



# First observations of the cold-water coral *Lophelia pertusa* in mid-Atlantic canyons of the USA



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## ABSTRACT

The structure-forming, cold-water coral *Lophelia pertusa* is widely distributed throughout the North Atlantic Ocean and also occurs in the South Atlantic, North Pacific and Indian oceans. This species has formed extensive reefs, chiefly in deep water, along the continental margins of Europe and the United States, particularly off the southeastern U.S. coastline and in the Gulf of Mexico. There were, however, no records of *L. pertusa* between the continental slope off Cape Lookout, North Carolina (NC) (~34°N, 76°W), and the rocky Lydonia and Oceanographer canyons off Cape Cod, Massachusetts (MA) (~40°N, 68°W). During a research cruise in September 2012, *L. pertusa* colonies were observed on steep walls in both Baltimore and Norfolk canyons. These colonies were all approximately 2 m or less in diameter, usually hemispherical in shape and consisted entirely of live polyps. The colonies were found between 381 m and 434 m with environmental observations of: temperature 6.4–8.6 °C; salinity 35.0–35.6; and dissolved oxygen 2.06–4.41 ml L<sup>-1</sup>, all of which fall within the range of known *L. pertusa* distributions. All colonies were observed on vertical walls or underneath overhangs in areas of high current, which differs from observations further south, where *L. pertusa* colonizes rocky ledges and outcroppings, often forming large bioherms. We discuss observations from Baltimore and Norfolk canyons in the context of the known distribution of this species in the North Atlantic.

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## 1. Introduction

The azooxanthellate colonial scleractinian *Lophelia pertusa* (Linnaeus, 1758) was first described over 250 years ago from Trondheim Fjord, Norway, but during the last two decades research on *L. pertusa* and other deep-water habitat-forming corals has expanded rapidly (Jensen and Fredericksen, 1992; Reed, 1992; Mortensen et al., 1995; Rogers, 1999; Roberts et al., 2006, 2009; Cairns, 2007; Lumsden et al., 2007; Freiwald et al., 2009), driven by a growing recognition of their environmental importance and concerns over negative human impacts. *Lophelia pertusa* has been recorded in every ocean apart from the polar seas, but is particularly abundant in the North Atlantic Ocean off the coasts of Europe (Roberts et al., 2009) and southeastern USA (Cairns, 1979, 1981, 2000). Extensive deep-coral communities dominated by this species also exist from NC through the Straits of Florida and into the Gulf of Mexico (Brooke and Schroeder, 2007; Ross and Nizinski, 2007; Messing et al., 2008). In most areas of the Atlantic, *L. pertusa* often forms large bioherms as well as attaches to exposed hard substrata. It usually occurs over a depth range of

370–800 m, but may occur as shallow as 200 m (Brooke and Ross, unpublished data). In cold temperate regions off the Atlantic coast of North America its distribution is patchy, and bioherms constructed by *L. pertusa* have not been reported (Packer et al., 2007). Structure-forming scleractinians in general appear to be relatively rare north of Cape Lookout, NC (Packer et al., 2007), which is unexpected considering their abundance in the eastern North Atlantic (Roberts et al., 2009).

Despite its wide distribution, the documented geographic range of *L. pertusa* is not continuous along the US east coast. In the southeastern US region, the northernmost sample of *L. pertusa* (a single dredged dead specimen) was collected from approximately 34°25'N, but multibeam bathymetry indicates the presence of several low relief *L. pertusa* mounds off NC, extending to 34°28'N (Ross et al., 2012). The next most northerly sample of *L. pertusa* was dredged from Oceanographer Canyon, southeast of Cape Cod, MA (US National Museum Invertebrate Zoology Collection: USNM 1116177, 20 May 1979, R/V *Eastward* station E-2B-79, 40°19.76'N, 68°06.37'W; 350–985 m). Hecker (1980) also reported dead *L. pertusa* rubble in Oceanographer Canyon between 700 and 1000 m. These were just south of two other records from Lydonia Canyon at 800 m (USNM 99232; Cairns, 2000) and 462 m (USNM 1116579). There was, therefore, a gap of approximately 930 km in the distribution of *L. pertusa* between Cape Lookout, NC, and Cape

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Cod, MA. Reviews by Rogers (1999) and Roberts et al. (2006, 2009) also noted this distributional gap.

Habitat suitability modeling predicted appropriate conditions for *L. pertusa* almost continuously along the slope of the US east coast (Davies and Guinotte, 2011); however, much of this steep topography north of Cape Lookout, NC, is consolidated mud rather than hard substratum and is probably not sufficiently stable to support large *L. pertusa* colonies. Lack of suitable settlement substrata may explain the apparent absence of *L. pertusa* in the mid-Atlantic region; however, *L. pertusa* is also rare in the more rocky canyons from Cape Cod, MA, to Canada where there are abundant hard substrata. In these canyons, *L. pertusa* occurs as isolated colonies and does not form the large complex structures that are abundant off the southeastern US and in the northeastern Atlantic (Packer et al., 2007; Gass and Willison, 2005). This paper presents the first records of *L. pertusa* from the mid-Atlantic region and describes the habitat and environmental conditions found at the coral sites.

## 2. Materials and methods

As part of a large, multidisciplinary study of mid-Atlantic submarine canyons, Baltimore and Norfolk canyons (Fig. 1) were explored during two research cruises. The first (15th August–2nd October 2012) used the NOAA ship *Nancy Foster* and the Remotely Operated Vehicle (ROV) *Kraken II* (University of Connecticut). The second (30th April–27th May, 2013) used the NOAA ship *Ronald H. Brown* and the ROV *Jason II* (Woods Hole Oceanographic Institute, WHOI). Sampling in Baltimore Canyon was emphasized in 2012,

