

Spatio-temporal variations of sea star *Asterias* spp. distributions between sea scallop *Placopecten magellanicus* beds on Georges Bank

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ABSTRACT: Presently 80 % of the biomass of sea scallop *Placopecten magellanicus* on Georges Bank is located within 3 large areas closed to fisheries. Sea stars *Asterias* spp., primary predators of scallops, are also aggregated within these closed areas. As prey becomes depleted within one scallop bed, sea stars may move to another food source, possibly to another scallop bed. We tested the hypothesis that sea star aggregations moved from one scallop bed to another within the Nantucket Lightship Closed Area (NLCA) on Georges Bank. We video surveyed 204 stations in the NLCA from 1999 to 2006 using a 1.57 km grid-centric systematic sampling design. The center of sea star abundance was calculated by averaging the sea star frequency-weighted latitude and longitude for all stations. Using multivariate analysis of variance and all-pairs comparisons (Hotelling's T^2), shifts in the center of sea star abundance were determined by assessing if the locations of the 2 aggregations were different. The sea star center of abundance, standard ellipse and 95 % confidence ellipse were superimposed on the scallop density distribution maps to determine the spatial overlap. The distributions of sea star aggregations in the NLCA significantly shifted between consecutive years from 1999 to 2006 and overlapped with areas of high densities of scallops. Shifts in the center of abundance reflect changes in distribution possibly resulting from movement, recruitment and mortality. As sea stars aggregate in these areas presumably due to high abundances of scallops, sea star movement between the scallop beds may increase natural mortality rates of the scallop population on Georges Bank.

KEY WORDS: *Asterias* spp. · Distribution patterns · *Placopecten magellanicus* · Predator–prey relationship · Spatiotemporal information

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INTRODUCTION

Georges Bank contains the world's largest natural sea scallop *Placopecten magellanicus* resource (Caddy 1989). Sea scallops are aggregated into 3 large grounds; each is made up of several scallop beds, areas with higher sea scallop densities than adjacent areas (Caddy 1989, Brand 2006, Orensanz et al. 2006). In 1994, 3 large areas of Georges Bank were closed to all mobile fishing gear in an effort to protect declining groundfish stocks (Murawski et al. 2000). These closed areas partitioned the historic scallop grounds and presently contain >80 % of the Georges Bank sea

scallop resource (Stokesbury 2002, Stokesbury et al. 2004).

Sea stars *Asterias* spp. are a primary predator in bivalve-dominated benthic communities, including sea scallop grounds (Dickie & Medcof 1963, Menge 1982, Stokesbury & Himmelman 1995). Sea stars on Georges Bank have a 'contagious' (aggregated) distribution with higher densities in the closed areas, which may influence densities of sea scallop prey (Marino et al. 2007).

The most frequent activity of sea stars is foraging (Barbeau & Scheibling 1994c, Himmelman et al. 2005). Sea stars move slowly in search of food or to avoid physical stress (Feder & Moller-Christensen 1966,

Sloan & Campbell 1982). Sea stars are non-visual predators that search for food using distance chemoreception or by relying on chance encounters (Dickie & Medcof 1963, Sloan & Campbell 1982, Barbeau and Scheibling 1994b,c). How well the sea star detects food with chemoreception seems to vary depending on the direction of water movement relative to the prey and predator, and the intensity and concentration of the perceptible matter released by the prey (Smith 1940, Feder & Moller-Christensen 1966). Most movements consist of random wandering that is modified when food is very close (Dickie & Medcof 1963, Feder & Moller-Christensen 1966).

Sea star aggregations and migrations are created by the summation of individual reactions to environmental stimuli, especially feeding (Sloan 1980). Sloan (1984) indicated that most sea stars, as responsive opportunistic predators, will aggregate on superabundant food sources (Menge 1972, 1982, Sloan 1980, Christie 1983). Local food limitation increased sea star searching activity associated with these migrations and aggregations (Sloan 1980).

Sea stars, including those common on Georges Bank (*Leptasterias polaris*, *Asterias vulgaris* and *A. forbesi*), prey on a resource until it is depleted and then move on in search of new prey sites (Sloan 1980, Dare 1982, Gaymer et al. 2001, Gaymer & Himmelman 2002). We hypothesized that sea star aggregations move from one scallop bed to another on Georges Bank in closed areas. To test the hypothesis, we first determined if sea star distributions were shifting and then examined whether these distributions and shifts overlapped sea scallop distributions. Sea scallop and sea star densities and spatial distribution (on scales of meters [density] and kilometers [spatial distribution]) were measured using video survey techniques in the Nantucket Lightship Closed Area (NLCA) from 1999 to 2006.

