Received: 28 May 2018 | Accepted: 3 January 2019
DOI: 10.1111/ivb.12243

ORIGINAL ARTICLE

Invertebrate Biology WILEY

Quantification of echinoderms (Echinodermata) on Georges Bank, and the potential influence of marine protected areas on these populations

Judith Rosellon-Druker | **Kevin D. E. Stokesbury**

School for Marine Science and Technology,
University of Massachusetts Dartmouth,
New Bedford, Massachusetts

Correspondence
Judith Rosellon-Druker, School for Marine Science and Technology, University of Massachusetts Dartmouth, 836 South Rodney French Boulevard, New Bedford, MA 02744.
Email: jrosellondruker@umassd.edu

Funding information
Fulbright fellowship; Mexican National Council of Science and Technology (CONACYT); Nature Conservancy, the Cooperative Institute for the North Atlantic Region (CINAR); NOAA Scallop Research Set-Aside Program; U.S. Sea Scallop Fishery Industry

Abstract

The spatiotemporal variation of the distribution of echinoderms in the Georges Bank ecosystem was examined from 2005 to 2012. Density and abundance of representatives from echinoderm classes (brittle stars, sand dollars, sea stars, and sea urchins) were estimated using a drop camera video survey of the benthos in areas open and closed to fish trawling. The influence of closed areas on these echinoderm populations relative to a suite of key environmental and biotic factors was evaluated using Canonical Correspondence Analysis (CCA). While marine protected areas appeared to influence the distribution of sand dollars and sea stars, the distribution of brittle stars and sea urchins seemed to be defined mainly by preferred habitat conditions. According to the CCA, depth, sediment stability, temperature, predator abundance, and management area were the most important factors explaining this echinoderm assemblage. On Georges Bank, echinoderms dominate the benthic biota and are present in a variety of habitats. They can alter marine communities and are preferred prey and main predators for several commercially targeted species. The detailed information presented here (on the scale of kilometers) on abundance and spatial distribution of these populations is thus valuable towards the implementation of ecosystem-based fisheries management.

KEYWORDS
density, fish trawling effects, invertebrates, spatial distribution, video survey

1 | INTRODUCTION

Echinoderms are strictly marine organisms, widely distributed in all oceans and extremely important for marine ecosystems (Brusca & Brusca, 1990). They can alter sediments with their burrowing activities (Smith, 1981). Fluctuations in their population size and distribution can cause changes in other marine communities (Meidel & Scheibling, 1998). Echinoderms are important primary consumers and predators (e.g., sea stars are the main predator of sea scallops [*Placopecten magellanicus*]), and the main prey for some juvenile and adult fish species, including American plaice (*Hippoglossoides platessoides*), haddock (*Melanogrammus aeglefinus*), and ocean pout (*Macrozoarces americanus*) (Link & Almeida, 2000; Marino, Juanes, & Stokesbury, 2009; Steimle, 1990). Therefore, echinoderms play major ecological roles in marine ecosystems and are keystone predators and grazers that can determine benthic community structure (Brusca & Brusca, 1990; Byrne, 1994; Link et al., 2012).

Georges Bank is located on the North American continental shelf between the New England states and Nova Scotia. It is a shallow area encompassing 40,000 km^2 within the 100 m isobath, and is delimited

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2019 The Authors. *Invertebrate Biology* published by Wiley Periodicals, Inc. on behalf of American Microscopical Society

by the deep-water Northeast Channel and the Great South Channel (Fogarty & Murawski, 1998). In 1994, three large areas on Georges Bank and southern New England (closed area I [CAI], closed area II [CAII], and Nantucket lightship closed area [NLSA]) were established, and all mobile fishing gear were banned (Murawski, Brown, Lai, Rago, & Hendrickson, 2000; Stokesbury, 2002). The selection of these protected areas was based on their historically high spawning and juvenile production of primary groundfish (i.e., cod, haddock, and yellowtail flounder) (Murawski et al., 2000). Some areas inside these closures have been periodically opened as rotational access areas in the last decade through the Scallop Fishery Management Plan of the New England Fisheries Management Council (Hart & Rago, 2006; Stokesbury, 2012; Valderrama & Anderson, 2007).

In general, the absence of or reduction in fishing inside closed or rotational access areas have resulted in changes in abundance (Asch & Collie, 2008; Collie, Hermsen, Valentine, & Almeida, 2005; Hart & Rago, 2006; Stokesbury, 2002), mean size (Hart & Rago, 2006; Stokesbury, Harris, Marino, & Nogueira, 2007), mean age (Coutré et al., 2013), distribution patterns (Langton & Robinson, 1990), and fishing effort redistribution (Murawski, Wigley, Fogarty, Rago, & Mountain, 2005) of several marine organisms (e.g., colonial epifauna, crabs, sea scallops, skates, haddock, and yellowtail flounder). Although some of these closures resulted in substantial increases in abundance for some shallow and sedentary fishes and invertebrates (Murawski et al., 2000; Stokesbury, 2002; Stokesbury, Harris, Marino, & Nogueira, 2004), other studies suggest that environmental factors have had a greater influence on these marine populations (Holland, 2000; Link et al., 2005). Consequently, the simultaneous examination of abiotic and biotic factors is necessary to determine if marine protected areas (MPAs) are the main drivers of modifications in patterns of species abundance and distribution.

Echinoderms are abundant and dominant on Georges Bank, representing almost half of the total biomass (wet weight g/m^2) of macrobenthic organisms in this ecosystem (Steimle, 1987, 1990; Stokesbury et al., 2004; Theroux & Wigley, 1998). Despite their abundance and ecological importance, detailed descriptions of these populations on the scale of kilometers for this region are lacking. Previous studies have employed coarse sampling designs that hinder the comparison of abundance between regions of the Georges Bank (e.g., marine closures versus areas open to fishing) (Link, 2004; Theroux & Wigley, 1998).

Here, we quantified echinoderm populations on Georges Bank and explored the potential effects of established MPAs on these populations. We estimated and compared annual density and abundance of echinoderms in closed (non-fishing), access (partially closed), and open areas, using video survey data collected from 2005 to 2012. We further assessed the influence of closed areas on echinoderm populations relative to a suite of biotic (predator and prey abundance) and abiotic (depth, sediment stability, sediment type, temperature) factors with the goal of delineating the optimal habitat conditions for given echinoderm taxa. Using a multivariate direct gradient analysis technique (canonical correspondence analysis, CCA), we explored the importance of each of the above variables in determining density and distribution of the echinoderm assemblage. In summary, we tested two null hypotheses: (a) echinoderm densities remained similar within the three management areas (access, closed, and open areas) across years of study and (b) MPAs do not have a significant effect on echinoderms populations when environmental and biotic covariates are controlled for statistically.

2 | METHODS

The School for Marine Science and Technology (SMAST) video survey research project was developed to provide a visual census of sea scallops on Georges Bank in southern New England and in the Mid-Atlantic Bight. A secondary objective of this survey was to analyze the distribution and abundance of other benthic marine organisms, including echinoderms (Stokesbury, 2002; Stokesbury et al., 2004). From 2005 to 2012, ~900 stations with depths ranging 20–160 m were annually sampled on Georges Bank, covering a total area of ~28,000 km^2. Survey stations were positioned over a grid with 5.6 km of separation between stations (Figure 1), using a centric systematic design with a random starting point (Krebs, 1989). A video sampling pyramid (Stokesbury, 2002; Stokesbury et al., 2004) was equipped with a set of nine lights and two downward-looking cameras mounted vertically at heights of 0.7 and 1.6 m from the base of the pyramid, providing view areas of 0.6 and 2.8 m^2, respectively, of the sea floor. Only the data from the 0.6-m^2 area camera were used in the present study, since the image resolution at that quadrat size allowed the identification of organisms smaller than 20 mm (Carey & Stokesbury, 2011). Two more cameras, one mounted parallel to the seafloor providing a side view of the area, and a digital still camera providing high-resolution images (quadrat size of 1.13 m^2), were only used for species identification.

At each station, the survey video pyramid was lowered from a scallop fishing vessel and placed on the sea floor. Video footage of the first quadrat was recorded on DVDs and DVRs, and then the pyramid was raised so the sea floor could no longer be seen. The vessel drifted ~30 m, and the pyramid was lowered to the sea floor again to obtain a second quadrat; this process was repeated four times at each station, resulting in a total sampled area of 2.4 m^2 at each station. For each quadrat, the time, depth, latitude, longitude, substrate, macroinvertebrates, and fishes were recorded. After each survey, the video footage was reviewed in the laboratory, and a still image of each quadrat was captured, digitized, and saved, using Image Pro Plus® software. Echinoderms were identified to class level as Asteroidea (sea stars), Echinoidea (sand dollars and sea urchins), and Ophiuroidea (brittle stars), with the class Echinoidea further resolved to the orders Clypeasteroida (sand dollars) and Echinoida (sea urchins).

The number of echinoderms present in each image was counted and standardized to individuals per m^2. Only echinoderms completely inside the quadrat were counted. Given the constant number of quadrats at every station, the mean density (and the standard error [SE] of echinoderms were estimated using the equations for a two-stage sampling design (Cochran, 1977):

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

where n = number of stations and $\bar{x}_i$ mean of the four quadrats at station i

$$\mathrm{SE}(\bar{\bar{x}}) = \sqrt{\frac{1}{n}(S^2)} \tag{2}$$

where

$$s^2 = \frac{\sum (\bar{x} - \bar{\bar{x}})^2}{n-1} \tag{3}$$

is the variance among stations

This simplified estimation of the SE is accurate when the sampling fraction (e.g., hundreds of individuals sampled from the millions of individuals present in the study area) is small (Krebs, 1989). We reported mean density and SE accounting for all surveyed stations, and also for "echinoderm habitats," defined here as stations where at least one echinoderm was observed. The abundance was obtained by multiplying number of individuals per m^2 by the total surveyed area.

Due to the large number (in the order of thousands) of sand dollars recorded at some stations, we subsampled a number of stations before undertaking the counting process. We selected an area (NLSA) and a random year (2005) with observed high variation in the presence of sand dollars, and we counted all the individuals. The mean density ($\bar{x}$ = 28.33) and the SE (SE = 17.22) were estimated following Equations 1 and 2. Then the subsample size was estimated assuming a Poisson distribution, using the equation

$$n = \left(\frac{100\mathrm{CV}t_{\alpha}}{r}\right)^2 \tag{4}$$

where n is the number of stations; CV the coefficient of variation = SE/observed mean; t_α is Student's t with an α = 0.05; r = desired relative error (as percentage) (Krebs, 1989). At least 24 stations per year were required to provide estimates of sand dollar density with 25% precision. To improve this precision, we randomly selected 100 stations per year as the subsample size. Increasing the subsample size beyond this number of stations was time-prohibitive.

The echinoderm density in closed, partial access, and open areas were compared to each other using a Kruskal–Wallis analysis of variance (Sokal & Rohlf, 1981) with α = 0.05 and post hoc comparisons using the Dunn's post hoc test (Zar, 1999). The same tests were used for annual comparisons. These statistical comparisons were based on densities observed in echinoderm habitats.

Density of echinoderms (accounting for all stations) was used as the dependent variable for the CCA. Environmental (depth, sediment, sediment stability, temperature) and biological (predator and prey abundance) data were used as the explanatory factors.

