

Post-settlement predation by sea stars and crabs on the sea scallop in the Mid-Atlantic Bight

Burton V. Shank^{1,*}, Deborah R. Hart¹, Kevin D. Friedland²

¹National Marine Fisheries Service, 166 Water St., Woods Hole, Massachusetts 02543, USA

²National Marine Fisheries Service, 28 Tarzwell Dr., Narragansett, Rhode Island 02882, USA

ABSTRACT: Year-class strength of benthic invertebrates is generally determined during early life-history stages. However, the contribution of different biotic and abiotic factors to the resulting abundance and spatial distribution of recruits is poorly understood. We infer the effect of post-settlement mortality by benthic invertebrate predators on recruitment of sea scallops *Placopecten magellanicus* based on an 11 yr time series of survey data from the east coast of the United States. We reconstructed predator densities at different life-history stages for scallops and identified the stages when scallop recruitment dynamics are best explained by predator densities. Based on spatial associations and temporal dynamics, we found evidence that sea stars *Astropecten americanus* and crabs *Cancer* spp. are causing localized depletion of sea scallop recruits. Both predator groups appear to be affecting scallop recruitment primarily in the first year post-settlement. The spatial and temporal coherence in predator–prey fluctuations partially explains the most dramatic recruitment events in the past 3 decades and suggests that predation on recruits may also limit the geographic distribution of sea scallops in this region.

KEY WORDS: Post-settlement predation · Recruitment · Spatial association · Predator–prey dynamics · *Placopecten magellanicus* · *Astropecten* sp. · *Asterias* spp. · *Cancer* spp.

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INTRODUCTION

Understanding the factors causing inter-annual variation in recruitment is a challenging and important topic in benthic ecology and fisheries research (Anderson 1988, Trippel & Chambers 1997). Recruitment variability can be controlled by multiple factors including water circulation (Gilbert et al. 2010), habitat availability (Beverton 1995), nutrition (Zenitani et al. 2007), environmental stress (Hare & Able 2007) and predation (Sissenwine 1984, Leggett & DeBlois 1994, Gosselin & Qian 1997, Hunt & Scheibling 1997, Bax 1998), but the main drivers of recruitment in any particular case are often difficult to determine.

Except in shallow habitats, direct observation of marine communities is limited and experimental ma-

nipulation is impractical. In these cases, inference of population drivers is necessarily made from spatial and temporal correlations between observational data and candidate environmental or biological variables, typically collected through routine resource monitoring (Sissenwine 1984). However, such inferences are necessarily correlative and are not strict inferential tests of causality (Levin 1992, Myers 1998). Population data collected across heterogeneous habitats commonly exhibit spatial trends and autocorrelation, obscuring causal relationships and increasing the probability of producing spurious correlations (Legendre & Fortin 1989, Lennon 2000, Diniz-Filho et al. 2003, Holt & Barfield 2003, Birkhofer et al. 2010).

The difficulty in analyzing relationships among variables in the presence of spatial autocorrelation

*Email: burton.shank@noaa.gov

has historically been ignored in many ecological studies despite the availability of statistical techniques that can quantify and address autocorrelation explicitly (Legendre & Fortin 1989, Lennon 2000, Pinheiro & Bates 2000, Dormann et al. 2007). Thus, to identify determinants of recruitment from observational data one must detect the effects of individual processes despite process-based error introduced by other, unmeasured processes and account for the temporally and spatially autocorrelated nature of the data.

Sea scallops *Placopecten magellanicus* Gmelin are one of the most valuable fisheries in the United States and the most valuable wild scallop fishery in the world (Hart & Rago 2006). The US fishery includes populations in the Mid-Atlantic Bight (MAB), Georges Bank (GB), and the Gulf of Maine, which are ecoregions within the US Northeast Continental Shelf large marine ecosystem (Hart & Chute 2004, Naidu & Robert 2006). The GB stock has historically been the largest producer of sea scallops in the fishery, but yields from the MAB stock have surpassed the GB stock in recent years due to increased recruitment in this region (Hart & Chute 2004, Hart & Rago 2006, Northeast Fisheries Science Center 2010). Recruitment events in the MAB are erratic, presumably due to the variability of environmental and ecological factors in this region (Bourne 1965, Serchuk et al. 1979, Hart & Chute 2004, Hart & Rago 2006).

Juvenile scallop abundance is difficult to quantify until after their first year. During their pre- and early post-settlement period, they are subject to multiple sources of mortality that influence their abundance and spatial distribution. Post-settlement mortality rates among juvenile sea scallops are high, mainly due to sea star and crab predators, but their natural mortality declines as the scallops grow (Elner & Jamieson 1979, Barbeau & Scheibling 1994, Stokesbury & Himmelman 1995, Hatcher et al. 1996, Hart 2006). We hypothesize that these predators are influencing the spatial distribution and temporal dynamics of scallop recruitment in the MAB.

Several benthic invertebrate predators are common in the MAB and are readily captured by survey scallop dredges. Common predators include the sea stars *Asterias vulgaris*, *A. forbesi*, *Leptasterias tenera* and *Astropecten americanus*, and the Atlantic rock and Jonah crabs (*Cancer irroratus*, *C. borealis*). *Asterias* spp. and *L. tenera* consume bivalves by prying open their prey and everting their stomachs into the shell and are capable of preying on scallops >20 mm in shell height (Sloan 1980, Barbeau & Scheibling 1994). *A. forbesi* is more tolerant of warm tempera-

tures and tends to occur in shallower and more southerly waters than do *A. vulgaris* and *L. tenera* (Franz et al. 1981).

The sea star *Astropecten americanus* is abundant in the middle and outer continental shelf of the MAB and is the dominant asteroid on the outer shelf (Boesch 1979, Franz et al. 1981, Hart 2006). Their upper depth limit decreases from 25 m at their southern limit off Cape Hatteras to 150 m at its northern limit on Georges Bank; their geographic range is limited by summer thermal stress in the south and winter thermal stress in the north (Franz et al. 1981). *A. americanus* are generalist predators on small invertebrates and feed by engulfing their prey whole. It preferentially consumes small molluscs, including juvenile *Placopecten magellanicus*; its prey size rarely exceeds 10 mm (Franz & Worley 1982, Smerreka 2003).

The third predator group consists of *Cancer* crabs (*C. irroratus* and *C. borealis*), which are found throughout the MAB (Hart 2006). They are visual predators capable of rapidly depleting juvenile sea scallops and can be a significant source of scallop mortality (Elner & Jamieson 1979, Barbeau et al. 1994, Hatcher et al. 1996). Based on these studies, medium- and large-sized crabs (carapace widths: 50 to 130 mm) prefer moderate-sized scallops with shell heights in the range of 25 to 55 mm.

We investigate the potential for the spatiotemporal dynamics of benthic invertebrate predators to explain sea scallop recruitment patterns in the MAB region using an 11 yr observational dataset. Because both sea scallops and their predators have a limited capacity to move across geographic distances of kilometers or more, we predict that predators, in sufficient densities, will cause localized depletion of sea scallops that will be evident as negative spatial and temporal associations between predators and prey. Further, because the geographic distribution of predators changes temporally, we hypothesize that the strength of the spatial association between predators and prey will also vary across scallop early life-history stages with the strongest predator-prey associations occurring in the stages when predators most affect prey populations.

MATERIALS AND METHODS

Data were collected from 2000 through 2010 as part of the Northeast Fisheries Science Center sea scallop *Placopecten magellanicus* dredge survey (Northeast Fisheries Science Center 2010). This sur-

vey occurred annually with sampling from mid-May through July. Data for this study were limited to tows from the continental shelf in the MAB that encompassed the primary habitat for sea scallops in this region. The study region extended from 36.5 to 41.0° N and 75.0 to 71.4° W, encompassing an area of ~62 700 km², with depths ranging from 23 to 113 m (Fig. 1a).

Dredge sampling was conducted with a stratified-random design using an 2.44 m wide modified New Bedford-style scallop dredge, with 5.1 cm rings and lined with 3.8 cm plastic mesh. Dredges were towed on the bottom for 15 min at 7.04 km h⁻¹ for an average distance of 1 nautical mile. All collected sea scallops were counted, and their shell heights (SH) were individually measured to the nearest 5 mm increment from 2000 through 2004 and the nearest millimeter thereafter. In approximately every third tow, crabs were enumerated and weighed in aggregate to the nearest 0.1 kg. Because they were often extremely abundant, sea star (*Asterias* spp., *Leptasterias tenera* and *Astropecten americanus*) abundances and weights were estimated by taking a random subsample of bycatch, which was then extrapolated to the whole catch. Because individuals of *Cancer irroratus* and *C. borealis* were not consistently distinguished from each other, we treated all *Cancer* crabs as a single group for analytical purposes (hereafter *Cancer*

spp.). Similarly, we treated *A. vulgaris*, *A. forbesi*, and *L. tenera* as a single group (hereafter *Asterias* spp.) because these species were not recorded separately in many sampling years.

For each tow from the dredge survey, we inferred the density of 2 yr old sea scallops (hereafter juvenile scallops) from the number of scallops collected within a range of shell heights. Minimum size for juvenile scallops was fixed at 40 mm SH due to gear selectivity, corresponding to the typical lower size distribution of 2 yr old sea scallops. Maximum recruit sizes for each tow were calculated from the growth model developed by Hart & Chute (2009) which accounts for spatial variation in sea scallop growth rates based on latitude and depth. The maximum calculated shell height for juvenile scallops ranged from 66 mm in high-latitude, deep locations to 88 mm in low-latitude, shallow locations.

