distinct demersal fish taxa (Table 3A), plus one taxon positively identified visually (*Scyliorhinus retifer*), but not captured on video, and two additional tentatively identified taxa. A few taxa that could be identified only to the family or genus level included more than one similar species not readily distinguishable on

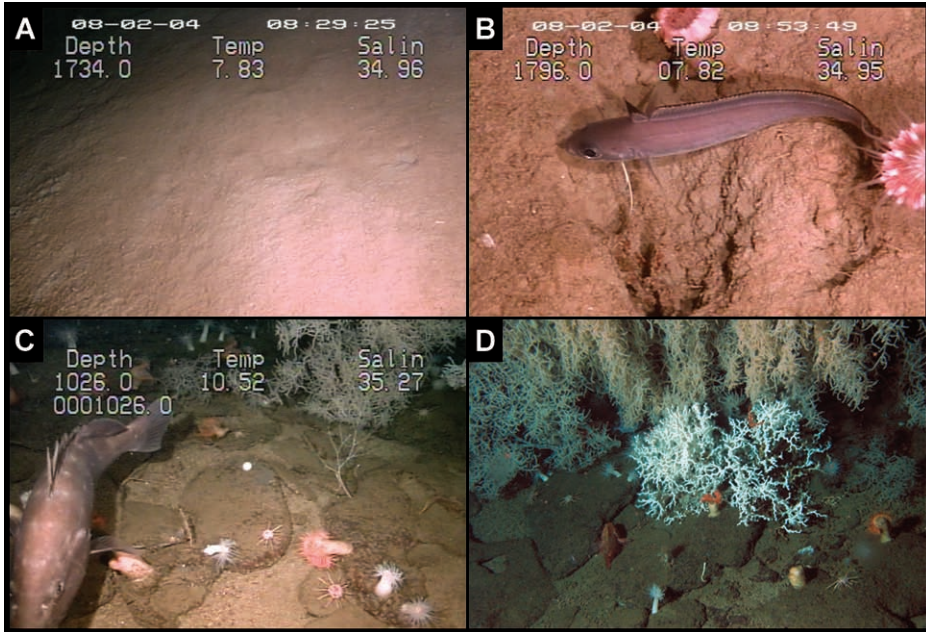


Figure 5. Examples of Viosca Knoll biotopes: (A) “Open” biotope, 528 m; (B) “Open” biotope, 547 m, with the hake *Laemonema goodebeanorum* and tube-dwelling cerianthid anemones; (C) “Plate” biotope, 316 m, with *Lophelia pertusa* hard coral and *Leiopathes* black coral bushes; (D) “Plate” biotope, 312 m, with *Epinephelus niveatus* snowy grouper.

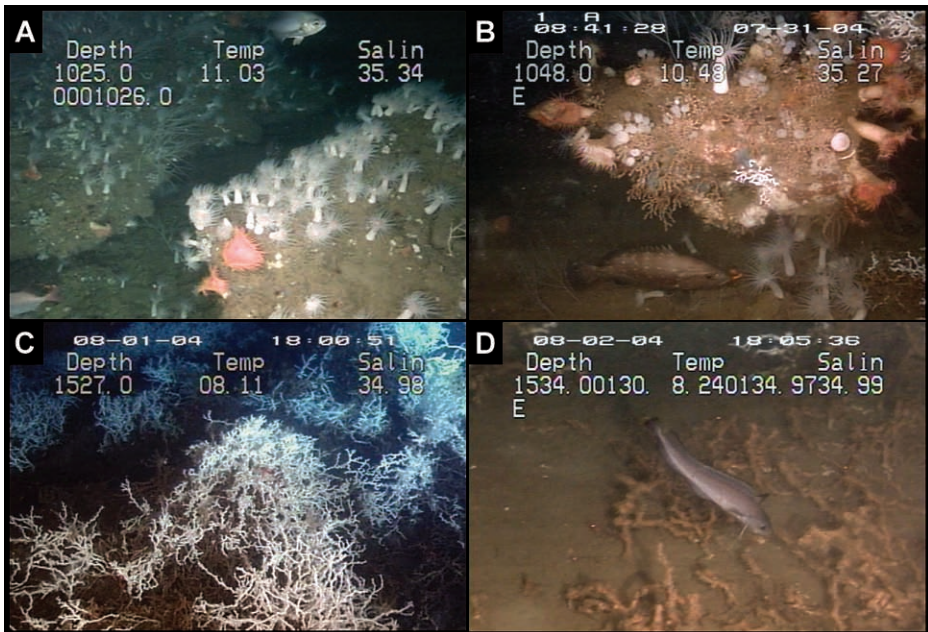


Figure 6. Examples of Viosca Knoll biotopes: (A) “Rock” biotope, 312 m, with *Hyperoglyphe perциformis* barrelfish; (B) “Rock” biotope, 320 m, supporting a diverse assemblage of sessile invertebrates, *Epinephelus niveatus* beneath; (C) “Thicket” biotope, 465 m, a monoculture of *Lophelia pertusa*, (D) “Rubble” biotope, rare on Viosca Knoll, 467 m, with *Laemonema goodebeanorum*.

Table 2. Biotope categories and descriptions, as applied to analysis of Viosca Knoll study sites.

Biotope Category	Criteria (Biotope Category covering > 50% of analyzed field of view; lower two-thirds of video screen = 15.0 m ²).
Open (non-coral)	Terrain flat or undulating, comprised of deep soft sediment, often hummocky with obvious biogenic burrows and mounds. Key indicator taxa: black cerianthiid anemones (burrowers).
Plate (non-coral)	Terrain flat or terraced hard-pan, or hard-pan with a thin veneer of sediment. Maximum relief < 10 cm. Substrate is typically populated by attached sessile invertebrates. Key indicator taxa: white anemones, glass sponges, gorgonians, bamboo corals, black corals.
Rock (non-coral)	Terrain uneven and either highly eroded, sculpted, or fragmented, with outcropping edge, and large crevices or pockets. Maximum relief > 10 cm. Substrate barren, or sparsely to densely populated by sessile invertebrates. Key indicator taxa: white anemones, glass sponges, gorgonians, bamboo corals, black corals.
Rubble (coral debris)	Terrain either hard or soft, but with live and/or dead <i>Lophelia pertusa</i> coral branches and fragments covering > 50% of field of view.
Thicket (live coral)	Terrain either hard or soft, predominantly live (white) coral developed into expanses of tall, extensively-branched bushes covering > 50% of field of view.

video. Twelve video species identifications were validated using submersible-caught specimens. Twenty-seven species were documented from remote traps, trawls, and benthic sleds (Table 3A), including 15 species not documented in submersible videos or by submersible collections. Comparison of the species list from USGS cruises with the list from NOAA Fisheries bottom trawl records within a comparative depth and geographic range (Fig. 1) yielded 30 species common to both databases (Table 3A). The NOAA database contained an additional 23 demersal fish species not documented during the present study (Table 3B), although four of these species may be identical in both databases (due to use of different taxonomic names for potentially synonymous taxa). Most of these additional NOAA species are fishes typically associated with soft substrate on the open slope (e.g., Macrouridae, Gadidae, Merluccidae, Rajidae, Alepocephalidae), away from hard bottom and reef biotopes. Examination of CSA video for 12 additional dives on Viosca Knoll sites added no further species to the overall USGS faunal list.

