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RESILIENCY OF MARINE BENTHIC COMMUNITIES IN SEA SCALLOP ROTATIONAL MANAGEMENT AREAS ON GEORGES BANK

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ABSTRACT Area closures allow fish and shellfish populations and associated habitats to recover from the effects of fishing. Determining the appropriate duration of rotational management closures for the Atlantic sea scallop (*Placopecten magellanicus*) fishery requires information on both the recovery of scallop populations for subsequent harvest and the resiliency of marine benthic ecosystems for conservation objectives. Here, the effects of scallop fishing on the benthic communities of the northern edge of Georges Bank were examined with a control-impact environmental study comparing an area that had been closed to fishing for over 20 y to an area continually fished. Substrate composition, faunal density, and taxonomic richness data were collected using drop camera surveys. These areas have similar substrate composition, mostly cobble and gravel. Sediment in the control area shifted to larger particle sizes over time, whereas the sediment in the impact area remained the same, suggesting fishing activity prevented this shift in the impact area. Comparing survey stations of like substrate showed that as fishing effort subsided from 2015 to 2017, there was a marked recovery of taxonomic richness and abundance in the impact area. The impact and control areas shifted in a similar manner but varied in the intensity of the shift. This suggests the benthic communities in this area of Georges Bank were relatively resilient to the effects of fishing effort with mean densities of all categories recovering within 2 years.

KEY WORDS: Scallop, Marine Protected Area, resilience

INTRODUCTION

Scallop dredging has a breadth of impacts on benthic communities including reduced megafaunal species and production (Collie et al. 1997, Hermsen et al. 2003), and homogenization of the substrate (Kaiser et al. 2006, Stewart & Howarth 2016). The magnitude of these impacts depends on the level of fishing disturbance relative to the level of natural disturbance (Auster &Langton 1999, Stokesbury & Harris 2006, Lambert et al. 2017). Designating spatial management areas, such as habitat areas of particular concern (HAPC), where high-priority habitat is accompanied by stricter conservation measures, may help mitigate the effects of bottom fishing (Rosenberg et al. 2000, Kaiser et al. 2002). Determining appropriate approaches to spatial management has been hindered, as many studies on the effects of bottom fishing lack unfished control areas (Jennings & Kaiser 1998, Sciberras et al. 2013, Leblanc et al. 2015).

Spatial management is successfully used in the sea scallop (*Placopecten magellanicus*) fishery off the northeastern coast of the USA. Three closed areas, including an HAPC, were implemented on Georges Bank in 1994, and yielded the highest scallop densities and largest sea scallop sizes ever observed in that area after just 5 y (Murawski et al. 2000, Stokesbury 2002, Stokesbury et al. 2016). Due to this success, fisheries managers permitted short-term openings to the scallop fishery in these areas (Murawski et al. 2000, Stokesbury 2002, NEFMC 2004, Stokesbury et al. 2007). Using a video survey, Stokesbury and Harris (2006) compared the changes in biological diversity, density, and sediment composition of two areas impacted by one of these short-term openings with two unimpacted areas. They found that scallop dredging had less of an impact on the epibenthic community and sediment composition than the natural disturbance, and that sediment composition shifted more among surveys than epibenthic faunal composition. This suggests that this community is adapted to a dynamic environment (Stokesbury & Harris 2006). These results differed from previous studies in this area that suggested that scallop dredging severely impacts the seafloor for 10–20 y (Collie et al. 1997, Hermsen et al. 2003, Asch & Collie 2008). These disparities were examined with an opportunity to use the Northern Edge HAPC within Closed Area II (CAII) as a control site (HAPC-control) and the ICJ Line Closure of Canada (C1) as an impact site (C1-impact) to conduct a control-impact environmental study (Fig. 1). The HAPC-control area has been closed to fishing for over 20 y and is the most pristine environment on Georges Bank. The C1-impact area was continuously open to fishing before a voluntary fisheries closure was implemented from January 1, 2014, to June 1, 2015, after which it was heavily fished for one season. Following the brief fishery, the area was allowed to rest. These areas are located adjacent to each other on either side of the Hague Line (Fig. 1). The hypothesis that changes in substrate and benthic communities of the impact area would be similar to changes in the control area by comparing the substrate composition, the number of taxa, and the densities of individuals within each taxonomic group of the areas were tested. This study clarifies conflicting results of previous studies on the ecological effects of scallop dredging (Collie et al. 1997, Hermsen et al. 2003, Stokesbury & Harris 2006). Information is provided on the effects the fishery has on the marine habitat, which is required by fisheries managers implementing rotational management strategies (Stokesbury 2002).

