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Spatial scaling of juvenile–adult associations in northwest Atlantic sea scallop *Placopecten magellanicus* populations

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ABSTRACT: High resolution images from 2008 and 2009 video surveys of Georges Bank and the Mid-Atlantic Bight were used to examine the association between juvenile and adult sea scallops over a range of spatial scales. Nearest neighbor and correlation analyses indicate that juvenile and adult scallops were negatively associated at small scales (cm) and positively associated at larger scales (>km) in both areas and years. However, the tipping point from negative to positive association occurred at a 10- to 100-fold larger spatial scale in the Mid-Atlantic than on Georges Bank. In both years, stronger negative correlation coefficients occurred in the Mid-Atlantic Bight. Differences between the Mid-Atlantic Bight and Georges Bank, with respect to larval supply, habitat quality and post-settlement movement and mortality are possible explanations that remain to be examined. The potential differences in population dynamics between these areas should be of interest to fishery managers and considered when devising harvest strategies in order to ensure the most efficient management of this valuable resource. This study presents an analysis method that has the potential to be a useful tool in understanding the spatial dynamics of populations and examining interactions both within and between species over a range of spatial scales.

KEY WORDS: *Placopecten magellanicus* · Sea scallop · Juvenile · Optical survey · Georges Bank · Mid-Atlantic Bight · Spatial scale patterns

INTRODUCTION

Interactions between juveniles and adults play an important role in the spatial distribution and population dynamics of a species, and understanding these interactions is essential to successful management of a resource. While the Atlantic sea scallop *Placopecten magellanicus* is the most valuable commercially fished species in the USA ($US 585 million in 2011, Van Voorhees & Lowther 2012), management of the resource has proven difficult due to the lack of a clear stock-recruitment relationship (Hart & Rago 2006, Stokesbury 2012). There are 2 main stocks that make up the Atlantic sea scallop resource: Georges Bank and the Mid-Atlantic Bight. Current understanding of the connectivity between these stocks is limited, adding further complexity to the management of the resource (Stokesbury 2012).

A series of terms has been coined to describe the spatial distribution of sea scallops across a range of scales; they are generally aggregated into 'clumps' (cm^2), 'patches' (m^2), 'beds' (km^2) and 'grounds' ($>10\ km^2$) (Brand 2006). Sea scallops are gonochoristic broadcast spawners and need to be in close proximity to one another to have high fertilization success (Stokesbury & Himmelman 1993, Smith & Rago 2004).

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Distribution and densities of sea scallops from clumps to beds are associated with sand-gravel substrate, low levels of predation and presence of filamentous flora and fauna (Stokesbury & Himmelman 1995, Henry & Kenchington 2004). Grounds are associated with oceanographic conditions which facilitate larval retention (Tremblay et al. 1994).

Most stock-recruitment models suggest that density dependent mortality will impact the rate of recruitment by reducing juvenile survival rates at levels of high adult biomass (Beverton & Holt 1957, Ricker 1975). Factors responsible for density dependent mortality include: cannibalism, disease transmission, intraspecific competition for living space and food, and attraction of predators resulting in increased predation (Hilborn & Walters 1992). For scallops, however, the presence of adults may enhance the settlement and survival of juvenile scallops. Settling post-larval scallops display a strong association with erect branching colonial fauna such as bryozoans and hydroids (Caddy 1972, Larsen & Lee 1978, Brand et al. 1980, Minchin 1992, Harvey et al. 1993). These organisms frequently colonize the shells of adult scallops, providing primary settlement substrate and possibly mitigating negative juvenile–adult interactions (Orensanz 1986, Stokesbury & Himmelman 1995, Henry & Kenchington 2004).

The detection and description of spatial patterns is important when assessing fishing strategies and making ecological inferences. Further, as patterns can change with scale, a variety of scales must be examined (Orensanz et al. 1998). In 2008 and 2009, we video surveyed the commercial sea scallop resource on Georges Bank and in the Mid-Atlantic Bight; here, we use the resultant data to examine the spatial relationship between juvenile and adult scallops over a range of spatial scales.

MATERIALS AND METHODS

Data collection

In cooperation with the US commercial sea scallop industry, the fishing grounds of Georges Bank and the Mid-Atlantic Bight were video surveyed between 28 April and 30 June in 2008 and between 27 April and 24 June in 2009. The video survey employed a centric systematic sampling design where the first station location was chosen randomly and each subsequent station was placed on a 5.6 km^2 grid (Fig. 1). At each station, the survey pyramid was deployed to the sea floor from a commercial fishing vessel. As the vessel drifted, 4 video quadrat samples were collected, separated by approximately 25 m. Using a custom field application, technicians recorded station and quadrat number, date and time, latitude and longitude, depth, number of sea scallops observed and other information regarding substrate and biota (Stokesbury 2002, Stokesbury et al. 2004).