Sediment and sediment stability maps were obtained from previous studies that also used SMAST video survey data (Harris, Cowles, & Stokesbury, 2012; Harris & Stokesbury, 2010). These

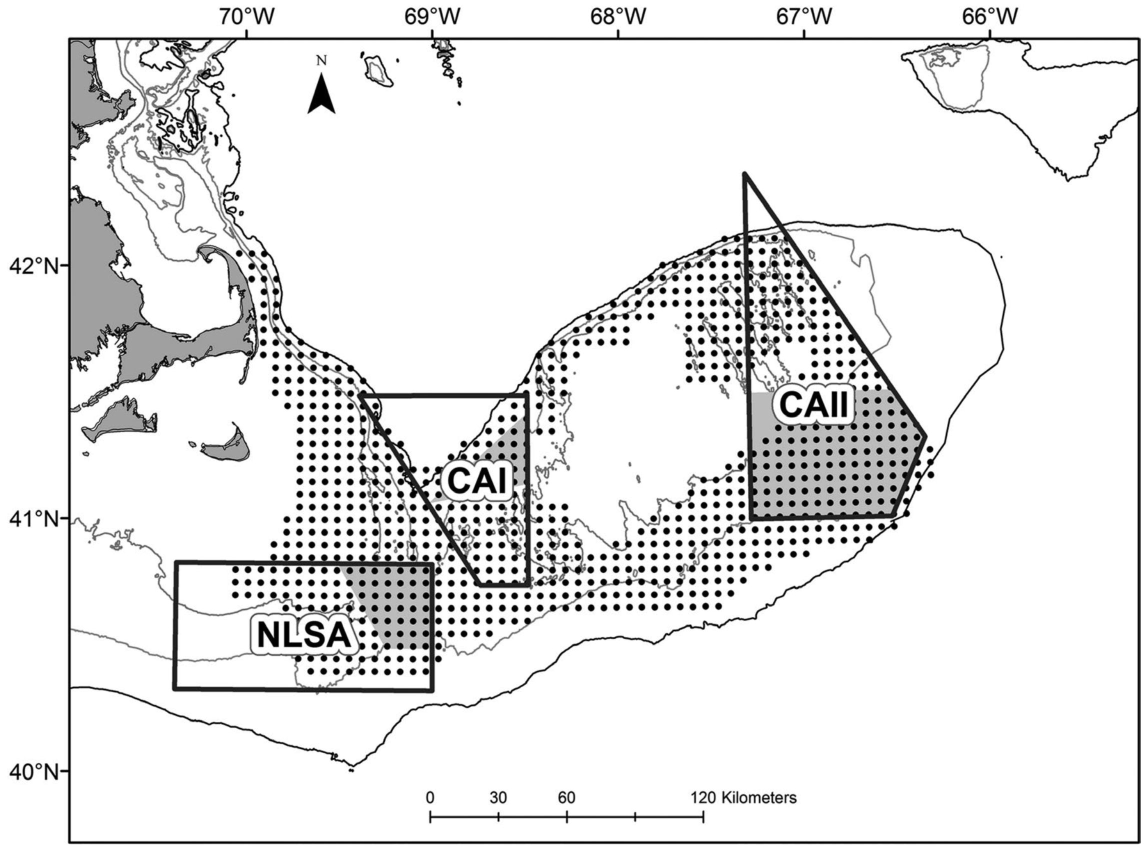

FIGURE 1 Georges Bank map. Location of SMAST video survey stations in a 5.6-km grid. Polygons represent the MPAs with access areas depicted in light grey. CAI, closed area I; CAII, closed area II; NLSA, Nantucket lightship closed area

maps provided an adequate spatial resolution (1 km raster grid) for habitat characterization. The dominant sediment (S_d) map showing most frequently occurring sediment type at each station (Harris & Stokesbury, 2010) was used. The sediment type from this analysis was based on Wentworth particle size categories (Wentworth, 1922). The sediment stability index (Harris et al., 2012) was defined as the shear stress to critical shear stress ratio ($\xi = \tau_0/\tau_{cr}$). Shear stress (τ_0) is the force per unit area exerted on the sediment by water, while critical shear stress (τ_{cr}) is the force needed to move a particle in the sediment (Harris et al., 2012). Therefore, a higher sediment stability index (>1) in the map, indicates unstable sediments and high shear stress conditions (Harris et al., 2012). Bathymetry and sea scallop density was also obtained directly from the SMAST video survey data set (Stokesbury, 2002; Stokesbury et al., 2004).

Temperature data and relative abundance (Catch per Unit Effort [CPUE] = fish/number of tows) of American plaice, haddock, and ocean pout were obtained yearly (2005–2012) from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey program from late spring, summer, and fall, which roughly matches the temporal scale at which the SMAST video survey is carried out (end of May through late September). Relative abundance data were adjusted for differences in trawl doors, gear types, and vessels used over time, applying calibration factors as specified by Miller et al. (2010). The NEFSC bottom trawl survey used a stratified random design. Strata were delineated by depth. Stations were allocated to strata in proportion to the area and were assigned to specific locations within strata at random (Azarovitz, 1981). A “Number 36 Yankee” bottom trawl has been used in all summer/fall surveys since 1981. This trawl has a 12.5-mm mesh in the cod end. At each station the net was towed for 30 min at 6.5 kph relative to the sea bottom. The catch (fish and invertebrates) was sorted by species, weighed to the nearest 0.1 kg, and measured in length. Sex and maturity stage were noted. Location, depth, and time were also recorded. Surface and bottom water temperature were obtained using SeaBird Electronics SBE19+ CTD units (Azarovitz, 1981; Despres-Patanjo, Azarovitz, & Byrne, 1988; Holzwarth & Mountain, 1990).

Spatial analyses were performed using Geographic Information System (ESRI ArcGIS©) mapping software. To examine the spatial relationship between echinoderm abundance and independent variables, a grid composed of cells each representing 5 km^2 was overlaid on the Georges Bank region. The rationale behind this grid resolution was to avoid having many cells with null values. To achieve that, we used a similar spatial scale to the one used in the SMAST video survey (grid with 5.5 km between stations). Furthermore, this meter-to-kilometer scale is consistent with the observed in several echinoderm bed formations (Broom, 1975; Merrill & Hobson, 1970; Warner, 1971). Creating and working with a grid was also necessary because the location of sampling stations varied among data sets. The product of this spatial analysis was a matrix with sites (cells) related to a specific value of each dependent and independent variable. Thus, mean depth (Figure 2A), mean sediment stability, most common sediment type (Figure 2B,C), mean temperature (Figure 2D), mean CPUE for groundfish species (Figure 3A,B,C), and mean density for scallops (Figure 3D) were allocated to each spatial cell. Additionally, each cell was identified with a binary code, where 0 = closed area and 1 = open area to fishing (management area).

With this matrix, CCA (Ter Braak, 1986) was used to simultaneously explore all the environmental factors and species to determine the independent variables that correspond as closely as possible to the major patterns of echinoderm abundance. This multivariate direct gradient analysis technique performs well in cases with skewed species distributions, with quantitative noise in species abundance data, with samples taken from unusual sampling designs, with highly intercorrelated environmental variables, and with situations in which only some of the factors determining species composition are known (Palmer, 1993).

This analysis determines a score for each echinoderm taxon that is constrained to a linear combination of the explanatory factors in the analysis (Methratta & Link, 2006). Those scores are displayed in an ordination diagram (biplot) that shows the echinoderm taxa (centers of abundance) and vectors representing the independent variables. The length and the angle of vectors on the biplot indicate the importance (e.g., magnitude of correlation) of independent variables in the ordination (Palmer, 1993). The longer and more parallel a vector is to a CCA axis, the stronger the relationship between the variable and the axis. Implicit correlations also extend equally in opposite directions from the vectors (Rakocinski, Lyczkowski-Shultz, & Richardson, 1996). The relative position of the echinoderm taxa along the vectors reflects how they are associated with each factor relative to the other echinoderm taxa in the ordination (Methratta & Link, 2006). Echinoderms found at the center of the ordination diagram are generally ubiquitous, while echinoderms found at the edges of the biplot are associated with more specific environmental or biological conditions (Ter Braak & Prentice, 1988). By analyzing the signs and the relative magnitudes of the intraset correlations (i.e., correlation coefficients) it is also possible to determine the importance of variables for each of the axes in the biplot. Coefficients >|0.4| were regarded conservatively as biologically significant for the CCA axes (Hair, Anderson, Tatham, & Grablowsky, 1984).

We added a positive small value (0.0001) to all the biotic variables to avoid a null marginal sum in a row or column of the input matrix. Any missing values were removed from the final matrix before running the CCA (final n = 550 cells). Variations in density for each individual echinoderm taxon within different environmental categories were also tested using a Kruskal–Wallis analysis of variance (Sokal & Rohlf, 1981), with $\alpha = 0.05$, and post hoc comparisons using the Dunn's post hoc test. All statistical tests were performed using XLSTAT version 2014.3.02 software (Addinsoft 1995–2014).

3 | RESULTS

3.1 | Quantification of echinoderms

Distribution and abundance of echinoderms varied significantly among taxa. While brittle star and sea urchin densities were similar

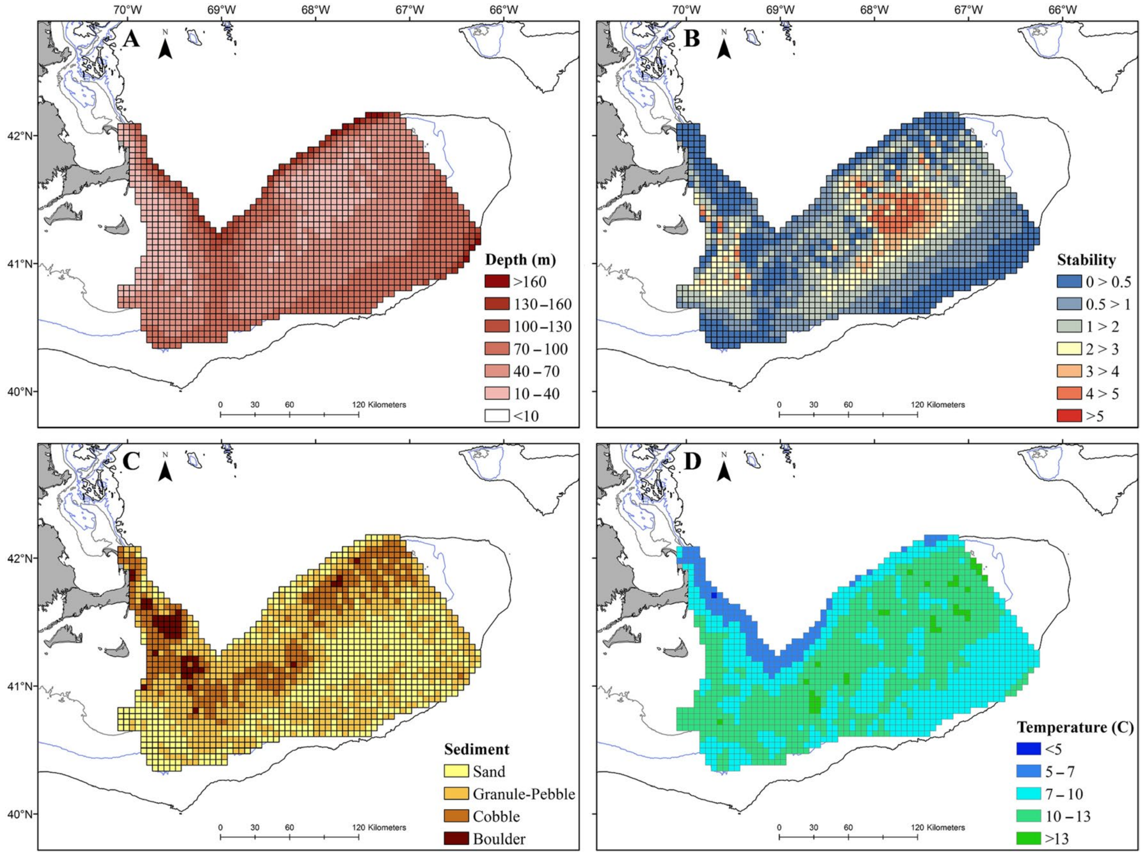

FIGURE 2 Independent environmental variables displayed on a grid of 5-km^2 cells. Each cell represents the average value of all the data points found inside. **A.** Depth (2005–2012). **B.** Sediment stability (1999–2010). **C.** Sediment type (1999–2009). **D.** Temperature (2005–2012). For sediment stability, a value <1 represent stable sediments and a value >1 represents unstable sediments. For sediment type, each cell represents the most common and largest type of sediment particle observed. In the case of temperature, yearly average was used for all statistical analyses

in closed and open areas, some of the highest densities of sand dollars and sea stars were observed inside closed areas. Brittle stars were observed in 54 stations on Georges Bank from 2005 to 2012, and 4,265 individuals were counted. Brittle stars generally occurred in high densities (>10 individuals per quadrat), and in some cases they completely covered the sea floor (Figure 4). Other megafauna in these brittle star beds were rare. The distribution of brittle stars was mainly confined to the northern edge, between CAI and the outside western edge of CAII (Figure 5). Yearly variations in brittle star densities were not significant (H = 9.81, df = 7, p = 0.200; Table 1).