MATERIALS AND METHODS

Experimental Design

A control-impact environmental experiment was conducted to evaluate the effects of scallop fishing on the

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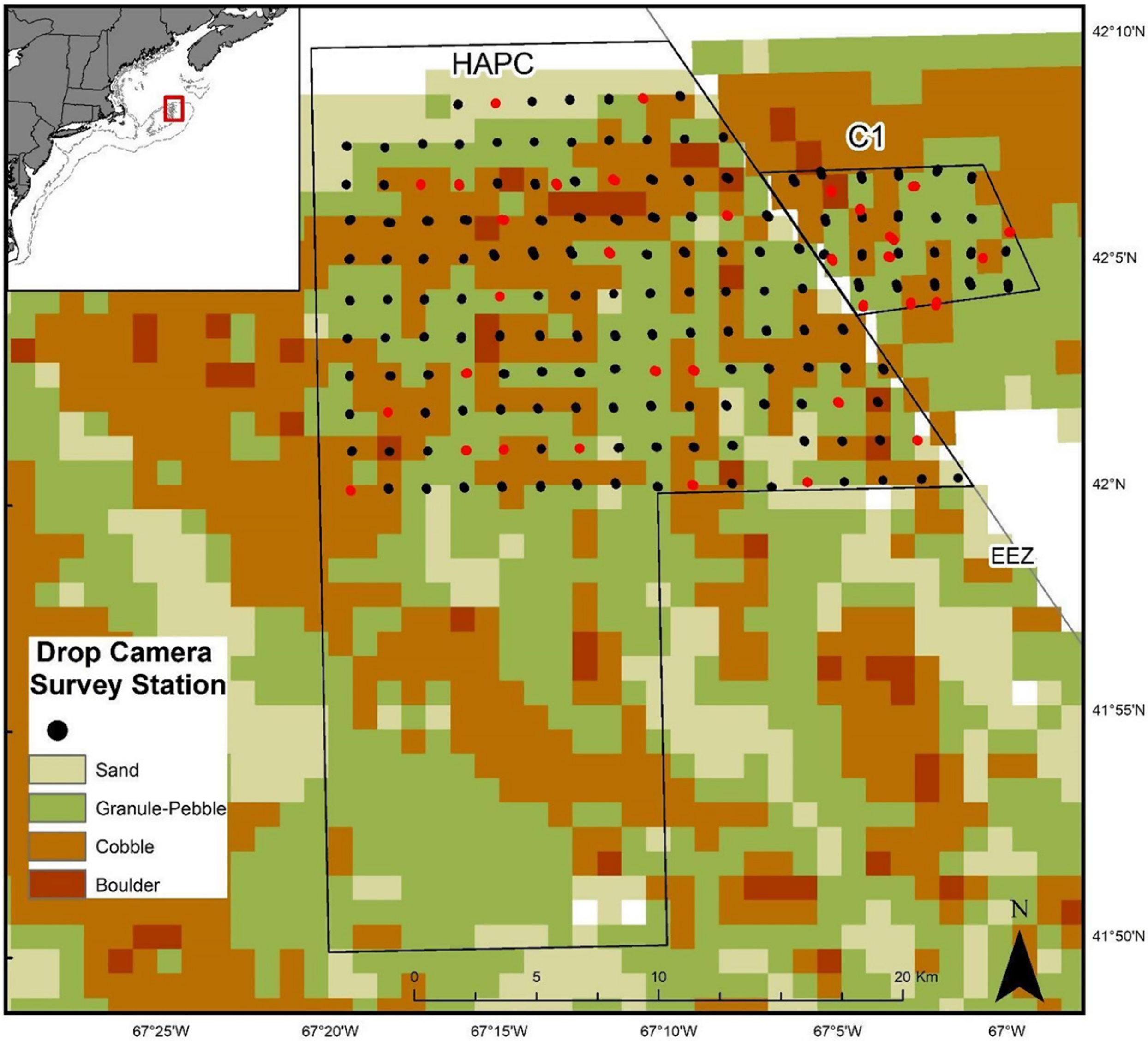

Figure 1. The survey stations in the HAPC-control in 2015 and C1 in 2014 were overlaid on the substrate distribution defined by Harris and Stokesbury (2010) showing the total number of stations sampled in each area. Subset stations are represented by red dots.

epibenthic communities against the background of the high natural disturbance of Georges Bank (Underwood 1992, Stokesbury & Harris 2006, Harris et al. 2012). The control-impact design assesses the effect of a stressor by comparing an affected area (impact) to a similar unaffected (control) area (Green 1979). To compare areas, the control and impact areas are assumed to have similar epibenthic communities and environmental conditions, and that these communities will change over time in the same fashion, except from any disturbances caused by scallop dredging in the impact areas (Stokesbury & Harris 2006).

The HAPC-control and C1-impact areas cover 340 km^2 and 50 km^2, respectively. The HAPC-control was designated because of the importance of its gravel substrate with patches of encrusting sessile species as nursery and spawning ground for several commercially important fish species (Auster et al. 1996, Murawski et al. 2000, Asch & Collie 2008, Harris & Stokesbury 2010, Howarth et al. 2011). Stations were used from the northern half of the HAPC-control for comparisons because the substrate composition was like the C1-impact area. Gravel and cobble made up 75% of the HAPC-control and 95% of the C1-impact area sediment compositions. The areas also had similar scallop densities and current structure. The mean water depths were 65 m and 57 m in the HAPC-control and C1-impact areas, respectively.

Survey Design

In 2014, 2015, and 2017, optical data were collected of the HAPC-control and C1-impact areas using the SMAST drop camera survey (Stokesbury & Harris 2006, Bethoney & Stokesbury 2018) (Table 1). Using a systematic sampling design, four quadrats were sampled with images and video of the seafloor at stations arranged in a grid pattern. Images and video were taken using a sampling pyramid made of a steel frame equipped with lights and cameras, lowered to the seafloor from a fishing vessel.

TABLE 1.

The camera type, grid spacing in square kilometers, number of total and subset stations and quadrat, and quadrat area in m² are listed by year and area.