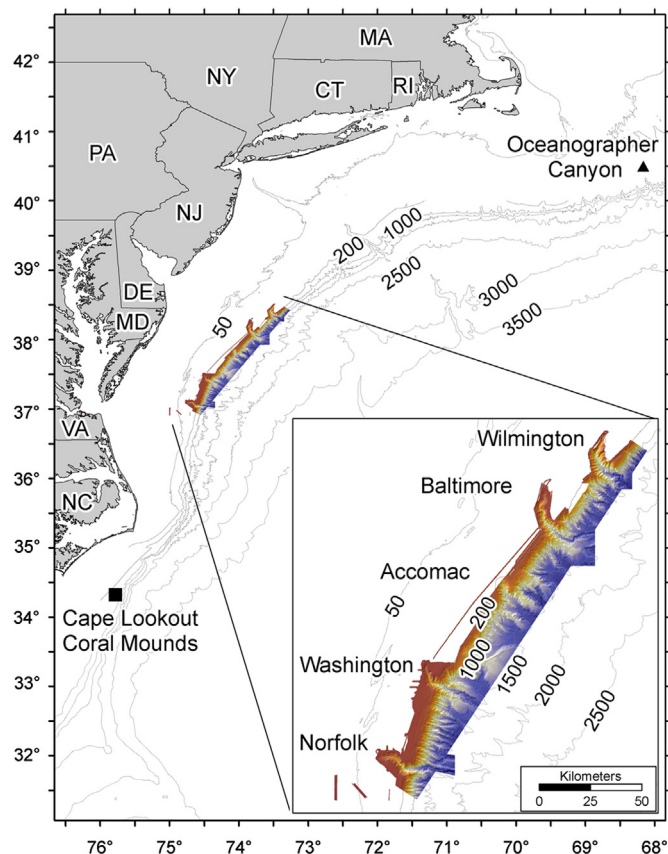


Fig. 1. Large area map showing the USA east coast between North Carolina and Massachusetts. Prior to the new observations, there were no records of *Lophelia pertusa* between the Cape Lookout coral mounds and Oceanographer Canyon. Inset map shows the major canyons off the mid-Atlantic, including Norfolk and Baltimore canyons. Shaded area represents coverage by multibeam sonar.

with some sampling in Norfolk Canyon, and in 2013 the emphasis was reversed, with most of the work being conducted in Norfolk Canyon.

Multibeam sonar bathymetry maps of the target canyons were generated during a mapping cruise using the NOAA ship *Nancy Foster* in 2011 and were used to facilitate ROV navigation and surveying. The ROV positions were continuously recorded using Ultrashort Baseline tracking systems with integrated navigation. The *Kraken II* ROV is a Max Rover science-configured vehicle capable of operating to 1000 m. The science video imagery was collected using a Kongsberg OE14–502 high-definition camera, with parallel lasers (10 cm apart) used for size reference. The ROV had a six-function manipulator arm, a suction device and a variety of collection containers for samples. The *Jason II* ROV was designed and built by the WHOI Deep Submergence Laboratory and can operate to depths of 6500 m. This is a two-body system comprised of the ROV (*Jason*) and an active tether management system (*Medea*) which buffers *Jason* from the movements of the ship during operations. The ROV was equipped with three high-definition video cameras (Insite Mini-Zeus) and a digital still camera (Nikon Coolpix 3 MP) with lasers (10 cm apart) on the main science camera. The *Jason* had two seven-function manipulator arms, a suction device and a variety of containers for sample collection.

During each ROV dive (both cruises) a SeaBird SBE 19+ CTD instrument was mounted on the vehicle to record turbidity (formazin turbidity units), dissolved oxygen ( $\text{mL L}^{-1}$ ), depth (m), salinity and temperature ( $^{\circ}\text{C}$ ). Two 6-L Niskin bottles were mounted on the ROV to collect water samples from close to the coral habitats. Samples were analyzed by NOAA's Pacific Marine Environmental Laboratory (PMEL) for dissolved inorganic carbon, pH, carbon dioxide partial pressure, and total alkalinity, from which aragonite saturation state ( $\Omega_{\text{arag}}$ ) was calculated. Analytical methods are detailed on the PMEL website (<http://pmel.noaa.gov/co2/story/Laboratory+Analysis>). Values of pH and  $\Omega_{\text{arag}}$  calculated from the water samples are reported in Table 1.

A total of 20 ROV dives were completed during the 2012 cruise and 13 dives during 2013. Most ROV dives followed a similar pattern, usually targeting steep hard substrata in search of deep coral communities. Dives began at the base of a slope, and progressed generally upwards with occasional lateral deviations to follow interesting features. The dives emphasized digital imagery along bottom transects and collection of specimens on or near the bottom. Position data were collected continuously throughout the dive, providing accurate coordinates for all imagery and samples.

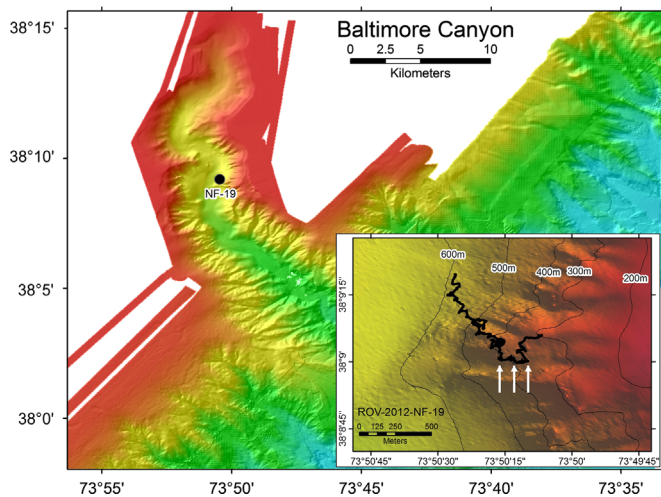
## 3. Results

*Lophelia pertusa* was initially observed and collected during an ROV dive in Baltimore Canyon (ROV-2012-NF-19) on 12th September 2012 (Fig. 2). The dive in Baltimore Canyon started at the base of a steep wall at 608 m, approximately mid-way down the east flank of the canyon ( $38^{\circ}09.317'N$ ,  $73^{\circ}50.436'W$ ), proceeded south-eastward up the wall to a plateau, then traveled north-westward to ascend along a small ridge, terminating the dive at the end of the ridge at 302 m ( $38^{\circ}09.099'N$ ,  $73^{\circ}50.118'W$ ) (Fig. 2). Towards the end of the dive, the ROV followed an almost vertical wall just below the ridge at 373 m. The wall appeared to be composed of hard-packed consolidated clay and supported an abundant sessile community of sponges (demosponges and hexactinellids), anemones, and octocorals (*Primnoa resedaeformis*, *Paramuricea placomus* and *Paragorgia arborea*). A few motile fauna included crabs and squat lobsters (*Cancer* cf. *borealis*, hermit crabs, *Eumunida picta*), small shrimp (species unknown) and fishes (*Laemonema*