Brittle stars were observed in 2.9% and 0.8% of all stations sampled in CAI and open areas, respectively. Within the stations with at least one brittle star observed in CAI, densities ranged between 4.1 and 34.1 individuals per m^2 (SE = 0.52 and 4.21, respectively; Table 1), with an annual average of ~19 individuals per m^2. In open areas, densities ranged from 0.4 to 93.0 individuals per m^2 (SE = 0.02 and 4.98, respectively; Table 1), with an annual average of ~41 individuals per m^2. Densities in brittle star habitats were similar between closed and open areas (H = 2.82, df = 1, p = 0.090). No brittle stars were observed in access areas. Abundance reflected similar patterns of density, with values ranging from 3.8×10^8 to 4.2×10^9 individuals in CAI and from 1.3×10^7 to 1.3×10^{10} individuals in open areas (Table 1).

In a subsample of 754 stations from 2005 to 2012, 56,683 sand dollars were counted. When aggregated, they formed beds of hundreds of individuals (Figure 4), and as with brittle stars, the presence of other megabenthic organisms within these beds was rare. Sand dollars were found mainly inside and outside the southwestern corner of CAII, the southern area of CAI, in the central-eastern portion of NLSA, and outside the northeastern portion of CAI (Figure 5). Annual density estimates did not differ significantly between years (H = 7.56, df = 7, p = 0.373) although temporal variability was observed (Table 1).

The subsample of stations containing sand dollars represented 29.0%, 18.1%, 25.8%, and 9.2% of the total stations sampled in CAI, CAII, NLSA, and open areas, respectively. Within stations with at least one sand dollar observed in CAI, density ranged between 11.9 and 125.5 individuals per m^2 (SE = 3.93 and 51.81, respectively; Table 1), with an average annual value of ~32 individuals per m^2. An unusually high density (125.5 individuals per m^2) was observed in 2008 in the non-fishing portion of this area. In CAII, densities ranged between 8.6 and 33.4 individuals per m^2 (SE = 2.60 and 16.16, respectively; Table 1), with an annual average

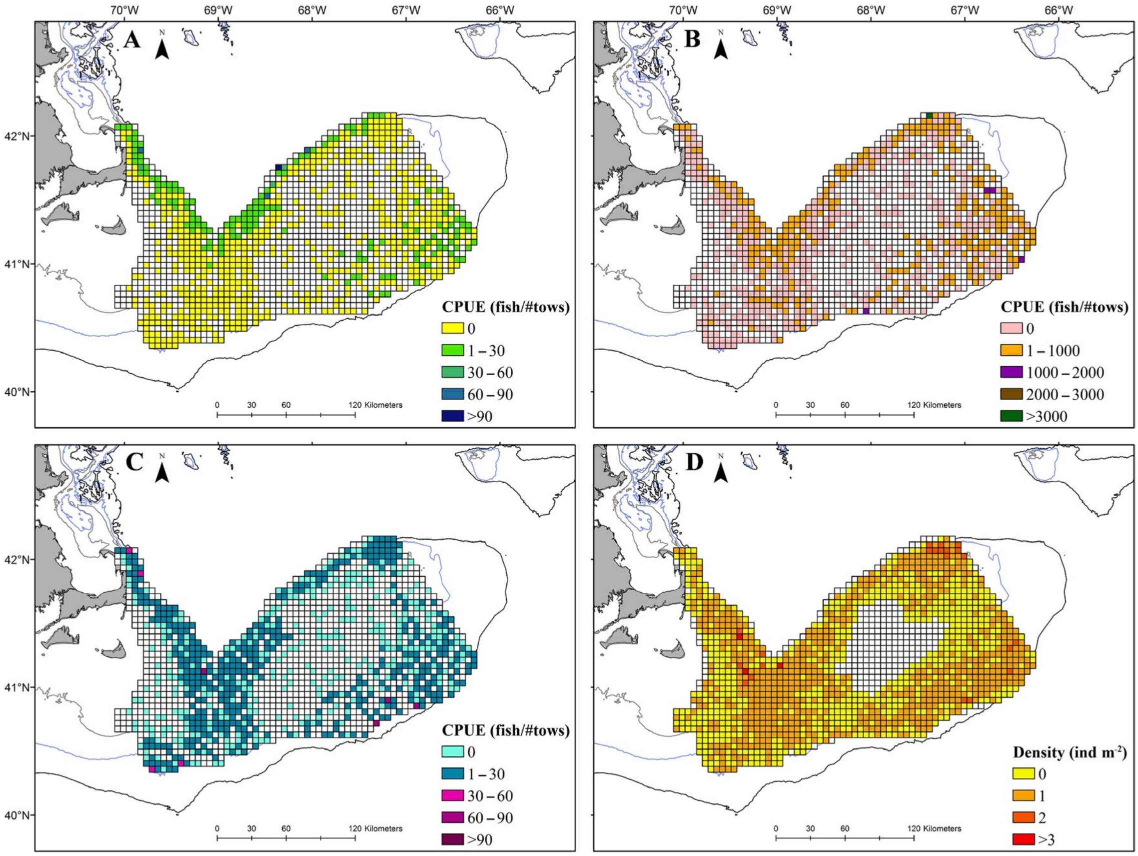

FIGURE 3 Independent biological variables displayed on a grid of 5-km^2 cells. Each cell represents the average abundance from 2005–2012 of American plaice (**A**), haddock (**B**), ocean pout (**C**), and scallops (**D**). Blank cells represent no data. For all statistical analyses, the yearly average was used

of ~19 individuals per m^2. Densities in NLSA ranged between 18.0 and 62.8 individuals per m^2 (SE = 6.00 and 18.49, respectively; Table 1), with an annual average value of ~44 individuals per m^2. In open areas sand dollar densities ranged between 24.5 and 92.6 individuals per m^2 (SE = 6.55 and 19.08, respectively; Table 1), with an annual average density of ~52 individuals per m^2. Differences in density by area in these sand dollar habitats were statistically significant ($H = 47.79$, $df = 3$, $p < 0.001$), with highest densities found in both NLSA and open areas and lowest densities in CAII (Dunn's post hoc test). Abundance followed similar patterns to density; the lowest value observed in CAII in 2008 was 6.4×10^9 sand dollars, and the highest value in open areas in 2012 was 7.1×10^{10} sand dollars (Table 1). In NLSA and CAII, densities were higher in the non-fishing portion of the area compared with the access area ($H = 4.61$, $df = 1$, $p = 0.032$; $H = 13.76$, $df = 1$, $p < 0.001$, respectively). For CAI, the differences in density between the non-fishing portion and the access area were not significant ($H = 1.00$, $df = 1$, $p = 0.320$).

We analyzed 2,866 stations containing sea stars between 2005 and 2012. We counted a total of 20,104 individuals. Although sea stars (Figure 4) had a widespread distribution throughout the entire study area (Figure 5), highest densities were observed in the southern edge of the bank, both in the non-fishing portion of NLSA and in the adjacent open areas (Figure 5). Density estimates revealed high and significant interannual variability ($H = 222.30$, $df = 7$, $p < 0.001$). Highest average density over the entire time series was observed in 2009. Conversely, in 2012, density was significantly lower than that observed in the 2005–2009 time period (Dunn's post hoc test; Table 1).

Sea stars were observed in 28.2%, 29.1%, 58.2%, and 44.7% of all stations sampled in CAI, CAII, NLSA, and open areas, respectively. In stations with at least one sea star observed inside CAI, densities ranged between 0.8 and 1.8 individuals per m^2 (SE = 0.13 and 0.28, respectively; Table 1). For CAII, densities ranged between 0.6 and 1.8 individuals per m^2 (SE = 0.04 and 0.17, respectively; Table 1). Both of these areas featured an annual average of ~1 individual per m^2. In NLSA, densities ranged between 4.5 and 9.6 individuals per m^2 (SE = 0.85 and 0.95, respectively; Table 1), with an annual average of ~8 individuals per m^2. In open areas, the stations had densities ranging from 1.3 to 5.1 individuals per m^2 (SE = 0.08 and 0.26, respectively; Table 1), with an annual average of ~2 individuals per m^2. Density differences by area in these sea star habitats were highly significant ($H = 476.02$, $df = 3$, $p < 0.001$). CAI and CAII had the lowest densities while NLSA had densities at least three times higher than any other area. Open areas had lower densities compared to NLSA but higher than in CAI and CAII (Dunn's post hoc

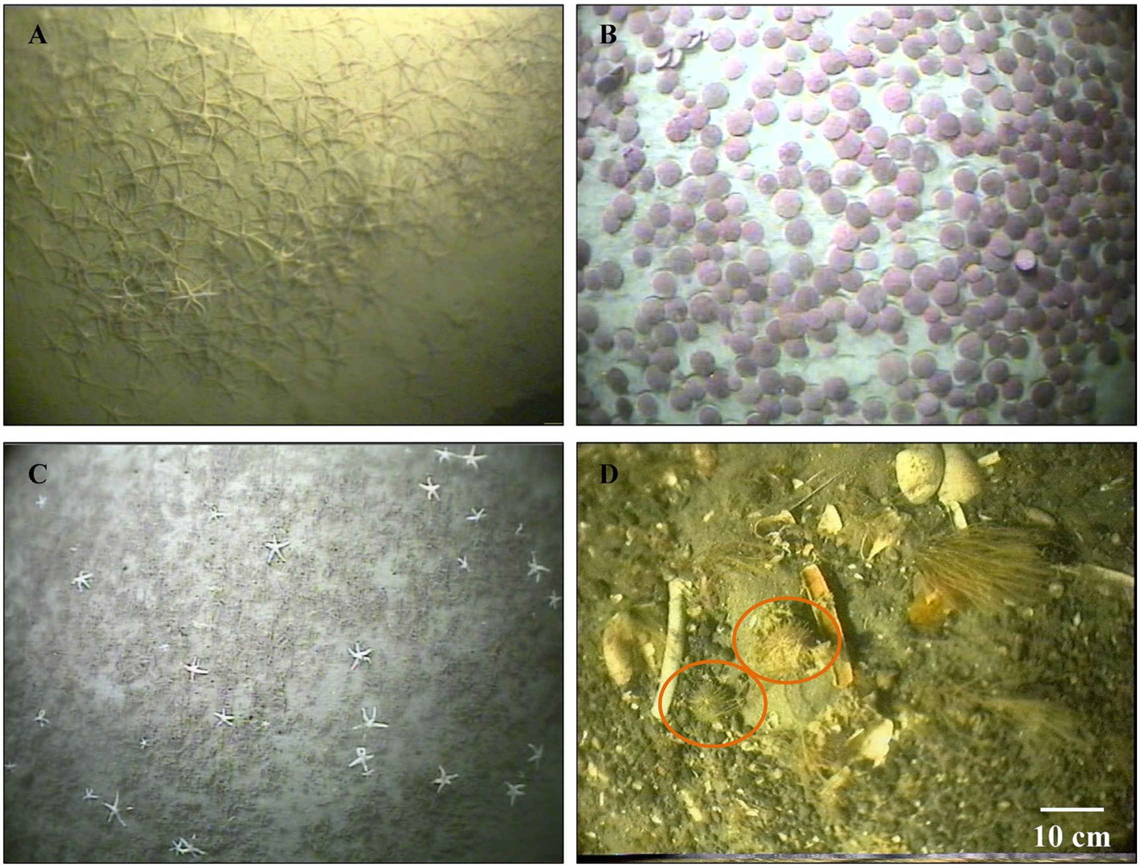

FIGURE 4 SMAST video survey images. Images collected with small camera providing a view area of 0.6 m^2. **A.** Brittle stars. **B.** Sand dollars. **C.** Sea stars. **D.** Sea urchins. Scale bar depicted in the last panel

test). Abundance followed similar patterns as to density with values ranging from 1.9×10^8 (in CAI) to 4×10^{10} (in open areas). Higher abundances in the open areas compared to NLSA, are due to greater number of stations in open areas with presence of sea stars (Table 1). There was significant difference between the non-fishing portion and the access area of all closed areas. In NLSA (H = 95.96, df = 1, p < 0.001) and CAI (H = 6.56, df = 1, p = 0.010) densities were higher in non-fishing areas. Conversely, in CAII (H = 5.38, df = 1, p = 0.020), higher densities were observed in the access areas.

