Sea scallops exhibit strong local spatiotemporal structure associated with seabed stability and high flows

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Abstract.   Sea scallops (*Placopecten magellanicus*) live along the Northwest Atlantic continental shelf and are aggregated over a broad range of spatial scales (m^2–10^5 km^2). However, little is known about the spatial distribution of local scallop neighborhoods, the scale at which spawning, intra-specific competition, and predator–prey interactions occur. We surveyed 30,995 km^2 of Georges Bank and the Great South Channel annually from 2003 to 2010 counting the number of scallops in 54,016 locally replicated 3.24-m^2 quadrats with underwater video. There were about 4 billion scallops occupying 11,200 km^2 of the study area in concentrations from 1 to 41 scallops per scallop. Scallop spatial distribution switched from dispersed to aggregated at a concentration of 3–4 scallops in every year. High concentrations (>3) occurred in 11% but were only persistent in 4% (449 km^2) of scallop habitat. There were 13 persistent high-concentration aggregations (7–217 km^2), and all but two occurred on gravel-dominated sediments left by prehistoric glacial retreat. Model-derived benthic boundary shear stresses in the persistent aggregations averaged two times higher than in scallop habitat, but the seabed was about two times more stable because it had significantly less sand and more granule–pebble and cobble sediment. The area occupied by scallops each year varied little (9%) despite a 49% increase in total scallop abundance between 2005 and 2007, suggesting Georges Bank scallops have a proportional density population structure. Most scallops occurred alone or at low concentrations (≤2) where fertilization success is probably poor. The persistent high-concentration aggregations we identified may be critical for successful reproduction and sustainable harvest. Observing organisms at scales corresponding to their individual interactions reveals important processes shaping their landscape-scale spatiotemporal distributions. These processes are obscured by the methods typically employed to estimate abundances of commercial fishery species. The spatiotemporal structure of sea scallop distribution has important implications for the design of abundance surveys and the assumptions underlying stock assessment methods. These should be investigated. Finally, this work suggests that natural disturbance (sediment stability) may play a substantial role in shaping spatiotemporal distributions and dynamics of benthic marine populations.

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INTRODUCTION

Scallops (*Placopecten magellanicus*) inhabit the Northwestern Atlantic continental shelf from Cape Hatteras, USA, to the northern Gulf of St. Lawrence, Canada (Posgay 1957, Squires 1962). Their adductor meats are valuable ($10–30 USD/kg), and U.S. commercial landings are worth nearly half a billion U.S. dollars annually (ex-vessel value; National Marine Fisheries Service 2017). Sea scallop spatial distributions are patchy and have been related to depth (Naidu and Robert 2006), substrate type (Thouzeau et al. 1991, Stokesbury 2002, Kostylev et al. 2003), water flow (Wildish and Saulnier 1992, Pilditch and Grant 1999), temperature and salinity (Stewart and Arnold 1994), food availability (Bordon 1928, Stevenson 1936, Shumway et al. 1987, Grant and Cranford 1991), and predator distribution (Medcof and Bourne 1964, Stokesbury and Himmelman 1995, Marino et al. 2009).

Important scallop intra- and inter-specific processes including broadcast spawning, competition for food and space, and predator–prey interactions occur in local neighborhoods of individuals (Stokesbury and Himmelman 1993, Orensanz et al. 2016). Understanding the role of spatiotemporal scales in uncovering these interactions has been and continues to be a hallmark of ecology (Allee 1931, Levins 1969, Turner et al. 2001, Sale et al. 2006). Due to the difficulties of sampling at the scale at which scallops occur, ranging from individuals (m^2) to large areas (10^2–10^4 km^2), little is known about the spatial distribution of scallop concentrations, and therefore, it limits our frame of inference about population-level processes (Orensanz et al. 2016). Most scallop population studies have used modified commercial scallop dredges which have sampling grains ~10^3 m^2 (e.g., a 2.6-m dredge towed for 1 km has a sampling grain = 2,660 m^2) and integrate local scallop distributions in the tow path (Caddy 1968, 1970, Brand 2006). Legendre and Legendre (1998) point out that the sampling grain defines the smallest scale at which a pattern can be detected. Stokesbury et al. (2016) have used video quadrats to sample scallops in U.S. waters since 1999, but the objective of these studies was area-based population assessment and local scallop concentration was not addressed.

Density (individuals/area) is the typical measure used to describe scallop populations; the goal is usually to estimate the total number of individuals in a given area. However, when the goal is to describe local scallop living conditions and to understand inter-organism interactions, then *concentration* (the number of scallops experienced by a scallop in a given neighborhood) is the appropriate measure (Iwao 1976, Clark 1982, Orensanz et al. 1998). Sampling species with patchy distributions typically yields many counts of zero, which causes mean densities to decrease; concentration is not affected (Orensanz et al. 1998). Further, the mean density for a given area does not necessarily correspond to local densities experienced by individual organisms. Ideally concentrations are calculated based on the exact locations of individuals and the distances to their neighbors. However, counting individuals in a fixed neighborhood (e.g., quadrat) also permits the calculation of local mean concentration (the average number of individuals per individual in the neighborhood; Orensanz et al. 1998).

The U.S. scallop fishery occurs primarily in Mid-Atlantic Bight and on Georges Bank, including the Great South Channel. Scallops have pelagic larvae (Bourne 1964), and owing to a residual clockwise gyre, Georges Bank is thought to have the largest self-sustaining scallop population (Posgay 1950, Tremblay et al. 1994). Stokesbury et al. (2010) estimated that between 2003 and 2009, there were about 4.2 billion scallops living on the U.S. side of Georges Bank. The Bank is a 40,000-km^2 bulge in the Northwest Atlantic continental shelf (Backus and Bourne 1987) which is hydrographically dominated by the principal lunar and solar semidiurnal tides (Butman and Beardsley 1987) and geologically dominated by a 12,000-km^2 gravelly prehistoric glacial moraine (Harris and Stokesbury 2010).

We have assessed scallop density and abundance with small- and large-scale video surveys since 1999 (Stokesbury et al. 2016). Based on our field observations and spatial analyses of some scallop beds (Adams et al. 2010), we hypothesize that there are persistent high-concentration scallop aggregations on Georges Bank. This idea is consistent with decades of observations by commercial scallop fishers but has never been formally investigated. In this paper, we assess local scallop concentration annually from 2003 to 2010 using 54,016 multi-view underwater video quadrats. Scallop concentration profiles were constructed using

geostatistical aggregation curves, and persistent high-concentration aggregations were mapped. We estimated the total number of scallops in these aggregations, and to better understand the conditions in these locations, we tested null hypotheses that the water depth, sediment, and shear stress conditions were no different from the remaining areas where scallops were observed (herein referred to as scallop habitat).

