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Effectiveness of a deep-water coral conservation area: Evaluation of its boundaries and changes in octocoral communities over 13 years

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ABSTRACT

Over the past 15 years, multiple areas in the North Atlantic have been closed to destructive fishing practices to protect vulnerable deep-water coral ecosystems, known to provide habitat for diverse associated fauna. Despite the growing number of conservation measures, long-term studies on the recovery of deep-water coral communities from fisheries impacts remain scarce. In the Gulf of Maine, the Northeast Channel Coral Conservation Area (NECCCA)¹ was established in 2002 to protect dense aggregations of the two numerically dominant octocoral species in the region, *Primnoa resedaeformis* and *Paragorgia arborea*. To evaluate the effectiveness of the conservation measures, we monitored shifts in abundance and size of these two coral species in the shallow section (400–700 m) of the NECCCA for 12 years after the fisheries closure. We also evaluated the appropriateness of the location of the deep boundaries of the NECCCA that were placed based on a precautionary approach with limited information on coral distribution at depths > 500 m. Video transects were conducted with ROV “ROPOS” in 2001, 2006, 2010 and 2014. We found potential signs of recovery from fisheries impact at some of the shallow locations in 2014: higher coral abundance and the presence of some very large colonies as well as recruits compared to 2001 and 2006. However, spatial heterogeneity was pronounced and small colonies (< 20 cm) indicative of successful recruitment were not found at all sites, underscoring the need for long-term protection measures to allow full recovery of impacted coral communities. At 700–1500 m different coral taxa were dominant than at the shallow locations and coral abundance peaked between 700 and 1200 m. High abundance and diversity of corals at this depth range, 8–10 km southwest of the NECCCA, suggest that an extension of the southwest boundary should be considered. Comparably low coral abundance was found at depths of 1200–1500 m inside the NECCCA indicating an appropriate initial placement of the southeast boundary. These are the first long-term observations of protected deep-water octocoral communities which are needed for the effective management of deep-water coral conservation areas.

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1. Introduction

Deep-water corals enhance the structural complexity of the seafloor and provide habitat for a diverse associated fauna (Roberts et al., 2006). Fish and invertebrates, such as echinoderms and crustaceans, are found on and among the colonies for protection, feeding and attachment (De Clippele et al., 2015; Du Preez and Tunnicliffe, 2011; Husebø et al., 2002; Krieger and Wing, 2002; Stone, 2006). The detrimental effects of bottom fishing activities on deep-water coral ecosystems have been widely demonstrated (Clark et al., 2015). Bottom trawling is known to

impact coral communities severely (Althaus et al., 2009; Fosså et al., 2002; Hall-Spencer et al., 2002; Krieger, 2001), but colonies can also get damaged by long lines (Fosså et al., 2002; Mortensen et al., 2005) and are often brought up as bycatch (Breeze et al., 1997; Edinger et al., 2007; Taylor et al., 2013).

Due to longevity and slow growth rates, many benthic deep-water communities, such as corals and sponges, are expected to show slow recovery from fishing impacts (Clark et al., 2015). The recognition of deep-water coral ecosystems as vulnerable habitats has led to increasing efforts in conservation measures in the last 15 years (Brock et al., 2009; Davies et al., 2007; Hall-Spencer et al., 2009; Hourigan, 2009) and multiple areas in the North Atlantic have been closed to destructive fishing practices to protect these habitats (ICES, 2007). Many of these areas were established to protect scleractinian coral aggregations including several reefs of *Lophelia pertusa* in Norwegian waters. In the first deep-water coral

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conservation area, *Oculina varicosa* was protected from bottom fishing and anchoring off the coast of Florida in 1984 (ICES, 2007; Reed et al., 2007). An example of protection measures for coral gardens is the Northeast Channel Coral Conservation Area (NECCCA) in Atlantic Canada, which harbours dense aggregations of gorgonian corals (Breeze and Fenton, 2007; Mortensen et al., 2005). Coral gardens were added to the OSPAR list of threatened and/or declining species & habitats in 2008, encouraging their consideration in future conservation measures (OSPAR Commission, 2008, 2010). Recent efforts in deep-water coral conservation in the USA include the proposal of the Mid-Atlantic Fishery Management Council in 2015 to protect an area of ~98,000 km² from destructive fishing in the U.S. Exclusive Economic Zone.

Effective management of a conservation area requires a management plan with clear objectives; effectiveness of a conservation action should then be evaluated based on the defined targets (Halpern, 2003; Pomeroy et al., 2005). The response of an ecosystem to protection measures is strongly linked to the biology of the targeted species. While some reserves can show increased biomass, density and diversity of species within a few years, the response of slow-growing organisms to protection is expected to require a much longer time frame (Halpern and Warner, 2002). Information on life history traits and recovery times of protected species is essential to ensure a powerful link between biological responses and policy that is often not achieved (Gnanalingam and Hepburn, 2015). Recovery of an impacted system is regarded as the return of that system to conditions similar to the pre-disturbance state (Clark et al., 2015; Williams et al., 2010). Since deep-water ecosystems generally harbour slow-growing and long-lived species (Clark et al., 2015), protection measures need to be long-lasting to ensure recovery and retention of these habitats. In addition to the duration of protection, size, location, extent of ongoing fisheries and enforcement of regulations can influence the success of a conservation area (Edgar et al., 2014). Despite the growing number of conservation measures, long-term studies on the recovery of benthic deep-water communities from fisheries impacts remain scarce (Clark et al., 2015).

To protect dense aggregations of the two dominant octocoral species, *Primnoa resedaeformis* and *Paragorgia arborea*, a 424-km² conservation area was established in 2002 by the Canadian government in the Northeast Channel in Atlantic Canada. A “restricted bottom fishing zone” covers ~90% of the NECCCA and is completely closed to bottom fishing gear, while the remaining 10% is a “limited bottom fishing zone”, open to bottom long-line fishing with an at-sea observer (ESSIM Planning Office, 2006). The legislation of the NECCCA is provided by the Fisheries Act that prohibits the destruction and detrimental alteration of fish habitat (Department of Justice Canada, 1985). While dense coral aggregations were recorded at depths < 500 m prior to the establishment of the NECCCA (Mortensen et al., 2005), distribution patterns of corals in deeper ranges remained largely unknown at that time and the deep boundaries of the conservation area were placed on a precautionary approach.

The deep-water coral communities in the NECCCA were sampled on 3 occasions since 2001 (Lacharité and Metaxas, 2013; Mortensen and Buhl-Mortensen, 2004; Mortensen and Buhl-Mortensen, 2005; Mortensen et al., 2005; Watanabe et al., 2009). Here, we combine these datasets with new data collected in 2014 to explore changes in the deep-water coral assemblages over 13 years. In a resilient ecosystem, we would expect coral aggregations to return to pre-impacted conditions after the fisheries impact ceased (Williams et al., 2010). However, since fishing activities have a long history in the Gulf of Maine and coral bycatch has been reported over the last century (Breeze et al., 1997), the pre-disturbance state of the monitored coral assemblages remains unknown.

To assess whether “highest densities of coral communities are effectively protected” in the NECCCA, we investigated whether: (1) signs of recovery of coral communities were present at different sampling locations 12 years after the fisheries closure; and whether (2) the boundaries of the NECCCA were placed appropriately. Firstly, we monitored shifts in abundance and size of the two dominant octocoral species at depths < 700 m over 13 years. Coral size is regarded a fundamental life-history trait and changes over time can provide information on responses of coral populations to disturbances such as from fishing activities (McClanahan et al., 2008). We present the first long-term observations of population dynamics in these protected deep-water octocoral communities. We assumed the observations in 2001 to represent the impacted state of coral communities, while the dataset in 2014 could potentially show first indications of recovery 12 years after the establishment of the NECCCA. Secondly, we analysed coral distribution in the offshore deeper margins of the conservation area (> 900 m depth) which have not been studied before, to evaluate the current placement of the NECCCA boundaries. Dives conducted off the southwest boundary of the NECCCA provided information on coral communities immediately outside the conservation area. These data were used to assess the potential of a possible extension of the boundaries of the conservation area.

2. Materials and methods

2.1. Study area and sites

The Northeast Channel is situated between Browns Bank and Georges Bank and provides the only deep passage into the Gulf of Maine (Ramp et al., 1985). Water circulation is largely influenced by tidal currents, where the inflowing water into the Gulf is composed of Warm Slope Water and Labrador Slope Water, while the outflow mainly consists of Maine Intermediate Water (Ramp et al., 1985). Along this Channel multiple canyons are found at depths of ~300 to 1100 m (Twomey and Signell, 2013) that harbour deep-water coral aggregations (Metaxas and Davis, 2005; Mortensen and Buhl-Mortensen, 2004).

Coral communities in and around the NECCCA in the Gulf of Maine were sampled with the ROV ROPOS in August 2001, July 2006, August 2010 and June 2014 (Fig. 1). Data collected in 2001 were used to establish the NECCCA in 2002 (Mortensen et al., 2005) and this is considered the baseline dataset.