MATERIALS AND METHODS

From 1999 to 2006, areas of high sea scallop densities, identified by New Bedford scallop fishers and literature searches, were video-surveyed, particularly within the 3 closed areas on Georges Bank (Stokesbury 2002, Stokesbury et al. 2004). The video survey was primarily designed to examine the distribution and abundance of sea scallops (Stokesbury 2002, Stokesbury et al. 2004). A secondary goal of the video sur-

vey was to observe the distribution and abundances of other macroinvertebrates, including sea stars. To test our hypothesis, we used the NLCA, as it was the only area that was continuously sampled over this time period, except during 2003 (Fig. 1).

Survey stations were positioned using a centric systematic design, as the design is simple and samples evenly across the entire survey area (Hilborn & Walters 1992, Krebs 1999, Stokesbury 2002). A total of 204 video stations were sampled on a grid with 1.57 km between stations (Stokesbury 2002) (Fig. 1). The precision (coefficient of variation) of this survey design ranged from 5 to 15% for the normal and negative binomial distributions, respectively, for sea scallop densities assessed in the NLCA in 1999 (Stokesbury 2002).

A video sampling pyramid (described in Stokesbury 2002, Stokesbury et al. 2004) was deployed from scallop fishing vessels. Two downward-looking DeepSea Power & Light® multi-Seacam underwater cameras and up to 9 DeepSea Power & Light® multi-Sealite 100 W lights provided 3.2 and 0.8 m² (nested within the 3.2 m²) views of the sea floor; however, only the data from the 3.2 m² view were used in the analysis. It was possible to identify sea scallops and sea stars to a minimum size of about 20 mm, and all individuals were counted, including those that were only partially visible along the edge of the quadrat image. Four quadrats were observed at each station which increased the sample area to 12.94 m².

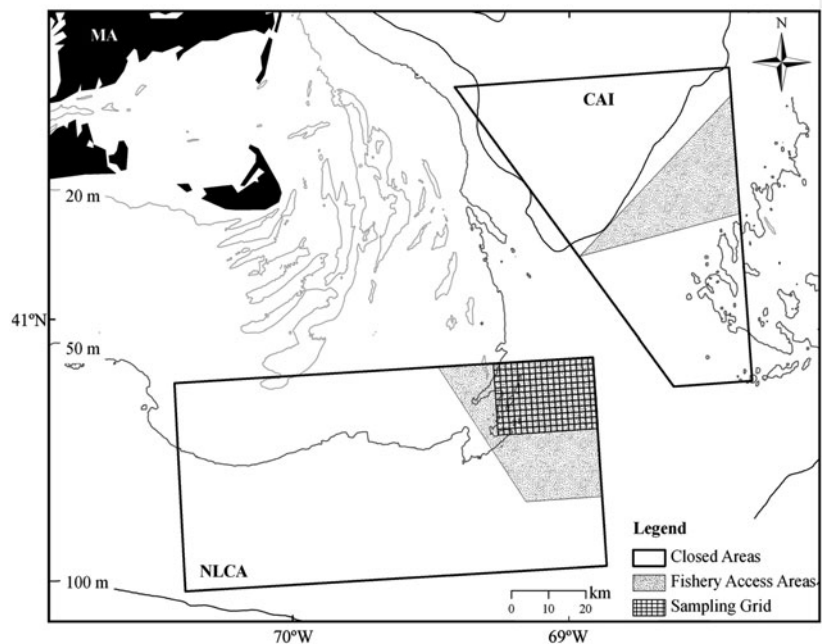


Fig. 1. Georges Bank, showing the Nantucket Lightship Closed Area (NLCA) and the video survey grid (1.57 km intervals) within the NLCA, which was sampled from 1999 to 2006. Both the NLCA and Closed Area I (CAI) have been closed to all mobile fishing gear since 1994, but limited access fisheries have been allowed within portions of these areas (shaded)

Video footage of the sea floor was recorded on S-VHS tapes and DVDs. A mobile studio, including monitors and S-VHS video and DVD recorders for each live camera, a monitor for the Captain controlling the vessel's hydraulic winches that deploy the pyramid, a laptop computer with Arcpad GIS[®] software integrated with a differential GPS and Wide Area Augmentation System receiver, and a laptop computer for data entry, was assembled in the wheelhouse. The survey grid was plotted prior to the cruise in Arcpad GIS[®]. For each quadrat, we recorded the time, depth, latitude and longitude, number of scallops and clappers (scallops that died of natural causes), substrate and the presence of other macroinvertebrates (including sea stars).

