

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

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5 Swaantje Bennecke (1)<sup>1</sup>, Anna Metaxas (2)

6 (1) GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstr. 1-3, 24148 Kiel,  
7 Germany; sbennecke@geomar.de

8 (2) Department of Oceanography, Dalhousie University, 1355 Oxford Street, PO Box 15000,  
9 Halifax, Nova Scotia, B3H 4R2, Canada; metaxas@dal.ca

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14 Subtheme 1: Conservation topics and stewardship

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<sup>1</sup> Corresponding author

16 **Abstract**

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18 Over the past 15 years, multiple areas in the North Atlantic have been closed to destructive  
19 fishing practices to protect vulnerable deep-water coral ecosystems, known to provide habitat  
20 for diverse associated fauna. Despite the growing number of conservation measures, long-  
21 term studies on the recovery of deep-water coral communities from fisheries impacts remain  
22 scarce. In the Gulf of Maine, the Northeast Channel Coral Conservation Area (NECCCA)<sup>2</sup>  
23 was established in 2002 to protect dense aggregations of the two numerically dominant  
24 octocoral species in the region, *Primnoa resedaeformis* and *Paragorgia arborea*. To evaluate  
25 the effectiveness of the conservation measures, we monitored shifts in abundance and size  
26 of these two coral species in the shallow section (400 -700 m) of the NECCCA for 12 years  
27 after the fisheries closure. We also evaluated the appropriateness of the location of the deep  
28 boundaries of the NECCCA that were placed based on a precautionary approach with limited  
29 information on coral distribution at depths > 500 m. Video transects were conducted with  
30 ROV “ROPOS” in 2001, 2006, 2010 and 2014. We found potential signs of recovery from  
31 fisheries impact at some of the shallow locations in 2014: higher coral abundance and the  
32 presence of some very large colonies as well as recruits compared to 2001 and 2006.  
33 However, spatial heterogeneity was pronounced and small colonies (< 20 cm) indicative of  
34 successful recruitment were not found at all sites, underscoring the need for long-term  
35 protection measures to allow full recovery of impacted coral communities. At 700 – 1500 m  
36 different coral taxa were dominant than at the shallow locations and coral abundance peaked  
37 between 700 and 1200 m. High abundance and diversity of corals at this depth range, 8 - 10  
38 km southwest of the NECCCA, suggest that an extension of the southwest boundary should  
39 be considered. Comparably low coral abundance was found at depths of 1200 – 1500 m  
40 inside the NECCCA indicating an appropriate initial placement of the southeast boundary.  
41 These are the first long-term observations of protected deep-water octocoral communities  
42 which are needed for the effective management of deep-water coral conservation areas.

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<sup>2</sup> NECCCA: Northeast Channel Coral Conservation Area

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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 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

71 measures (OSPAR Commission, 2008, 2010). Recent efforts in deep-water coral  
72 conservation in the USA include the proposal of the Mid-Atlantic Fishery Management  
73 Council in 2015 to protect an area of ~98000 km<sup>2</sup> from destructive fishing in the U.S.  
74 Exclusive Economic Zone.

75         Effective management of a conservation area requires a management plan with clear  
76 objectives; effectiveness of a conservation action should then be evaluated based on the  
77 defined targets (Halpern, 2003; Pomeroy et al., 2005). The response of an ecosystem to  
78 protection measures is strongly linked to the biology of the targeted species. While some  
79 reserves can show increased biomass, density and diversity of species within a few years,  
80 the response of slow-growing organisms to protection is expected to require a much longer  
81 time frame (Halpern and Warner, 2002). Information on life history traits and recovery times  
82 of protected species is essential to ensure a powerful link between biological responses and  
83 policy that is often not achieved (Gnanalingam and Hepburn, 2015). Recovery of an  
84 impacted system is regarded as the return of that system to conditions similar to the pre-  
85 disturbance state (Clark et al., 2015; Williams et al., 2010). Since deep-water ecosystems  
86 generally harbour slow-growing and long-lived species (Clark et al., 2015), protection  
87 measures need to be long-lasting to ensure recovery and retention of these habitats. In  
88 addition to the duration of protection, size, location, extent of ongoing fisheries and  
89 enforcement of regulations can influence the success of a conservation area (Edgar et al.,  
90 2014). Despite the growing number of conservation measures, long-term studies on the  
91 recovery of benthic deep-water communities from fisheries impacts remain scarce (Clark et  
92 al., 2015).

93         To protect dense aggregations of the two dominant octocoral species, *Primnoa*  
94 *resedaeformis* and *Paragorgia arborea*, a 424-km<sup>2</sup> conservation area was established in  
95 2002 by the Canadian government in the Northeast Channel in Atlantic Canada. A “restricted  
96 bottom fishing zone” covers ~ 90% of the NECCCA and is completely closed to bottom  
97 fishing gear, while the remaining 10% is a “limited bottom fishing zone”, open to bottom long-  
98 line fishing with an at-sea observer (ESSIM Planning Office, 2006). The legislation of the

99 NECCCA is provided by the Fisheries Act that prohibits the destruction and detrimental  
100 alteration of fish habitat (Department of Justice Canada, 1985). While dense coral  
101 aggregations were recorded at depths < 500 m prior to the establishment of the NECCCA  
102 (Mortensen et al., 2005), distribution patterns of corals in deeper ranges remained largely  
103 unknown at that time and the deep boundaries of the conservation area were placed on a  
104 precautionary approach.

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

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

127 current placement of the NECCCA boundaries. Dives conducted off the southwest boundary  
128 of the NECCCA provided information on coral communities immediately outside the  
129 conservation area. These data were used to assess the potential of a possible extension of  
130 the boundaries of the conservation area.

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## 133 **2. Materials and Methods**

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### 135 *2.1 Study Area and Sites*

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

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

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

154 Details on the methods and data collection can be found in Mortensen and Buhl-Mortensen  
155 (2004) and Watanabe et al. (2009).

156 Additional dives were conducted inside (Fig. 1, Table 2; R1359, 2010) the NECCCA,  
157 along the deep boundary (R979, 2006 and R1358, 2010) and outside the NECCCA (R1705,  
158 2014) to determine coral distribution and abundance at depths of 685 – 1583 m.

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

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## 163 2.2 Abundance

164 In 2014, we measured coral abundance using 10 (site 1, site 2) or 8 (site X) parallel  
165 video transects of ~100 m in length taken by a downward-oriented HD camera at altitudes of  
166 2.7 – 4.3 m above the seafloor. The downward-looking position was adjusted during the  
167 transects to account for changes in the slope of the seafloor. To avoid underestimation of the  
168 field of view due to slightly varying angles of the camera, corals were only counted if they  
169 appeared on the same plane as 2 scaling lasers. To minimize perspective distortion towards  
170 the sides of the 16:9 frame, 1/6 on both sides of the video frame were not included in the  
171 analysis, leading to a 10.7:9 aspect ratio. Every coral colony that was inside the remaining  
172 2/3 of the frame width was counted, but colonies were excluded if their base was outside the  
173 defined area. For dense aggregations of *P. resedaeformis*, individual bases were often  
174 indistinguishable and the extent of colonies was estimated based on their shape and the  
175 assumed position of the bases.

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

182 view. The actual length of each transect was measured in ArcGIS 10.1. The area analysed  
183 per transect was the product of the width of the field of view and transect length. Abundance  
184 of coral colonies was calculated for each transect relative to the transect area.

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

201 Sections of transects in dives R639 and R640 in 2001 were done at site 1. Dive R640  
202 directly intersected the transect area sampled in 2014, while dive R639 only reached the  
203 northwest corner of site 1 at the end of the dive. Dives R637 and R642 in 2001 directly  
204 intersected the abundance transects done at site 2 in 2014, while dives R636 and R637 were  
205 done at a maximum distance of 150 m from the measurements in 2014. Abundances of  
206 corals were reported by Mortensen and Buhl-Mortensen (2004) for the entire length of each  
207 dive in 2001. Watanabe et al. (2009) presented abundance of corals around site X (dive  
208 R974-NEC3) and site Z (dive R974-NEC4 and R978-NEC4) in 25-m depth intervals, without



209 providing precise locations of the analysed area. For those sites, we used abundances that  
210 were in the same depth range as the dives in 2014.

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

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

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### 225 2.3 *Size frequency*

226 Size frequency distribution of *P. resedaeformis* and *P. arborea* was measured at two  
227 sites in 2001 (site 1, site 2) and at four sites in 2014 (site 1, site 2, site X, site Z). In 2014, the  
228 ROV landed on the seafloor and the forward-looking camera including scaling lasers (10 cm  
229 apart) directly pointed onto the coral colony to be measured. If the lasers could not be  
230 projected onto the colony, they were placed onto the same plane, e.g. the substrate. To  
231 minimize the error of 2D measurements in a 3D environment, only colonies growing in a ~  
232 90° ( $\pm 20^\circ$ ) angle to the camera were measured. Overturned but alive colonies were  
233 included, while colonies with mainly dead branches were excluded. Corals growing on a wall  
234 were measured while the ROV was moving. A few colonies of *P. arborea* were measured  
235 when the ROV was not touching the ground, but the 90°  $\pm$  20° requirement was maintained.  
236 Colony length was defined as the linear extension along the main direction of growth starting

237 at the base of the coral. A box was projected around each colony and its dimensions  
238 specified length and width of the colony. For tall colonies of *P. arborea* with very large bases,  
239 length was measured from the estimated origin of the main stem. Frame grabs of every  
240 colony were taken with OFOP and size was measured with the image processing software  
241 ImageJ.