Deployment of the Secchi-disk signpost target resolved maximum horizontal visibility to a scientist in the submersible sphere as 12.2 m for the neutral gray half (representing most fishes), and 19.8 m for the flat white half (representing white or silver fishes). However, by comparative video vs sonar reference to both the metal frame and the signpost at various distances from the submersible, it was determined that fishes viewed by the videocamera could be reliably identified to species only within a distance of 5 m ahead of the sphere (i.e., approximately 3 m ahead of the camera).

Quantitative video analysis.—Video records for 32 moving transects from seven USGS submersible dives were converted into 8486 1-s frame grabs. Analysis of these frames documented at least 37 total demersal species identified from video (Table 3A). Additional taxa could be resolved only to a higher taxonomic level. Of the total frame grab record, 4498 frames represented transects accomplished on the 325 m depth ho-

Table 3A. Demersal fish taxa documented by USGS submersible (JSL) video and collections on Viosca Knoll study sites, versus those from comparative USGS trawl, sled, and trap collections, and NOAA bottom trawls collections. NOAA records are from 300–550 m between lat. 28°55'–29°20'N, long. 87°29'–88°40'W. Key: DFG = digital frame grab from JSL video, LP = Layout digital image, UDP = JSL digital still image, VS = visual JSL record (not tallied in totals), X = positive record, XX = taxon recorded both in present study and NOAA bottom trawl database, XXO = taxon also recorded in NOAA trawl database, but under an earlier species name, XXX = taxon recorded in present study both by JSL and in trawl, trap, or sled collections, ?? = tentative record (not tallied in totals).

Demersal fish taxa:	USGS	USGS	USGS	USGS	USGS	USGS	USGS
	Video record n = 12	JSL coll. n = 4	Trawl coll. n = 2	Sled coll. n = 4	Trap coll. n = 265	Trawl coll. n = 265	USGS Voucher image
<i>Anthias nicholsi</i> Firth, 1933	??						
<i>Argentina striata</i> Goode and Bean, 1896	X		X				
<i>Bassogigas</i> sp.	X	X					LP
<i>Bathygadus melanobranchus</i> Vaillant, 1888			XX			XXO	
<i>Bathypterois</i> cf. <i>bigelowi</i> Mead, 1958	XX					XX	
<i>Bembrops anatirostris</i> Ginsburg, 1955			XX			XX	LP
<i>Caristius</i> sp.	X						DFG
<i>Chlorophthalmus agassizi</i> Bonaparte, 1840			XX			XX	LP
<i>Coelorinchus caribbaeus</i> (Goode and Bean, 1885)	XX		XX	X		XX	LP, DFG
<i>Conger oceanicus</i> (Mitchill, 1818)	XX		XX		XX	XX	LP, DFG
<i>Cyttopsis rosea</i> (Lowe, 1843)	X		X				DFG
<i>Dibranchius atlanticus</i> Peters, 1876	XX		XX			XX	LP, DFG
<i>Epigonus pandionus</i> Goode and Bean, 1881	XX					XX	DFG
<i>Epinephelus niveatus</i> (Valenciennes, 1828)	X						DFG
<i>Facciolella</i> sp.	X	X					LP
<i>Gephyroberyx darwini</i> (Johnson, 1866)	X						DFG,UDP
<i>Glossanodon</i> sp.	XX					XX	DFG
<i>Gnathagnus egregius</i> (Jordan and Thompson, 1905)			XX			XX	LP
<i>Grammicolepis brachiusculus</i> Poey, 1873	XX	XX				XX	LP, DFG
<i>Helicolenus dactylopterus</i> (Delaroche, 1809)	XX	XX	XX		XX	XX	LP, DFG
<i>Hemanthias aureorubens</i> (Longley, 1935)	X		X				LP, DFG
<i>Hoplostethus mediterraneus</i> Cuvier, 1829	??		??			XX	DFG
<i>Hoplostethus occidentalis</i> Woods, 1973	XX	XX				XX	LP, DFG
<i>Hymenocephalus</i> sp.			XX			XX	LP
<i>Hyperoglyphe perciformis</i> (Mitchill, 1818)	X						DFG
<i>Laemonema goodebeanorum</i> Meléndez and Markle, 1997	XXX	XXX	XXX			XXO	LP, DFG
<i>Lophius gastrophysus</i> Miranda Ribeiro, 1915	XX	XX				XX	LP, DFG
<i>Lopholatilus chamaeleonticeps</i> Goode and Bean, 1879	X						DFG
<i>Malacocephalus occidentalis</i> Goode and Bean, 1885			XX			XXO	LP
<i>Monomitopus</i> sp.	X	X					LP
<i>Neobythites marginatus</i> Goode and Bean, 1896	X	X					LP
<i>Nezumia aequalis</i> (Günther, 1878)	XX					XX	DFG
<i>Odontaspis ferox</i> Risso, 1810	X						DFG
<i>Paralichthys albigutta</i> Jordan and Gilbert, 1882			X				
<i>Parasudis truculentus</i> (Goode and Bean, 1896)			XX			XX	LP
<i>Physiculus karrerae</i> Paulin, 1989	XXX	XXX			X	XXO	LP, DFG
<i>Poecilopsetta beani</i> Goode, 1881			X				LP
<i>Polyprion americanus</i> (Bloch and Schneider, 1801)	X						DFG
<i>Pontinus longispinis</i> Goode and Bean, 1896			X				LP

Table 4. Abundance scores per taxon for Viosca Knoll study sites demersal fish taxa from transect frame-by-frame analysis for USGS 2004–2005 submersible video records. Taxon list is coordinated with that in Table 5 for comparison of abundance and occurrence scores.