METHODS

Sampling

Sea scallops were sampled on Georges Bank and the Great South Channel (30,995 km^2) in water depths ranging from 10 to 100 m from 2003 to 2010 with underwater video quadrats (3.24 m^2; Fig. 1; Stokesbury et al. 2016). We used a two-stage design with stations sampled on regular grids (stage 1) and four quadrats sampled at each station (stage 2; Krebs 1989). The survey vessel stopped at each station and a 700-kg steel pyramid with live-feed video cameras was lowered to the seabed for 15–30 s, raised until the seabed was beyond view, and then dropped again. This process was repeated until four samples were taken. The number of scallops in each quadrat was counted in real time, and the latitude and longitude of the vessel was used as the quadrat position. The position, date, time, and quadrat identification were overlaid on the video during recording to digital versatile disk. In the laboratory, the video was reviewed, the scallop counts were verified, and a digital still image from the video footage at each quadrat was archived. The shell heights (mm) of the scallops
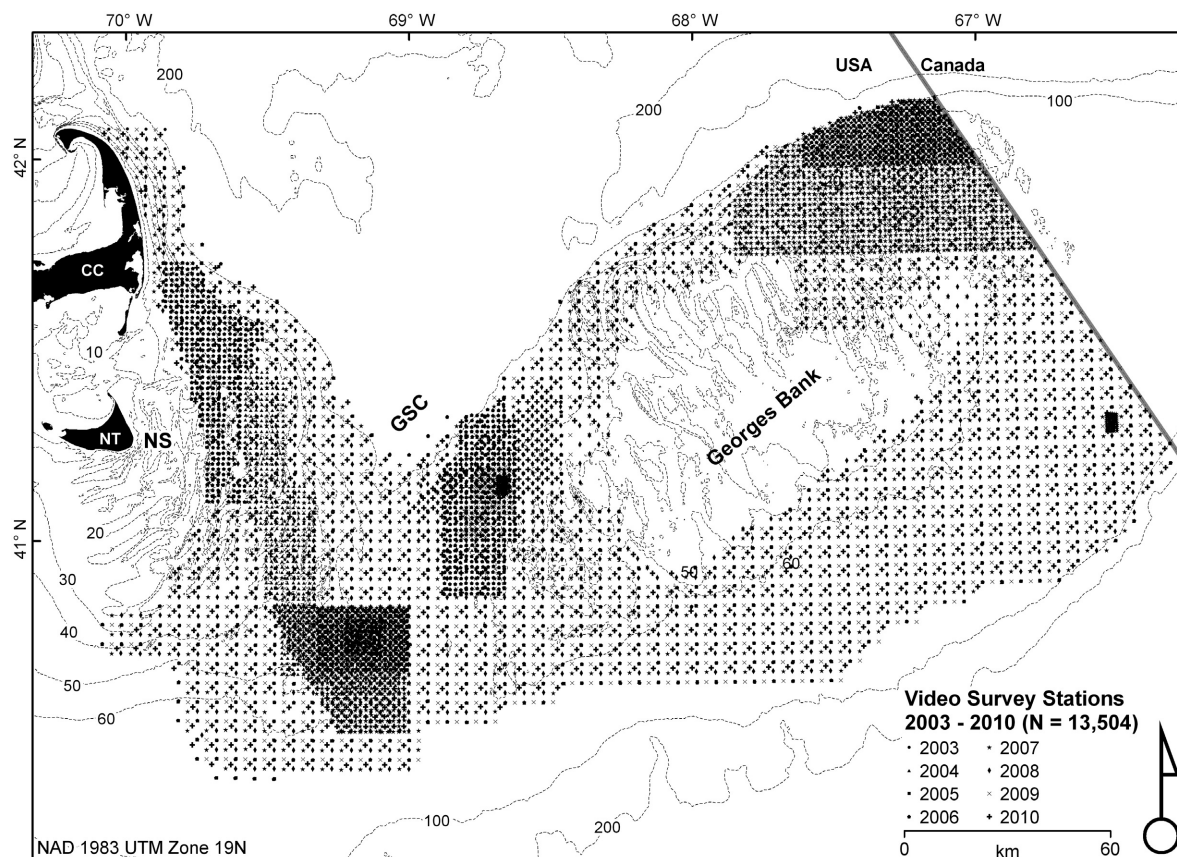

Fig. 1. Scallop video survey stations sampled from 2003 to 2010 (N = 13,504); four 3.24-m^2 quadrats were viewed at each station. The Great South Channel (GSC), Nantucket Shoals (NS), Nantucket Island (NT), and Cape Cod (CC) are provided for spatial reference. The dashed lines indicate depth contours (m).

in each still image were measured using Image-Pro Plus software (Media Cybernetics, Bethesda, Maryland, USA). For survey design and sampling equipment details, see Stokesbury et al. (2016) and Carey and Stokesbury (2011), respectively. Data organization and analyses were conducted using Microsoft Excel v.2013 (Chicago, Illinois, USA), unless otherwise stated.

Between 2003 and 2010, we conducted 61 video survey research cruises on Georges Bank (Fig. 1). The initial survey in 2003 used a 5.5-km station grid covering the U.S. water portion of the Bank from 10 to 100 m depth with the exception of the center and southwestern parts where scallops are rare (Stokesbury et al. 2004). A 5.5-km sampling grid was also used from 2004 to 2010, but additional higher resolution (1- to 1.5-km grid) surveys were conducted in the Great South Channel and on northeastern Georges Bank (Stokesbury et al. 2009). From 2007 to 2010, the 5.5-km sampling grid points were shifted annually to the midpoints of the previous year's grid to decrease the multiyear sampling lag to support habitat mapping (Harris and Stokesbury 2010, Stokesbury et al. 2010, and Harris et al. 2012).

Scallop concentration

The mean scallop concentration (C_a) in each survey station was calculated following Orensanz et al. (1998):

$$C_a = \frac{\sum_{i=1}^{q} n_i^2}{N},$$

where Q = number of quadrats (4) at each station, n_i is the number of scallops in quadrat i, and N is the total number of scallops at the station. Therefore, C_a gives the mean number of scallops experienced by each individual scallop in the four 3.24-m^2 quadrats and thus has units of scallops per scallop (Orensanz et al. 1998). For simplicity, we will give C_a in scallops. The C_a values sampled each year were interpolated to a standard 1-km raster grid using Sibson's natural neighbor method (Sibson 1981, Harris and Stokesbury 2010). The fit of the interpolated annual maps was examined by subtracting the predicted scallop concentration value from the observed data at each station j, to obtain the residual value r_j. Mean r_j, the mean absolute

error (MAE), and the mean squared error (MSE) were calculated for the 2003–2010 C_a raster maps:

$$\text{MAE} = \frac{1}{\text{st}} \sum_{j=1}^{n} |r_j|,$$

$$\text{MSE} = \frac{1}{\text{st}} \sum_{j=1}^{n} |r_j^2|,$$

where st is the number of stations (Zar 1999, see Harris and Stokesbury 2010).