After each survey the videotapes were reviewed in the laboratory and a still image of each quadrat was digitized and saved using Image Pro Plus[®] software (TIFF file format). Counts of sea stars and sea scallops were standardized to individuals per square meter. Mean densities (ind. m⁻²) and SE of macroinvertebrates were calculated using equations for a 2-stage sampling design (Cochran 1977, Stokesbury 2002).

The sea stars *Asterias vulgaris* (= *A. rubens*, Franz et al. 1981) and *A. forbesi* are sympatric species on Georges Bank and the feeding ecology and movement of both species are similar (Feder & Moller-Christensen 1966). We could not reliably differentiate between *A. vulgaris* and *A. forbesi* (hereafter referred to as *Asterias* spp.) in the video images (Marino et al. 2007).

The center of sea star abundance was calculated as the average latitude and longitude of all stations, weighted by the observed frequency of sea stars. The difference between the average latitude and the longitude from one year to the next is a bivariate quantity (Batschelet 1981). Five statistics, the sample means and SD of *X* (latitude) and *Y* (longitude) and a correlation coefficient, are required to represent bivariate data as an ellipse (Batschelet 1981). Ellipses were used to describe the central tendency and orientation of the sea star distributions. The standard ellipse was used as

a descriptive tool to visualize the variability of the data. To statistically compare the aggregations from year to year, 95% confidence ellipses, regions that cover the population center with a 95% probability, were calculated (Table 1) (Batschelet 1981). The average center of abundance and 95% confidence ellipse based on the average for each year were plotted for temporal comparisons. Overlapping confidence ellipses represent similar centers of abundance from one year to the next, indicating a stationary aggregation.

A multivariate analysis of variance (MANOVA) and all-pairs comparisons (Hotelling's T^2) were used to determine whether the centers of abundance (average latitude and average longitude) significantly differed between years (Zar 1999). The null hypothesis of the MANOVA is that the centers of abundance are equal. Transformations did not normalize the data; therefore the raw data were used, as departures from normality have only a slight affect on the Type I error rate using MANOVA (Zar 1999, Anderson 2003).

We examined the spatial overlap between sea stars and sea scallops on a macroscale (study area subpopulation; 10s to 100s of km) using Hotelling's 2-sample T^2 tests. Hotelling's 2-sample T^2 tests were used to determine whether the sea star and sea scallop centers of abundance significantly differed (Batschelet 1981). Transformations did not normalize the data; therefore, the raw data were used in the Hotelling's 2-sample tests, which are robust to departures from normality, because sample sizes were large (Everitt 1979, Anderson 2003). Despite differences in scale, we were interested in the spatial overlap of the sea star center of abundance and sea scallops on the mesoscale (scallop beds; 10s of km), so we compared the distributions using visual inspection, superimposing the average sea star center of abundance, standard ellipse and 95% confidence ellipse on the sea scallop density distribution maps. Distributions of sea stars and sea scallops (m⁻²) were plotted using ESRI[®] ArcGIS software. MANOVA and Hotelling's 2-sample T^2 tests were calculated using Systat 11 (SYSTAT Software).

Table 1. Bivariate sea star sample statistics (sample size, average latitude [lat], longitude [long], SD, covariance [COV] and correlation coefficient [r]) collected using a systematic multistage video survey in the Nantucket Lightship Closed Area (NLCA). During 2006, the NLCA was surveyed in June and August

Year	Month	n	Avg lat (°N)	Avg long (°W)	Lat SD	Long SD	COV	r
1999	July	857	40.7267	-69.1143	0.0413	0.0711	-0.001	-0.217
2000	August	319	40.7495	-69.1276	0.0455	0.0835	0.000	0.081
2001	July	746	40.7404	-69.1057	0.0464	0.0680	0.000	0.000
2002	July	1137	40.7274	-69.1204	0.0445	0.0717	-0.001	-0.185
2004	May	674	40.7214	-69.1258	0.0454	0.0683	0.000	-0.114
2005	October	494	40.7306	-69.1278	0.0492	0.0718	-0.001	-0.219
2006	June	527	40.7328	-69.1055	0.0459	0.0676	-0.001	-0.164
2006	August	1786	40.7423	-69.1428	0.0495	0.0895	-0.001	-0.302

RESULTS

Sea star distributions were aggregated in the NLCA sample area with the highest densities occurring in the southeast corner from 1999 to 2006 (Fig. 2). Sea star aggregations shifted their positions between years from 1999 to 2006 as the 95% confidence ellipses were generally separate (Fig. 3), although

there was some overlap between 2002–2004 and 2004–2005. These annual shifts, and a bimonthly shift in 2006, between centers of sea star aggregations were all significantly different (MANOVA, Pillai's Trace, $F_{14,13066} = 27.63$, $p < 0.001$). Planned multiple comparison tests indicated that all chronological shifts were significantly different (Hotelling's 2-sample T^2 statistic; Table 2).