**Table 1**

Locations of living colonies of *Lophelia pertusa* and associated environmental data in Baltimore and Norfolk canyons. The  $\Omega_{\text{arag}}$  and pH were calculated from water samples collected at or near the coral sites. Other environmental data were recorded by a Seabird SBE+19 instrument on the ROV. The  $\Omega_{\text{arag}}$  and pH values were derived from water samples collected at or near the coral sites in 2012. The water sample from Baltimore Canyon was taken adjacent to the first coral colony, and the sample from Norfolk Canyon was collected on 4th September from 37°04.10'N, 74°38.89'W, depth 513 m.

| Canyon (dive #)   | Date     | Colony | Depth (m) | Latitude (N) | Longitude (W) | Temperature (°C) | Salinity | DO (mL/L) | Turbidity (FTU) | $\Omega_{\text{arag}}$ | pH   |
|-------------------|----------|--------|-----------|--------------|---------------|------------------|----------|-----------|-----------------|------------------------|------|
| Baltimore (NF-19) | 09/12/12 | 1      | 381       | 38°09.010'   | 73°50.265'    | 7.23             | 35.08    | 4.09      | 55.62           | 1.44                   | 7.94 |
|                   |          | 2      | 379       | 38°09.012'   | 73°50.224'    | 6.99             | 35.08    | 4.21      | 58.37           |                        |      |
|                   |          | 3      | 379       | 38°09.012'   | 73°50.224'    | 6.99             | 35.08    | 4.21      | 58.37           |                        |      |
| Norfolk (NF-20)   | 09/13/12 | 1      | 434       | 37°03.020'   | 74°37.299'    | 6.39             | 35.04    | 4.41      | 64.08           | 1.41                   | 7.97 |
| Norfolk (RB-681)  | 05/06/13 | 1      | 425       | 37°03.018'   | 74°37.158'    | 7.92             | 35.20    | 2.41      | 32.62           |                        |      |
| Norfolk (RB-684)  | 05/10/13 | 1      | 406       | 37°04.127'   | 74°38.680'    | 7.24             | 35.11    | 3.54      | 53.71           |                        |      |
| Norfolk (RB-686)  | 05/13/13 | 1      | 479       | 37°03.516'   | 74°36.349'    | 7.09             | 35.55    | 2.36      | 17.93           |                        |      |
|                   |          | 2      | 479       | 37°03.515'   | 74°36.349'    | 6.56             | 35.05    | 3.41      | 20.03           |                        |      |
| Norfolk (RB-687)  | 05/14/13 | 1      | 394       | 37°03.639'   | 74°34.690'    | 7.63             | 35.11    | 2.80      | 19.95           |                        |      |
|                   |          | 2      | 402       | 37°03.635'   | 74°34.706'    | 7.26             | 35.14    | 2.24      | 17.05           |                        |      |
|                   |          | 3      | 390       | 37°03.632'   | 74°34.719'    | 7.26             | 35.10    | 2.71      | 65.39           |                        |      |
|                   |          | 4      | 387       | 37°03.625'   | 74°34.720'    | 8.11             | 35.12    | 2.59      | 26.25           |                        |      |
|                   |          | 5      | 386       | 37°03.363'   | 74°34.720'    | 7.44             | 35.11    | 2.59      | 46.62           |                        |      |
|                   |          | 6      | 391       | 37°03.617'   | 74°34.722'    | 7.79             | 35.11    | 2.06      | 24.80           |                        |      |
|                   |          | 7      | 399       | 37°03.609'   | 74°34.716'    | 7.99             | 35.13    | 2.87      | 14.42           |                        |      |
| Norfolk (RB-691)  | 05/18/13 | 1      | 420       | 37°01.912'   | 74°38.116'    | 8.49             | 35.21    | 2.45      | 23.31           |                        |      |
|                   |          | 2      | 420       | 37°01.909'   | 74°38.117'    | 8.55             | 35.18    | 2.27      | 24.91           |                        |      |
|                   |          | 3      | 420       | 37°01.921'   | 74°38.140'    | 8.39             | 35.18    | 2.44      | 27.73           |                        |      |
|                   |          | 4      | 421       | 37°01.947'   | 74°38.175'    | 8.29             | 35.18    | 2.41      | 32.46           |                        |      |
|                   |          | 5      | 423       | 37°01.909'   | 74°38.103'    | 7.48             | 35.12    | 2.82      | 43.37           |                        |      |
|                   |          | 6      | 424       | 37°01.911'   | 74°38.106'    | 7.96             | 35.10    | 2.13      | 52.57           |                        |      |
|                   |          | 7      | 424       | 37°01.911'   | 74°38.106'    | 7.94             | 35.10    | 2.13      | 52.57           |                        |      |