Abundance of the two dominant octocoral species, *Primnoa resedaeformis* and *Paragorgia arborea*, was documented at three locations (site 1, site 2, site X; Fig. 2, Table 1) and size frequency distributions at four sites (site 1, 2, X, Z) inside the NECCCA between 26 and 27 June 2014. Mortensen and Buhl-Mortensen (2004) reported coral abundances for ROV dives in 2001, the location of which partially overlapped with our sites 1 and 2; we measured size frequency distributions at these locations using video collected in 2001. Both parameters were also investigated at site X and site Z in 2006 (Watanabe et al., 2009). Details on the methods and data collection can be found in Mortensen and Buhl-Mortensen (2004) and Watanabe et al. (2009).

Additional dives were conducted inside (Fig. 1, Table 2; R1359, 2010) the NECCCA, along the deep boundary (R979, 2006 and R1358, 2010) and outside the NECCCA (R1705, 2014) to determine coral distribution and abundance at depths of 685–1583 m.

In 2014, ROV tracks were reconstructed with 1 Hz positioning data. The Ocean Floor Observation Protocol 3.3.5.i (OFOP) was used to remove obvious outliers and smooth the tracks. Using OFOP, dive tracks were linked to videos and all coral locations were annotated.

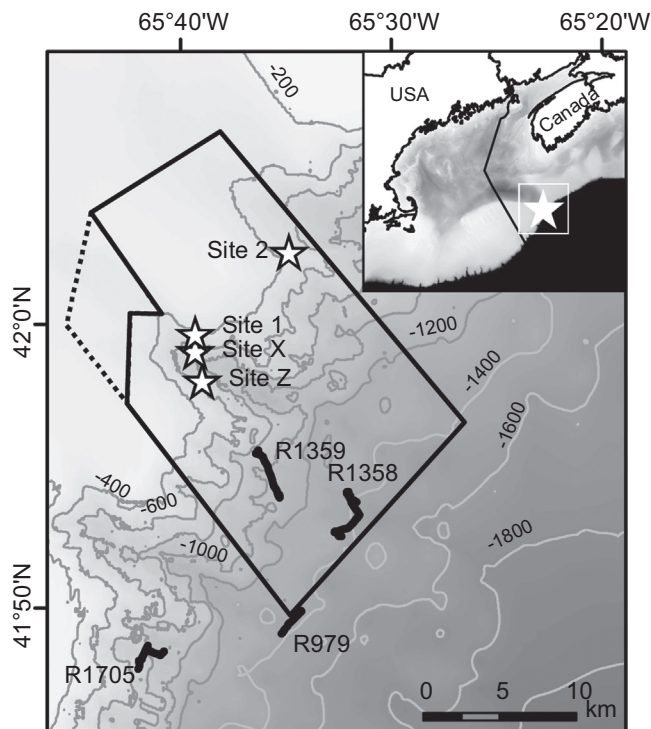


Fig. 1. Dive locations for measurements of coral abundance and/or size frequency (white stars) and ROV tracks (black lines) with associated dive numbers for deep dives in and around the Northeast Channel Coral Conservation Area (restricted (solid polygon) and limited (dashed line) bottom fisheries zones) in the Gulf of Maine between 2001 and 2014. A 3-arcsecond bathymetry grid was provided by the U.S. Geological Survey (Twomey and Signell, 2013). All maps were created in ArcGIS 10.1 and are displayed in a projected WGS 1984 UTM 20N coordinate system.

2.2. Abundance

In 2014, we measured coral abundance using 10 (site 1, site 2) or 8 (site X) parallel video transects of ~100 m in length taken by a downward-oriented HD camera at altitudes of 2.7–4.3 m above the seafloor. The downward-looking position was adjusted during the transects to account for changes in the slope of the seafloor. To avoid underestimation of the field of view due to slightly varying angles of the camera, corals were only counted if they appeared on the same plane as 2 scaling lasers. To minimise perspective distortion towards the sides of the 16:9 frame, 1/6 on both sides of the video frame were not included in the analysis, leading to a 10.7:9 aspect ratio. Every coral colony that was inside the remaining 2/3 of the frame width was counted, but colonies were excluded if their base was outside the defined area. For dense aggregations of *P. resedaeformis*, individual bases were often indistinguishable and the extent of colonies was estimated based on their shape and the assumed position of the bases.

The width of field of view was measured every 10 m along transects and averaged for each 100-m transect. In strong currents, the ROV moved laterally which also altered the camera angle (e.g. in case of a 90° change of direction of the ROV the camera aspect ratio would change from 16:9 to 9:16). The angle for lateral movement of the ROV was calculated using the forward and sideward velocity vectors provided by ROPOS, which relate the course over ground to the heading. This angle was used to calculate an angle-corrected field of view. The actual length of each transect was measured in ArcGIS 10.1. The area analysed per transect was the product of the width of the field of view and transect length. Abundance of coral colonies was calculated for each transect relative to the transect area.

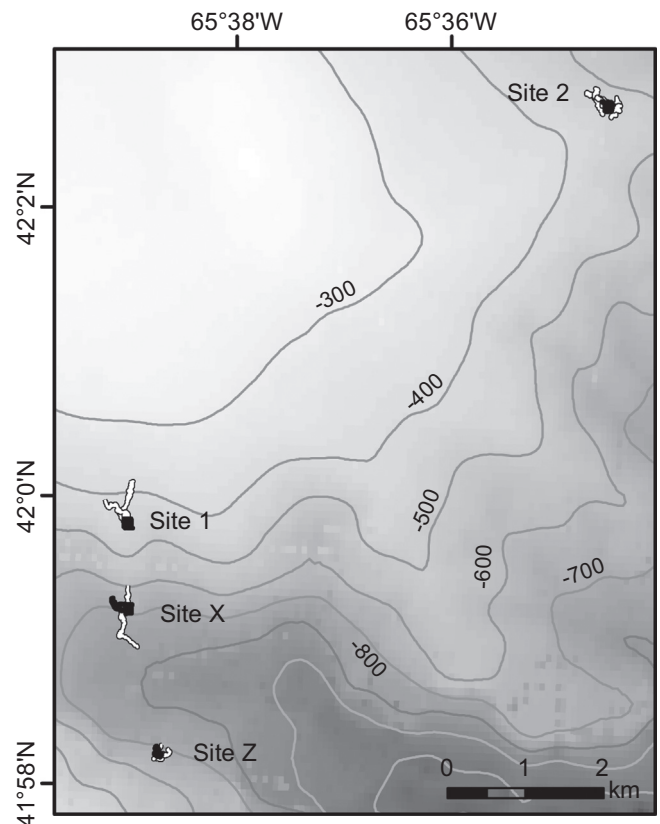


Fig. 2. Locations of measurements of coral abundance and/or size frequency during ROV dives in 2001 (site 1, 2; white lines), 2006 (site X, Z; white lines) and 2014 (site 1, 2, X, Z; black lines) inside the Coral Conservation Area in the Gulf of Maine. Detailed maps of coral locations used for size frequency measurements at each site can be found in the appendix (S1–S4). Bathymetry by U.S. Geological Survey (Twomey and Signell, 2013).

For the first transect at site 1 and site 2, the positioning signal was not stable. For these sections, contiguous frame grabs were taken from the video and the analysed area was measured for each image. At site X, recording of the downward-looking camera failed during the first 5 transects. Additionally, the downward-looking setup could not be maintained during sections of the remaining 3 transects because of a rapid change in topography. Only 3 transects (54, 55 and 71 m in length, respectively) on top of the steep feature were suitable for analysis. To better represent coral patterns for the entire site, video footage from the forward-looking camera was also utilised at this site. In this case, width of field of view was measured every 5 m. Overall, 9 transects of different lengths were analysed that were divided into three categories: lower plateau, wall and upper plateau. For two transects along the wall, only the middle 40% of the frame area could be used due to the camera angle. For sections where the ROV was moving vertically along the steep wall, the 3D transect length was calculated in ArcGIS. Since the forward-facing camera was laterally adjustable, the width of field of view was not angle-corrected. A higher smoothing level was applied to the positioning data to minimize overestimation of transect length by erratic positioning signals that occurred particularly at the wall parts.

Sections of transects in dives R639 and R640 in 2001 were done at site 1. Dive R640 directly intersected the transect area sampled in 2014, while dive R639 only reached the northwest corner of site 1 at the end of the dive. Dives R637 and R642 in 2001 directly intersected the abundance transects done at site 2 in 2014, while dives R636 and R637 were done at a maximum distance of 150 m from the measurements in 2014. Abundances of corals were reported by Mortensen and Buhl-Mortensen (2004) for the entire

length of each dive in 2001. Watanabe et al. (2009) presented abundance of corals around site X (dive R974-NEC3) and site Z (dive R974-NEC4 and R978-NEC4) in 25-m depth intervals, without providing precise locations of the analysed area. For those sites, we used abundances that were in the same depth range as the dives in 2014.

