



The fish fauna associated with deep coral banks off the southeastern United States

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Abstract

Deep-sea or cold-water corals form substantial habitat along many continental slopes, including the southeastern United States (SEUS). Despite increasing research on deep coral systems and growing appreciation of their importance to fishes, quantitative data on fish communities occupying these ecosystems are relatively lacking. Our overall goals were to document the fish species and their relative abundances and to describe the degree of general habitat specificity of the fishes on and around deep coral habitats on the SEUS slope. From 2000 to 2006, we used the Johnson-Sea-Link (JSL) submersible (65 dives, 366–783 m), supplemented with otter trawls (33 tows, 365–910 m) to document fishes and habitats from off North Carolina to east-central Florida. Eight areas with high concentrations of deep-sea corals were surveyed repeatedly. Three general habitat types (prime reef, transition reef, and off reef) were defined to determine large-scale habitat use patterns. Throughout the area, at least 99 fish species were identified, many (19%) of which yielded new distributional data. Most species observed with the JSL were on prime reef ($n = 50$) and transition reef ($n = 42$) habitats, but the off reef habitat supported a well developed, but different fauna ($n = 25$ species). Prime reef was characterized by *Laemonema melanurum* (21% of total), *Nezumia sclerorhynchus* (17% of total), *Beryx decadactylus* (14% of total), and *Helicolenus dactylopterus* (10% of total). The off reef areas were dominated by *Fenestraja plutonia* (19% of total), *Laemonema barbatulum* (18% of total), *Myxine glutinosa* (8% of total), and *Chlorophthalmus agassizi* (7% of total). Transition habitat exhibited a mixture of species that were also found on either prime reef or off reef habitats. *Nezumia sclerorhynchus* was the most abundant (25% of total) transition habitat species, followed by *L. barbatulum* (16% of total) and *L. melanurum* (14% of total). Several species (e.g., *Anthias woodsi*, *B. decadactylus*, *Conger oceanicus*, and *Dysommia rugosa*) demonstrated specificity to deep-reef habitats, while others (e.g., *C. agassizi*, *Benthobatis marcida*, *F. plutonia*, and *Phycis chesteri*) were always more common away from reefs. In addition to new distributional data, we provide behavioral and biological observations for dominant species.

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1. Introduction

Deep-sea or cold-water corals form important habitat along many continental slopes and are receiving increasing attention worldwide. There is growing appreciation of their functions as fish

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habitat (Costello et al., 2005; Stone, 2006), as repositories of data on past environmental conditions (Adkins et al., 1998; Williams et al., 2006), and as focal points of biodiversity. Deep coral habitats are much more extensive than previously known, and they face a number of threats (Rogers, 1999; Koslow et al., 2000; Morgan et al., 2006; Roberts et al., 2006). These high-profile features may concentrate exploitable resources and enhance local productivity in ways similar to seamounts (Rogers, 1994; Koslow, 1997). Also, like seamounts, the unique, diverse habitats occurring along the continental slope of the southeastern United States (SEUS) have escaped detailed examination not only because of their depths, but because the bottom topography is rugged and overlain by strong currents (i.e., Gulf Stream). Deep coral reefs populate the SEUS continental slope in great abundance (Stetson et al., 1962; Paull et al., 2000; Popenoe and Manheim, 2001; Reed, 2002a; Reed and Ross, 2005; Reed et al., 2006). By one estimate (Hain and Corcoran, 2004), the SEUS and Gulf of Mexico have the most extensive deep coral populations in US waters; however, the deeper parts of these large regions are poorly explored.

Habitat association data for deep-sea fishes are lacking, leading to a general assumption that habitat selection is opportunistic. Deep-sea fishes have often been grouped by depth (e.g., Jacob et al., 1998; Bull et al., 2001); however, even this basic habitat parameter may not accurately or strictly classify fish assemblages (Snelgrove and Haedrich, 1985; Haedrich and Merrett, 1990; Chave and Mundy, 1994). Compared with continental shelf and estuarine systems, deep-sea bottoms on the scale of 100s to 1000s of meters are more homogeneous, soft substrata. There are large, rugged structures (canyons, mid-ocean ridges, trenches, seamounts) in the deep-sea, but much of the habitat diversity that exists there, particularly deeper than 1000 m, may result from biological constructs (e.g., tubes, mudballs) that have ecological impacts (e.g., increased species richness) at a micro scale (Gage and Tyler, 1991). In contrast, there are abundant cases for close, often obligate, fish associations with various shallow-water marine and estuarine habitats (e.g., corals/hardgrounds: Parker and Ross, 1986; Lough et al., 1989; Stein et al., 1992; Chittaro, 2004; Quattrini and Ross, 2006; vegetation: Adams, 1976; Lubbers et al., 1990; other: Pederson and Peterson, 2002). While any of the biological or physical/chemical parameters composing a habitat may

influence the distribution or survival of an organism, it is generally impossible to quantify all of these. For this paper we concentrated on the influence of deep-sea coral or rock (reef) structures on the composition of benthic slope fish assemblages. We considered the reefs to be mesoscale features (similar scale to hydrothermal vents or food falls) falling between megascale deep-sea structures, such as mid-ocean ridges, canyons, or seamounts, and microscale structures such as crevices, burrows, or ripples.

Basic habitat affinities have been established for shallow-water (<200 m) reef fishes because such habitats lend themselves readily to direct observation methods that allow faunal classifications based on habitat features. Stark (1968) defined levels of habitat affinity (i.e., primary, secondary) for reef fishes, which has facilitated general sea-floor habitat classifications (Miller and Richards, 1980; SEAMAP-SA, 2001). Choat and Bellwood (1991) defined “reef fish” based on an array of characteristics (e.g., group features, ecological, habitat, distributional, taxonomic, body morphology). In the deep-sea, however, conclusions about fish and habitat relationships are likely biased by the indirect sampling (e.g., dredges, trawls) used to collect most data. These methods confound and integrate fish/habitat associations over the distances sampled, and in many cases the habitat sampled is unknown. Long term, replicated, direct observation is the preferred methodology for gathering explicit data on faunal relationships to habitat in marine environments (Starr et al., 1995; Connell et al., 1998; Cailliet et al., 1999). Such methods are rarely applied in the deep-sea, and when used, results ranged from only qualitative fish/habitat descriptions (e.g., Wenner and Barans, 2001; Reed et al., 2006) to detailed habitat association data indicating that several fishes were correlated with rocky, reef habitats (Percy et al., 1989; Stein et al., 1992; Chave and Mundy, 1994; Yoklavich et al., 2000).

Despite increasing research on deep coral systems, quantitative data on fishes associated with these habitats are relatively lacking. In the cool temperate to boreal northeastern Atlantic Mortensen et al. (1995), Husebø et al. (2002), and Costello et al. (2005) noted that reefs formed by *Lophelia pertusa* seemed to be important to some fishes. However, Auster (2005) suggested that in the northwestern Atlantic deep corals were no more important to fishes than other reef structures.

A similar conclusion of habitat opportunism was reached for fishes associated with corals and sponges at moderate depths off southern California (Tissot et al., 2006). Deep coral ecosystem data for fishes from the SEUS and Gulf of Mexico are limited, with studies reporting only a few taxa, many not identified to species, from only a few locations (Messing et al., 1990; Wenner and Barans, 2001; Reed et al., 2005, 2006). Data presented here represent the first extensive, quantitative treatment of fishes on deep coral and hardground slope habitats of this region. Our overall goals were to document species occurrences and relative abundances and to describe the degree of general habitat specificity of fishes on and around deep reef habitats on the SEUS slope. By documenting fish distributions and abundances over reef and non-reef habitats, we determined the degree to which fishes were specifically and predictably associated with these continental slope habitats.

2. Materials and methods

2.1. Study areas

Some deep coral study areas in the SEUS region have been named (e.g., Reed and Ross, 2005; Reed et al., 2005, 2006), giving the impression that coral habitats are disjunct. Coral habitats on the Blake Plateau (North Carolina to Cape Canaveral, FL) are generally larger and more continuous than these names imply. Detailed mapping of the region combined with ground truthing are needed to clarify coral habitat distributions and the extent to which areas require discrete names.

Based on literature and our surveys, we designated eight general research areas where deep corals occurred in order to conduct replicate sampling over several years (Fig. 1). During this study (2000–2006) we steadily expanded our sampling to include larger areas of the SEUS slope. Deep coral

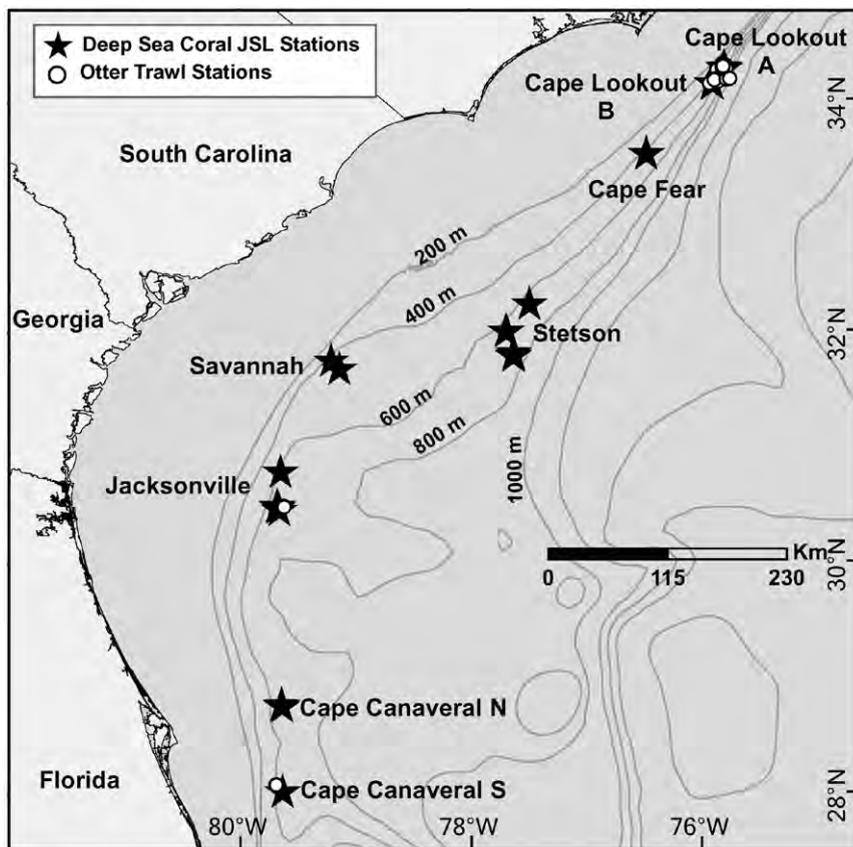


Fig. 1. Deep-sea coral habitat study areas along the southeastern United States slope sampled during this study, 2000–2006.

habitats within the eight study areas vary in bottom topography, coral development, and depth; however, all of these reefs occur under the Gulf Stream and experience strong bottom currents.

Off North Carolina, large mounds and ridges have been formed, which appear to be a sediment/coral rubble matrix topped with almost monotypic stands (up to 3 m high) of live and dead *L. pertusa*. The three North Carolina *Lophelia* banks (designated as Cape Lookout A, Cape Lookout B, and Cape Fear, Fig. 1) are the northernmost deep-sea coral banks off the SEUS and the shallowest of our study sites (Table 1). The banks are generally similar in physical attributes, rising about 80–100 m above the seafloor over <1 km distance and exhibiting slopes up to 60°. Extensive coral rubble zones surround the mounds for large distances, and in places seem to be quite thick (several cm at least).

South of Cape Fear, deep coral habitat is more variable and diverse and occurs deeper than off North Carolina. Sediment/coral mounds (Popenoe and Manheim, 2001) are topped with a variety of anthozoans. The abundant hard bottoms (often exhibiting high-profile) on the Blake Plateau also provide substantial substrata for *L. pertusa* and other anthozoans. The Stetson area, a large region of extremely rugged topography and diverse bottom types (Stetson et al., 1962; Reed, 2002a; Reed et al., 2006), supports a variety and often a high density of corals (e.g., *L. pertusa*, *Enallopsammia profunda*, *Leiopathes* spp., *Keratoisis* spp.) and sponges. The Savannah area is composed of numerous mounds and ridges of varying topography, and appears to have a heavier sediment load compared with other sites. The bottom is covered with mostly dead *Lophelia*, both rubble and standing thickets, with scattered low-profile living corals (e.g., *L. pertusa*, *Stylaster* spp.) and sponges (Reed, 2002a; Reed et al., 2006; pers. obs.). Many habitats in the Jacksonville area, especially on the northern end, are composed of large, high-profile rock ledges with varying quantities and types of attached corals. Bottom types in this area are diverse, and some sampling sites are composed of *Lophelia* mounds with mixed soft corals and sponges. Topographic highs, most with coral development, are abundant and nearly continuous from the Jacksonville area to south of Cape Canaveral (Ayers and Pilkey, 1981; Paull et al., 2000; Reed, 2002a; Reed et al., 2006). Our southernmost study sites, divided into North Cape Canaveral and South Cape Canaveral, are composed of *L. pertusa* with mixed soft corals and

sponges on tops of mounds/ridges, which are surrounded by sand and rubble.

2.2. Collection methods

During eight (2000–2006) summer–fall cruises, benthic and benthopelagic fishes on and near deep-water coral banks were documented along the SEUS slope at depths of 356–910 m (Table 1, Fig. 1). Benthic sampling was conducted at eight general localities (Fig. 1, see above) along the slope from central North Carolina to central Florida using the Johnson-Sea-Link (JSL) submersible (Harbor Branch Oceanographic Inst.), supplemented with otter trawls.

The JSL was the primary gear used to collect data on fishes and associated habitats. Usually two daytime dives (ranging from ca. 1.5–3 h each) were made with the JSL each day on or near coral banks (Table 1). Our goal was to survey a variety of habitat types during each dive; however, since our priority was the largely unexplored coral mounds, more time was spent in that habitat. Scientists in both bow and stern compartments made frequent observations and operated hand-held digital, color video cameras (Sony TRV 950) and digital audio recorders. In addition, an external, bow-mounted digital color video camera (Sony 3-chip CCD camera with Canon 6–48 mm zoom lens) recorded continuously throughout most dives. Two (2001–2005) or four (2000) laser pointers (25 cm apart) mounted on the camera were used to estimate fish lengths and measure habitat characteristics. Depth, temperature, salinity, date, and time were logged at $\leq 1 \text{ scan s}^{-1}$ intervals (data were overlain on the external camera video tapes) using a real-time data logger (Sea-Bird SBE 25 or 19plus) attached to the submersible. Digital still images were taken with an externally mounted Nikon 955 camera (3.34 megapixel CCD, 4 × 8–115 mm zoom lens) at irregular intervals during dives in 2003–2005. During all dives, the submersible's position was tracked from the surface support ship using a Trackpoint II system.