Depth horizon	325 m	325 m	500 m	500 m
Abundance	n	Rank	n	Rank
Taxa				
<i>Hyperoglyphe perciformis</i>	579	1	0	
<i>Gephyroberyx darwini</i>	55	2	0	
<i>Epinephelus niveatus</i>	0		0	
Unidentified Scorpaenidae	0		0	
<i>Urophycis</i> + <i>Laemonema</i>	1	4.5	10	1
<i>Conger oceanicus</i>	1	4.5	6	2.5
<i>Helicolenus dactylopterus</i>	5	3	1	6.5
<i>Cyttopsis rosea</i>	0		0	
<i>Polyprion americanus</i>	0		0	
<i>Physiculus karrerae</i>	0		0	
Unidentified Gadiformes	0		1	6.5
<i>Lopholatilus chamaeleonticeps</i>	0		0	
Macrouridae	0		1	6.5
<i>Hoplostethus occidentalis</i>	0		2	4
<i>Grammicolepis brachiusculus</i>	0		6	2.5
<i>Trachyscorpia cristulata</i>	0		1	6.5
<i>Squalus</i> spp. (2 species)	0		0	
<i>Lophius gastrophysus</i>	0		0	
All other identified taxa	2		1	
Images unidentifiable to taxon	4		8	
Totals all taxa	648		38	
Database				
Total 1-s frame grabs	4,498		3,988	
Total area sampled (m ²)	4,516		4,004	
Population density (fish ha ⁻¹)	1,435		95	

rizon (VK-906/907), yielding 648 individual fishes scored among seven species (Table 4). Frames representing the five biotope categories were scored as follows: “Open”—383 frames; “Plate”—2800; “Rock”—1315; Rubble—0, “Thicket”—0. Only 51 “Rock” biotope frames contained substantial (but < 50%) *Lophelia* coral cover. Thus “Plate” and “Rock” hard-substrate biotopes without *Lophelia* (but almost always populated by anemones, sponges, bamboo corals, and black corals) appeared to dominate the VK-906/907 landscape, accounting for all but three of 648 fish scores. The 3988 frames representing the 500 m depth horizon (VK-826) yielded 38 individual fishes scored among 10 species (Table 4). Frames representing biotope categories were scored as follows: “Open”—1671 frames; “Plate”—1052; “Rock”—335; “Rubble”—0; “Thicket”—925; plus six frames over open space as the submersible crested a ridge top. *Lophelia* coral was much more prevalent on the 500 m depth horizon, and was typically developed as dense coral monoculture thickets. This three-dimensional coral biotope contrasted dramatically with the dominant low-relief, sparsely populated (sessile invertebrates other than *Lophelia*) “Open” and “Plate” biotopes. Dominant fish biotopes were “Open” (non-coral) (18 fishes scored) and “Thicket” (15 fishes scored). For both depth horizons, “Rubble” biotope was essentially absent.

In the general absence of food habits data for deep-living fishes that occur on *Lophelia* reefs, we have hypothesized probable assignments to trophic guilds by analogy with the known food habits of better-known shallow-water reef and shelf fishes. Large, mobile, schooling fishes that are probable macrocarnivores or mesocarnivores (sensu guilds defined by Ebeling and Hixon, 1991) dominated the 325 m depth horizon (submersible visual observations), including *Hyperoglyphe perciformis* (barrelfish) and *Epinephelus niveatus* (snowy grouper), but the former was under-represented and the latter un-represented in the transect analysis abundance summary (Table 4). Both species typically remained just outside the analyzed field of view during moving transects, as did *Polyprion americanus*, also un-represented in Table 4 relative to submersible visual observations. Other numerically dominant species included the probable sit-and-wait ambush mesocarnivores, *Helicolenus dactylopterus*, and *Conger oceanicus* (this cryptic species also under-represented during moving transects, although frequently observed by the diving scientists), and the apparent hover-and-wait mesocarnivore, *Gephyroberyx darwini*. All of these species were highly associated with hard substrate biotopes, "Plate" and "Rock", particularly in areas with extensive sessile invertebrate live cover. Overall population density of demersal fishes on the VK-906/907 study site estimated from summary of 1-s frame grabs (each representing approximately 1.0 m²) was 1435 fish ha⁻¹ (Table 4).

On the 500 m depth horizon, large cruising predators were essentially absent. Moreover, the suite of dominant species scored (Table 4) was more diverse in probable feeding modes. The top-ranking taxon was comprised of three species of benthic euryphagous "hakes" (*Laemonema goodebeanorum*, *Urophycis cirrata*, and *Urophycis floridana*), which probably feed opportunistically as both mesocarnivores and microcarnivores. Also important was the apparent ambush predator, *C. oceanicus*, the hover-and-wait strategist, *Hoplostethus occidentalis*, and a morphologically very specialized epifaunal picker, *Grammicolepis brachiusculus*, all three species closely associated with *Lophelia* "Thicket" biotope on VK-826. Four species of Scorpaenidae and Gadiformes completed the dominant species list. Overall population density of demersal fishes on the VK-826 study site estimated from summary of 1-s frame grabs (each representing approximately 1.0 m²) was 95 fish ha⁻¹ (Table 4). Thus, despite extensive three-dimensional habitat in the form of *Lophelia* thickets, population density on the deeper study site was lower by a factor of 15.

Non-transect frames analysis.—A total of 6879 frame grabs were analyzed for demersal fish occurrence (presence of a given taxon in the analyzed field of view) from the 20 dives, documenting at least 3 distinct species (Table 5). The 325 m depth horizon analysis included 2368 frame grabs, yielding 598 fish occurrences (622 individual fish) among 16 species. The 500 m depth horizon analysis included 4512 frame grabs yielding 230 fish occurrences (233 individual fish) among 23 species. All individuals of all identified species recorded during video analyses appeared to be adults or subadults; no obvious juveniles were observed. Nor were obvious juveniles observed in close-up imaging using the digital still camera. Dominant species, determined via frequency of occurrence in non-transect segments of dives, are given in Table 5. On the 325 m depth horizon, dominant taxa (orders and families) included the Perciformes (Stromateidae, Serranidae, Polyprionidae, Scorpaenidae), Beryciformes (Trachichthyidae), Zeiformes (Grammicolepidae, Zeidae), Gadiformes (Gadidae, Moridae), and Anguilliformes (Congridae). On the 500 m depth horizon, faunal composition by major taxa was similar, except that the large mobile foraging Stromateidae, Serranidae, and Polyprionidae dropped out, and

Table 5. Dominance rank by total occurrences per taxon for Viosca Knoll study sites demersal fish taxa from frame-by-frame analysis of non-transect time segments of all USGS 2004–2005 submersible dive video records.