Kriging was used to interpolate sea scallop recruit densities from the surveyed points to a regular grid (Pebesma 2004, Bivand et al. 2008). Kriging assumes that the degree of spatial autocorrelation is equal in all directions and does not change within the study area (Burrough & McDonnell 1998). However, scallop distributions in the study area are anisotropic (exhibiting directional dependence of spatial autocorrelation), with stronger gradients across isobaths than along isobaths (Adams et al. 2008). Further, the

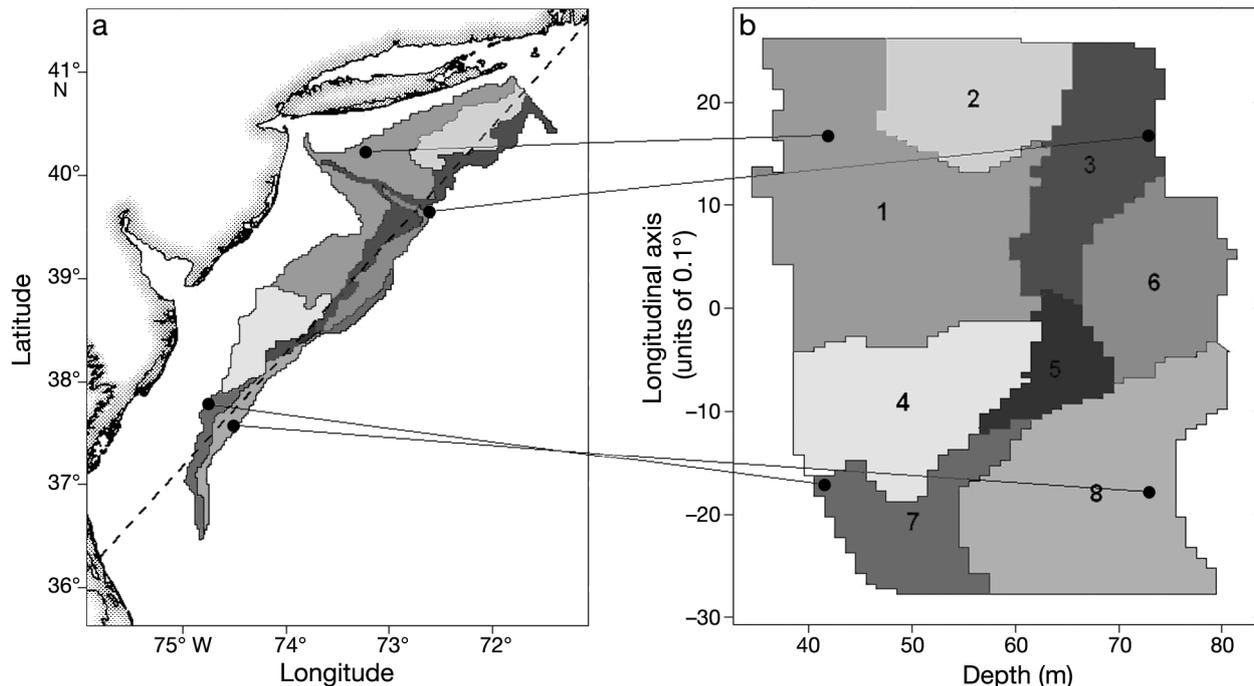


Fig. 1. (a) Mid-Atlantic Bight study area. Dashed line: orientation of the longitudinal axis. (b) Study area after coordinates were re-projected to relieve anisotropy. Shaded subregions in both maps: results of the cluster analysis for temporally synchronous scallop *Placopecten magellanicus* recruitment. Reference lines show corresponding points on the 2 maps

degree of anisotropy varied within the study area due to changes in the width of the continental shelf. We resolved the anisotropy by re-projecting the coordinates of our data to a longitudinal axis that roughly paralleled the isobaths, and a depth axis, which accounted for the changing width of the continental shelf (Fig. 1b). Replacing the spatial coordinates with the longitudinal and depth axis coordinates resulted in stationary, isotropic variance patterns throughout the study area. We used this coordinate system to represent our study area and the distances among survey sites in all subsequent spatial analysis. In this coordinate projection, 1 unit on the x-axis corresponds to a change of 1 m of depth, and 1 unit on the y-axis corresponds to 0.1 degrees (11.5 km) along the longitudinal axis. While this re-projection is an effective manner of dealing with complex anisotropy patterns over a large geographic region, we are not aware of the use of similar methods in other studies.

To address the spatial variability in recruitment dynamics across the study area, we used cluster analysis to divide the study area into subregions that had distinct temporal dynamics. The kriged estimates of recruitment were, for each grid cell, centered across time to a mean of zero to calculate recruitment anomalies for each year. The cluster analysis was then performed with the centered recruitment at each grid cell as a sampling unit, and years as repeated measures. We visually examined the clustering dendrogram and the spatial subregions resulting from different sets of retained clusters and cut the dendrogram at a compromise between accurately depicting spatial heterogeneity in recruitment dynamics and dividing the study area into too many subregions to be practical for analysis or management.

To estimate predator densities at different early life-history stages, we reconstructed the time series of predator densities at each scallop sampling site for the year of sampling (Year-2) and the 2 yr prior to sampling (Year-1 and Year-0). The Year-0 estimate of predator density corresponds to the summer that scallop recruits were spawned, 2 yr before recruits were recorded in the dredge survey. The Year-0 time period occurs when scallops from the spring spawning would be settling and ~4 mo before spat from the fall spawning would be settling. The Year-1 estimate corresponds to the summer sampling 1 yr before scallop densities were quantified, ~1 yr post-settlement. The Year-2 estimate corresponds to the summer sampling when recruit densities were actually recorded in the survey, ~2 yr post-settlement. To eliminate zeroes in the predator dataset, we added 0.1 kg to all observations before log-transforming the data. We then esti-

mated predator abundance at un-sampled locations using lognormal co-kriging, using the spatial abundance pattern from the year before and after the target year to stabilize predictions, as well as a bias-correction technique adapted from Yamamoto (2007).

We examined the spatial association between scallop recruits and predators at a regional scale using spatial cross-correlation (Veit et al. 1993, Fortin & Dale 2005). We calculated the spatial cross-correlations between log-transformed scallop recruit densities and predator densities for each year, predator species, and lag time (Year-0 to Year-2). We then calculated a weighted average across years within distance intervals to get a single cross-correlogram for each predator and lag time. Statistical significance of resulting correlations was determined by permutation testing.

To further test the hypothesis that predators cause depletion of scallop recruits, the spatial relationship between predator biomass and juvenile scallop densities on subregional scales was examined using linear mixed-effect models (Pinheiro et al. 2009). Predator-prey relationships were examined using 2 simple linear models: a log-log relationship and a log-linear relationship, with predator densities as a fixed effect and all combinations of year and subregion as random effects (i.e. random intercept models). The log-log model used log-transformed recruit densities and the kriged estimates of predator biomass to model the geographic association between recruits and predators with lognormal errors.

Log-log model:

$$\log(r_{ijk}) = \beta_0 + \beta_1 \cdot \log(p_{ijk}) + b_{ij} + \epsilon_{ijk} \quad (1)$$

where r_{ijk} is the number of scallop recruits observed in subregion i in year j from tow k , β_0 and β_1 are estimated intercept and slope parameters, p_{ijk} is the estimated predator density for dredge tow ijk , b_{ij} is the geometric mean number of recruits for subregion i and year j [random effect, $b_{ij} \sim N(0, \sigma^2)$] and ϵ_{ijk} is the error $\sim N(0, \sigma^2)$ and assumed to be independent (see Appendix 1 for details). The log-linear model also used log-transformed recruit densities but used back-transformed estimates of predator biomass:

Log-linear model:

$$\log(r_{ijk}) = \beta_0 + \beta_1 \cdot p_{ijk} + b_{ij} + \epsilon_{ijk} \quad (2)$$

The log-linear model predicts that prey density would decline as a negative exponential function of predator density and, thus, implies a more causative relationship between predator and prey than the log-log relationship. However, a simple exponential decline would only occur if there were no density-

dependent effects (e.g. no predator satiation or non-linear functional responses of predators to prey densities; Bjørnstad et al. 1999). Both models account for temporal and larger scale (across subregions) spatial variance with the random effects and, thus, analyze only the relationships between predator and prey at subregional spatial scales. Intra-cohort density-dependent mortality can occur in juvenile sea scallops (Wong & Barbeau 2005, Hart & Shank 2011), but this cannot be detected using our methods since we only have data on the abundance of sea scallop recruits after the density-dependent recruitment processes have occurred.

We developed the log-log and log-linear models through a constrained, forward-selection process with model selection based on AIC (Akiake's information criteria) values and coefficients of the fixed effects (Burnham & Anderson 2004, Hoeting et al. 2006). The purpose of the model-building exercise was not to identify a single, best model but rather to identify which predators were affecting scallop recruitment and the time lag where predator density best described prey density. We constrained model selection because we wished to avoid multiple testing errors associated with the re-testing of parameters in stepwise model building but we lacked strong, *a priori* hypotheses for the life-history stage where scallops would be most affected by predation (Anderson & Burnham 2002, Whittingham et al. 2006). For our model-building process we first built individual mixed-effect linear models for each predator at each scallop age (Year-0 through Year-2). We then compared each model AIC to a common null model that contained only the random effects (Appendix 1, Eq. 1). Thus, models with an AIC below the null model (a negative Δ AIC) are interpreted as an improvement over the null model. For each predator species, we then selected the temporal lag that produced the best model and added random slope terms to assess variations in predator-prey relations across time or subregions (Pinheiro & Bates 2000, present study Appendix 1, Eq. 3). Finally, we combined the best models from each predator into multispecies models and assessed potential predator interactions. We assessed the total variance explained by each model by computing the pseudo- R^2 (Kissling & Carl 2008).

For model validation, model residuals were visually examined using quantile-quantile and residual scatterplots. We examined assumptions of linearity using general additive mixed models (GAMMs) with the same model structure but with smoothers instead of linear estimators (Wood 2006). We also assessed the spatial autocorrelation of residuals as the weighted

average of the absolute Moran's I values with a spatial lag of <2 distance units (Legendre & Fortin 1989, Kissling & Carl 2008, Birkhofer et al. 2010). Because spatial autocorrelation was evident in the residuals, we repeated the above model-building process with exponential spatial correlation structures (SCSs) included in each linear model (Pinheiro & Bates 2000, Dormann et al. 2007, present study Appendix 1). All statistical analyses were conducted on the R statistical platform (R Development Core Team 2009).

We tested if predator temporal dynamics is negatively correlated with scallop recruitment with a similar set of log-log models that only examined temporal predator-prey associations. To this end, all spatial associations between predators and prey were removed by regressing predator biomass against scallop recruit density for each subregion and year. We then built a set of log-log mixed-effect models using the un-centered residual predator densities and subregion as a random effect:

Temporal log-log model:

$$\log(r_{ijk}) = \beta_0 + \beta_1 \cdot \log(p_{ijk}^*) + b_i + \epsilon_{ijk} \quad (3)$$

where p_{ijk}^* is the spatially detrended predator data and b_i is the geometric mean of recruits in subregion i . For each model, temporal autocorrelation was computed as the mean correlation among residuals with a 1 yr time lag. Because temporal autocorrelation was negligible beyond 1 yr, we determined if observed patterns were robust to the removal of temporal autocorrelation by repeating each model with a first-order autoregressive structure (Pinheiro & Bates 2000).

Finally, to examine the effect of spatially aggregating data on apparent predator-prey relationships and to visualize temporal predator-prey trajectories, we calculated the geometric means for juvenile scallop density and predator biomass for each subregion and year. A linear, mixed-effect analysis was then performed on the aggregated data with *Astropecten americanus* and *Cancer* spp. in Year-0 as fixed effects and subregion as a random effect, and results were compared to a null model with only the random effect. *Asterias* spp. was excluded from this analysis because our spatial and temporal analysis did not provide sufficient evidence for inclusion at any time lag.