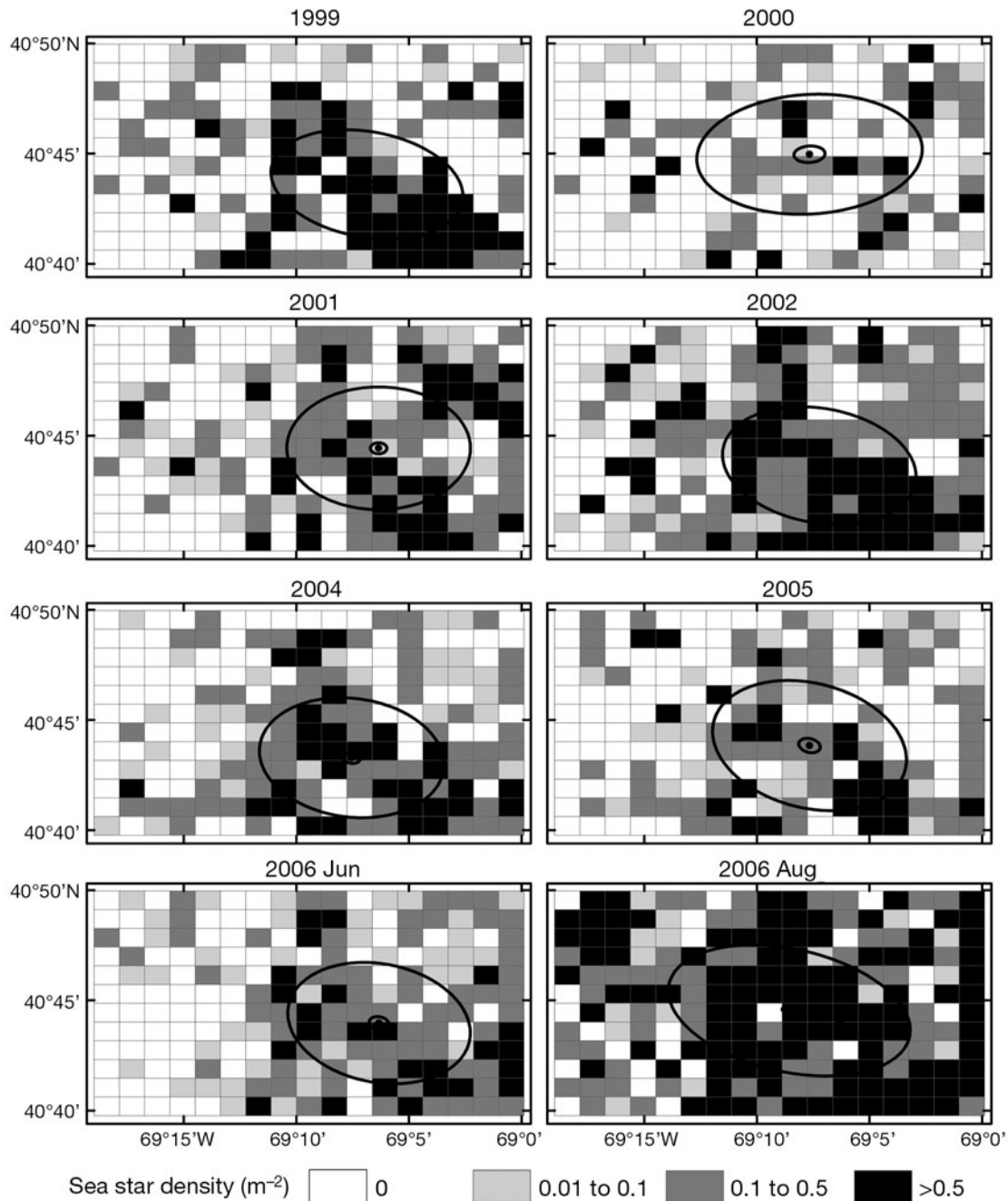


Fig. 2. *Asterias* spp. Sea star standard (outer ellipse) and 95% confidence ellipse (inner ellipse) overlaid on the sea star density (sea stars m^{-2}) distribution maps in the Nantucket Lightship Closed Area (NLCA) sample area observed during the video survey from 1999 to 2006, with the exception of 2003. During 2006, the NLCA was surveyed in June and August