242 For 2001, Mortensen and Buhl-Mortensen (2005) reported size frequency  
243 distributions pooled along different locations in the Northeast Channel, including data from  
244 ROV ROPOS dives. We extracted coral images from these videos for our specific locations  
245 at site 1 and site 2 that met the same requirements for camera angle and laser pointers as in  
246 2014. A 150-m radius was drawn around the location of coral measurements in 2014 and  
247 only corals within this radius were measured for 2001. Size frequency distribution was  
248 measured at site 1 and site 2 mostly while the ROV was moving.

249 Watanabe et al. (2009) reported size frequency distributions around site X and site Z  
250 in 50-m depth intervals. At site X, we extracted size data at the corresponding depth range of  
251 600 – 700 m. Since this yielded only 7 measurements for *P. arborea*, data from 700 - 750 m  
252 depth were added to increase sample size. At site Z, coral sizes measured at depths of 650  
253 – 700 m were extracted for comparison with sizes in 2014.

254 During abundance transects at site 2, a fishing line was observed in 2014. In 2001, a  
255 fishing line was documented 50 – 80 m northwest of the 2014 observations. No line was  
256 found there in 2014. Since both lines seem to follow a similar pattern, we assume it is the  
257 same fishing line and that there was a positional offset in the 2001 dataset. Based on this  
258 offset, we believe that the 150-m radius around the 2014 measurement locations should  
259 include all colonies in the direct proximity measured in 2001.

260

#### 261 2.4 Statistical Analyses

262 Mean coral sizes were compared between 2001 and 2014 at site 1 and 2 and  
263 between 2006 and 2014 at site X and Z with Student's t-tests, if variances were homogenous  
264 and distributions were normal. Welch's t-test was used in cases of heterogeneous variances.

265 If distribution was not normal, data were ln-transformed. This led to an approximate normal  
266 distribution only for *P. resedaeformis* at site Z. If normal distribution could not be achieved  
267 using transformations, Mann-Whitney-Wilcoxon tests were conducted instead.

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

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

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### 275 **3. Results**

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#### 277 *3.1 Spatial and temporal patterns in abundance*

278 Abundance of corals ranged between 2.06 and 53.66 colonies 100 m<sup>2</sup> for *P.*  
279 *resedaeformis*, and 0.12 and 7.54 colonies 100 m<sup>2</sup> for *P. arborea* in 2014 (Table 3). The  
280 minimum detectable size was 4 cm and although two smaller colonies of *P. arborea* were  
281 observed during one transect at site 2, they were not included in the analysis. Abundance  
282 was lowest at site 1 for both species where no corals were found on two transects, and a  
283 total of 3 colonies of *P. arborea* were recorded (Fig. 3A). Abundance was similar to 2001 for  
284 *P. resedaeformis* and slightly lower for *P. arborea* at this site. Highest abundances were  
285 found at site 2 for both species where a maximum of 234 *P. resedaeformis* and 30 *P.*  
286 *arborea* occurred per transect (Fig. 3B). Abundance at this site was much higher in 2014  
287 than in 2001 for both species (Table 3). At site X, abundance of *P. resedaeformis* was  
288 slightly higher in 2014 compared to the same depth range in 2006. Abundance of *P. arborea*  
289 was > 10x higher in 2014 than in 2006, when Watanabe et al. (2009) observed only 2  
290 colonies. Most colonies of *P. arborea* (55 out of 87, Table 4) were found on the steep wall  
291 (Fig. 3C). The ROV transect in 2006 crossed through the observed steep features only once.

292 *P. resedaeformis* was by far the dominant species at all locations, but at the wall it was only  
293 slightly more abundant than *P. arborea*.

294 Statistical comparisons of abundance data among the different years were not  
295 possible due to different sampling and analysis approaches in 2001, 2006 and 2014.

296

### 297 3.2 *Size frequency distribution*

298 Across all years, length of *P. resedaeformis* ranged from 8 to 134 cm (Table 5). There  
299 was a single colony < 10 cm in length (site 2, 2014), and the tallest colony was found at site  
300 X in 2014. Colonies were significantly larger at site X than all other sites in 2014 (Wilcoxon  
301 rank sum test, site X vs. 1:  $p = 0.012$ ; site X vs. 2 and Site X vs. Z:  $p < 0.001$ ) and were  
302 significantly smaller at site 2 than at site X and site 1 ( $p = 0.032$ ).

303 Colonies of *P. resedaeformis* at site 1 covered a similar size range in 2001 and 2014,  
304 lacking colonies < 20 cm in length. Colonies were on average larger in 2001 than in 2014,  
305 but not significantly so (Student's t-test,  $p = 0.233$ ) and the sample size was low ( $n = 12$ ) in  
306 2001. At site 2, mean colony length did not change significantly between 2001 and 2014  
307 (Welch's t-test,  $p = 0.874$ ), but the range of size classes was wider in 2014 (Table 5). At site  
308 X, colonies of *P. resedaeformis* were significantly larger in 2014 than in 2006 (Mann-  
309 Whitney-Wilcoxon test,  $p < 0.001$ ) and the skewness of the distribution was lower due to a  
310 larger number of large corals in 2014 (Fig. 4). This led to an approximately normal  
311 distribution in 2014, while the few colonies in larger size classes caused a right-tailed  
312 distribution in 2006. Significant positive skewness was indicated for the distribution in 2006  
313 (Table 5), but the large sample sizes (here  $n = 159$ ) suggest caution in the interpretation  
314 (Field et al., 2012). At site Z, corals were slightly larger in 2014 than in 2006, with a broader  
315 size range because of a small number of large corals in the high size classes. Both  
316 distributions were right tailed.

317 The length of *P. arborea* over all sites ranged from 4 to 227 cm (Fig. 5, Table 6). The  
318 smallest colonies on average were found at site 2 and the largest at site 1 in 2014. Colonies  
319 were significantly smaller at site 2 than at site 1 and site Z in 2014 (Wilcoxon rank sum test,

320 site 2 vs. 1:  $p = 0.041$ , site 2 vs. Z:  $p = 0.017$ ). At site 1, mean size did not vary significantly  
321 between years (Student's t-test,  $p = 0.970$ ) and was highest of all sampling sites, although  
322 sample sizes were small for both years. At site 2, colonies were significantly smaller in 2014  
323 than in 2001 (Mann-Whitney-Wilcoxon test,  $p = 0.013$ ). Multiple colonies were observed in  
324 the smallest size classes in 2014, including 3 colonies  $< 10$  cm. Skewness of the distribution  
325 changed from slightly negative in 2001 to positive in 2014 due to the prevalence of small  
326 colonies in 2014. At site X, colony size did not change significantly over time. At 600 – 700 m  
327 depth, only 7 colonies were measured that were on average larger in 2006 than in 2014 but  
328 not significantly so (Student's t-test,  $p = 0.746$ ). Colony size at 600 – 750 m in 2006 was  
329 smaller than in 2014 (Welch's t-test,  $p = 0.473$ ). Size range was wider in 2014 (178 cm) than  
330 in 2006 (78 and 107 cm), including multiple colonies  $< 10$  cm long and a few very large  
331 individuals (133, 162 and 185 cm). At site Z, colonies were significantly larger in 2014 than  
332 colonies at 650 – 700 m in 2006 (Mann-Whitney-Wilcoxon test,  $p = 0.005$ ). The distribution  
333 was shifted towards larger colonies in 2014 where the smallest colony was 47 cm long,  
334 whereas in 2006, the smallest coral colony was 25 cm (Fig. 5).

335

### 336 3.3 *Patterns in coral abundance at the deeper margins of the NECCCA*

337 Seventeen coral taxa were recorded during the three dives between 700 and 1500 m  
338 depth (Fig. 6, Table 7) and *Acanella* sp. and *Anthomastus* sp. were among the numerically  
339 most dominant corals. Coral abundance and diversity was lowest at the deepest dive (1239 –  
340 1521 m), and most of the corals were present at the shallower (~1300 m), southern section  
341 of the dive (Fig. 7). In contrast, corals were present throughout the other deep dive within the  
342 NECCCA (Fig. 8). Abundance was greatest for *Anthomastus*, but this taxon was sparse in  
343 the southwest section of the dive. Many colonies ( $> 200$ ) of *Acanella*, the whip coral  
344 *Radicipes* sp., a *Keratoisis*-like bamboo coral and the sea pen *Halipteris* sp. were recorded,  
345 mostly in the deeper section of the dive (transect 2,  $> 1000$  m). During dive R1705,  
346 *Anthomastus* and colonies of the family Nephtheidae were the numerically dominant taxa  
347 (Table 7), with most Nephtheidae occurring on the most shallow transect (700 - 800 m, Fig.

348 9). Due to their transparent texture, corals of the family Nephtheidae were difficult to detect  
349 and we likely underestimated their abundance. *Acanella* and other Isidids were observed in  
350 high numbers ( $n \geq 195$ ) over the entire dive with only a few *Keratoisis*-like colonies at the  
351 shallow transect (Fig. 9D). A small white sea pen (Order Pennatulacea) was present on this  
352 dive but was difficult to see resulting in underestimates of abundance.

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

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

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## 373 **4. Discussion**

374

### 375 *4.1 Fisheries impact and recovery potential of coral communities*

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

383

384 The presence of higher numbers of large colonies in 2014 than in previous years  
385 could indicate recovery from fisheries impact. Bycatch and damage of corals by lines and  
386 nets likely has a bigger impact on large colonies, since they are more easily entangled in  
387 fishing gear than small recruits (Krieger, 2001). In Atlantic Canada, Mortensen et al. (2005)  
388 observed a lower average size for colonies of *P. arborea* in 2001 than reported by Verrill  
389 (1922) for the late 19th century. They speculated that Verrill's dataset may have been biased  
390 towards large specimens, since their sampling material was mainly collected as bycatch from  
391 longlines. The establishment of the NECCCA in 2002 should have enabled the growth of  
392 large colonies that were experiencing fisheries-induced mortality previously. The largest  
393 colonies of both species were found at all sites (except for *P. resedaeformis* at site 1) in  
394 2014. To a certain extent, this may be explained by the continued growth of tall colonies that  
395 were not damaged by fishing gear inside the conservation area. This can be regarded as a  
396 sign of recovery of the system now harbouring colonies in large size classes that likely were  
397 abundant at the pre-impact state. However, growth rates for *P. resedaeformis* are assumed  
398 to decrease with age (Mortensen and Buhl-Mortensen, 2005; Sherwood and Edinger, 2009)  
399 and full regrowth of tall colonies requires a much longer time frame than the study period of  
400 13 years.