RESULTS

A total of 2389 regular scallop *Placopecten magellanicus* survey tows were conducted within the study area between 2000 and 2010, with data on benthic predators collected from 869 tows. Juvenile scallop

densities were strongly right-skewed, ranging from 0 (14% of observations) to 15288 recruits, with a median of 22 recruits tow^{-1} . The spatial cluster analysis of recruitment dynamics identified 10 subregions with synchronous dynamics. We excluded the shallowest and deepest subregions due to insufficient data, retaining 8 subregions with depths ranging from 36 to 80 m. Subregion 4, a central and inshore portion of the study area, initially segregated from the rest of the study area as distinct. In successive splits, the northern portion of the study area (Subregions 1 to 3) segregated from the southern portion (Subregions 5 to 8), followed by the deeper habitats segregating from the shallower habitats.

Yearly mean recruitment ranged from a low of 62 scallops tow^{-1} in 2009 to highs of 386 and 299 scallops tow^{-1} in spawning years 2001 and 2002, respectively (Fig. 2a, note that recruitment in the figure is lagged back 2 yr from the sampling year to the spawning year). Scallop stock biomass increased rapidly from 1998 to 2003, with little change in biomass thereafter (Fig. 2a).

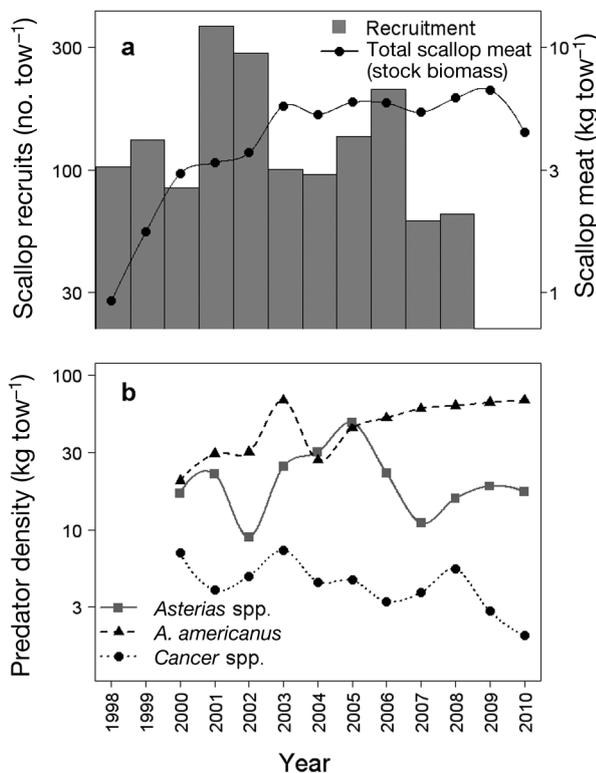


Fig. 2. *Placopecten magellanicus*. (a) Mean sea scallop recruit abundance and total scallop meat weight (stock biomass) per tow and (b) predator (*Asterias* spp., *Astropecten americanus*, *Cancer* spp.) biomass per tow in the Mid-Atlantic during the study period. Recruitment is lagged back 2 yr to indicate the approximate year of settlement rather than the year of observation

The spatial distribution of juvenile scallops was roughly centered but irregularly distributed across the study area (Fig. 3a), with 3 areas of high interannual variability (Fig. 3e). The observed recruitment peaks in 2001 and 2002 were largely constrained to the center of the study area (Subregions 4 and 5), while a second recruitment peak in 2006 occurred in the southern portion of the study area (Subregions 5, 6, and 8).

All predators exhibited right-skewed distributions with biomass ranging from 0 to 83 kg tow^{-1} for *Asterias* spp. (16% of samples were zeros), 0 to 173 kg tow^{-1} for *Astropecten americanus* (21% zero values), and 0 to 79 kg tow^{-1} for *Cancer* spp. (<1% zero values). There were no clear temporal trends in mean *Asterias* spp. biomass during the study period, with low densities in 2002 and 2007 and a peak in 2005 (Fig. 2b). High densities of *Asterias* spp. were generally constrained to the shallower inshore portions of the study area (Fig. 3b), with regions of temporal variability on the northern and southern boundaries of the study region (Fig. 3f).

Astropecten americanus biomass showed an increasing trend through the study period, and its densities were highest in deeper waters (Fig. 3c), with high temporal variability at intermediate depths (Figs. 2b & 3c,g). *Cancer* crab biomass declined slightly during our study, with peak biomasses in 2000, 2003, and 2008, and a historic low in 2010 (Fig. 2b). *Cancer* spp. densities were highest in the southern portion of the study area (Fig. 3d), with regions of higher temporal variability in the northern and southern extents of the study area (Fig. 3h).

The fitted variogram models used for interpolating predator densities indicated differences among predators and across years in the spatial structures of the populations. This resulted in varying precision in our estimation of predator densities. Variogram models for all species and all years had non-zero nuggets, suggesting the presence of small-scale variability and sampling error (Bivand et al. 2008). Relative nugget values, scaled to the variogram sill, were lowest for *Astropecten americanus* (interannual mean = 22%, range = 13 to 37%), suggesting good potential for precise interpolation. Relative nuggets were higher for *Asterias* spp. (mean = 42%, range = 26 to 60%), while *Cancer* spp. showed intermediate precision (mean relative nugget = 31%, range = 15 to 46%), with the exception of years 2000 and 2001 when small-scale variability was unusually high with relative nuggets of 70 and 89%, respectively.

Predators had different spatial associations with scallop recruits at regional scales in the cross-corre-

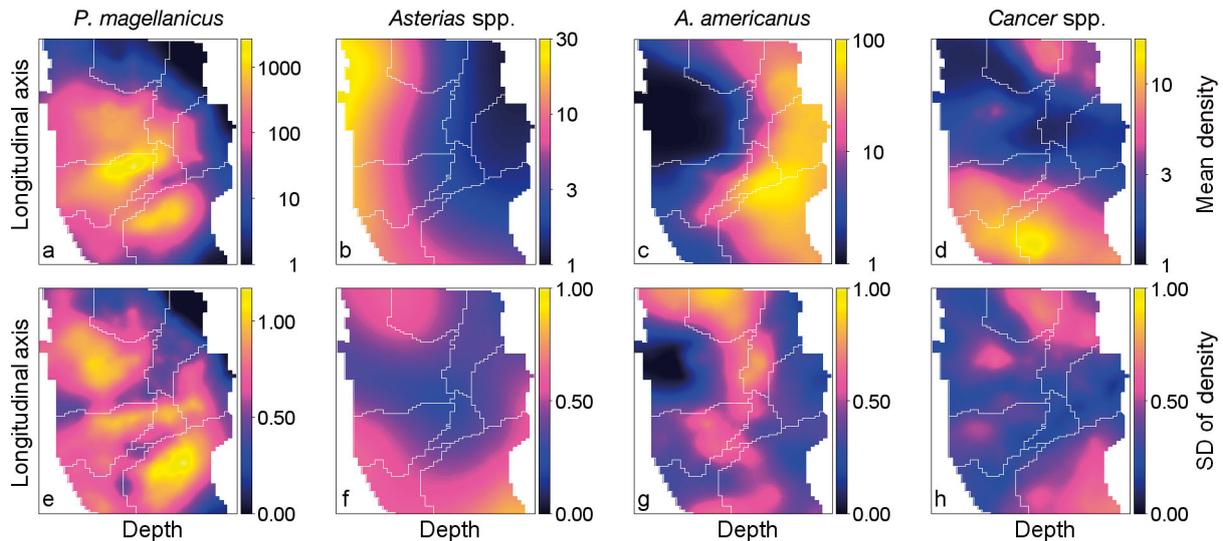


Fig. 3. *Placopecten magellanicus*. Maps of mean density (a–d) and standard deviation (SD; e–h) of sea scallop recruitment and predator density from 2000 to 2010 plotted by longitudinal axis and depth. Means are arithmetic means of sea scallop density (no. tow⁻¹) and predator biomass (kg tow⁻¹), while SD are in orders of magnitude (SD of log₁₀-transformed densities). Plots are (biomass and SD each): (a,e) juvenile sea scallop *P. magellanicus* density, (b,f) *Asterias* spp., (c,g) *Astropecten americanus*, and (d,h) *Cancer* spp.

lation analysis (Fig. 4). *Asterias* spp. was positively associated with scallop recruitment at small scales, with cross-correlations of about 0.1 and similar correlograms for all time lags (Fig. 4a). *Astropecten americanus* was negatively associated with scallop recruits, with distinct correlograms for different time lags (Fig. 4b). The spatial correlation between *A. americanus* and scallop recruitment was strongest for Year-0 (–0.21) and weakened through Year-1 and Year-2 (–0.16 and –0.10, respectively). The regional spatial association between *Cancer* spp. and scallop recruitment was positive, and the correlograms for different time lags were also distinct (Fig. 4c). However, the small-scale association between *Cancer* spp. and scallop recruits is strongest for Year-2 (0.07) and weakens through Year-1 and Year-0 (0.04 and 0.004, respectively; Fig. 4c). The spatial association between *Cancer* spp. in Year-0 and scallop recruits increases from nearly zero at short distances to a positive correlation at intermediate distances before declining to zero at larger distances.

Analysis of predator–prey relationships at subregional scales differed from regional scales for *Asterias* spp. and *Cancer* spp. In the spatial log-log model analysis, both *Cancer* spp. and *Astropecten americanus* were negatively associated with sea scallop densities, but there was no strong relationship between *Asterias* spp. and sea scallop densities (Table 1). For both *Cancer* spp. and *A. americanus*, predator densities in Year-0 (the summer of spawning) were the best predictors, and models for both predators

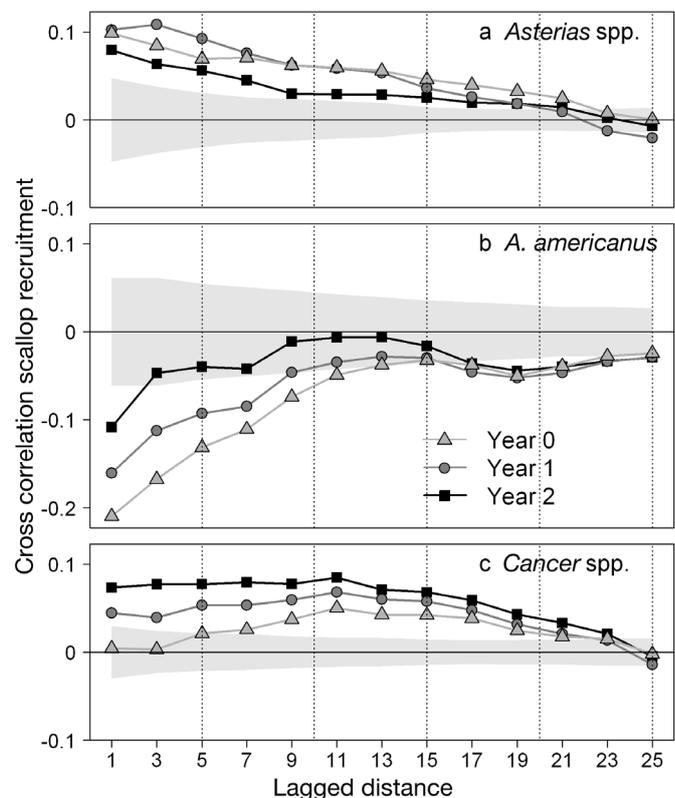


Fig. 4. *Placopecten magellanicus*. Spatial cross-correlations for predators (*Asterias* spp., *Astropecten americanus*, *Cancer* spp.) and juvenile scallop densities with separate correlograms for different time lags. Lagged distance is in re-projected coordinates and represents changes in depth or position along the longitudinal axis. Shaded areas: points outside the shaded areas are significant at $p < 0.05$

were improved by including random slope terms. The model without the predator interaction term performed better than the model with the interaction term. The best log-log spatial model included random intercept and slope terms for both *A. americanus* and *Cancer* spp.