Taxa	325 m horizon Occurrences	325 m horizon Rank	500 m horizon Occurrences	500 m horizon Rank
<i>Hyperoglyphe perciformis</i>	213	1		
<i>Gephyroberyx darwini</i>	74	2	5	10
<i>Epinephelus niveatus</i>	45	3		
Unidentified Scorpaenidae (2 spp.)	14	4	17	5
<i>Urophycis</i> + <i>Laemonema</i> (3 spp.)	9	5	26	2.5
<i>Conger oceanicus</i>	7	6	56	1
<i>Helicolenus dactylopterus</i>	3	7	16	6
<i>Cyttopsis rosea</i>	2	8		
<i>Polyprion americanus</i>	1	11		
<i>Physiculus karrerae</i>	1	11		
Unidentified Gadiformes	1	11		
<i>Lopholatilus chamaeleonticeps</i>	1	11		
Macrouridae (2 spp.)	1	11	9	9
<i>Hoplostethus occidentalis</i>			26	2.5
<i>Grammicolepis brachiusculus</i>			19	4
<i>Trachyscorpia cristulata</i>			14	7
<i>Squalus</i> spp. (2 species)			13	8
<i>Lophius gastrophysus</i>			3	11
All other identified taxa			8	
Images unidentifiable to taxon Database	17		25	
Total 1-s frame grabs	2,368		4,512	
Total fish occurrences (N grabs)	368		230	
Total identified fish taxa	16		23	
Occurrences on coral biotopes	14		153	
Occurrences on non-coral biotopes	354		77	

the open-slope Macrouridae (rattails) and Squalidae (dog sharks) entered as important contributors to the fauna (Table 5). Despite the similarity in composition among major taxa at the two depth horizons, there was substantial faunal transition between these horizons at the species level (Table 5). Species dominance rank by occurrence during non-transect video frames roughly paralleled dominance rank by abundance during moving transect frames. However, many more species were documented during the non-transect video segments, particularly including shy, cryptic, and smaller fish species. Such species were more readily documented when the submersible was stationary and the video camera used to zoom in on the substrate or the *Lophelia* thicket.

Lophelia colonies were sparse and poorly developed at the 325 m depth horizon. *Lophelia* coral largely occurred as small isolated bushes within an assemblage of mixed sessile invertebrates (sponges, anemones, black corals). No “Thicket” biotope was scored among all frame grabs analyzed. Fish taxa were primarily found on non-coral biotopes. Species occurrences were overwhelmingly scored from non-coral biotopes (Table 5: 354 of 368 frames). In contrast, the reverse situation was observed at the 500 m depth horizon where abundant coral “Thicket” biotope was scored during video frame analysis (Table 5).

Biotope associations among dominant fish species.—As advanced by Elliott (1977), a hypothesis of random distribution is appropriate for low density populations, a model which obtains for fish taxa inhabiting Viosca Knoll biotopes. The χ^2 goodness of fit test of observed vs expected counts from occurrence data for 12 key taxa (occurrences ≥ 10) from non-transect segments analyzed revealed that no taxon was randomly distributed among the comparative biotopes (Table 6).

Remote sampling results.—Twenty-seven species were captured in bottom trawl and benthic sled collections (Table 3A). Traps returned six species, adding three different species, making the total of 30 remotely collected species. Remote sampling added 15 new species to our overall Viosca Knoll taxonomic list (Table 3A), yielding a total of at least 53 species documented by the USGS study.

Discussion

Methodological limitations.—Moving quantitative belt transects conducted as per pre-defined criteria from the JSL submersible have inherent limitations that affect video estimates of demersal fish diversity and population density. During a moving transect, the JSL cannot deviate from its course for the purpose of identifying or photographing an individual fish. Nor can the submersible stop to collect a fish specimen to validate species identification. The video camera cannot be turned or zoomed in, when the objective is to maintain a consistent field of view to score species abundances. Thus, certain individual fishes cannot be identified to species, genus, or family. Furthermore, small species, juveniles, and cryptic fishes may be under-represented in species scores, or go undetected. The lights, sounds, and motion of the JSL are unusual disturbances in the typically dark, quiet, and still environment of the deep slope. Qualitatively, some species appeared to be repelled by the submersible, at least initially (e.g., *E. niveatus*, *P. americanus*), or more continuously (e.g., *H. perciformis*, *Hemanthias aureorubens*). Some may slowly retreat into cover as the submersible advances (e.g., *H. occidentalis*). A few species appear to be attracted to the submersible (e.g., *E. niveatus* and *C. oceanicus*) following a period of accommodation, such that individuals following the JSL during moving transects may be under-counted initially, then over-counted later in the same dive. Schooling species with large numbers of fish constantly moving (e.g., *H. perciformis*) are difficult to score, and individuals may re-enter and leave the video field multiple times. Despite such limitations, fish species occurrence and abundance on *Lophelia* reefs have previously been successfully quantified using underwater video (Mortensen et al., 1995; Fössa et al., 2002; Costello et al., 2005). The present study, however, is the first to conduct quantitative fish faunal structure on *Lophelia* and associated biotopes based upon tightly-standardized submersible moving transects rendered into sequential equal-time, equal-area high-quality digital still frames for objective scoring. It is also the first quantitative analysis of fish community structure for *Lophelia*-associated biotopes in the Gulf of Mexico and western Atlantic.

The number of dives per each of the two study sites was limited. Under perfect conditions, two dives per day were possible. However, due to competition with other objectives for bottom time, the number of quantitative transects that could be undertaken per dive was limited. Moreover, effort was very unevenly apportioned per biotope category since the hard-bottom and coral areas were the central focus of multidisciplinary objectives in the overall USGS program of investigations. Thus, although hard-substrate biotopes

Table 6. Chi-square test of observed vs expected count data by biotope for 12 key Viosca Knoll demersal fish taxa ($n \geq 10$). Observed count data are from frame-by-frame analysis of all non-transect time segments. Expected counts for a hypothesized random distribution of a given taxon across biotopes were determined as the proportion of total frame grabs times the total observed count for that taxon. Critical value = 11.14 (4 df), $P > 0.05$.