Year	Area	Camera	Grid (km^2)	Total stations	Subset stations	Total quadrats	Subset quadrats
2014	HAPC	Large	5.56	12	11	48	44
–	C1	–	0.93	44	–	176	–
2015	HAPC	Large	5.56, 1.57	151	22	604	88
–	C1	–	0.93	22	–	88	–
2017	HAPC	DSC	5.56	11	10	44	40
–	C1	–	1.48	22	–	88	–

HAPC, habitat areas of particular concern.

The deep-sea large camera used in 2014 and 2015 and the Imperx camera used in 2017 provided quadrat images of 2.8 m^2 and 2.39 m^2, respectively (Bethoney 2020). Images were analyzed by counting fishes and macroinvertebrates as well as defining substrate composition. To account for individuals only partially visible along the edge of the quadrat image, an edge effect (based on half the average shell height of the scallops observed) was added to each edge of the quadrat image (Bethoney & Stokesbury 2018, Bethoney 2020). When possible, fishes and macroinvertebrates to a minimum size of about 40 mm were identified to species and animals were grouped into categories based on taxonomic order (similar to Table 2 of Stokesbury & Harris 2006). Counts were standardized to individuals per meter-squared at quadrat level. Colonial organisms that were difficult or impossible to count were marked as present or absent in each quadrat. Sediment type and shell debris were visually identified and the sediment for each quadrat was categorized based on the largest grain size present, ranked according to the Wentworth particle grade scale, where sand = 0.625–2.0 mm, gravel = 2.0–64.0 mm, cobble = 64.0–256.0 mm, and rock ≥256.0 mm (Harris & Stokesbury 2010).

To balance the experimental design, an equal number of stations of each sediment type in the control and impact area were selected for each year. This standardized the design as scallops have a strong association with certain substrates (Stokesbury 2002). This subset of stations was used to compare changes in species composition. The number of subset stations was based on the minimum number in stations of like substrate; for example, there were 12 gravel stations in C1-impact and 61 in the HAPC-control in 2015, so 12 gravel stations were randomly selected from the 61 gravel stations in the HAPC-control. There were 11, 22, and 10 stations in each area in 2014, 2015, and 2017, respectively. Data from cameras of the same models were compared (Table 1).

TABLE 2.

The mean densities for count taxonomic categories and mean proportion of presence for presence/absence taxonomic categories including standard errors for each are listed by area and year.

Year	2014				2015				2017			
Area	C1-impact		HAPC-control		C1-impact		HAPC-control		C1-impact		HAPC-control	
N	11		11		22		22		10		10	
Taxa	11		7		9		14		11		10	
Counts	**Density**	**SE**	**Density**	**SE**	**Density**	**SE**	**Density**	**SE**	**Density**	**SE**	**Density**	**SE**
Sea star	0.61	0.168	0.04	0.022	0.13	0.026	0.34	0.149	0.49	0.099	0.74	0.284
Scallop	1.27	0.280	0.66	0.190	0.60	0.129	0.50	0.211	1.88	0.439	0.53	0.251
Crab	0.00	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.01	0.008
HermitCrab	0.01	0.010	0.32	0.055	0.02	0.011	0.32	0.039	0.33	0.060	0.33	0.059
Lobster	0.01	0.007	0.00	0.000	0.00	0.000	0.00	0.004	0.02	0.016	0.00	0.000
Buccinum	0.01	0.007	0.02	0.021	0.01	0.006	0.00	0.000	0.03	0.013	0.04	0.013
Moon snail	0.00	0.000	0.02	0.021	0.00	0.000	0.00	0.004	0.02	0.012	0.00	0.000
Skate	0.02	0.011	0.01	0.009	0.00	0.004	0.01	0.007	0.00	0.000	0.00	0.000
Flatfish	0.01	0.007	0.00	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00	0.000
Pres/Abs	–	–	–	–	–	–	–	–	–	–	–	–
SandDollar	0.00	0.000	0.00	0.000	0.00	0.000	0.01	0.011	0.00	0.000	0.03	0.025
Anemone	0.00	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.03	0.025	0.25	0.112
Bryo/hydro	0.05	0.030	0.00	0.000	0.26	0.056	0.71	0.077	0.50	0.118	0.33	0.124
Clam	0.02	0.023	0.18	0.096	0.01	0.011	0.30	0.078	0.00	0.000	0.00	0.000
Sponge	0.21	0.074	0.00	0.000	0.14	0.039	0.08	0.034	0.78	0.069	0.20	0.062
Urchin	0.00	0.000	0.00	0.000	0.00	0.000	0.01	0.011	0.15	0.076	0.00	0.000
Tunicate	0.02	0.023	0.00	0.000	0.01	0.011	0.14	0.075	0.23	0.087	0.23	0.079
Brittle star	0.00	0.000	0.00	0.000	0.00	0.000	0.01	0.004	0.00	0.000	0.00	0.000

Number of stations (N) and number of taxonomic categories (Taxa) are given for each area and year. Count taxonomic categories are listed first followed by presence/absence taxonomic categories with the mean proportion presented.
HAPC, habitat areas of particular concern.

Data Analysis

The sediment composition was calculated by finding the proportion of each sediment type for all sampled stations in each area for each year. To assess whether these proportions changed over time, the proportions of sediment composition in each year were compared using chi square tests ($\alpha < 0.05$).