We analyzed 98 stations with sea urchins present from 2005 to 2012; 208 sea urchins (Figure 4) were counted. They were distributed throughout all the areas of Georges Bank (Figure 5) but mainly observed in the central portion of CAI, in the northern peak of CAII and in the northwestern portion of the bank (Figure 5). We rarely observed aggregations of >5 individuals per quadrat (Figure 4). Density differences between years were significant (H = 14.69, df = 7, p = 0.040) and were mainly caused by high densities observed in 2010 and 2012 and low densities in 2007 (Dunn's post hoc test; Table 1).

Sea urchins were present in 2.4%, 2.1%, 1.0%, and 1.2% of the total stations analyzed in CAI, CAII, NLSA, and open area, respectively. In CAI stations with presence of urchins, density ranged from 0.4 to 2.9 individuals per m^2 (SE = 0.06 and 0.34, respectively; Table 1). In CAII densities ranged between 0.4 and 1.4 individuals per m^2 (SE = 0.03 and 0.14, respectively; Table 1). In NLSA densities ranged between 0.4 and 0.8 individuals per m^2 (SE = 0.04 and 0.08, respectively; Table 1). Finally, in open areas, densities ranged between 0.6 and 1.4 individuals per m^2 (SE = 0.03 and 0.07, respectively; Table 1). In all areas, an annual average density of ~ 1 individual per m^2 was observed. Densities in urchin habitats were not significantly different between closed and open areas (H = 6.29, df = 3, p = 0.098). Additionally, densities were similar between non-fishing and access portion of any closed area (For CAI, H = 0.07, df = 1, p = 0.791; for CAII, H = 1.93, df = 1, p = 0.164; no urchins were observed in the non-fishing portion of NLSA). Abundance ranged across all areas from 1.3×10^7 to 3.1×10^8 sea urchins (Table 1).

3.2 | Canonical correspondence analysis

The canonical relationship between matrices of independent and dependent variables was highly significant (p < 0.0001, Monte Carlo permutation test, pseudo F = 0.196, 1,000 permutations). Eigenvalues provided three factors that represented 100% of the constrained variance or inertia (Table 2). The first two canonical axes accounted for 98.2% of the constrained variance explained by the independent variables (Table 2). Depth (r = −0.53), American plaice abundance (r = −0.54), and management area (r = −0.85) were the variables with greatest contribution to the first axis (Table 3), while

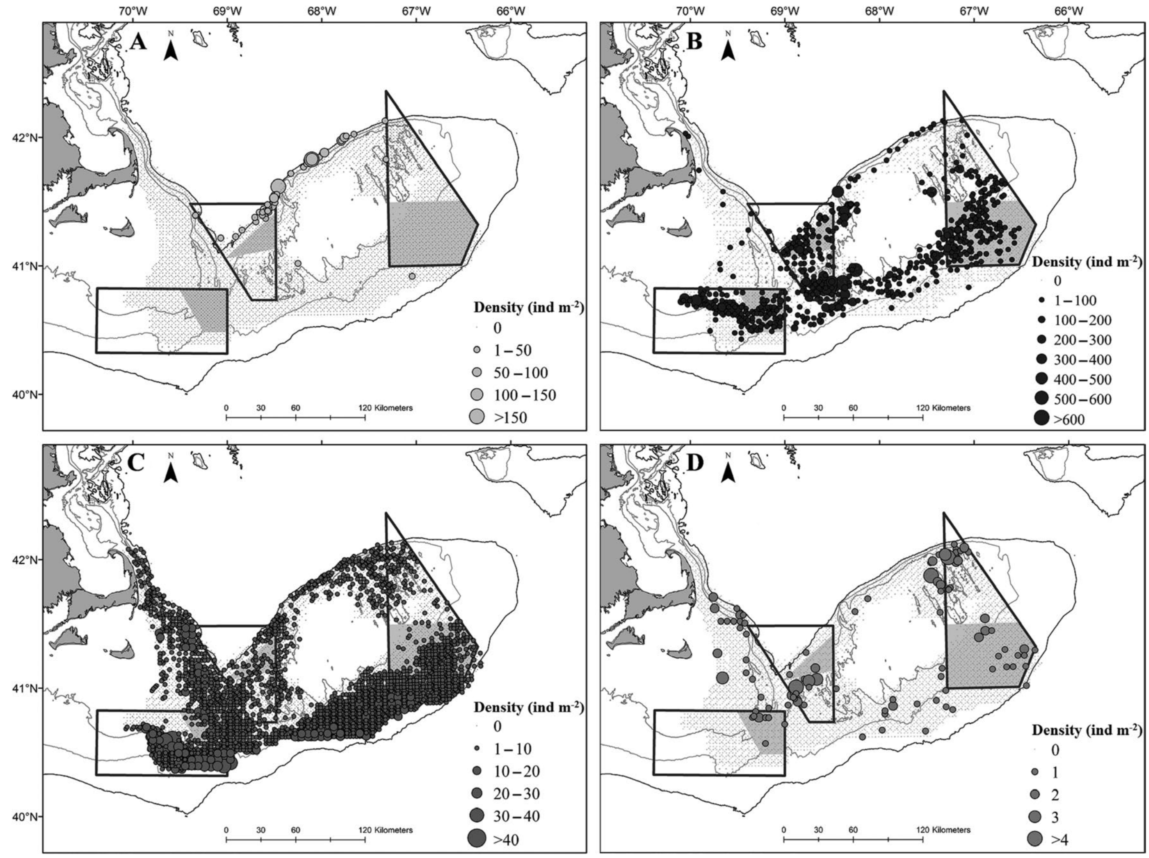

FIGURE 5 Distribution and density (number of individuals per m^2) of echinoderms from 2005 to 2012, relative to location of MPAs. **A.** Brittle stars. **B.** Sand dollars. **C.** Sea stars. **D.** Sea urchins

sediment stability ($r = -0.60$), temperature ($r = 0.65$), and ocean pout abundance ($r = 0.79$) were the variables with greatest contribution to the second axis (Table 3).

Most brittle stars were found in depths ranging 90–130 m ($H = 145.32$, $df = 2$, $p < 0.001$) and in cold (<10°C) waters ($H = 44.71$, $df = 3$, $p < 0.001$). Highest densities were found in stable sand or granule sediments (sediment, $H = 13.74$, $df = 3$, $p < 0.001$; sediment stability, $H = 20.27$, $df = 5$, $p < 0.001$). The CCA biplot (Figure 6) indicates that brittle stars were primarily associated with increasing depth and American plaice abundance. They were also the only echinoderm associated with open areas, as represented by the management area vector (Figure 6).

Most sand dollars were observed between 30 and 70 m ($H = 223.48$, $df = 4$, $p < 0.001$) and in unstable sandy and granule sediments (sediment, $H = 160.20$., $df = 3$, $p < 0.001$; sediment stability, $H = 352.64$, $df = 5$, $p < 0.001$). Highest sand dollar densities occurred in temperatures >10°C, with lower densities occurring in the lowest temperatures (~5°C) ($H = 46.96$, $df = 3$, $p < 0.001$). The CCA biplot depicts that sand dollars were associated with unstable sediments, management area (closed areas), and were negatively (but weakly) correlated with ocean pout abundance and positively (and strongly) correlated with haddock abundance (Figure 6).

Sea stars occurred in all depth ranges, but highest densities occurred between 70 and 100 m ($H = 717.17$, $df = 4$, $p < 0.001$) and in sandy substrates ($H = 82.31$, $df = 3$, $p < 0.001$). Most sea stars were found in stable sediments ($H = 1162.28$, $df = 5$, $p < 0.001$). Highest sea star densities occurred between 7 and 13°C ($H = 427.28$, $df = 3$, $p < 0.001$) with lower densities occurring in temperatures >13°C ($H = 101.92$, $df = 3$, $p < 0.001$). According to the CCA biplot, sea stars were associated with areas of high stability, and they were positively correlated with temperature and abundance of ocean pout (Figure 6).

Higher urchin densities were observed in coarser sediments (boulder and cobble) ($H = 69.33$, $df = 3$, $p < 0.001$). These organisms occurred mainly in depths ranging 40–100 m ($H = 12.71$, $df = 4$, $p < 0.001$). Their density decreased with sediment instability ($H = 50.87$, $df = 5$, $p < 0.001$) and increased with water temperatures >10°C ($H = 10.45$, $df = 3$, $p < 0.001$). According to the CCA biplot, sea urchin density was mainly associated with coarser and stable sediments, management area (closed areas), and was positively correlated with temperature and abundance of ocean pout (Figure 6).

4 | DISCUSSION

On Georges Bank, echinoderms contribute significantly to species diversity and abundance of the benthic fauna (Steimle, 1987; Stokesbury et al., 2004; Theroux & Wigley, 1998) and play a

TABLE 1 Brittle star, sand dollar, sea star, and sea urchin density (individuals per m^2) and abundance in closed and open areas of Georges Bank from 2005 to 2012. Values are given for all sampled stations and for those stations with at least one echinoderm observed (echinoderm habitat). Abundance (number of individuals) is also provided