Biotope	Open	Plate	Rock	Rubble	Thicket	Total	χ^2
Frame grabs (n)	775	2,671	1,628	1	1,797	6,872	
Proportion of Total Count	0.1128	0.3887	0.2369	0.0001	0.2615	1.0000	
<i>Hyperoglyphe perciformis</i>	obs 0	126	86	0	1	213	6,699.26
	exp 24	83	50	0	56	79	
<i>Gephyroberyx darwini</i>	obs 0	13	62	0	4	79	2,543.92
	exp 9	31	19	0	21	63	
<i>Conger oceanicus</i>	obs 0	5	7	0	51	63	1,685.05
	exp 7	24	15	0	16	45	
<i>Epinephelus niveatus</i>	obs 0	15	30	0	0	45	544.44
	exp 5	17	11	0	12	35	
<i>Urophycis + Laemonema</i>	obs 16	9	1	0	9	35	219.66
	exp 4	14	8	0	9	31	
Unidentified Scorpaenidae	obs 9	10	3	2	7	31	58.57
	exp 3	12	7	0	8	26	
<i>Hoplostethus occidentalis</i>	obs 4	2	2	0	18	26	209.61
	exp 3	10	6	0	7	19	
<i>Helicolenus dactylopterus</i>	obs 4	9	0	0	6	19	27.38
	exp 2	7	5	0	5	19	
<i>Grammicolepis brachiusculus</i>	obs 1	1	4	0	13	19	106.83
	exp 2	7	5	0	5	14	
<i>Trachyscorpia cristulata</i>	obs 1	9	1	0	3	14	18.80
	exp 2	5	3	0	4	10	
Macrouridae	obs 8	2	0	0	0	10	63.24
	exp 1	4	2	0	3	10	
Squaloid sharks (4 species)	obs 4	3	0	0	3	10	14.80
	exp 1	4	2	0	3	10	

(“Plate” and “Rock”) without *Lophelia* coral (but almost always populated by anemones, sponges, bamboo corals, and black corals) appeared to comprise the dominant landscape of VK-906/907, video footage was skewed toward such biotopes. The same was true on the 500 m depth horizon, where *Lophelia* “Thicket” biotope appeared as a prevalent biotope. Comparative areas of “Open” soft-substrate biotope away from reef influence were less frequently traversed during all dives on the Viosca Knoll study sites, particularly when coral collection was the primary objective. However, open soft substrate does appear to be relatively rare on the elevated, carbonate-capped topographic features of Viosca Knoll. Only one dive into the 100 m deep depression on the northwestern corner of VK-826 (Fig. 2, reference “B”) encountered extensive soft substrate throughout the dive. The relative rarity of many otherwise dominant open-substrate, middle-slope taxa (e.g., Macrouridae, Halosauridae, Synphobranchidae) tends to confirm that soft-substrate is disproportionately unavailable in the study area. Thus, comparison of fish assemblages associated with hard-bottom and *Lophelia* biotopes, vs those associated with open soft substrate biotopes is basically limited to the comparative lists of USGS submersible documented taxa vs USGS trawl/sled and NOAA trawl taxa (Tables 3A,B).

Demersal fish faunal and trophic structure.—The deep slope biotopes investigated, including *Lophelia* reefs, are sparsely populated with demersal fishes. Only 686 total fishes were scored over 141 min during 32 moving transects, averaging < 5 fish min⁻¹. Species biotope affinities were better revealed during opportunistic non-transect intervals, which allowed for closer observations of fishes and their habitats, including observations with the submersible stationary and the video camera free to pan, tilt, and zoom.

Biotopes populated by sessile invertebrates differed substantially between the two depth horizons. On the 325 m depth horizon, a broad suite of sessile invertebrates (anemones, glass sponges, black corals, gorgonians, and *Lophelia*) contributed substantially to forming mixed live cover. Large expanses of “Rock” and “Plate” biotope were densely populated with this type of cover. *Lophelia* occurred primarily as individual small bushes, within the mix of sessile invertebrates. When it occurred in isolation, *Lophelia* was found mostly on bare hard substrate, varying in size from small sprigs with < 10 polyps to bushes up to 1 m high and 1 m in diameter. Typically, such small bushes were composed entirely of live white coral. No “Thicket” biotope was observed on the shallower VK-906/907 site. In contrast, *Lophelia* was the dominant sessile invertebrate on the 500 m depth horizon at the VK-826 site. In places, it formed extensive monospecific thickets covering ridge flanks and crests, sometimes in sequential parallel windrow formations. Thickets were alternatively developed atop thick soft sediment, or on carbonate pavement coated with a thin veneer of sediment. Typically, thickets ended abruptly, giving way to barren sediment or pavement without transitional habitat. Coral rubble was scarce, but sometimes found immediately at the base of thickets. Wherever found, it had the appearance of having been rapidly degraded. Elsewhere, *Lophelia* existed as isolated colonies on otherwise barren carbonate rock.

In terms of taxonomic and probable trophic diversity, the demersal fish fauna of the Viosca Knoll sites, including *Lophelia* reefs, appears rather rarified compared to shallower reef systems. The total fauna documented in this study included 53 species, 37 of which were documented from hard-substrate or coral biotopes. However, only a few were common or abundant, and fewer still highly associated with *Lophelia* “Thicket” biotope. On the 325 m depth horizon site, the fauna was dominated by Serranidae (1 species),

Stromateidae (Centrolophidae) (1), Beryciformes (1), Congridae (1), and Gadiformes (1). Faunal composition of the deeper site was similar, except that the Serranidae and Stromateidae (plus Polyprionidae) dropped out. Thus, large, highly-mobile, benthopelagic visual predators were prominent only on the shallower site where ambient light must still be sufficient to sustain a strategy of visual predation. Nonetheless, in terms of foraging guilds recognized among coral reef fishes (Ebeling and Hixon, 1991) large macrocarnivores and mesocarnivores dominated both *Lophelia* depth horizons in the northern Gulf of Mexico. Among predatory fishes of shallow coral reefs, Hobson (1975, 1979) distinguished five categories [summary based on Hixon (1991), adapted here for Gulf of Mexico *Lophelia* reefs with examples from the present study]: (1) open-water pursuers (*H. perciformis*, *Squalus* spp., *Odontaspis ferox*), (2) cryptic ambush predators (*H. dactylopterus*, *Trachyscorpia cristulata*), (3) tactical predators (*E. niveatus*, *P. americanus*), (4) slow stalkers (*H. occidentalis*, *G. darwini*, *G. brachiusculus*), (5) crevice predators (*C. oceanicus*). All five were present on the shallow *Lophelia* depth horizon; category 1 was greatly depleted in abundance and occurrence on the deeper horizon; category 3 was absent; categories 2 and 5 were important on both depth horizons.