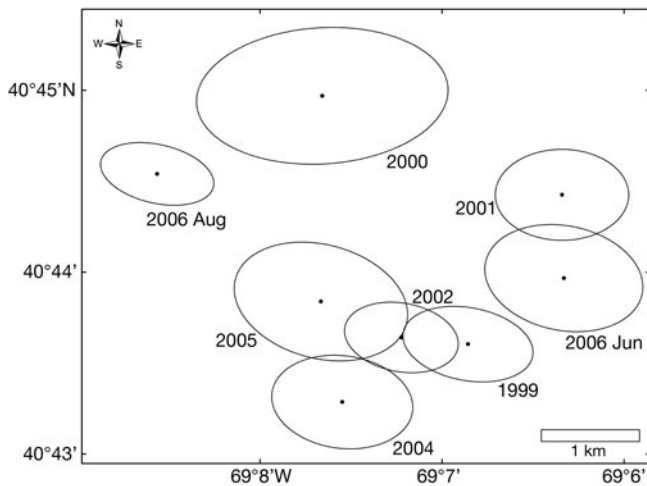


Fig. 3. *Asterias* spp. Average center of sea star abundance and 95 % confidence ellipses observed in the Nantucket Lightship Closed Area (NLCA) sample area from 1999 to 2006, with the exception of 2003. Note difference in scale from previous and subsequent figures

The highest densities of scallops in the NLCA sample area from 1999 to 2006 occurred in the middle and southeast portions of the survey area, with the beds elongated north to south (Stokesbury 2002) (Fig. 4). The spatial overlap between the sea star and sea scallop centers of abundance were significantly different in each of the years surveyed (Hotelling's 2-sample T^2 statistic; Table 3); however, finer scale analysis detected interesting patterns (see below, this section) associated with areas of high scallop abundance.

In 1999, the center of the sea star aggregation was observed east of the high density scallop bed, with the standard ellipse overlapping with the high density of scallops in the center of the NLCA sample area (Fig. 4). The center of sea star abundance shifted 2930 m to the

Table 2. Multiple analysis of variance pairwise comparisons (Hotelling's 2-sample tests) used to determine whether the centers of the 2 consecutively surveyed samples of sea stars within the Nantucket Lightship Closed Area (NLCA) deviated significantly from each other. J: June; A: August

Comparison	df	Hotelling's T^2	p	Distance (m)
1999 vs. 2000	1173	57.66	<0.001	2929.6
2000 vs. 2001	1062	23.03	<0.001	2637.4
2001 vs. 2002	1880	64.00	<0.001	2184.8
2002 vs. 2004	1808	10.88	0.004	890.7
2004 vs. 2005	1165	11.30	0.004	1045.7
2005 vs. 2006 (J)	1018	24.29	<0.001	2481.4
2006 (J) vs. 2006 (A)	2310	101.90	<0.001	4268.6

Table 3. Hotelling's 2-sample tests used to determine whether the sea star and sea scallop centers of abundance within each year in the Nantucket Lightship Closed Area (NLCA) deviated significantly from each other. J: June; A: August

Comparison	df	Hotelling's T^2	p
1999	1864	466.33	<0.001
2000	1370	59.85	<0.001
2001	2377	171.43	<0.001
2002	3295	164.22	<0.001
2004	3245	57.84	<0.001
2005	1479	54.06	<0.001
2006 (J)	1734	109.80	<0.001
2006 (A)	3337	107.06	<0.001

northwest by August of 2000, towards the high density sea scallop bed and the standard ellipse covered a large portion of the sea scallop bed.

The sea star center of abundance shifted 2637 m east from 2000 to 2001, with the center of the aggregation and standard ellipse overlapping with the highest densities of scallops in the eastern scallop bed.

The eastern scallop bed became more defined as sea scallop densities increased in the eastern portion of the NLCA sample area from 2001 to 2002 (Fig. 4). By 2002, the center of sea star abundance shifted back 2185 m to the southwest, similar to the location of the center of the aggregation in 1999, overlapping with high densities of sea scallops. The standard ellipse in 2002 completely overlapped with the high density sea scallop beds in the south-central portion of the NLCA sample area.

The scallop beds in the central and eastern portions of the NLCA sample area continued to expand from 2002 to 2004 to form one continuous bed elongated from north to southeast (Fig. 4). Sea star distributions shifted 891 m southwest, but the center of abundance remained in the high density bed of scallops.