For the deeper dives in 2010 (R1358, R1359) and 2014 (R1705) a different approach was used to determine coral abundance because these dives covered large areas and were done along individual long transects. Images from the downward-looking camera were taken every 10 m along transects and reduced by 1/6 on each side. Coral abundance was related to the analysed area measured in each frame. Additionally, every coral seen in the forward-facing camera was annotated to detect potentially rare coral species. Visual identification was particularly difficult in case taxa were rare ($n \leq 3$) and no close-ups of the colonies could be obtained. These corals are not included here.

Image subsamples taken every minute along transects during a ROV dive (R979) at the southeast boundary of the NECCCA between 1410 and 1583 m depth in 2006 were not analysed in detail and only used to confirm the presence of corals annotated in the live logs during the dive.

2.3. Size frequency

Size frequency distribution of *P. resedaeformis* and *P. arborea* was measured at two sites in 2001 (site 1, site 2) and at four sites in 2014 (site 1, site 2, site X, site Z). In 2014, the ROV landed on the seafloor and the forward-looking camera including scaling lasers (10 cm apart) directly pointed onto the coral colony to be measured. If the lasers could not be projected onto the colony, they were placed onto the same plane, e.g. the substrate. To minimize the error of 2D measurements in a 3D environment, only colonies growing in a $\sim 90^\circ$ ($\pm 20^\circ$) angle to the camera were measured.

Table 1
Characteristics of dive sites and dives conducted with the ROV ROPOS in the Northeast Channel Coral Conservation Area for measurements of coral abundance and size frequency distributions in 2001, 2006 and 2014.

Location	Dive	Date	Bottom time (h:mm)	Latitude start	Longitude start	Latitude end	Longitude end	Depth (m)
Site 1	R639	21.08.2001	1:04	41.998874	-65.648410	41.998274	-65.649306	421-427
Site 1	R640	21./22.08.2001	2:28	41.996730	-65.647590	41.998504	-65.649316	422-455
Site 1	R1703-1	26.06.2014	2:46	41.997481	-65.647985	41.997553	-65.648040	428-466
Site 2	R636	20.08.2001	1:45	42.047578	-65.574066	42.045780	-65.574944	462-498
Site 2	R637	20./21.08.2001	2:21	42.046800	-65.574960	42.048236	-65.577870	463-486
Site 2	R638	21.08.2001	1:36	42.046262	-65.576256	42.047702	-65.577170	457-476
Site 2	R642	22.08.2001	2:24	42.047084	-65.576382	42.047980	-65.577188	457-486
Site 2	R1704	26./27.06.2014	5:12	42.047321	-65.575948	42.047489	-65.576358	466-489
Site X	R974-NEC3	16.07.2006	2:03	41.982731	-65.645815	41.989855	-65.647565	600-751
Site X	R1703-x	26.06.2014	5:41	41.987527	-65.647713	41.986971	-65.647098	636-691
Site Z	R974-NEC4	16./17.07.2006	0:44	41.971073	-65.640457	41.969837	-65.642763	650-701
Site Z	R978-NEC4	19.07.2006	5:33	41.971546	-65.641575	41.970372	-65.642393	651-702
Site Z	R1703-z	26.06.2014	1:12	41.970133	-65.641751	41.970515	-65.641763	664-699

Positions, depths and bottom times for the dives in 2001 are given for dive sections inside a 150-m radius from measurements in 2014. In 2006, dive parts inside the same depth ranges as in 2014 are listed.

Table 2
Characteristics of ROPOS dives in deeper regions inside and outside the Coral Conservation Area to measure coral distribution and abundance in 2006, 2010 and 2014.

Dive	Date	Bottom time (h:mm)	Latitude start	Longitude start	Latitude end	Longitude end	Depth (m)	Area analysed (m ²)
R979	19.07.2006	2:01	41.834937	-65.559166	41.823001	-65.572213	1410-1583	223
R1358	09.08.2010	4:46	41.902352	-65.521091	41.882977	-65.532942	1239-1521	376
R1359	10.08.2010	3:19	41.902442	-65.577759	41.928051	-65.597321	900-1187	470
R1705	27.06.2014	4:23	41.809348	-65.665125	41.798851	-65.684938	685-1021	426

Bottom time is the total dive time spent on transects for coral abundance.

Table 3
Primnoa resedaeformis and *Paragorgia arborea*. Mean abundance at four locations inside the Coral Conservation Area in 2001 (site 1 and site 2), 2006 (site X and site Z) and 2014 (site 1, site 2, site X). Ranges for multiple dives are provided at site 1 and site 2 in 2001. For 2014, the weighted mean abundance and weighted SD are given.

Site	Year	Depth m	Area analysed m ^{2a}	<i>Primnoa resedaeformis</i>			<i>Paragorgia arborea</i>			Reference
				n	100 m ⁻²	SD ^a	n	100 m ⁻²	SD ^a	
1	2001	387-452	na	12-36	1.9-3.6	na	1-5	0.2-1.1	na	Mortensen and Buhl-Mortensen (2004)
1	2014	431-459	2473	51	2.06	1.79	3	0.12	0.19	This study
2	2001	457-498	na	162-582	10.6-37.6	na	16-89	0.9-4.0	na	Mortensen and Buhl-Mortensen (2004)
2	2014	467-487	2678	1437	53.66	20.21	202	7.54	2.96	This study
X	2006	625-700	446	183	41.03	30.85	2	0.45	1.90	Watanabe et al. (2009)
X	2014	639-691	1174	604	51.45	22.65	87	7.41	11.56	this study
Z	2006	650-700	381	139	36.47	36.63	30	7.87	13.94	Watanabe et al. (2009)

n=number of recorded colonies, SD=standard deviation.

^a na=not available in Mortensen & Buhl-Mortensen (2004).

Overtaken but alive colonies were included, while colonies with mainly dead branches were excluded. Corals growing on a wall were measured while the ROV was moving. A few colonies of *P. arborea* were measured when the ROV was not touching the ground, but the $90 \pm 20^\circ$ requirement was maintained. Colony length was defined as the linear extension along the main direction of growth starting at the base of the coral. A box was projected around each colony and its dimensions specified length and width of the colony. For tall colonies of *P. arborea* with very large bases, length was measured from the estimated origin of the main stem. Frame grabs of every colony were taken with OFOP and size was measured with the image processing software ImageJ.

For 2001, Mortensen and Buhl-Mortensen (2005) reported size frequency distributions pooled along different locations in the Northeast Channel, including data from ROV ROPOS dives. We extracted coral images from these videos for our specific locations at site 1 and site 2 that met the same requirements for camera angle and laser pointers as in 2014. A 150-m radius was drawn around the location of coral measurements in 2014 and only corals within this radius were measured for 2001. Size frequency distribution was measured at site 1 and site 2 mostly while the ROV was moving.

Watanabe et al. (2009) reported size frequency distributions around site X and site Z in 50-m depth intervals. At site X, we extracted size data at the corresponding depth range of 600–700 m. Since this yielded only 7 measurements for *P. arborea*, data from 700–750 m depth were added to increase sample size. At site Z, coral sizes measured at depths of 650–700 m were extracted for comparison with sizes in 2014.

During abundance transects at site 2, a fishing line was observed in 2014. In 2001, a fishing line was documented 50–80 m northwest of the 2014 observations. No line was found

there in 2014. Since both lines seem to follow a similar pattern, we assume it is the same fishing line and that there was a positional offset in the 2001 dataset. Based on this offset, we believe that the 150-m radius around the 2014 measurement locations should include all colonies in the direct proximity measured in 2001.

2.4. Statistical analyses

Mean coral sizes were compared between 2001 and 2014 at site 1 and 2 and between 2006 and 2014 at site X and Z with Student's t-tests, if variances were homogenous and distributions were normal. Welch's t-test was used in cases of heterogeneous variances. If distribution was not normal, data were ln-transformed. This led to an approximate normal distribution only for *P. resedaeformis* at site Z. If normal distribution could not be achieved using transformations, Mann–Whitney–Wilcoxon tests were conducted instead.

Since size frequency distributions were not normal for all sampling locations, we tested differences in coral size among site 1, site 2, site X and site Z using Kruskal–Wallis rank sum tests. Pairwise comparisons were done using Wilcoxon rank sum tests with Bonferroni adjusted *p*-values.

All analyses were conducted in R Studio (Version 0.98.1103).