401 The significantly higher average size of *P. resedaeformis* in 2014 at site X than at all  
402 other sampling locations, and the presence of colonies > 90 cm in 2006 and 2014 could  
403 indicate low fisheries impact in terms of removal of large colonies. The steep terrain features

404 might have limited access of bottom fishing gear to this area. Similarly, Clark et al. (2010)  
405 found intact coral colonies on a section of a seamount that was too heterogeneous for  
406 fishing.

407

408         Signs of recovery of coral communities in terms of abundance and recruitment were  
409 variable among our four sampling sites. Reproductive output in some octocorals is known to  
410 increase with size (Coma et al., 1995; Santangelo et al., 2003) and thus the removal of large  
411 colonies could have led indirectly to an overall lower recruitment rate of the coral populations.  
412 Without fisheries-induced mortality, signs of recovery would be manifested as increased  
413 coral abundance over time due to successful recruitment, in turn indicated by the presence of  
414 small colonies. Growth rates of small-sized colonies of *P. resedaeformis* can only be  
415 estimated from very few observations, while data for *P. arborea* are lacking completely.  
416 Growth rates of  $\sim 2$  cm yr<sup>-1</sup> were reported for colonies of *P. resedaeformis* < 30 years old  
417 (Buhl-Mortensen and Mortensen, 2005) and the largest recruit of *P. resedaeformis* found on  
418 settlement collectors deployed for 4 years in the NECCCA was 1.2 cm in size (Lacharité and  
419 Metaxas, 2013) leading to a minimum possible growth rate of 0.3 cm yr<sup>-1</sup>. A recruit of *P.*  
420 *resedaeformis* in the NECCCA at 863 m grew from  $\sim 1.7$  to  $\sim 23.2$  cm in 8 years leading to a  
421 growth rate of  $\sim 2.7$  cm yr<sup>-1</sup> (Bennecke et al., in press). From these observations, we assume  
422 a time span of  $\sim 15$  years to be sufficient to yield newly recruited colonies of *P. resedaeformis*  
423  $\sim 20$  cm in size. However, this assumption is based on single observation and certainly not  
424 every colony < 20 cm will have recruited in the past 15 years.

425         In 2014, successful recruitment was indicated by the presence of small colonies (< 20  
426 cm) at two of our four sites for each of the two coral species. In striking contrast were the  
427 patterns at the two shallow sites (440 - 490 m) between 2001 and 2014. With low abundance  
428 of both species before and after the NECCCA establishment and the lack of small colonies,  
429 site 1 seems to harbour comparably old coral communities. The smallest colony of *P.*  
430 *arborea* was 72 cm long. Assuming growth rates of about 1.6 cm yr<sup>-1</sup> (Sherwood and Edinger,  
431 2009), the last recruitment event of *P. arborea* must have occurred  $\sim 45$  years ago. Since



432 only a few colonies of *P. arborea* were found overall, recruitment appears to be very sporadic  
433 at this location. Over the study period, the presence of large colonies alone was not sufficient  
434 to suggest successful recruitment of both coral species. At this location, we found the lowest  
435 coral abundance of all sampling sites. Abundance may have been too low to sustain a  
436 community and ensure recovery capacity. Contrasting patterns were found at site 2, where  
437 the presence of colonies < 20 cm and higher abundances of *P. resedaeformis* and *P.*  
438 *arborea* in 2014 than in 2001 suggested successful recruitment. These observations indicate  
439 some recovery capacity of these coral communities.

440         Spatial variation among coral communities is likely influenced by various parameters  
441 including larval supply, substrate composition and availability or biological disturbances, such  
442 as by the high abundance of brittle stars observed in the Northeast Channel (Metaxas and  
443 Giffin, 2004). Predictive habitat models have shown *P. arborea* and *P. resedaeformis* to  
444 preferably inhabit slopes or topographic highs (Bryan and Metaxas, 2007; Tong et al., 2012).  
445 While the abundance of *P. resedaeformis* was lower at the steep wall features at site X  
446 compared to areas of lower slope in 2014, *P. arborea* occurred more frequently on these  
447 features than at plateaus. These small-scale terrain features may reflect different preferred  
448 habitats of these two species that often, but not always, co-occur. Site 1, where coral  
449 abundance was extremely low and no recruits were found, and site X are located 1 km apart  
450 and separated by a 200-m depth gradient. These observations indicate the important  
451 influence of small-scale patterns on population dynamics of deep-water octocorals. The  
452 critical role of local patterns has been suggested previously based on differences in size and  
453 abundance of coral recruits at site X and Z between 2006 and 2010 (Lacharité and Metaxas,  
454 2013).

455  
456         The low frequency of colonies of *P. resedaeformis* < 20 cm (except at Site 2 in 2014)  
457 could indicate low recruitment overall. However, recruitment of *P. resedaeformis* may be  
458 cryptic and at least some of the colonies in our study may have been aggregations of  
459 multiple smaller colonies. In dense aggregations of *P. resedaeformis*, it was often difficult to

460 identify individual colonies and coral branches without a distinguishable separate base were  
461 regarded as belonging to a single colony. However, basal structures of old colonies of  
462 *Primnoa* spp. can provide settlement substrate for recruits (Andrews et al., 2002; Krieger,  
463 2001), and a single specimen may be composed of colonies of different ages. We observed  
464 recruits of *P. resedaeformis* at the base of an old colony at site X, but could not measure  
465 them accurately and did not include them in our analysis. The complete lack of small corals  
466 at site 1 and X in 2014 could have been the result of a limitation of the non-invasive sampling  
467 method. In contrast, the presence of multiple colonies < 20 cm at sites 2 and Z indicated  
468 recent recruitment. Continuous recruitment of *P. resedaeformis* was suggested for our  
469 sampling sites X and Z, where *P. resedaeformis* recruited between 2006 and 2010 (Lacharité  
470 and Metaxas, 2013). Most recruits were in the primary polyp stage and high mortality of this  
471 life stage was assumed (Lacharité and Metaxas, 2013). High post-settlement mortality and  
472 cryptic recruitment may explain the apparent lack of small colonies at some of our sites.

473

474 Overall, most size-frequency distributions of *P. resedaeformis* were normal with few  
475 very small and few very large colonies. Similarly, Watanabe et al. (2009) found that the most  
476 abundant size class for the same species in Northeast Channel was 50 cm. Approximate  
477 normal distributions of size frequency measurements were also found for some populations  
478 of the gorgonian corals *Paramuricea clavata* and *Eunicella singularis* in the Mediterranean  
479 Sea (Gori et al., 2011; Linares et al., 2008). For *P. resedaeformis*, decreasing growth rates  
480 with age (Mortensen and Buhl-Mortensen, 2005; Sherwood and Edinger, 2009) and low  
481 mortality of large colonies may explain the accumulation of corals in a size range of 40 – 70  
482 cm. Reduced mortality rates with size have been observed for *Paramuricea* spp. in the Gulf  
483 of Mexico (Doughty et al., 2014). In contrast, determinate colony size may explain the low  
484 frequency of very large corals, as in the shallow-water Caribbean octocoral  
485 *Pseudopterogorgia elisabethae* (Lasker et al., 2003). Drag forces over-turning large corals  
486 (Mortensen and Buhl-Mortensen, 2005; Tunnicliffe and Syvitski, 1983; Watanabe et al.,  
487 2009) could also induce a maximum size limit of colonies (Lasker et al., 2003). However,

488 observations of broken colonies of *P. resedaeformis* were infrequent at our sampling  
489 locations.

490

491

#### 492 4.2 *Limitations of temporal comparisons*

493 Abundance was estimated in 2001 (Mortensen and Buhl-Mortensen, 2004), 2006  
494 (Watanabe et al., 2009) and 2014 (this study) using different methods, possibly leading to  
495 uncertainties in the comparisons. In 2001, coral abundance was reported for entire dives and  
496 was not restricted to our sampling locations but rather intersecting them (Mortensen and  
497 Buhl-Mortensen, 2004). Still, similar trends were observed in 2001 as in 2014 with lower  
498 coral abundance around site 1 and higher at site 2. The higher abundances we observed at  
499 site 2 in 2014 compared to 2001 may partly be explained by better video quality. The  
500 minimum detectable coral size during abundance transects was 4 cm in 2014, and 7 cm in  
501 2001 (Mortensen and Buhl-Mortensen, 2004). However, if we only include observations of  
502 corals > 7 cm in 2014, abundances were still higher than in 2001 (52 colonies 100 m<sup>-2</sup> for *P.*  
503 *resedaeformis* and 6.5 colonies 100 m<sup>-2</sup> for *P. arborea*). Although site 2 could also have been  
504 an area of particularly high abundance, while other areas had lower coral numbers in 2001,  
505 most sections of the four dives in 2001 were conducted < 150 m away from the transects in  
506 2014. We therefore maintain that the higher coral abundance in 2014 is likely explained by  
507 successful recruitment since 2001. Watanabe et al. (2009) reported a detection limit of 8 cm  
508 for the measurements of abundance and size at sites X and Z in 2006. We observed only  
509 one colony of *P. arborea* < 8 cm at site X in 2014 and thus assume that the error induced by  
510 varying detection limits is negligible for abundance. At site X, transects crossed the wall  
511 features exhibiting high densities of *P. arborea* multiple times in 2014, while the ROV  
512 transect in 2006 only intersected this area once, which may explain the low abundance of *P.*  
513 *arborea* in that year (Watanabe et al., 2009).