Aside from macrocarnivores and mesocarnivores that appear to depend on vision, several trophic categories were absent from our *Lophelia* study reefs compared to shallower reef systems. The absence of herbivores below the depth of photosynthesis is unsurprising. However, the fundamental absence of microplanktivores (aside from rare individuals of *H. aureorubens* and *Anthias nicholsi*) is remarkable since microplanktivores represent a characteristic component of the world reef fish fauna (Hobson, 1991). Planktivores dominated numerically on the deep reef at Enewetak Atoll, Marshall Islands, down to 300 m (Thresher and Colin, 1986), and also dominated on northern Gulf of Mexico shelf-edge reefs, at least to 180 m (Weaver et al., 2002). Undoubtedly, structurally complex *Lophelia* reefs function in the same way as shallow reefs in concentrating particulate matter and plankton (Wolanski and Hamner, 1998), accelerating the delivery of such food items, and providing shelter from predation (Hobson, 1991). The abundance of planktonic prey on the Viosca Knoll sites is evidenced by the diversity and density of sessile particulate-feeding invertebrates populating these sites. But, sessile invertebrates are stationary contact feeders or filter feeders. In contrast, planktivorous fishes must actively select individual prey animals from the water column, and feed via discrete visual strikes (Zaret, 1972; Confer and Blades, 1975; Durbin, 1979). At the depth of Gulf of Mexico *Lophelia* reefs, ambient light is apparently insufficient to support this feeding strategy. Thus despite abundant shelter available in the form of anemone, sponge, black coral forests, and *Lophelia* thickets, planktivorous fishes are absent from the Viosca Knoll sites. The notable absence of juvenile fishes from our *Lophelia* biotopes, and from comparative eastern North Atlantic reefs (Husebø et al., 2002; Costello et al., 2005) is perhaps similarly explained, since early juveniles of most marine fishes typically depend on a plankton diet (Durbin, 1979). In contrast to our findings for the Viosca Knoll fauna, microplanktivory has been reported by Costello et al. (2005) among fishes inhabiting well-developed *Lophelia* reefs on the Sula Ridge off Norway. Shoals of *Sebastes* spp. are reported to hover over the reef tops, facing into the current at 230–320 m depth. Apparently, sufficient ambient light is available on Norwegian *Lophelia* reefs to enable visual microplanktivory. A diet consisting entirely of zooplankton has been confirmed for *Sebastes* spp. in a separate *Lophelia* reef study off southwestern Norway (Husebø et al., 2002).

A further notable attribute of the fauna of the Viosca Knoll study sites is the rarity of epifaunal croppers and benthivores. Much of the fish diversity of shallow coral reefs consists of species that either crop sessile invertebrates (Harmelin-Vivien, 2002) or exploit small benthic invertebrates (Choat and Bellwood, 1991). Sessile megafaunal invertebrates, including *Lophelia*, are abundant on northern Gulf of Mexico hard-bottom slope biotopes. The diversity and abundance of benthic and epibenthic invertebrates (e.g., crustaceans, mollusks) has yet to be assessed for *Lophelia* reefs in the Gulf of Mexico. However, *Lophelia* reefs in the eastern North Atlantic are reported to sustain a high diversity of benthic/epibenthic macrofaunal invertebrates (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Fosså and Mortensen, 1998; Husebø et al., 2002; Costello et al., 2005), with population densities up to three times higher than on adjacent soft substrate (Mortensen et al., 1995). Additionally, Reed (2002) reported that *Lophelia* reefs along the Florida-Hatteras slope support large, but unstudied, populations of sponges, gorgonians, and small macroinvertebrates.

The apparent absence of demersal microcarnivores (epifaunal croppers) among the fish fauna of Viosca Knoll may be a consequence of the limiting energetic cost of processing low-quality prey in a cold-water regime (Harmelin-Vivien, 2002). The negative correlation between increasing latitude and diversity in the world's shallow-water fish fauna (Mead, 1970; Briggs, 1974; Ehrlich, 1975; Springer, 1982; Ebeling and Hixon, 1991; Hobson, 1994; Harmelin-Vivien, 2002) has previously been explained by the progressive loss at higher latitudes of trophic specialists (Ebeling and Hixon, 1991; Harmelin-Vivien, 2002). Sessile invertebrate croppers are diverse and important on tropical reefs (Randall, 1967; Hobson, 1974; Harmelin-Vivien, 1979), but apparently absent from temperate reefs (Harmelin-Vivien, 2002). Low-quality invertebrate prey is energetically expensive to process for low-caloric return (Brey et al., 1988), and may contain high concentrations of anti-predator metabolites (Hay, 1996). Utilizing low-quality prey such as sessile invertebrates (Cummins and Wuycheck, 1971; Brey et al., 1988) may have evolved only on tropical reefs where intense competition for high-quality resources has favored trophic radiation, and only in shallow tropical waters where sustained high temperatures facilitate metabolism of refractory food resources (Harmelin-Vivien, 2002). Tropical reefs are dominated by perciform and tetraodontiform fishes (Randall et al., 1990; Ebeling and Hixon, 1991). These taxa include the most recently evolved and most highly derived forms, including almost all fishes adapted to feed as herbivores or sessile invertebrate croppers (Harmelin-Vivien, 2002). The trophic rarity of benthic microcarnivores on deep cold-water reefs reflects the phylogenetic rarity of percomorph taxa on these reefs. Among more ancient groups occurring on deep reefs, only the Zeiformes seem to contain species adapted for specialized microcarnivory.

Specialized reef microcarnivores that pick small mobile crustaceans off the substrate or off sessile invertebrates appear to be largely absent from the Viosca Knoll demersal fish fauna. There is one notable exception, the zeiform species *G. brachiusculus*, highly adapted morphologically (deep, strongly compressed body), behaviorally (slow, deliberate maneuvering using dorsal and anal fin undulation), and trophically (small tubular mouth with fixed funnel-like opening) to prey upon small reef-dwelling prey, probably small epibenthic and hyperbenthic crustaceans sheltering within *Lophelia* reefs. A second zeiform fish, *Neocyttus helgae* (Holt and Byrne, 1908), from eastern North Atlantic deep reefs (Costello et al., 2005) may represent a trophic analog to *G. brachiusculus*.