	All stations				Echinoderm habitat				
Year	No. stations	Density	SE	CV (%)	No. stations	Density	SE	CV (%)	Abundance
Brittle stars									
Closed area I									
2005	86	0.32	0.32	98.48	2	13.87	2.07	14.93	8.6×10^8
2006	96	1.42	0.87	61.19	4	34.15	4.21	12.32	4.2×10^9
2007	99	0.12	0.09	74.86	3	4.06	0.52	12.92	3.8×10^8
2008	29	–	–	–	–	–	–	–	–
2009	95	0.91	0.64	70.48	3	28.72	3.56	12.39	2.7×10^9
2010	99	–	–	–	–	–	–	–	–
2011	97	0.42	0.39	93.82	5	8.15	1.73	21.18	1.3×10^9
2012	46	1.09	1.05	96.62	2	25.01	4.98	19.92	1.5×10^9
Open areas									
2005	532	0.64	0.26	40.8	9	37.55	1.98	5.28	1.0×10^{10}
2006	548	0.78	0.46	59.17	9	47.59	3.6	7.56	1.3×10^{10}
2007	507	0.3	0.16	54.32	5	30.69	1.65	5.38	4.7×10^9
2008	525	0	0	100	1	0.42	0.02	4.36	1.3×10^7
2009	422	–	–	–	–	–	–	–	–
2010	531	0.01	0.01	59.51	4	1.16	0.06	5.15	1.4×10^8
2011	518	0.54	0.38	70.5	3	93.04	4.98	5.35	8.6×10^9
2012	507	0.47	0.28	59.13	3	79.02	3.58	4.54	7.3×10^9
Sand dollars									
Closed area I									
2005	89	2.73	1.71	62.52	17	14.32	8.59	60.01	7.5×10^9
2006	94	5.99	3.72	62.14	24	23.47	14.21	60.52	1.7×10^{10}
2007	87	3.3	1.21	36.83	24	11.95	3.93	32.93	8.9×10^9
2008	31	56.68	25.6	45.16	14	125.51	51.81	41.28	5.4×10^{10}
2009	69	11.98	5.88	49.12	24	34.44	16.14	46.88	2.6×10^{10}
2010	99	9.08	3.7	40.76	24	37.44	13.94	37.23	2.8×10^{10}
2011	75	14.97	7.36	49.15	24	46.79	21.9	46.81	3.5×10^{10}
2012	42	10.61	6.33	59.67	19	23.45	13.6	58.01	1.4×10^{10}
Closed area II									
2005	152	2.68	1.53	57.14	24	16.95	9.31	54.94	1.3×10^{10}
2006	150	3.13	1.6	51	22	21.35	10.24	47.96	1.4×10^{10}
2007	167	5	2.55	50.99	25	33.43	16.16	48.35	2.6×10^{10}
2008	161	1.28	0.45	35.21	24	8.59	2.6	30.25	6.4×10^9
2009	86	2.89	1.24	42.99	24	10.37	4.14	39.9	7.7×10^9
2010	137	1.77	0.74	41.79	24	10.12	3.85	38.08	7.5×10^9
2011	97	7.55	2.53	33.46	25	29.31	4.8	16.39	2.3×10^{10}
2012	115	4.79	2.54	52.94	25	22.04	11.17	50.67	1.7×10^{10}
Nantucket lightship closed area									
2005	102	15.22	5.93	38.98	25	62.11	21.98	35.4	4.8×10^{10}
2006	100	11.4	3.74	32.77	25	45.59	12.86	28.2	3.5×10^{10}
2007	100	15.71	5.31	33.81	25	62.82	18.49	29.43	4.8×10^{10}
2008	68	11.85	2.96	24.94	20	40.29	6.66	16.54	2.5×10^{10}

(Continues)

TABLE 1 (Continued)

	All stations				Echinoderm habitat				
Year	No. stations	Density	SE	CV (%)	No. stations	Density	SE	CV (%)	Abundance
2009	132	5.89	2.48	42.03	24	32.41	12.44	38.39	2.4×10^{10}
2010	103	8.78	3.11	35.43	25	36.19	11.32	31.29	2.8×10^{10}
2011	81	5.54	2.05	36.95	25	17.96	6	33.41	1.4×10^{10}
2012	61	20.81	8.05	38.71	24	52.89	18.88	35.7	3.9×10^{10}
Open areas									
2005	485	2.2	1.31	59.74	25	42.64	24.55	57.57	3.3×10^{10}
2006	338	4.68	2.46	52.41	25	63.34	31.46	49.67	4.9×10^{10}
2007	227	3.84	1.57	40.83	24	36.36	13.32	36.65	2.7×10^{10}
2008	166	5.31	1.7	32	25	35.27	9.37	26.58	2.7×10^{10}
2009	183	7.38	2.71	36.71	24	56.24	17.97	31.94	4.2×10^{10}
2010	221	2.77	0.9	32.32	25	24.52	6.55	26.71	1.9×10^{10}
2011	258	6.22	2.31	37.2	25	64.21	20.9	32.55	5.0×10^{10}
2012	258	8.97	2.49	27.78	25	92.61	19.08	20.61	7.1×10^{10}
Sea stars									
Closed Area I									
2005	86	0.18	0.05	28.62	18	0.84	0.1	12.33	4.7×10^{8}
2006	93	0.22	0.05	24.72	24	0.86	0.1	11.7	6.4×10^{8}
2007	92	0.26	0.07	26.71	21	1.16	0.14	11.98	7.5×10^{8}
2008	29	0.29	0.14	47.79	8	1.05	0.25	23.64	2.6×10^{8}
2009	91	0.6	0.17	28.08	31	1.76	0.28	15.61	1.7×10^{9}
2010	88	0.49	0.11	22.61	29	1.48	0.18	11.96	1.3×10^{9}
2011	96	0.34	0.06	18.88	35	0.92	0.1	10.28	1.0×10^{9}
2012	41	0.15	0.06	40.22	8	0.79	0.13	16.63	1.9×10^{8}
Closed area II									
2005	171	0.21	0.03	15.51	50	0.71	0.05	7.63	1.1×10^{9}
2006	178	0.21	0.03	15.53	49	0.78	0.06	7.42	1.2×10^{9}
2007	199	0.47	0.05	10.59	88	1.06	0.06	6.1	2.9×10^{9}
2008	195	0.3	0.04	12.31	67	0.86	0.05	6.36	1.8×10^{9}
2009	144	0.86	0.12	14.55	67	1.84	0.17	9.01	3.8×10^{9}
2010	193	0.21	0.03	14.84	54	0.76	0.05	7.15	1.3×10^{9}
2011	200	0.09	0.02	18.83	31	0.6	0.04	6.96	5.7×10^{8}
2012	195	0.07	0.02	22.47	24	0.6	0.04	7.52	4.4×10^{8}
Nantucket lightship closed area									
2005	110	4.04	0.57	14.23	67	6.63	0.67	10.07	1.4×10^{10}
2006	108	5.35	0.83	15.49	64	9.03	0.99	10.93	1.8×10^{10}
2007	115	6.01	0.87	14.56	74	9.34	1.01	10.78	2.1×10^{10}
2008	65	4.44	0.77	17.35	37	7.8	0.9	11.53	8.9×10^{9}
2009	110	6.04	0.83	13.78	69	9.63	0.95	9.88	2.1×10^{10}
2010	101	3.16	0.55	17.36	54	5.91	0.69	11.67	9.8×10^{9}
2011	106	3.64	0.58	15.98	55	7.02	0.73	10.42	1.2×10^{10}
2012	70	2.39	0.65	27.16	37	4.52	0.85	18.81	5.2×10^{9}
Open areas									
2005	532	0.81	0.09	10.71	219	1.97	0.13	6.53	1.3×10^{10}
2006	533	0.88	0.08	9.24	247	1.9	0.11	5.91	1.5×10^{10}

(Continues)

TABLE 1 (Continued)

	All stations				Echinoderm habitat				
Year	No. stations	Density	SE	CV (%)	No. stations	Density	SE	CV (%)	Abundance
2007	495	1.28	0.12	9.66	245	2.58	0.17	6.41	2.0×10^{10}
2008	500	1.03	0.1	9.48	231	2.23	0.13	6.04	1.6×10^{10}
2009	422	3.06	0.22	7.32	255	5.06	0.26	5.16	4.0×10^{10}
2010	527	0.72	0.08	10.61	206	1.85	0.12	6.29	1.2×10^{10}
2011	518	0.58	0.06	10.29	196	1.53	0.09	5.96	9.2×10^{9}
2012	506	0.52	0.05	9.82	206	1.28	0.08	5.87	8.2×10^{9}
Sea urchins									
Closed area I									
2005	72	0.04	0.04	100	1	2.94	0.34	11.7	9.1×10^{7}
2006	94	0.02	0.01	60.69	3	0.56	0.06	10.69	5.2×10^{7}
2007	99	–	–	–	–	–	–	–	–
2008	34	0.05	0.05	99.96	1	1.68	0.28	16.9	5.2×10^{7}
2009	93	0.03	0.02	74.21	2	1.26	0.42	33.33	7.8×10^{7}
2010	99	0.1	0.05	49.31	6	1.47	0.19	12.59	2.7×10^{8}
2011	97	–	–	–	–	–	–	–	–
2012	46	0.02	0.01	69.92	2	0.42	0.06	14.26	2.6×10^{7}
Closed area II									
2005	141	0.02	0.01	62.01	3	0.84	0.08	8.96	7.8×10^{7}
2006	178	0.01	0.01	74.37	2	0.63	0.05	7.84	3.9×10^{7}
2007	199	0.01	0	57.44	3	0.42	0.03	7	3.9×10^{7}
2008	195	0.02	0.01	65.24	3	0.98	0.08	8.04	9.1×10^{7}
2009	144	–	–	–	–	–	–	–	–
2010	193	0.03	0.02	71.57	4	1.37	0.14	10.28	1.7×10^{8}
2011	200	0.04	0.01	40.67	8	0.89	0.07	8.01	2.2×10^{8}
2012	200	0.05	0.02	40.14	7	1.32	0.1	7.39	2.9×10^{8}
Nantucket lightship closed area									
2005	110	0.01	0.01	100	1	0.84	0.08	9.49	2.6×10^{7}
2006	108	0.02	0.01	57.19	4	0.63	0.07	10.85	7.8×10^{7}
2007	115	–	–	–	–	–	–	–	–
2008	65	–	–	–	–	–	–	–	–
2009	110	0.01	0.01	74.26	2	0.63	0.06	9.93	3.9×10^{7}
2010	101	0	0	100	1	0.42	0.04	9.9	1.3×10^{7}
2011	106	–	–	–	–	–	–	–	–
2012	70	–	–	–	–	–	–	–	–
Open areas									
2005	367	0.03	0.01	50.49	9	1.12	0.09	7.87	3.1×10^{8}
2006	533	0.01	0	34.76	10	0.59	0.03	4.72	1.8×10^{8}
2007	495	0.01	0	42.23	7	0.6	0.03	4.99	1.3×10^{8}
2008	500	0.01	0	49.85	5	0.67	0.03	4.97	1.0×10^{8}
2009	422	0.01	0	48.81	6	0.7	0.04	5.79	1.3×10^{8}
2010	527	0.01	0	50.48	5	0.92	0.05	4.9	1.4×10^{8}
2011	518	0	0	74.48	2	0.63	0.03	4.62	3.9×10^{7}
2012	506	0.01	0.01	55.88	4	1.37	0.07	4.95	1.7×10^{8}

Dashes represent years with no observations.

Abbreviations: CV, coefficient of variation; SE, standard error.

TABLE 2 Canonical eigenvalues and constrained inertia

	F1	F2	F3
Eigenvalue	0.60	0.32	0.02
Constrained inertia (%)	64.35	33.82	1.83
Cumulative (%)	64.35	98.17	100

Variance explained by the three factors. The first two factors combined carry a total of 98.2% of the total inertia.

TABLE 3 Correlation coefficients between the first (F1) or second (F2) factors in the canonical correspondence analysis and individual independent variables including species abundance, environmental variables, and management area

	F1	F2
American plaice	−0.54	−0.17
Haddock	0.28	−0.28
Ocean pout	0.06	0.79
Scallops	−0.38	0.00
Depth	−0.53	0.01
Temperature	0.31	0.65
Stability	0.29	−0.60
Sediment	0.10	0.00
Management area	−0.85	0.06

Variables for which $|r| > 0.40$ were considered to be biologically meaningful for the CCA axes.