Estimates for the mean densities and standard errors of scallops were calculated using equations for a two-stage sampling design (Cochran 1977):

$$\bar{x}_i = \sum_{j=1}^{n} \left(\frac{x_{ij}}{m} \right) \tag{1}$$

$$\bar{\bar{x}} = \sum_{i=1}^{n} \left(\frac{\bar{x}_i}{n} \right) \tag{2}$$

where, n = primary sample units (stations), m = elements per primary sample unit (quadrats), x_{ij} = measured value (counts of scallops) for element j in primary unit i, $\bar{x}_i$ = sample mean per element (quadrat) in primary unit i (stations), and $\bar{\bar{x}}$ = the mean over the two stages. The standard error of this mean is:

$$S.E.(\bar{x}) = \sqrt{\frac{1}{n}\left(S^2\right)} \tag{3}$$

where, $s^2 = \sum^{n}\left(\bar{x}_i - \bar{\bar{x}}\right)^2 / (n-1)$ is the variance among primary unit (stations) means.

This simplified version of the two-stage variance is possible when the sampling fraction n/N is small (Cochran 1977). This is the case for the drop camera survey, where thousands of m^2 are sampled compared to millions of m^2 in the study area. In addition, the quadrat sizes within each zone were increased based on the average scallop shell height in the zone to adjust for partially visible scallops counted along the edge of the image (Bethoney and Stokesbury, 2018). Average shell height for each area was calculated as a simple mean. This was done only for scallops all other densities are the fixed quadrat area.

A t-test ($\alpha < 0.05$) on the C1-impact area to compared mean densities of scallops between 2014 and 2015 to identify any effect of the opening of the fishery on the scallops. Also, two-way and one-way analysis of variance (ANOVA) ($\alpha < 0.05$) were used to test the statistical significance of shifts in mean individuals per m^2 within each taxonomic category among surveys for each area (Underwood 1981). Two-way ANOVA with replication examined the influence of area and year on the mean density of each taxonomic category. The one-way ANOVA used the mean individuals per m^2 and the standard error of each taxonomiccategory with the number of stations as the sample size. Holm–Sidak method posthoc tests on statistically significant comparisons were conducted to identify the differences among years to accept/reject the null hypothesis (Cardillo 2020). Density data were $\log_{10}(x + 1)$ transformed emphasizing relative differences and improving homogeneity of variance.

The similarity in species composition among the areas was measured using the Bray–Curtis dissimilarity statistic and percent similarity (Wolda 1981, Krebs 1989). The Bray–Curtis measure uses counts and relative proportions of species, ignores cases in which the species is absent in both community samples, and it is dominated by the abundant species so that rare species add very little to the value of the coefficient (Krebs 1989). Percentage similarity uses the percent composition of stations to compare counts and relative proportions of taxonomic categories present in each area. Both indices of similarity standardize similarity as a percentage. Bray–Cutis dissimilarity statistic ranges from 0% for identical communities to 100% for those that are completely different. Percent similarity ranges from 100% for identical communities to 0% for those that are completely different.

To understand whether the community composition is similar among stations within each year and area, and whether there are differences by area or year when looking at the community composition, a cluster analysis and principal coordinate analysis was performed (Carmichael & Sneath 1969, Legendre & Anderson 1999).

RESULTS

Gravel and cobble comprised most of the sediment for all areas and years by at least 75%. The HAPC-control in 2014 had the smallest overall particle size with 25% sand, 58.3% gravel, 16.7% cobble, and no rock. The HAPC-control in 2017 had the largest overall particle size with no sand, 9.1% gravel, 72.7% cobble, and 18.2% rock. Sand was present in the HAPC-control, but not in C1-impact. Rock was present in all areas and years except in the HAPC-control in 2014 (Fig. 2).

The sediment composition within each area did not differ from 2014 to 2015 (n_{2014} = 12, n_{2015} = 151, χ^2 = 7.24, df = 3, P = 0.065, HAPC-control) (n_{2014} = 44, n_{2015} = 22, χ^2 = 1.29, df = 2, P = 0.526, C1-impact) or from 2015 to 2017 (n_{2015} = 151, n_{2017} = 11, χ^2 = 7.33, df = 3, P = 0.062, HAPC-control) (n_{2015} = 22, n_{2017} = 22, χ^2 = 0.1, df = 2, P = 0.95, C1-impact). Sediment composition was different among areas for 2014 ($n_{\text{HAPC-control}}$ = 12, $n_{\text{C1-impact}}$ = 44, χ^2 = 12.12, df = 3, P = 0.007), 2015 ($n_{\text{HAPC-control}}$ = 151, $n_{\text{C1-impact}}$ = 22, χ^2 = 245.36, df = 3, P < 0.001), and 2017 ($n_{\text{HAPC-control}}$ = 11, $n_{\text{C1-impact}}$ = 22, χ^2 = 22.72, df = 2, P < 0.001).

The sediment composition differed significantly from 2014 to 2017 in the HAPC-control area (n_{2014} = 12, n_{2017} = 11, x^2 = 13.08, df = 3, P = 0.004) but not in the C1-impact area (n_{2014} = 44, n_{2017} = 22, x^2 = 0.59, df = 2, P = 0.746).