3. Results

3.1. Spatial and temporal patterns in abundance

Abundance of corals ranged between 2.06 and 53.66 colonies 100 m^{-2} for *P. resedaeformis*, and 0.12 and 7.54 colonies 100 m^{-2} for *P. arborea* in 2014 (Table 3). The minimum detectable size was

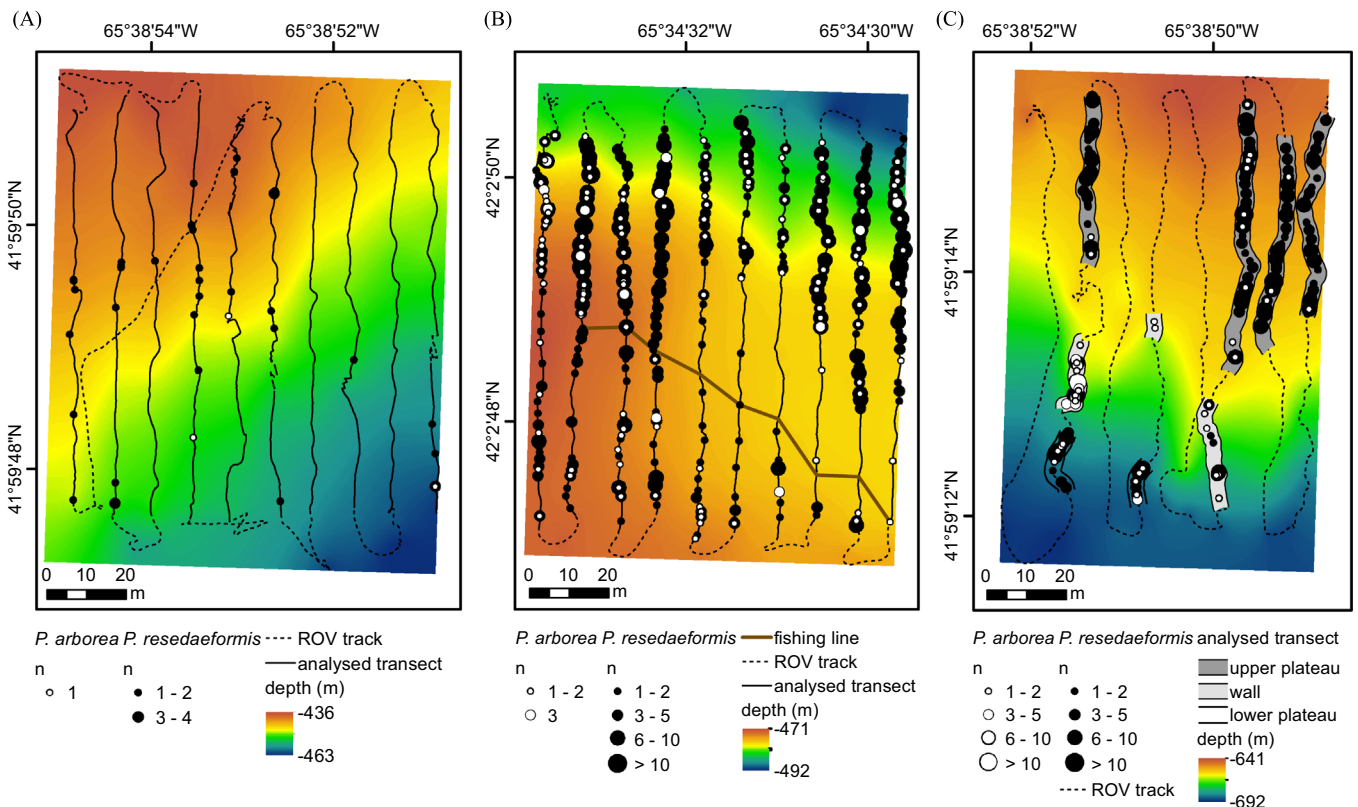


Fig. 3. *Paragorgia arborea* and *Primnoa resedaeformis*. Coral locations along abundance transects at site 1 (A), site 2 (B) and site X (C) inside the Coral Conservation Area in 2014. At site 1 and 2, the bathymetry grid was interpolated from ROV depth and altitude along 10 transects and at site X it was interpolated from ROV depth along 8 transects in ArcGIS.

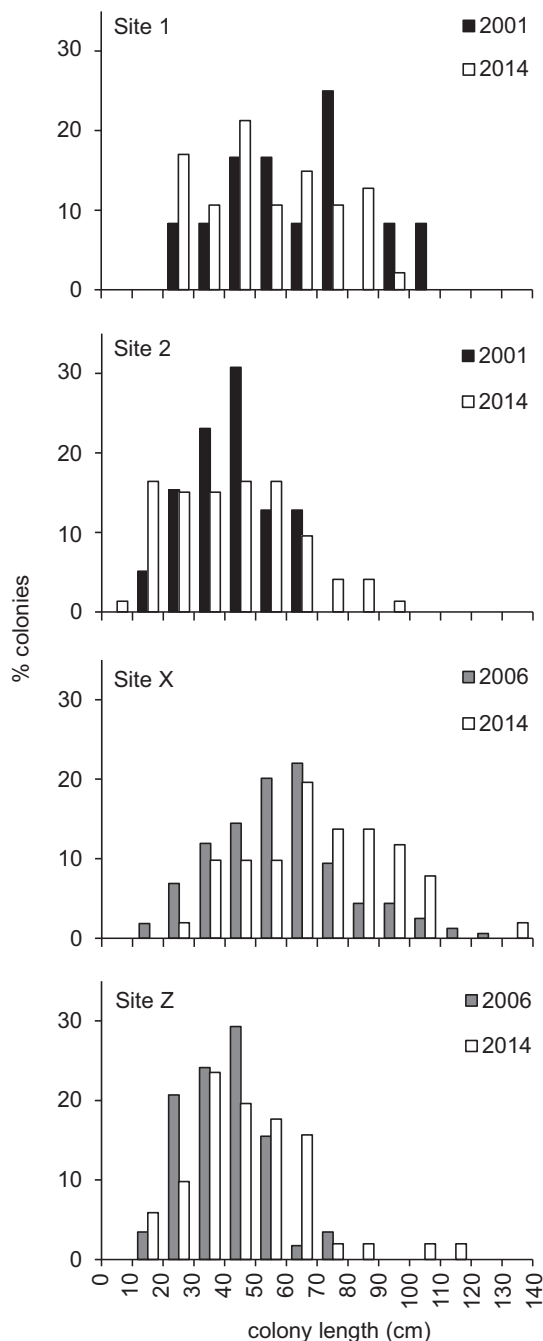


Fig. 4. *Primnoa resedaeformis*. Size frequency distributions at each of four sites inside the Coral Conservation Area in 2014 (white), 2001 (black) and 2006 (grey). For 2001, measured colonies included those ≤ 150 m from colonies measured in 2014. In 2006, corals at depth ranges of 600–700 m (site X) and 650–700 m (site Z) were included (see methods).

3.3. Patterns in coral abundance at the deeper margins of the NECCA

Seventeen coral taxa were recorded during the three dives between 700 and 1500 m depth (Fig. 6, Table 7) and *Acanella* sp. and *Anthomastus* sp. were among the numerically most dominant corals. Coral abundance and diversity was lowest at the deepest dive (1239–1521 m), and most of the corals were present at the shallower (~ 1300 m), southern section of the dive (Fig. 7). In contrast, corals were present throughout the other deep dive within the NECCA (Fig. 8). Abundance was greatest for *Anthomastus*, but this taxon was sparse in the southwest section of the

dive. Many colonies (> 200) of *Acanella*, the whip coral *Radicipes* sp., a *Keratoisis*-like bamboo coral and the sea pen *Halipteris* sp. were recorded, mostly in the deeper section of the dive (transect 2, > 1000 m). During dive R1705, *Anthomastus* and colonies of the family Nephtheidae were the numerically dominant taxa (Table 7), with most Nephtheidae occurring on the most shallow transect (700–800 m, Fig. 9). Due to their transparent texture, corals of the family Nephtheidae were difficult to detect and we likely underestimated their abundance. *Acanella* and other Isidids were observed in high numbers ($n \geq 195$) over the entire dive with only a few *Keratoisis*-like colonies at the shallow transect (Fig. 9D). A small white sea pen (Order Pennatulacea) was present on this dive but was difficult to see resulting in underestimates of abundance.

All coral taxa were identified visually by their morphotype from HD videos of the two cameras. For corals showing very characteristic features or occurring frequently (*Acanella*, *Anthomastus*, *Halipteris*, *Paragorgia*, *Primnoa*, *Pennatula*) identification was more accurate than for rare and small taxa. *Acanthogorgia*-like, *Anthothela*-like, *Clavularia*-like and *Radicipes*-like corals were observed and are also presented with the genus name. Due to their shape, smaller size or low abundance detailed identification was difficult for some observations. Close-ups for some of these records were obtained and corals were identified as belonging to these taxa. Similar looking colonies were labelled accordingly. Many observations of white bamboo corals were obtained and most of the larger colonies were likely *Keratoisis* sp., but especially small corals of 1–2 branches could not be identified in detail, although they could be recruits of *Keratoisis*. These observations are grouped as “Isididae b”. Since another taxa of the family Isididae could clearly be distinguished, they are listed separately as “Isididae a” (Table 7). Small corals, such as the cup corals *Javania* sp. and *Desmophyllum* sp. are often difficult to distinguish visually and are easily missed on videos taken by the wide angled forward-looking camera and actual abundance could thus be higher than presented.

The presence of *Acanella* and *Anthomastus* was confirmed from images taken along the southeast boundary of the Coral Conservation Area at 1410–1583 m depth in 2006.