We attempted to employ video transects standardized by time or distance (Parker and Ross, 1986; Sulak and Ross, 1996); however, highly variable and rugged bottom topography coupled with often strong currents made this impractical. Video recorded when the JSL was stationary and moving (“transecting”) was used for both qualitative and quantitative fish and habitat assessments. When

Table 1
2000–2006 Johnson-Sea-Link (JSL) submersible (S) and otter trawl (T) station data at deep-water coral sites off the southeastern US

Station	Gear	Date	Time	Total Time (min)	Start Latitude (°N)	Start Longitude (°W)	End Latitude (°N)	End Longitude (°W)	Depth Range (m)	Temp (°C)	Salinity	
<i>Cape Lookout A</i>												
JSLI-4206	S	28-Jul-00	M	114	34° 19.63	75° 46.33	34° 19.45	75° 47.25	385–470	8.6 (5.6–10.6)	35.2 (34.0–35.8)	
JSLI-4207	S	28-Jul-00	A	109	34° 19.57	75° 47.13	34° 19.42	75° 47.29	388–418	8.6 (6.2–9.4)	35.2 (34.1–35.6)	
CH-01-092	T	28-Aug-01	M	30	34° 20.14	75° 48.05	34° 19.66	75° 47.94	397–398			
CH-01-094	T	28-Aug-01	M	45	34° 19.46	75° 47.84	34° 18.52	75° 47.53	409–434			
CH-01-096	T	28-Aug-01	M	45	34° 19.53	75° 48.03	34° 18.93	75° 47.84	390–420			
CH-01-097	T	28-Aug-01	A	45	34° 19.64	75° 46.42	34° 18.79	75° 46.26	467–474			
CH-01-100	T	28-Aug-01	A	45	34° 19.93	75° 46.71	34° 19.31	75° 46.48	445–460			
CH-01-109	T	29-Aug-01	M	29	34° 19.12	75° 46.64	34° 18.36	75° 46.19	470–488			
CH-01-110	T	29-Aug-01	M	29	34° 19.94	75° 46.83	34° 19.10	75° 47.12	442–445			
CH-01-111	T	29-Aug-01	M	30	34° 20.57	75° 47.69	34° 19.65	75° 47.36	399–424			
CH-01-112	T	29-Aug-01	A	30	34° 20.60	75° 48.16	34° 19.56	75° 47.99	378–403			
CH-01-113	T	29-Aug-01	A	30	34° 20.55	75° 48.19	34° 19.38	75° 47.98	378–408			
JSLI-4361	S	22-Sep-01	M	159	34° 19.68	75° 47.37	34° 19.69	75° 47.53	381–427	9.5 (9.1–9.9)	35.2 (35.0–35.6)	
JSLI-4362	S	22-Sep-01	A	135	34° 19.43	75° 47.49	34° 19.42	75° 47.51	367–399	10.1 (9.2–10.6)	35.3 (34.9–35.7)	
JSLI-4363	S	23-Sep-01	M	165	34° 19.42	75° 47.45	34° 19.41	75° 47.50	370–417	10.5 (9.9–10.8)	35.3 (35.1–35.5)	
JSLI-4364	S	23-Sep-01	A	171	34° 18.84	75° 47.01	34° 18.77	75° 47.13	398–443	10.1 (9.0–10.9)	35.3 (35.0–35.5)	
SJ-02-034	T	10-Aug-02	M	30	34° 18.69	75° 48.12	34° 18.49	75° 49.27	393–413			
SJ-02-035	T	10-Aug-02	A	30	34° 17.65	75° 50.34	34° 17.28	75° 51.21	356–374			
SJ-02-036	T	10-Aug-02	N	33	34° 19.13	75° 48.04	34° 19.08	75° 48.39	396–405			
SJ-02-037	T	10-Aug-02	N	39	34° 19.05	75° 48.19	34° 18.99	75° 48.33	400–402			
JSLII-3304	S	11-Aug-02	M	148	34° 19.71	75° 47.04	34° 19.51	75° 46.21	384–447	9.6 (6.3–10.9)	35.3 (33.9–36.0)	
JSLII-3305	S	11-Aug-02	A	149	34° 19.46	75° 47.20	34° 19.48	75° 47.20	381–416	9.2 (9.0–10.1)	35.2 (34.7–35.7)	
JSLII-3306	S	12-Aug-02	M	147	34° 19.4	75° 47.2	34° 19.45	75° 47.25	382–418	10.9 (8.9–12.0)	35.4 (34.0–36.1)	
JSLII-3307	S	12-Aug-02	A	47	34° 19.48	75° 47.45	34° 19.50	75° 47.55	367–416	10.1 (9.8–10.5)	35.3 (35.0–35.5)	
JSLII-3430	S	23-Aug-03	A	155	34° 19.37	75° 47.33	34° 19.40	75° 47.25	384–415	6.3 (5.9–6.9)	35.1 (34.9–35.2)	
JSLII-3431	S	24-Aug-03	M	136	34° 19.52	75° 47.04	34° 19.42	75° 47.24	382–432	7.1 (6.2–8.3)	35.1 (34.9–35.2)	
JSLII-3432	S	24-Aug-03	A	130	34° 19.43	75° 47.16	34° 19.48	75° 47.21	381–424	8.3 (7.5–9.0)	35.1 (34.8–35.3)	
JSLI-4692	S	15-Jun-04	M	124	34° 19.43	75° 47.17	34° 19.44	75° 47.22	380–426	9.8 (9.5–10.0)	35.3 (35.2–35.4)	
JSLI-4693	S	15-Jun-04	A	127	34° 19.44	75° 47.14	34° 19.51	75° 47.15	392–431	9.1 (8.0–9.8)	35.2 (35.0–35.3)	
SJ-04-025	T	15-Jun-04	A	30	34° 20.06	75° 48.08	34° 19.34	75° 47.90	370–407			
JSLI-4890	S	17-Oct-05	M	127	34° 19.59	75° 47.09	34° 19.47	75° 47.22	386–420	8.1 (5.5–9.0)	35.1 (34.9–35.3)	
JSLI-4891	S	17-Oct-05	A	115	34° 19.49	75° 47.44	34° 19.37	75° 47.56	366–433	9.0 (8.4–9.6)	35.2 (35.1–35.4)	
CH-06-044	T	21-Sep-06	M	30	34° 18.35	75° 47.88	34° 17.58	75° 48.00	430–441			
<i>Cape Lookout B</i>												
JSLI-4365	S	24-Sep-01	M	153	34° 11.34	75° 53.80	34° 11.41	75° 53.74	410–428	10.0 (9.6–10.4)	35.3 (35.1–35.4)	
JSLI-4366	S	24-Sep-01	A	74	34° 10.75	75° 53.51	34° 10.77	75° 53.37	437–450	9.8 (9.6–10.2)	35.3 (35.0–35.4)	
SJII-01-053	T	24-Sep-01	A	30	34° 12.61	75° 52.17	34° 12.27	75° 52.50	468–478			
JSLII-3429	S	23-Aug-03	M	136	34° 11.15	75° 54.03	34° 11.42	75° 53.75	412–450	5.8 (5.4–6.0)	35.0 (35.0–35.1)	

Table 1 (continued)

Station	Gear	Date	Time	Total Time (min)	Start Latitude (°N)	Start Longitude (°W)	End Latitude (°N)	End Longitude (°W)	Depth Range (m)	Temp (°C)	Salinity	
JSLI-4694	S	16-Jun-04	M	132	34° 11.28	75° 53.62	34° 11.28	75° 53.79	387–440	10.5 (9.4–11.2)	35.4 (35.2–35.5)	
JSLI-4695	S	16-Jun-04	A	130	34° 11.41	75° 53.65	34° 11.41	75° 53.74	407–442	9.9 (9.7–11.3)	35.3 (35.0–35.8)	
SJ-04-035	T	16-Jun-04	A	30	34° 12.56	75° 46.29	34° 12.94	75° 44.54	657–910			
JSLI-4892	S	18-Oct-05	M	140	34° 13.90	75° 52.44	34° 14.08	75° 52.33	370–411	8.8 (8.6–9.7)	35.1 (35.0–35.3)	
JSLI-4893	S	18-Oct-05	A	121	34° 14.00	75° 52.30	34° 14.19	75° 52.28	366–420	9.1 (8.4–9.6)	35.2 (35.0–35.3)	
JSLI-4894	S	19-Oct-05	M	157	34° 10.66	75° 53.59	34° 11.00	75° 53.36	397–450	7.5 (6.3–8.2)	35.1 (35.0–35.2)	
JSLI-4895	S	19-Oct-05	A	149	34° 12.96	75° 53.09	34° 12.96	75° 53.02	390–413	7.8 (7.6–7.9)	35.0 (35.0–35.1)	
CH-06-012	T	19-Sep-06	M	33	34° 14.23	75° 52.47	34° 13.42	75° 53.02	395–411			
CH-06-013	T	19-Sep-06	M	30	34° 12.94	75° 53.27	34° 11.99	75° 53.85	411–419			
CH-06-015	T	19-Sep-06	M	30	34° 12.37	75° 52.83	34° 11.54	75° 53.14	423–443			
CH-06-016	T	19-Sep-06	A	30	34° 14.00	75° 52.11	34° 13.13	75° 52.13	406–440			
CH-06-017	T	19-Sep-06	A	30	34° 12.33	75° 52.76	34° 10.68	75° 53.15	430–438			
CH-06-018	T	19-Sep-06	A	30	34° 11.37	75° 52.74	34° 10.43	75° 53.15	458–465			
CH-06-019	T	19-Sep-06	A	30	34° 10.36	75° 53.33	34° 09.48	75° 53.69	461–469			
CH-06-021	T ^a	19-Sep-06	N	14	34° 11.65	75° 53.56	34° 10.74	75° 54.09	0–431			
CH-06-026	T	20-Sep-06	M	30	34° 15.28	75° 51.55	34° 14.28	75° 51.90	419–425			
CH-06-027	T	20-Sep-06	M	31	34° 14.40	75° 51.85	34° 13.43	75° 52.19	419–430			
CH-06-028	T	20-Sep-06	M	30	34° 12.78	75° 52.76	34° 11.95	75° 53.04	408–455			
CH-06-029	T	20-Sep-06	A	30	34° 11.88	75° 53.82	34° 11.08	75° 54.25	415–431			
CH-06-031	T	20-Sep-06	A	30	34° 11.44	75° 50.53	34° 10.68	75° 50.98	500–504			
<i>Cape Fear</i>												
JSLII-3308	S	13-Aug-02	M	149	33° 34.33	76° 29.05	33° 34.43	76° 27.90	369–449	9.1 (8.4–9.5)	35.2 (34.8–35.4)	
JSLII-3425	S	21-Aug-03	M	146	33° 34.38	76° 27.93	33° 34.46	76° 27.87	369–394	9.2 (9.4–9.7)	35.2 (35.1–35.3)	
JSLII-3426	S	21-Aug-03	A	147	33° 34.38	76° 27.91	33° 34.33	76° 27.91	368–431	10.2 (9.3–11.2)	35.3 (35.0–35.6)	
JSLII-3427	S	22-Aug-03	M	138	33° 34.28	76° 27.75	33° 34.48	76° 27.70	380–434	8.7 (7.9–9.8)	35.1 (34.8–35.3)	
JSLII-3428	S	22-Aug-03	A	126	33° 34.38	76° 27.95	33° 34.44	76° 27.89	368–397	9.1 (8.7–9.4)	35.2 (35.1–35.2)	
JSLI-4696	S	17-Jun-04	M	114	33° 34.37	76° 27.71	33° 34.36	76° 27.67	389–402	9.1 (9.0–9.5)	35.1 (35.1–35.3)	
JSLI-4697	S	17-Jun-04	A	120	33° 34.57	76° 27.83	33° 34.59	76° 27.77	394–411	11.7 (11.2–12.1)	35.5 (35.4–35.7)	
JSLI-4896	S	20-Oct-05	M	146	33° 34.18	76° 27.89	33° 34.17	76° 27.77	372–399	8.1 (7.9–8.3)	35.1 (35.0–35.1)	
JSLI-4897	S	20-Oct-05	A	125	33° 34.64	76° 27.98	33° 34.65	76° 27.95	404–443	8.0 (7.8–8.2)	35.1 (35.0–35.1)	
<i>Stetson</i>												
JSLII-3419	S	17-Aug-03	M	131	32° 01.75	77° 40.44	32° 02.01	77° 40.49	592–622	10.9 (10.8–11.0)	35.4	
JSLII-3420	S	17-Aug-03	A	126	32° 02.01	77° 40.71	32° 02.04	77° 40.93	624–640	9.9 (9.8–10.0)	35.2	
JSLI-4689	S	13-Jun-04	M	120	31° 49.15	77° 36.77	31° 49.15	77° 36.20	666–672	12.2 (12.1–12.3)	35.5 (35.5–35.6)	

JSLI-4698	S	18-Jun-04	M	109	31° 49.45	77° 36.69	31° 49.56	77° 36.79	660–703	11.0 (10.9–11.8)	35.4 (35.3–35.5)
JSLI-4699	S	18-Jun-04	A	130	31° 50.89	77° 36.72	31° 50.75	77° 36.77	658–721	11.0 (10.9–11.1)	35.4 (35.3–35.5)
JSLI-4898	S	21-Oct-05	M	118	32° 15.94	77° 28.42	32° 16.17	77° 28.47	549–646	8.0 (7.2–8.7)	35.1 (35.0–35.2)
JSLI-4899	S	21-Oct-05	A	123	32° 15.84	77° 28.82	32° 15.83	77° 29.02	540–603	8.6 (8.1–9.2)	35.1 (35.0–35.3)
JSLI-4903	S	27-Oct-05	M	111	32° 01.12	77° 40.00	32° 00.95	77° 40.16	613–633	7.6 (7.3–8.0)	35.2 (35.1–35.2)
JSLI-4904	S	27-Oct-05	A	143	31° 50.81	77° 36.83	31° 50.79	77° 36.74	649–705	9.7 (8.2–11.8)	35.3 (34.9–35.8)
<i>Savannah</i>											
JSLI-4687	S	12-Jun-04	M	101	31° 44.36	79° 06.09	31° 44.52	79° 05.66	497–541	9.1 (9.0–9.1)	35.1
JSLI-4688	S	12-Jun-04	A	93	31° 46.45	79° 11.70	31° 46.56	79° 11.59	505–532	8.2 (8.2–8.3)	35.0
JSLI-4900	S	22-Oct-05	A	134	31° 44.36	79° 06.16	31° 44.57	79° 05.53	500–544	9.2 (9.1–9.3)	35.1 (35.1–35.2)
JSLI-4901	S	23-Oct-05	M	9	31° 42.36	79° 07.42	31° 42.30	79° 07.39	507–508		
JSLI-4902	S	26-Oct-05	A	139	31° 42.26	79° 07.88	31° 42.32	79° 07.31	497–519	8.1 (8.1–8.2)	35.0 (35.0–35.1)
JSLI-4905	S	30-Oct-05	A	143	31° 46.91	79° 12.26	31° 46.43	79° 12.10	505–558	7.7 (7.5–7.8)	35.0
JSLI-4906	S	30-Oct-05	A	86	31° 46.49	79° 11.64	31° 46.62	79° 11.56	507–543	7.4 (7.4–7.6)	35.0
<i>Jacksonville</i>											
JSLI-4683	S	10-Jun-04	M	143	30° 31.05	79° 39.62	30° 30.97	79° 39.72	543–581	10.5 (10.3–10.9)	35.3 (35.1–35.5)
JSLI-4684	S	10-Jun-04	A	126	30° 30.94	79° 39.62	30° 30.84	79° 39.62	548–571	9.6 (9.0–10.5)	35.2 (34.9–35.5)
SI-04-009	T	10-Jun-04	A	30	30° 30.29	79° 36.14	30° 29.86	79° 36.12	802–809		
JSLI-4685	S	11-Jun-04	M	135	30° 48.81	79° 37.81	30° 48.70	79° 37.93	626–652	7.8 (7.8–8.0)	35.0 (34.9–35.0)
JSLI-4686	S	11-Jun-04	A	113	30° 30.13	79° 39.09	30° 30.10	79° 39.18	591–638	9.9 (9.8–10.0)	35.2 (35.2–35.3)
JSLI-4700	S	19-Jun-04	M	90	30° 30.76	79° 39.68	30° 30.85	79° 39.60	558–567	7.6 (7.5–8.3)	35.0 (34.9–35.1)
JSLI-4701	S	19-Jun-04	A	99	30° 28.94	79° 38.50	30° 28.93	79° 38.38	645–674	7.4 (7.3–7.5)	34.9 (34.9–35.0)
JSLI-4907	S	1-Nov-05	M	139	30° 48.15	79° 38.39	30° 48.03	79° 38.50	517–553	7.9 (7.5–8.3)	35.0 (34.9–35.1)
JSLI-4908	S	1-Nov-05	A	137	30° 31.12	79° 39.63	30° 31.26	79° 39.41	568–628	7.3 (7.2–7.6)	35.0 (34.9–35.0)
<i>North Cape Canaveral</i>											
JSLI-4681	S	9-Jun-04	M	122	28° 47.55	79° 37.19	28° 47.60	79° 37.31	709–783	6.7 (6.7–6.9)	34.9
JSLI-4682	S	9-Jun-04	A	122	28° 47.76	79° 37.30	28° 47.75	79° 37.24	760–773	6.8 (6.8–7.0)	34.9 (34.8–35.0)
JSLI-4702	S	20-Jun-04	M	124	28° 47.70	79° 37.40	28° 47.61	79° 37.38	712–738	6.6 (6.5–6.7)	34.9 (34.9–35.0)
JSLI-4703	S	20-Jun-04	A	104	28° 46.62	79° 36.96	28° 46.62	79° 36.96	741–755	6.7 (6.7–6.8)	34.9
<i>South Cape Canaveral</i>											
JSLI-4704	S	21-Jun-04	M	124	28° 02.64	79° 36.82	28° 02.53	79° 36.75	735–745	6.3 (6.3–6.4)	34.9
JSLI-4705	S	21-Jun-04	A	110	28° 02.16	79° 36.84	28° 02.38	79° 36.78	679–725	6.3	34.9
SI-04-043	T	21-Jun-04	A	30	28° 05.24	79° 39.89	28° 05.46	79° 40.25	549–560		