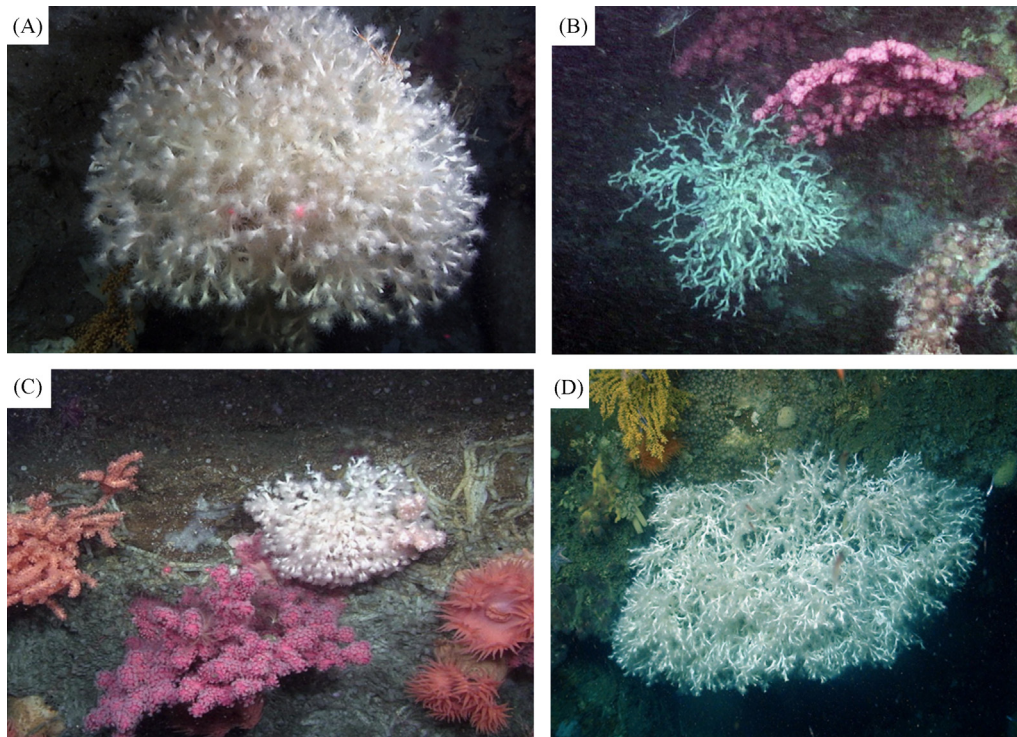
**Fig. 2.** Multibeam image of Baltimore Canyon showing dive location where *Lophelia pertusa* colonies were observed in 2012; smaller scale inset shows bottom tracks for ROV Kraken dive. White arrows indicate locations of *Lophelia pertusa* colonies.

*barbatulum*, *Helicolenus dactylopterus*). The ROV then descended to 376 m to a small ledge, below which was another vertical consolidated clay wall approximately 7 m high covered with abundant hexactinellid sponges (probably *Acanthascus* sp. and *Polymastia* sp.) and a few octocorals. The first colony of *L. pertusa* was observed at 381 m near the bottom of this wall under a slight overhang. The colony was hemispherical, 55 cm in diameter and 43 cm tall, and with closely packed branches. The whole colony was alive and appeared to be healthy as the polyps were open (Fig. 3A). A few small fragments of broken coral accompanied by small scattered boulders were observed on a gentle sediment slope at the base of the wall, but there was no accumulation of coral rubble. After documenting the colony and taking samples,

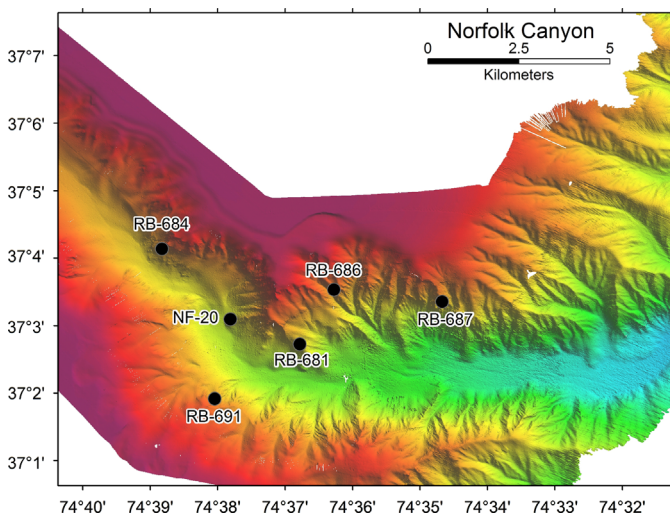
the ROV continued to follow this vertical wall, traveling eastward at 379 m. Three more colonies of *L. pertusa* were observed in a cleft in the wall, two on opposite sides near the mouth at 379 m, and the third towards the back of the cleft. The latter could not be fully documented as the ROV could not maneuver sufficiently close to the colony. The two more accessible colonies were attached to the vertical wall of the cleft ~3 m from the base and 9 m from the top (Fig. 3B). Both colonies were completely alive; the colony on the western side was hemispherical, ~1 m across and 55 cm tall, with tightly packed branches, whereas the one on the opposite side was irregularly shaped, ~75 cm across, with more open branching. As before, there were no signs of dead coral rubble in the area. Surrounding sessile fauna included octocorals (*Paragorgia arborea*, *Paramuricea placomus*, and an unidentified plexaurid), and small hexactinellid sponges.

The second observation and collection of *L. pertusa* was from Norfolk Canyon (ROV-2012-NF-20) on 13th September 2012 (Fig. 4). This dive began at the base of a steep wall at 766 m, approximately mid-way along the north flank of the canyon (37°03.058'N, 74°37.939'W), traveled northeastward up a ridge, then ran southeastward along a wall, and terminated at 385 m near the top of the wall (37°03.038'N, 74°37.198'W) (Fig. 5A). Near the end of the dive, the ROV was traveling southeasterly along the top of the wall, which consisted of a series of steep steps. The substratum was consolidated mud with attached sessile fauna including *Pargorgia arborea*, *Primnoa resedaeformis*, Venus flytrap anemones, large unidentified pink anemones, hexactinellid sponges, and abundant dense patches of soft worm tubes (species unknown). Mobile fauna was similar to that seen at the coral sites in Baltimore Canyon. A single small hemispherical colony (50 × 30 cm<sup>2</sup>) of *L. pertusa* was observed at 434 m near the top of the wall underneath a slight overhang. The colony was completely alive and appeared to be healthy (Fig. 3C); no dead coral was observed. This area exhibited high current speeds during the ROV dive; actual current speeds were not measured but the ROV had difficulty maintaining station, and the octocoral branches





**Fig. 3.** *Lophelia pertusa* colonies observed in Baltimore Canyon (A,B) and Norfolk Canyon (C,D). Colony in panel (A) is  $55 \times 43 \text{ cm}^2$ , depth 381 m; colony in panel (B) is 75 cm in diameter, depth 379 m; colony in panel (C) is  $50 \times 30 \text{ cm}^2$ , depth 434 m; and colony in panel (D) is  $48 \times 30 \text{ cm}^2$ , depth 390 m. Note *Paragorgia arborea* colonies surrounding *L. pertusa* in panels (B) and (C).