Spatial aggregation

Relative geostatistical aggregation curves were used to construct scallop concentration profiles for each year (Matheron 1981, Orensanz et al. 1998, Petitgas 1998). The curves give the proportion of total scallops $P(z)$, in areas where C_a was greater than z, plotted against the area occupied $T(z)$, by scallop C_a greater than z:

$$P(z) = \sum_{e=1}^{y} \frac{n_e}{N},$$

$$T(z) = \sum_{e=1}^{y} \frac{a_e}{A},$$

where y is the survey year, n_e is the number of scallops in C_a class e, a_e is the area occupied by the scallops in class e, and A is the total area scallops occupied. Area occupied (km^2) was determined by constructing Voronoi polygons of the survey stations sampled in each year (Legendre and Legendre 1998). The $P(z)$ and $T(z)$ vectors were calculated for sequential C_a classes (whole scallops), and the $P(T)$ curves were constructed by sorting C_a classes in descending order (Petitgas 1998).

Each curve's 45° tangent indicates where scallop spatial distribution shifts from dispersed to aggregated (Petitgas 1998). The C_a class corresponding to the 45° tangent is the concentration at which more scallops occur in less area. Following Colloca et al. (2009), the 45° tangent was used to define high concentration. We used the geostatistical aggregation curves to empirically derive this threshold based on station-level mean concentration across the study domain for each year, not the counts of scallops in individual quadrats.

Persistence

We calculated an index of persistence (I_i) for each map grid cell to identify how often cells were classed as high-concentration (Fiorentino

et al. 2003, Colloca et al. 2009). I_i gives the proportion of years that the scallop concentration in cell k (C_{ak}) was classed as high:

$$I_i = \frac{1}{y} \sum\nolimits_{j=1}^{y} \delta_{kj},$$

where y is the total number of years j that cell k was surveyed; $\delta_{ij} = 1$ when C_{ak} is high (>3) in year j; otherwise, $\delta_{ij} = 0$. The index (I_i) ranges from 0 (indicating C_{ak} was never high) to 1 (C_{ak} was always high). We considered cells where C_{ak} was high for at least five of the eight years ($I_i \geq 0.625$) to be persistent high-concentration scallop aggregations (see, e.g., Colloca et al. 2009). Hereafter, we refer to these persistent high-concentration scallop aggregations as scallop aggregations. The scallop aggregations were mapped and the size (km^2) of each was calculated, along with the total proportion (%) of the study area and of scallop habitat (ArcGIS ESRI v.10.1, Redland, California, USA). The total number and density (individuals/km^2) of scallops occupying the aggregations in each year was estimated using methods detailed in Stokesbury et al. (2016).

Habitat conditions

We compared the surficial sediment characteristics, mean water depth, benthic boundary shear stress, and sediment stability conditions in surveyed areas with no scallops in all years and those in scallop habitat ($C_a \geq 1$ in any year) and between scallop habitat and the locations which met our scallop aggregation criteria. Sediment characteristics were extracted from the Harris and Stokesbury (2010) maps of surficial sediment dominance, coarseness, heterogeneity, and maximum type. Sediment areal proportions were calculated for each area and compared with χ^2 tests (Zar 1999). In addition, we examined the degree of spatial correspondence between scallop aggregations and the glacial-lag gravel outcrops mapped by Harris and Stokesbury (2010).

Water depth (z) in the study area was mapped to the 1-km raster grid using 401,793 depth sounding records queried from the U.S. National Ocean Service data portal (www.ngdc.noaa.gov. html) using Sibson's natural neighbor interpolation method (Sibson 1981, ArcGIS ESRI v.10.1, Redland, California, USA). The benthic boundary

shear stress (τ_{0s}), sediment critical shear stress (τ_{cr}), and sediment stability (ξ) conditions in each aggregation were extracted from the maps published by Harris et al. (2012). Mean water depth, τ_{0s}, τ_{cr}, and ξ values in the aggregations and scallop habitat were compared with a two-sample Welch's t-test and the nonparametric Mann-Whitney U-test; post hoc comparisons were made between each aggregation and scallop habitat (Bonferroni-adjusted P-values, Zar 1999; SYSTAT v.12; Systat Software, San Jose, California, USA).

RESULTS

Sampling

A total of 13,504 video survey stations (54,016 quadrats) were used in our scallop concentration analysis (Fig. 1). The annual sampling extent was 30,995 km^2, the mean station lag (distance between stations) for all years was 3.80 km (SD 1.145), and the sampling grain was the quadrat area (3.24 m^2). Mean scallop concentration was calculated for each station, so C_a values reflect the scallops sampled in four quadrats along a drift that averaged 84.7 m^2 (SD 9.25 m^2) in area (for annual sampling scales, see Appendix S1: Table S1). Therefore, the following results give an 8-year perspective of scallop concentration based on the number of individuals counted in four 3.24-m^2 quadrats sampled along ~85-m^2 drifts.

Scallop concentration

Scallops occupied 11,201 km^2 of the study area (scallop habitat) and were observed at 40% of stations with C_a ranging from 1 to 41.2 scallops (Appendix S1: Fig. S1). The distribution of C_a values was highly skewed with about 78% ($\pm$ 8.1%) of scallops occurring at stations where C_a was <4. The median scallop C_a for all years was 1.67 scallops with annual median C_a ranging from 1 in 2003 to 1.86 in 2004. Scallop concentration was patchy, but there were consistent hotspots along the southern and eastern Great South Channel, on the Northern Edge, and on the Southern Flank near the U.S.–Canada boundary (Appendix S1: Fig. S1).