Habitat and apparent trophic associations.—The microcarnivore *G. brachiusculus* is non-randomly distributed, and appears to be associated primarily with the “Thicket” biotope. Despite its large body size and weak swimming abilities (one specimen was plucked from open water using the JSL manipulator claw), *G. brachiusculus* adults have rarely been collected in bottom trawls (eight total records over six decades of NOAA Fisheries bottom trawling in the Gulf and Caribbean. This is probably due to a high association with reef and rock biotopes that are difficult to trawl. All three Gulf of Mexico bottom trawl records came from within the Viosca Knoll region rectangle, suggesting an association with continental slope reefs in the northern Gulf of Mexico. Such an association is consistent with USGS submersible data, in which 68% of *G. brachiusculus* video records were from the “Thicket” biotope, and 21% from the high-relief “Rock” biotope. Aside from this sole specialist, medium-sized generalized macro- and mesocarnivores (Ebeling and Hixon, 1991), to which category we would tentatively assign beryciform species (*H. occidentalis*, *G. darwini*) and hake-like gadiform species (*L. goodebeanorum*, *Physiculus karrerae*, and species of *Urophycis*), appear to be the predominant predators of small benthic and epibenthic organisms on Viosca Knoll hard-substrate biotopes. However, the hake-like gadiform species appear equally at home on soft-substrates, with roughly equivalent occurrences on “Open” soft-substrate biotope vs hard-substrate and structured biotopes.

A first-order statistical test of habitat affinities of 12 numerically-dominant Viosca Knoll demersal fish species via χ^2 goodness of fit revealed that none of these key species were randomly distributed across the four biotopes. However, three taxa, *H. dactylopterus*, *Trachyscorpia cristulata*, and squaloid sharks (4 spp.) closely approached the critical value for a random distribution. Bias in the frequency of occurrence data by taxon (observed vs expected) in Table 6 suggests the habitat affinities of individual taxa. Departure from randomness was greatest for *H. perciformis* and *G. darwini*, both of which occurred predominantly on “Plate” and “Rock” biotopes (i.e., non-reef hard substrates), never on the “Open” biotope. *Epinephelus niveatus* displayed a similar pattern, never occurring on the “Open” or *Lophelia* “Thicket” biotopes. *Conger oceanicus* occurred disproportionately on the “Thicket” biotope, corresponding to its observed behavior of burrowing into the base of *Lophelia* bushes. *Grammicolepis brachiusculus* also occurred disproportionately on the “Thicket” biotope. Macrouridae displayed an affinity for unstructured low-relief biotope (“Open” and “Plate”). Extensive coral rubble was recorded only once among 6879 Viosca Knoll video frames analyzed. Thus, no association with this rare biotope was documented in the data.

Fish faunas from comparative investigations.—The fish fauna of *Lophelia* reefs in the western North Atlantic, including the Gulf of Mexico, has previously been reported only incidentally. In an appendix to their report on deep-water lithoherms (some topped by *Lophelia*) of the northeastern Straits of Florida, Messing et al. (1990) noted these species observed from submersible: a small macrourid, *P. americanus*, *Chaunax* cf. *pictus* Lowe, 1846, *Polymixia* sp., *Beryx decadactylus*, *Odontaspis noronhai*, and an ophidiid/bythitid. Of these species, only *P. americanus* has also been documented from Viosca Knoll in the present study. Reed et al. (2005) reported on the invertebrate and fish faunas inhabiting deep-water sinkholes and bioherms off South Florida, none of which were populated by *Lophelia*. However, these authors noted the following species common to Pourtales Terrace bioherms populated by stylasterid corals, and to Blake Plateau *Lophelia* reefs (based on unpublished data): *H. dactylopterus*, *Hoplostethus* sp,

Laemonema melanurum Goode and Bean, 1896, *Chlorophthalmus agassizi*, *Nezumia* spp., and *Xiphias gladius* Linnaeus, 1758. Only the first two species listed also occurred frequently on Viosca Knoll coral biotope. While *L. melanurum* was not observed during USGS missions on Viosca Knoll, three potential ecological analogs (species of *Urophycis* and *Laemonema*) were recorded on coral biotope, but more frequently on unstructured “Open” and “Plate” biotopes. *Chlorophthalmus agassizi* and *Nezumia* spp. are characteristic open-slope species. These species were not recorded by us from “Thicket”, “Rock” or “Plate” biotopes, and are probably not highly associated with such biotopes. Other demersal fish species reported by Reed et al. (2005) from three-dimensional deep-water habitats off South Florida, and shared with the Viosca Knoll fauna, include *G. darwini*, *E. niveatus*, and congrid eels (probably *C. oceanicus*).

In contrast to the poorly-known fish fauna of western Atlantic *Lophelia* reefs, that of eastern North Atlantic reefs has been relatively well studied (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Husebø et al., 2002; Costello et al., 2005). Based on multiple imaging data, Costello et al. (2005) found 25 fish species in 17 families inhabiting *Lophelia*-associated habitats (coral reef, transition zone, coral debris zone) at eight sites over a depth range of 39–1015 m off Ireland, the Faroe Islands, and Scandinavia. The transition zone of patchy coral was earlier defined by Mortensen et al. (1995) and Freiwald et al. (2002). Both zones are essentially lacking from Viosca Knoll *Lophelia* reefs. Costello et al. (2005, table 4) reported considerable overlap in habitat affinities among species recorded from four natural seafloor habitats: *Lophelia* reef (16 total species), transitional habitat (21), coral debris habitat (18), and open seabed (21). (Note that the original totals by respective habitat in Costello et al.’s table 4 are each erroneously summed). Only one species (*N. helgae*) was exclusively associated with reef. Only two species each were exclusively found on transitional or coral debris habitats, and only three exclusively on open seabed. Eleven species were found in common among all four habitats. However, no single species reported in Costello et al. (2005) that was found on all three coral-associated habitats was not also found on open seabed habitat. Gadoid fishes predominated, along with the Scorpaenidae (Sebastidae). Species associated exclusively or more consistently with open seabed habitats were typified by families Macrouridae, Rajidae, Lophiidae, and Pleuronectidae.

No species reported from eastern North Atlantic *Lophelia* reefs were shared with Gulf of Mexico reefs. However, prominently contributing to the faunas of both eastern North Atlantic *Lophelia* reefs and Viosca Knoll study sites were the Gadiformes (Gadidae, Moridae), Beryciformes (Trachichthyidae), and Scorpaeniformes (Scorpaenidae). All may be trophic generalists. The gadiform and scorpaeniform taxa exploit both open and structured biotopes on the continental slope, while beryciform taxa are more consistently associated with structured biotopes. All appear to be facultatively associated with *Lophelia* reefs. However, Husebø et al. (2002) reported that long-line catches yielded seven times more scorpaenid species (*Sebastes marinus* Linnaeus, 1758) from coral vs non-coral habitats, and nearly twice as many of two gadid species (*Brosme brosme* Ascanius, 1772; *Molva molva* Linnaeus, 1758). No single demersal fish species in the eastern North Atlantic has been reported to be an obligate *Lophelia* associate (Husebø et al., 2002), matching similar findings among reef-associated invertebrates (Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992). In the Gulf of Mexico, however, at least the highly-specialized zeiform fish, *G. brachiusculus*, may be an obligate *Lophelia* inhabitant.