Data are only for the period when the JSL or trawl was on the bottom. For JSL stations, mean temperatures (and ranges), mean salinities (and ranges), and depth ranges were determined from Seabird data loggers (at stations where no ranges are listed, there was no variability in data). M = morning (0600–1200 h EDT), A = afternoon (1200–1900 h EDT), N = night (1900–0600 h EDT).

^aTucker trawl towed throughout the water column (~0–409 m) and on the bottom (~409–431 m).

moving, we standardized operations as much as possible by keeping the JSL as close to the bottom as practical, maintaining slow speed, tilting the external camera somewhat downward (toward the seafloor), and videotaping on wide-angle view. The consistent camera field of view and motion of the JSL across all transects helped standardize the fish counts among transects across different habitats. Each “transect” could have multiple video segments (see below) used for statistical analyses. When the JSL stopped, the camera was variously set from wide-angle to close-up views depending on subject matter and objectives. During the frequent stops, specimens were first videotaped and then collected using a suction device or grab, often supplemented with rotenone. Collections with associated video were critical in confirming species identifications on video. When specimens could not be collected, we recorded as much high-quality video as possible. Specimens were preserved at sea in 10% formalin seawater solution and later transferred to 40% isopropanol, identified and measured. Most species were measured in mm standard length (SL); myxinids, sharks, anguilliforms and macrourids were measured in mm total length (TL); batoids were measured in mm disk width (DW).

Otter trawls were deployed around coral banks to sample benthic fishes (Fig. 1). Prior to trawling, the area was surveyed with single beam sonar to ensure that trawls avoided major coral areas; however, the trawling objective was to tow as close to coral mounds as possible. During 2001–2002, 2004 and 2006 the otter trawl (4.9 m head rope, 38.1 mm mesh) was towed for 29–45 min at ~2 knot (3.7 km/h) ground speed. A Tucker Trawl (4 m² opening, 1.59 mm mesh), deployed for a mid-water sample, was accidentally towed on the bottom (409–431 m) in 2006 for 14 min at ~2 knot ground speed. Since this produced an obvious sample of the bottom (collection included several bottom fishes and substantial amounts of coral, brittle stars, urchins), data from this tow were included with the otter trawl data. Trawl catches were preserved, identified and measured (mm SL, TL, or DW) as described above. Voucher specimens were deposited in the North Carolina Museum of Natural Sciences ichthyology collection.

2.3. Habitat definitions

To determine large-scale habitat use patterns, three general habitat types were designated. More

specifically, a main objective was to determine whether there is a primary (possibly obligate) reef fish fauna on deep coral habitat; therefore, broad generic habitat classification was appropriate. Videotapes and scientist observations were used to develop the three general habitat classifications: prime reef, transition reef, and off reef (Fig. 2).

Prime reef habitat had variable profile (≥ 1 m) and usually occurred on or near tops of mounds (Fig. 2a–c). Prime reef generally had dense coverage of corals (e.g., scleractinians, stylasterines, alcyonaceans, gorgonians, and antipatharians) and/or sponges (e.g., hexactinellids, desmosponges). A high (>50%) percentage of live coral frequently occurred in prime reef habitat. Some prime reef areas, however, consisted of high profile, standing bushes of dead coral (*L. pertusa*), while others consisted of extensive, moderate to high-profile (≥ 1 m) rock ledges with or without attached fauna. Sand channels were often interspersed throughout prime reef habitat. Transition reef included areas of mostly dead coral rubble with occasional scattered live corals and/or sponges. Transition reef usually had moderate to low (<1 m) profile and occurred on the faces of steep slopes, near bottoms of slopes, or on the tops of slopes adjacent to prime reef areas (Fig. 2d–f). At times, small rock outcrops with low-profile (<1 m) were present in transition habitat. Patches of soft sediment often occurred in this habitat. Off reef habitat was on relatively flat bottom (Fig. 2g–i), and soft sediment with occasional coral or rock rubble was the dominant substratum.

2.4. Data analyses

External video camera recordings were the main data used to describe the fish community and associated habitats on and around deep coral banks. Videos from each dive were split chronologically into distinct time segments during which fishes were identified and counted and habitats were classified (see Section 2.3). Video segments were designated when the JSL stopped or started movement, the camera zoom changed, the video quality changed (e.g., “dead time”), or when the habitat changed. Depth was recorded at the beginning and end of each video segment. All video “dead time” was removed from the dataset; this occurred when fish data could not be recorded because video was turned off, was out of focus or clouded by sediment, the camera was too high off the bottom, or digital

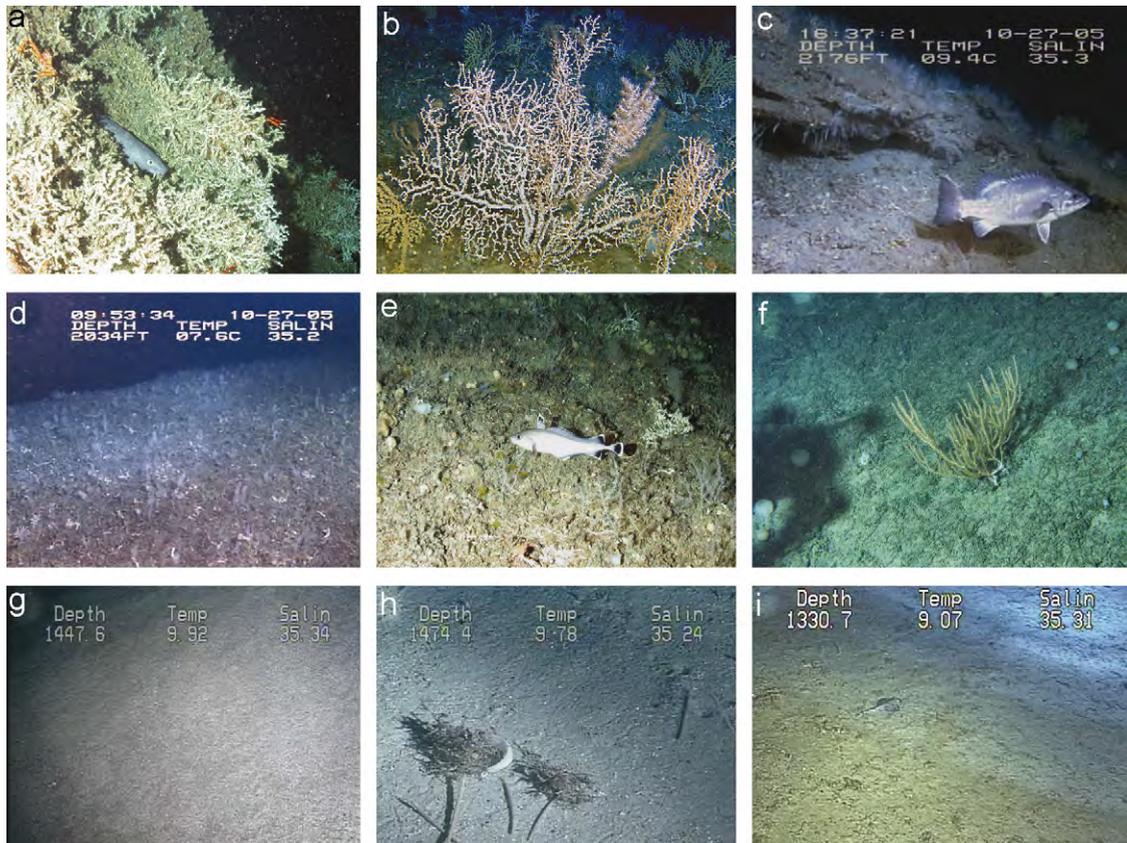


Fig. 2. Examples of habitat types: (a) *Conger oceanicus* in a prime *Lophelia pertusa* reef off North Carolina—JSLII-3432, 385 m; (b) mixed corals in prime reef in Stetson area—JSLI-4699, 669 m; (c) *Polyprion americanus* near a rock ledge in Stetson area—JSLI-4904, 663 m; (d) transition reef in Stetson area—JSLI-4903, 620 m; (e) *Laemonema melanurum* in Stetson transition reef—JSLII-3419, 610 m; (f) bamboo coral and sponges in transition area off Jacksonville, Florida—JSLI-4907, 541 m; (g) off reef, soft substrate habitat off North Carolina—JSLI-4366, 441 m; (h) debris on bottom in North Carolina off reef habitat—JSLI-4366, 449 m; and (i) *Breviraja claramaculata* in North Carolina off reef—JSLII-3304, 406 m.

still images were taken. When data were difficult to extract from the external camera videotapes, the internal bow videotapes aided in species identifications and habitat classifications. Specimens collected (and videotaped) with the JSL enabled us to visually distinguish various species, many of which have rarely or never been seen in situ.

Species composition and relative abundances were compared among prime, transition, and off reef habitat types. To compare abundances of all species within a particular habitat, relative (%) abundances were calculated (number of individuals per species per habitat/total number of individuals observed per habitat \times 100) using wide-angle transect video segment data (wide-angle transect observations represent a subset of all observations). Species occurrences were noted for all other times, when the submersible was stopped or the camera was videotaping in close-up mode.

Habitat specificity of benthic fishes was determined using wide-angle transect video data. This analysis was restricted to fishes positively identified to unique taxa, with overall abundances ≥ 3 individuals. A smaller abundance cutoff would not allow for the possibility of a species occurring in all three-habitat types. For each species, relative (%) abundances were calculated by dividing the number of individuals in a particular habitat by the total number of individuals of the same species from all habitats.

Multivariate analyses were used to determine differences in benthic fish assemblages among reef habitat types. All analyses were conducted in PRIMER 6 and based on guidelines in Clarke and Warwick (2001) and Clarke and Gorley (2006). First, (using only transect data) sample units were established as numbers of each species per habitat category (prime, transition, or off reef) per dive; the few samples with no species present were removed

from the dataset. Second, species' abundances were standardized per sample by dividing the number of individuals per species by the total number of fishes per sample. Standardization was used because transect times were variable. Standardized abundances were then fourth root transformed to down weight the abundant species relative to the rare species. Similarities between samples were then calculated using a Bray–Curtis similarity coefficient. A non-metric multidimensional scaling ordination (MDS) plot and a dendrogram with group average linking were created based on the Bray–Curtis similarity matrix. Finally, a one-way analysis of similarities (ANOSIM) and post-hoc multiple comparison tests were used to determine whether there were significant differences among fish assemblages in different reef types. SIMPER exploratory analysis was used to determine which species contributed to the dissimilarities among reef types.

In addition, inverse hierarchical cluster analysis (PRIMER 6) was used to group species with similar numerical distributions across samples. To minimize rare species confounding the cluster analysis (Field et al., 1982; Clarke and Warwick, 2001), species that were <1% abundant across all habitats were removed from the dataset. Numbers of fishes were then standardized per species (number of individuals per species per sample/the total number of individuals per species), which reduced disparities in species counts yet maintained ratios of occurrences between species (Field et al., 1982; Clarke

and Warwick, 2001). The Bray–Curtis similarity coefficient was used to calculate similarities between species across samples. The resulting similarities were clustered using group average linking to construct a dendrogram. On the dendrogram, each habitat was listed after each species in decreasing order of usage by the species.

Otter trawl catch data supplemented video observations, adding to the overall species composition of deep coral bank areas. Since all trawls were towed near the banks in areas of low relief, the catches represented transition or off reef habitats. Catches that included dead coral rubble, live coral colonies, sponges and/or hard substrata represented tows in transition reef habitat. All other tows were classified as off reef habitat.