The diagnostics for the spatial log-log models indicated that model errors are spatially correlated and the relationships between predators and scallop recruit densities are nonlinear (Table 1, Fig. 5). Residual spatial autocorrelation (RSA) was evident in all linear models. Models with lower AIC values had lower RSAs, with RSA declining from 0.17 in the null model to 0.06 in the best model, indicating that residuals in the best model are still weakly autocorrelated and justifying the examination of models with spatial correlation structures (SCSs). The inclusion of SCSs in the models weakened the relationships between predators and scallop recruits (Table 1). For models with SCSs, only models with *A. americanus* terms are supported over the null model with the strongest relationship again occurring in Year-0. Both of the 2-

species SCS models with random slope terms for *A. americanus* resulted in singular convergences and could not be evaluated. The response curves for the GAMM models suggested that predator–prey relationships are nonlinear with near-zero slopes at low predator densities and increasingly negative slopes at high densities for both *A. americanus* and *Cancer* spp. (Fig. 5a,b). The predator–prey relationships for additive SCS models are also nonlinear for *A. americanus* (Fig. 5c). However, the relationship for additive *Cancer* spp. SCS models is linear and not statistically relevant (Fig. 5d).

Results from the spatial log-linear models were similar to the log-log models, but the shape of the response curves were different (Table 2, Fig. 6). Both *Astropecten americanus* and *Cancer* spp. were negatively associated with scallop recruitment and predator–prey relationships were strongest for Year-0 scallops. *Asterias* spp. densities showed a negative association with scallop recruits, with more support for Year-1 than Year-0, though the strength of the association was comparatively weak and not ana-

Table 1. *Placopecten magellanicus*. Spatial log-log models for predators (*Asterias* spp., *Astropecten americanus*, *Cancer* spp.) and scallop juveniles. Δ AIC (Akaike's information criterion) values are relative to the null random intercept model. RSA is the model residual spatial autocorrelation. Notation for model representations (left column) are in Appendix 1. Yr denotes scallop age (0 to 2 yr) and SR-Y denotes the subregion-year random effect. Model parameters joined to SR-Y with * indicate random slope terms. SC indicates models that were not solved due to singular convergences in parameter estimates

Model	Models without spatial correlation structures			Models with spatial correlation structures	
	Coefficient \pm SE	Δ AIC	RSA	Coefficient \pm SE	Δ AIC
SR-Y (null model)	–	0.0	0.171	–	0.0
<i>Asterias</i> Yr2 + SR-Y	0.155 \pm 0.061	–0.5	0.169	0.266 \pm 0.089	–3.8
<i>Asterias</i> Yr1 + SR-Y	0.087 \pm 0.065	3.8	0.171	0.244 \pm 0.092	–2.0
<i>Asterias</i> Yr0 + SR-Y	0.058 \pm 0.065	4.8	0.172	0.275 \pm 0.091	–4.1
<i>A. americanus</i> Yr2 + SR-Y	–0.193 \pm 0.033	–27.8	0.159	–0.154 \pm 0.044	–5.7
<i>A. americanus</i> Yr1 + SR-Y	–0.231 \pm 0.032	–42.8	0.162	–0.199 \pm 0.044	–13.6
<i>A. americanus</i> Yr0 + SR-Y	–0.291 \pm 0.032	–72.0	0.155	–0.250 \pm 0.044	–25.7
<i>A. americanus</i> Yr0 * SR-Y	–0.351 \pm 0.064	–140.1	0.084	–0.269 \pm 0.096	–24.2
<i>Cancer</i> Yr2 + SR-Y	–0.142 \pm 0.054	–0.3	0.168	–0.023 \pm 0.074	5.3
<i>Cancer</i> Yr1 + SR-Y	–0.207 \pm 0.055	–7.4	0.168	–0.042 \pm 0.077	5.0
<i>Cancer</i> Yr0 + SR-Y	–0.363 \pm 0.054	–37.1	0.161	–0.187 \pm 0.074	–0.4
<i>Cancer</i> Yr0 * SR-Y	–0.385 \pm 0.103	–92.8	0.115	–0.187 \pm 0.078	3.6
<i>A. americanus</i> Yr0 ^a	–0271. \pm 0.033	–96.7	0.145	–0.239 \pm 0.044	–22.2
+ <i>Cancer</i> Yr0 + SR-Y	–0.305 \pm 0.053			–0.106 \pm 0.076	
<i>A. americanus</i> Yr0	–0273. \pm 0.036	–90.6	0.146	–0.244 \pm 0.046	–16.8
* <i>Cancer</i> Yr0 + SR-Y	–0.307 \pm 0.057			–0.117 \pm 0.082	
	–0.005 \pm 0.050			0.024 \pm 0.067	
<i>A. americanus</i> Yr0 * SR-Y	–0.325 \pm 0.062	–153.9	0.077	SC	–
+ <i>Cancer</i> Yr0 + SR-Y	–0.257 \pm 0.056				
<i>A. americanus</i> Yr0 + SR-Y	–0.226 \pm 0.034	–125.8	0.116	–0.239 \pm 0.044	–18.2
+ <i>Cancer</i> Yr0 * SR-Y	–0.303 \pm 0.088			–0.011 \pm 0.077	
<i>A. americanus</i> Yr0 * SR-Y	–0.286 \pm 0.061	–170.5	0.062	SC	–
+ <i>Cancer</i> Yr0 * SR-Y	–0.234 \pm 0.087				

^aResults for corresponding additive model are shown in Fig. 5

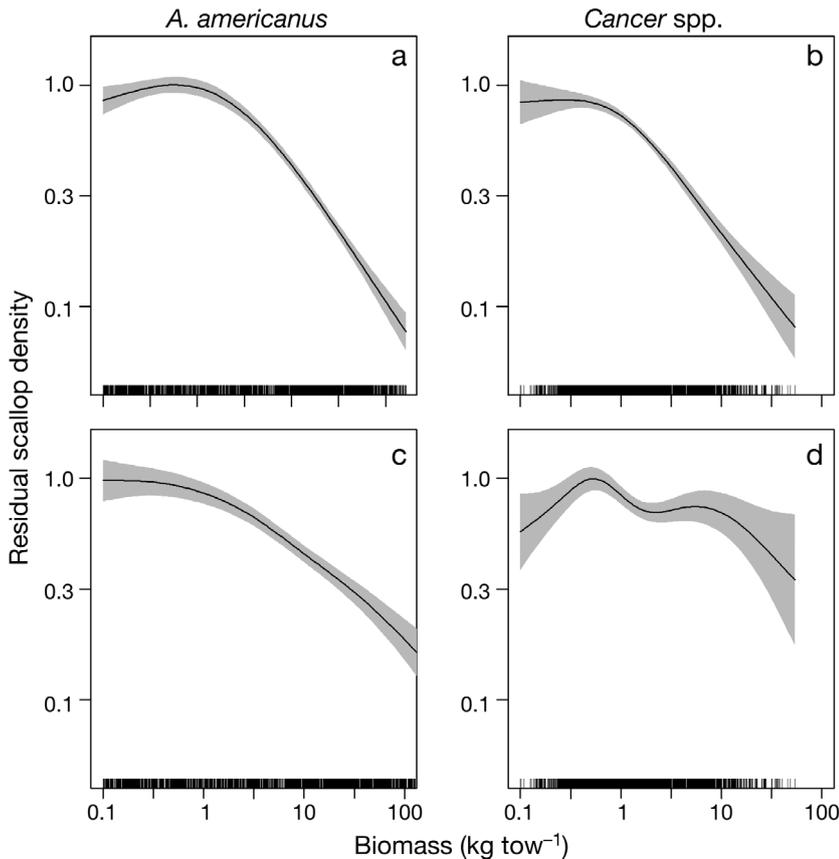


Fig. 5. *Placopecten magellanicus*. Predator–prey response curves for the spatial log-log general additive mixed models without random slope terms (* in Table 1) based on models with (a,b) and without (c,d) spatial autocorrelation structures for *Astropecten americanus* (a,c) and *Cancer* spp. (b,d). Tick marks along the x-axis indicate the presence of survey data

lyzed further. The inclusion of random slope terms for both *A. americanus* and *Cancer* spp. provided improvement over simpler random intercept models, and 2-species models improved single-species models, though there is no evidence for predator interactions. Like the log-log model, the best log-linear model had random intercept and slope terms for both predators. Most predator–prey relationships were stronger for log-linear models than comparable log-log models, though not consistently for the models for *Cancer* spp.

Similar to the log-log models, the diagnostics for the log-linear models indicated spatially structured model errors and nonlinear relationships between predator biomass and scallop recruitment. Models with lower RSAs also had lower AIC values relative to the null model, and the model with random slope terms for both *Astropecten americanus* and *Cancer* spp. had the lowest RSA (0.082), again suggesting that SCSs are appropriate additions to the log-linear models (Table 2). Models with SCSs had weaker

predator–prey relationships, and only models for *A. americanus* are supported over the null model, again with the strongest relationship occurring in Year-0.

The response curves from the additive models indicate that prey depletion rates increase with increased predator biomass for low to moderate predator biomass but approach a threshold at high predator biomass (Fig. 6). However, additive models with spatial autocorrelation structures estimate linear responses for both *Astropecten americanus* and *Cancer* spp. densities, suggesting that the log-linear model may be appropriate for modeling these predator–prey relationships. The best log-linear model had a pseudo- R^2 of 0.41, compared to a pseudo- R^2 of 0.11 for the null model. Thus, predation accounts for ~30% of the total deviance in this model.