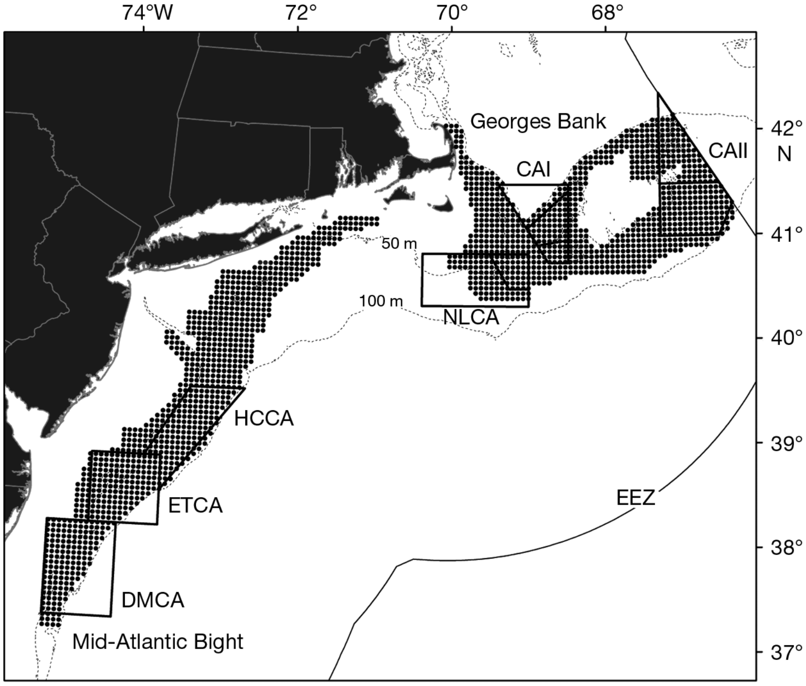

Fig. 1. Video survey station locations on a 5.6 km grid. Georges Bank closed areas are the Nantucket Lightship Closed Area (NLCA), Closed Area 1 (CA I) and Closed Area 2 (CA II). Mid-Atlantic Bight closed areas are the Hudson Canyon Closed Area (HCCA), Elephant Trunk Closed Area (ETCA) and Delmarva Closed Area (DMCA). EEZ: exclusive economic zone

The survey pyramid was equipped with 8 DeepSea® MultiSeaLites for illumination, 3 DeepSea® MultiSeaCam-2060 live-feed underwater video cameras and an Ocean Imaging Systems DSC-10,000 high-resolution digital still camera. Two downward facing video cameras were mounted 1.58 m and 0.70 m above the sea floor. The higher camera, or 'large camera', provided a quadrat view area of 2.84 m^2 and easily detected scallops of commercially harvestable sizes.

The lower camera, or 'small camera', provided a smaller quadrat view area of 0.60 m^2, but was capable of detecting smaller scallops that were missed by the large camera. The third video camera provided a side profile, aiding species identification (Stokesbury 2002, Stokesbury et al. 2004). Lastly, the digital still camera (DSC) provided high-resolution quadrat images of 1.04 m^2, nested within the view area of the large camera, and was capable of detecting scallops as small as 10 mm in shell height (Stokesbury et al. 2010b, Carey & Stokesbury 2011).

In the laboratory, technicians used the 'Digitizer', a custom application, to digitize video footage and verify or update information collected in the field, including scallop counts. Once identified, fully visible scallops that were completely within the image were measured from the umbo to the outer shell margin using ImagePro® image analysis software, with appropriate measurement calibrations for each camera (Stokesbury et al. 2004, Carey & Stokesbury 2011).

Nearest neighbor analysis

We conducted a nearest neighbor analysis using all DSC images with 2 or more measureable scallops (densities > 1.9 scallops m^{-2}). For each scallop, we measured shell height, distance to nearest neighbor and the nearest neighbor's shell height. In this type of analysis, it is important to consider uncertainty about neighbors beyond the borders of an image. A scallop near the edge of an image may have a neighbor outside the image that is closer than its visible neighbor within the image. As a result, individuals near the perimeter will tend to have greater nearest neighbor distances than those further inside (Clark & Evans 1954, Sinclair 1985).