Scallop density in the NLCA sample area declined by 50% between 2004 and 2005, resulting in the contraction of the central scallop bed (Stokesbury et al. 2007) (Fig. 4). The center of sea star abundance shifted 1046 m north towards the high density scallop bed and the standard ellipse included this scallop bed in 2005.

From 2005 to June 2006, scallop densities increased in the central portion of the NLCA sample area, followed by a decrease in August 2006 corresponding to the limited access fishery in this area between June and August (Fig. 4). Sea star distributions shifted away from the scallop bed to the east 2481 m by June 2006. However, sea star distributions shifted 4269 m back to the west by August 2006. In both June and August, sea star standard ellipses overlapped with large portions of the central scallop bed.

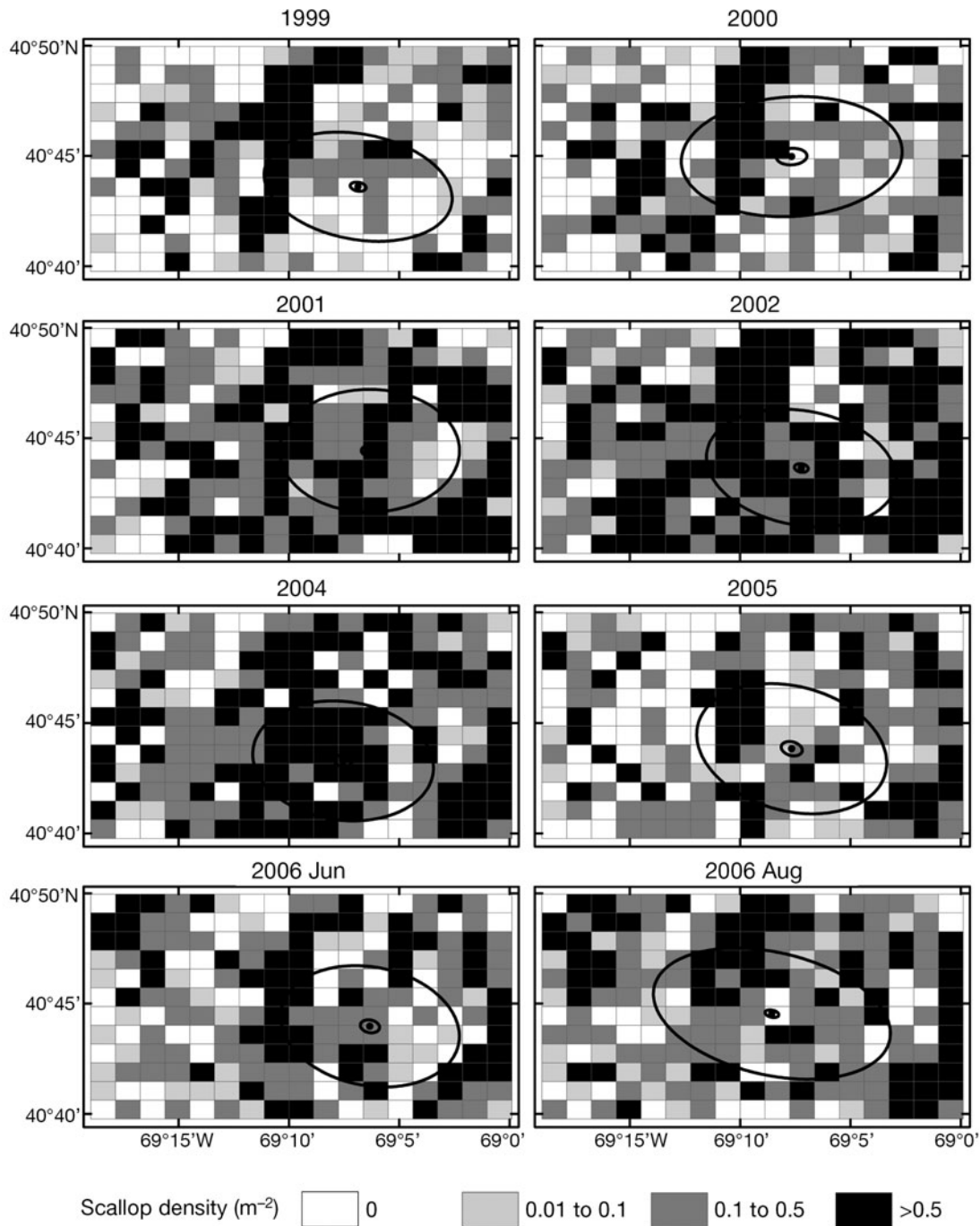


Fig. 4. *Asterias* spp. and *Placopecten magellanicus*. Sea star standard (outer ellipse) and 95% confidence ellipse (inner ellipse) overlaid on the sea scallop density (scallops m^{-2}) distribution maps in the Nantucket Lightship Closed Area (NLCA) sample area from 1999 to 2006, with the exception of 2003