Spatial aggregation

Scallop concentration was spatially aggregated in all years with 41–70% of scallops occurring in
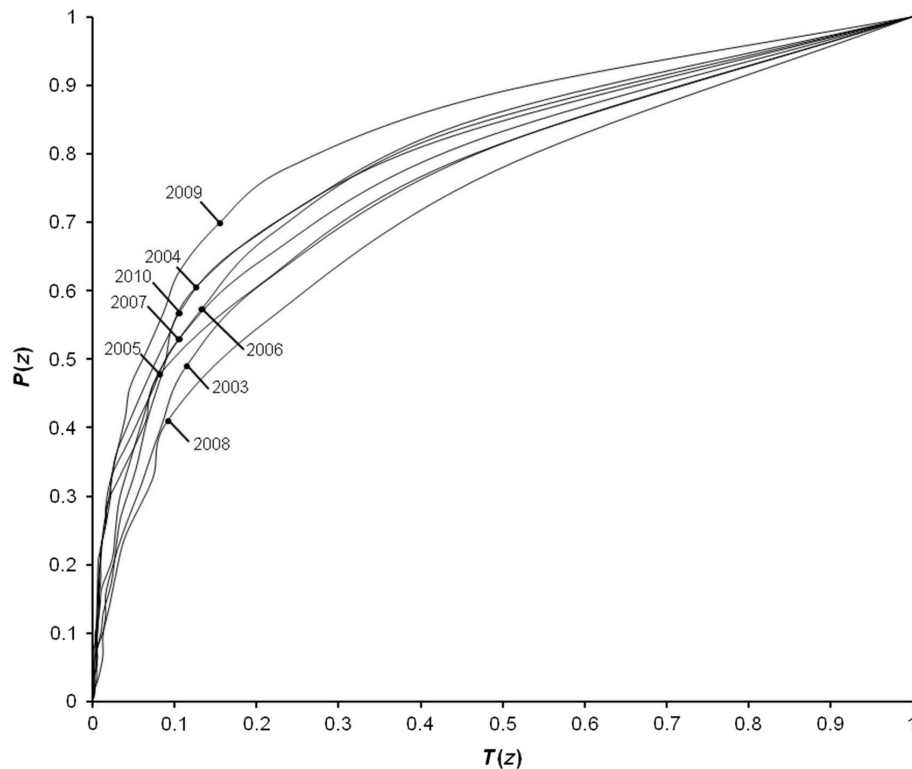
Fig. 2. Geostatistical aggregation curves of scallop concentration (C_a) for Georges Bank from 1999 to 2010. $P(z)$ is the proportion of the total number of scallops in areas where C_a was greater than z, and $T(z)$ is the proportion of the total study area where C_a was greater than z. Solid dots mark the C_a level nearest the 45° tangent to the curve (values are in Table 1).

8–16% of the study area (Fig. 2, Table 1). Surprisingly, every year the C_a value nearest the 45° tangent to the geostatistical aggregation curves was 4 scallops. The angles associated with $C_a = 4$ were

Table 1. The geostatistical aggregation curve tangent angles (θ_{45}) nearest 45°, the corresponding aggregation concentration levels (C_a), and $P(z)$ and $T(z)$ values for each year.

Year	θ_{45}	C_a	$P(z)$	$T(z)$
2003	52	4	0.49	0.12
2004	43	4	0.60	0.13
2005	47	4	0.48	0.08
2006	52	4	0.57	0.13
2007	49	4	0.53	0.11
2008	51	4	0.41	0.09
2009	45	4	0.70	0.16
2010	52	4	0.57	0.11

all slightly >45° (except in 2009), so we used $C_a > 3$ to define high concentration (Table 1). The interpolated C_a maps (Appendix S1: Fig. S1) were good representations of the video survey data; all the mean residual, MAE, and MSE values were near 0 (Appendix S1: Table S2).

Persistence

We identified 13 locations where scallop C_a was >3 for at least five of the eight years surveyed ($I_i \geq 0.625$; Fig. 3). These persistent high-concentration scallop aggregations ranged in size from 7 to 217 km² and occupied 1.5% (449 km²) of the study area; about 4% of scallop habitat (Fig. 4). The aggregations were named using terms common to commercial scallop fishers: from west to east: Nantucket Shoals (NS)-North and Nantucket Shoals-South (NS-N, NS-S); Asia Rip (AR); Nantucket Lightship (NL)-South (NL-S) and Nantucket Lightship-East (NL-E); Hambone (HB)-
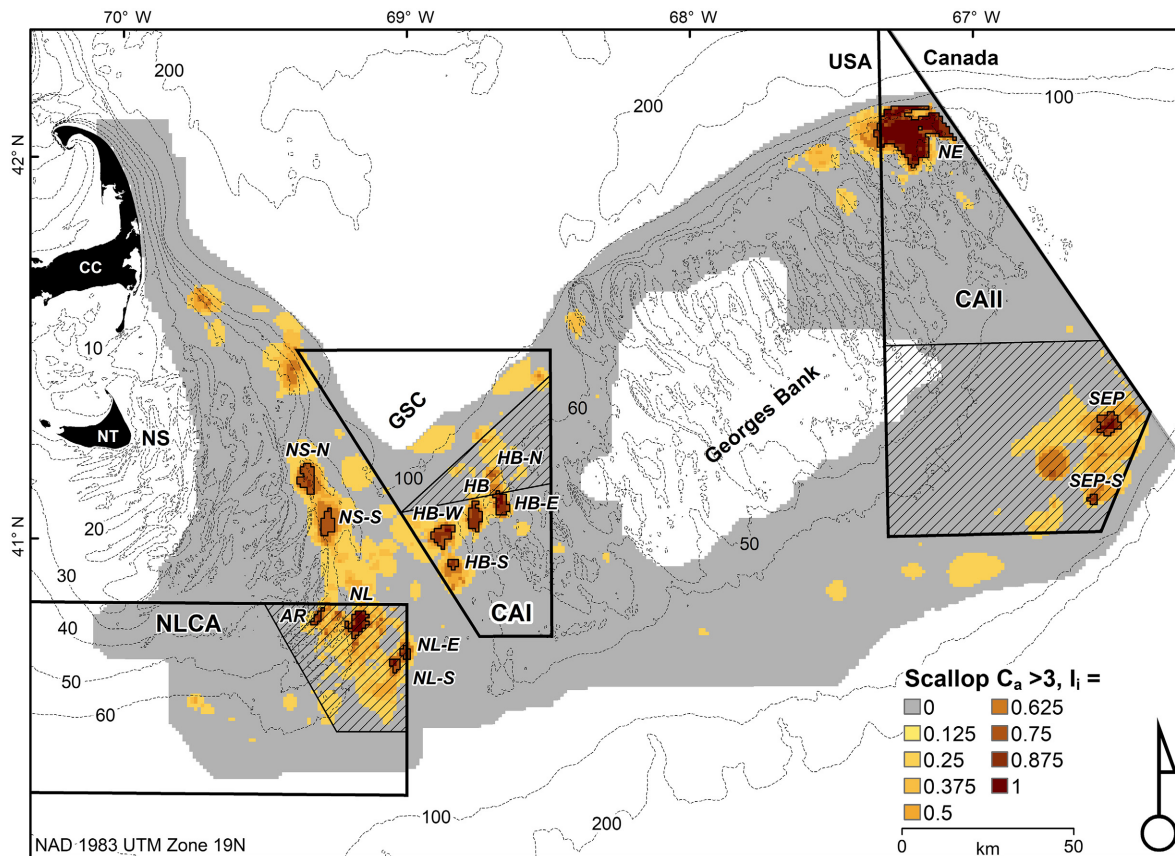
Fig. 3. The persistence (I_i) of locations where $C_a > 3$ scallops. Persistent high-concentration aggregations are outlined in black with abbreviated names. The Great South Channel (GSC), Nantucket Shoals (NS), Nantucket Island (NT), and Cape Cod (CC) are provided for spatial reference. The dashed lines indicate depth contours (m). Nantucket Shoals (NS)-North and Nantucket Shoals-South (NS-N, NS-S); Asia Rip (AR); Nantucket Lightship (NL)-South (NL-S) and Nantucket Lightship-East (NL-E); Hambone (HB)-South (HB-S), Hambone-West (HB-W), and Hambone-East (HB-E); Northern Edge (NE); and Southeast Parts (SEP)-South (SEP-S). The Georges Bank groundfish MPAs including the Nantucket Lightship Closed Area (NLCA), Closed Area I (CAI), and Closed Area II (CAII) are shown with back boundaries; the hashed areas are scallop fishery access zones.