**Fig. 4.** Multibeam image of Norfolk Canyon showing dive locations where *Lophelia pertusa* was observed. NF-20 represents the 2012 ROV *Kraken* dive and the others represent the 2013 ROV *Jason* dives.

were being obviously moved by the flow. The long term current regime is unknown.

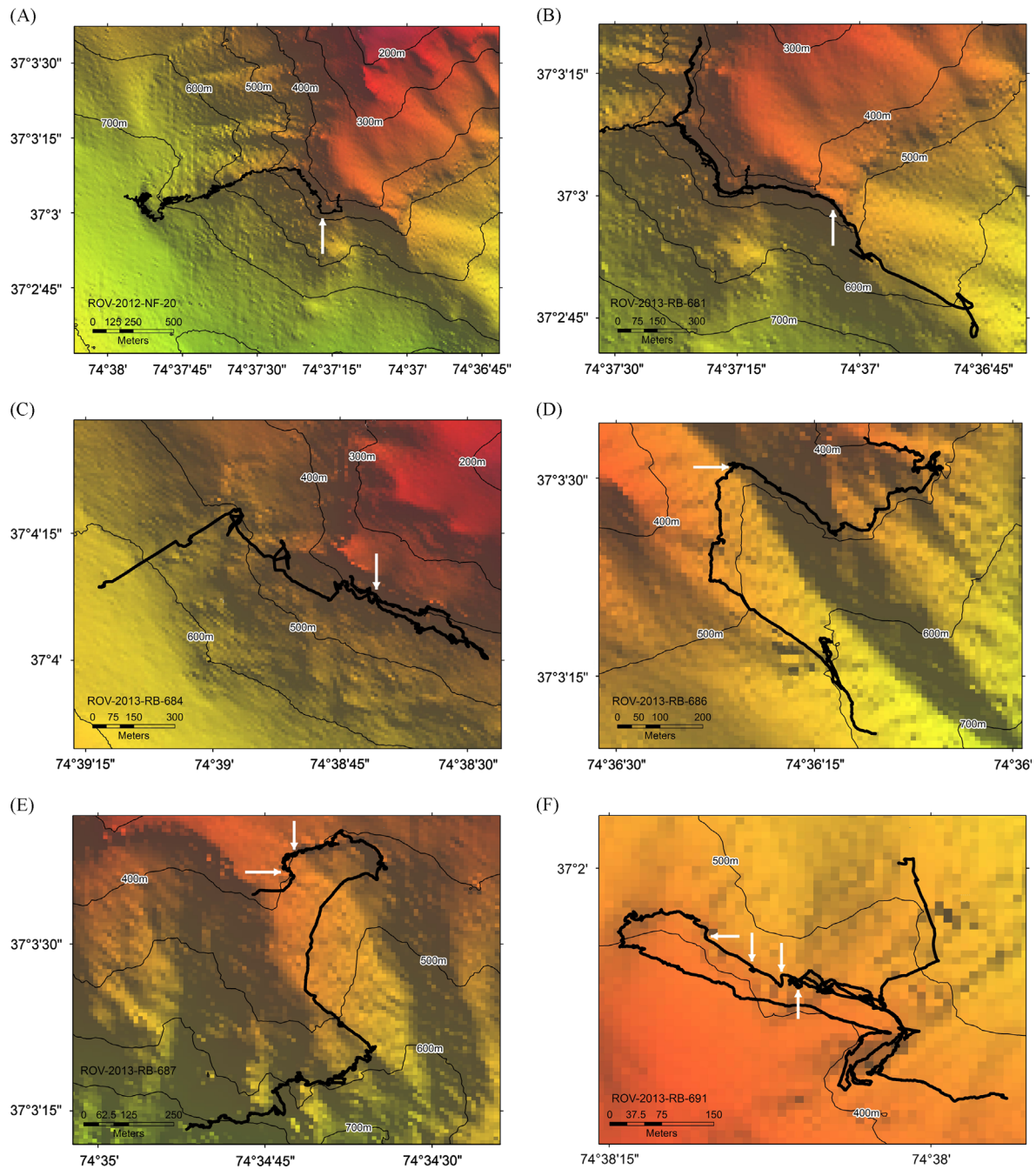
In Norfolk Canyon in 2013, we targeted steep rugged areas in depths between 350 and 500 m that appeared similar to those where *Lophelia pertusa* had been found the previous year. We found a total of 18 additional colonies of *L. pertusa* on five ROV dives (Figs. 4 and 5B–F). The depth of these observations ranged from 386 m to 479 m which was similar to the previous observations. The overall size range of all colonies observed in both years was 10–2 m diameter across the widest axis (average = 62.55 cm; SD = 55.08), and one of the largest 2013 colonies had some dead exposed skeleton, which differed from the earlier observations.

Although most environmental conditions were similar for all the coral observations, dissolved oxygen and turbidity (with a single exception) were lower in 2013 than 2012 (Table 1). It is not clear whether these differences were due to spatial or temporal variation, and more long term environmental data are necessary to determine how much variability occurs around these coral sites. The habitat characteristics of these additional colonies were very similar to those found in our initial discoveries; colonies were found on steep walls usually under overhangs (Fig. 3D) or in clefts. There were always other sessile invertebrates such as gorgonians, anemones and sponges in the vicinity. Dominant mobile fauna included galatheid crabs, echinoderms and synphobranchid eels.

During ROV dives the visibility was usually poor, due to high levels of organic material rather than suspended sediment. This was particularly true in 2013, when we observed a persistent layer of dense brown organic suspension at approximately 500–700 m depth. This suspension often reduced the visibility to < 3 m. Table 1 shows the locations of *Lophelia pertusa* observations and associated environmental data in both canyons during 2012 and 2013.

#### 4. Discussion

Although there has been extensive bottom-sampling of the mid-Atlantic region, these efforts have primarily used trawls and dredges, which are not generally effective over rugged terrain. Visual explorations of hard-bottom habitats in the mid-Atlantic canyons have been limited to a few submersible dives (mostly in the heads of the canyons) and towed camera surveys. The limited sampling effort on hard-bottom habitats within the canyons, and the apparent restriction of *L. pertusa* distribution to isolated colonies in relatively inaccessible locations (based on our observations), likely explains why this species has not previously been documented from this region.