The use of a buffer zone is recommended to minimize edge effects (Campbell 1996). To account for uncertainty beyond the edge of DSC images, we examined analogous large camera images. Since DSC images are fully nested within the large camera view area, we used the large camera to provide information beyond the perimeter of DSC images to determine the accuracy of each nearest neighbor pair. Only confirmed nearest neighbor pairs were included in the analysis.

From the measurements, each scallop and its nearest neighbor were classified as either juvenile or adult. Juveniles were scallops less than 70 mm in shell height, as this roughly marks the beginning of gonadal development and most effectively separated year classes in all 4 data sets (Stokesbury et al. 2011, Carey & Stokesbury 2011). The above results were organized into 2 × 2 contingency tables of observed nearest neighbor interactions for Georges Bank and the Mid-Atlantic Bight in 2008 and 2009 (Table 1) (Pielou 1961).

Table 1. Layout of contingency tables depicting nearest neighbor interactions, where JA' represents the number of juvenile scallops (J) with adult nearest neighbors (A')

Nearest neighbor	Base individual		Total
	Juvenile	Adult	
Juvenile	JJ'	AJ'	$N_{j'}$
Adult	JA'	AA'	$N_{a'}$
Total	N_j	N_a	N

If spatial segregation is occurring at the cm scale, juvenile scallops would more likely be nearest other juveniles and adults near other adults. Therefore, observed frequencies in the JJ' and AA' cells would be higher than expected frequencies. We tested for cm scale spatial segregation between juveniles and adults by comparing the above observed nearest neighbor contingency table frequencies to expected frequencies assuming independence between base individual and nearest neighbor. Expected frequencies of nearest neighbor interactions were calculated as:

$$N(JJ') = \frac{N_j \times N_{j'}}{N} \quad (1) \qquad N(AA') = \frac{N_a \times N_{a'}}{N} \quad (2)$$

$$N(JA') = \frac{N_j \times N_{a'}}{N} \quad (3) \qquad N(AJ') = \frac{N_a \times N_{j'}}{N} \quad (4)$$

A chi-square analysis was used to compare observed and expected contingency table frequencies (Zar 1999). To test with an α of 0.01, average expected frequencies must be greater than 10 (Roscoe & Byars 1971).

Correlation analysis

To examine juvenile–adult interactions beyond the cm scale, we conducted a series of correlation analyses of juvenile counts versus adult counts at 8 spatial scales ranging from 1 m^2 to over 10^9 m^2. The first and smallest scale examined counts of juvenile and adult scallops within individual quadrats and represents a scale of 1 m^2. We next summed scallop counts from the first and second quadrats and the third and fourth quadrats of each station and treated these as 'quadrat pairs.' As each quadrat is separated by approximately 25 m and the direction in which the survey