4. Discussion

4.1. Fisheries impact and recovery potential of coral communities

We found signs of potential recovery at some of our sampling locations 12 years after the fisheries closure, as indicated by higher coral abundance and the presence of some very large colonies and of recruits. However, the absence of small colonies at other sampling sites indicated slow recovery potential from fisheries impact which is generally assumed to be the case for benthic deep-sea ecosystems (Clark et al., 2015). We assumed that abundance and size distributions at site 1 and site 2 in 2001 (1 year before the closure came into effect) indicate the impacted state of coral communities.

The presence of higher numbers of large colonies in 2014 than in previous years could indicate recovery from fisheries impact. Bycatch and damage of corals by lines and nets likely has a bigger impact on large colonies, since they are more easily entangled in fishing gear than small recruits (Krieger, 2001). In Atlantic Canada, Mortensen et al. (2005) observed a lower average size for colonies of *P. arborea* in 2001 than reported by Verrill, (1922) for the late 19th century. They speculated that Verrill’s dataset may have been biased towards large specimens, since their sampling material was mainly collected as bycatch from longlines. The establishment of the NECCA in 2002 should have enabled the growth of large colonies that were experiencing fisheries-induced mortality

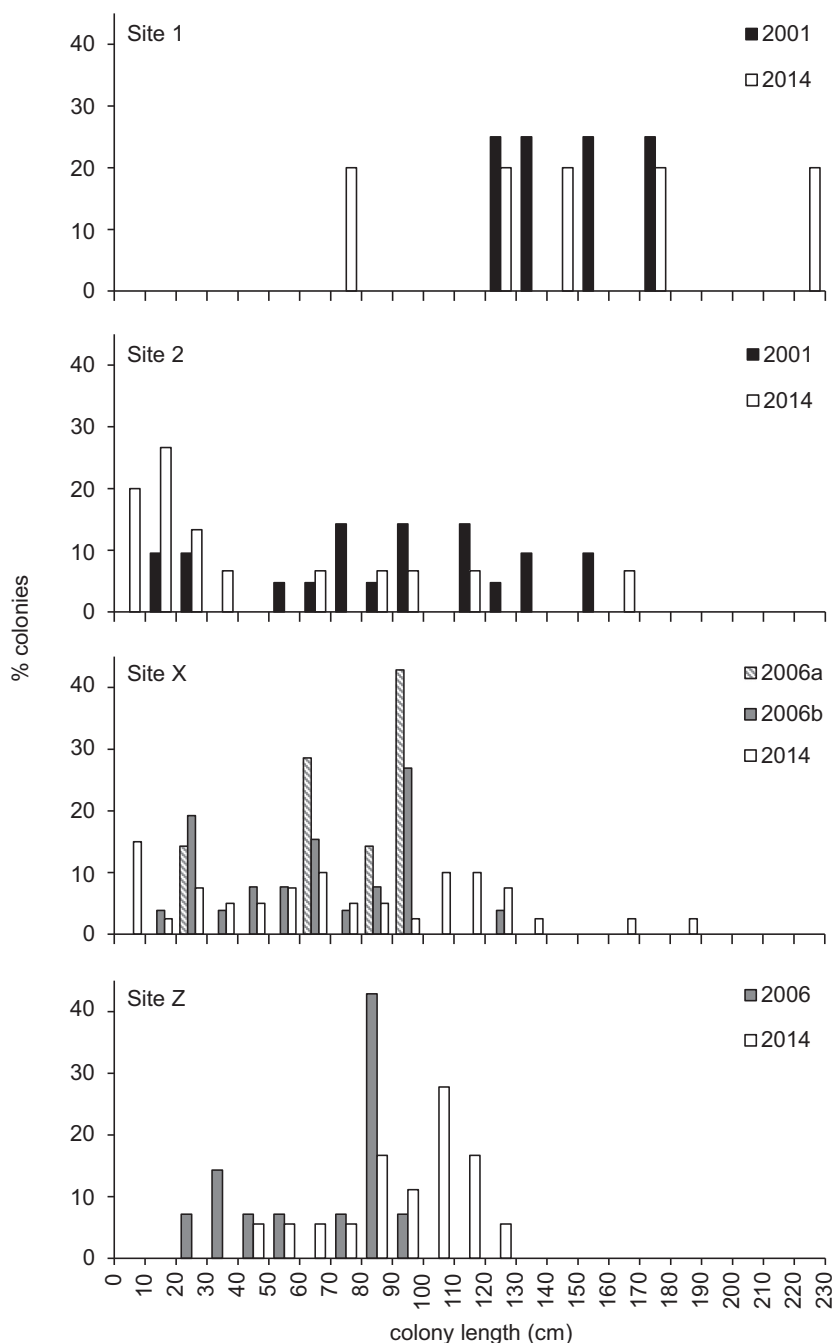


Fig. 5. *Paragorgia arborea*. Size frequency distribution at four sites inside the Coral Conservation Area in 2014 (white), 2006 (grey) and 2001 (black). For 2001, measured colonies included those ≤ 150 m from colonies measured in 2014 (solid black). In 2006, corals at 600–750 m (site X, 2006a, grey stripes), 600–700 m (site X, 2006b, solid grey) and 650–700 m (site Z) depth were included.

previously. The largest colonies of both species were found at all sites (except for *P. resedaeformis* at site 1) in 2014. To a certain extent, this may be explained by the continued growth of tall colonies that were not damaged by fishing gear inside the conservation area. This can be regarded as a sign of recovery of the system now harbouring colonies in large size classes that likely were abundant at the pre-impact state. However, growth rates for *P. resedaeformis* are assumed to decrease with age (Mortensen and Buhl-Mortensen, 2005; Sherwood and Edinger, 2009) and full regrowth of tall colonies requires a much longer time frame than the study period of 13 years.

The significantly higher average size of *P. resedaeformis* in 2014 at site X than at all other sampling locations, and the presence of

colonies > 90 cm in 2006 and 2014 could indicate low fisheries impact in terms of removal of large colonies. The steep terrain features might have limited access of bottom fishing gear to this area. Similarly, Clark et al. (2010) found intact coral colonies on a section of a seamount that was too heterogeneous for fishing.

Signs of recovery of coral communities in terms of abundance and recruitment were variable among our four sampling sites. Reproductive output in some octocorals is known to increase with size (Coma et al., 1995; Santangelo et al., 2003) and thus the removal of large colonies could have led indirectly to an overall lower recruitment rate of the coral populations. Without fisheries-induced mortality, signs of recovery would be manifested as increased coral abundance over time due to successful