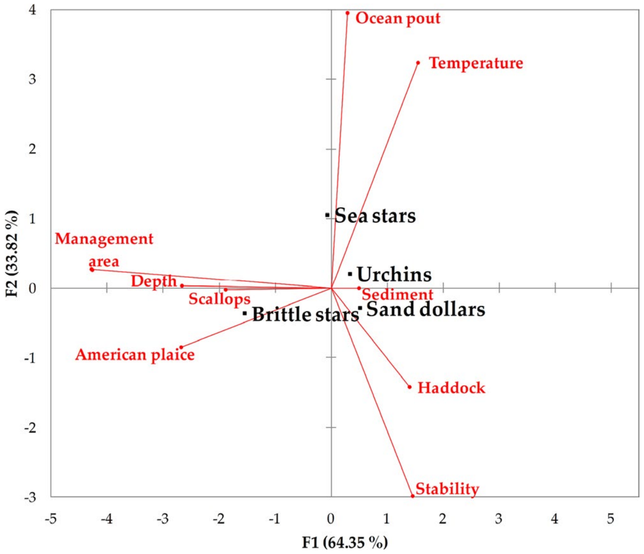

FIGURE 6 Canonical correspondence analysis. Statistical modeling examining relationship of echinoderms and environmental and biological factors. These results are depicted in an ordination diagram with the axes (F1, F2) that, when combined, explained 98.2% of the constrained variance. Vectors (red lines) represent explanatory factors. Echinoderms are represented with black squares

significant role in the transfer of energy from the benthos to upper trophic levels (Steimle & Terranova, 1985; Zamarro, 1992). The most comprehensive research to date regarding the main echinoderm taxa on Georges Bank relies on a series of surveys from offshore New England waters conducted from the mid-1950s to the mid-1960s by the National Marine Fisheries Service in cooperation with the Woods Hole Oceanographic Institution. Two technical reports (Theroux & Wigley, 1998; Wigley & Theroux, 1981) and one book chapter (Steimle, 1987) quantitatively and qualitatively described abundance and distribution of major macrobenthic invertebrates, including echinoderms, on the Atlantic continental shelf. Spatial resolution of these studies was on the scale of tens to hundreds of kilometers. More recent studies have generally investigated echinoderm abundance and distribution as part of benthic assemblages (i.e., phylum taxonomic resolution) or are focused on specific areas of the bank (e.g., Collie, Escanero, & Valentine, 1997; Hermsen, Collie, & Valentine, 2003; Link, 2004; Link et al., 2005; Marino, Juanes, & Stokesbury, 2007; Marino et al., 2009; Packer, Watling, & Langton, 1994; Thouzeau, Robert, & Ugarte, 1991).

We spatially described and quantified echinoderm populations on Georges Bank at a spatial resolution of square kilometers (improving available spatial resolution by at least an order of magnitude). Abundance and distribution varied significantly among the four echinoderm groups and between management areas. Brittle stars were mainly restricted to the northern edge of the bank, between CAI and CAII. Sand dollars dominated the central areas of the bank as well as the central portion of NLSA. Sea stars dominated the southern edge of the bank and were highly aggregated in the southern non-fishing portion of NLSA and in the adjacent southern open areas. Sea urchins were found in all sampled areas of the bank with the exception of the southern edge. The lack of overlap in the density hotspots of these echinoderm groups suggest that echinoderm populations in Georges Bank are habitat-specific.

Echinoderms are ubiquitous, persistent, dominant, and resilient organisms but have distinct patterns of habitat preference (Cusson & Bourget, 2005; Ellis & Rogers, 2000; Freeman & Rogers, 2003; Thouzeau et al., 1991). All of these were characteristics observed in this study. The preferred environmental conditions (driven primarily by depth, sediment stability, and temperature), along with predator abundance, were the most important factors in explaining the patterns of echinoderm assemblage on Georges Bank. These environmental descriptors of echinoderm habitat generally agreed with related literature. For example, an examination of global patterns of marine benthic macroinvertebrate production determined that temperature was the most important variable explaining the variance of echinoderm populations (Cusson & Bourget, 2005). Kostylev et al. (2001) found a strong association of echinoderm taxa with depth and specific hydrodynamic conditions of Browns Bank on the southwestern Scotian Shelf, off the Canadian Atlantic coast. The influence of management area in our study was also significant. Thus, higher abundances of echinoderms in closed areas than in adjacent open areas that share similar biological and environmental conditions may be indicative of an indirect, positive effect of reduced fishing over these populations.

Depth was the most important explanatory environmental factor for the abundance of brittle stars. Although ophiuroids are present in depths ranging from the intertidal zone down to 8,000 m (Summers & Nybakken, 2000), some species have depth-specific preferences (Gage & Tyler, 1991; García, Yeh, & Ohta, 2002; Piepenburg, Voss, & Gutt, 1997). On Georges Bank, brittle star abundance increased with depth. Deeper waters, with characteristics that include abundant food supply (e.g., suspended matter), may provide a more constant hydrodynamic environment for these organisms. Common brittle stars of Georges Bank, such as *Ophiura sarsi* Lütken 1855 (Steimle, 1987), are suspension and deposit feeders, which may benefit from increased flux of fine particulate matter into the sediment. Other favorable characteristics for brittle stars of these deep waters include stable sediments, low temperatures, and reduction in competition and predation pressure (Aronson, 1992; Haedrich, Rowe, & Polloni, 1980; Harris et al., 2012; Howell, Billett, & Tyler, 2002).

Sediment stability and temperature were strongly related with the distribution of sea stars and sea urchins. Stable sediments reduce the potential of suffocation and burial of these organisms in comparison with highly unstable sediments (Aronson, 1992; Hinchey, Schaffner, Hoar, Vogt, & Batte, 2006). Strong currents and high shear stress also compromise the directional swimming ability of sea urchin larvae (Sameoto, Ross, & Metaxas, 2010). Conversely, sand dollars were the only echinoderm associated with relatively unstable sediments (sediment index >1), but their density decreased in the most unstable regimes (sediment index >3). Feeding of these flat sand dollars is actually enhanced under unstable conditions, because more food in the form of suspended particles is readily available (O'Neill, 1978). However, at higher water velocities associated with a storm surge event, sand dollars bury themselves for protection (O'Neill, 1978), and these storm events may negatively influence their survival. Stable sediments and temperatures ranging 7–13°C appeared to be related to the narrow center of distribution of sea stars in the southern areas of the bank. Sea star distribution on the North Atlantic coast may be controlled by temperature (Khanna & Yadav, 2005). Furthermore, mortality of *Asterias vulgaris* Verrill 1866, one of the most representative species of this ecosystem (Bigelow & Schroeder, 2002; Link & Almeida, 2000; Theroux & Wigley, 1998), is associated with temperatures >25°C (Khanna & Yadav, 2005). For sea urchins, temperatures >15°C have a considerable detrimental effect on the development of larvae (Stephens, 1972) and increased mortality of adults (Scheibling & Stephenson, 1984).

Predator abundance was as strongly correlated with echinoderm abundance as the environmental factors. High densities of American plaice and brittle stars were observed in the same northern areas of the bank. Brittle stars are a preferred prey of American plaice in this ecosystem (Link & Almeida, 2000; Packer et al., 1994). Similarly, haddock prey on sand dollars (Link & Almeida, 2000), and their densities were also positively correlated. We were expecting to observe a stronger correlation between ocean pout and sand dollars, because they are a preferred prey (Buzulutskaya, 1983; Link & Almeida, 2000). The weakly negative correlation may have resulted from a stronger association between ocean pout and urchins because both share similar substrates (e.g., cobble, boulder). Ocean pout distribution may be related to coarse sediments because their fertilized eggs are laid in rocky crevices (Steimle, Morse, Berrien, Johnson, & Zetlin, 1999).

Sea scallops and sea star distribution were weakly associated, although previous studies indicate that sea star distribution can be influenced by the location of their prey (Marino et al., 2009). Predator and prey densities are influenced by the spatial scale used in the analysis (Rose & Leggett, 1990). Stronger species-specific relationships may only be determined at local scales, rather than at the regional scales used in our analysis. Georges Bank is considered a predator-controlled ecosystem (Worm & Myers, 2003) and our results support this hypothesis, because the influence of predators in echinoderm populations was stronger than that of prey availability. Therefore, a stronger association between sea stars and scallops may only be discernible by analyzing these populations separately.

Several studies indicate that the establishment of MPAs leads to significant differences in invertebrate populations after a period of time, with a general consensus that abundance, biomass, and diversity are modified as a result of diminishing the impacts of fishing disturbance (Ashworth, Ormond, & Sturrock, 2004; Collie et al., 1997; Hermsen et al., 2003; Marino et al., 2007; Stokesbury, 2002). The types of fishing disturbance include direct removal of invertebrates by fishing gear, body breakage, enhanced predation and migration rates, along with modification of sediments via re-suspension of finer particles or dispersion of coarser sediments (Asch & Collie, 2008; Prena et al., 1999; Stokesbury & Harris, 2006).

Initially, brittle stars were expected to be more abundant in undisturbed areas than in open areas, because there would likely be less removal, burial, or body breakage caused by bottom fishing gear (Collie et al., 1997; Hansson, Lindegarth, Valentinsson, & Ulmestrand, 2000; Prena et al., 1999). The high abundance of brittle stars in open areas seen in the present study may have several explanations, including a possible reduction in predation pressure, and the capacity of brittle stars (with the capability to regenerate lost arms and portions of the central disk; Hendler, Miller, Pawson, & Kier, 1995; Kaiser & Spencer, 1995) to survive damage induced by bottom trawls. Furthermore, trawling may increase food availability in the form of damaged organisms and disturbed sediment particles, and thus may be beneficial to brittle stars (Ramsay, Kaiser, & Hughes, 1998; Tuck, Hall, Robertson, Armstrong, & Basford, 1998).

Estimates of brittle star density were limited by the distribution of survey stations, which provided few records within brittle star habitat. The SMAST video survey was designed primarily to examine the distribution and abundance of scallops, thus habitats outside their distribution range were not sampled. These include stations with depths >160 m. Brittle stars may be found in waters well below the 100 m isobath. Therefore, brittle star habitat is underrepresented in the present study and unambiguous evidence about the lack of impact of MPAs on these populations cannot be adequately evaluated.

Sand dollars have high survival rates when they are discarded from bottom trawls, and may have the ability to recover fast from potential damage inflicted on the test during trawling. Sand dollars also re-aggregate rapidly after a disruption of their beds (Murawski & Serchuk, 1989). Therefore, the presence and high-density aggregation of sand dollars in different areas of Georges Bank, regardless of the presence of fishing pressure, was expected. However, some studies have also found significantly lower biomasses in trawled areas compared to undisturbed sites (Murawski & Serchuk, 1989; Prena et al., 1999). The unusual high density observed inside the closed portion of CAI is likely the result of a high recruitment and survivorship of sand dollars prior to 2008. High survivorship may be partly related to low fishing disturbance in this area, while retention of larvae in this area is primarily determined by current and wind patterns (Tian et al., 2009). Higher density of sand dollars observed in the non-fishing portion of NLSA compared to the partial access area, also suggests a positive effect of the closure itself. Higher densities inside closed areas, in combination with preferred habitat conditions, may indicate a positive effect of the closure via enhanced reproduction (improving the external fertilization rate in undisturbed beds) and higher recruitment (Highsmith, 1982; Merrill & Hobson, 1970).

A caveat of the sand dollar population estimates in open areas is that the center of the bank was not sampled. Based on their distribution, it is likely that densities in this area are high and therefore sand dollar abundance is underestimated in open areas. Nevertheless, the SMAST video survey covers an important part of the distribution range of these individuals because sea scallops (the target species of study in this survey) and sand dollars share similar habitats (Stokesbury & Harris, 2006).

Highest densities of sea stars were found inside NLSA. The environmental conditions (e.g., temperature and sediment stability) found inside this closed area are similar to those observed in the adjacent southern open areas, suggesting a direct positive impact of this MPA on these populations. Reducing the impacts of fishing disturbance may enhance recruitment of sea stars in this area. This hypothesis is supported by the presence of smaller individuals inside closed areas compared to open areas (Marino et al., 2007; Rosellon-Druker, 2017). As with sand dollars, sea stars were also persistent and abundant in open areas, indicating natural resilience. Furthermore, fishing activities in open areas may provide food for scavenging sea stars in the form of other damaged animals that are left in the track of a trawl or dredge (Ramsay et al., 1998).

The similarity in density of sea urchins among management areas was expected, since these organisms were strongly associated with hard bottoms (Meidel & Scheibling, 1998), which are found both in closed and open areas (Harris & Stokesbury, 2010) and are generally avoided by fishing gears (Collie et al., 1997). Sea urchin population estimations in this study are uncertain because of the small sample size. Sea urchins were the most difficult echinoderm to identify in the video survey, since they can be confounded with the substrate (e.g., pebbles and small rocks).