**Fig. 5.** Multibeam maps showing bottom tracks for individual ROV dives. (A) Dive NF-20 using the ROV *Kraken* in 2012 represents the first observation of *L. pertusa* in Norfolk Canyon and (B–F) dives RB-681, 684, 686, 687 and 691 represent ROV *Jason* dives conducted in 2013. White arrows indicate locations where *Lophelia pertusa* colonies were observed. There were sometimes multiple colonies at each location. Refer to Table 1 for details on location of each individual colony.

It is unclear why *L. pertusa*, which is abundant elsewhere in the North Atlantic, should be uncommon in these canyons, whereas other deep coral species (especially octocorals) seem to be abundant and widely distributed. Very little information is available on the distribution of *L. pertusa* in the canyons off Cape Cod, but records indicate it occurs much deeper (700–1100 m) than our observations from the mid-Atlantic canyons. Several factors may influence the distribution of *L. pertusa*, including availability of suitable substrata, temperature, food availability, sediment load, current regime, larval supply and recruitment rates (Davies et al., 2008; Brooke et al., 2009; Roberts et al., 2009; Larsson and Purser, 2011; Wagner et al., 2011; Davies et al., 2014). The steep, rugged habitat in the mid-Atlantic canyons consists of hard-packed clay rather than rock and supports abundant large octocoral colonies,

such as those of *P. arborea*, even on vertical walls. However, we observed numerous dislodged live and dead *P. arborea* colonies during dives in both canyons near the bases of steep walls. Presumably, colony weight became too great for support by the clay substratum, especially in strong currents. The substratum that supported the *L. pertusa* colonies also seemed to be the same hard clay as the octocoral habitat; therefore, lack of hard substrata does not seem to be driving the scarcity of *L. pertusa* in the canyons. This species was only seen in two of the 20 ROV dives in 2012, and then only in a small area. In 2013, more colonies were observed, but all within a fairly restricted habitat type and depth range.

Temperature is thought to be an important controlling factor for *L. pertusa* distribution (Roberts et al., 2009). In Baltimore and



Norfolk canyons, colonies of this species were found at temperatures (6.39–8.55 °C) that fall well within the observed range for this species (4–13.9 °C, usually 6–9 °C) (Rogers, 1999; Roberts et al., 2003; Freiwald et al., 2009; Brooke et al., 2013). All other environmental variables measured at the *L. pertusa* sites (Table 1) also fell within reported ranges for this coral (Dodds et al., 2007; Mienis, 2008; Davies et al., 2010; Lunden et al., 2012), except turbidity, which was much higher in these canyons (58.37–64.09 FTU) than documented by Davies et al. (2010) at similar depths near the coral habitat in the Gulf of Mexico (0.12–0.22 FTU) and near coral mounds off the southeastern US (0.28–1.09 FTU) (Ross et al., unpublished data). High turbidity values can be produced by organic material, very fine sediment or a combination of both. Some corals, including *L. pertusa*, can tolerate relatively high suspended sediment (Rice and Hunter, 1992; Brooke et al., 2009), but accumulation of sediment can suffocate coral polyps, clog delicate feeding mechanisms and increase metabolic demand as energy is allocated to cleaning mechanisms (Dallmeyer et al., 1982; Riegl and Branch, 1995). High suspended sediment levels can also affect larval survival and recruitment (Babcock and Davies, 1991; Gilmour, 1999). Whether the high turbidity is ecologically limiting is unclear and requires additional observations and experimentation.

Deep-sea corals occur predominantly in areas of elevated current speed; current regimes control food delivery, oxygen and sediment levels around coral ecosystems and are generally accepted as primary drivers of coral distribution (White et al., 2005, 2007; Orejas et al., 2009). The *L. pertusa* colonies were all found on steep walls, usually under overhangs, (which may help prevent sediment deposition on the colony), in areas of strong current. Whether the current speeds observed during the ROV dives were representative of long-term currents is not known, but are likely as *L. pertusa* is normally found in areas of moderate to high current speed (Roberts et al., 2009). In summary, there is no evidence from the available data that the environmental conditions in the canyons are unsuitable for *L. pertusa* survival and growth, with turbidity being the possible exception; however, we have not completed a detailed habitat assessment, and it may be that *L. pertusa* requires a specific habitat type that is uncommon in the canyons. The larger number of colonies discovered in Norfolk Canyon than Baltimore may have been just due to chance; however Obelcz et al. (2014) note fine scale differences in geomorphology among four mid-Atlantic canyons, which may account for the observed differences in *L. pertusa* distribution.

Populations of *L. pertusa* in the Gulf of Mexico, southeastern USA and the New England Seamounts (which clustered with the northeast Atlantic) are genetically distinct (Morrison et al., 2011). There are no genetic data from elsewhere in the northwest Atlantic, and the source of larvae for the canyons is currently unclear. The closest known locations of *L. pertusa* to the canyon's colonies are Oceanographer Canyon (548 km north of Baltimore Canyon) and Cape Lookout (307 km south of Norfolk Canyon). With a possible larval lifespan of three weeks or more (Stromberg et al., unpublished data), a linear current of 15.43 cm s<sup>-1</sup> could carry *L. pertusa* larvae from Cape Lookout to Norfolk Canyon, and a current of 30.87 cm s<sup>-1</sup> would enable larvae to reach Baltimore Canyon from Oceanographer Canyon within the larval lifespan. These are not fast current speeds; therefore, the distances between known records could theoretically be traveled; however, without genetic analysis the source of the canyons colonies remains speculative.

There are no data on recruitment rates of *L. pertusa* larvae on natural substrata. Limited larval supply and recruitment could account for the rarity of this species in the canyons; however, even with infrequent recruitment, over hundreds or thousands of years the number of colonies in an area should accumulate unless

restricted by other factors. The coral colonies observed in the canyons ranged from a minimum of 10 cm in diameter to a maximum of 2 m. Growth rates for *L. pertusa* have been measured using a variety of approaches, including inferences from colonies on artificial structures (Gass and Roberts, 2006), isotopic analysis of skeletons (Freiwald et al., 1997; Mortensen and Rapp, 1998), growth in aquaria (Mortensen, 2000; Orejas et al., 2008) and *in situ* measurements (Brooke and Young, 2009; Lartaud et al., 2013). These approaches have produced a wide range of growth estimates from 2.44–35 mm yr<sup>-1</sup>. The higher values were derived from *in situ* estimates of colony age, and the lower values from direct measurement or isotopic analysis. Using the slowest of these growth rates, the largest colony observed in the canyons would have a maximum age of approximately 400 years, and the smallest colonies of approximately 20 years. This indicates that recruitment has occurred over an extended time period, and the observed colonies were not the result of a single vicarious event.