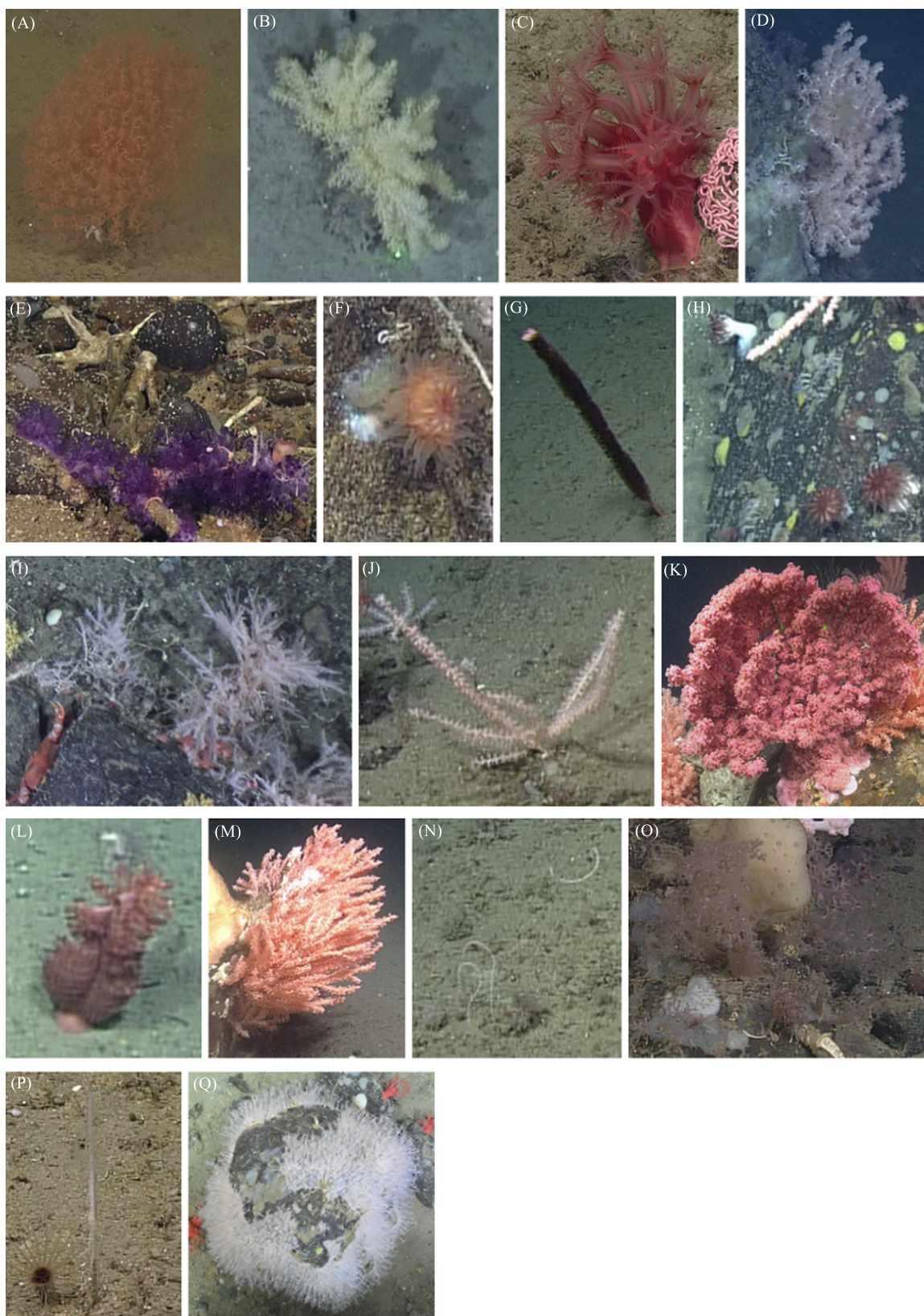


Fig. 6. Coral observations along deep dives at 685–1583 m depth. *Acanella* sp. (A), *Acanthogorgia* sp. (B), *Anthomastus* sp. (C), *Anthothela* sp. (D), *Clavularia* sp. (E), cup coral, likely *Desmophyllum* sp. (F), *Halipterus* sp. (G), cup coral, likely *Javania* sp. (H), Isididae, likely *Isidella* sp. (I), Isididae, likely *Keratoisis* sp. (J), *Paragorgia* sp. (K), *Pennatula* sp. (L), *Primnoa* sp. (M), *Radicipes* sp. (N), Nephtheidae (O), Pennatulacea (P), Stolonifera (Q).

recruitment, in turn indicated by the presence of small colonies. Growth rates of small-sized colonies of *P. resedaeformis* can only be estimated from very few observations, while data for *P. arborea* are

lacking completely. Growth rates of $\sim 2 \text{ cm yr}^{-1}$ were reported for colonies of *P. resedaeformis* < 30 years old (Mortensen and Buhl-Mortensen, 2005) and the largest recruit of *P. resedaeformis* found

Table 7
Occurrences of corals obtained from forward- and downward-looking cameras and coral abundance for deep dives R1358 (1239–1521 m), R1359 (900–1187 m) and R1705 (685–1021 m) inside (R1358, R1359) and outside (R1705) the Coral Conservation Area. Weighted mean abundance and weighted SD are given.

	R1358				R1359				R1705			
	Coral observations		Abundance	SD	Coral observations		Abundance	SD	Coral observations		Abundance	SD
	Forward n	Downward n	(100 m ⁻²)		Forward n	Downward n	(100 m ⁻²)		Forward n	Downward n	(100 m ⁻²)	
<i>Acanella</i>	60	3	0.80	8.36	276	8	1.70	12.14	310	16	3.76	11.44
<i>Acanthogorgia</i>					36	2	0.43	4.71	47	1	0.23	3.72
<i>Anthomastus</i>	23	13	3.45	50.79	2603	95	20.21	54.47	805	80	18.80	58.66
<i>Anthothela</i>									2			
<i>Clavularia</i>					13	1	0.21	4.96	3			
<i>Desmophyllum</i>									8			
<i>Halipteris</i>	2				235	8	1.70	12.62	40	2	0.47	3.51
<i>Javania</i>					36	7	1.49	13.56	1			
<i>Paragorgia</i>					9				10			
<i>Primnoa</i>									25			
<i>Pennatula</i>					15				1	1	0.23	1.87
<i>Radicipes</i>	4				262	20	4.25	21.66	28	11	2.58	33.09
Isididae ^a					6	1	0.21	3.75				
Isididae ^b	1				549	22	4.68	20.33	195	12	2.82	11.71
Nephtheidae		1	0.27	5.68					825	168	39.47	110.11
Pennatulacea ^c									6	2	0.47	3.57
Stolonifera, white ^d					7				6			

n=number of recorded colonies, SD=standard deviation.

^a White colonies of the family Isididae, likely *Isidella* sp.

^b White colonies of the family Isididae, most of them likely *Keratoisis* sp.

^c Small white sea pen.

^d Aggregations of white stoloniferous colonies could not be identified visually in more detail than the suborder.

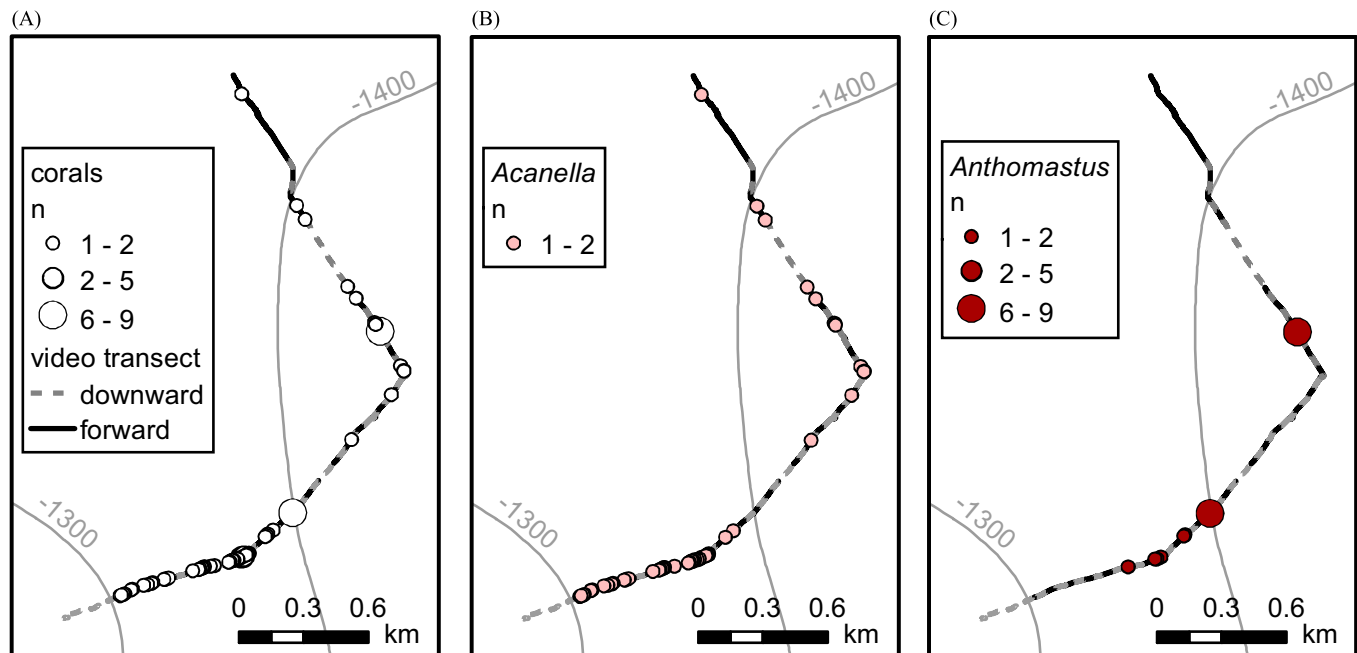


Fig. 7. Coral locations along video transects of the forward-looking camera (solid black line) during dive R1358 at 1239–1521 m depth inside the Coral Conservation Area in 2010 for all corals (A), *Acanella* sp. (B) and *Anthomastus* sp. (C). Bathymetry grid lines were extracted from a 3-arcsecond digital elevation model of the Gulf of Maine (Twomey and Signell, 2013) and do not necessarily follow small-scale patterns observed during the dives.

on settlement collectors deployed for 4 years in the NECCA was 1.2 cm in size (Lacharité and Metaxas, 2013) leading to a minimum possible growth rate of 0.3 cm yr⁻¹. A recruit of *P. resedaeformis* in the NECCA at 863 m grew from ~1.7 to ~23.2 cm in 8 years leading to a growth rate of ~2.7 cm yr⁻¹ (Bennecke et al., 2016). From these observations, we assume a time span of ~15 years to be sufficient to yield newly recruited colonies of *P. resedaeformis* ~20 cm in size. However, this assumption is based on a single

observation and certainly not every colony < 20 cm will have recruited in the past 15 years.