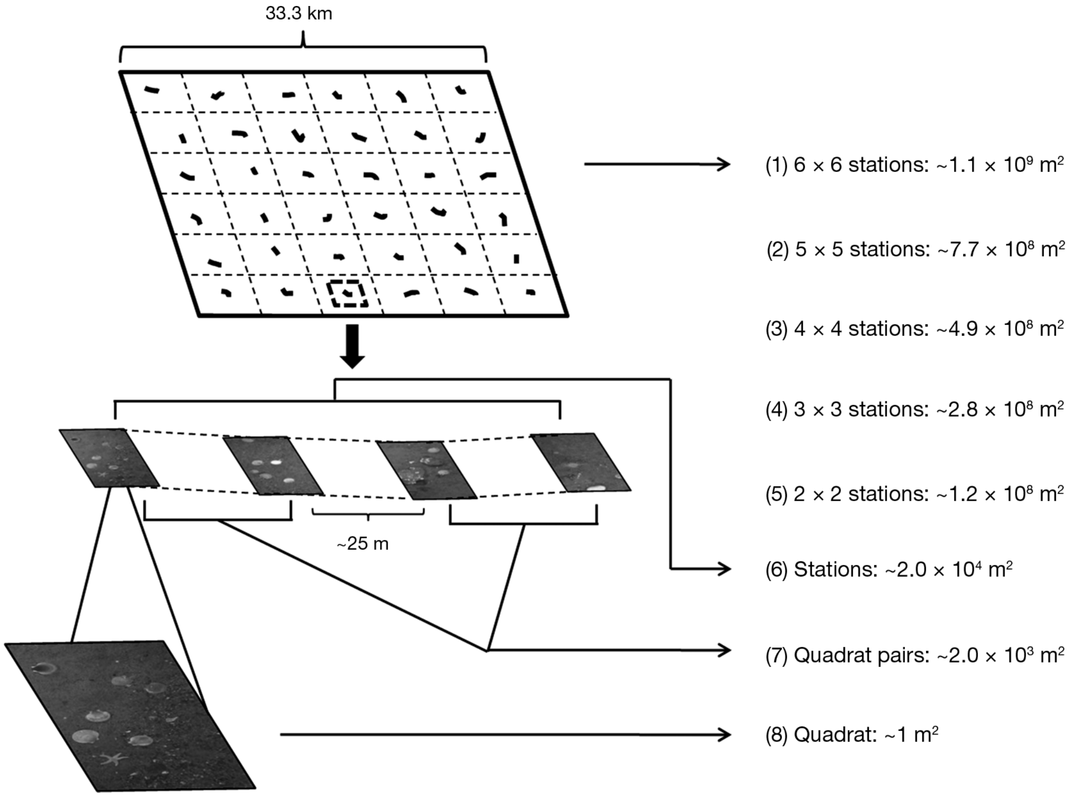

Fig. 2. Breakdown of 8 spatial scales assessed in correlation analyses, ranging from 1 m^2 (individual quadrats; bottom) to 1.1 × 10^9 m^2 (blocks of 36 stations [6 × 6]; top). See 'Materials and methods: Correlation analysis' for further description

vessel drifts between quadrats is random at every station, we suggest that these samples represent a scale of 2.0 × 10^3 m^2 (area of a circle with ~25 m radius). The third scale examined included scallop counts per station (sum of all 4 quadrats). As the average distance between the first and last quadrats was approximately 75 m and the direction in which the survey vessel drifts between quadrats is random, these samples represented a scale of 2 × 10^4 m^2 (area of a circle with ~75 m radius). Lastly, we grouped stations into 2 × 2, 3 × 3, 4 × 4, 5 × 5 and 6 × 6 blocks. As each station is separated by 5.6 km, these blocks represent scales of 1.2 × 10^8 m^2, 2.8 × 10^8 m^2, 4.9 × 10^8 m^2, 7.7 × 10^8 m^2 and 1.1 × 10^9 m^2, respectively (Fig. 2).

Sea scallops display a highly aggregated distribution, thus the majority of quadrats sampled contained zero scallops. These quadrats were excluded from the analysis, as the goal was to evaluate associations between juvenile and adult scallops over a range of spatial scales. All quadrats containing one or more scallops were included in the data set for each area and year. With each increasing spatial scale, the counts of juvenile and adult scallops were aggregated into the appropriate spatial unit so that all scallops were included at every scale of the analysis. For the Georges Bank and Mid-Atlantic Bight data sets in 2008 and 2009, we conducted correlation analyses at each of the 8 scales and provide Pearson correlation coefficients with associated 95% confidence intervals. Resulting correlation coefficients were plotted against log transformed scale for both areas and years to depict changes in juvenile–adult association with scale. Linear trendlines were fit to these plots.

RESULTS

Survey results

In 2008, we surveyed 932 stations (3728 quadrats) in the Mid-Atlantic Bight and 933 stations (3732 quadrats) on Georges Bank. Of these, measureable scallops were observed in 457 quadrats (from 284 different stations) in the Mid-Atlantic Bight and 266 quadrats (from 157 different stations) on Georges Bank. In the Mid-Atlantic Bight, juvenile and adult scallops were observed together in 33 individual quadrats and in 48 stations when quadrat counts were summed by station. On Georges Bank, juvenile and adult scallops were observed together in 42 individual quadrats and in 35 stations when quadrat counts were summed by station (Table 2).

Table 2. Summary of the 2008 and 2009 video survey data sets by quadrat and aggregated by station (groups of 4 quadrats). Also shown are the number of samples with one or more scallops present, the number of samples with multiple scallops present and the number of samples with both juvenile (juv.) and adult scallops present

	N	With scallops	With multiple scallops	With juv. and adults
Quadrats				
Mid-Atlantic Bight				
2008	3728	457	137	33
2009	3732	406	84	18
Georges Bank				
2008	3732	266	104	42
2009	3820	330	128	56
Stations				
Mid-Atlantic Bight				
2008	932	284	131	48
2009	933	286	110	37
Georges Bank				
2008	933	157	82	35
2009	955	178	99	45

In 2009, we surveyed 933 stations (3732 quadrats) in the Mid-Atlantic Bight and 955 stations (3820 quadrats) on Georges Bank. Of these, measureable scallops were observed in 406 quadrats (from 286 different stations) in the Mid-Atlantic Bight and 330 quadrats (from 178 different stations) on Georges Bank. In the Mid-Atlantic Bight, juvenile and adult scallops were observed together in 18 individual quadrats and in 37 stations when quadrat counts were summed by station. On Georges Bank, juvenile and adult scallops were observed together in 56 individual quadrats and in 45 stations when quadrat counts were summed by station (Table 2).