*Lophelia pertusa* exhibits many different growth forms, from individual colonies to thickets or large bioherms, with branches ranging from stout and densely packed to slender and loosely arranged. On vertical habitats such as oil platforms (Gass and Roberts, 2006) and fjords (SDB, pers. obs.), *L. pertusa* colonies eventually become so large and heavy that they may break away from the substrata, as observed for large *Paragorgia arborea* in the canyons. Especially, given the clay rather than rock substrata in the canyons, we would expect an attrition of older colonies as they break away from the wall and become buried in sediment perhaps accelerated by the canyon environment. This might explain our discovery of relatively small colonies. In other locations where *L. pertusa* is attached to steep walls (such as the Norwegian Fjords) dead colonies and rubble accumulate at the base of the walls (SDB pers. obs.). We observed very little dead *L. pertusa* colonies or accumulations of coral rubble in either canyon; exceptions were small fragments of broken coral at the base of the wall below the first colony observed in Baltimore Canyon, and a slightly larger piece in Norfolk Canyon during dive RB-684. The ROV usually traveled along the sides or tops of steep walls rather than at the base and so dead colonies may have been overlooked; however if dead material had been common, it likely would have been observed.

In conclusion, the relative rarity of *L. pertusa* in the north-western Atlantic in general, and specifically the mid-Atlantic canyons, may be due to a combination of infrequent larval delivery, specific habitat requirements (i.e., steep, rocky, current-swept walls with clefts or overhangs) and loss of older colonies. Future work involving *L. pertusa* reproductive and larval biology, genetic studies and oceanographic modeling would help explain why this species is rare north of NC in the western north Atlantic.