3. Results

Sixty-five JSL dives were completed on deep coral habitats from off Cape Lookout, NC to just south of Cape Canaveral, FL (Table 1, Fig. 1). The dives resulted in 136 h of bottom time and 116 h of useable video time (Tables 1 and 2). In all eight locations, prime reef was observed during 60 dives (366–770 m) and transition reef was observed during 64 dives (367–783 m). Off reef habitat was observed during 25 dives (390–783 m) in seven locations (Table 2); it was not observed in the Stetson area. Time spent among methods (transects and stops) and habitats varied (Table 2). The JSL completed

Table 2

Fishes observed using submersibles (2000–2005) across three general habitat types. Number of dives and depth ranges (in parentheses) are under habitat type

Taxa	Prime Reef 60 (366–770 m)		Transition Reef 64 (367–783 m)		Off Reef 25 (390–783 m)	
	T	O	T	O	T	O
	14.8 h	50.7 h	16.1 h	29.8 h	2.6 h	2.7 h
Myxinidae						
Undetermined	0.27	X	0.11	X	0.27	X
<i>Eptatretus</i> sp. (2, 175–202)	0.18	X		X		
<i>Eptatretus minor</i> (1, 227)		X				
<i>Myxine glutinosa</i>				X	7.69	X
Chimaeridae						
<i>Chimaera monstrosa</i>	0.09		0.11		0.27	
Squalidae						
<i>Squalus</i> spp.	0.09		0.11	X		
<i>Cirrhigaleus asper</i> (1, 785)	0.36	X	0.11			
<i>Squalus cubensis</i>	0.27	X	1.35	X	0.27	X
Odontaspidae						
<i>Odontaspis ferox</i>				X		

Table 2 (continued)

Taxa	Prime Reef 60 (366–770 m)		Transition Reef 64 (367–783 m)		Off Reef 25 (390–783 m)	
	T 14.8 h	O 50.7 h	T 16.1 h	O 29.8 h	T 2.6 h	O 2.7 h
Scyliorhinidae						
<i>Scyliorhinus</i> spp.	0.18		0.34			
<i>Scyliorhinus hesperius</i>	0.18					
<i>Scyliorhinus meadi</i>	0.27	X	0.45	X		
<i>Scyliorhinus retifer</i> (1, 440)	0.45	X	2.47	X	0.27	
Carcharhinidae						
<i>Carcharhinus altimus</i>		X		X		
Narcinidae						
<i>Benthobatis marcida</i> (1, 172)					2.39	
Rajidae						
Undetermined			0.22		2.39	X
<i>Breviraja claramaculata</i>					0.53	
<i>Dactylobatus armatus</i>				X		
<i>Dipturus</i> cf. sp.		X			0.27	
<i>Fenestraja plutonia</i> (1, 98)			0.90	X	18.83	X
Mobulidae						
<i>Mobula hypostoma</i>		X				
Synaphobranchidae						
<i>Dysommia rugosa</i> (6, 130–215)	0.90	X				
<i>Synaphobranchus</i> spp.	1.81	X	5.62	X	5.31	X
<i>Synaphobranchus kaupii</i> (2, 233–341)	0.09	X				
Congridae						
Undetermined				X		
<i>Conger oceanicus</i>	7.78	X				
Nettastomatidae						
<i>Nettenchelys exoria</i> (5, 93–447)	0.27	X	0.22	X		
Argentinidae						
<i>Argentina</i> cf. <i>striata</i>	1.27	X	0.22	X	0.27	
Sternoptychidae						
<i>Maurolucus weitzmani</i> (128, 35–45)	7.87	X	11.36	X	2.92	X
<i>Polyipnus clarus</i> (5, 46–56)	0.45	X	0.34	X	12.20	X
<i>Sternoptyx</i> sp.				X		
Stomiidae						
<i>Chauliodus sloani</i>		X				
Ateleopodidae						
Undetermined			0.11			
Chlorophthalmidae						
<i>Chlorophthalmus agassizi</i> (2, 100–125)			1.12	X	6.63	X
Paralepididae						
Undetermined		X	0.11		0.27	
Myctophidae						
Undetermined		X	1.24	X		
<i>Diaphus dumerilii</i> (215, 17–63)				X		
Bythitidae						
<i>Bellottia apoda</i> (1, 44)		X				
<i>Bythites gerdae</i> (1, 71)		X				
<i>Bythites</i> cf. <i>gerdae</i>	0.45	X				
<i>Diplacanthopoma brachysoma</i> (1, 221)		X				
Macrouridae						
Undetermined			0.45		2.12	
<i>Nezumia</i> spp.			0.22	X	0.80	X
<i>Nezumia aequalis</i>			0.22	X	0.27	X
<i>Nezumia</i> cf. <i>bairdii</i>	0.09	X				
<i>Nezumia sclerorhynchus</i> (6, 145–228)	17.01	X	25.08	X	4.24	X

Table 2 (continued)

Taxa	Prime Reef 60 (366–770 m)		Transition Reef 64 (367–783 m)		Off Reef 25 (390–783 m)	
	T 14.8 h	O 50.7h	T 16.1 h	O 29.8 h	T 2.6 h	O 2.7 h
Moridae						
<i>Laemonema</i> spp.	1.00	X	1.46	X	0.80	
<i>Laemonema barbatulum</i> (10, 63–158)	3.53	X	15.97	X	17.51	X
<i>Laemonema melanurum</i> (1, 220)	20.81	X	14.40	X	0.80	
<i>Physiculus</i> cf. <i>fulvus</i>	0.09	X		X		
<i>Physiculus karrerae</i> (1, 250)	0.09	X				
Phycidae						
<i>Phycis chesteri</i>			0.22	X	2.39	
<i>Urophycis</i> cf. <i>chuss</i>	0.18					
Merlucciidae						
<i>Merluccius albidus</i>			0.34	X	3.45	X
Lophiidae						
<i>Lophiodes beroe</i> (6, 280–400)	0.36	X	1.12	X		
<i>Lophiodes monodi</i> (1, 325)		X				
<i>Lophius gastrophysus</i> (1, 210)	0.09		0.11			
Chaunacidae						
<i>Chaunax stigmaeus</i> (6, 95–255)			0.67			
Ogcocephalidae						
<i>Dibranchius atlanticus</i>			0.22			X
Trachichthyidae						
<i>Hoplostethus occidentalis</i> (11, 91–164)	5.61	X	1.01	X		
Berycidae						
<i>Beryx decadactylus</i>	13.94	X				
Zeidae						
<i>Zenopsis conchifera</i>		X				
Scorpaenidae						
Undetermined	0.45	X	0.56	X	0.80	X
<i>Helicolenus dactylopterus</i> (8, 66–252)	10.32	X	7.87	X	5.57	X
<i>Idiastion kyphos</i> (7, 65–109)	0.36	X	0.22	X		
<i>Phenacoscorpius nebris</i> (1, 55)		X				
<i>Pontinus rathbuni</i> (2, 119–185)		X		X		
<i>Setarches guentheri</i> (2, 106–132)	0.09		0.22		0.27	X
<i>Trachyscorpia cristulata</i> (3, 60–230)	1.27	X	2.02	X		X
Acropomatidae						
<i>Synagrops</i> sp. A				X		
<i>Synagrops</i> sp. B			0.34	X	0.27	
Polyprionidae						
<i>Polyprion americanus</i>	0.36	X	0.67	X		
Serranidae						
Anthiinae	0.18	X				
<i>Anthias woodsi</i>	0.81	X				
<i>Hemanthias aureorubens</i>		X				
Epigonidae						
Undetermined		X				
Echeneidae						
Undetermined		X				
Trichiuridae						
Undetermined		X		X		
Xiphiidae						
<i>Xiphias gladius</i>		X				

Hours of observation spent in each habitat are listed by method. Species % relative abundances were calculated for each habitat during transects (T). Occurrences (denoted by X) during other (O) times are noted. Number of individuals collected via submersible, followed by length (mm) range, are indicated (in parentheses) after each species.

14.8 and 16.1 h of transects in prime and transition habitats, respectively, and 2.6 h of transects in off reef habitat.

Salinities at deep-coral banks were stable across study areas, while temperatures fluctuated among dives within and across all study areas (Table 1). Over all dives and study areas, mean bottom salinities ranged from 34.9 to 35.5 (± 0.0 SE). Mean bottom temperatures ranged from 5.8 °C (± 0.0 SE) at a location within Cape Lookout B to 12.2 °C (± 0.0 SE) at a location within the Stetson area. During a few dives, observers noted benthic temperature fluctuations over short distances, where temperatures increased or decreased briefly, and during these events, the observers saw mixing of density layers in the water column.

To supplement the JSL data, 33 otter trawl (includes the bottom Tucker trawl) tows were completed around deep coral banks in 356–910 m depth (Table 1). In the Cape Lookout A area (356–488 m), eleven tows were completed in transition reef, and five tows were in off reef. Ten tows were completed in off reef habitat, and four tows were in transition reef habitat in the Cape Lookout B area (395–504 m). One tow was in deep (657–910 m) off reef habitat east of the Cape Lookout B area. Farther south, only one tow was made off Jacksonville in transition habitat (802–809 m), and one tow was completed off South Cape Canaveral in off reef habitat (549–560 m).

3.1. Submersible data

We identified at least 66 unique fish taxa in 38 families from the submersible data over all locations and years (Table 2). While most of the species richness was within prime reef or transition habitats (50 and 42 species, respectively), the soft substrata off reef habitats also supported a well developed, but different fish fauna (25 species) (Table 2). The ichthyofauna of all three general habitat types was dominated by relatively few species, with little overlap in species between prime reef and off reef habitats. In particular, prime reef was characterized by *Laemonema melanurum* (21% of prime reef total), *Nezumia sclerorhynchus* (17% of total), *Beryx decadactylus* (14% of total), and *Helicolenus dactylopterus* (10% of total). The off reef areas were dominated by *Fenestraja plutonia* (19% of off reef total), *Laemonema barbatulum* (18% of total), *Myxine glutinosa* (8% of total) and *Chlorophthalmus agassizi* (7% of total). Transition habitat

exhibited a mixture of species that could also be found on either prime reef or off reef. *N. sclerorhynchus* was the most abundant (25% of transition reef total) transition habitat species, followed by *L. barbatulum* (16% of total) and *L. melanurum* (14% of total).

We used multivariate analyses on the video data to examine fish assemblage differences among habitat types. MDS and hierarchical clustering analyses were performed on 42 benthic fish species observed across 142 samples in prime, transition, and off reef habitat types. The ANOSIM test revealed weak, but significant (Global $R = 0.2$, $p = 0.1\%$), fish assemblage differences among the three reef types; however, the post-hoc comparison tests indicated moderate difference between prime and off reef habitats ($R = 0.5$) and no differences between off and transition habitats ($R = 0.2$) and transition and prime habitats ($R = 0.1$) ($R = 0$ when groups are the same and $R = 1$ when groups are different; Clarke and Warwick, 2001). The low Global R value was a result of the similarity between transition and prime reef and transition and off reef habitat types. Since transition reef habitat is an ecotone between prime and off reef habitats, the lack of significant fish assemblage differences between transition reef and the other two habitat types was not surprising.

To examine off and prime reef fish assemblage differences in greater detail, we reanalyzed the dataset (PRIMER 6, Section 2.4) using only fish counts from these two reef types (39 species, 78 samples). The resulting MDS plot (Fig. 3) displayed

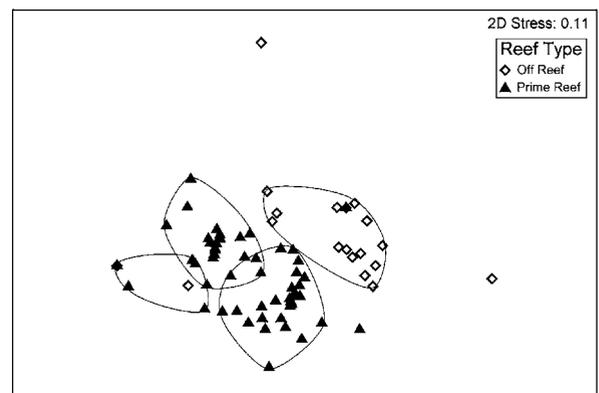


Fig. 3. Multidimensional scaling (MDS) ordination of 78 off and prime reef samples based on the Bray-Curtis similarity matrix calculated from standardized, fourth root transformed fish abundances (39 species). Clusters are defined at a 30% (black outlines) similarity level.

a good representation (Stress = 0.11) of the samples in two-dimensional space (Clarke and Warwick, 2001). The MDS indicated three off reef groupings (two groupings consisted of one sample each) and four prime reef groupings (one consisted of only one sample) at a 30% level of similarity. The ANOSIM test revealed moderate, but significant, differences (Global $R = 0.5$, $p = 0.1\%$) between the two habitats, while SIMPER exploratory analysis indicated that prime and off reef assemblages were 88% dissimilar. Species driving the differences included the following abundant species: *L. barbatulum* (off reef), *L. melanurum* (prime), *N. sclerorhynchus* (prime), *H. dactylopterus* (prime) and *F.*

plutonina (off). SIMPER analysis also indicated low average similarity of samples within each habitat (off reef samples: 32% similar, prime reef samples: 33% similar). The relatively moderate statistical difference between off and prime reef habitats, combined with the low average similarity of samples within a particular habitat, resulted from a location (eight study sites along the SEUS) effect on the dataset. Location differences will be discussed in a future paper where data will be further analyzed by study site (Ross and Quattrini, manuscript in preparation).

We further examined the habitat specificity of the abundant benthic species observed during transects

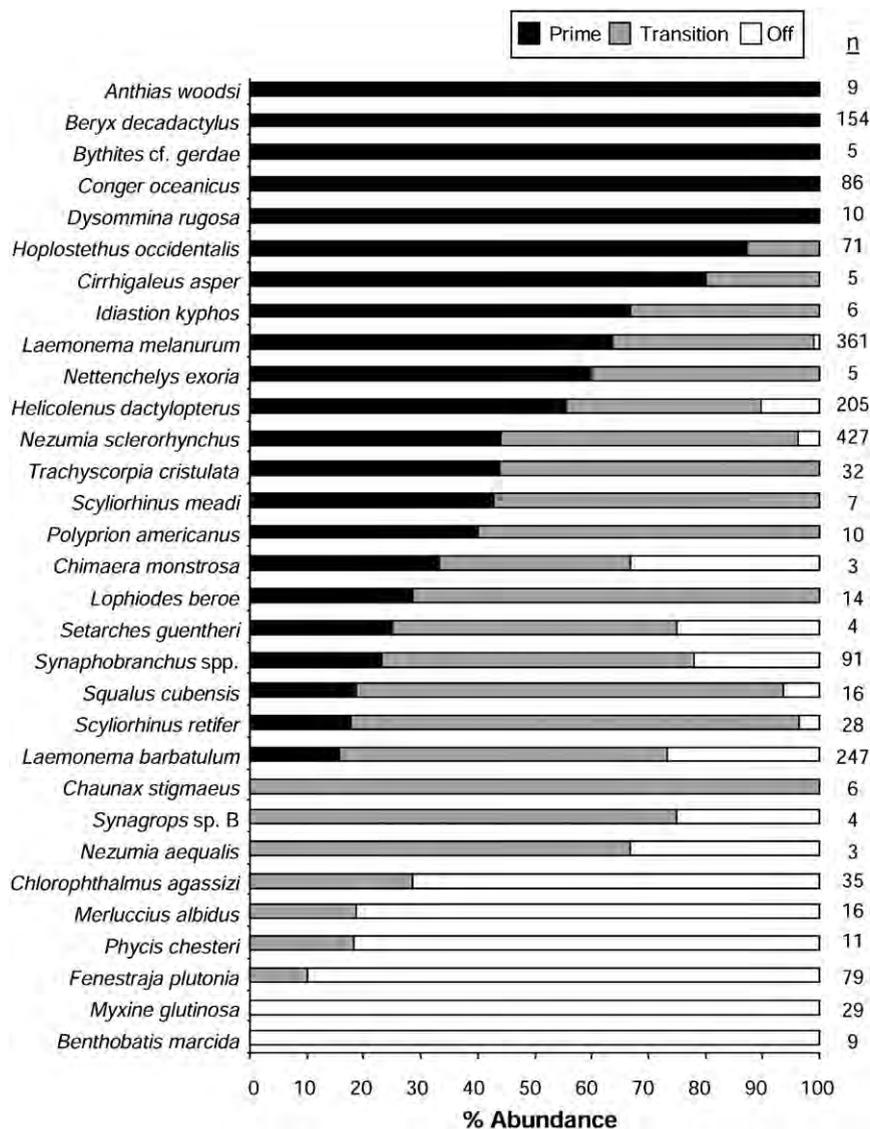


Fig. 4. Within species relative (%) abundances across three habitat types. n = number of individuals observed during wide-angle transects.