South (HB-S), Hambone-West (HB-W), and Hambone-East (HB-E); Northern Edge (NE); and Southeast Parts (SEP)-South (SEP-S; Fig. 3). The persistence of locations with high scallop concentration ($C_a > 3$) was inversely related to area occupied ($km^2 = 2475.6 \times I_i^{-1636}$, $R^2 = 0.98$; Fig. 3; Appendix S1: Fig. S2).

Between 10.2% and 20.3% (5.5 and 7.7×10^8) of the scallops on Georges Bank occurred in these 13 aggregations, and mean scallop density was 1.38×10^6 km^{-2} (SD = 2.8×10^5; Appendix S1: Fig. S3). Most notable was the NE aggregation, which was 217 km^2 (6–31 times larger than the other aggregations) and contained 5.7–12.0% of all the scallops on Georges Bank, despite being 1.9% of scallop habitat.

Habitat conditions

The sediments in scallop habitat were proportionally coarser and more heterogeneous and contained less mud and sand and more granule–pebble, cobble, and boulder by area compared to areas with no scallops (Fig. 4; Appendix S1: Figs. S4 and S5). While the differences were significant (χ^2 test, $P < 0.0001$), they were relatively small (3–10%). The mean water depth in scallop habitat was 13.1 m deeper than the rest of the study area, shear stress was 1.6 times lower, and the
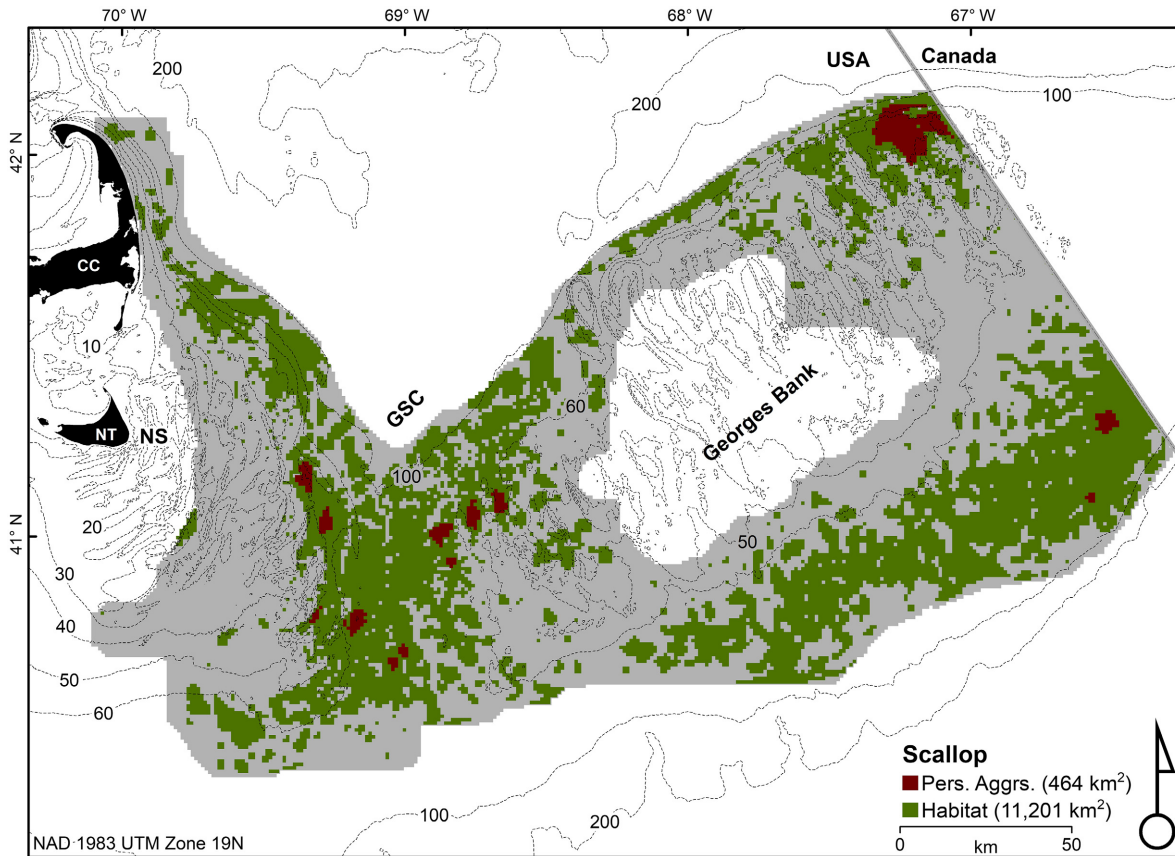
Fig. 4. Map showing scallop habitat ($C_a \geq 1$) in green and the persistent high-concentration aggregations in red. The area shown in gray had no scallops. The Great South Channel (GSC), Nantucket Shoals (NS), Nantucket Island (NT), and Cape Cod (CC) are provided for spatial reference. The dashed lines indicate depth contours (m).

sediment critical shear stress levels were 1.5 times higher. As a result, the seabed in scallop habitat was 2.3 times more stable than the areas of Georges Bank with no scallops (Table 2).

Compared with scallop habitat, the persistent high-concentration aggregations occurred in much coarser, more heterogeneous sediments which contained significantly less sand and more

Table 2. Results of a comparison of the conditions in areas with no scallops and scallop habitat ($C_a > 0$).

Parameters	z (m) Mean (SD)	τ_0 (N/m^2) Mean (SD)	τ_{cr} (N/m^2) Mean (SD)	ξ Mean (SD)
Scallop habitat	69.0 (15.54)	0.56 (0.457)	11.18 (19.732)	0.58 (0.459)
Aggregations	58.9 (12.01)	1.08 (0.486)	30.47 (19.548)	0.20 (0.267)
Difference	10.08 ± 1.15	−0.520 ± 0.046	−19.290 ± 1.849	0.380 ± 0.262
t	17.21	22.28	20.49	28.52
df	510	480.0	485	560
P	<0.0001	<0.0001	<0.0001	<0.0001
U	3.43×10^6	1.0×10^6	9.57×10^5	3.85×10^6
P	<0.0001	<0.0001	<0.0001	<0.0001

Notes: Comparisons were made using Welch's t-statistic and the Mann–Whitney U-statistic. The means, standard deviations (SD), and mean differences in water depth (z), shear stress (τ_0), sediment critical shear stress (τ_{cr}), and stability index (ξ) along with the test statistic and degrees of freedom (df) and P-values (P) are reported.