Nearest neighbor analysis

In 2008, the nearest neighbor analysis was based on 405 scallops from 137 quadrats in the Mid-Atlantic Bight and 371 scallops from 104 quadrats on Georges Bank. Using large camera images as a buffer zone, these images yielded 265 and 243 confirmed nearest neighbor pairs in the Mid-Atlantic Bight and on Georges Bank, respectively. In 2009, the nearest neighbor analysis was based on 204 scallops from 84 quadrats in the Mid-Atlantic Bight and 470 scallops from 128 quadrats on Georges Bank. Using large camera images as a buffer zone, these images yielded 96 and 318 confirmed nearest neighbor pairs in the Mid-Atlantic Bight and on Georges Bank, respectively.

Table 3. *Placopecten magellanicus.* Nearest neighbor contingency tables of juvenile–adult scallop interactions with observed and expected (in parentheses) proportions. Juvenile (N_j) and adult (N_a) sample-sizes, chi-square values and corresponding p-values are provided for each area and year

Neighbor	Base individual	
	Juvenile	Adult
Mid-Atlantic Bight		
2008		
Juvenile	0.43 (0.26)	0.08 (0.25)
Adult	0.08 (0.25)	0.41 (0.24)
$N_j = 135$, $N_a = 130$, $\chi^2 = 123.6$, $p < 0.01$		
2009		
Juvenile	0.18 (0.08)	0.10 (0.20)
Adult	0.11 (0.21)	0.60 (0.51)
$N_j = 28$, $N_a = 68$, $\chi^2 = 20.8$, $p < 0.01$		
Georges Bank		
2008		
Juvenile	0.48 (0.39)	0.14 (0.23)
Adult	0.15 (0.24)	0.23 (0.14)
$N_j = 154$, $N_a = 89$, $\chi^2 = 36.1$, $p < 0.01$		
2009		
Juvenile	0.44 (0.29)	0.11 (0.25)
Adult	0.09 (0.24)	0.36 (0.21)
$N_j = 169$, $N_a = 149$, $\chi^2 = 112.7$, $p < 0.01$		

Partial segregation was observed between juvenile (*J*) and adult (*A*) scallops at the cm scale in both areas and years. Chi-square values ranged from 20.77 to 123.59, yielding p-values of <0.01 for each dataset, indicating moderate levels of segregation (Table 3). Sample sizes were adequate for all datasets, as mean expected frequency was greater than 10 in all cases. The distribution of nearest neighbor pairs within the contingency tables (more *JJ*'s and *AA*'s) suggests that juveniles and adults are significantly more likely to be found near members of their own group than of the other (Table 3).

Correlation analysis

In the Mid-Atlantic Bight, correlation analyses displayed similar trends in 2008 and 2009. Correlation coefficients were significantly negative ($p < 0.01$) at the smallest scales, and gradually increased with increasing scale, becoming significantly positive ($p < 0.05$) at the largest scales. They ranged from −0.379 to 0.358 in 2008 and from −0.446 to 0.644 in 2009 (Table 4). On Georges Bank, correlation analyses also displayed similar trends in 2008 and 2009. Correlation coefficients were negative only at the smallest scale (individual quadrats), but significant only in

Table 4. *Placopecten magellanicus.* Correlation analyses for juvenile scallop versus adult scallop counts over increasing spatial scale from the Mid-Atlantic Bight and Georges Bank in 2008 and 2009