DISCUSSION

Our data support the hypothesis that sea star aggregations moved from one scallop aggregation to another within the NLCA sample area on Georges Bank. Sea star 95% mean confidence ellipses and Hotelling's 2-

sample T^2 tests indicated sea star distributions shifted (average of 2348 m) in year-to-year comparisons. Sea star distributions generally overlapped with areas of high densities of sea scallops. Shifts in the center of abundance reflect changes in distribution possibly resulting from movement, recruitment and mortality.

Changes in sea star density related to recruitment and natural disturbances can influence the distribution and observed shifts in the center of abundance. Studies on *Asterias vulgaris* (= *A. rubens*) in the Woods Hole region and southwest coast of the United Kingdom indicate that peak gonadal development occurs from May to early July (Lillie 1941, Vevers 1949, Barker & Nichols 1983). The planktotrophic pelagic life lasts about 90 d, suggesting a settlement on Georges Bank from August to early October (Barker & Nichols 1983). Balch & Scheibling (2000) observed a similar settlement of *Asterias* spp. between late July and early October along the coast of Nova Scotia. Settlement of new recruits may influence the distribution of sea stars by increasing their density. Natural disturbances, such as severe storms, can also influence sea star distributions, since natural disturbances can alter the substrate and decrease the number of sea stars (Butman 1987a,b, Stokesbury & Harris 2006, Marino et al. 2007).

Sea stars in the wild can travel 100s of m in 1 yr individually and as a group (Smith 1940, Dare 1982). Smith (1940) stained sea stars *Asterias vulgaris* and observed an individual sea star traveled a maximum distance of 200 m in 4 mo, with an average distance of ca. 20 m over 4 mo for the rest of the sea stars studied. Dare (1982) observed a large swarm of sea stars *A. rubens* traveled 200 m in 1 mo and 700 m in 3 mo. Based on behavioral studies, combining the average searching time ($19.9 \pm 6.2\%$ of time budget) and an average movement velocity of 4.5 cm min^{-1} would equate to an average of 4642 m yr^{-1} per sea star (Barbeau & Scheibling 1994b,c). These estimates may be high, as experiments were conducted in aquaria. A more conservative estimate, based on *in situ* observations with a mean movement velocity of $1.1 \pm 0.1 \text{ cm min}^{-1}$ (Barbeau & Scheibling 1994a), would equate to an average of 1135 m yr^{-1} per sea star.

These distances (Smith 1940, Dare 1982, Barbeau & Scheibling 1994b,c) are comparable to those shifts we observed in the center of sea star abundance in the NLCA on Georges Bank, which ranged from 891 to 4269 m in year-to-year comparisons. However, the farthest shift (4269 m), which occurred between June and August 2006, was unrealistic within a 3 mo period, but it may be explained by a redistribution of the sea stars associated with the pulse fishery during this time period (Ramsay et al. 1998, Marino et al. 2007). This shift was also associated with a mean (\pm SE) sea star density increase from 0.20 ± 0.019 to 0.68 ± 0.048 sea stars m^{-2} (Fig. 5), suggesting a recruitment event.

Spatial patterns of sea star aggregations may have influenced the survivorship of settling scallops. Scallop densities increased in the NLCA sample area from 1999 to 2002, indicating recruitment into the area. The center of sea star abundance shifted during this period, but

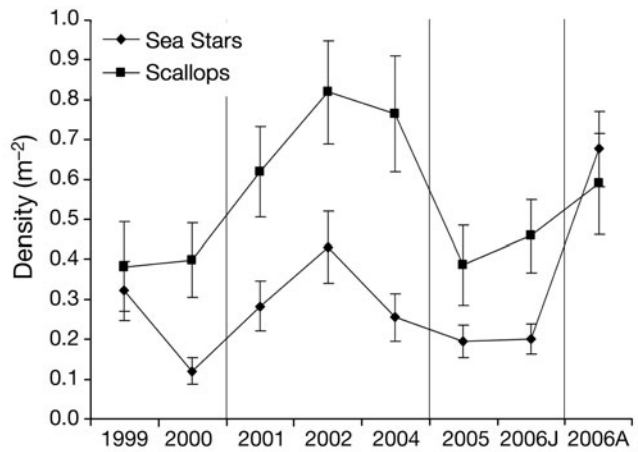


Fig. 5. *Asterias* spp. and *Placopecten magellanicus*. Average ($\pm 95\%$ CI) sea star and sea scallop densities in the Nantucket Lightship Closed Area (NLCA) sample area surveyed from 1999 to 2006, with the exception of 2003. Vertical lines: limited access sea scallop fisheries. J: June; A: August