Table 3. Results of a comparison of the conditions in scallop habitat ($C_a > 0$) and the persistent high-concentration scallop aggregations.

Parameters	z (m) Mean (SD)	τ_0 (N/m^2) Mean (SD)	τ_{cr} (N/m^2) Mean (SD)	ξ Mean (SD)
No scallops	55.4 (20.69)	0.94 (0.711)	8.07 (18.073)	1.34 (1.068)
Scallop habitat	68.9 (15.54)	0.56 (0.457)	11.18 (19.732)	0.58 (0.459)
Difference	-13.60 ± 0.41	0.378 ± 0.013	-3.107 ± 0.446	0.76 ± 0.017
t	65.07	52.48	13.67	86.18
df	28566	30222	21751	28623
P	<0.0001	<0.0001	<0.0001	<0.0001
U	6.15×10^7	1.35×10^8	8.92×10^7	1.61×10^8
P	<0.0001	<0.0001	<0.0001	<0.0001

Notes: Comparisons were made using Welch's *t*-statistic and the Mann–Whitney *U*-statistic. The means, standard deviations (SD), and mean differences in water depth (z), shear stress (τ_0), sediment critical shear stress (τ_{cr}), and stability index (ξ) along with the test statistic and degrees of freedom (df) and *P*-values (*P*) are reported.

granule–pebble and cobble by area (Fig. 4; Appendix S1: Figs. S4 and S6). The differences were significant and ranged from 20 to 50% (χ^2 test, $P < 0.0001$). The aggregations occurred in shallower water (10.1 m) where shear stress forces were 1.9 times higher, but where the sediment critical shear stress was 2.7 times higher owing to larger particles resulting in much more stable seabed compared to scallop habitat (Table 3).

The mean water depth in scallop habitat was 69 m (SD 15.54); all the aggregations except SEP and SEP-S were shallower (HB-S, HB-W, and NL-S were not significant; Fig. 5, Table 3). The mean shear stress in scallop habitat was 0.56 N/m^2 (SD 0.457); all the aggregations except SEP, SEP-S, NL-E, and NL-S had higher shear stress.

The mean sediment critical shear stress level in scallop habitat was 11.18 N/m^2 (SD 19.732); the aggregations all had higher levels except SEP and SEP-S (Fig. 5, Table 3). The critical shear stress levels in the Nantucket Lightship aggregations (NL, NL-S, NL-E) were not significantly different from scallop habitat.

The mean sediment stability (ξ) value for scallop habitat was 0.58 (SD 0.459); the aggregations were all more stable (lower values) although the HB-W, HB-S, and NL-S aggregations were not significantly different from scallop habitat (Fig. 5, Table 3).

The boundaries of the Nantucket Shoals, Asia Rip, Hambone, and the Northern Edge aggregations were all either completely within or closely matched the glacial-lag gravel outcrops mapped by Harris and Stokesbury (2010; Appendix S1: Fig. S7). The NL and NL-S aggregations had partial overlap with the outcrops, but the Southeast Parts aggregations did not.

Discussion

There are about 4 billion scallops occupying Georges Bank and the Great South Channel in local mean concentrations ranging from 1 to 41 scallops per scallop in a 3.24-m^2 neighborhood. Most scallops on the Bank occurred alone or at low concentrations (≤2). High concentrations (>3) occurred in 11% but were only persistent in 4% (449 km^2) of the areas occupied by scallops (scallop habitat). All but two of the 13 persistent high-concentration aggregations we detected occurred on gravel-dominated sediments left by prehistoric glacial retreat and were positioned where benthic boundary shear stresses were two times higher than in scallop habitat. Importantly, owing to their high critical shear stress thresholds, these sediments remain stable even under the high-flow conditions at all 13 aggregations. Despite large changes (e.g., 49%) in total scallop abundance during the study, the median concentration and the area occupied by scallops each year area were stable.

The local scallop spatial structure changed from dispersed to aggregated at concentrations of 3–4 in all eight years of this study regardless of changes in total population abundance. The biological significance of this concentration level is unknown, but our results align with Stokesbury and Himmelman (1993) who found scallops in the Port Daniel Bay, Canada, were locally aggregated with an average of 3 scallops in
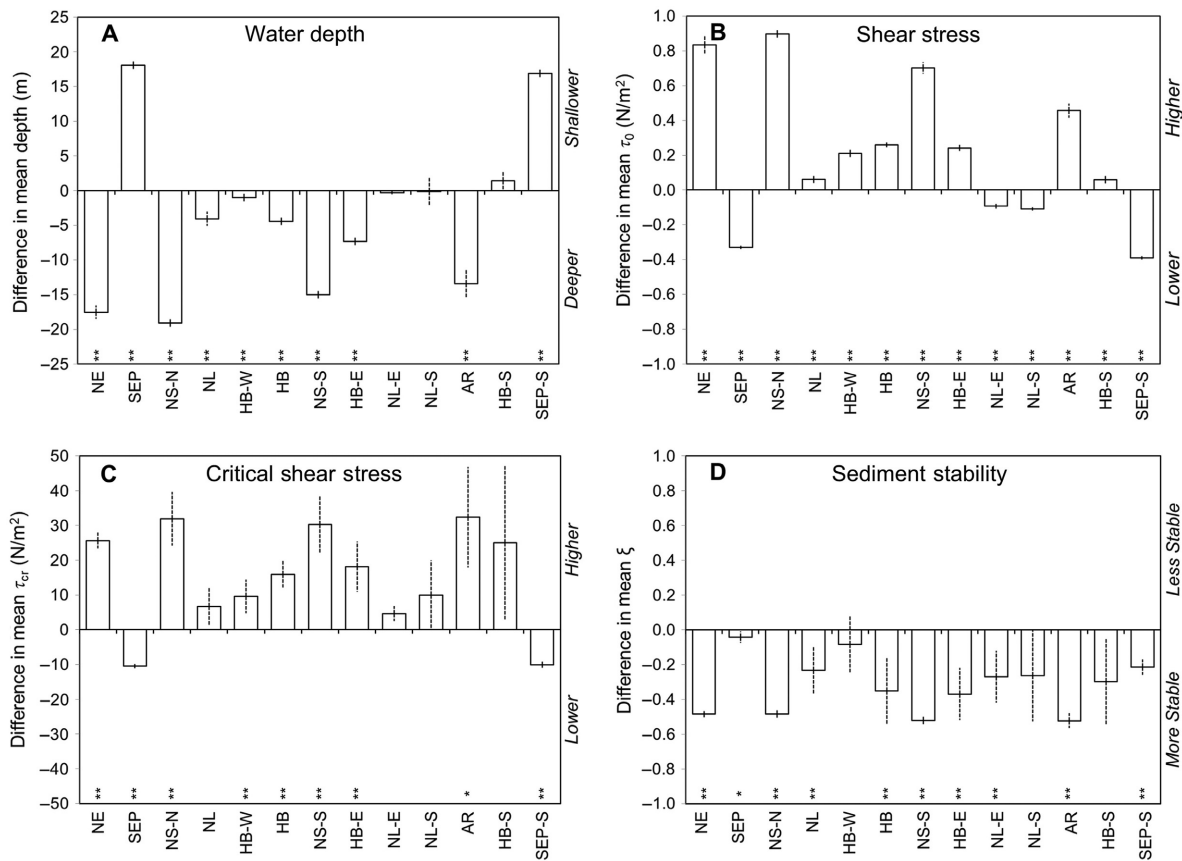
Fig. 5. The differences in mean water depth (z), shear stress (τ_0), critical shear stress (τ_{cr}), and sediment stability index (ξ) between persistent scallop aggregations and scallop habitat. Dashed lines are 95% confidence limits, *indicates the Bonferroni-adjusted P-values ≤ 0.05, and **indicates $P \leq 0.01$.