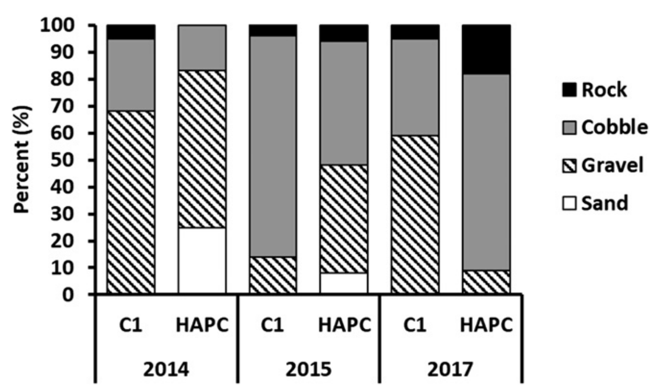

Figure 2. Sediment composition in control and impact areas observed in 2014, 2015, and 2017.

Taxonomic richness decreased in the C1-impact area between 2014 and 2015 from 11 to 9 taxonomic categories, whereas taxonomic richness increased from 7 to 14 taxonomic categories in the HAPC-control area. Taxonomic richness increased in the C1-impact area between 2015 and 2017 from 9 to 11 taxonomic categories, whereas taxonomic richness decreased in the HAPC-control from 14 to 10 taxonomic categories (Table 2). The C1-impact area in 2017 had the overall greatest mean density of all taxonomic categories, whereas the C1-impact area in 2015 had the overall lowest mean density of all taxonomic categories (Table 2). Sea scallop and starfishes comprised the majority of individuals for all areas and years. In addition to sea stars and scallops, hermit crabs were consistently abundant throughout areas and years. Bryozoans/Hydrozoans and sponges were also prominent categories except in the HAPC-control area in 2014, where both were absent.

The fishing event occurred between 2014 and 2015. The mean density of scallops decreased significantly from 2014 (t-test; $\bar{x}$ = 1.273, SD = 0.916) to 2015 ($\bar{x}$ = 0.596, SD = 0.605) in the C1-IMPACT-impact area; $t(31) = 2.546$, $P = 0.0161$. The differences in mean densities of taxonomic categories over time were statistically clear using the one-way ANOVA (Table 3). From 2014 to 2015, sea star density decreased in the C1-impact area and remained the same in the HAPC-control area and tunicate density increased in the HAPC-control area and remained the same in the C1-impact area. Bryozoans/hydrozoan density increased in both areas (Table 3, Fig. 3). From 2015 to 2017, scallop, sea stars, scallops, hermit crabs, moon snails, sponges, urchins, and tunicates densities in the C1-impact area significantly increased, while these faunal densities remained the same in the HAPC-control. Bryozoans/hydrozoans densities increased in the C1-impact area and decreased in the HAPC-control. Brittle stars decreased in the HAPC-control area and remained the same in the C1-impact

TABLE 3.

Comparison of mean number of individuals per m^2 within each taxonomic category from 2014 to 2017, using one-way ANOVA.

HAPC	–	Df	SS	MS	F	P
Bryozoans/ hydrozoans	Between Groups	2	3.801	1.900	18.605	<0.001
–	Residual	40	4.086	0.102	–	–
Anemone	Between Groups	2	0.480	0.240	8.527	<0.001
–	Residual	40	1.125	0.028	–	–
Buccinum	Between Groups	2	0.012	0.006	3.52	0.39
–	Residual	40	0.065	0.002	–	–
Sponge	Between Groups	2	0.212	0.106	–	–
–	Residual	40	0.898	0.023	–	–
Brittle Star	Between Groups	2	0.001	0.001	4.763	0.014
–	Residual	40	0.006	0.000	–	–
C1	–	–	–	–	–	–
Scallop	Between Groups	2	11.895	5.948	7.107	0.002
–	Residual	40	33.473	0.837	–	–
Bryozoans/ hydrozoans	Between Groups	2	1.082	0.541	7.767	0.001
–	Residual	40	2.787	0.070	–	–
Moon Snail	Between Groups	2	0.005	0.002	6.578	0.003
–	Residual	40	0.014	0.019	–	–
Hermit Crab	Between Groups	2	0.761	0.381	39.014	<0.001
–	Residual	40	0.390	0.010	–	–
Sea Star	Between Groups	2	1.982	0.991	9.229	<0.001
–	Residual	40	4.295	0.107	–	–
Sponge	Between Groups	2	2.945	1.473	33.672	<0.001
–	Residual	40	1.749	0.044	–	–
Tunicate	Between Groups	2	0.339	0.169	8.497	<0.001
–	Residual	40	0.798	0.020	–	–
Urchin	Between Groups	2	0.173	0.086	6.578	0.003
–	Residual	40	0.525	0.013	–	–

All taxonomic categories were tested. Only significant results are shown. Power with alpha set at 0.05.
ANOVA, analysis of variance.