Results from the analysis of temporal associations in predator–prey abundances support the results from the spatial analysis. Interannual variations in both *Cancer* spp. and *Astropecten americanus* densities were negatively associated with sea scallop recruitment in Year-0 and Year-1, with the strongest relationships in Year-0

(Table 3). Models containing both *A. americanus* and *Cancer* spp. improved only minimally over models with *A. americanus* alone, suggesting some temporal correlation between these predators. Again, including an interaction term between the predators did not improve model fit. Temporal fluctuations in *Asterias* spp. densities again showed no association with scallop recruitment dynamics.

We constructed mortality curves using the coefficients from the spatial log-linear models as depreciation rates (Table 2, Fig. 7). We used the best single-species models with and without SCSs as reasonable higher and lower estimates of predation rates. The higher estimates of predation rates for both predators suggest the potential for >90% juvenile sea scallop mortality during their first 2 yr post-settlement at high predator densities. At a moderately high *Astropecten americanus* density of 50 kg tow⁻¹ (about the upper 13th percentile of observed samples) the models predict juvenile sea scallop mortality between 48 and 76%. A high *Cancer* spp.

Table 2. *Placopecten magellanicus*. Results of spatial log-linear models for predators (*Asterias* spp., *Astropecten americanus*, *Cancer* spp.) and scallop juveniles. Δ AIC (Akaike's information criterion) values are relative to the random effects model. RSA is the model residual spatial autocorrelation. Notation for model representations (left column) are in Appendix 1. Yr denotes scallop age (0 to 2 yr) and SR-Y denotes the subregion-year random effect. Model parameters joined to SR-Y with an asterisk indicate random slope terms. Depreciation curves for models in **bold** are shown in Fig. 7

Model	Models without spatial correlation structures			Models with spatial correlation structures	
	Coefficient \pm SE	Δ AIC	RSA	Coefficient \pm SE	Δ AIC
SR-Y (null model)	–	0.0	0.171	–	0.0
<i>Asterias</i> Yr2 + SR-Y	-0.014 ± 0.004	1.9	0.169	0.003 ± 0.006	9.9
<i>Asterias</i> Yr1 + SR-Y	-0.026 ± 0.005	-15.1	0.162	-0.008 ± 0.008	8.9
<i>Asterias</i> Yr0 + SR-Y	-0.024 ± 0.005	-9.2	0.165	-0.003 ± 0.008	9.7
<i>A. americanus</i> Yr2 + SR-Y	-0.008 ± 0.001	-87.0	0.132	-0.006 ± 0.001	-19.4
<i>A. americanus</i> Yr1 + SR-Y	-0.009 ± 0.001	-102.0	0.136	-0.008 ± 0.001	-33.9
<i>A. americanus</i> Yr0 + SR-Y	-0.009 ± 0.001	-112.1	0.126	-0.008 ± 0.001	-41.0
<i>A. americanus</i> Yr0 * SR-Y	-0.013 ± 0.002	-143.2	0.088	-0.008 ± 0.001	-37.0
<i>Cancer</i> Yr2 + SR-Y	-0.018 ± 0.005	-2.6	0.175	-0.002 ± 0.007	10.0
<i>Cancer</i> Yr1 + SR-Y	-0.019 ± 0.005	-3.1	0.173	-0.005 ± 0.007	9.6
<i>Cancer</i> Yr0 + SR-Y	-0.029 ± 0.005	-25.1	0.168	-0.014 ± 0.007	6.1
<i>Cancer</i> Yr0 * SR-Y	-0.038 ± 0.015	-50.0	0.143	-0.014 ± 0.007	10.2
<i>A. americanus</i> Yr0 ^a + <i>Cancer</i> Yr0 + SR-Y	-0.010 ± 0.001 -0.036 ± 0.005	-158.2	0.123	-0.008 ± 0.001 -0.015 ± 0.007	-35.4
<i>A. americanus</i> Yr0 * <i>Cancer</i> Yr0 + SR-Y	-0.010 ± 0.001 -0.038 ± 0.005 0.000 ± 0.000	-140.8	0.125	-0.008 ± 0.001 -0.016 ± 0.008 0.000 ± 0.000	-17.8
<i>A. americanus</i> Yr0 * SR-Y + <i>Cancer</i> Yr0 + SR-Y	-0.012 ± 0.002 -0.032 ± 0.005	-170.7	0.092	-0.008 ± 0.001 -0.015 ± 0.007	-31.4
<i>A. americanus</i> Yr0 + SR-Y + <i>Cancer</i> Yr0 * SR-Y	-0.010 ± 0.001 -0.031 ± 0.007	-157.0	0.117	-0.008 ± 0.001 -0.015 ± 0.007	-31.5
<i>A. americanus</i> Yr0 * SR-Y + <i>Cancer</i> Yr0 * SR-Y	-0.012 ± 0.002 -0.025 ± 0.008	-180.3	0.082	-0.008 ± 0.001 -0.015 ± 0.007	-25.5

^aResults for corresponding additive model are shown in Fig. 6

density of 10 kg tow⁻¹ (the upper fourth percentile of the sampled densities) is predicted to result in scallop mortality rates of between 21 and 68% in their first 2 yr post-settlement.

Relationships between predators and scallop recruitment were weaker when data were aggregated to the subregion level (Fig. 8). The best model had only *Astropecten americanus* in Year-0 as a fixed effect (Δ AIC = -7.0 relative to null model), with no support for the inclusion of *Cancer* spp. or random slope effects for either predator. A general pattern of declining scallop recruitment and increasing predator densities is present in multiple subregions and particularly clear in Subregion 4 (Fig. 8d), but is not evident in all subregions.

DISCUSSION

We found varying levels of evidence for predators influencing sea scallop *Placopecten magellanicus* recruitment. There is strong evidence that *Astropecten americanus* has affected scallop recruitment in our

study area. Predator–prey relationships are consistently negative in the spatial log-log, log-linear, and temporal models, with stronger relationships in the earliest life-history stages. These models also remain relevant with the inclusion of autocorrelation structures, suggesting that this relationship is not an artifact of autocorrelation effects (Diniz-Filho et al. 2003). Additionally, the linear nature of the additive log-linear models suggests that the log-linear models are more appropriate, implying a causative relationship between predator and prey rather than a geographic association. These results support the hypothesis that predation by *A. americanus* is taking place primarily in the first year after settlement (between Year-0 and Year-1 observations), as expected, because the scallops would be too large to be consumed by *A. americanus* after the first year.

Our analysis provides moderate evidence that *Cancer* crabs are structuring scallop recruitment patterns. The relationship between *Cancer* crabs and sea scallops is persistently negative at subregional scales, including both spatial and temporal analysis. Additionally, there are clear differences in the

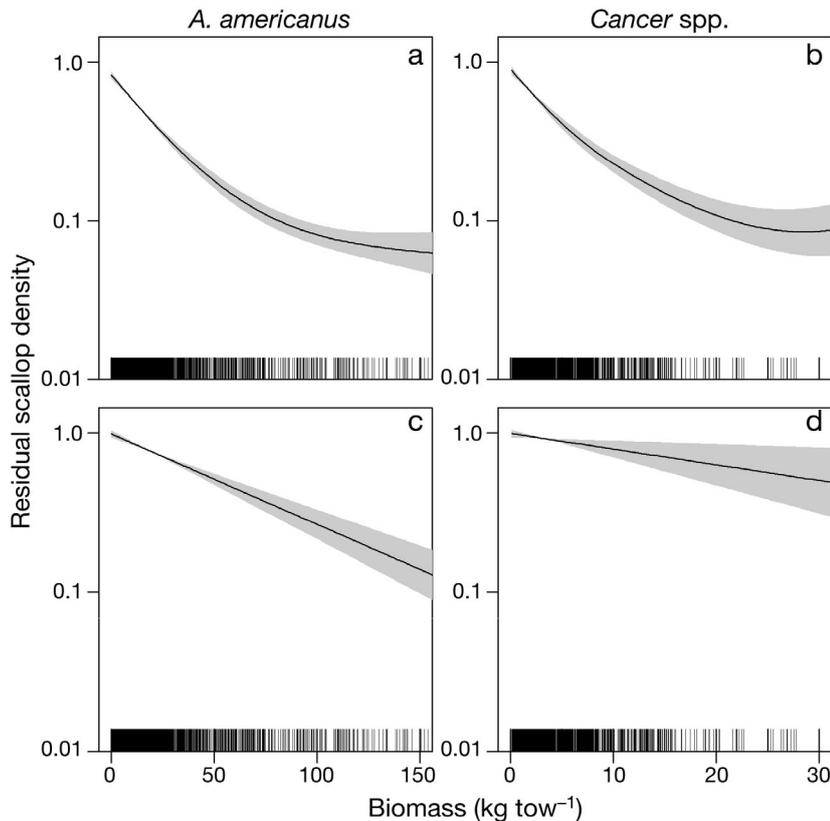


Fig. 6. *Placopecten magellanicus*. Predator–prey response curves for the spatial log-linear general additive mixed models without random slope terms (superscript a in Table 2) based on models with (a,b) and without (c,d) spatial autocorrelation structures for *Astropecten americanus* (a,c) and *Cancer* spp. (b,d). Tick marks along the x-axis indicate the presence of survey data

strength of the predator–prey relationship in different scallop life-history stages, suggesting that predation effects are age specific. Conversely, there is more support for the spatial log-log model than the log-linear model, based on Δ AICs, and there is no support for *Cancer* effects in models that include spatial correlation structures, suggesting that this relationship is partially confounded by common environmental processes.

There was no clear evidence that *Asterias* spp. were affecting recruitment in our study area. *Asterias* spp. densities are unrelated to sea scallop recruitment in the spatial log-log model, have weak negative relationships in the spatial log-linear model that are not robust to inclusions of spatial autocorrelation terms, and model fit does not vary by life-history stage. Further, temporal fluctuations in predator density are not correlated with fluctuations in prey density.

Comparison of the spatial distributions of predators and prey at regional scales (cross-correlation analysis) versus subregional scales (mixed-effect models)

provides insight into the importance of unmeasured environmental variables on predator–prey associations. The negative relationship between *Astropecten americanus* and scallop recruitment is consistent between the regional and subregional analyses, with stronger relationships in earlier life-history stages, suggesting a spatial association that is largely causative. For *Cancer* crabs, the regional association was positive, while the subregional association was negative. We interpret this pattern as the combined influence of both environmental correlates and causative interactions. At regional scales, a common response to environmental gradients results in a positive relationship, but at smaller, subregional scales predator depletion results in a negative association between scallops and *Cancer* crabs (Ciannelli et al. 2008). *Asterias* spp. were positively associated with scallop recruits at regional scales, but unassociated at subregional scales. Such changes of associations between prey and mobile predators have been reported in other ecological systems and may represent shifts between top-down and bottom-up control (Rose & Leggett 1990, Fauchald & Erikstad 2002, Tobin & Bjørnstad 2003, Frank et al. 2007, Santora et al. 2011). The positive regional-scale relationship may be a result of a latent, environmental variable that is removed by the random-effects term and the reduced spatial scale (Keitt et al. 2002).