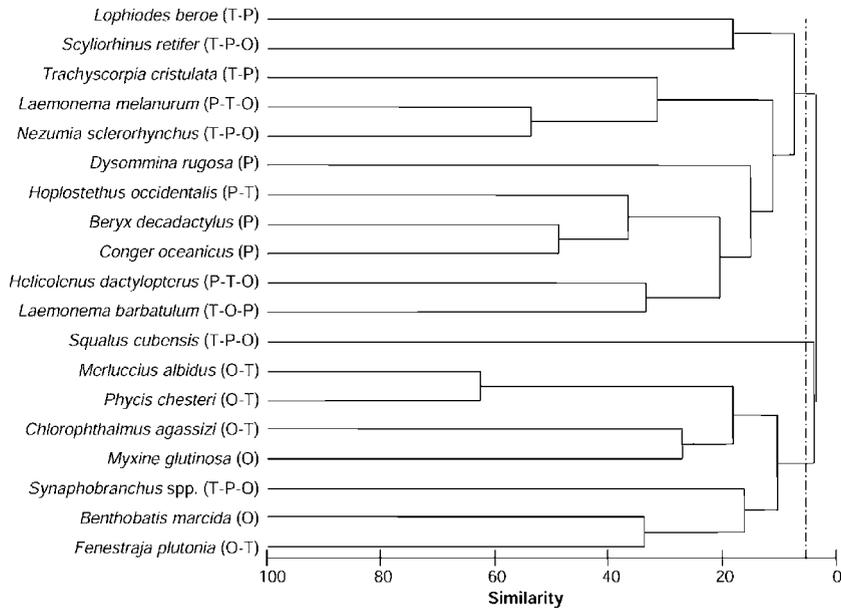


Fig. 5. Dendrogram of fish species using group average linking from a Bray-Curtis species similarity matrix calculated from standardized abundances. The 19 most abundant benthic species were included in this analysis. Three major groups are 95% dissimilar, denoted by the dotted vertical line through the dendrogram. Letters (in parentheses) denote order of abundance in habitats, P = prime reef, T = transition reef, O = off reef.

by comparing the relative abundances within a species across habitat types (Fig. 4). Five species were observed only in prime reef: *Anthias woodsi*, *B. decadactylus*, *Bythites cf. gerdae*, *Conger oceanicus* and *Dysommima rugosa*. Species that were most abundant in prime reef habitat and were rarely observed in off or transition reef areas included *Hoplostethus occidentalis*, *Cirrhigaleus asper*, *L. melanurum*, *Nettenchelys exoria*, and *H. dactylopterus*. Some species were more abundant in off reef habitat, and never occurred on prime reef, including *Benthobatis marcida*, *C. agassizi*, *Merluccius albidus*, *M. glutinosa*, *F. plutonia* and *Phycis chesteri*. Certain species were more abundant in transition reef compared with other habitats, including *Chauliognathus stigmaeus* (observed only in this habitat), *Lophiodes beroe*, *Scyliorhinus retifer* and *L. barbatulum*. The large, commercially important wreckfish (*Polyprion americanus*) was also commonly observed in transition habitat. These data clearly illustrated (Fig. 4) species-specific general habitat use differences.

Inverse cluster analysis also indicated habitat-related groupings of fish species. The 19 most abundant species from 142 video samples clustered into three major groups that were 95% dissimilar from one another (Fig. 5). Fishes that were most

abundant in prime and transition reefs clustered together, and fishes most abundant in off reef areas grouped together, except *Synaphobranchus* spp. that were most abundant in transition habitats clustered with the off reef group. The third major cluster consisted of only one species, *Squalus cubensis*, which was more abundant in transition reef than other habitats and was seen most frequently in the Savannah study area. Within the prime/transition reef species group, there were two subgroups at high (50%) similarity levels; one subgroup consisted of *B. decadactylus* with *C. oceanicus*, and another subgroup consisted of *L. melanurum* with *N. sclerorhynchus*. *B. decadactylus* and *C. oceanicus* were abundant in prime reef habitats, especially off North Carolina, while *L. melanurum* and *N. sclerorhynchus* were abundant in both prime and transition habitats in several deep coral bank areas. Within the off reef species group, *M. albidus* and *P. chesteri* grouped together at a high (~60%) similarity level, and these two species were common only off North Carolina.

While our analyses concentrated on benthic fishes, several species of pelagic and midwater fishes also visited these deep reefs. Three solitary *Xiphias gladius* were observed briefly in prime reef coral habitat during dives at the Cape Lookout coral

banks. One individual swam rapidly up a steep reef face, whereupon it struck the submersible and swam away. Three very large *Mobula hypostoma* also occupied the Cape Lookout coral banks during a few dives. Individuals occurred singly and were observed circling above the crests of *Lophelia* mounds. An unidentifiable echeneid was attached on the dorsal head region of one *M. hypostoma*. Additionally, several species of mesopelagic fishes, including *Diaphus dumerilii*, *Maurolicus weitzmani* and *Polyipnus clarus*, were observed in aggregations near the bottom in all three habitats (Table 2).

3.2. Otter trawl data

We collected 69 fish species (including mesopelagics) in transition and off reef habitats using the otter trawl (Table 3). Of these, 49 species were caught in tows from transition reef habitat, and 49 species were collected in off reef habitat tows. Trawling added 34 benthic species to the overall composition of fishes on and around SEUS deep coral banks and included several families that were not observed with the JSL (e.g., Draconettidae, Etmopteridae, Grammicolepidae, Ipnopidae, Paralichthyidae and Peristediidae). Several species collected by trawl may have been observed with the JSL, but they could not be accurately identified on video. These included *Dipturus teevani*, *Epigonus pandionis*, *Synagrops bellus*, *S. spinosus* and *S. trispinosus*.

Of the total number of fishes collected by trawl in each habitat, *H. dactylopterus* was the most abundant in both transition (44%) and off reef (22%) habitats (Table 3). Also, *L. barbatulum* (18%) and *P. chesteri* (17%) were abundant in transition and off reef habitats, respectively. Some fishes that were common in trawl collections, such as *Dibranchius atlanticus*, *Setarches guentheri* and *Urophycis regia*, were rarely observed with the JSL probably because of reduced observation time in off reef habitats.

Juveniles of several species whose adults were commonly observed with the JSL in transition or prime reef habitats were collected with the otter trawl in off reef habitat (Table 3). These included *Nezumia* spp. (*aequalis* or *sclerorhynchus*, species identification not resolvable because of damage or missing scales), *L. barbatulum*, *Trachyscorpia cristulata* and *H. occidentalis*. Juvenile *H. occidentalis* may have been collected in the water column because in the otter trawl tow containing this

Table 3

Numbers of fishes followed by length (mm) ranges (in parentheses) collected with the otter trawl in two habitats

Taxa	Transition Reef <i>n</i> = 16 (370–809 m)	Off Reef <i>n</i> = 17 (356–910 m)
Myxinidae		
<i>Eptatretus</i> sp.		1 (202)
<i>Myxine glutinosa</i>	5 (250–320)	54 (186–345)
Etmopteridae		
<i>Etmopterus bullisi</i>	2 (135–190)	
Scyliorhinidae		
<i>Scyliorhinus retifer</i>	5 (123–330)	1 (183)
Torpedinidae		
<i>Torpedo nobiliana</i>	1 (231)	
Rajidae		
<i>Breviraja claramaculata</i>	3 (124–171)	3 (45–128)
<i>Dipturus teevani</i>	2 (234–255)	1 (261)
<i>Fenestraja plutonia</i>	26 (72–118)	69 (28–129)
Synphobranchidae		
<i>Dysommia rugosa</i>	21 (79–210)	2 (180–183)
<i>Synphobranchus kaupii</i>	1 (316)	
Ophichthidae		
<i>Ophichthus</i> sp.		1 (292)
Congridae		
<i>Bathycongrus vicinalis</i>	1 (115)	
Nettastomatidae		
<i>Nettanchelys exoria</i>	1 (345)	
Serrivomeridae		
<i>Serrivomer</i> sp. (damaged)	1 (148)	
Argentinidae		
<i>Argentina striata</i>	1 (131)	
Gonostomatidae		
<i>Cyclothone</i> spp. (damaged)		9
<i>Cyclothone microdon</i>		1 (44)
<i>Cyclothone pallida</i>		3 (37–53)
Sternoptychidae		
<i>Maurolicus weitzmani</i>	1 (37)	
<i>Polyipnus clarus</i>		1 (23)
<i>Sternoptyx diaphana</i>		1 (32)
Stomiidae		
<i>Chauliodus sloani</i>		3 (87–160)
Ateleopodidae		
<i>Ateleopus</i> spp.	2 (451–520)	2 (340–365)
<i>Ijimaia antillarum</i>	1 (208)	
Chlorophthalmidae		
<i>Chlorophthalmus agassizi</i>	41 (51–121)	58 (49–129)
<i>Parasudis truculenta</i>	1 (180)	
Ipnopidae		
<i>Bathypterois bigelowi</i>		2 (127–146)
Neoscopelidae		
<i>Neoscopelus macrolepidotus</i>		4
Myctophidae		
<i>Benthosema glaciale</i>		1 (52)
<i>Diaphus dumerilii</i>	10 (56–60)	
Polymixiidae		
<i>Polymixia lowei</i>		1 (153)
Ophidiidae		
<i>Benthocometes robustus</i>	1 (112)	
Bythitidae		
<i>Bythites gerdae</i>	1 (52)	

Table 3 (continued)

Taxa	Transition Reef <i>n</i> = 16 (370–809 m)	Off Reef <i>n</i> = 17 (356–910 m)
Macrouridae		
Undetermined (damaged)	1	
<i>Caelorinchus caelorhincus</i>	1 (209)	6 (177–260)
<i>Hymenocephalus italicus</i>		19 (105–170)
<i>Malacocephalus occidentalis</i>	1 (362)	1
<i>Nezumia</i> sp. (damaged)		1
<i>Nezumia</i> sp. (<i>aequalis</i> / <i>sclerorhynchus</i>)	3	22 (60–82)
<i>Nezumia bairdii</i>	2 (260–299)	
<i>Nezumia sclerorhynchus</i>	3 (94–160)	1 (107)
<i>Ventrifossa macropogon</i>	1 (290)	
Moridae		
<i>Gadella imberbis</i>	3 (114–147)	3 (102–134)
<i>Laemonema barbatulum</i>	161 (62–188)	128 (54–192)
<i>Physiculus karrerae</i>	4 (130–190)	
Phycidae		
<i>Phycis chesteri</i>	12 (195–284)	147 (162–254)
<i>Urophycis regia</i>	61 (93–310)	13 (142–217)
<i>Urophycis tenuis</i>	1 (373)	
Lotitidae		
<i>Enchelyopus cimbrius</i>		1 (105)
Merlucciidae		
<i>Merluccius albidus</i>	11 (132–388)	10 (112–241)
Lophiidae		
<i>Lophiodes beroe</i>	1 (235)	
<i>Lophius gastrophysus</i>		4 (135–237)
Chaunacidae		
<i>Chaunax suttkusi</i>	1 (28)	1 (121)
Ogocephalidae		
<i>Dibranchius atlanticus</i>	34 (29–117)	53 (26–138)
Trachichthyidae		
<i>Hoplostethus mediterraneus</i>		4 (22–50)
<i>Hoplostethus occidentalis</i>	3 (77–131)	2 (19–63)
Grammicolepidae		
<i>Xenolepidichthys dalgleishi</i>	1 (73)	
Scorpaenidae		
<i>Helicolenus dactylopterus</i>	385 (30–335)	190 (50–220)
<i>Idiastion kyphos</i>	1 (94)	
<i>Setarches guentheri</i>	24 (34–144)	12 (51–129)
<i>Trachyscorpia cristulata</i>	11 (65–160)	14 (47–156)
Peristediidae		
<i>Peristedion ecuadorensis</i>	1 (140)	4 (42–153)
<i>Peristedion greyae</i>	5 (64–120)	2 (102–109)
<i>Peristedion truncatum</i>	1 (48)	1 (68)
Acropomatidae		
<i>Synagrops bellus</i>	8 (15–146)	1 (148)
<i>Synagrops spinosus</i>	1 (106)	3 (63–133)
<i>Synagrops trispinosus</i>		1 (73)
Epigonidae		
<i>Epigonus pandionis</i>	8 (105–145)	2 (109–121)
Percophidae		
<i>Bembrops gobioides</i>		1 (152)
Draconettidae		
<i>Centrodraco acanthopoma</i>	6 (80–97)	2 (83–90)
Bothidae		
<i>Monolene sessilicauda</i>		1 (40)

Table 3 (continued)

Taxa	Transition Reef <i>n</i> = 16 (370–809 m)	Off Reef <i>n</i> = 17 (356–910 m)
Paralichthyidae		
<i>Hippoglossina oblonga</i>		1 (180)
Cynoglossidae		
<i>Symphurus nebulosus</i>		1 (63)
Total Number	884	870

n = number of tows, followed by sample depth ranges (in parentheses). Damaged specimens could not be positively identified to species and/or accurately measured.

species, several mesopelagic species (e.g., *Cyclothone* spp., *Sternoptyx diaphana*) were also collected. Juvenile *Hoplostethus mediterraneus* were collected by otter trawl in off reef habitat; this species was not collected in any other habitat. Also, juveniles of common off reef species were collected in non-reef habitat, including newly hatched *Breviraja claramaculata* (*n* = 1, 45 mm DW) and *F. plutonia* (*n* = 11, 28–44 mm DW).

3.3. Behavioral observations

A unique advantage of using submersibles is the ability to observe and record behaviors of fishes in situ. Despite possible observational artifacts introduced by the submersible (from noise and lighting), many fishes exhibit few reactions to the submersible, and the direct observations seem worthwhile because many of these fishes have not been observed in the wild, and literature generally lacks data on behavioral attributes of deep-sea fishes. Costello et al. (2005) reported in situ behaviors of fishes associated with coral banks, noting that 75% of species did not react to the underwater cameras. Other studies reported wide ranges of reactions to submersibles or ROVs, but maintained that direct observations were valuable (Chave and Mundy, 1994; Uiblein et al., 2002, 2003; Lorange and Trenkel, 2006). Behavioral observations for the dominant species (Fig. 4) are summarized below, except such data appear in Sections 3.4 and 3.5 for fishes yielding new distributional information, and lophiiform observations were discussed by Caruso et al. (2007).

M. glutinosa was frequently observed with JSL and collected with the otter trawl in off reef habitat. This species was never observed buried in soft sediments in this study, but it was always observed

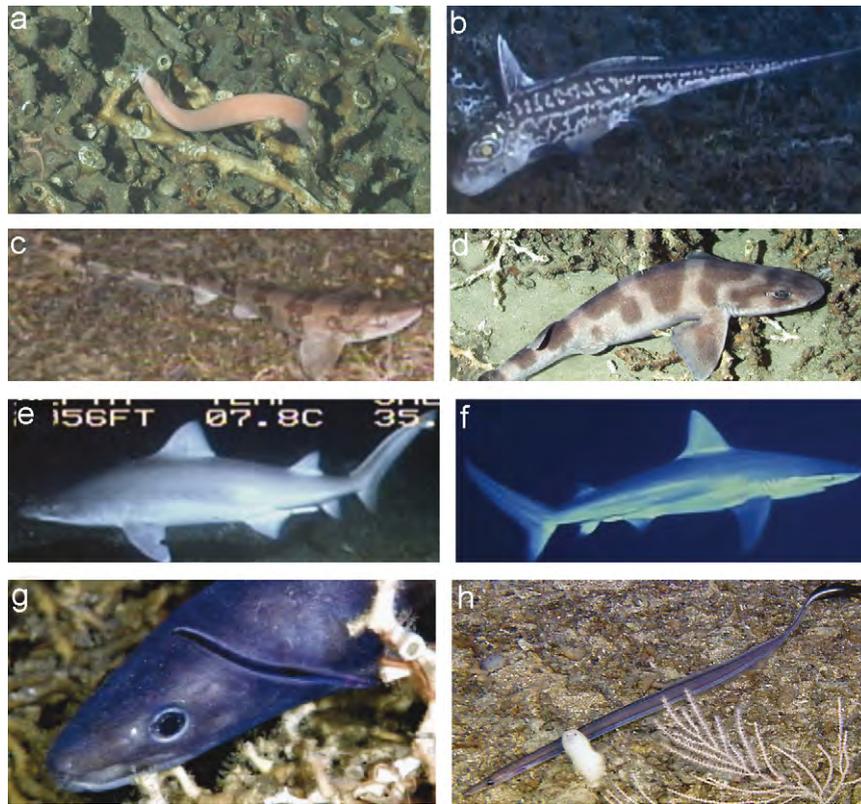


Fig. 6. In situ photographs of noteworthy species: (a) *Eptatretus* sp.—JSLI-3429, 415 m; (b) *Chimaera monstrosa*—JSLI-4905, 506 m; (c) *Scyliorhinus hesperius*—JSLI-4686, 604 m; (d) *Scyliorhinus meadi*—JSLI-3431, 409 m; (e) *Odontaspis ferox*—JSLI-4903, 627 m; (f) *Carcharhinus altimus*—JSLI-4365, 393 m; (g) *Conger oceanicus* (large eel) and *Dysommima rugosa* (small eel)—JSLI-4694, 387 m; and (h) *Nettenchelys exoria*—JSLI-4699, 717 m.

swimming rapidly over the bottom. At a soft substratum study site off Cape Hatteras it was one of the most abundant fishes, often observed buried with only the snout exposed (SWR, pers. obs.).