Spatial scales	Scale (m^2)	*N*	Correlation coefficient	95% CI Lower	95% CI Upper	p	r^2
Mid-Atlantic							
2008							
Quadrats	1.0	457	−0.379	−0.455	−0.298	<0.01	0.144
Quadrat pairs	2.0×10^{3}	371	−0.240	−0.334	−0.142	<0.01	0.058
Stations	2.0×10^{4}	284	−0.133	−0.246	−0.017	0.03	0.018
2 × 2 stations	1.23×10^{8}	158	−0.010	−0.166	0.146	0.90	0.000
3 × 3 stations	2.78×10^{8}	92	0.066	−0.141	0.267	0.53	0.004
4 × 4 stations	4.94×10^{8}	63	0.090	−0.161	0.330	0.48	0.008
5 × 5 stations	7.72×10^{8}	50	0.346	0.075	0.570	0.01	0.119
6 × 6 stations	1.11×10^{9}	36	0.358	0.033	0.614	0.03	0.128
2009							
Quadrats	1.0	406	−0.446	−0.521	−0.365	<0.01	0.199
Quadrat pairs	2.0×10^{3}	360	−0.306	−0.397	−0.209	<0.01	0.094
Stations	2.0×10^{4}	286	−0.148	−0.260	−0.033	0.01	0.022
2 × 2 stations	1.23×10^{8}	157	0.070	−0.088	0.224	0.39	0.005
3 × 3 stations	2.78×10^{8}	95	0.130	−0.073	0.323	0.21	0.017
4 × 4 stations	4.94×10^{8}	64	0.416	0.190	0.600	<0.01	0.173
5 × 5 stations	7.72×10^{8}	52	0.448	0.199	0.642	<0.01	0.201
6 × 6 stations	1.11×10^{9}	38	0.644	0.408	0.799	<0.01	0.415
Georges Bank							
2008							
Quadrats	1.0	266	−0.060	−0.179	0.061	0.33	0.004
Quadrat pairs	2.0×10^{3}	213	0.113	−0.022	0.244	0.10	0.013
Stations	2.0×10^{4}	157	0.342	0.196	0.473	<0.01	0.117
2 × 2 stations	1.23×10^{8}	89	0.425	0.238	0.582	<0.01	0.181
3 × 3 stations	2.78×10^{8}	59	0.481	0.256	0.656	<0.01	0.231
4 × 4 stations	4.94×10^{8}	44	0.501	0.240	0.695	<0.01	0.251
5 × 5 stations	7.72×10^{8}	33	0.631	0.367	0.801	<0.01	0.398
6 × 6 stations	1.11×10^{9}	30	0.609	0.319	0.795	<0.01	0.371
2009							
Quadrats	1.0	330	−0.161	−0.264	−0.054	<0.01	0.026
Quadrat pairs	2.0×10^{3}	254	0.000	−0.123	0.123	1.00	0.000
Stations	2.0×10^{4}	178	0.108	−0.040	0.251	0.15	0.012
2 × 2 stations	1.23×10^{8}	108	0.266	0.081	0.433	0.01	0.071
3 × 3 stations	2.78×10^{8}	73	0.413	0.202	0.587	<0.01	0.171
4 × 4 stations	4.94×10^{8}	54	0.596	0.390	0.745	<0.01	0.355
5 × 5 stations	7.72×10^{8}	38	0.528	0.251	0.725	<0.01	0.279
6 × 6 stations	1.11×10^{9}	35	0.580	0.306	0.765	<0.01	0.337

2009 ($p = 0.33$ in 2008, $p < 0.01$ in 2009). They increased with increasing scale ranging from −0.060 to 0.609 in 2008 and from −0.161 to 0.580 in 2009 (Table 4).

Differences were apparent between Georges Bank and the Mid-Atlantic Bight. In the Mid-Atlantic Bight, correlation coefficients were more strongly negative at the smallest scale and remained negative into larger spatial scales than on Georges Bank (Table 4, Fig. 3). Trendlines of correlation coefficient plotted against the log of area were shifted to the right in the Mid-Atlantic Bight compared to Georges Bank. The *x*-intercepts of these trendlines indicate the scale at which correlation coefficients change from negative to positive, where juvenile and adult scallops shift from negatively associated to positively associated. In 2008 and 2009, *x*-intercepts were 6.2 and 5.4 in the Mid-Atlantic Bight, and 0.8 and 2.7 on Georges Bank, respectively (Fig. 3). These values translate into scales of 1.5×10^{6} m^2 and 2.3×10^{5} m^2 in the Mid-Atlantic Bight and 6 m^2 and 5.0×10^{2} m^2 on Georges Bank in 2008 and 2009, respectively. This implies that segregation between juvenile and adult scallops extends into larger spatial scales in the Mid-Atlantic Bight than on Georges Bank.