The strength of the relationship between predators and scallop recruit dynamics parallels our capacity to precisely estimate predator densities at small spatial scales. Moderate to high variogram nugget values, relative to the sill values, indicate that much of the process-based variance in predator and prey population dynamics occurs at scales smaller than the resolution of our data, limiting our capacity for inference. Our data on scallop and predator densities are based on dredge tows collected over 1 nautical mile. Sea scallops and the predators in our study are known to exhibit high variability on smaller spatial scales due to fine-scale habitat variability and tendencies to actively aggregate (Stokesbury & Himmelman 1993, 1995, Barbeau et al. 1996, S. Gallagher pers. comm.). The variogram models used to characterize the spa-

Table 3. *Placopecten magellanicus*. Results from the temporal log–log models with spatially detrended predator (*Asterias* spp., *Astropecten americanus*, *Cancer* spp.) densities. Δ AIC (Akaike's information criterion) values are relative to the null random effects model. RTA is the model residual temporal autocorrelation. Notation for model representations (left column) are in Appendix 1. Yr denotes scallop age (0 to 2 yr) and SR denotes the subregion random effect. Model parameters joined to SR with an asterisk indicate random slope terms

Model	Models without spatial autocorrelation structures			Models with spatial autocorrelation structures	
	Coefficient \pm SE	Δ AIC	RSA	Coefficient \pm SE	Δ AIC
SR (null model)	–	0.0	0.070	–	0.0
<i>Asterias</i> Yr2 + SR	0.014 \pm 0.051	6.1	0.070	0.011 \pm 0.049	6.1
<i>Asterias</i> Yr1 + SR	0.059 \pm 0.051	4.8	0.069	0.053 \pm 0.050	5.0
<i>Asterias</i> Yr0 + SR	0.082 \pm 0.054	3.7	0.063	0.076 \pm 0.052	3.9
<i>A. americanus</i> Yr2 + SR	–0.033 \pm 0.037	6.0	0.070	–0.026 \pm 0.035	6.3
<i>A. americanus</i> Yr1 + SR	–0.135 \pm 0.035	–7.7	0.062	–0.118 \pm 0.034	–5.1
<i>A. americanus</i> Yr0 + SR	–0.145 \pm 0.033	–11.6	0.057	–0.128 \pm 0.032	–8.6
<i>A. americanus</i> Yr0 * SR	–0.105 \pm 0.079	–31.2	0.034	–0.093 \pm 0.072	–24.7
<i>Cancer</i> Yr2 + SR	0.041 \pm 0.052	5.5	0.072	0.044 \pm 0.050	5.4
<i>Cancer</i> Yr1 + SR	–0.145 \pm 0.056	–0.4	0.067	–0.124 \pm 0.054	1.0
<i>Cancer</i> Yr0 + SR	–0.203 \pm 0.055	–7.2	0.062	–0.176 \pm 0.053	–4.6
<i>Cancer</i> Yr0 * SR	–0.190 \pm 0.055	–14.6	0.045	–0.129 \pm 0.087	–10.5
<i>A. americanus</i> Yr0 + <i>Cancer</i> Yr0 + SR	–0.139 \pm 0.034 –0.190 \pm 0.055	–17.2	0.049	–0.123 \pm 0.032 –0.164 \pm 0.053	–11.9
<i>A. americanus</i> Yr0 * <i>Cancer</i> Yr0 + SR	–0.136 \pm 0.036 –0.186 \pm 0.059 –0.009 \pm 0.053	–9.2	0.050	–0.120 \pm 0.035 0.160 \pm 0.057 –0.012 \pm 0.051	–5.9
<i>A. americanus</i> Yr0 * SR + <i>Cancer</i> Yr0 + SR	–0.096 \pm 0.078 –0.176 \pm 0.057	–34.5	0.030	–0.085 \pm 0.071 –0.154 \pm 0.054	–26.4
<i>A. americanus</i> Yr0 + SR + <i>Cancer</i> Yr0 * SR	–0.122 \pm 0.033 –0.153 \pm 0.087	–20.8	0.038	–0.110 \pm 0.032 –0.130 \pm 0.080	–15.1
<i>A. americanus</i> Yr0 * SR + <i>Cancer</i> Yr0 * SR	–0.087 \pm 0.069 –0.144 \pm 0.076	–32.9	0.024	–0.079 \pm 0.063 –0.121 \pm 0.071	–24.8

tial autocorrelation of predators exhibit varying degrees of spatial structure and local predictability, both across predators and across years. Small-scale variance (scales smaller than our sampling units) actually exceeded the total geographic variance in predator densities in some years for *Asterias* spp. and *Cancer* spp. (i.e. the variogram nugget exceeds the partial sill). The calculation of predator densities at unsampled locations by interpolation further decreases precision and weakens inferential testing (de Knecht et al. 2010). As a result, the weaker predator–prey relationships detected for *Cancer* spp. and *Asterias* spp. may be partially due to our inability to model processes and population structures at an appropriately small scale with our data.

Coefficients from our log-linear models suggest that moderate to high densities of either *Astropecten americanus* or *Cancer* crabs are capable of consuming the majority of juvenile sea scallops in their vicinity. For *A. americanus*, our models predict an upper scallop mortality rate of 76% at sea star densities of 50 kg tow^{–1}, corresponding to a median density of 13 100 sea stars tow^{–1}. Survey dredge efficiency for

A. americanus is unknown, but estimated efficiency for scallops is about 0.4 (Northeast Fisheries Science Center 2010). If dredge efficiency is similar for *A. americanus*, then 50 kg tow^{–1} would correspond to densities of about 7.25 m^{–2}. Though *A. americanus* can only consume small juvenile scallops, they are capable of consuming multiple juvenile scallops per day (Franz & Worley 1982, Smereka 2003). Thus, such high densities of *A. americanus* would certainly be capable of consuming the majority of scallop recruits in their area. Our results and the spatial distribution of *A. americanus* further support the assertion by Hart (2006) that predation by *A. americanus* may functionally exclude sea scallops from the deeper depths of the Mid-Atlantic Bight.

Similarly, *Cancer* spp. are predicted to result at an upper mortality rate of 62% at densities of 10 kg tow^{–1}. Again, correcting for dredge efficiency, this would translate into actual densities of 0.1 crabs m^{–2} for crabs large enough to be retained in the dredge. *Cancer* crabs are capable of eating up to 3 scallops d^{–1}, and scallops are susceptible to crab predation over a broader range of sizes (Nadeau et al. 2009).

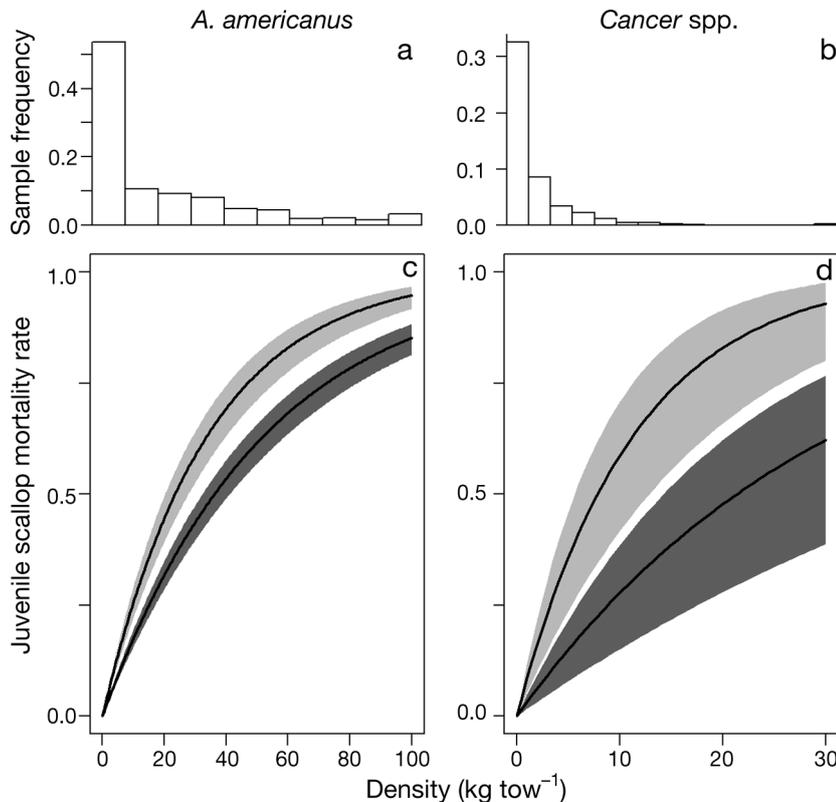


Fig. 7. *Placopecten magellanicus*. Estimated predation rates of juvenile sea scallops by *Astropecten americanus* (a,c) and *Cancer* spp. (b,d) based on parameter estimates for best single-species log-linear models (Table 2). (a,b) Frequency of sample densities. (c,d) Predicted (\pm SE) mortality rates for models with (dark gray) and without (light gray) spatial autocorrelation structures

Additionally, crab predation rates on scallops are density dependent and may account for a recent scallop mortality event in this region (Wong & Barbeau 2005, Hart & Shank 2011). Given the broader range of scallop sizes that are susceptible to crab predation and that *Cancer* crabs have been recorded to eat up to 3 scallops d⁻¹, it is again reasonable that crabs at these densities would be sufficient to consume the majority of scallop recruits in their area (Nadeau et al. 2009).

Based on the literature, we had expected *Cancer* crabs to affect sea scallops populations primarily between Year-1 and Year-2, when recruits are larger, rather than in Year-0 as suggested by the analysis. Laboratory experiments have found *Cancer* crabs to prefer scallops in the 20 to 50 mm SH range over smaller scallops due to difficulties in capturing and handling small prey and the decreased profitability in consuming small prey when larger prey are available (Elnor & Jamieson 1979, Barbeau & Scheibling 1994). However, these studies also demonstrated that preferred prey size scales with predator size, suggesting that smaller crabs may be more capable of

consuming small sea scallops. These studies used crabs from 45 to 130 mm carapace width. In comparison, modal size for *Cancer* spp. from the dredge survey is <60 mm (Shank unpubl. data), and survey dredges presumably undersample smaller crabs due to the 38 mm mesh liner. Thus, there may be an unsampled portion of the *Cancer* spp. population affecting scallop recruitment. Finally, *Cancer* crabs exhibit prey switching, targeting less preferable prey when preferred prey are not abundant (Wong & Barbeau 2005), so crabs may facultatively switch to smaller prey when encounter rates with scallops in the preferred size range are low.