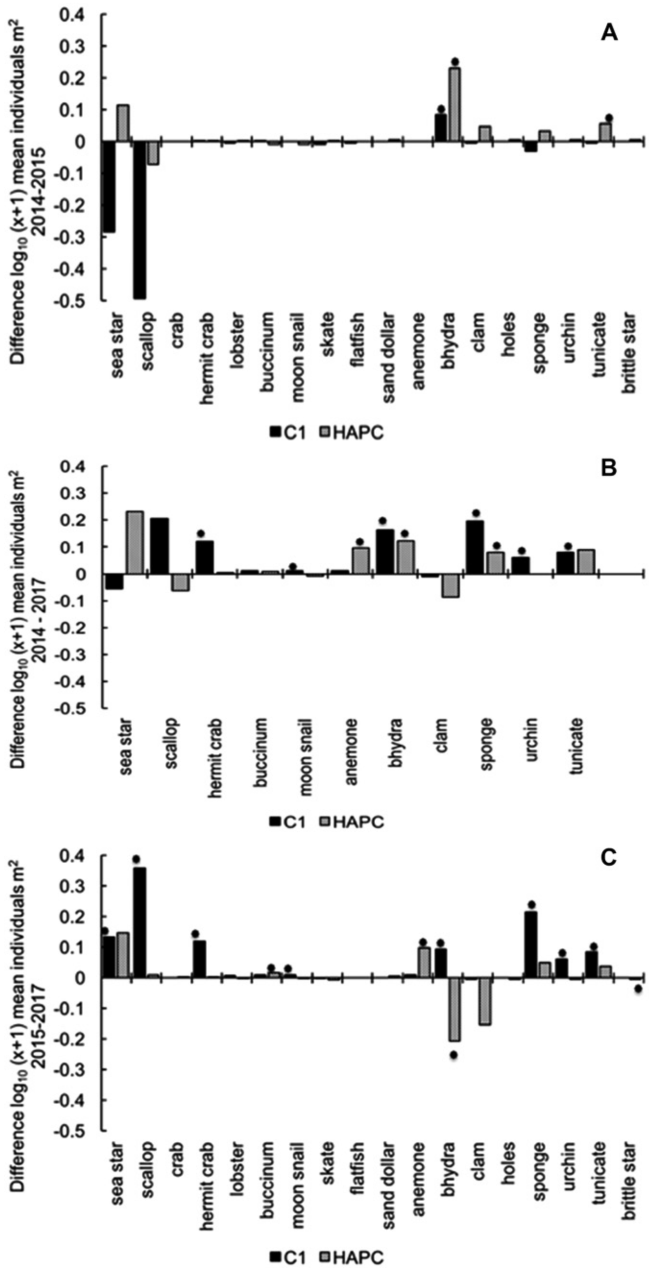

Figure 3. Difference in mean densities for taxonomic categories observed in HAPC-control and C1-impact areas between (A) 2014 and 2015, (B) 2015 and 2017, and (C) 2014 and 2017. Both areas were tested for significance using one-way ANOVA. *Statistical significant difference at P = 0.05.

area. In the HAPC-control area, *Buccinum* sp. and anemone increased, while these faunal densities remained the same in the C1-impact area (Table 3, Fig. 3). From 2014 to 2017, hermit crabs, moon snails, urchins, and tunicate densities increased in the C1-impact area and remained the same in the HAPC-control area. Bryozoans/hydrozoans and sponges increased in both areas. Anemone increased in the HAPC-control area and remained the same in the C1-impact area (Table 3, Fig. 3).

Overall, five taxonomic categories changed significantly in the HAPC-control and eight in the C1-impact (Table 3). There were no significant differences in mean densities between areas or through time for any category and no interaction between area and time (two-way ANOVA). Mean densities of all taxonomic groups in both areas either increased or remained the same from 2014 to 2017 (Table 3). A greater number of category densities increased in the C1-impact area than in the HAPC-control area. Sea star density decreased after the area opened, but recovered to its original state by 2017. Sessile categories, such as sponge and bryozoans/hydrozoans, which were expected to be most vulnerable to bottom fishing (Asch & Collie 2008), increased despite the presence of fishing. Also, scallop density was higher in the C1-impact area than the HAPC-control area for all years. Mean density of anemone remained the same in the C1-impact area but increased in the HAPC-control (Table 3, Fig. 3).

Similarities calculated using the Bray–Curtis statistic indicated that HAPC-control area benthic communities were less similar from 2014 to 2015 (52.9%) than from 2015 to 2017 (36.8%). In the C1-impact area, benthic communities were more similar from 2014 to 2015 (20.5%) than from 2015 to 2017 (28.4%). Similarities calculated by percent similarity indicated that the benthic communities were the most similar between areas in 2014 and the least similar in 2017 (Table 3). In the HAPC-control area, the percent similarity of the benthic communities was lower from 2014 to 2015 (53.5%) than from 2015 to 2017 (64.4%). In the C1-impact area, the percent similarity of the benthic communities was higher from 2014 to 2015 (85.6%) than from 2015 to 2017 (83.0%). Overall, the Bray–Curtis statistic indicated that the HAPC-control area was less similar than the C1-impact area from 2014 to 2017 (57.6% versus 25.4%). The percent similarity of the benthic communities was lower in the HAPC-control than in the C1-impact from 2014 to 2017 (35.5% versus 75.0%).

The cluster analysis and principal coordinate analysis suggest some grouping of data according to area and year (Fig. 4). By year, the first linear discriminant explains 85.3% of the total between-group variation, and the second explains 14.7%. By area and year, the first linear discriminant explains 51.36% of the total variation, the second 23.42%, the third, 12.69%, the fourth 9.55%, and the fifth 2.97%. The linear discriminants explained for most of the variance for each of the models.

DISCUSSION

The impacts of scallop fishing were evaluated on benthic communities and habitats on the highly productive northern edge of Georges Bank. The C1-impact area was exposed to a year and a half closure followed by a concentrated scallop fishing effort. The directly adjacent HAPC-control area has been closed to fishing for over 20 y.