the center of the sea star aggregation stayed in the area of increasing scallop densities, suggesting sea stars remained in the areas where scallops recruited. This may explain the low recruitment in this area (Stokesbury 2002, Stokesbury et al. 2004), as juvenile scallops are highly vulnerable to sea star predation (Barbeau et al. 1996). Although sea star predation could not explain the mass mortality event that occurred from 2004 to 2005, as average sea star arm length in this area was relatively small compared to scallop shell heights (Stokesbury et al. 2007), there was not enough recruitment to replace the mass mortality which may be related to the sea star movement and predation.

Sea stars respond rapidly to short-term changes in feeding conditions (Menge 1972, Anger et al. 1977, Barbeau & Scheibling 1994b, Barbeau et al. 1996) and are capable of assimilating large quantities of food, if available (Feder & Moller-Christensen 1966). For example, *Asterias rubens* increases feeding activity in the presence of enhanced food availability (Sloan 1984), and Caddy (1989) observed sea stars aggregating, presumably in response to olfactory stimuli, on high-density patches of scallops.

Sea stars swarm and form efficient feeding aggregations in bivalve communities in many contexts. Volkov et al. (1983) observed sea star aggregations following dispersing aggregations of seeded scallops. Dare (1982) concluded that large, dense aggregations of *Asterias rubens* are highly-efficient predators, which can have catastrophic impacts on local bivalve fisheries. Dare (1982) observed the seasonal swarming behavior of *A. rubens*, with densities up to 300–400 sea stars m^{-2} traveling up to 300 m in 2 mo, totally clearing

0.5 km² of seed mussels (equivalent to 3900 to 4900 t). Brun (1968) observed sea star aggregations feeding on beds of Icelandic scallops *Chlamys islandica*: the extreme densities of sea stars were observed in a band-like formation (10 m wide by 100 m long) devouring all scallops in its path. Stokesbury et al. (2004) observed a similar aggregation of sea stars, possibly responsible for a mass mortality (>25% of population) of sea scallops in the southern portion of Closed Area II. These observations along with the present study indicate sea star aggregations may be moving through the area in a feeding front (Lauzon-Guay et al. 2008). However, this hypothesis requires further analysis on a larger spatial and temporal scale.

The use of a species' center of abundance as a metric for examining population shifts and/or movements is rare. Previous studies have used the center of abundance (also referred to as centroid or center of gravity), but few have statistically tested the spatio-temporal patterns (Kendall & Picquelle 1990, Hollowed 1992, Murawski 1993, Atkinson et al. 1997, Brodie et al. 1998, Loher & Armstrong 2005, Woillez et al. 2007). Video surveys utilizing centric systematic sampling techniques allowed us to determine temporal shifts in the center of sea star abundances and relate these to their prey. This work highlights the use of the statistical ellipse as an inferential tool for population shifts. These techniques may also be used in future work to examine inter- and intraspecific spatial variation according to sex, age and size, and temporal variation related to environmental conditions such as depth, temperature and habitat.

Stokesbury (2002) found that the spatial distribution of scallops on Georges Bank was not always described by the negative binomial distribution, and suggested examining the dynamics of these scallop aggregations using different spatial analysis techniques, such as geostatistics. C. F. Adams & K. D. E. Stokesbury (unpubl. data) are currently employing geostatistics to describe the mesoscale (km) distribution of scallop beds in the NLCA, Closed Area I and Northern Edge from 1999 to 2007 using the fine-scale (1.57 km) grid survey data. This analysis is being done by year, thus allowing interannual comparisons. Future work will involve the use of geostatistical techniques to further explore the spatio-temporal overlap of sea stars and sea scallops.

In the present study, we found video survey techniques combined with circular statistics to be a useful tool for examining predator–prey interactions. Our data suggest sea star aggregations moved between sea scallop beds in the NLCA sample area on Georges Bank from 1999 to 2006. These 2 dominant benthic species appear to be experiencing similar oscillating density changes (Fig. 5), which is characteristic of the

classical predator–prey relationship (Volterra 1926). The interactions between these 2 species and the limited access fisheries could have severe ramifications. As sea stars aggregate in these areas due to the high abundances of sea scallops, sea star movement between sea scallop beds may increase the natural mortality of the sea scallop population on Georges Bank.

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