514

515 Differences in minimum detectable size between the three sampling years could have  
516 influenced size frequency measurements. Corals < 10 cm of either species were not  
517 observed in 2001. In 2014, a single colony of *P. arborea* and no colony of *P. resedaeformis*  
518 were found below the 2001 detection limit of 7 cm. The influence of the different detection  
519 limits in 2001 and 2014 is thus assumed to be minimal for size frequency distributions. In  
520 2006 and 2014, no colonies of *P. resedaeformis* < 10 cm were found at site X and Z during  
521 size measurements, while four colonies of *P. arborea* < 8 cm were present at site X in 2014.  
522 It is possible that colonies in that size class were also abundant but were not detected in  
523 2006.

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

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

532

533

#### 534 4.3 Effectiveness of coral conservation – coral recovery

535 In general, the effectiveness of conservation areas is associated with large size, long  
536 closure periods and good enforcement (Claudet et al., 2008; Edgar et al., 2014), when  
537 beneficial relationships of conservation areas with species richness, biomass, density and  
538 size of fish and invertebrates are often observed in shallow-water reserves (Lester et al.,  
539 2009). The vast majority of these studies focus on fish abundance, while only few include  
540 benthic sessile communities. Protection of deep-water coral habitats mainly occurred over  
541 the past 15 years (Davies et al., 2007) and long-term datasets for their recovery potential and  
542 conservation efficiency remain scarce.

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

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

570 for comparisons with protected communities. However, the densest coral aggregations  
571 observed at that time were inside the NECCCA.

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

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

585

586

#### 587 4.4 Effectiveness of coral conservation - placement of boundaries

588 In 2002, abundance of *P. resedaeformis* and *P. arborea* had been mainly  
589 documented at depths < 500 m (Mortensen et al., 2005) and the placement of the southeast  
590 boundary of the NECCCA was based on a precautionary approach to protect potential coral  
591 habitats at greater depths (Breeze and Fenton, 2007; ESSIM Planning Office, 2006). After  
592 the fisheries closure, Watanabe et al. (2009) reported these corals to occur in depths of 865  
593 and 910 m, respectively. In our study, the deepest *P. arborea* colony was found at 1074 m  
594 inside and at 909 m outside the NECCCA, while *P. resedaeformis* outside the NECCCA was  
595 only observed at a maximum depth of 757 m. Abundance of both species is reported to  
596 decline with depth in the Northwest Atlantic (Quattrini et al., 2015; Watanabe et al., 2009)  
597 and although they have a similar depth range, abundance of *P. arborea* peaks at greater

598 depths than *P. resedaeformis* (Bryan and Metaxas, 2006; Watanabe et al., 2009). In this  
599 study, the abundance of *P. resedaeformis* decreased below 700 m and other coral species  
600 occurred more frequently with diverse coral communities at 900 – 1200 m inside the  
601 NECCCA. Changes in coral communities with depth likely occur in relation to patterns in  
602 environmental parameters (Baker et al., 2012). In the northeast Pacific, the composition of  
603 the most abundant coral families varied with depth (Etnoyer and Morgan, 2005) suggesting  
604 differences in habitat preferences. Protection of these diverse coral habitats is needed for  
605 conservation measures to follow a holistic approach (Baker et al., 2012). The newly  
606 documented coral assemblages other than the comparably shallow aggregations of *P.*  
607 *resedaeformis* and *P. arborea* have been successfully protected in the NECCCA due to the  
608 precautionary placement of the southeast boundary.

609         Although corals were present along the southeast boundary of the NECCCA between  
610 1239 and 1521 m, their abundance and diversity was lower than at shallower dives. Due to  
611 their morphology the dominant taxa in these areas, *Anthomastus* and *Acanella*, are  
612 considered to be of lower sensitivity to physical disturbance than sea fans (Clark et al., 2015)  
613 found along shallower transects. If the main purpose of the NECCCA is to protect regions of  
614 high diversity and abundance of corals, the placement of the southeast boundary of this area  
615 appears to be adequate.

616

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

626 and could be regarded as a precautionary measure based on the anticipation that fisheries  
627 efforts will increase at these depths in the future.

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

631

632

#### 633 4.5 *Management implications*

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

639 The precautionary approach is regarded as a fundamental tool for the conservation of  
640 deep-water coral habitats (Auster, 2001, 2005; Clark et al., 2015). It is presented as one of  
641 the management principles in the Coral Conservation Plan for the Maritimes (ESSIM  
642 Planning Office, 2006) and was successful in protecting coral aggregations in the NECCCA.  
643 Video surveys are widely used in deep-sea research and allow fine scale observations, while  
644 their spatial coverage is limited. Thus, conservation measures often need to be based on a  
645 precautionary approach using locally gathered data and management needs to be adaptive  
646 to respond to new findings.

647 Conservation measures targeting deep-water corals need to be long-lasting due to slow  
648 growth rates and mostly unknown recruitment patterns that to date have not allowed  
649 accurate estimations of recovery times. Our results show that management actions with time-  
650 frames of < 10 years will not be sufficient to ensure full recovery of impacted deep-water  
651 coral ecosystems (s. also Williams et al., 2010) and effectiveness of deep-water conservation  
652 measures needs to be evaluated on a much longer time-frame. Following a holistic  
653 conservation approach, a variety of coral habitats that are representative for different depth



654 ranges should be protected. Representative coral communities need to be monitored  
655 consistently over time to further investigate the effectiveness of the conservation measures.  
656 The NECCCA is a unique set-up for future monitoring of population dynamics in protected  
657 deep-water coral communities where the recovery capacity of these systems can be studied  
658 over a long time frame.

659

660

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662

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673

674

## 675 **Supplementary material**

676

677 S1 Locations of size frequency measurements at site 1

678 S2 Locations of size frequency measurements at site 2

679 S3 Locations of size frequency measurements at site X

680 S4 Locations of size frequency measurements at site Z

681 S5 Images of colonies of *P. resedaeformis* < 20 cm

682 S6 Images of colonies of *P. arborea* < 20 cm

683

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862

863

864 **Figure captions**

865

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

872

873 **Fig. 2** Locations of measurements of coral abundance and/or size frequency during ROV dives in  
874 2001 (site 1, 2; white lines), 2006 (site X, Z; white lines) and 2014 (site 1, 2, X, Z; black lines) inside  
875 the Coral Conservation Area in the Gulf of Maine. Detailed maps of coral locations used for size  
876 frequency measurements at each site can be found in the appendix (A1 – A4). Bathymetry by U.S.  
877 Geological Survey (Twomey & Signell, 2013).

878

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

883

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

888

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

893

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

899

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

905

906 **Fig. 8** Coral locations along two transects during dive R1359 at 900 – 1187 m depth inside the Coral  
907 Conservation Area in 2010 for all corals (A), *Acanella* sp. (B), *Anthomastus* sp. (C), *Halipteris* sp. (D),  
908 white *Keratoisis*-like Isididae (E), *Radicipes* sp. (F). Bathymetry grid lines were extracted from a 3-  
909 arcsecond digital elevation model of the Gulf of Maine (Twomey & Signell, 2013) and do not  
910 necessarily follow small-scale patterns observed during the dives.

911

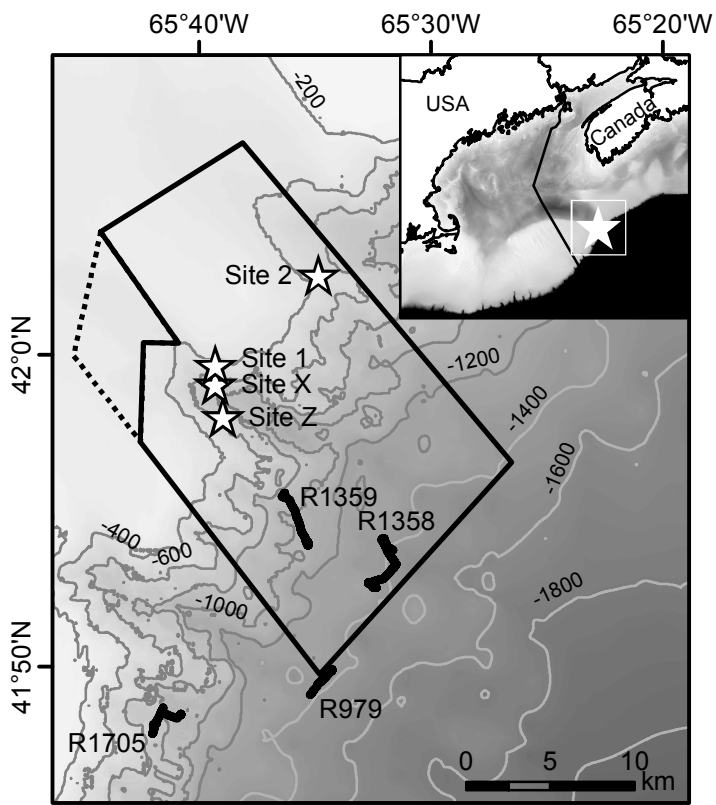
912 **Fig. 9** Coral locations along four transects during dive R1705 at 685 – 1021 m depth outside the Coral  
913 Conservation Area in 2014 for all corals (A), *Acanella* sp. (B), *Anthomastus* sp. (C), white *Keratoisis*-  
914 like Isididae (D), Nephtheidae (E). Bathymetry grid lines were extracted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