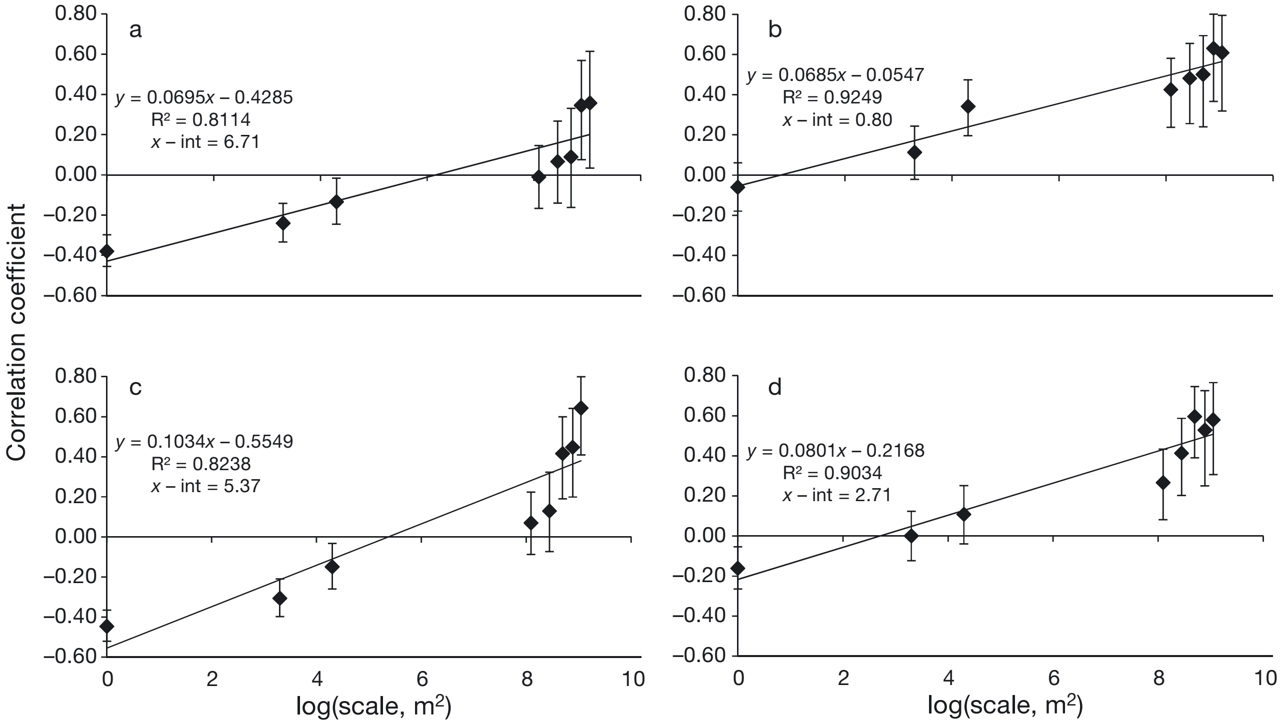

Fig. 3. *Placopecten magellanicus*. Scatter plots of juvenile−adult scallop correlation coefficients against log-transformed scales, with linear trendlines for the (a,c) Mid-Atlantic Bight and (b,d) Georges Bank in (a,b) 2008 and (c,d) 2009. Error bars represent 95% confidence intervals

DISCUSSION

Juvenile and adult sea scallops were negatively associated at small scales. This spatial segregation is likely the result of a number of factors, beginning with spatial variability in larval transport and dispersal across cohorts. Yearly differences in environmental conditions will result in inter-annual variability in larval settlement sites, likely causing an initial negative association between juvenile and adult scallops at small scales (Brand 2006, Tian et al. 2009a,b, Stokesbury 2012).

After settlement, the association between juveniles and adults will continue to be modified by dispersal, growth and mortality. Scallops between 30 and 100 mm in shell height are effective swimmers, but as they grow larger, size and weight begin to limit their swimming efficiency (Dadswell & Weihs 1990). Given their ability to swim well, juvenile scallops may move in search of more suitable habitat, to escape predators or to exploit available food sources (Brand 2006). As scallops mature, aggregating with other adults is likely to also confer reproductive benefits through enhanced fertilization success (Stokesbury & Himmelman 1993, Harris 2011). The reproductive benefits of aggregating are widely reported in free spawners (Pennington 1985, Levitan 1991); however, empirical evidence of sea scallop fertilization dynamics in the field is lacking. Adult aggregation may enhance the negative juvenile−adult association, but not necessarily through avoidance of juveniles. Stokesbury & Himmelman (1993) observed a positive association between immature and mature scallops at low population densities, but at high densities the association became random. The role of density-dependent factors in driving fine-scale adult-juvenile associations requires further research.

As scale increased, correlation between juvenile and adult scallop density became more positive. Scallop distributions on the scale of grounds (>10 km^2) are determined by the effect of physical and environmental factors on the population level and the need for common habitat. Sea scallops require certain habitat characteristics for survival, including suitable depth, water temperature, substrate and food availability. An appropriate combination of these essential habitat characteristics is available only in certain areas and as the scale assessed increases to encompass these areas, we would expect to see a positive association between juvenile and adult scallops.