clumps of 1.13 and 4.5 m². Additionally, Adams et al. (2010) found strong spatial structure at 1.24 scallops/m² ($\sim C_a = 3$–4 scallops; Appendix S1: Table S3) on southwestern and northeastern Georges Bank. Stokesbury and Himmelman (1993) thought local scallop clumping might be due to small-scale movement by individuals to enhance fertilization, while other workers have suggested movements may be to escape predators (e.g., Caddy 1968, Thayer 1972, Peterson et al. 1982).

Juvenile sea scallops can swim short distances (<10 m, Caddy 1989), but swimming ability decreases with size (Stokesbury and Himmelman 1995), so the mechanisms creating persistent high concentrations of scallops at the scale of this study likely include high localized recruitment and/or low localized mortality relative to the rest

of Georges Bank scallop habitat. Despite efforts to explore the spatiotemporal drivers of scallop recruitment (e.g., Tian et al. 2009*a, b, c*), to date no stock–recruitment relationship has been established for scallops on Georges Bank and the spatial patterns in recruitment are unknown (Brand 2006, Hart and Rago 2006, Stokesbury 2012). Along similar lines, the drivers of local mortality such as predation and fishery discards have been explored broadly (e.g., Marino et al. 2009, Stokesbury et al. 2016), but the spatiotemporal patterns of localized mortality are unknown.

The strong inverse relationship between the persistence of locations with high scallop concentration ($C_a > 3$) and area (km²) suggests there may be higher rates of mortality with increasing distance from each aggregation's persistent core

(Fig. 3; Appendix S1: Fig. S2). Mechanisms for improved survival at these locations could be the availability of stable sediments, increased food supply in higher flow (indicated by higher shear stress), and shallower water (Brand 2006). While scallops are ideally shaped for living in high-flow conditions (Gould 1971), many of their predators are not (e.g., lobsters, crabs; Massel 1999, Marino et al. 2009). Therefore, high-shear stress conditions may provide scallops a refuge from predators with less streamlined bodies.

For marine benthic broadcast-spawning organisms such as scallops, the dilution of gametes limits fertilization success (Petersen and Levitan 2001, Gaudette et al. 2006, Bayer et al. 2016). Conversely, in highly fecund species relatively small high-concentration aggregations of adults may serve as population epicenters with the potential to contribute a large proportion of the total zygotes in a population and consequently support a high sustainable exploitation (MacCall 1990, Claereboudt 1999, Walters and Kitchell 2001). Pennington (1985) and Gaudette et al. (2006) demonstrated that sea urchin (*Strongylocentrotus droebachiensis*) fertilization success dropped exponentially with inter-adult distance and was between 1% and 10% at 1 m. To better understand our results in terms of these other studies, we conducted a post hoc simulation to explore the probability that scallops in C_a levels from 2 to 8 in our 3.24-m^2 quadrats have at least one neighbor within distances of 1 m or 2 m. Assuming scallops to each occupy about 10 cm^2, we constructed simulations which randomly assigned scallop locations within a quadrat to generate a distribution of potential neighbor distances (Microsoft Excel v.2013) for each level of concentration. The probability that a scallop would be within 1 or 2 m of another was estimated using 10,000 Monte Carlo simulations assuming replacement (Edgington and Onghena 2007). The *P*-values were calculated in the R statistical programming environment (R Core Team 2016; version 3.2.2) with permp function in the package statmod (Phipson and Smyth 2010). For $C_a = 4$, there was a 94% probability that a scallop would have a neighbor within 1 m and a 99.9% probability of a neighbor within <2 m (Appendix S1: Table S3). This suggests that the persistent high-concentration aggregations we detected are areas with close scallop proximity and therefore have

the potential to contribute large numbers of scallop larvae relative to their area. This potential was demonstrated by Claereboudt (1999) using simulations and more recently by Bayer et al. (2016) using laboratory fertilization trials.

The persistent high-concentration scallop aggregations we mapped have been known by name to members of the U.S. commercial scallop fleet for decades (D. Eilertsen, J. Kendal, *personal communication*). This is the first analysis to define them empirically. Commercial fishers who inspected Fig. 3 verified the existence of the aggregations and told us their names. They also indicated that the scallop concentration hotspots in the northwestern Great South Channel and in the area just north of the NL aggregation, neither of which met our criteria for persistence, were indeed persistent aggregations which had supported high catch-per-unit-effort fishing for decades. Inspection of the Harris and Stokesbury (2010) sediment maps and the shear stress and sediment maps in Harris et al. (2012) shows that these two hotspots probably have similar sediment and flow conditions to the persistent aggregations defined in this analysis.

In 1994, the New England Fisheries Management Council created three large Marine Protected Areas (MPAs) on Georges Bank, USA, to limit fishing mortality on overfished haddock and flounder stocks (Murawski et al. 2000, Fig. 3). Fishing with scallop dredges and all other gears capable of retaining groundfish was initially prohibited in these areas. In subsequent years, scallop fishing was permitted in access zones within the MPAs (Stokesbury et al. 2016). Incidentally, all three MPAs included historically productive scallop fishing grounds which supported pre-closure catches accounting for more than 50% of total U.S. landings (Stokesbury 2002, Stokesbury et al. 2004, Hart and Rago 2006). Six years after closure (2000), the scallop biomass in the MPAs had increased 18-fold (Murawski et al. 2000, Hart et al. 2013). Since 2000, the abundance of scallops inside and outside the MPAs has remained at least 10 times the 1994 level (Stokesbury et al. 2016).