In conclusion, we provided the first estimates of density and absolute abundance of the main echinoderm taxa of Georges Bank at a spatial resolution of kilometers, allowing the examination of these populations in relation with different management regimes. This spatial and temporal characterization of echinoderm populations on Georges Bank has important ecological applications. Echinoderm beds, with hundreds of individuals per square meter, may directly and indirectly affect other species (Fujita & Ohta, 1989; Highsmith, 1982; Howell et al., 2002; Merrill & Hobson, 1970). Indirect impacts of these echinoderm aggregations include physical alterations to the habitats where they are present, such as the mechanical disruption of sediments by burrowing (Smith, 1981). Direct impacts of echinoderm aggregations include the intensification of biological interactions with other species that might be of economic importance. For example, the average annual density of sand dollars at Georges Bank (35 individuals per m^2) was 30-fold greater than the density of scallops (0.14 individuals per m^2) in the same time period (2005–2012), while the average annual density of sea stars (six individuals per m^2) was sixfold greater than scallops. Sand dollars and scallops share essential habitats (Stokesbury, 2002; Stokesbury et al., 2004), and thus competitive exclusion for space may be occurring. Sea stars are main predators of scallops (Marino et al., 2009), and therefore location of hotspots of sea star density may help to delineate areas where consumption is enhanced.

Finally, an important management application of this work is the incorporation of these echinoderm population estimates into stock assessment models. Echinoderms are not commonly included in available models because of limited information about the distribution and abundance of these organisms at appropriate temporal and spatial scales (Schückel, Ehrich, Kröncke, & Reiss, 2010). The improved spatial resolution of echinoderm density provided here can remove some of these constraints, and has important implications for implementation of multispecies models and, as a result, ecosystem-based fisheries management.

ACKNOWLEDGMENTS

We thank all the students, digitizers, and collaborators of the Marine Fisheries Field Research Group and the Marine Fisheries Biology and Assessment Lab in SMAST, for all the help provided during the development of this study, including image analysis, collection of live samples and manuscript reviews. This manuscript benefitted immensely from discussions and critical reviews of Drs. Steven X. Cadrin, Gavin Fay, Jason S. Link, Timothy Miller, Brian J. Rothschild, and three anonymous reviewers. Funding was provided by the Fulbright fellowship, the Mexican National Council of Science and Technology (CONACYT) scholarship, the Nature Conservancy, the Cooperative Institute for the North Atlantic Region (CINAR), the NOAA Scallop Research Set-Aside Program, and the U.S. Sea Scallop Fishery Industry. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any other agencies.

ORCID

Judith Rosellon-Druker https://orcid.org/0000-0003-1788-7202

REFERENCES

Aronson, R. B. (1992). Biology of a scale-independent predator-prey interaction. *Marine Ecology Progress Series*, *89*, 1–13. https://doi.org/10.3354/meps089001

Asch, R. G., & Collie, J. S. (2008). Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure. *Fishery Bulletin*, *106*, 438–456.

Ashworth, J. S., Ormond, R., & Sturrock, H. T. (2004). Effects of reef-top gathering and fishing on invertebrate abundance across take and no-take zones. *Journal of Experimental Marine Biology and Ecology*, *303*, 221–242. https://doi.org/10.1016/j.jembe.2003.11.017

Azarovitz, T. R. (1981). A brief historical review of the Woods Hole Laboratory trawl survey time series. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *58*, 62–67.

Bigelow, H. B., & Schroeder, W. C. (2002). *Bigelow and Schroeder's fishes of the Gulf of Maine*. Washington, DC: Smithsonian Institution Press, 882 pp.

Broom, D. M. (1975). Aggregation behavior of the brittle star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the UK*, *55*, 191–197. https://doi.org/10.1017/S0025315400015836

Brusca, R. C., & Brusca, G. J. (1990). *Invertebrates*. Sunderland, MA: Sinauer Associates Inc, 922 pp.

Buzulutskaya, A. (1983). Feeding of ocean pout Macrozoarces americanus in the Northwest Atlantic. Northwest Atlantic Fisheries Organization. Scientific Council Research Document 83-76, Dartmouth, NS, 9 pp.

Byrne, M. (1994). Ophiuroidea. In F. W. Harrison & F. S. Chia (Eds.), *Microscopic anatomy of invertebrates, Echinodermata* (pp. 247–343). New York, NY: Wiley-Liss, Inc

Carey, J. D., & Stokesbury, K. D. E. (2011). An assessment of juvenile and adult sea scallop, *Placopecten magellanicus*, distribution in the northwest Atlantic using high-resolution still imagery. *Journal of Shellfish Research*, *30*, 569–582. https://doi.org/10.2983/035.030.0301

Cochran, W. G. (1977). *Sampling techniques*. New York, NY: John Wiley & Sons 444 pp.

Collie, J. S., Escanero, G. A., & Valentine, P. C. (1997). Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series*, *155*, 159–172. https://doi.org/10.3354/meps155159

Collie, J. S., Hermsen, J. M., Valentine, P. C., & Almeida, F. P. (2005). Effects of fishing on gravel habitats: Assessment and recovery of benthic megafauna on Georges Bank. In P. W. Barnes & J. P. Thomas (Eds.), *Benthic habitats and the effects of fishing* (pp. 325–343). Bethesda, MD: American Fisheries Society Symposium.

Coutré, K., Gedamke, T., Rudders, D. B., Driggers, W. B. III, Koester, D. M., & Sulikowski, J. A. (2013). Indication of density-dependent changes in growth and maturity of the barndoor skate on Georges Bank. *Marine and Coastal Fisheries*, *5*, 260–269. https://doi.org/10.1080/19425120.2013.824941

Cusson, M., & Bourget, E. (2005). Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series*, *297*, 1–14. https://doi.org/10.3354/meps297001

Despres-Patanjo, L. I., Azarovitz, T. R., & Byrne, C. J. (1988). Twenty-five years of fish surveys in the northwest Atlantic: The NMFS Northeast Fisheries Center's bottom trawl survey program. *Marine Fisheries Review*, *50*, 69–71.

Ellis, J. R., & Rogers, S. I. (2000). The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea. *Journal of the Marine Biological Association of the UK*, *80*, 127–138. https://doi.org/10.1017/S0025315499001642

Fogarty, M. J., & Murawski, S. A. (1998). Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. *Ecological Applications*, *8*, S6–S22. https://doi.org/10.2307/2641359

Freeman, S. M., & Rogers, S. I. (2003). A new analytical approach to the characterization of macro-epibenthic habitats: Linking species to the environment. *Estuarine, Coastal and Shelf Science*, *56*, 749–764. https://doi.org/10.1016/S0272-7714(02)00297-4

Fujita, T., & Ohta, S. (1989). Spatial structure within a dense bed of the brittle star *Ophiura sarsi* (Ophiuroidea: Echinodermata) in the bathyal zone off Otsuchi, northeastern Japan. *Journal of the Oceanographical Society of Japan*, *45*, 289–300. https://doi.org/10.1007/BF02123483

Gage, J. D., & Tyler, P. A. (1991). *Deep-sea biology: A natural history of organisms at the deep-sea floor*. Cambridge, MA: Cambridge University Press, 504 pp. https://doi.org/10.1017/CBO9781139163637

García, J., Yeh, H., & Ohta, S. (2002). Distribution and bathymetric zonation of deep-sea brittle stars (Echinodermata: Ophiuroidea) off the Japanese Pacific coast. *Journal of the Marine Biological Association of the UK*, *82*, 345–346. https://doi.org/10.1017/S0025315402005544

Haedrich, R. L., Rowe, G. T., & Polloni, P. T. (1980). The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology*, *57*, 165–179. https://doi.org/10.1007/BF00390735

Hair, J. F., Anderson, R. E., Tatham, L., & Grablowsky, B. J. (1984). *Multivariate data analysis*. New York, NY: Macmillan, 360 pp.

Hansson, M., Lindegarth, M., Valentinsson, D., & Ulmestrand, M. (2000). Effects of shrimp-trawling on abundance of benthic macrofauna in Gullmarsfjorden, Sweden. *Marine Ecology Progress Series*, *198*, 191–201. https://doi.org/10.3354/meps198191

Harris, B. P., Cowles, G. W., & Stokesbury, K. D. E. (2012). Surficial sediment stability on Georges Bank, in the Great South Channel and on eastern Nantucket Shoals. *Continental Shelf Research*, *49*, 65–72. https://doi.org/10.1016/j.csr.2012.09.008

Harris, B. P., & Stokesbury, K. D. E. (2010). The spatial structure of local surficial sediment characteristics on Georges Bank, USA. *Continental Shelf Research*, *30*, 1840–1853. https://doi.org/10.1016/j.csr.2010.08.011

Hart, D. R., & Rago, P. J. (2006). Long-term dynamics of U.S. Atlantic sea scallop *Placopecten magellanicus* populations. *North American Journal of Fisheries Management*, *26*, 490–501. https://doi.org/10.1577/M04-116.1

Hendler, G., Miller, J. E., Pawson, D. L., & Kier, P. M. (1995). *Sea stars, sea urchins and allies: Echinoderms of Florida and the Caribbean*. Washington, DC: Smithsonian Institution Press, 390 pp.

Hermsen, J. M., Collie, J. S., & Valentine, P. C. (2003). Mobile fishing gear reduces benthic megafaunal production on Georges Bank. *Marine Ecology Progress Series*, *260*, 97–108. https://doi.org/10.3354/meps260097

Highsmith, R. C. (1982). Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: Adult sand dollar beds. *Ecology*, *63*, 329–337. https://doi.org/10.2307/1938950

Hinchey, E. K., Schaffner, L. C., Hoar, C. C., Vogt, B. W., & Batte, L. P. (2006). Responses of estuarine benthic invertebrates to sediment burial: The importance of mobility and adaptation. *Hydrobiologia*, *556*, 85–98. https://doi.org/10.1007/s10750-005-1029-0

Holland, D. S. (2000). A bioeconomic model of marine sanctuaries on Georges Bank. *Canadian Journal of Fisheries and Aquatic Science*, *57*, 1307–1319. https://doi.org/10.1139/f00-061

Holzwarth, T. J., & Mountain, D. G. (1990). Surface and bottom temperature distributions from the Northeast Fisheries Center spring and fall bottom trawl survey program, 1963-1987. Ref Doc 90-03 NEFSC, Woods Hole, MA. 97 pp.

Howell, K. L., Billett, D. S. M., & Tyler, P. A. (2002). Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E Atlantic. *Deep Sea Research*, *49*, 1901–1920. https://doi.org/10.1016/S0967-0637(02)00090-0

Kaiser, M. J., & Spencer, B. E. (1995). Survival of by-catch from a beam trawl. *Marine Ecology Progress Series*, *126*, 31–38. https://doi.org/10.3354/meps126031

Khanna, D. R., & Yadav, P. R. (2005). *Biology of Echinodermata*. New Delhi, IN: Discovery Publishing House, 339 pp.

Kostylev, V. E., Todd, B. J., Fader, G. B., Courtney, R. C., Cameron, G. D., & Pickrill, R. A. (2001). Benthic habitat mapping on the Scotian Shelf based on multibeam bathymetry, surficial geology and sea floor photographs. *Marine Ecology Progress Series*, *219*, 121–137. https://doi.org/10.3354/meps219121

Krebs, C. J. (1989). *Ecological methodology*. New York, NY: Harper & Row, 654 pp.