Opportunities to compare the effects of this fishing effort to a practically pristine area are rare. The HAPC-control area on the United States side of the northern edge of Georges Bank has been closed for 28 y. The adjacent C1-impact area was continually fished then closed for 1.5 y followed by a concentrated scallop fishing effort. Benthic communities and sediments are constantly shifting due to the highly dynamic environment of Georges Bank (Harris et al. 2012). This experimental design distinguished these natural changes from those caused by fishing by comparing how both areas changed over time. Some limitations of this design are that any difference that occurred between the two areas is assumed to be from the impact, even if it was not caused by human disturbance, and that if the abundance in the control area changed in the same direction as the impact area, it would cancel the effects of an impact (Underwood 1992). Also, as stations closer together are more likely to be similar and the control area was broader than the impact area, there may be more variability among the selected stations in the control area than those in the impact area. This study did not account for biomass or the size of individuals. Biomass is an important indicator in determining the effects of fishing as it describes the effects on body size and age structure as well as abundance, which greatly correlate to ecosystem functioning (Hiddink et al. 2020). Despite these potential limitations, this study strongly suggests that the benthic communities were relatively resilient to the effects of fishing.

Sediment in the HAPC-control area shifted to larger particle sizes over time, whereas the sediment in the C1-impact area remained the same, perhaps fishing activity prevented this shift in the C1-impact area. Scallop dredging can homogenize substrate (Collie et al. 2000a), shift particle sizes of surface sediments (Collie et al. 2000a, Hall-Spencer & Moore 2000, Bradshaw et al. 2002), and remove larger stones from fishing grounds (Collie et al. 2000a, Bradshaw et al. 2002). Collie et al. (2000a) found that undisturbed sites had more heterogeneous sediments with higher frequencies of sand and cobble than disturbed sites using a photographic survey. They suggested that scallop dredging might have exposed sand and pebbles in the disturbed sites. Bradshaw et al. (2002) also found that sediments became finer over 40–60 y of scallop fishing grounds in the Irish Sea. Hall-Spencer and Moore (2000) found that scallop dredging brought mud and sand to the surface and that fished areas had a higher proportion of fine sediments at the surface than unfished areas using a combination of a remotely operated vehicle, self-contained underwater breathing apparatus (SCUBA), and core samples of maerl beds in the Clyde Sea. These previous studies strengthen the conclusion that scallop fishing prevented the shift of sediment composition to larger particle sizes.

As fishing effort subsided from 2015 to 2017, there was a marked recovery of taxonomic richness and abundance in the C1-impact area. The decrease in faunal density and diversity was undetectable after 2 y suggesting that the recovery of benthic communities exceeded the damage caused by fishing for this dynamic region. This is a rapid recovery suggesting a relatively resilient benthic community in this area, agreeing with other studies conducted in high-energy environments (Stokesbury & Harris 2006, LeBlanc et al. 2015, Lambert et al. 2017). The northern edge of Georges Bank is a high-energy environment with strong tidal currents where only cobble or sediments dominated by gravel remain stable (Harris et al. 2012). Stokesbury and Harris (2006) examined the impacts of a short-term sea