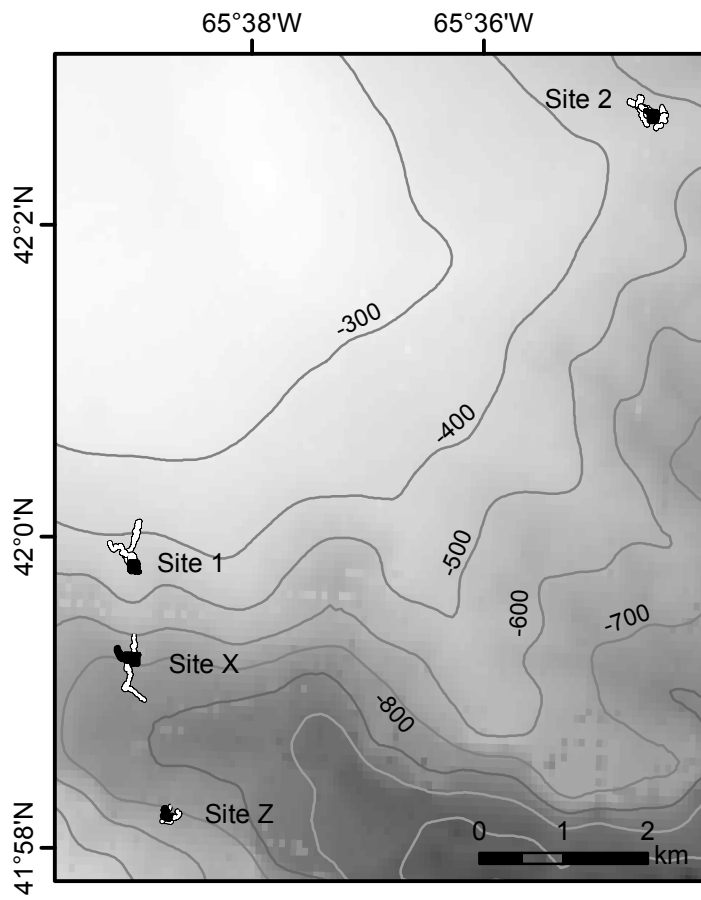
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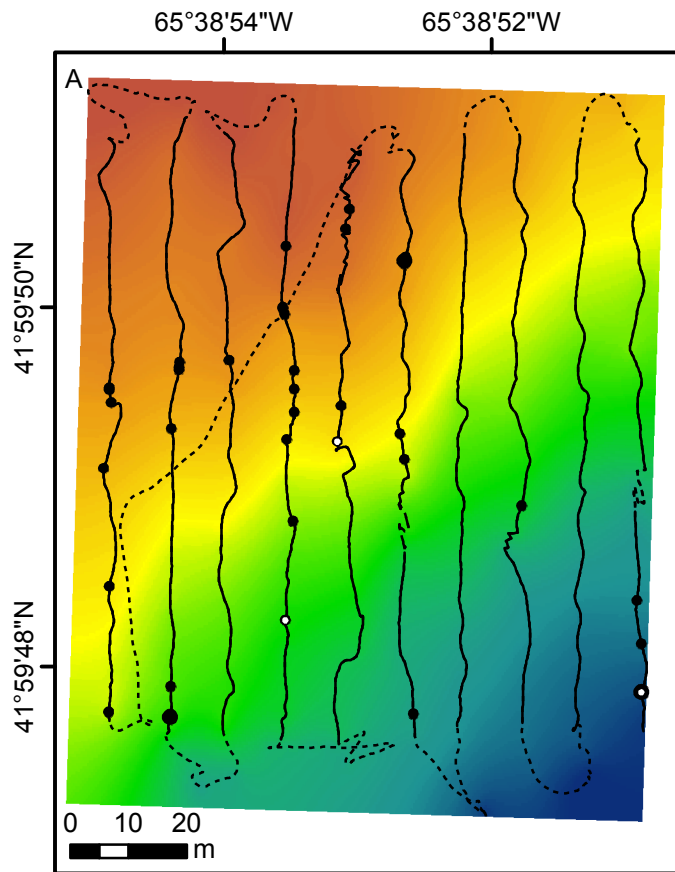
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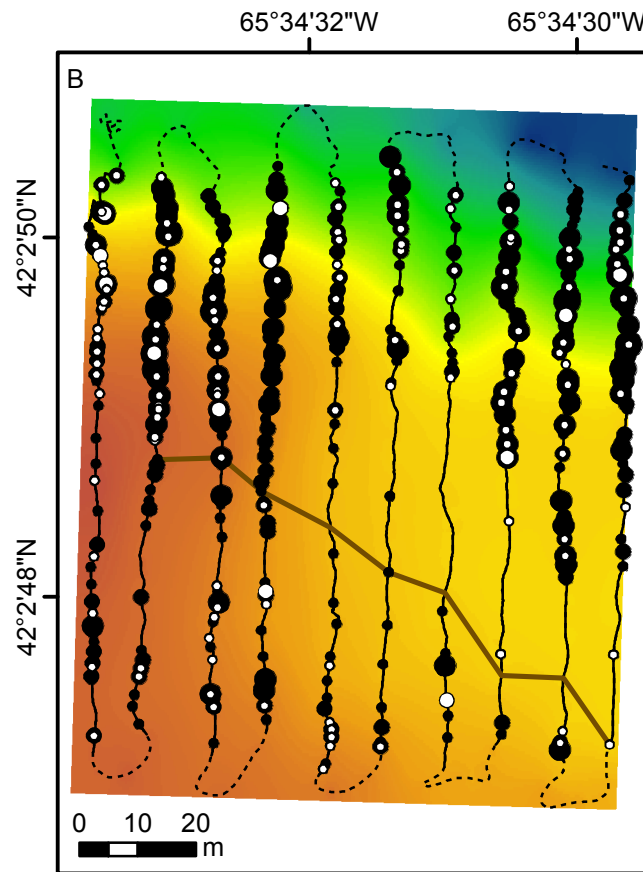




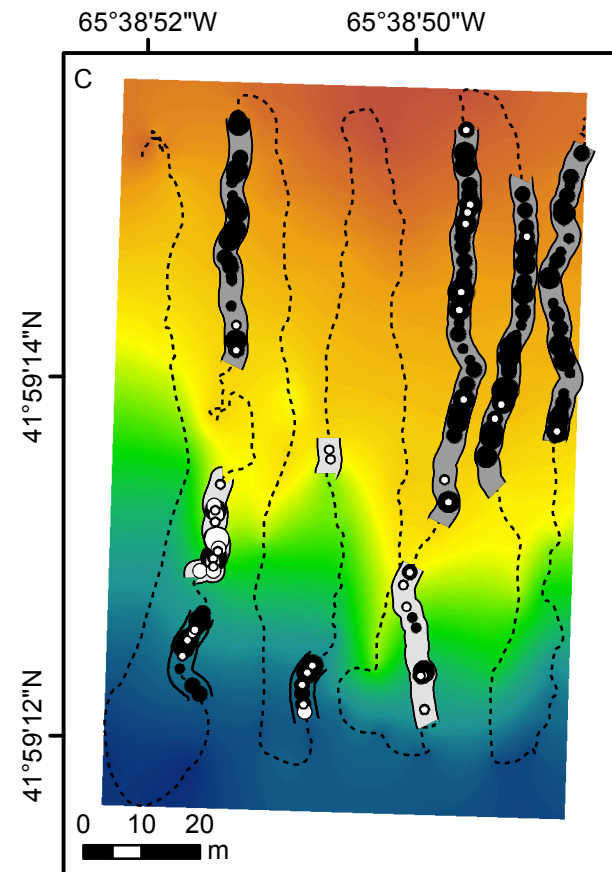




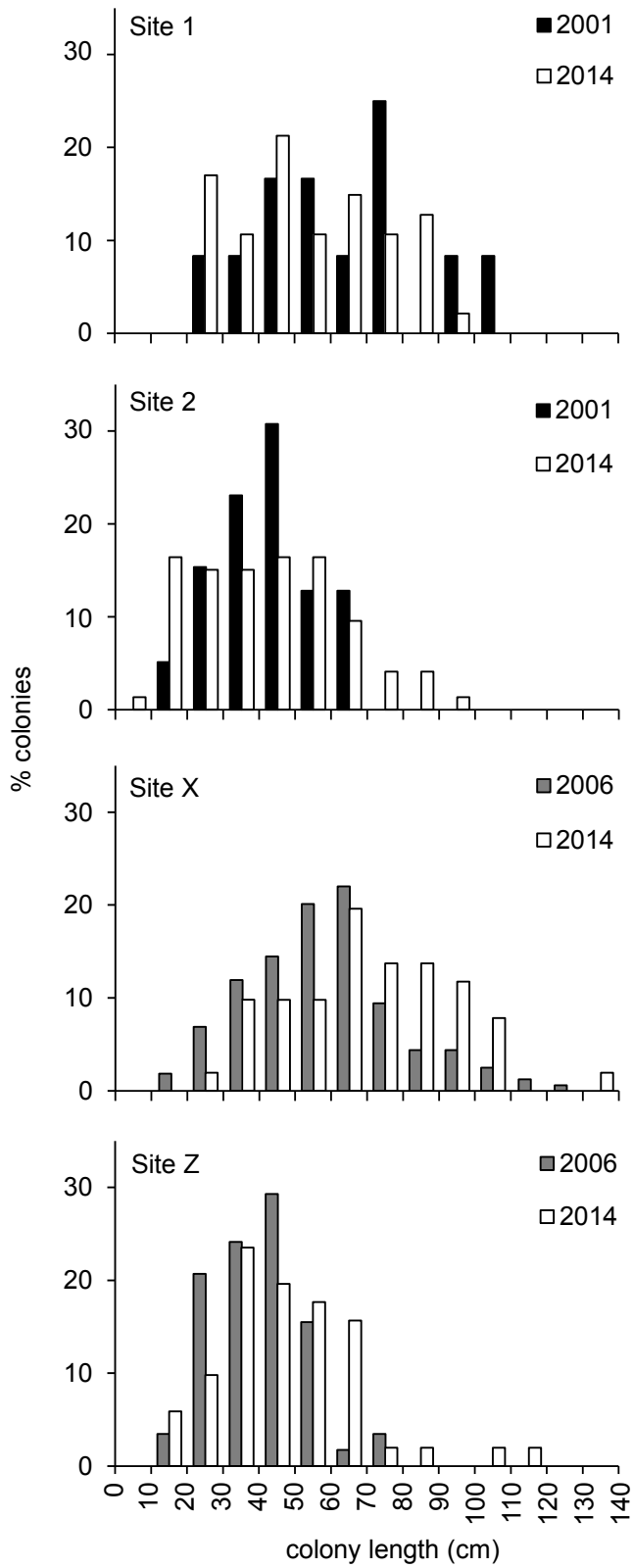
*P. arborea* *P. resedaeformis* ---- ROV track  
 — analysed transect  
 n ○ 1 ● 1-2 ● 3-4  
 depth (m)  
 -436  
 -463