Langton, R. W., & Robinson, W. E. (1990). Faunal associations on scallop grounds in the western Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, *144*, 157–171. https://doi.org/10.1016/0022-0981(90)90026-9

Link, J. S. (2004). Using fish stomachs as samplers of the benthos: Integrating long-term and broad scales. *Marine Ecology Progress Series*, *269*, 265–275. https://doi.org/10.3354/meps269265

Link, J. S., & Almeida, F. P. (2000). An overview and history of the food web dynamics program of the Northeast Fisheries Science Center. NOAA Technical Memorandum NMFS NE-159, Woods Hole, MA. 64 pp.

Link, J. S., Almeida, F. P., Valentine, P., Auster, P., Reid, R., & Vitaliano, J. (2005). The effects of area closures on Georges Bank. In P. W. Barnes & J. P. Thomas (Eds.), *Benthic habitats and the effects of fishing* (pp. 345–368). Bethesda, MD: American Fisheries Society Symposium.

Link, J. S., Bell, R., Auster, P. J., Smith, B. E., Overholtz, W. J., Methratta, E., … Stockhausen, W. (2012). Food web and community dynamics of the northeast US large marine ecosystem. Ref Doc 12-15 NEFSC, Woods Hole, MA, 96 pp.

Marino, M. C. II, Juanes, F., & Stokesbury, K. D. E. (2007). Effect of closed areas on populations of sea star *Asterias* spp. on Georges Bank. *Marine Ecology Progress Series*, *347*, 39–49. https://doi.org/10.3354/meps07057

Marino, M. C. II, Juanes, F., & Stokesbury, K. D. E. (2009). Spatio-temporal variations of sea star *Asterias spp*. distributions between sea scallop *Placopecten magellanicus* beds on Georges Bank. *Marine Ecology Progress Series*, *382*, 59–68. https://doi.org/10.3354/meps08011

Meidel, S. K., & Scheibling, R. E. (1998). Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. *Marine Biology*, *131*, 461–478. https://doi.org/10.1007/s002270050338

Merrill, R. J., & Hobson, E. S. (1970). Field observations of *Dendraster excentricus*, a sand dollar of Western North America. *American Midland Naturalist*, *83*, 595–624. https://doi.org/10.2307/2423965

Methratta, E. T., & Link, J. S. (2006). Seasonal variation in groundfish habitat associations in the Gulf of Maine-Georges Bank region. *Marine Ecology Progress Series*, *326*, 245–256. https://doi.org/10.3354/meps326245

Miller, T. J., Das, C., Politis, P. J., Miller, A., Lucey, S. M., Legault, C. M., … Rago, P. J. (2010). Estimation of Albatross IV to Henry B. Bigelow calibration factors. US Department of Commerce. Northeast Fisheries Science Center Reference Document 10-05, Woods Hole, MA. 233 pp.

Murawski, S. A., Brown, R., Lai, H. L., Rago, P. J., & Hendrickson, L. (2000). Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science*, *66*, 775–798.

Murawski, S. A., & Serchuk, F. M. (1989). *Environmental effects of offshore dredge fisheries for bivalves*. Copenhagen, Denmark: ICES Shellfish Committee Meeting. 12 pp.

Murawski, S. A., Wigley, S. E., Fogarty, M. J., Rago, P. J., & Mountain, D. G. (2005). Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science*, *62*, 1150–1167.

O'Neill, P. L. (1978). Hydrodynamic analysis of feeding in sand dollars. *Oecologia*, *34*, 157–174. https://doi.org/10.1007/BF00345164

Packer, D. B., Watling, L., & Langton, R. W. (1994). The population structure of the brittle star *Ophiura sarsi* Lütken in the Gulf of Maine and its trophic relationship to American plaice (*Hippoglossoides platessoides* Fabricius). *Journal of Experimental Marine Biology and Ecology*, *179*, 207–222. https://doi.org/10.1016/0022-0981(94)90115-5

Palmer, M. W. (1993). Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology*, *74*, 2215–2230. https://doi.org/10.2307/1939575

Piepenburg, D., Voss, J., & Gutt, J. (1997). Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off Northeast Greenland (Arctic): A comparison of diversity and abundance. *Polar Biology*, *17*, 305–322. https://doi.org/10.1007/PL00013372

Prena, J., Schwinghamer, P., Rowell, T. W., Gordon, D. J., Gilkinson, K. D., Vass, W. P., & McKeown, D. L. (1999). Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: Analysis of trawl bycatch and effects on epifauna. *Marine Ecology Progress Series*, *181*, 107–124.

Rakocinski, C. F., Lyczkowski-Shultz, J., & Richardson, S. L. (1996). Ichthyoplankton assemblage structure in Mississippi Sound as revealed by canonical correspondence analysis. *Estuarine, Coastal and Shelf Science*, *43*, 237–257. https://doi.org/10.1006/ecss.1996.0067

Ramsay, K., Kaiser, M. J., & Hughes, R. N. (1998). Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *Journal of Experimental Marine Biology and Ecology*, *224*, 73–89. https://doi.org/10.1016/S0022-0981(97)00170-6

Rose, G. A., & Leggett, W. C. (1990). The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. *Ecology*, *71*, 33–43. https://doi.org/10.2307/1940245

Rosellon-Druker, J. (2017). Describing echinoderm (Echinodermata) populations on Georges Bank and evaluating direct and indirect effects of marine protected areas on these populations. Doctoral thesis, University of Massachusetts Dartmouth, Dartmouth, MA, 162 pp.

Sameoto, J. A., Ross, T., & Metaxas, A. (2010). The effect of flow on larval vertical distribution of the sea urchin, *Strongylocentrotus droebachiensis*. *Journal of Experimental Marine Biology and Ecology*, *383*, 156–163. https://doi.org/10.1016/j.jembe.2009.11.014

Scheibling, R. E., & Stephenson, R. L. (1984). Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Marine Biology*, *78*, 153–164. https://doi.org/10.1007/BF00394695

Schückel, S., Ehrich, S., Kröncke, I., & Reiss, H. (2010). Linking prey composition of haddock *Melanogrammus aeglefinus* to benthic prey availability in three different areas of the northern North Sea. *Journal of Fish Biology*, *77*, 98–118. https://doi.org/10.1111/j.1095-8649.2010.02657.x

Smith, A. L. (1981). Comparison of macrofaunal invertebrates in sand dollar (*Dendraster excentricus*) beds and in adjacent areas free of sand dollars. *Marine Biology*, *65*, 191–198. https://doi.org/10.1007/BF00397085

Sokal, R. R., & Rohlf, F. J. (1981). *Biometry the principles and practice of statistics in biological research*. San Francisco, CA: W.H. Freedman, 859 pp.

Steimle, F. W. (1987). Benthic faunal production. In R. H. Backus (Ed.), *The Georges Bank* (pp. 310–314). Cambridge, MA: MIT Press.

Steimle, F. W. (1990). Population dynamics, growth, and production estimates for the sand dollar *Echinarachnius parma*. *Fishery Bulletin*, *88*, 179–189.

Steimle, F. W., Morse, W. W., Berrien, P. L., Johnson, D. L., & Zetlin, C. A. (1999). Essential fish habitat source document: Ocean pout, Macrozoarces americanus, life history and habitat characteristics. National Oceanic and Atmospheric Administration Tech Memo. National Marine Fisheries Service NE-129, Woods Hole, MA. 34 pp.

Steimle, F. W., & Terranova, R. J. (1985). Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *Journal of Northwest Atlantic Fishery Science*, *6*, 117–124.

Stephens, R. E. (1972). Studies on the development of the sea urchin *Strongylocentrotus droebachiensis*. I. Ecology and normal development. *Biological Bulletin*, *142*, 132–144. https://doi.org/10.2307/1540251

Stokesbury, K. D. E. (2002). Estimation of sea scallop abundance in closed areas of Georges Bank, USA. *Transactions of the American Fisheries Society*, *131*, 1081–1092. https://doi.org/10.1577/1548-8659(2002)131<1081:EOSSAI>2.0.CO;2

Stokesbury, K. D. E. (2012). Stock definition and recruitment: Implications for the U.S. sea scallop (*Placopecten magellanicus*) fishery from 2003 to 2011. *Reviews in Fisheries Science*, *20*, 154–164. https://doi.org/10.1080/10641262.2012.695816

Stokesbury, K. D. E., & Harris, B. P. (2006). Impact of limited short-term sea scallop fishery on epibenthic community of Georges Bank closed areas. *Marine Ecology Progress Series*, *307*, 85–100. https://doi.org/10.3354/meps307085

Stokesbury, K. D. E., Harris, B. P., Marino, M. C. II, & Nogueira, J. I. (2004). Estimation of sea scallop abundance using a video survey in off-shore US waters. *Journal of Shellfish Research*, *23*, 33–40.

Stokesbury, K. D. E., Harris, B. P., Marino, M. C. II, & Nogueira, J. I. (2007). Sea scallop mass mortality in a marine protected area. *Marine Ecology Progress Series*, *349*, 151–158. https://doi.org/10.3354/meps07113

Summers, A. C., & Nybakken, J. (2000). Brittle star distribution patterns and population densities on the continental slope off central California (Echinodermata: Ophiuroidea). Deep Sea Res. Part 2 Top. *Studies in Oceanography*, *47*, 1107–1137. https://doi.org/10.1016/S0967-0645(99)00138-1

Ter Braak, C. J. (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology*, *67*, 1167–1179. https://doi.org/10.2307/1938672

Ter Braak, C. J., & Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, *18*, 271–317. https://doi.org/10.1016/S0065-2504(08)60183-X

Theroux, R. B., & Wigley, R. L. (1998). *Quantitative composition and distribution of the macrobenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States*. Woods Hole, MA: NOAA Technical Memorandum NMFS, 246 pp.

Thouzeau, G., Robert, G., & Ugarte, R. (1991). Faunal assemblages of benthic megainvertebrates inhabiting sea scallop grounds from eastern Georges Bank, in relation to environmental factors. *Marine Ecology Progress Series*, *74*, 61–82. https://doi.org/10.3354/meps074061

Tian, R. C., Chen, C., Stokesbury, K. D. E., Rothschild, B. J., Cowles, G. W., Xu, Q., … Marino, M. C. II (2009). Dispersal and settlement of sea scallop larvae spawned in the fishery closed areas on Georges Bank. *ICES Journal of Marine Science*, *66*, 2155–2164. https://doi.org/10.1093/icesjms/fsp175

Tuck, I. D., Hall, S. J., Robertson, M. R., Armstrong, E., & Basford, D. J. (1998). Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology Progress Series*, *162*, 227–242. https://doi.org/10.3354/meps162227

Valderrama, D., & Anderson, J. L. (2007). Improving utilization of the Atlantic sea scallop resource: An analysis of rotational management of fishing grounds. *Land Economics*, *83*, 86–103. https://doi.org/10.3368/le.83.1.86

Warner, G. F. (1971). On the ecology of a dense bed of the brittle star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the UK*, *51*, 267–282. https://doi.org/10.1017/S0025315400031775

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology*, *30*, 377–392. https://doi.org/10.1086/622910

Wigley, S. E., & Theroux, R. B. (1981). Atlantic Continental Shelf and Slope of the United States. Macrobenthic Invertebrate Fauna of the Middle Atlantic Bight Region. Faunal Composition and Quantitative Distribution. US Geological Survey Professional Paper 529-N, Washington, District of Columbia, 198 pp.

Worm, B., & Myers, R. A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, *84*, 162–173. https://doi.org/10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2

Zamarro, J. (1992). Feeding behavior of the American plaice (*Hippoglossoides platessoides*) on the southern Grand Bank of Newfoundland. *Netherlands Journal of Sea Research*, *29*, 229–238. https://doi.org/10.1016/0077-7579(92)90023-8

Zar, J. H. (1999). *Biostatistical analysis*. Upper Saddle River, NJ: Prentice Hall, 662 pp.

How to cite this article: Rosellon-Druker J, Stokesbury KDE. Quantification of echinoderms (Echinodermata) on Georges Bank, and the potential influence of marine protected areas on these populations. *Invertebr Biol*. 2019;138:e12243. https://doi.org/10.1111/ivb.12243