Most sharks were observed in reef areas and exhibited various behaviors. Squalids were highly mobile throughout reef habitats, occurring ~1–5 m off the bottom. Several individuals, especially *S. cubensis*, were usually in constant motion and at times appeared to be attracted to the submersible. Small *S. cubensis* were also observed resting on the bottom. *Cirrhigaleus asper* was usually mobile, but some individuals were observed in close contact with the bottom. *S. retifer* exhibited many behaviors, including sitting motionless on the bottom (mostly on coral rubble or dead coral matrix), moving rapidly around coral mounds or the nearby open substrate, and occasionally rubbing their bodies on dead *Lophelia* branches.

The batoid fishes, *F. plutonia* and *B. marcida*, were consistently observed lying motionless on the

bottom on soft substrata, off reef habitats. At times individuals buried into the sediments. Occasionally, *F. plutonia* was observed lying on dead coral rubble in transition habitat.

Species of Anguilliformes, a dominant group of fishes, exhibited various behaviors on deep coral banks. *Synaphobranchus* spp., nearly ubiquitous throughout habitats off Florida, were observed in constant motion swimming ~0.5–5 m above the substrate. *Synaphobranchus* spp. occurred singly or in small groups (<10 individuals). We collected two *Synaphobranchus kaupii*; but because species within the genus *Synaphobranchus* cannot be visually identified, we could not confirm whether all individuals observed were this species. *S. kaupii* exhibited a variety of locomotion behaviors (forward movement, station holding, and drifting) that varied with habitat (including depth, substrate type, and current speed) in the Bay of Biscay (Uiblein et al., 2002, 2003). *C. oceanicus* adults (~700–1000 mm TL), never observed off-reef, were intimately



Fig. 7. In situ photographs of noteworthy species: (a) undetermined ateleopodid—JSLI-4894, 443 m; (b) *Nezumia sclerorhynchus*—JSLI-3419, 613 m; (c) *Helicolenus dactylopterus*—JSLII-3431, 413 m; (d) *Idiastion kyphos*—JSLI-4693, 416 m; (e) *Setarches guentheri*—JSLI-4906, 542 m; (f) *Trachyscorpia cristulata*—JSLI-4687, 499 m; (g) *Hoplostethus occidentalis* within coral matrix—JSLII-3305, 383 m (h) *Beryx decadactylus*—JSLII-3431, 384 m; and (i) *Anthias woodsi*—JSLI-4362, 368 m.

associated with the coral habitat. On a few occasions individuals were observed swimming around the corals, but most observations were of single individuals with either the heads or tails protruding from the coral matrix (Figs. 2a and 6g). This eel was rarely observed in rocky habitat and was most abundant where corals (especially *Lophelia*) were the dominant substratum. *D. rugosa* was observed several times in the vicinity of *C. oceanicus* (Fig. 6g). Several individuals, all relatively small (collected individuals, 130–215 mm TL), were observed swimming around the heads of *C. oceanicus*. *D. rugosa* occurred only in prime reef habitat, and was frequently observed with head in, tail out of high-profile *Lophelia* bushes. Occasionally, this eel was not seen until flushed out from coral rubble or bushes using rotenone, indicating that they spend some time deeper within the coral matrix.

The mostly off reef species, *C. agassizi*, *M. albidus* and *P. chesteri*, generally occurred as solitary individuals closely associated with the bottom.

These three species were observed resting on, hovering over, or slowly swimming above soft substrata or coral rubble. On occasion, pairs of *M. albidus* and pairs of *P. chesteri* were observed.

An abundant fish of deep coral banks, *N. sclerorhynchus*, was regularly observed south of Cape Fear, NC. Most individuals hovered <0.5 m from the substrate with their heads angled downward toward the seafloor. Several individuals were also observed swimming over the open substrate, and no individuals were observed within the coral bushes. *N. sclerorhynchus* was easily identified in videos because of its small size, slender body, and tall, white first dorsal fin (Fig. 7b).

L. melanurum was frequently and consistently observed around coral areas. Although its distribution was highly skewed toward reef habitat, it was observed over less dense reef cover as our surveys expanded toward the southern Blake Plateau. A wide range of sizes (~150–350 mm TL) was observed, and individuals were easily recognized

by the distinct black markings on the caudal and posterior anal and dorsal fins (Fig. 2e). They were usually moving slowly just above the bottom. On several occasions, *L. melanurum* were observed in pairs, and generally, one individual was much smaller than the other. Its congener, *L. barbatulum*, overlapped *L. melanurum* in habitat usage but also ranged further away from reefs, occurring over soft substrata.

B. decadactylus occurred occasionally as single individuals, but was more often observed in aggregations ranging from <10 to >50 individuals. All were large adults that were usually swimming over (1–3 m above) and around the reef (Fig. 7h); however, a few individuals were seen under ledges created by *Lophelia* bushes. *B. decadactylus* were most common around the highest profile reefs (usually at the tops of mounds) with dense coral coverage. *B. decadactylus* appears to be closely associated with rugged, steep terrain; other studies have also documented this same pattern of habitat usage (Chave and Mundy, 1994; Popenoe and Manheim, 2001).

Literature and our data indicate that *H. dactylopterus* uses a wide range of habitats. It was the most common scorpaenid on the reefs, and adults and juveniles were observed perched under coral bushes, perched on top of coral (live or dead), or sitting on the substrate near corals (Fig. 7c). This species is also common on coral habitat at Rockall Banks off Ireland where it displays the same behavior as noted above (SWR, pers. obs.). When observed away from reef habitat, it was nearly always closely associated with whatever structure was available (burrows, anemones). This species is widely known from trawl samples over supposedly soft substrata (Haedrich and Merrett, 1988; Gordon et al., 1996), but trawls obscure habitat data. Regardless of habitat details, *H. dactylopterus* is strongly associated with the bottom (Uiblein et al., 2003).

S. guentheri, a common scorpaenid on open, soft substrata (S.W. Ross, unpubl. data), was rarely observed during this study. When observed, individuals were on soft substrata or on coral rubble, sometimes sitting next to structures (e.g., *Lophelia* colony). Live coloration of *S. guentheri* is pale red, with darker red, diagonal bands and markings along its body and a dark red to black spinous dorsal fin, tipped in pale red/white (Fig. 7e). This coloration seems more pronounced in smaller individuals. Upon reaching the surface, the coloration of *S.*

guentheri dramatically changes as the diagonal bands disappear and the body becomes brick red or orange, with dark reddish to black spots along its body and a dark reddish to black stripe along its ventral midline. This fresh dead coloration is commonly described in the literature (e.g., Poss and Eschmeyer, 2002).

T. cristulata was common, especially on deep coral banks south of North Carolina (Fig. 7f). All individuals sat motionless on the bottom, also the dominant behavior of the subspecies *T. c. echinata* in the eastern Atlantic (Lorance and Trenkel, 2006). A few were observed resting on top of *Lophelia* branches, but most were on coral rubble, either on open substrata or next to black corals, bamboo corals, sponges, or *Lophelia* bushes. The coloration of *T. cristulata* was generally red, with light, small spots scattered on the body and reddish-brown bars from the head to caudal peduncle. Additionally, pale to white blotches were apparent on the head, and beneath the dorsal fin.

P. americanus was the largest fish consistently observed (Fig. 2c) in this study. Usually we observed these fish in loose aggregations of 3–>20 individuals. They hovered just above the bottom, sometimes touching it, or swam slowly 1–2 m above the bottom. Individuals often exhibited no response to the submersible, or at times seemed distracted by it and moved away. While only observed in reef habitats, it tended to be most common around the bases and slopes of reef mounds. *Polyprion americanus* was observed on tops of mounds only when the coral was low profile and mostly dead, or where rock ledges occurred (Stetson area). They were never observed in dense, high profile, live coral habitat. Several studies have documented *P. americanus* to be abundant in coral mound and high relief rock habitats on the Charleston Bump (see Sedberry, 2001).

3.4. New fish distributional data for the SEUS slope

Nineteen fish species that we observed or collected yielded new depth and/or geographic range data. Caruso et al. (2007) also documented four Lophiiform fishes collected during this study that were new to the region.

The genus *Eptatretus* may be more often associated with coral (and/or structure) than previously thought (Fernholm and Quattrini, in press). *Eptatretus minor* was collected with the JSL in prime reef habitat in the Stetson area in 561 m (NCSM 44650,

227 mm TL, JSLI-4899). We examined an additional specimen of *E. minor* (GMBL 97-39) that was trapped on hard bottom habitat in 201 m off South Carolina (D.M. Wyanski, pers. commun.), an unusually shallow depth for this genus in the western North Atlantic. These records substantially extend the geographic and depth ranges of *E. minor*. Previously, this species was known from the northeastern Gulf of Mexico to the Dry Tortugas, FL in 300–472 m (Fernholm and Hubbs, 1981; McEachran and Fechhelm, 1998). Fernholm and Hubbs (1981) reported that coral and mud were collected in two trawls that caught *E. minor*. They assumed that *E. minor* probably bury into sediment and thus, were caught in mud habitat. Two individuals of an undescribed species of *Eptatretus* (Fig. 6a) (Fernholm and Quattrini, in press) were collected by JSL (UF 165853, JSLI-4364) in transition, rubble habitat in the Cape Lookout A site, and one individual was trawled (UF 165852, CH-06-017) in off reef habitat adjacent to the Cape Lookout B site. In addition, 19 individuals of this new species were observed with the JSL in prime and transition reef habitats, swimming over the bottom and/or moving through (or protruding from) the coral matrix (Fig. 6a). The unique bright pink color of this hagfish allowed us to easily distinguish it from other hagfish species.

We observed three, solitary adult *Chimaera monstrosa* (all ~600 mm TL) in prime, transition, and off reef habitats from the Savannah (506–528 m, JSLI-4905, 4906) and North Cape Canaveral (770 m, JSLI-4682) study areas (Fig. 6b). In addition, we examined a specimen of this species collected by trawl in the Tongue of the Ocean, Bahamas in 1483 m (UF 166362, 880 mm TL). This specimen appears to be the one reported by Sulak (1982). These represent the first records for the western Atlantic. *C. monstrosa* was previously known from the eastern Atlantic in depths of 300–1171 m from off Greenland, Norway, the North Sea, and Iceland to the Azores, including the Mediterranean Sea (Stehmann and Bürkel, 1984; Moller et al., 2004; Mytilineou et al., 2005). It may occur in shallower areas (40–100 m) during summer in the northern part of its range (Stehmann and Bürkel, 1984). Although we did not collect *C. monstrosa*, we recorded high quality video and identified this species using the following characters: anal fin separate from ventral caudal fin, silver color with brown spots and undulating stripes, grayish fins, and black distal margins of unpaired fins

(Stehmann and Bürkel, 1984; Didier, 1998; identification confirmed by D. Didier Dagit, pers. commun.). Individuals were observed alone, hovering over coral rubble, hard coral, or sandy substrate. Upon the submersible's approach, individuals were disturbed and swam away. In the northeastern Atlantic, *C. monstrosa* was also reported from off reef (Mortensen et al., 1995; Freiwald et al., 2002; Costello et al., 2005) and coral rubble habitats near *Lophelia* reefs (Costello et al., 2005).

An uncommon catshark, *Scyliorhinus hesperius*, was observed twice off Jacksonville, FL resting on thick coral rubble in 580 m (JSLI-4908) and 604 m (JSLI-4686) in prime reef habitat (Fig. 6c). Their sizes were estimated to be ~500 mm TL. This species was readily identified by unique coloration consisting of white spots scattered within black saddles (identification confirmed by G.H. Burgess, pers. commun.). These are the first records for the SEUS continental slope and the deepest yet for the species. Previously, this species was known from depths of 274–530 m on the continental slopes of the western Caribbean Sea (Springer, 1966, 1979; Springer and Sadowsky, 1970; Compagno, 1984).

Six *B. claramaculata* were collected off Cape Lookout, NC by otter trawl (NCSM 44430, 132 mm DW, 409–434 m, CH-01-094; NCSM 44434, 124 and 171 mm DW, 390–420 m, CH-01-096; NCSM 44436, 117 and 128 mm DW, 445–460 m, CH-01-100; NCSM 44649, 45 mm DW, 500–504 m, CH-06-031). In addition, two adults were observed by JSL (Fig. 2i) in off reef habitat resting on the bottom off Cape Lookout, NC (406–469 m, JSLI-4206, JSLII-3304). Previously, *B. claramaculata* was known from South Carolina to the Florida Keys in 293–896 m (McEachran and Matheson, 1985). An additional individual was collected off North Carolina in 640 m (UF 29868).

A single ophichthid eel was collected by trawl adjacent to the Cape Lookout B coral bank (CAS 224335, CH-06-016). This eel represents a new species of *Ophichthus* (McCosker and Ross, in press).

One *Bathycongrus vicinalis* was collected off Cape Lookout, NC from a transition reef area with a Tucker trawl (NCSM 44646, 115 mm TL, 409–431 m, CH-06-021). This juvenile specimen possessed its larval pigmentation, three lateral rows of melanophores (D.G. Smith, pers. commun.). The Tucker trawl was towed both in midwater and on the bottom (409–431 m), but most likely this species

was collected on the bottom. *B. vicinalis* is known from the eastern Gulf of Mexico, northwestern Bahamas, West Indies, and Central and South America from 101 to 503 m (Smith and Kanazawa, 1977; Smith, 1989a; McEachran and Fechhelm, 1998).