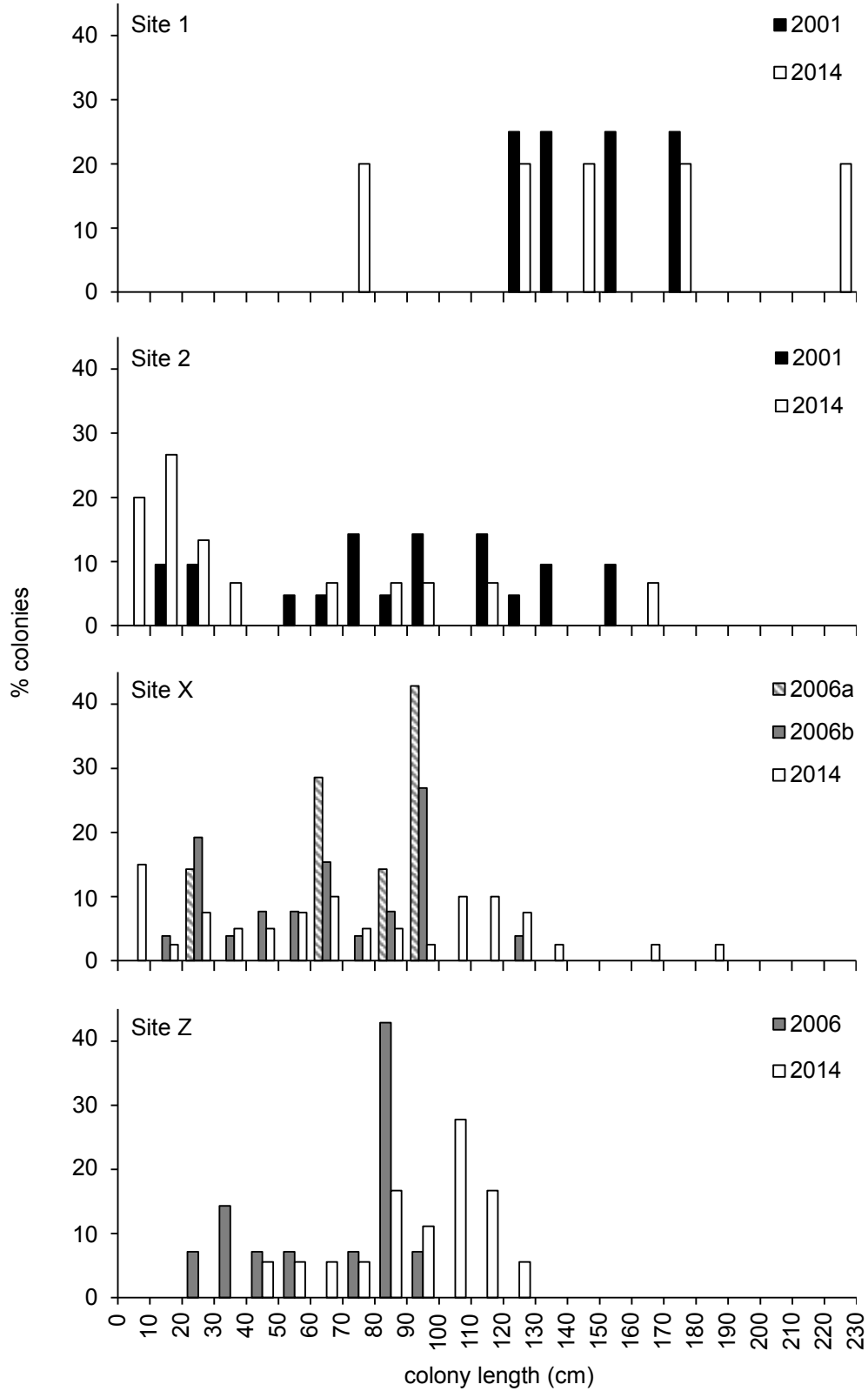


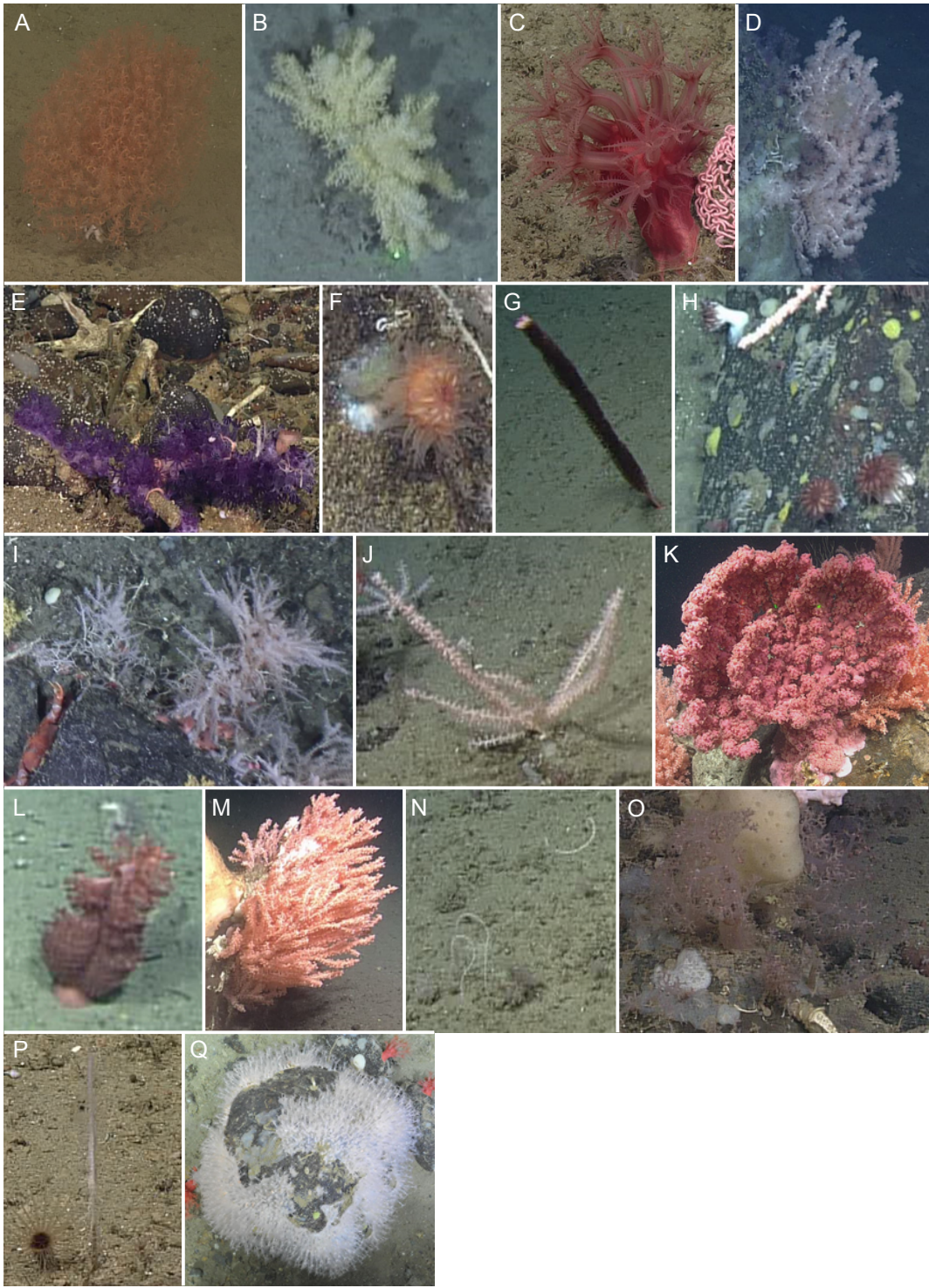
*P. arborea* *P. resedaeformis* — fishing line  
 ---- ROV track  
 — analysed transect  
 n ○ 1-2 ● 1-2 ● 3-5 ● 6-10 ● >10  
 ○ 3  
 depth (m)  
 -471  
 -492