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## References

- Babcock, R., Davies, P., 1991. Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* 9, 205–208.
- Brooke, S., Schroeder, W.W., 2007. State of deep coral ecosystems in the Gulf of Mexico Region: Texas to the Florida Straits. In: Lumsden, S.E., Hourigan, T.F., Bruckner, A.W., Dorr, G. (Eds.), *The State of Deep Coral Ecosystems of the United States*. NOAA Technical Memorandum CRCP-3. Silver Spring, MD, pp. 271–306.
- Brooke, S., Young, C.M., 2009. Direct measurements of *in situ* survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 397, 153–161.
- Brooke, S., Holmes, M.W., Young, C.M., 2009. Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 390, 137–144.
- Brooke, S., Ross, S.W., Bane, J.M., Seim, H.E., Young, C.M., 2013. Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. *Deep Sea Res. II* (<http://dx.doi.org/10.1016/j.dsr2.2012.12.001>).
- Cairns, S.D., 1979. The deep-water scleractinia of the Caribbean Sea and adjacent waters. *Studies on the Fauna of Curacao and Other Caribbean Islands*, 57; p. 341.
- Cairns, S.D., 1981. Marine flora and fauna of the northeastern United States. Scleractinia. NOAA Technical Report NMFS Circular 438.
- Cairns, S.D., 2000. A revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic. *Stud. Nat. Hist. Caribb. Reg.* 75, 1–231.
- Cairns, S.D., 2007. Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bull. Mar. Sci.* 81, 311–322.
- Dallmeyer, D.G., Porter, J.W., Smith, G.J., 1982. Effects of particulate peat on the behavior and physiology of the Jamaican reef-building coral *Montastrea annularis*. *Mar. Biol.* 68, 229–233.
- Davies, A.J., Wisshak, M., Orr, J.C., Roberts, J.M., 2008. Predicting suitable habitat for the deep-water reef framework-forming coral *Lophelia pertusa* (Scleractinia). *Deep Sea Res. I* 55, 1048–1062.
- Davies, A.J., Duineveld, G.A., van Weering, T.C., Mienis, F., Quattrini, A.M., Seim, H.E., Bane, J.M., Ross, S.W., 2010. Short-term environmental variability in cold-water coral habitat at Viosca Knoll, Gulf of Mexico. *Deep Sea Res. I* 57, 199–212.
- Davies, A.J., Guinotte, J.M., 2011. Global habitat suitability for framework-forming cold-water corals. *PLoS One* 6 (4), e18483, <http://dx.doi.org/10.1371/journal.pone.0018483>.
- Davies, J.S., Howell, K.L., Stewart, H.A., Guinan, J., Golding, N., 2014. Defining biological assemblages (biotopes) of conservation interest in the submarine canyons of the South West Approaches (offshore United Kingdom) for use in marine habitat mapping. *Deep-Sea Research II* 104, 208–229.
- Dodds, L.A., Roberts, J.M., Taylor, A.C., Marubini, F., 2007. The cold-water coral *Lophelia pertusa* (Scleractinia) reveals metabolic tolerance to temperature and dissolved oxygen change. *J. Exp. Mar. Biol. Ecol.* 349, 205–214.
- Freiwald, A., Henrich, R., Pätzold, J., 1997. Anatomy of a deep-water coral reef mound from Stjernsund, West-Finnmark, Northern Norway. *SEPM Spec.* 56, 141–162.
- Freiwald, A., Beuck, L., Rüggeberg, A., Taviani, M., Hebbeln, D., R/V Meteor cruise M70-1 participants, 2009. The white coral community in the central Mediterranean Sea revealed by ROV surveys. *Oceanography* 22, 58–74.
- Gass, S.E., Willison, J.H.M., 2005. An assessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, pp. 223–245.
- Gass, S.E., Roberts, J.M., 2006. The occurrence of the cold water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: colony growth, recruitment and environmental controls on distribution. *Mar. Poll. Bull.* 52, 549–559.
- Gilmour, J., 1999. Experimental investigation into the effects of suspended sediment on fertilization, larval survival and settlement in a scleractinian coral. *Mar. Biol.* 135, 451–462.
- Hecker, B., 1980. Scleractinians (stony corals) encountered in this study: Appendix C. Canyon Assessment Study no. BLM-AA551-CT8-49. U.S. Department of Interior, Bureau of Land Management, Washington, DC.
- Jensen, A., Fredericksen, R., 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. *Sarsia* 77 (1), 53–69.
- Larsson, A.I., Purser, A., 2011. Sedimentation on the cold-water coral *Lophelia pertusa*: cleaning efficiency from natural sediments and drill cuttings. *Mar. Poll. Bull.* 62, 1159–1168.
- Lartaud, F., Pareige, S., de Rafelis, M., Feuillasseir, L., Bideau, M., Peru, E., Romans, P., Alcalá, F., Le Bris, N., 2013. A new approach for assessing cold-water coral growth *in situ* using fluorescent calcein staining. *Aquat. Living Res.* 26, 187–196 <http://dx.doi.org/10.1051/alr/2012029>.
- Lumsden, S.E., Hourigan, T.F., Bruckner, A.W., Dorr, G. (Eds.), 2007. NOAA Technical Memorandum CRCP-3.
- Lunden, J.J., Georgian, S.E., Cordes, E.E., 2012. Aragonite saturation states at cold-water coral reefs structured by *Lophelia pertusa* in the Northern Gulf of Mexico. *Limnol. Oceanogr.* 58, 354–362.
- Messing, C.G., Reed, J.K., Brooke, S.D., Ross, S.W., 2008. Ch. 27: Deep-Water Coral Reefs of the United States. In: Riegl, B., Dodge, R.E. (Eds.), *Coral Reefs of the USA*. Springer, pp. 763–788.
- Mienis, F., 2008. Environmental constraints on cold water coral growth and carbonate mound formation. Ph.D. dissertation, Royal Netherlands Institute for Sea Research. ISBN978-90-9023457-1.
- Morrison, C.M., Ross, S.W., Nizinski, M.S., Brooke, S., Jarnegren, J., Waller, R., Johnson, R.L., King, T.L., 2011. Genetic discontinuity between regional populations of *Lophelia pertusa* in the north Atlantic ocean. *Conserv. Genet.* 12, 713–729.
- Mortensen, P.B., 2000. *Lophelia pertusa* (Scleractinia) in Norwegian waters. Distribution, growth, and associated fauna. Thesis, Department of Fisheries and Marine Biology, University of Bergen, Norway.
- Mortensen, P.B., Rapp, H.T., 1998. Oxygen- and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L.) (Anthozoa: Scleractinia): implications for determination of linear extension rates. *Sarsia* 83, 433–446.
- Mortensen, P.B., Hovland, M., Brattegard, T., Farestveit, R., 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64 degrees N on the Norwegian shelf: structure and associated megafauna. *Sarsia* 80 (2), 145–158.
- Orejas, C., Gori, A., Gili, J.M., 2008. Growth rates of live *Lophelia pertusa* and *Madrepora oculata* form the Mediterranean Sea maintained in aquaria. *Coral Reefs* 27, 255.
- Orejas, C., Gori, A., Iacono, C.L., Puig, P., Gili, J.M., Dale, M.R.T., 2009. Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. *Mar. Ecol. Prog. Ser.* 397, 37–51.
- Packer, D.B., Boelke, D., Guida, V., McGee, L.-A., 2007. State of deep coral ecosystems in the northeastern US region: Maine to Cape Hatteras. In: Lumsden, S.E., Hourigan, T.F., Bruckner, A.W., Dorr, G. (Eds.), *The State of Deep Coral Ecosystems of the United States*. NOAA Technical Memorandum CRCP-3. Silver Spring, MD, pp. 195–232.
- Reed, J.K., 1992. Submersible studies of deep-water *Oculina* and *Lophelia* coral banks off southeastern U.S.A. *Proc. Am. Acad. Underwater Sci. 12th Ann. Scien. Diving Symp.*, 143–151.
- Riegl, B., Branch, G.M., 1995. Effects of sediment on the energy budgets of four scleractinians (Bourne 1900) and five alcyonaceans (Lamouroux 1816) corals. *J. Exp. Mar. Biol. Ecol.* 186, 259–275.
- Rice, S.A., Hunter, C.L., 1992. Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. *Bull. Mar. Sci.* 51, 429–442.
- Roberts, J.M., Long, D., Wilson, J.B., Mortensen, P.B., Gage, J.D., 2003. The cold-water coral *Lophelia pertusa* (Scleractinia) and enigmatic seabed mounds along the north-east Atlantic margin: are they related? *Mar. Poll. Bull.* 46, 7–20.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312, 543–547.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., Cairns, S.D., 2009. *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats*. Cambridge University Press, Cambridge p. 352.
- Rogers, A.D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *Int. Rev. Hydrobiol.* 84, 315–406.
- Ross, S.W., Nizinski, M.S., 2007. State of deep coral ecosystems in the U.S. southeast region: Cape Hatteras to southeastern Florida. In: Lumsden, S.E., Hourigan, T.F., Bruckner, A.W., Dorr, G. (Eds.), *The State of Deep Coral Ecosystems of the United States*. NOAA Technical Memorandum CRCP-3. Silver Spring, MD, pp. 233–270.
- Ross, S.W., Carlson, M.C.T., Quattrini, A.M., 2012. The utility of museum records for documenting distributions of deep-sea corals off the southeastern United States. *Mar. Biol. Res.* 8 (2), 101–114.
- Wagner, H., Purser, A., Thomsen, L., Cesar Jesus, C., Lundalv, T., 2011. Particulate organic matter fluxes and hydrodynamics at the Tisler cold-water coral reef. *J. Mar. Sys.* 85, 19–29.
- White, M., Mohn, C., de Stigter, H., Mottram, G., 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-Water Corals and Ecosystems*. Springer Verlag, Berlin, pp. 503–514.
- White, M., Roberts, J.M., van Weering, T., 2007. Do bottom intensified diurnal tidal currents shape the alignment of carbonate mounds in the NE Atlantic? *Geo. Mar. Lett.* 27, 391–397.