In 2014, successful recruitment was indicated by the presence of small colonies (< 20 cm) at two of our four sites for each of the two coral species. In striking contrast were the patterns at the two shallow sites (440–490 m) between 2001 and 2014. With low abundance of both species before and after the NECCA establishment and the lack of small colonies, site 1 seems to harbour comparably old coral

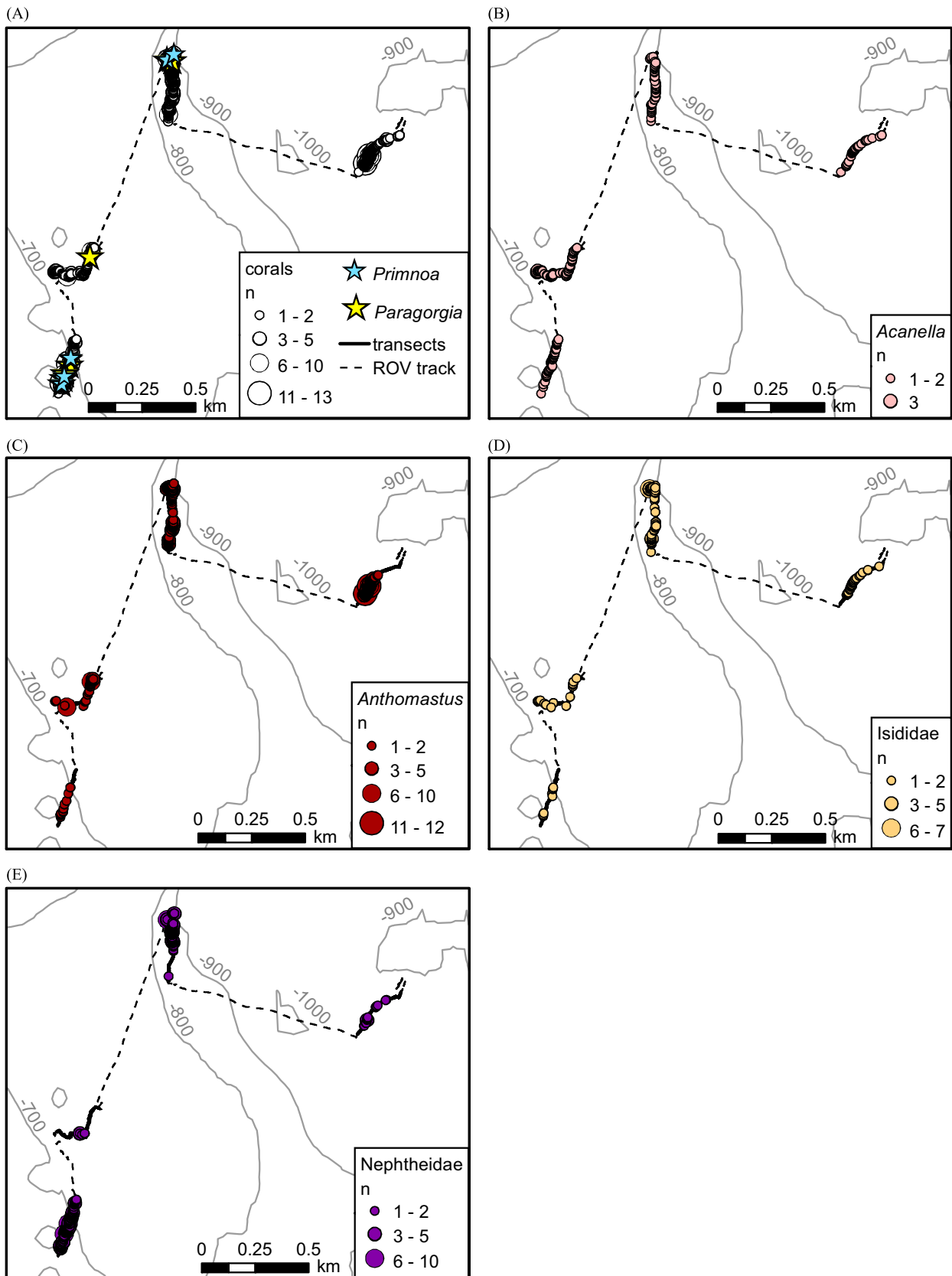


Fig. 9. Coral locations along four transects during dive R1705 at 685–1021 m depth outside the Coral Conservation Area in 2014 for all corals (A), *Acanella* sp. (B), *Anthomastus* sp. (C), white *Keratoisis*-like Isididae (D), Nephtheidae (E). Bathymetry grid lines were extracted from a 3-arcsecond digital elevation model of the Gulf of Maine (Twomey and Signell, 2013) and do not necessarily follow small-scale patterns observed during the dives.

composition and availability or biological disturbances, such as by the high abundance of brittle stars observed in the Northeast Channel (Metaxas and Giffin, 2004). Predictive habitat models have shown *P. arborea* and *P. resedaeformis* to preferably inhabit slopes or topographic highs (Bryan and Metaxas, 2007; Tong et al., 2012). While the abundance of *P. resedaeformis* was lower at the steep wall features at site X compared to areas of lower slope in 2014, *P. arborea* occurred more frequently on these features than at plateaus. These small-scale terrain features may reflect different preferred habitats of these two species that often, but not always, co-occur. Site 1, where coral abundance was extremely low and no recruits were found, and site X are located 1 km apart and separated by a 200-m depth gradient. These observations indicate the important influence of small-scale patterns on population dynamics of deep-water octocorals. The critical role of local patterns has been suggested previously based on differences in size and abundance of coral recruits at site X and Z between 2006 and 2010 (Lacharité and Metaxas, 2013).

The low frequency of colonies of *P. resedaeformis* < 20 cm (except at Site 2 in 2014) could indicate low recruitment overall. However, recruitment of *P. resedaeformis* may be cryptic and at least some of the colonies in our study may have been aggregations of multiple smaller colonies. In dense aggregations of *P. resedaeformis*, it was often difficult to identify individual colonies and coral branches without a distinguishable separate base were regarded as belonging to a single colony. However, basal structures of old colonies of *Primnoa* spp. can provide settlement substrate for recruits (Andrews et al., 2002; Krieger, 2001), and a single specimen may be composed of colonies of different ages. We observed recruits of *P. resedaeformis* at the base of an old colony at site X, but could not measure them accurately and did not include them in our analysis. The complete lack of small corals at site 1 and X in 2014 could have been the result of a limitation of the non-invasive sampling method. In contrast, the presence of multiple colonies < 20 cm at sites 2 and Z indicated recent recruitment. Continuous recruitment of *P. resedaeformis* was suggested for our sampling sites X and Z, where *P. resedaeformis* recruited between 2006 and 2010 (Lacharité and Metaxas, 2013). Most recruits were in the primary polyp stage and high mortality of this life stage was assumed (Lacharité and Metaxas, 2013). High post-settlement mortality and cryptic recruitment may explain the apparent lack of small colonies at some of our sites.

Overall, most size-frequency distributions of *P. resedaeformis* were normal with few very small and few very large colonies. Similarly, Watanabe et al. (2009) found that the most abundant size class for the same species in Northeast Channel was 50 cm. Approximate normal distributions of size frequency measurements were also found for some populations of the gorgonian corals *Paramuricea clavata* and *Eunicella singularis* in the Mediterranean Sea (Gori et al., 2011; Linares et al., 2008). For *P. resedaeformis*, decreasing growth rates with age (Mortensen and Buhl-Mortensen, 2005; Sherwood and Edinger, 2009) and low mortality of large colonies may explain the accumulation of corals in a size range of 40–70 cm. Reduced mortality rates with size have been observed for *Paramuricea* spp. in the Gulf of Mexico (Doughty et al., 2014). In contrast, determinate colony size may explain the low frequency of very large corals, as in the shallow-water Caribbean octocoral *Pseudopterogorgia elisabethae* (Lasker et al., 2003). Drag forces over-turning large corals (Mortensen and Buhl-Mortensen, 2005; Tunnicliffe and Syvitski, 1983; Watanabe et al., 2009) could also induce a maximum size limit of colonies (Lasker et al., 2003). However, observations of broken colonies of *P. resedaeformis* were infrequent at our sampling locations.

4.2. Limitations of temporal comparisons

Abundance was estimated in 2001 (Mortensen and Buhl-Mortensen, 2004), 2006 (Watanabe et al., 2009) and 2014 (this study) using different methods, possibly leading to uncertainties in the comparisons. In 2001, coral abundance was reported for entire dives and was not restricted to our sampling locations but rather intersecting them (Mortensen and Buhl-Mortensen, 2004). Still, similar trends were observed in 2001 as in 2014 with lower coral abundance around site 1 and higher at site 2. The higher abundances we observed at site 2 in 2014 compared to 2001 may partly be explained by better video quality. The minimum detectable coral size during abundance transects was 4 cm in 2014, and 7 cm in 2001 (Mortensen and Buhl-Mortensen, 2004). However, if we only include observations of corals > 7 cm in 2014, abundances were still higher than in 2001 (52 colonies 100 m⁻² for *P. resedaeformis* and 6.5 colonies 100 m⁻² for *P. arborea*). Although site 2 could also have been an area of particularly high abundance, while other areas had lower coral numbers in 2001, most sections of the four dives in 2001 were conducted < 150 m away from the transects in 2014. We therefore maintain that the higher coral abundance in 2014 is likely explained by successful recruitment since 2001. Watanabe et al. (2009) reported a detection limit of 8 cm for the measurements of abundance and size at sites X and Z in 2006. We observed only one colony of *P. arborea* < 8 cm at site X in 2014 and thus assume that the error induced by varying detection limits is negligible for abundance. At site X, transects crossed the wall features exhibiting high densities of *P. arborea* multiple times in 2014, while the ROV transect in 2006 only intersected this area once, which may explain the low abundance of *P. arborea* in that year (Watanabe et al., 2009).