The Georges Bank Groundfish MPAs contain 11 of the 13 persistent aggregations identified in this analysis (Fig. 3). The Asia Rip, Nantucket Lightship, and Southeast Parts aggregations have been subject to periodic fishing due to a rotational harvest strategy which allows scallop fishing in

the access zones. It is possible that the inadvertent closure of these persistent high-concentration aggregations contributed to the subsequent scallop population boom by increasing fertilization success. Scallop fecundity increases with age and size (e.g., eggs = shell height$^{3.7}$; see Langton et al. 1987 and Smith and Rago 2004) and fertilization success increases with increased gamete density (see Bayer et al. 2016) resulting from a number of mechanisms including close proximity of adult scallops. Further, owing to seasonally persistent oceanographic conditions, scallop larvae spawned on Georges Bank may settle just about anywhere else on the Bank or may be transported southwest to the Mid-Atlantic Bight (see Tian et al. 2009*a, b, c*). Hart et al. (2013) suggest that spillover effects might explain the post-MPA increases in scallop abundance. Overlaying the Georges Bank tidal mixing fronts mapped by Hu et al. (2008) on the locations of the persistent high-concentration aggregations we identified revealed that they all lay in line with or between the fall and winter tidal fronts (Appendix S1: Fig. S8). This suggests an oceanographic mechanism for delivery of recruits to and export of larvae from these aggregations. We suggest further work exploring the level of connectivity of among aggregations and with scallop habitat.

Georges Bank total scallop abundance has fluctuated ± 16.3% over the 8-year study period (Stokesbury et al. 2010), and although total area of scallop habitat followed a similar annual trend, it varied only ±6.0% (Fig. 6). Additionally, the similarity in the geostatistical aggregation curves from the years with the lowest (2005) and highest abundances (2003 and 2007) suggests that Georges Bank scallops exhibited a proportional density population structure in which local concentrations change proportional to total scallop abundance while total scallop habitat area (km^2) remains roughly constant from year to year (Fig. 6; Hilborn and Walters 1992, Petitgas 1998). This pattern did not hold for 2008–2009 (Fig. 2). This may be due to three new scallop concentration hotspots in the northeastern Great South Channel in 2009 (see the 2009 map in Appendix S1: Fig. S1). To further explore this, we investigated the quadrat imagery and scallop shell height data sampled at these locations and found large aggregations of juvenile scallops with concentrations >10 and mean shell
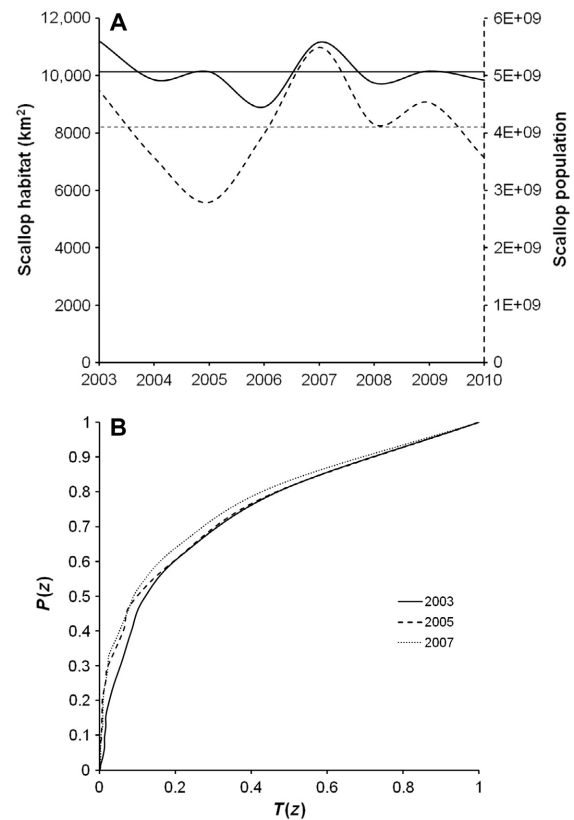

Fig. 6. (A) Mean and annual scallop habitat area (solid lines, left vertical axis, km^2) and mean and annual scallop abundance (dashed lines, right vertical axis) on Georges Bank from 2003 to 2010. (B) $P(T)$ curves from the years with highest (2003, 2007) and lowest (2005) abundances. Both plots suggest a proportional density population structure.

height = 56.3 mm (SD 12.92, N = 193). It is notable that only two of these areas persisted to 2010 and that the C_a in both had already dropped to ~2 scallops per scallop.

Conclusions

Important intra- and inter-specific processes driving spatiotemporal distributions (e.g., spawning, feeding, and predator–prey interactions) occur in local neighborhoods of individuals. These processes are often invoked in the literature but seldom investigated at scales supporting regional inference (Orensanz et al. 2016). This work demonstrates that counting individuals in fixed neighborhoods via video quadrats at

the continental shelf scale is plausible and supports the exploration of species concentrations in local neighborhoods leading to improved understanding of the relationships between their spatiotemporal distributions and local environmental conditions. Elucidation of these relationships and our consequent understanding of scallop proximity and aggregation persistence are critical for a deeper understanding of population-level processes (Orensanz et al. 2016, cf. Fogarty and Botsford 2006).

Sea scallops are a highly valued commercial species, and the influences of environmental factors on their spatiotemporal distributions have been the subject of many scientific investigations (see Orensanz et al. 2016). However, the pervasive use of modified fishing gears (dredges in the case of scallops) to generate most of the scallop density estimates reported in the literature may have obscured the strong spatiotemporal signals detected in this study. By sampling the scallops on Georges Bank at the scale of individuals for eight consecutive years, we successfully described and mapped the spatial distribution of local scallop concentration. This revealed that of the roughly 4 billion scallops inhabiting Georges Bank annually, most live alone or in low concentrations. Only 4% of scallop habitat supported persistent high-concentration aggregations which occurred on outcrops of gravel–cobble sediments where benthic boundary shear stresses were high. It is plausible that the persistent high-concentration aggregations may be among the few places where scallops on Georges Bank have life-cycle closure on a consistent basis and therefore strongly influence trends in total scallop abundance. This aligns with Sinclair's (1988) member–vagrant hypothesis and Orensanz's ideas about shellfish metapopulations (Orensanz et al. 2016). In addition, it is also possible that the spatial management actions aimed at rebuilding groundfish stocks ultimately served to increase scallop concentrations in key aggregations and thereby influenced the temporal frequency of extreme recruitment events observed in recent years (see Bethoney et al. 2016). Work investigating the role of persistent high-concentration aggregations on scallop recruitment, mortality, and reproductive dynamics is warranted. Further, the influences of sediment stability, and of natural disturbance in general, in shaping spatiotemporal distributions and dynamics of benthic marine populations is a promising area of future study. Finally, the spatiotemporal structure we detected likely has important implications for the design of sea scallop abundance surveys and the assumptions underlying current stock assessment methods; these should be investigated.

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