N. exoria was observed and collected frequently from deep coral banks along the SEUS (Fig. 6h). Off North Carolina, one individual was collected by otter trawl (NCSM 44467, 345 mm TL, 396–405 m, SJ-02-036), and five were collected by JSL (NCSM 44444, 143 mm TL, 374 m, JSLI-4363; NCSM 44448, 190 mm TL, 425 m, JSLI-4365; NCSM 44450, 447 mm TL, 440 m, JSLI-4366; NCSM 44454, 107 mm TL, 414 m, JSLI-4695; NCSM 44455, 93 mm TL, 402 m, JSLI-4696). Also, an adult was observed by JSL off North Carolina (442 m, JSLI-4366); five adults (all ~300 mm TL) were observed in the Stetson area (641–717 m, JSLI-4689, 4699, 4898); two adults were observed off Jacksonville, FL (614–631 m, JSLI-4686); and two were observed off Cape Canaveral, FL (687–748 m, JSLI-4703, 4705). *N. exoria* was often observed with head in, tail out of the *Lophelia* coral matrix, but a few individuals were observed in the open, swimming near the bottom. This poorly documented species was previously reported off Cuba (Claro et al., 2000), the northeast coast of Florida and the Bahamas in 227–494 m (Smith et al., 1981; Smith, 1989b).

Ateleopodidae is a poorly known family in need of revision (Smith, 1986; Moore, 2002a) whose species have a circumtropical distribution (Prokofiev, 2006) and have been infrequently collected in 200–800 m (Moore, 2002a). *Ijimaia antillarum* was collected by otter trawl off Cape Lookout, NC (NCSM 44438, 208 mm SL, 378–403 m, CH-01-112). This species has been reported from Cuba, the Gulf of Mexico (Howell Rivero, 1935; McEachran and Fechhelm, 1998) and New England (Moore et al., 2003). Species of the genus *Ateleopus* have been reported from the eastern Atlantic (e.g., Smith, 1986), Pacific (e.g., Prokofiev, 2006), and Indian oceans (e.g., Smith, 1986), and in the western Atlantic, *Ateleopus* spp. have been reported from off Suriname (Shimizu, 1983) and the Gulf of Mexico (Moore, 2002a). Four individuals of *Ateleopus* spp. (not assignable to species) were collected by otter trawl off Cape Lookout, NC (NCSM 44431, 520 mm SL, CH-01-096; NCSM 44437, 451 mm SL, 399–424 m, CH-01-111; NCSM 44465, 340 and 365 mm SL, 356–374 m, SJ-02-035).

One ateleopodid (visual identification not possible beyond family level) was observed (Fig. 7a) with the JSL off Cape Lookout, NC swimming close to the bottom on the edge of *Lophelia*-sand habitat (443 m, JSLI-4894). Our records extend the geographic ranges of these genera.

One *Benthocometes robustus* was collected by otter trawl from transition reef habitat in the Cape Lookout B area (NCSM 44743, 112 mm SL, 423–443 m, CH-06-015). This species was previously reported in the eastern Atlantic off northwest Africa and in the Mediterranean (Nielsen et al., 1999). In the western Atlantic, *B. robustus* was reported from off Cuba (Goode and Bean, 1895), northern Straits of Florida (Staiger, 1970), and along the northeast US coast from Norfolk Canyon (USNM 326148) to Hudson Canyon (Musick et al., 1992; Moore et al., 2003). This species was collected in bottom depths of 200–1652 m (Moore et al., 2003). Nielsen and Evseenko (1989) proposed that the disjunct distribution of *B. robustus* could result from an extended pelagic larval phase. While possible, it seems likely that the distribution of this rarely collected fish will prove to be more continuous on both sides of the Atlantic.

Bellottia apoda was collected with the JSL off Jacksonville, FL in 629 m (NCSM 44451, 44 mm SL, JSLI-4685) in prime, rocky reef habitat, extending both its geographic and depth ranges. This species was flushed out of a crevice in a rock ledge with rotenone. *B. apoda* was previously known from the subtropical eastern and western Atlantic, the Mediterranean Sea, the Galapagos Archipelago and the Philippines, occurring at bottom depths of 30–569 m (Nielsen et al., 1999; Mytilineou et al., 2005).

Four *Physiculus karrerae* individuals were collected by otter trawl (NCSM 44429, 130 mm SL, 409–434 m, CH-01-094; NCSM 44433, 175 and 190 mm SL, 390–420 m, CH-01-096; NCSM 44643, 137 mm SL, 423–443 m, CH-06-015). In addition, one was collected and observed with the JSL (NCSM 44442 250 mm SL, 383 m, JSLI-4361), and three other adults were observed only with the JSL (384–424 m, JSLI-4361, 4365, JSLII-3429). All were observed in prime, *Lophelia* reef habitats under coral bushes or dead coral matrices. Upon the submersible's attempts to collect specimens with rotenone, individuals swam out from the coral and appeared to quickly seek shelter under another coral bush/matrix. *P. karrerae* is known from a few records off Bermuda (Smith-Vaniz et al., 1999), the

Gulf of Mexico (Sulak et al., in press), the Caribbean, Brazil, St. Helena (Paulin, 1989), Tristan da Cunha (Andrew et al., 1995) and the Walvis Ridge (Trunov, 1991) in 240–800 m (Smith-Vaniz et al., 1999).

Off Cape Lookout, NC six *Idiastion kyphos* specimens were collected with the JSL (NCSM 44443, 95 mm SL, 398 m, JSLI-4361; NCSM 44445, 82 mm SL, 374 m, JSLI-4363; NCSM 44460, 65 mm SL, 397 m, JSLII-3305; NCSM 44462, 107 mm SL, 387 m, JSLII-3306; NCSM 44452, 81 mm SL, 416 m, JSLI-4693; NCSM 44457, 90 mm SL, 443 m, JSLI-4894), and another was collected by a bottom Tucker trawl tow (NCSM 44647, 94 mm SL, 409–431, CH-06-021). An additional specimen was collected in the Stetson area (NCSM 44458, 109 mm SL, 569 m, JSLI-4899). Ten other individuals (all ~80–100 mm TL) were observed with the JSL off North Carolina (385–443 m, JSLI-4206, 4365, 4693, 4697, 4890, JSLII-3304, 3306, 3430, 3431, 3432); one (~90 mm TL) was observed in the Stetson area (560 m, JSLI-4899), and another (~90 mm TL) was observed in the Savannah study area (519 m, JSLI-4905). Several *I. kyphos* were observed perched on branches of live or dead *L. pertusa*. Some individuals were sitting well within, while others were on the fringes of, low to high relief coral bushes. All sat motionless and were not disturbed by the submersible. All *I. kyphos* were pale red, but some individuals had large white blotches covering the posterior portion of the head to under the spiny dorsal fin (Fig. 7d). When brought to the surface, the blotches disappeared. *I. kyphos* was previously known from scattered records in the Atlantic (Poss and Eschmeyer, 2002): off Venezuela (Eschmeyer, 1965), northeastern Florida and the eastern South Atlantic (Anderson et al., 1975) in depths of 229–622 m.

Phenacoscorpius nebris was collected with the JSL as it was sitting motionless on outer branches of a *Lophelia* bush in the Savannah study area in 499 m (NCSM 44459, 55 mm SL, JSLI-4902). This collection extends both its geographic and depth ranges. This species was reported in the tropical eastern Atlantic (Mandritsa, 1992) in 320 m and in the western Atlantic (Venezuela and the Gulf of Mexico) in 347–475 m (Eschmeyer, 1965, 1969).

Synagrops trispinosus was collected by otter trawl off Cape Lookout, NC (NCSM 44464, 73 mm SL, 356–374 m, SJ-02-035). A few specimens (*Synagrops* spp.) that we observed with the JSL (Table 2) may

also have been this species. Previously, this species was known from the Caribbean to Brazil (Mochizuki and Sano, 1984; Cervigón, 1993; Mejia et al., 2001; Lopes et al., 2003) and the northeastern Gulf of Mexico (Ruiz-Carus et al., 2004) from depths of 137–550 m (Mochizuki and Sano, 1984; Ruiz-Carus et al., 2004). Additional trawl collections (MCZ 62079, 160714, 166112, 166167) exist from off Cape Hatteras, NC in 66–127 m.

A. woodsi was observed (14 adults, ~300 mm TL) with the JSL (Fig. 7i) off Cape Lookout, NC (367–407 m, JSLI-4362, 4363, 4891, 4892, 4893, 4895, JSLII-3306) in prime, *Lophelia* reef habitats. Individuals were solitary, closely associated with reef habitat, and several were observed in or darting into the *Lophelia* matrix. This species was previously known from collections off South Carolina, the east coast of Florida, and the Dry Tortugas (Anderson and Heemstra, 1980) in 175–475 m (Heemstra et al., 2002).

Ten *E. pandionis* were collected by otter trawl off Cape Lookout, NC (NCSM 44428, 145 mm SL, 409–434 m, CH-01-094; NCSM 44435, 109 mm SL, 445–460 m, CH-01-100; NCSM 44439, 378–403 m, 113 and 121 mm SL, CH-01-112; NCSM 44441, 108 and 117 mm SL, 378–408 m, CH-01-113; NCSM 44466, 105, 117 and 118 mm SL, 396–405 m, SJ-02-036; NCSM 44645, 121 mm SL, 406–440 m, CH-06-016). This amphi-Atlantic species was recorded in the western Atlantic from the southern New England slope (Moore et al., 2003), New Jersey, Straits of Florida, the Gulf of Mexico and the Caribbean to French Guiana in 210–751 m (Staiger, 1970; Mayer, 1974). Our records are the first documented for the SEUS south of Cape Hatteras.

Eight *Centrodraco acanthopoma* individuals were collected by otter trawl off Cape Lookout, NC (NCSM 44427, 83 mm SL, 409–434 m, CH-01-094; NCSM 44432, 81 mm SL, 390–420 m, CH-01-096; NCSM 44469, 97 mm SL, 370–407 m, SJ-04-025; NCSM 44642, 80, 83, and 85 mm SL, 423–443 m, CH-06-015; NCSM 44644, 83 and 90 mm SL, 406–440 m, CH-06-016). This species occurs in both the eastern and western Atlantic (Fricke, 1992). In the western Atlantic, adults are known from Georgia to the Florida Keys (Briggs and Berry, 1959) and the Gulf of Mexico (McEachran and Fechhelm, 2005) in depths of 384–594 m (Briggs and Berry, 1959; Davis, 1966). Several pelagic juveniles have also been reported off New England (Moore et al., 2003).

3.5. Noteworthy records

Several poorly known species, rarely recorded in SEUS waters, were documented during this study. *Odontaspis ferox* is a deep-water shark infrequently reported throughout most of the world's oceans (Compagno, 1984; Bonfil, 1995) in 13–420 m (Compagno, 2002). In the western Atlantic, it is known from the Yucatán shelf (Bonfil, 1995), the northern Gulf of Mexico (Sulak et al., in press), Cuba (Claro and Parenti, 2001), Brazil (Compagno, 2002) and off Cape Hatteras, NC (Sheehan, 1998). We add records of two individuals of *O. ferox* to continental US waters, both observed swimming slowly near the bottom around the JSL: one individual (~2000 mm TL, Fig. 6e) in the Stetson area (627 m, JSLI-4903), and one (~2500 mm TL) off Jacksonville, FL (573 m, JSLI-4683). *O. ferox* was visually distinguished by the presence of five gill slits all anterior to the pectoral fin, high dorsal fins (second slightly smaller than the first), the first dorsal originating well in advance of pelvic fin, a markedly high anal fin placed well behind second dorsal, and coloration (identification confirmed by G.H. Burgess, pers. commun.). Twelve individuals (all ~600 mm TL) of the poorly documented *Scyliorhinus meadi* (Fig. 6d) were observed off North Carolina (374–442 m, JSLI-4207, 4361, 4364, 4693, 4892, 4893, JSLII-3428, 3431, 3432) and one (~600 mm TL) was observed in the Savannah study area (498 m, JSLI-4687). This species was visually identified by unique coloration of conspicuous dark saddles without light or dark spots. Individuals were usually solitary and were generally observed swimming close to the bottom, often contacting or rubbing their bodies on the corals. They were also observed resting on the bottom usually near coral formations (Fig. 6d). Few records of *S. meadi* have been reported in the western Atlantic from off North Carolina, Florida, the Bahamas to Cuba, and the Yucatán in the Gulf of Mexico in 329–549 m (Springer, 1966, 1979; Springer and Sadowsky, 1970; Burgess et al., 1979; Compagno, 2002). Four *Carcharhinus altimus* (all ~2000 mm TL) were observed with the JSL (Fig. 6f) swimming rapidly near the bottom off North Carolina (380–424 m, JSLI-4365, 4890, JSLII-3307, 3427). Visual identification (confirmed by G.H. Burgess, pers. commun.) was based on a combination of characters: posterior gill slits located above pectoral fin origin, midlength of first dorsal fin base closer to pectoral fin than pelvic fin insertion, first dorsal fin moderately high with a straight anterior

margin, second dorsal fin smaller than first, and coloration. This deep-water carcharhinid has a circumglobal distribution; however, records of it are sporadic (Compagno, 1984, 2002). In the western Atlantic, *C. altimus* was recorded from near the surface (at night over deep-water) to 430 m (Compagno, 1984; Anderson and Stevens, 1996) off Florida, the Bahamas, Cuba, the Atlantic coast of Mexico, the Yucatán, Costa Rica, Nicaragua, Venezuela, Brazil, the northeastern Gulf of Mexico (Compagno, 1984; McEachran and Fechhelm, 1998; Compagno, 2002) and off Cape Hatteras, NC (Stillwell and Casey, 1976).

Four specimens of *Bythites gerdae* were reported from off Cape Hatteras, NC in 204–562 m (Nielsen and Cohen, 2002), resulting from a related study (S.W. Ross et al., unpubl. data). *B. gerdae* is also known from a few records in the Florida Straits in 786–832 m (Nielsen and Cohen, 1973). We add records for this species off the SEUS: one individual collected by otter trawl in transition reef habitat off Cape Lookout, NC (NCSM 44426, 52 mm SL, 409–434 m, CH-01-094), and one collected by JSL within a crevice in a *Lophelia* mound in the South Cape Canaveral study area (NCSM 44456, 71 mm SL, 687 m, JSLI-4705). Also, a few undetermined bythitids, possibly *B. gerdae*, were observed frequently in prime, *Lophelia* habitat off North Carolina. Individuals were observed protruding from or darting into large coral bushes.

One *Ventrifossa macropogon* was collected by otter trawl off Cape Lookout, NC (NCSM 44440, 290 mm TL, 378–403 m, CH-01-112). *V. macropogon* was previously known from North Carolina (two records), the east coast of Florida, the Caribbean to Guyana, and the Gulf of Mexico in 439–1000 m (Marshall, 1973; Cohen et al., 1990).

Adult *H. occidentalis* (all ~100–200 mm TL) were commonly observed ($n = 130$) with the JSL off North Carolina and Jacksonville, FL. Eleven other individuals were collected using the JSL from reef areas off North Carolina (NCSM 44446, 116 mm SL, 372 m, JSLI-4363; NCSM 44447, 120, 135, 137, 140, 155, and 164 mm SL, 400 m, JSLI-4364; NCSM 44449, 151 mm SL, 423 m, JSLI-4365; NCSM 44461, 135 mm SL, 382 m, JSLII-3305; NCSM 44463, 98 mm SL, 427 m, JSLII-3427; NCSM 44453, 91 mm SL, 394 m, JSLI-4693). Five more individuals were collected off North Carolina by otter trawl, two of which were juveniles (NCSM 44468, 110 mm SL, 396–405 m, SJ-02-036; NCSM 44470, 19 and 63 mm SL, 657–910 m, SJ-04-035;

NCSM 44648, 77 and 131 mm TL, 415–431 m, CH-06-029). This species was thought to be rare along the coast of the SEUS (Moore, 2002b), with previous records from off New England (Moore et al., 2003), Bermuda (Smith-Vaniz et al., 1999), North Carolina (MCZ 75974, 137247), the east coast of Florida, Florida Straits, the northern Gulf of Mexico, the Caribbean, southern Brazil, Venezuela, the Guianas (Woods and Sonoda, 1973; Kotlyar, 1986), Cuba (Claro et al., 2000) and Suriname (Uyeno and Sato, 1983) in 124–823 m (McEachran and Fechhelm, 1998; Smith-Vaniz et al., 1999). *H. occidentalis* is closely associated with coral habitat and was one of the most cryptic fishes documented on coral habitats. Single individuals were usually observed hidden deep within coral branches (Fig. 7g) and were rarely observed swimming over the reef substrate. We were unable to identify species-specific colorations or morphologies to visually distinguish the two *Hoplostethus* spp. (*H. mediterraneus* and *H. occidentalis*) known from SEUS waters. However, since we only collected *H. occidentalis* with JSL, we recorded all observed individuals as this species. Their cryptic behavior and association with rugged habitats, indicate they may be more abundant than our data suggest and also may explain why captures were previously lacking in the region.