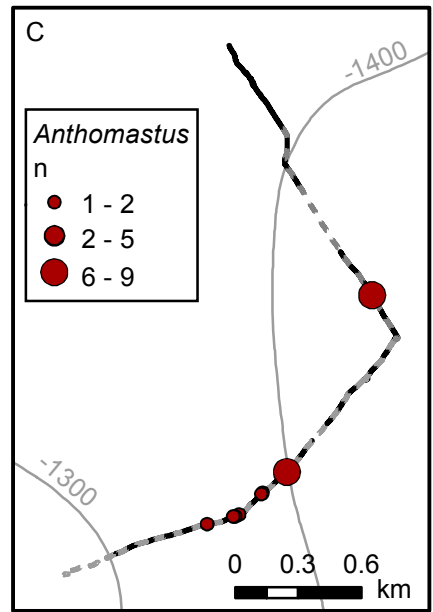
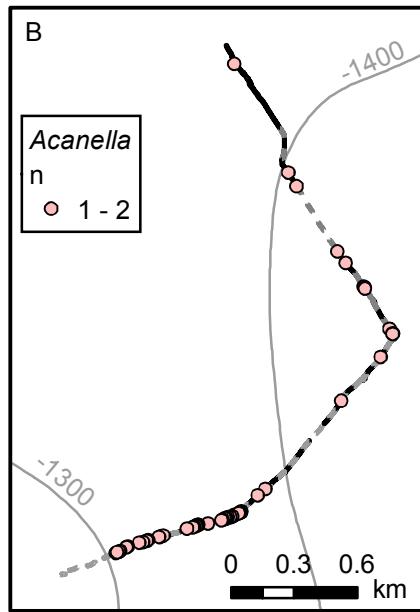
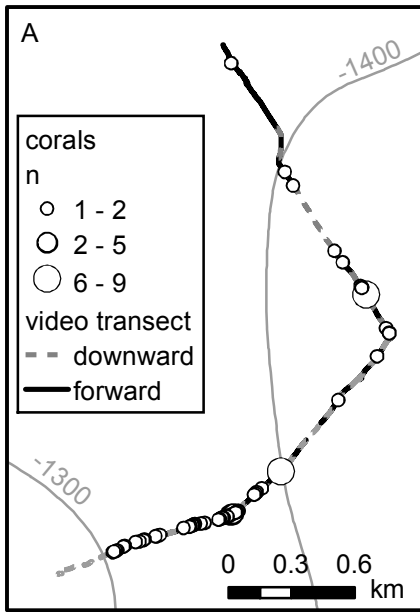


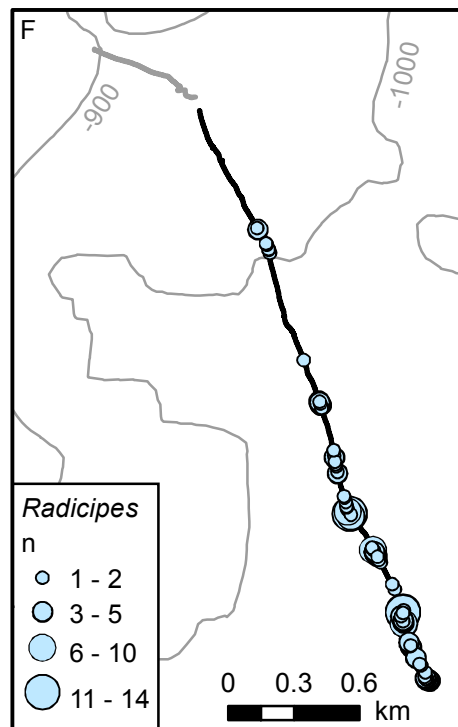
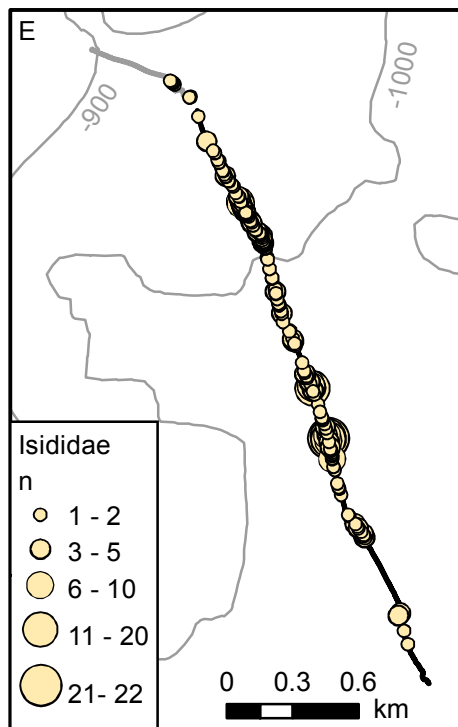
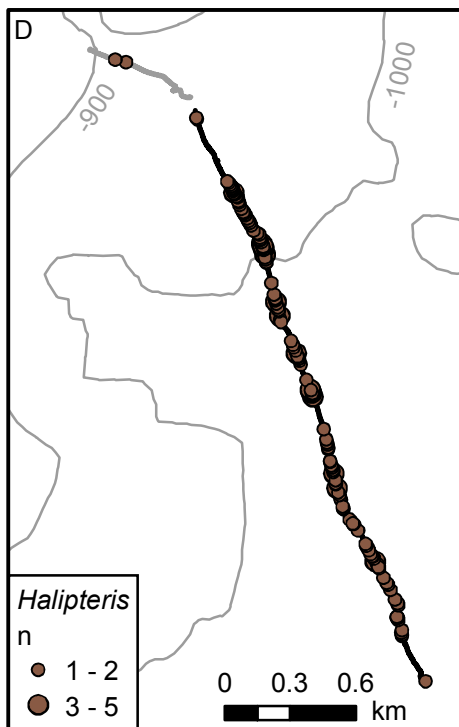
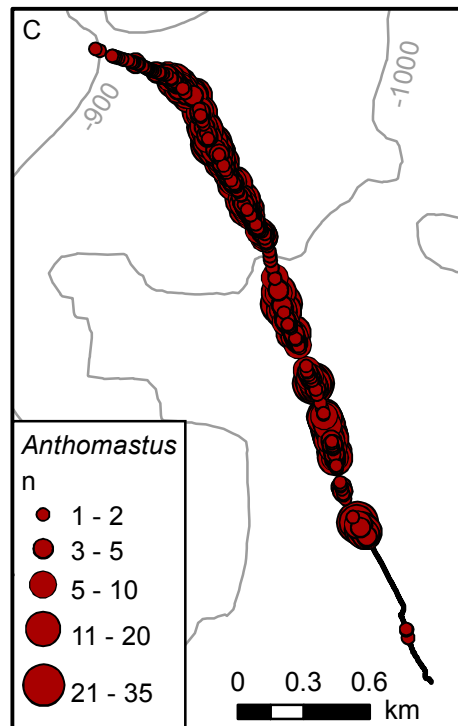
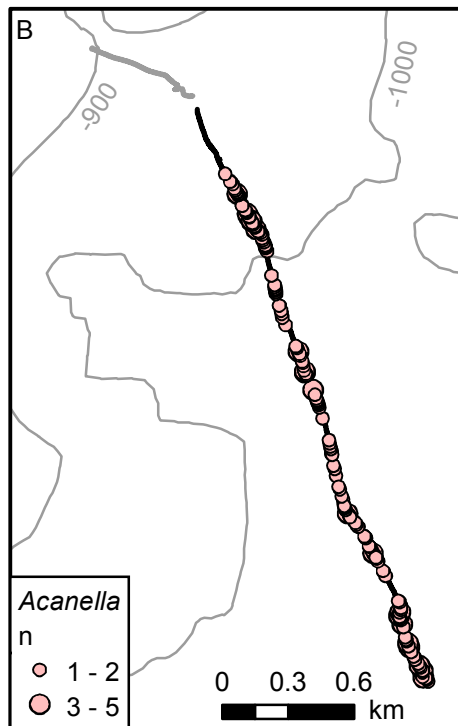
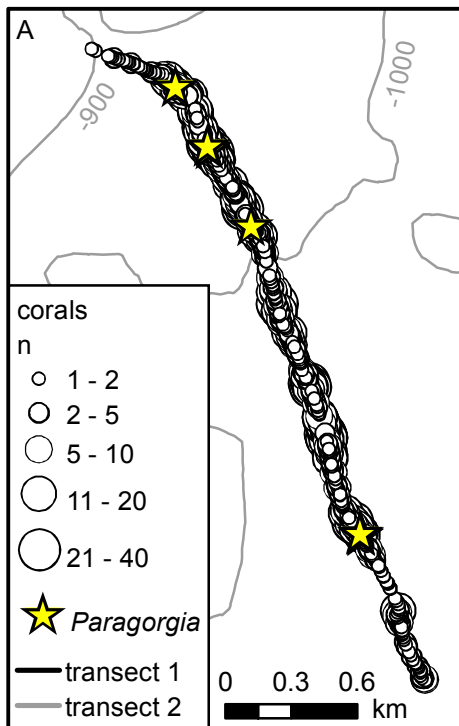
*P. arborea* *P. resedaeformis* analysed transect  
 n ○ 1-2 ● 1-2 ● 3-5 ● 6-10 ● >10  
 ○ 3-5 ● 3-5 ● 6-10 ● >10  
 upper plateau  
 wall  
 lower plateau  
 depth (m)  
 -641  
 -692  
 ---- ROV track