The negative association between juvenile and adult scallops was more pronounced and extended into larger scales in the Mid-Atlantic Bight than in Georges Bank. This may suggest differences in population dynamics between the 2 locations. Stokesbury & Himmelman (1995) identified 3 critical factors in determining the location of sea scallop aggregations: gravel substratum, low decapod predation and presence of erect, branching flora and fauna, which provide an initial settlement habitat. Georges Bank and the Mid-Atlantic Bight differ dramatically with respect to these factors, suggesting that the development of persistent scallop beds is more likely on Georges Bank.

Georges Bank substrate is heterogeneous, with abundant patches of gravel substratum (Harris & Stokesbury 2010). In the Mid-Atlantic Bight, the substrate is much more homogeneous, dominated by sand (Stokesbury et al. 2010a). Taking these differences into consideration, we would expect spatial variations in juvenile scallop survivorship on Georges Bank, with consistently higher survival in areas of preferred gravel substratum year after year. Over time, this would facilitate a positive association between juvenile and adult scallops at smaller spatial scales. Conversely, in the Mid-Atlantic Bight, the effects of substrate on juvenile survivorship should be more consistent across the resource.

Sea stars are a major scallop predator (Barbeau et al. 1994, Nadeau & Cliché 1998) and were the most abundant macroinvertebrate on Georges Bank and the Mid-Atlantic Bight. Although sea star densities were high on Georges Bank, they did not generally overlap in space with scallop aggregations. In the Mid-Atlantic Bight, however, sea stars were highly abundant across the entire sea scallop range (Stokesbury et al. 2010a). Sea stars display a size preference in their prey, consuming more small scallops than medium or large scallops (Barbeau & Scheibling 1994). This may result in increased rates of predation on juvenile scallops by sea stars. Furthermore, sea scallops respond to contact with sea stars by swimming (Barbeau & Scheibling 1994, Wong et al. 2006). More prevalent interactions with sea stars in the Mid-Atlantic Bight may increase rates of scallop mortality and dispersal, in turn preventing the formation of stable scallop beds.

Filamentous flora and fauna, such as bryozoans and hydrozoans, were much more abundant on Georges Bank than in the Mid-Atlantic Bight (Stokesbury et al. 2010a). Settling scallops display a strong association with these organisms, which frequently colonize the shells of adult scallops (Harvey et al. 1993, Stokesbury & Himmelman 1995, Henry & Kenchington 2004). This provides primary settlement substrate and could help mitigate any small-scale negative associations between juvenile and adult scallops.

Lastly, differences in hydrography may cause different recruitment patterns between Georges Bank and the Mid-Atlantic Bight. The prevailing currents on Georges Bank form a clockwise gyre which can allow for increased larval retention and a more consistent annual supply of larvae (Tremblay et al. 1994, Tian et al. 2009a,b). In the Mid-Atlantic Bight, prevailing currents are southwesterly, allowing for little larval retention. Thus, scallop recruitment in the Mid-Atlantic Bight may be highly dependent on favorable currents, resulting in more episodic large year classes (Hart & Rago 2006, Stokesbury et al. 2011).

These potential differences in population dynamics may help to explain the differences we observed in the spatial relationships between juvenile and adult scallops. The distribution of scallops in the Mid-Atlantic Bight may be established primarily at larval settlement, as successful scallop recruitment seems to be highly dependent on favorable currents causing episodic large year classes, and post-settlement factors appear consistent across the region. On Georges Bank, larvae may be retained more effectively by the gyre of currents, providing a more consistent supply of young scallops into the population. Here, the distribution of scallops may be influenced more after larval settlement, as the heterogeneity of habitat quality can result in spatially variable but temporally stable levels of juvenile scallop survivorship. This may lead to a more persistent, well defined scallop bed structure on Georges Bank and a more 'boom and bust' cohort driven population structure in the Mid-Atlantic Bight.

While the potential differences in population dynamics and juvenile–adult spatial associations between the Georges Bank and Mid-Atlantic sea scallop stocks should be of interest to managers, additional years of data should be examined to determine whether these trends persist over time. Additionally, further research into the causes of the spatial patterns observed in this study would prove helpful to managers. These differences need to be considered when devising harvest strategies to ensure the most efficient management of this valuable resource.

The methods used in this study provide direct, useful insight into the relationships between individuals over a range of spatial scales. In plotting correlation coefficient against spatial scale, as in Fig. 3, the x-intercept represents the tipping point between positive and negative spatial associations of 2 groups of individuals. This type of analysis has the potential to be a useful tool in understanding the spatial dynamics of populations and examining interactions both within and between species.

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