4. Discussion

We documented a diverse ichthyofauna (99 species) on and near deep coral habitats of the SEUS slope between 356 and 910 m. This represents the most fish species yet recorded from deep reef/coral ecosystems in the Atlantic. There are few other deep coral (>200 m) ecosystem references in the SEUS region with which to compare our fish data, and those are generally qualitative (fishes neither collected nor counted). All 12 of the fishes visually identified to species level by Reed et al. (2006) from three study areas (Stetson, Savannah, Jacksonville) overlapping with our sites were also reported in our study. Their identification of fewer fishes could result from lack of voucher specimen collections (precluding some species level identifications), difficulty of visual identifications for many species (many never before seen in situ), and lack of literature documentation for the region's fishes (many new records for the region). We found *Lophiodes* (two species) to be the most common lophiid (Caruso et al., 2007), while Reed et al.

(2006) listed *Lophius* sp. from one location. We never saw or collected *Raja* sp., which they listed from three areas, but instead we observed and collected several other Rajidae taxa throughout the region. They indicated that *Nezumia* sp. might be three species one of which was *N. atlanticus*; our data suggested *N. sclerorhynchus* to be more likely. Reed et al. (2006) did not report abundances or habitat associations, so no further comparisons are possible. George (2002) reported 24 fish species (13 of which we report here) trawled from a possible coral area north of the Stetson sites. Recent multibeam sonar mapping of that area (S.W. Ross, unpubl. data), however, suggests a soft substrate habitat with no elevation.

The Charleston Bump area (roughly between our Savannah and Stetson sites) contains rugged hard bottom with various coral coverage (Sedberry, 2001). Weaver and Sedberry (2001) listed 15 fish taxa from the Charleston Bump, and only six of those coincided with species from our surveys. Differences in habitat (less coral and more rock at Charleston Bump) and sampling methods could account for the fish biota differences between their study and ours. Popenoe and Manheim (2001) observed that *P. americanus*, *Beryx* spp., and Trachichthyidae used large undercut ledges as shelter in the Charleston Bump area. Undercut ledges of the size noted by Popenoe and Manheim (2001) were not encountered in our surveys; yet, we also observed *B. decadactylus* and *H. occidentalis* under ledges created by *Lophelia* bushes and lower profile rock ledges, suggesting a general tendency for these species to seek shelter.

Two adjacent deep coral sites (in 308–536 m) were surveyed in the north-central Gulf of Mexico (Sulak et al., in press). Most of the 36 fish taxa positively identified to species from JSL video occurred on reef habitat (mixed rock, corals and sponges). A few species (*Hyperoglyphe perciformis*, *Gephyroberyx darwini*, *Epinephelus niveatus*, *H. occidentalis*, *Grammicolepis brachiusculus*, *C. oceanicus*) were seen almost exclusively on reef habitat (Sulak et al., in press). Although all of the above species are known from the SEUS slope, only two (*H. occidentalis*, *C. oceanicus*) occurred in our study primarily in reef habitat. The lack of *E. niveatus* on SEUS slope reefs was likely due to greater depths sampled compared to the Gulf of Mexico sites where this species was seen only around 310 m. Differences in data treatment preclude further habitat related comparisons between these studies. Reed et al. (2006)

reported nine fish taxa from coral and hard bottom habitats in the western Gulf of Mexico (412–558 m), all of which we also observed or collected on SEUS sites.

Compared with other deep regions of the western Atlantic (Haedrich and Merrett, 1988; Diaz et al., 1994; Sulak and Ross, 1996; Moore et al., 2003; Powell et al., 2003), the slope environment of the Blake Plateau has been poorly sampled for benthic and benthopelagic macrofauna. This area has a disproportionate amount of high-profile rugged substrata, which has probably hampered extensive sampling via traditional means (dredges, trawls). Most of the species documented from off reef and to some extent transition reef habitats were species known from the area, and were those we expected to find. In contrast, many of the prime and transition reef species were either previously unknown to the area (19% of total) or were thought to be rare (or both). The apparent abundance and widespread occurrence of many of these fishes are further indications of close association with reef habitat, which seems to have secluded them from discovery. Outer continental shelf hardgrounds in the SEUS are also difficult to sample, and, as for the deep coral reefs, there were many additions to the fish fauna when these areas were better sampled (Quattrini et al., 2004; Quattrini and Ross, 2006). In comparison, none of the 23 fish species recorded from cold-water coral reef habitats from off Norway to the Porcupine Seabight were new to the region (Costello et al., 2005), probably because these reefs and nearby habitats have been historically better sampled. Also, if northeastern Atlantic slope fishes were habitat generalists, they would have greater opportunity for their ranges to be well documented (i.e., not secluded in hard to sample habitats).

The fish fauna of Blake Plateau deep reefs is completely different from that of the relatively better studied SEUS shelf hardgrounds. The shallower (≤ 200 m) continental shelf reef systems of the SEUS consist of one *Oculina* reef off central Florida (Reed, 2002b) and extensive emergent hardgrounds from Cape Hatteras to southern Florida (SEAMAP-SA, 2001). These hardground communities are subtropical and are best developed along the shelf edge (Grimes et al., 1982; Barans and Henry, 1984; Parker and Ross, 1986; Quattrini and Ross, 2006). Using similar methodology as in this study, we documented 113 fish species on several southern North Carolina shelf edge hardgrounds (57–128 m

depths) 37–48 km southwest of the Cape Fear deep coral reef (Quattrini and Ross, 2006), and only one species (*C. oceanicus*) was shared between shelf edge and slope reefs. Reed et al. (2006) noted that 73 fish species occurred on the *Oculina* Bank off east-central Florida (70–100 m), none of which were shared with coral/hardground systems deeper than 300 m. These examples typify the disparity between the shelf and slope reef faunas in terms of species richness and composition. Differences in temperature (usually $> 15^\circ$ on outer shelf vs. $\leq 12^\circ$ C on slope) probably play the biggest role in maintaining the faunal separation of the two different SEUS reef fish communities (shelf, subtropical versus slope species).

In contrast to many shallow water fish species, the lack of habitat association data for deep-water fishes has hampered our understanding of deep reef communities and the roles of complex habitats in structuring or maintaining deep-sea communities. While fish associations with deep corals may be more opportunistic in some areas (Husebø et al., 2002; Auster, 2005; Costello et al., 2005; Stone, 2006), our direct observation data, spanning several years and a wide geographic area, suggest a stronger tie to reef habitats along the SEUS slope. Our data, and those of Sulak et al. (in press), support the hypothesis that deep, slope reefs function much like shallow coral reefs, hosting a unique, probably obligate, ichthyofauna and concentrating food resources. Although not quantified, we observed abundant small invertebrates (amphipods, krill, shrimps), a potential forage base, more frequently around dense coral habitat than over non-reef areas. Costello et al. (2005) reported similar observations. Whether corals themselves or only the structure made by the corals (with its related benefits) are the attracting factors is unclear (Auster, 2005); nevertheless, corals are a major contributor to deep-sea habitat complexity and structure (Roberts et al., 2006). Comparisons of mobile macrofauna at slope depths between rocky habitat with no or few attached invertebrates (corals, sponges) and habitat with dense coral cover would be instructive for evaluating the role of deep-sea corals in attracting non-sessile fauna.

Unfortunately, most data on deep-sea fishes result from trawl or other indirect sampling, with little specific information on habitat. Several species important on Blake Plateau deep coral habitat (e.g., *Synphobranchus* spp., *H. occidentalis*, *B. decadactylus*, *H. dactylopterus*) have been captured

elsewhere, but details of habitat were missing and often obscured by sampling techniques (e.g., Haedrich and Merrett, 1988; Merrett et al., 1991; Massuti et al., 2001; Moore et al., 2003). Some of the previous investigations of deep reef fishes do not help elucidate the extent of the habitat use patterns we report because studies were either restricted to a few species, were geographically or temporally restricted, did not include non-reef habitat, lacked explicit habitat data, or resulted from indirect sampling methods (Husebø et al., 2002; Uiblein et al., 2003; Auster, 2005; Lorange and Trenkel, 2006; Stone, 2006). Despite compilation from a variety of video methods not specifically designed for fish surveys, the extensive data of Costello et al. (2005) from the northeastern Atlantic provide some of the best comparisons with our data. They reported low species richness (5–12 species per site) across eight sites, with most individuals and species associated with reef or near reef rubble/debris zones. Scorpaenids and gadioids were common in reef habitats, macrourids and morids were common in transition type habitats, and rajids and *Synphobranchus* spp. were prevalent away from reefs, patterns generally similar to the SEUS. Costello et al. (2005) argued that three-dimensional habitats in the deep-sea of the northeastern Atlantic attract and concentrate fishes, yet no species are restricted to reef habitat. Sulak et al. (in press) also reported a depauperate fish fauna on a deep *Lophelia* reef in the Gulf of Mexico, with some species that seemed restricted to deep reef environments, but they surveyed only a small geographic area. Determining the geographic and bathymetric variability of deep reef habitat usage awaits additional data.

The ecological advantages of reef structural complexity (reduction of competition and predation, influences on water column physics) that operate on shallow reefs (Almany, 2004) should also exist in deep water. The physical structure of deep coral habitats often rivals that of shallow systems, with dense coral matrices (or rocky ledges) full of interstitial spaces forming high profile and providing substrata for other sessile invertebrates. The growing reef alters the physics of the water column, accelerating bottom currents and enhancing the environment for corals and attached filter-feeders (Genin et al., 1986; pers. obs.). The less complex transition reef habitat appears similar (i.e., lower profiles, smaller habitat units, more interspersed soft substrate) to the patch reef and back reef formations common to shallow coral reef

systems. Although limited, data on the ages of western Atlantic deep coral systems indicate they have provided habitat for tens of thousands of years (Ayers and Pilkey, 1981; Paull et al., 2000), thus allowing substantial time for a deep reef fauna to evolve close habitat associations.

An important function of most shallow complex structure habitats (whether reef, vegetation, or anthropogenic) is that they serve as nursery areas for juvenile fishes. The deep reefs of the SEUS represented a large departure from this pattern as we rarely observed or collected small juveniles of most fish species. One explanation could be that we missed early recruitment phases because we sampled in summer or fall; however, it seems unlikely that all species would have the same seasonal patterns of recruitment or that individuals would grow from settlement sizes to the sizes we observed without our detecting intermediate sizes. Costello et al. (2005) also reported a lack of juvenile fishes from *Lophelia* reefs, which they attributed to cryptic behavior. It seems unlikely that juveniles of multiple species could completely escape detection. Our frequent rotenone stations on the SEUS deep reefs never flushed juvenile fishes from hiding. Sulak et al. (in press) attributed the lack of juvenile fishes on Gulf of Mexico deep coral sites to an inability to visually feed because of low light levels; however, this hypothesis lacks evidence. In fact, juveniles of most species are lacking from shelf edge reefs in the SEUS, where ambient light is plentiful (Quattrini and Ross, 2006). It is not uncommon for juvenile fishes to occupy habitats different from those of the adults (Day et al., 1989; Jones, 1991), and deep-sea fishes, like those using SEUS deep reefs, may have life history strategies that place juveniles in habitats different from those of adults (Mead et al., 1964). Juveniles of several deep-water species (e.g., *P. americanus*, *N. bairdii*) occupy surface or mesopelagic environments (Sedberry et al., 1994, 1998; Merrett and Barnes, 1996; Haedrich, 1997). It is also possible that juvenile fishes inhabit open, soft bottom habitats away from deep reefs, where predation may be less severe. We collected juveniles of a few species (*Hoplostethus* spp., *L. barbatulum*, and *Nezumia* spp.) in otter trawls during surveys of off reef habitat.

Most of the deep-sea bottom is composed of soft sediments (increasingly so with depth), a relatively simple, unstructured habitat (Gage and Tyler, 1991). Thus, there may be depth and geographic limits to which deep reef fishes are restricted simply

due to lack of reef habitat. Beyond these limits fish habitat use may be more opportunistic; however, such a conclusion seems premature, as most of the deep-sea remains poorly explored. Seamounts in particular are an abundant and under-studied environment where deep reef fauna may thrive (Rogers, 1994). Aside from the availability of structure, the depth limit of deep reef ecosystems could be related to the exponential decline in transport of labile carbon to the bottom and the decline of detrital quality with increasing depth (Carney, 2005), where at some depth there is too little food to support extensive, structure forming, sessile anthozoan or sponge colonies. More explicit data on habitats occupied by deep-sea fishes would help determine whether certain species are merely concentrated by structure, are only present periodically, or whether they are restricted to these areas.

The concept of fish communities (co-adapted, interacting groups) in the deep-sea was challenged, to be replaced with the proposal that there are only loose aggregations of individuals whose distributions are independent of one another (Haedrich and Merrett, 1990; Haedrich, 1997). A lack of cohesive, identifiable communities could suggest that strong associations with particular habitats are unlikely. The premise that marine communities may be nothing more than species collected together, a fortuitous or random assemblage, (Haedrich and Merrett, 1990) was derived from sampling methods that integrated all species caught and obscured small scale patterns. Koslow (1993) suggested that Haedrich and Merrett's conclusions were based on inadequate data and analyses, and upon reanalysis of some of these data species distribution patterns were revealed. Various collections (usually by trawls) have been used to represent, perhaps inappropriately, deep-sea benthic fish distributions. Obviously, a trawl sample delivers a catch of fishes which group together in terms of geography or depth (assuming the trawl did not cover vertical extremes), but whether the species caught formed habitat-related patterns would not be discernable. We doubt that this inefficient, indiscriminate methodology is adequate for determining the existence of deep-sea fish communities. We hypothesize that some slope fishes have experienced similar selective pressures controlling habitat usage and distributions as shallow species and responded to them in ways leading to communities closely tied to structured habitat. The deep reef fishes we identified exhibited some variation in distributional

patterns over this SEUS area (Ross and Quattrini, manuscript in preparation), but their usage of deep reef habitat is predictable, not random. Although data on species interactions (competition, predation) are lacking, we propose that the fishes strongly associated with deep coral (or hard bottom) habitats in this study constitute a deep reef community. In contrast to Haedrich and Merrett's (1990) interpretation of Mills (1969), our data are consistent with Mills' definition of community as "a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups." Perhaps without the strong organizing influence of physical structure, deep-sea fishes occurring on soft bottoms, especially beyond slope depths, in fact, are just loose aggregations (Haedrich and Merrett, 1990); however, this hypothesis awaits more detailed data (Koslow, 1993). We hope that this study encourages research on deep-sea fish distributions that incorporates more explicit data on fish behavior and habitat usage.

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