Our conclusions on which predators are affecting recruit densities differ somewhat from the previous analysis by Hart (2006) who found evidence that *Astropecten americanus* and *Asterias* spp. were potentially affecting scallop recruitment but not *Cancer* crabs. The disparity between the previous study and the current analysis is due to our segregation of the study area into subregions and the benefit of a longer time series as Hart (2006) only

had data for 2000 to 2002. The inclusion of subregions as a random variable disrupts the large-scale biogeographic patterns that otherwise result in the spurious spatial correlation between *Asterias* spp. and scallop recruits seen in Hart (2006). The current analysis is unable to discriminate between persistent geographical patterns and causal predation relationships for *Asterias* spp.; we cannot conclude that *Asterias* spp. has no effect on scallop recruitment, but only that it cannot be detected with our data.

The mobility of *Cancer* spp. likely obscured its effects on scallop recruitment using the methodology of Hart (2006). The extended time series now available allowed us to include time lags to the models which strengthened effects for *Astropecten americanus* but were crucial for detecting the effects for *Cancer* crabs. Without time lags in the models, our results are similar to those of Hart (2006), with moderate effects for *A. americanus* and little effect for *Cancer* spp. The observed difference between Year-2 and Year-0 results for these predators suggests that spatial patterns of *Cancer* spp. were temporally more variable than those of *A. americanus*. *Cancer* crabs

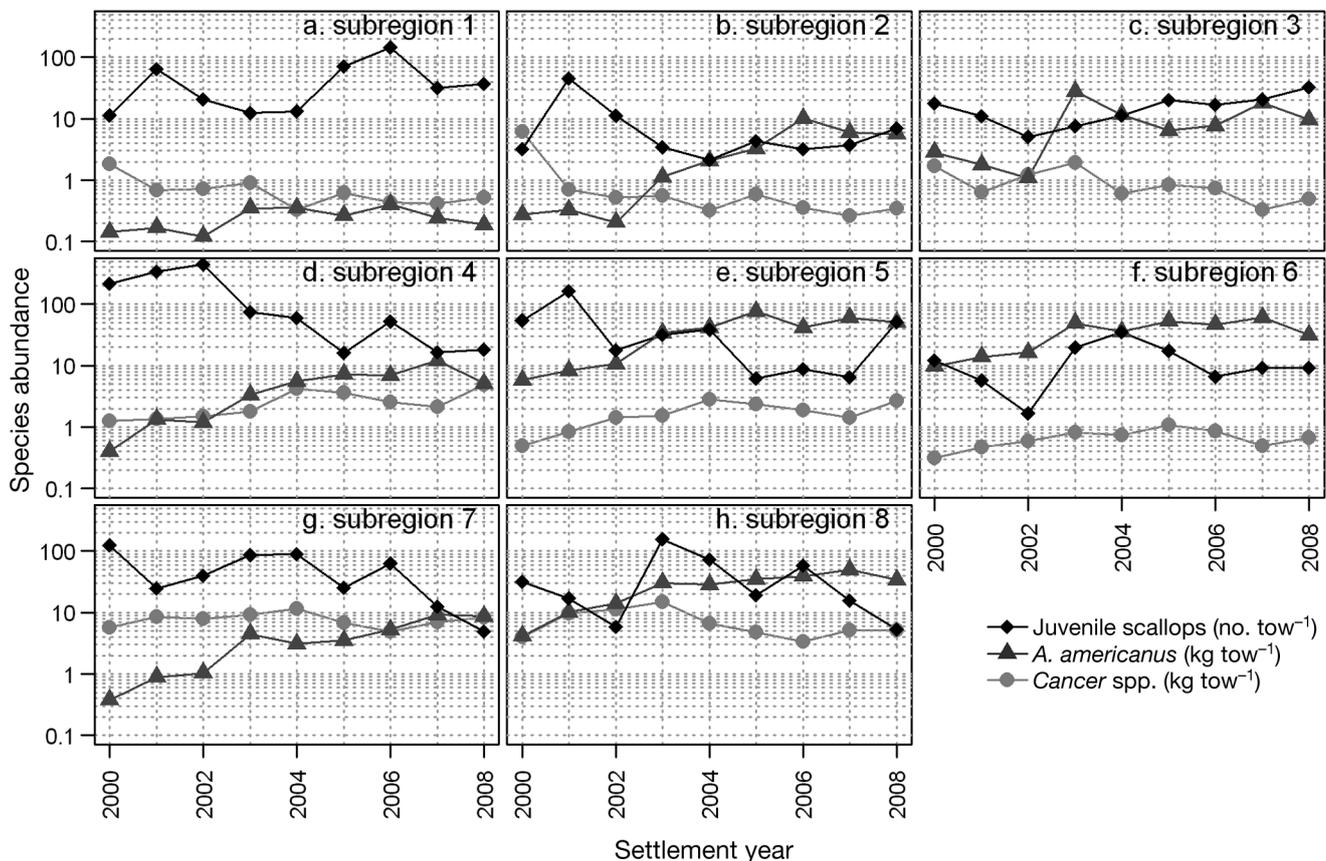


Fig. 8. *Placopecten magellanicus*. Time series of sea scallop recruitment and predator (*Astropecten americanus*, *Cancer* spp.) density, aggregated to subregion scales. (a to h) Subregions 1 to 8. Settlement year: spawning year for scallops with estimated predator biomasses for that year. *Asterias* spp. was not plotted for simplicity

are active foragers that aggregate in response to changes in prey availability, are capable of moving long distances seasonally and interannually, and may have high mortality rates (Barbeau et al. 1996, Hatcher et al. 1996). This temporal variability in *Cancer* crab densities makes the inclusion of temporal lags crucial to understanding the relationship between predator and prey and explains why this relationship was not detected by Hart (2006). In contrast, *A. americanus* are more sedentary and tend to be more opportunistic foragers with aggregations of sea stars persisting for periods of years (Hart 2006). Thus, the inclusion of time lags in the analysis is more important for predators like *Cancer* spp. whose densities are more temporally variable than *A. americanus* whose temporal dynamics are more stable.

The presence of spatial autocorrelation in model residuals may be indicative of additional endogenous or exogenous processes that are not included in our models (Keitt et al. 2002, Diniz-Filho et al. 2003). Our analysis only considers a limited subset of the predators that are preying on juvenile scallops

and does not account for other post-settlement processes (environmental stress, starvation, etc.). Further, we do not consider pre-settlement processes that are known to fluctuate inter-annually, including the biomass and spatial distribution of spawning stock and larval supply (Tian et al. 2009, Gilbert et al. 2010, Northeast Fisheries Science Center 2010). Therefore, the observed high spatial autocorrelation of residuals, especially in models that do not include random slope terms, may be the result of pre-settlement processes or unmeasured environmental variables, and the spatial structure of residuals may provide a basis for investigating these additional processes (Keitt et al. 2002).

Three regions of both high recruit density and temporal variability were evident in this study: Subregion 1 in the north, Subregions 4 and 5 in the center, and Subregion 8 in the south. The degree to which these predator species can explain temporal variation in juvenile scallop densities varies spatially within our study area with good agreement between model predictions and observed recruit dynamics in

Subregions 4 and 5. Subregions 4 and 5 had record densities of scallop recruits in 2003 and 2004, corresponding to the year classes that settled in 2001 and 2002. Densities of both *Cancer* spp. and *Astropecten americanus* were particularly low in these settlement years, but have increased in recent years with a corresponding decrease in scallop recruitment. Thus, a lack of predation pressure during the critical early post-settlement period potentially contributed to this recruitment anomaly. Recruitment dynamics in other subregions are not well explained solely by predator densities. This does not invalidate the importance of these predators in sea scallop mortality in other subregions, but rather emphasizes the spatial nature of multiple processes that structure the scallop population in our study area. We note that predator effects accounted for 30% of the total deviance in the best spatial model. Measurement error presumably accounts for a considerable amount of the unexplained variance, given the effective scales of our sampling equipment and the estimation of predator densities at unsampled locations. However, we expect that much of the unexplained variance is attributable to other processes that are not included in this study, such as variations in larval supply, nutrition, habitat quality, and other predators.

CONCLUSIONS

Our analysis finds evidence that 2 of the 3 predator groups studied, *Astropecten americanus* and *Cancer* spp., are negatively correlated with both the spatial distribution and temporal dynamics of juvenile sea scallops *Placopecten magellanicus* and affect sea scallops primarily in the first year post-settlement. The comparison of different statistical models further supports a causal relationship between predator and prey rather than non-causal spatial associations. Thus, post-settlement predation is a major determinant in the observed spatial and temporal recruitment dynamics of sea scallops in the Mid-Atlantic Bight.

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LITERATURE CITED

- Adams CF, Harris BP, Stokesbury KDE (2008) Geostatistical comparison of two independent video surveys of sea scallop abundance in the Elephant Trunk Closed Area, USA. *ICES J Mar Sci* 65:995–1003
- Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J Northwest Atl Fish Sci* 8:55–66
- Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. *J Wildl Manag* 66: 912–918
- Barbeau MA, Scheibling RE (1994) Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Ver-rill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)). *J Exp Mar Biol Ecol* 180:103–136
- Barbeau MA, Scheibling RE, Hatcher BG, Taylor LH, Hennigar AW (1994) Survival analysis of tethered juvenile sea scallops *Placopecten magellanicus* in field experiments: effects of predators, scallop size and density, site and season. *Mar Ecol Prog Ser* 115:243–256
- Barbeau MA, Hatcher BG, Scheibling RE, Hennigar AW, Taylor LH, Risk AC (1996) Dynamics of juvenile sea scallop (*Placopecten magellanicus*) and their predators in bottom seeding trials in Lunenburg Bay, Nova Scotia. *Can J Fish Aquat Sci* 53:2494–2512
- Bax NJ (1998) The significance and prediction of predation in marine fisheries. *ICES J Mar Sci* 55:997–1030
- Beverton RJH (1995) Spatial limitation of population size; the concentration hypothesis. *Neth J Sea Res* 34:1–6
- Birkhofer K, Scheu S, Wiegand T (2010) Assessing spatio-temporal predator-prey patterns in heterogeneous habitats. *Basic Appl Ecol* 11:486–494
- Bivand RS, Pebesma EJ, Gómez-Rubio V (2008) Applied spatial data analysis with R. Springer, New York, NY
- Bjørnstad ON, Fromentin JM, Stenseth NC, Gjøsæter J (1999) A new test for density-dependent survival: the case of coastal cod populations. *Ecology* 80:1278–1288
- Boesch DF (1979) Benthic ecological studies: macrobenthos, Chapter 6. In: Special report in applied marine science and ocean engineering, No. 194. Virginia Institute of Marine Science, Gloucester Point, VA
- Bourne N (1965) A comparison of catches by 3- and 4-inch rings on offshore scallop drags. *J Fish Res Board Can* 22: 313–333
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Burrough PA, McDonnell RA (1998) Principles of geographical information systems. Oxford University Press, Oxford
- Ciannelli L, Fauchald P, Chan KS, Agostini VN, Dingsor GE (2008) Spatial fisheries ecology: recent progress and future prospects. *J Mar Syst* 71:223–236
- de Knegt HJ, van Langevelde F, Coughenour MB, Skidmore AK and others (2010) Spatial autocorrelation and the scaling of species-environment relationships. *Ecology* 91:2455–2465
- Diniz-Filho JAF, Bini LM, Hawkins BA (2003) Spatial autocorrelation and red herrings in geographical ecology. *Glob Ecol Biogeogr* 12:53–64
- Dormann CF, McPherson JM, Arújo MB, Bivand R and others (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628