Differences in minimum detectable size between the three sampling years could have influenced size frequency measurements. Corals < 10 cm of either species were not observed in 2001. In 2014, a single colony of *P. arborea* and no colony of *P. resedaeformis* were found below the 2001 detection limit of 7 cm. The influence of the different detection limits in 2001 and 2014 is thus assumed to be minimal for size frequency distributions. In 2006 and 2014, no colonies of *P. resedaeformis* < 10 cm were found at site X and Z during size measurements, while four colonies of *P. arborea* < 8 cm were present at site X in 2014. It is possible that colonies in that size class were also abundant but were not detected in 2006.

The significant size increase of *P. resedaeformis* in 2014 compared to 2006 at site X might be attributed to the different sampling tracks. While we measured corals around the steep features, Watanabe et al. (2009) likely included many corals from the upper and lower plateau that could have had a different size structure.

These potential impacts of varying sampling methods demonstrate the importance of regular and consistent monitoring in the NECCA to evaluate the effectiveness of the protection measures over time. Consistent monitoring practices will be needed to be able to document fine-scale changes in the coral communities.

4.3. Effectiveness of coral conservation – coral recovery

In general, the effectiveness of conservation areas is associated with large size, long closure periods and good enforcement (Claudet et al., 2008; Edgar et al., 2014), when beneficial relationships of conservation areas with species richness, biomass, density and size of fish and invertebrates are often observed in shallow-water reserves (Lester et al., 2009). The vast majority of these studies focus on fish abundance, while only few include benthic sessile communities. Protection of deep-water coral habitats mainly occurred over the past 15 years (Davies et al.,

2007) and long-term datasets for their recovery potential and conservation efficiency remain scarce.

The effectiveness of a specific conservation management action needs to be evaluated in relation to its conservation objectives. The NECCCA was established to protect dense communities of mainly two octocoral species (ESSIM Planning Office, 2006). While fisheries can have detrimental effects on deep-water coral ecosystems (Edinger et al., 2007; Krieger, 2001; Mortensen et al., 2005), other factors such as temperature, substrate composition and water flow also affect coral distribution (Roberts et al., 2009). Many of these factors, including globally rising temperatures, cannot be managed locally and thus the management of conservation areas is largely restricted to local human activities. In addition to the fisheries management, research activities in the NECCCA are regulated by Fisheries and Oceans Canada and a moratorium on oil and gas exploration for the Georges Bank area comprising the Northeast Channel currently adds to the coral protection. Fisheries management is enforced by surveillance overflights and vessel-based controls (Breeze and Fenton, 2007).

The signs of recovery from fisheries impact observed at site 2 (increased abundance, presence of colonies < 20 cm and of very large colonies) suggest that the fisheries closure can be effective in protecting and sustaining coral communities. However, the variability in patterns among sampling locations within the NECCCA calls for long-term protection to allow full recovery of all coral habitats. For the octocoral *Corallium rubrum*, it was estimated that a time span of 14 years of protection was not sufficient for its recovery from commercial harvesting in shallow waters (Tsounis et al., 2006) and recovery of seamount ecosystems harbouring aggregations of *Solenosmilia variabilis* failed 5–10 years after trawling had ceased (Williams et al., 2010). Watanabe et al. (2009) observed extremely low coral abundance at a distance of 6 km from the southwest boundary of the NECCCA at 650–900 m depths and suggested that the effects of continuing fishing activities may prevent settlement of recruits. This underscores the value of the NECCCA as an area without fisheries disturbance that can allow the growth of coral communities. Documented coral locations outside the NECCCA in 2000 and 2001 could be used as further reference points for comparisons with protected communities. However, the densest coral aggregations observed at that time were inside the NECCCA.

Since deep-water ecosystems are influenced by multiple factors, the fisheries ban alone can only explain partially the observed patterns. Measurements of *in situ* growth rates and drivers of recruitment and connectivity of coral aggregations inside the conservation area that may explain the variation in community structure at our sampling sites are necessary to accurately estimate recovery times.

In summary, partial recovery was indicated by the presence of large colonies at all sampling sites, while indications of recovery through recruitment and increased abundance were only found at some of the locations. Thus, the conservation measures were effective in protecting existing coral communities and allowing the growth of large colonies. However, for a system to fully recover from fisheries induced mortality, successful recruitment is necessary. Higher abundance and small colonies were only documented at some of our sampling sites in 2014. The studied time-span was not sufficient to allow recovery of all studied coral communities.

4.4. Effectiveness of coral conservation – placement of boundaries

In 2002, abundance of *P. resedaeformis* and *P. arborea* had been mainly documented at depths < 500 m (Mortensen et al., 2005) and the placement of the southeast boundary of the NECCCA was based on a precautionary approach to protect potential coral habitats at greater depths (Breeze and Fenton, 2007; ESSIM

Planning Office, 2006). After the fisheries closure, Watanabe et al. (2009) reported these corals to occur in depths of 865 and 910 m, respectively. In our study, the deepest *P. arborea* colony was found at 1074 m inside and at 909 m outside the NECCCA, while *P. resedaeformis* outside the NECCCA was only observed at a maximum depth of 757 m. Abundance of both species is reported to decline with depth in the Northwest Atlantic (Quattrini et al., 2015; Watanabe et al., 2009) and although they have a similar depth range, abundance of *P. arborea* peaks at greater depths than *P. resedaeformis* (Bryan and Metaxas, 2006; Watanabe et al., 2009). In this study, the abundance of *P. resedaeformis* decreased below 700 m and other coral species occurred more frequently with diverse coral communities at 900–1200 m inside the NECCCA. Changes in coral communities with depth likely occur in relation to patterns in environmental parameters (Baker et al., 2012). In the northeast Pacific, the composition of the most abundant coral families varied with depth (Etnoyer and Morgan, 2005) suggesting differences in habitat preferences. Protection of these diverse coral habitats is needed for conservation measures to follow a holistic approach (Baker et al., 2012). The newly documented coral assemblages other than the comparably shallow aggregations of *P. resedaeformis* and *P. arborea* have been successfully protected in the NECCCA due to the precautionary placement of the southeast boundary.

Although corals were present along the southeast boundary of the NECCCA between 1239 and 1521 m, their abundance and diversity was lower than at shallower dives. Due to their morphology the dominant taxa in these areas, *Anthomastus* and *Acanella*, are considered to be of lower sensitivity to physical disturbance than sea fans (Clark et al., 2015) found along shallower transects. If the main purpose of the NECCCA is to protect regions of high diversity and abundance of corals, the placement of the southeast boundary of this area appears to be adequate.

There has been a global trend for fisheries to extend to increasing depths over the last centuries (Morato et al., 2006), including in the North Atlantic. Fishing with bottom contacting gear currently occurs mainly at depths < 800 m in the Canadian Maritimes region (S. Coffen-Smout, DFO, pers. communication). This, however, may change in the future, highlighting the need for precautionary conservation measures. Coral diversity was high along our transects at 685–1021 m depth at ~8 to 10 km from the southwest boundary of the conservation area, harbouring some coral taxa that were not present inside the NECCCA. We also observed lost fishing gear at depths of 874 and 1001 m during this dive. A possible extension of the conservation area towards the southwest should be considered and could be regarded as a precautionary measure based on the anticipation that fisheries efforts will increase at these depths in the future.

While the shallow northwest boundary has been studied prior to the establishment of the NECCCA, the exploration of the northeast section is encouraged to further evaluate the boundaries of the conservation area.

4.5. Management implications

Spatial heterogeneity was pronounced both in the temporal comparisons of coral size and abundance and in the deeper parts of the conservation area. Drivers of the observed heterogeneity are complex, likely influenced by small-scale patterns, and remain largely unknown. The NECCCA encompasses a complex network of different habitat types, which needs to be afforded full protection.

The precautionary approach is regarded as a fundamental tool for the conservation of deep-water coral habitats (Auster, 2001, 2005; Clark et al., 2015). It is presented as one of the management principles in the Coral Conservation Plan for the Maritimes (ESSIM Planning Office, 2006) and was successful in protecting coral

aggregations in the NECCA. Video surveys are widely used in deep-sea research and allow fine scale observations, while their spatial coverage is limited. Thus, conservation measures often need to be based on a precautionary approach using locally gathered data and management needs to be adaptive to respond to new findings.

Conservation measures targeting deep-water corals need to be long-lasting due to slow growth rates and mostly unknown recruitment patterns that to date have not allowed accurate estimations of recovery times. Our results show that management actions with time-frames of < 10 years will not be sufficient to ensure full recovery of impacted deep-water coral ecosystems (s. also Williams et al., 2010) and effectiveness of deep-water conservation measures needs to be evaluated on a much longer time-frame. Following a holistic conservation approach, a variety of coral habitats that are representative for different depth ranges should be protected. Representative coral communities need to be monitored consistently over time to further investigate the effectiveness of the conservation measures. The NECCA is a unique set-up for future monitoring of population dynamics in protected deep-water coral communities where the recovery capacity of these systems can be studied over a long time frame.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.06.005>.

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