Although bottom trawl sampling added 15 species to the overall USGS missions demersal fish species list for Viosca Knoll, most additions were fishes not typically associated with three-dimensional biotopes. Accordingly, most of these same species pertain to families characteristic of the two-dimensional open slope biome, and otherwise broadly and ubiquitously distributed. These include the Macrouridae (*Hymenocephalus* sp., *Malacocephalus occidentalis*), Steindachneriidae (*Steindachneria argentea*), Chlorophthalmidae (*C. agassizi*, *Parasudis truculentus*), Paralichthyidae (*Paralichthys albigutta*), Poecilopsettidae (*Poecilopsetta beani*), Cynoglossidae (*Symphurus marginatus*), Percophidae (*Bembrops anatirostris*), Scorpaenidae (*Pontinus longispinis*, *Setarches guentheri*), Uranoscopidae (*Gnathagnus egregius*), and Ophichthyidae (*Pseudomyrophis nimius*). Many of the fish species identified from eastern North Atlantic *Lophelia* reefs (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Husebø et al., 2002; Costello et al., 2005) similarly pertain to taxa more generally characteristic of the open slope biome than to *Lophelia* reefs. When found on deep coral biotopes, such taxa may be considered as either facultative or incidental, i.e., not distinctly associated with coral habitat. Such typical open-slope taxa (e.g., Macrouridae, Synphobranchidae, Ophidiidae, Ipnopidae, Halosauridae) were barely represented on Viosca Knoll where soft substrate is uncommon. Thus, direct ecological interaction between coral-associated fishes and typical open-slope deep-sea fishes may be limited. Midwater fishes were also very rarely observed during USGS Viosca Knoll dives, again suggesting limited interaction between the hard-bottom fauna and the mesopelagic deep-sea fauna.

Trawl samples from the Viosca Knoll vicinity also returned juveniles of at least one species, *C. oceanicus*, that inhabits *Lophelia* "Thicket" biotope as adults. Thus, at least for this species, the absence of juveniles from coral biotope can be explained. Furthermore, an ontogenetic linkage has been documented between the soft-substrate and coral biomes of the continental slope. Populated by macrocarnivores to a large extent, *Lophelia* reefs in all regions may represent a high predation risk habitat for juvenile fishes.

Regional biotope contrasts.—A striking difference between Viosca Knoll *Lophelia* reefs and eastern North Atlantic *Lophelia* reefs is the virtual absence of the coral rubble and patch reef transition zones (Mortensen et al., 1995; Freiwald et al., 2002) on the northern Gulf of Mexico reefs, and the apparently very high proportion of living white coral in the Gulf of Mexico (Schroeder, 2002). Both *Lophelia* rubble and dead coral have been reported to be important high-density, high-diversity invertebrate habitats in the eastern North Atlantic (Wilson, 1979; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Costello et al., 2005). In the western North Atlantic, Messing et al. (1990) reported that the upcurrent ends of *Lophelia*-topped lithoherms in the Florida Straits were covered with *Lophelia* rubble. Rubble was reported to extend beyond the foot of the lithoherms forming a talus apron, much like the rubble zones described for *Lophelia* reefs in the eastern North Atlantic. Among Norwegian bioherms studied, dead coral has been reported to cover an average basal area nearly eight-fold larger than that occupied by living coral (Mortensen et al., 1995). *Lophelia* rubble is also utilized as habitat by demersal fish species (Costello et al., 2005), and may form a distinct biotope for species such as *Lophiodes beroe* Caruso, 1981 and *Chaunax stigmaeus* Fowler, 1946, both found preferentially on *Lophelia* rubble on the Blake Plateau (Caruso et al., 2007).

In contrast, in the northern Gulf of Mexico, there is typically a dramatic and abrupt discontinuity between live *Lophelia* bushes or *Lophelia* reef thicket and adjacent barren substrate. Among 8486 frame grabs analyzed from 32 moving video transects on the

Viosca Knoll study sites, not one frame was scored as representing the “Rubble” biotope. Among 6879 additional still frames analyzed from non-transect video segments, only one frame was scored as containing > 50% rubble substrate in the field of view.

The remarkable rarity of *Lophelia* rubble from northern Gulf of Mexico reefs begs explanation. Among hypotheses that could be advanced, we offer the following alternatives: (1) The reefs are very young, as suggested by the preponderance of living white coral, such that time has been insufficient for extensive accumulation of rubble; (2) In the hydrocarbon seep environment of Gulf of Mexico salt diapers, rubble is rapidly degraded chemically, biologically, or both; (3) Active bottom currents continuously or episodically sweep rubble from the underlying hardpan substrate, transporting it down-ridge to be buried in sediment-filled valleys. None of these hypotheses has yet been tested.

Our finding that the shallower VK-906/907 depth horizon had 15-fold greater abundance of demersal fishes than the deeper depth horizon corresponds with a similar bathymetric trend in fish abundance for the faunas of eastern North Atlantic *Lophelia* reef habitats (Costello et al., 2005). As depth increases, fish trophic diversity and abundance both decline, paralleling findings for the invertebrate macrofauna (R.A.B., unpubl. data). Two trophic guilds of demersal fishes predominate on the deeper Viosca Knoll study site, large macrocarnivores and medium-sized opportunistic mesocarnivores.

New regional faunal records.—Documentation of *P. americanus* in the present study represents the first record of this species from the Gulf of Mexico, although *P. americanus* is known from deep habitats off the adjacent southeastern U.S. (Messing et al., 1990; Sedberry et al., 1999; Sedberry, 2002; Reed et al., 2007). This species and may utilize *Lophelia* biotope for spawning (Reed et al., 2007). The Viosca Knoll video record of the shark *O. ferox* (smalltooth sand tiger) is the third from the western Atlantic, second from the Gulf of Mexico (Bonfil, 1995), and second from within the U.S. EEZ (Sheehan, 1998). The video record of *Caristius* sp. (Table 3A) appears to represent the second record of this taxon from the Gulf (Trolley et al., 1990).

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