- Elnor RW, Jamieson GS (1979) Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster *Homarus americanus*. J Fish Res Board Can 36:537–543
- Fauchald P, Erikstad KE (2002) Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. Mar Ecol Prog Ser 231:279–291
- Fortin MJ, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, New York, NY
- Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. Trends Ecol Evol 22:236–242
- Franz DR, Worley EK (1982) Seasonal variability of prey in the stomachs of *Astropecten americanus* (Echinodermata: Asteroidea) from off southern New England, USA. Estuar Coast Shelf Sci 14:355–368
- Franz DF, Worley EK, Merrill AS (1981) Distribution patterns of common seastars of the Middle Atlantic Continental Shelf of the Northwest Atlantic (Gulf of Maine to Cape Hatteras). Biol Bull 160:394–418
- Gilbert CS, Gentleman WC, Johson CL, DiBacco C, Pringle JM, Chen C (2010) Modelling dispersal of sea scallop (*Placopecten magellanicus*) larvae on Georges Bank: the influence of depth-distribution, planktonic duration and spawning seasonality. Prog Oceanogr 87:37–48
- Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. Mar Ecol Prog Ser 146:265–282
- Hare JA, Able KW (2007) Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Microphogonias undulatus*). Fish Oceanogr 16:31–45
- Hart DR (2006) Effects of sea stars and crabs on sea scallop *Placopecten magellanicus* recruitment in the Mid-Atlantic Bight (USA). Mar Ecol Prog Ser 306:209–221
- Hart DR, Chute AS (2004) Essential fish habitat source document: sea scallop, *Placopecten magellanicus*, life history and habitat characteristics, 2nd edn. NOAA Tech Memo NMFS NE-189
- Hart DR, Chute AS (2009) Estimating von Bertalanffy growth parameters from growth increment data using a linear mixed-effects model, with an application to the sea scallop *Placopecten magellanicus*. ICES J Mar Sci 66: 2165–2175
- Hart DR, Rago P (2006) Long-term dynamics of U.S. Atlantic sea scallop (*Placopecten magellanicus*) populations. N Am J Fish Manag 26:490–501
- Hart DR, Shank BV (2011) Mortality of sea scallops *Placopecten magellanicus* in the Mid-Atlantic Bight: comment on Stokesbury et al. (2011). Mar Ecol Prog Ser 443: 293–297
- Hatcher BG, Scheibling RE, Barbeau MA, Hennigar AW, Taylor LH, Windust AJ (1996) Dispersion and mortality of a population of sea scallop (*Placopecten magellanicus*) seeded in a tidal channel. Can J Fish Aquat Sci 53:38–54
- Hoeting JA, Davis RA, Merton AA, Thompson SE (2006) Model selection for geostatistical models. Ecol Appl 16: 87–98
- Holt RD, Barfield M (2003) Impacts of temporal variation on apparent competition and coexistence in open ecosystems. Oikos 101:49–58
- Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155:269–301
- Keitt TH, Bjornstad ON, Dixon PM, Citron-Pousty S (2002) Accounting for spatial pattern when modeling organism environment interactions. Ecography 25:616–625
- Kissling WD, Carl G (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecol Biogeogr 17:59–71
- Legendre P, Fortin M (1989) Spatial pattern and ecological analysis. Vegetatio 80:107–138
- Leggett WC, DeBlois E (1994) Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Neth J Sea Res 32:119–134
- Lennon JJ (2000) Red-shifts and red herrings in geographical ecology. Ecography 23:101–113
- Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967
- Myers RA (1998) When do environment–recruitment correlations work? Rev Fish Biol Fish 8:285–305
- Nadeau M, Barbeau MA, Brêthes JC (2009) Behavioural mechanisms of sea stars (*Asterias vulgaris* Verrill and *Leptasterias polaris* Müller) and crabs (*Cancer irroratus* Say and *Hyas araneus* Linnaeus) preying on juvenile sea scallops (*Placopecten magellanicus* Gmelin), and procedural effects of scallop tethering. J Exp Mar Biol Ecol 374:134–143
- Naidu KS, Robert G (2006) Fisheries sea scallop, *Placopecten magellanicus*. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture. Elsevier, Amsterdam
- Northeast Fisheries Science Center (2010) 50th Northeast Regional Stock Assessment Workshop (50th SAW) Assessment Report. Northeast Fish Sci Cent Ref Doc 10-09, US Department of Commerce, Washington, DC
- Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. Comput Geosci 30:683–691
- Pinheiro J, Bates DM, DebRoy S, Sarkar D and the R Core team (2009) nlme: linear and nonlinear mixed effects models. R package Version 3.1-93, R Foundation for Statistical Computing, Vienna
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springer, New York, NY
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rose GA, Leggett WC (1990) The importance of scale to predator–prey spatial correlations: an example of Atlantic fishes. Ecology 71:33–43
- Santora JA, Ralston S, Sydeman WJ (2011) Spatial organization of krill and seabirds in the central California Current. ICES J Mar Sci 68:1391–1402
- Serchuk FM, Wood PW Jr, Posgay A, Brown BE (1979) Assessment and status of sea scallop (*Placopecten magellanicus*) populations off the northeast coast of the United States. Proc Natl Shellfish Assoc 69:161–191
- Sissenwine MP (1984) Why do fish populations vary? In: May RM (ed) Exploitation of marine communities. Springer, Berlin
- Sloan NA (1980) Aspects of the feeding biology of asteroids. Oceanogr Mar Biol Annu Rev 18:57–124
- Smereka P (2003) Dietary preference and foraging patterns in the sea star *Astropecten americanus* (Echinodermata: Asteroidea). Distinction thesis, Boston University, Boston, MA
- Stokesbury KDE, Himmelman JH (1993) Spatial-distribution of the giant scallop *Placopecten magellanicus* in unharvested beds in the Baie Des Chaleurs, Quebec. Mar Ecol Prog Ser 96:159–168

- Stokesbury KDE, Himmelman JH (1995) Biological and physical variables associated with aggregations of the giant scallop *Placopecten magellanicus*. *Can J Fish Aquat Sci* 52:743–753
- Tian RCC, Chen CS, Stokesbury KDE, Rothschild BJ and others (2009) Dispersal and settlement of sea scallop larvae spawned in the fishery closed areas on Georges Bank. *ICES J Mar Sci* 66:2155–2164
- Tobin PC, Bjørnstad ON (2003) Spatial dynamics and cross-correlation in a transient predator–prey system. *J Anim Ecol* 72:460–467
- Trippel EA, Chambers RC (1997) The early life history of fishes and its role in recruitment processes. In: Chambers RC, Trippel EA (eds) *Early life history and recruitment in fish populations*. Chapman & Hall, New York, NY
- Veit RR, Silverman ED, Everson I (1993) Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *J Anim Ecol* 62: 551–564
- Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* 75:1182–1189
- Wong MC, Barbeau MA (2005) Prey selection and the functional response of sea stars (*Asterias vulgaris* Verrill) and rock crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)) and blue mussels (*Mytilus edulis* Linnaeus). *J Exp Mar Biol Ecol* 327:1–21
- Wood SN (2006) *Generalized additive models; an introduction with R*. Chapman & Hall, London
- Yamamoto JK (2007) On unbiased backtransform of lognormal kriging estimates. *Comput Geosci* 11:219–234
- Zenitani H, Kono N, Tsukamoto Y (2007) Fluctuation in the great fisheries of northern Europe reviewed in the light of biological research. *Fish Oceanogr* 16:473–478

Appendix 1. Standard linear mixed effect models and model representations.

Model	Representation
1 $\log(r_{ijk}) = \beta_0 + b_{ij,0} + \varepsilon_{ijk}$	SR-Y
2 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{ijk} + b_{ij,0} + \varepsilon_{ijk}$	PredatorYrX + SR-Y
3 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{ijk} + b_{ij,0} + b_{ij,1} p_{ijk} + \varepsilon_{ijk}$	PredatorYrX * SR-Y
4 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{1ijk} + \beta_2 p_{2ijk} + b_{ij,0} + \varepsilon_{ijk}$	Predator1YrX + Predator2YrX + SR-Y
5 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{1ijk} + \beta_2 p_{2ijk} + \beta_3 p_{1ijk} \cdot p_{2ijk} + b_{ij,0} + \varepsilon_{ijk}$	Predator1YrX * Predator2YrX + SR-Y
6 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{1ijk} + \beta_2 p_{2ijk} + b_{ij,0} + b_{ij,1} p_{1ijk} + \varepsilon_{ijk}$	Predator1YrX * SR-Y + Predator2YrX + SR-Y
7 $\log(r_{ijk}) = \beta_0 + \beta_1 p_{1ijk} + \beta_2 p_{2ijk} + b_{ij,0} + b_{ij,1} p_{1ijk} + b_{ij,2} p_{2ijk} + \varepsilon_{ijk}$	Predator1YrX * SR-Y + Predator2YrX * SR-Y

where r_{ijk} is the number of scallop recruits observed in subregion i , year j , and tow k , p_{ijk} is the estimated predator density for dredge tow ijk at a given time lag, and p_{1ijk} and p_{2ijk} represent densities of different predators, $b_{ij,0}$ is the geometric mean of recruits for subregion i and year j [random effect, $b_{ij,0} \sim N(0, \sigma^2)$] and $b_{ij,x}$ represents a random slope term with predator x .

For models without spatial autocorrelation structures, ε_{ijk} is the error assumed to be independent distributed as $N(0, \sigma^2)$. For models with spatial autocorrelation structures, $\varepsilon_{ijk} \sim N(0, \Lambda_{ij})$, where Λ_{ij} is the variance–covariance matrix estimated from residual autocorrelation.

For model notation, SR-Y denotes the random effect of subregion, year. PredatoryYrX represents the predator density at a given scallop age (e.g. *Asterias*Yr2 is the density of *Asterias* spp. at scallop age 2). *: indicate random slope terms.

For GAMM models, the linear coefficients are replaced with smoothing terms.