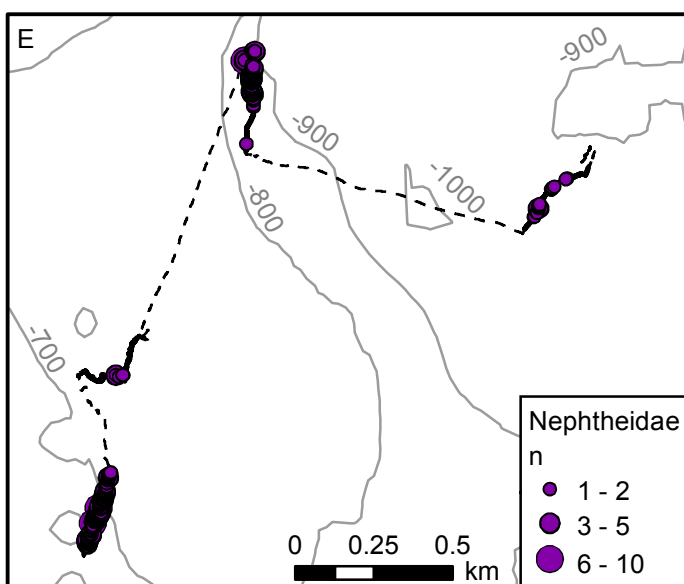
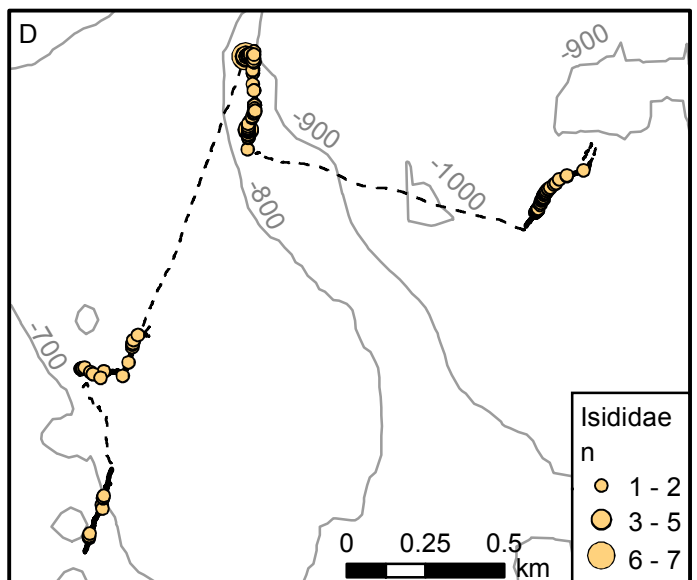
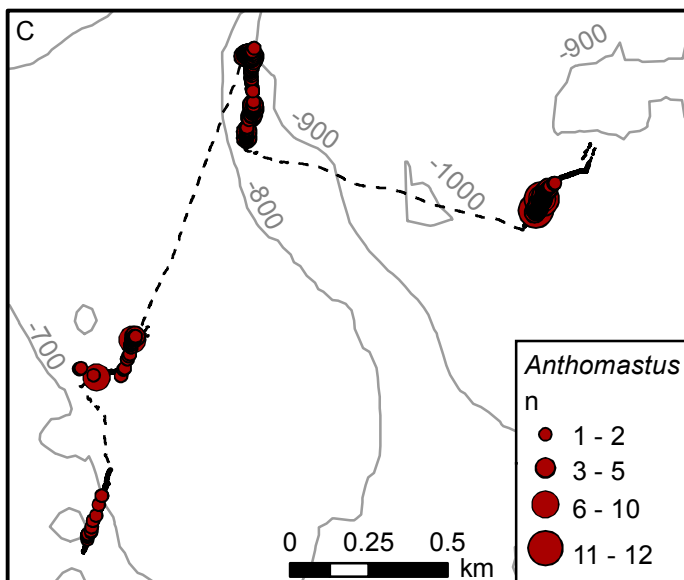
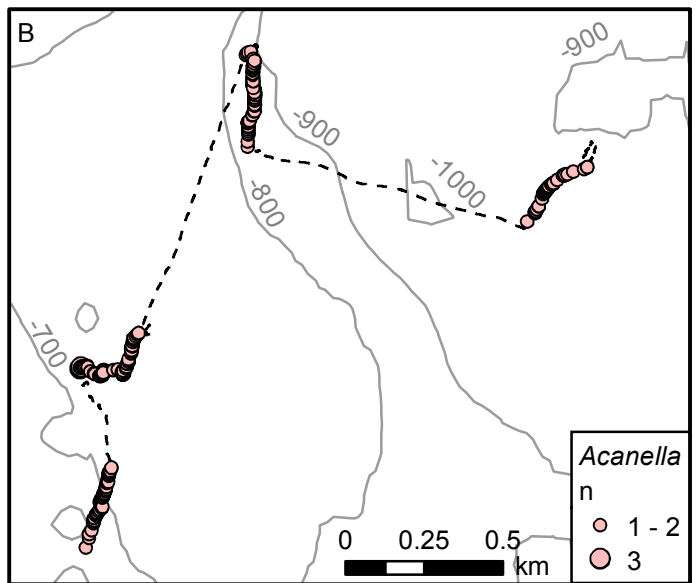
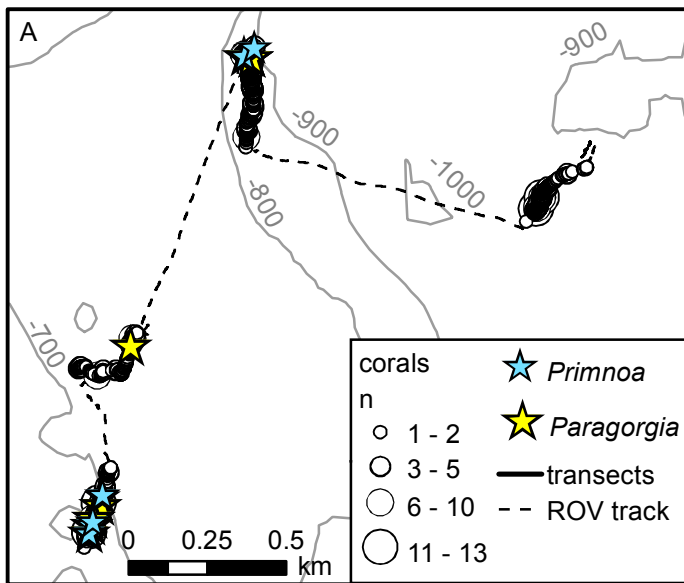












**Table 1.** Characteristics of dive sites and dives conducted with the ROV ROPOS in the Northeast Channel Coral Conservation Area for measurements of coral abundance and size frequency distributions in 2001, 2006 and 2014

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 <sup>2</sup> )
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 <sup>2a</sup>	<i>Primnoa resedaeformis</i>			<i>Paragorgia arborea</i>			Reference
				n	100 m <sup>-2</sup>	SD <sup>a</sup>	n	100 m <sup>-2</sup>	SD <sup>a</sup>	
1	2001	387 - 452	na	12 - 36	1.9 - 3.6	na	1 - 5	0.2 - 1.1	na	Mortensen & 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 & 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

<sup>a</sup> na = not available in Mortensen & Buhl-Mortensen (2004)

**Table 4.** *Primnoa resedaeformis* and *Paragorgia arborea*.

Weighted mean coral abundance at three sub-sections of site X  
in 2014

Habitat,feature	Analysed area (m <sup>2</sup> )	<i>P. resedaeformis</i>		<i>P. arborea</i>	
		n	(100 m <sup>-2</sup> )	n	(100 m <sup>-2</sup> )
lower plateau	158	92	58.14	13	8.22
wall	263	71	27.04	55	20.95
upper plateau	753	441	58.56	19	2.52

**Table 5.** *Primnoa resedaeformis*. Size frequency parameters at four locations inside the Coral Conservation Area in 2001 (site 1 and site 2), 2006 (site X and site Z) and 2014 (all sites).

Site <sup>a</sup>	Year	n	Mean (cm)	SD (cm)	Median (cm)	Min (cm)	Max (cm)	Skewness*
Site 1	2001	12	63	24	60	27	105	0.24
Site 1	2014	47	54	21	52	21	92	0.10
Site 2	2001	39	42	14	41	16	68	-0.05
Site 2	2014	73	43	21	45	8	93	0.35
Site X	2006	159	58	21	57	13	120	0.46*
Site X	2014	51	70	24	68	27	134	0.15
Site Z	2006	58	41	14	40	17	88	0.83*
Site Z	2014	51	48	20	48	11	113	0.80*

<sup>a</sup> For 2001, coral colonies  $\leq$  150 m away from colonies measured in 2014 were analysed. In 2006, corals at depth ranges of 600 - 700 m (site X) and 650 – 700 m (site Z) were included.

\* Significant skewness: Skewness divided by its standard error  $>$  2 (Field et al., 2012)

**Table 6.** *Paragorgia arborea*. Size frequency parameters at four locations inside the Coral Conservation Area in 2001 (site 1 and site 2), 2006 (site X and site Z) and 2014 (all sites).

Site <sup>a</sup>	Year	n	Mean (cm)	SD (cm)	Median (cm)	Min (cm)	Max (cm)	Skewness*
Site 1	2001	4	147	23	143	127	176	0.27
Site 1	2014	5	148	58	149	72	227	0.03
Site 2	2001	21	86	44	91	10	156	-0.26
Site 2	2014	15	47	49	22	5	167	1.08
Site Xa	2006	7	75	27	89	21	99	-0.96
Site Xb	2006	26	64	30	66	14	121	-0.09
Site X	2014	40	71	47	70	4	182	0.22
Site Z	2006	14	69	25	81	25	103	-0.49
Site Z	2014	18	93	22	99	47	128	-0.59

<sup>a</sup> For 2001 coral colonies  $\leq$  150 m away from colonies measured in 2014 were analysed (site 1, site 2b). In 2006, corals at depth ranges of 600 - 700 m (site Xa), 600 - 750 m (site Xb) and 650 – 700 m (site Z) were included.

\* Significant skewness: Skewness divided by its standard error  $>$  2 (Field et al., 2012)

**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 (100 m <sup>-2</sup> )	SD	Coral observations		Abundance (100 m <sup>-2</sup> )	SD	Coral observations		Abundance (100 m <sup>-2</sup> )	SD
Forward n	Downward n	Forward n			Downward n	Forward n			Downward n			
<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 <sup>a</sup>					6	1	0.21	3.75				
Isididae <sup>b</sup>	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 <sup>c</sup>									6	2	0.47	3.57
Stolonifera, white <sup>d</sup>					7				6			

n = number of recorded colonies, SD = standard deviation

<sup>a</sup>White colonies of the family Isididae, likely *Isidella* sp.

<sup>b</sup>White colonies of the family Isididae, most of them likely *Keratoisis* sp.

<sup>c</sup>Small white sea pen

<sup>d</sup>Aggregations of white stoloniferous colonies could not be identified visually in more detail than the suborder