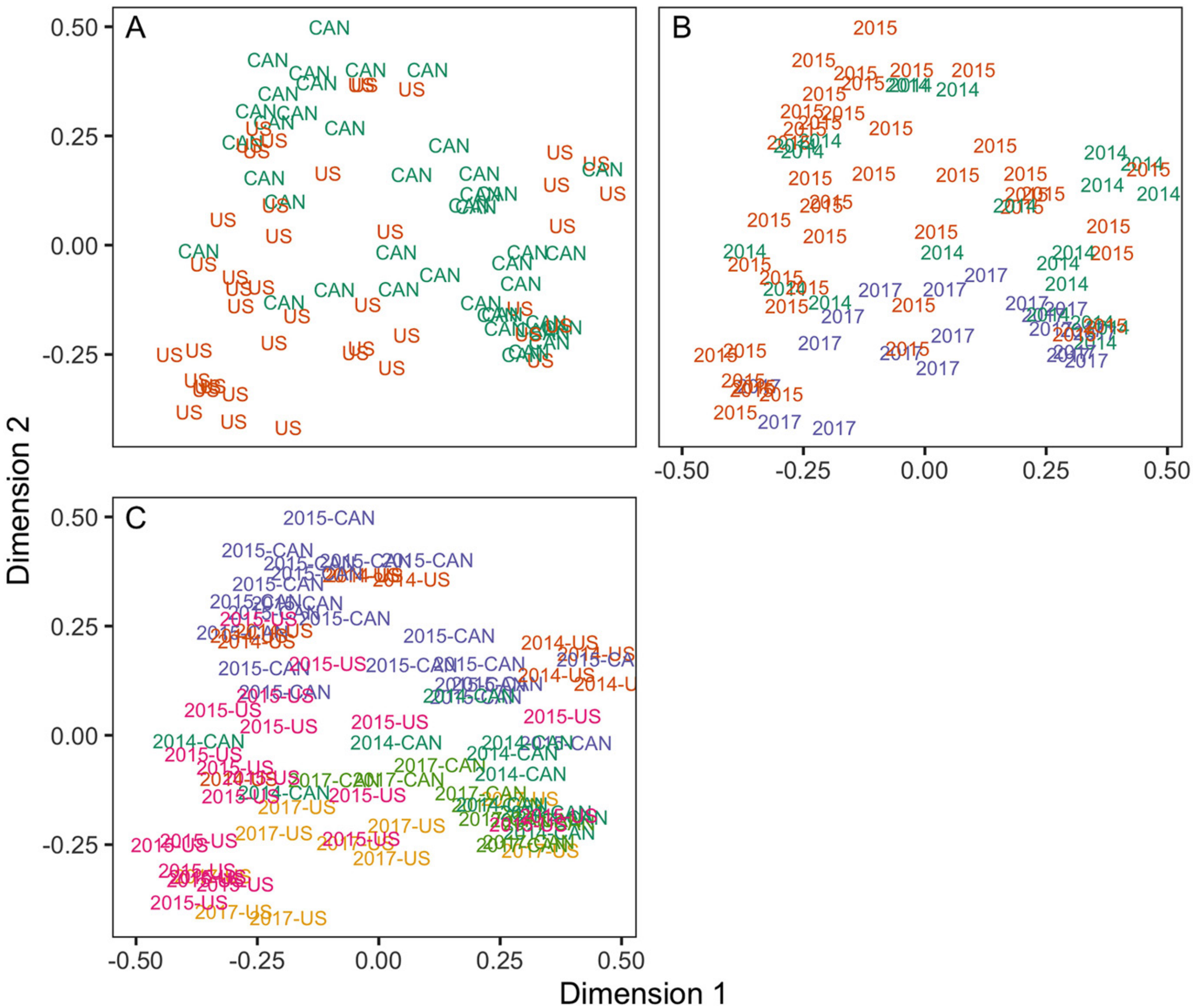

Figure 4. The grouping of stations shown here was calculated using principal coordinate analysis. The stations on plot A are labeled by area [HAPC-control (US) is orange and C1-impact (CAN) is green]. Plot B has the same grouping of stations, but the stations are labeled by year (2014 is green, 2015 is orange, and 2017 is purple). The stations on plot C are labeled by area and year [2014 HAPC-control (US) is orange, 2014 C1-impact (CAN) is turquoise, 2015 HAPC-control (US) is pink, 2015 C1-impact (CAN) is purple, 2017 HAPC-control (US) is yellow, and 2017 C1-impact (CAN) is green].

scallop fishery for benthic communities on Georges Bank using a drop camera survey. They found that the fishery appeared to alter the benthic community less than the environmental conditions. In 2014, Lambert et al. (2017) conducted a BACI fishing intensity gradient experiment within a marine protected area in Cardigan Bay, United Kingdom. They found that the natural temporal variation in community metrics exceeded the effects of fishing in this highly dynamic study site, also suggesting that highly dynamic areas appear relatively resilient to the effects of scallop dredging.

The rapid recovery of the C1-impact area is consistent with the recovery observed by Hermsen et al. (2003) who examined the same area. They monitored CA II for the first 7 y, it was closed to fishing using dredge surveys, and found that production was higher at recovering sites than disturbed sites and that the production to biomass ratio decreased over time. Similarly, more taxonomic category densities increased in the C1-impact area than in the HAPC-control area. Two years after the fishing event, faunal density and diversity in the C1-impact area had recovered to their previous level.

Despite the resilience of the benthic communities, scallop fishing could be keeping this area in a stable altered state. The benthic communities and sediment composition in the C1-impact area experienced less change over the 4-y study than the HAPC-control area. Scallop fishing could be altering the benthic community, favoring those species that are resilient to scallop fishing (Collie et al. 2000b, Szostek et al. 2015, Leblanc et al. 2015). Szostek et al. (2015) acknowledged that they may not have found correlations between fishing intensity and species richness, species diversity, or species composition in the English Channel because decades of scallop dredging had altered the habitats and shaped the benthic communities, resulting in communities resilient to fishing disturbance. Intensively fished areas are likely to be maintained in a permanently altered state inhabited by fauna adapted to frequent physical disturbance (Collie et al. 2000b). If the disturbance caused by fishing is greater in magnitude or frequency than natural disturbance, it could alter community structure and function (Hiddink et al. 2006).

Collie et al. (1997) found higher species abundance, richness, diversity, and evenness in areas undisturbed by fishing than in disturbed sites. Within the first 6 y of the CA II closure, Hermsen et al. (2003) and Asch and Collie (2008) examined the recovery of benthic communities. They predicted that because benthic communities in this area changed consistently throughout their studies that this area was still recovering from the effects of fishing and would need about 10 y to fully recover. On the northern edge after over 20 y of closure, the benthic communities and substrate in this area are still shifting. Constant change may be the normal state for this highly dynamic environment, and it is likely that there will never be an "endpoint" benthic community, rather these communities will shift naturally through time. The ability to use a 20-y closure as the control area allowed for the results to be viewed in a different perspective than the two previous studies. Determining the recovery of this area in all studies is complicated as data gathered prior to intensive bottom fishing is sparse (Collie et al. 2000b).

This study exemplified the importance of different types of area management. The 20-y absence of fishing in the HAPC gives a long-term perspective highlighting the importance of permanently closed areas for research. After a year and a half of closure, the scallop population in the C1-impact area was able to support a fishery and reestablished their abundance after a 2-y period. Fishing effort held within the bounds of natural disturbance, combined with intermittent closures, seems a productive approach to scallop fisheries management in this area.

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