

Original Article

Spillover of sea scallops from rotational closures in the Mid-Atlantic Bight (United States)

Deborah R. Hart ^{1*}, Daphne M. Munroe^{2,3}, Joseph C. Caracappa^{2,3}, Dale Haidvogel³, Burton V. Shank¹, David B. Rudders⁴, John M. Klinck⁵, Eileen E. Hofmann⁵, and Eric N. Powell⁶

¹National Oceanic and Atmospheric Administration Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, USA

²Haskin Shellfish Research Laboratory, Rutgers University, Port Norris, NJ, USA

³Department of Marine and Coastal Science, Rutgers University, New Brunswick, NJ, USA

⁴Department of Fisheries Science, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, USA

⁵Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, VA, USA

⁶Department of Coastal Sciences, Gulf Coast Research Laboratory, The University of Southern Mississippi, Ocean Springs, MS, USA

*Corresponding author: tel: +1 508 495 2369; e-mail: deborah.hart@noaa.gov.

Hart, D. R., Munroe, D. M., Caracappa, J. C., Haidvogel, D., Shank, B. V., Rudders, D. B., Klinck, J. M., Hofmann, E. E., and Powell, E. N. Spillover of sea scallops from rotational closures in the Mid-Atlantic Bight (United States). – ICES Journal of Marine Science, 77: 1992–2002.

Received 17 January 2020; revised 7 May 2020; accepted 15 May 2020; advance access publication 29 June 2020.

We examined evidence for larval spillover (increased recruitment outside the closures) of Atlantic sea scallops (*Placopecten magellanicus*) due to rotational closures in the Mid-Atlantic Bight using a 40-year fisheries survey time series and a larval transport model. Since the first closure of the Hudson Canyon South (HCS) area in 1998, mean recruitment in the two areas directly down-current from this closure, Elephant Trunk (ET) and Delmarva (DMV), increased significantly by factors of about 7 and 2, respectively. Stock–recruit plots indicate that low biomasses in HCS were associated with reduced mean recruitment in ET and DMV. Simulations indicate that larvae spawned in HCS often settle in the two downstream areas and that model-estimated settlement (based on gonad biomass in HCS and year-specific larval transport between the areas) is correlated with observed recruitment. This study gives strong evidence that the rotational closure of HCS has induced increased recruitment in down-current areas.

Keywords: invertebrate fishery, larval transport model, marine protected areas, pectinidae, *Placopecten magellanicus*, rotational fishery management

Introduction

The use of permanent fishery closed areas, often termed “marine reserves” or “marine protected areas” (MPAs), as a fishery management tool has received considerable interest. In the absence of spillover, that is movement of larvae or adult fish from the closed area to areas open to fishing, such closures will reduce fishery yield because fish that settle in the closed area will no longer be

available for harvesting by the fishery. For a closure to increase fishery yield, landings due to spillover must be greater than this direct loss from the lack of access to the harvestable stock in the closure; in particular, the existence of spillover by itself does not necessarily indicate that the closure has increased yields (Hart, 2006; Botsford *et al.*, 2009). An analysis comparing these two effects (spillover vs. direct loss) showed that marine reserves only

increase yields when recruitment limitation is sufficiently strong due to low spawning stock biomass (SSB), which typically occurs only when the stock is overfished (Hart, 2006).

Reserve siting can also be important for stocks with metapopulation structures, with spillover maximized when closures are located in upstream “source” areas (Crowder *et al.*, 2000; Gaines *et al.*, 2003; Munroe *et al.*, 2014). For this reason, larval transport studies, which predict the settlement locations of larvae spawned in a given area, are useful both for the design of MPAs and the analysis of their effects (Crowder *et al.*, 2000; Lipcius *et al.*, 2008).

Rotational or dynamic closures, where areas are first closed and then opened to fishing, are another potential fishery management tool (Hart, 2003; Hart and Rago, 2006; Cohen and Foale, 2013; Plagányi *et al.*, 2015; Goetze *et al.*, 2018). By protecting juveniles inside the closure, thereby allowing them to grow to a larger size before the area is reopened to be fished, yield per recruit, and hence total stock yields, can be potentially increased even in the absence of spillover (Hart, 2003). In such a case, larval spillover, resulting in increased recruitment outside the rotational closure, would be an additional benefit to the increased yield inside the rotational area. Fishery closures can also be valuable as large-scale experiments (Jensen *et al.*, 2012). Rotational closures can be particularly useful in this regard; unlike permanent marine reserves that often suffer from limited replication (Claudet and Guidetti, 2010), rotational closures are temporally replicated, permitting improved evaluation of their effects.

Sedentary broadcast spawners such as scallops need to be in relatively close proximity to achieve successful fertilization (Levitan *et al.*, 1992; Levitan and Petersen, 1995; Claereboudt, 1999; Bayer *et al.*, 2016). On the other hand, fishers tend to optimize their harvest rates by targeting areas of high densities (Caddy, 1975; Hart, 2001; Truesdell *et al.*, 2016; Smith *et al.*, 2017). By removing or thinning dense aggregations, fishing may disproportionately reduce larval output and hence recruitment. By keeping these aggregations intact, permanent or rotational closures may increase fertilization success and hence induce greater larval spillover than would be expected from increases in spawning biomass alone (Botsford, 1993; Hart, 2003; Smith and Rago, 2004).

In this article, we examine evidence for larval spillover from rotational closures for sea scallops (*Placopecten magellanicus*) in the Mid-Atlantic Bight (United States), i.e. increased recruitment in the areas down-current of the closures. We use data from a 40-year scallop dredge survey in which the first rotational closure occurred almost exactly halfway through the time series. We also use a larval transport model (Munroe *et al.*, 2018) to predict settlement locations and to further investigate the causal linkages between increased larval production in the rotationally closed source area and recruitment in the down-current areas.

Methods

Study site

The three rotationally closed areas for sea scallops are located in the Mid-Atlantic Bight, off the states of New Jersey, Delaware, Maryland, and Virginia in the eastern United States (Figure 1, Table 1). These areas are Hudson Canyon South (HCS), which was closed in 1998, 2008, and 2014 and reopened in 2001, 2011, and 2015; Elephant Trunk (ET), which was closed in 2004 and 2012 and then reopened in 2007, 2015 (one portion) and 2017 (the other portion); and Delmarva (DMV), which was closed in

2007 and 2012 and reopened in 2009 and 2014. A fourth closure, known as Virginia Beach, south of DMV, was closed between 1998 and 2001 but was not successful. Few fishable scallops have been observed in this area since 2002, probably due to warming bottom temperature (Wallace *et al.*, 2018), which has been noted for other shellfish in the southern Mid-Atlantic as well (Weinberg, 2005; Narváez *et al.*, 2015). This area will not be examined further in this study.

Survey data

A random-stratified scallop dredge survey has been conducted since 1979 using a 2.44-m New Bedford-style scallop dredge with 5.1-cm diameter rings and a 3.8-cm² plastic liner (Serchuk and Wigley, 1986; Hart and Rago, 2006). Tows targeted a 7.04-km/h speed for 15 min. Catches were adjusted for tow length and standardized to a tow length of 1 nautical mile (Northeast Fisheries Science Center, 2010). The survey has been conducted on three research vessels (R/V *Albatross IV*, R/V *Oregon II*, R/V *Hugh Sharp*) and in recent years on commercial scallop vessels as well. Inter-vessel comparisons indicate no significant vessel effects after standardization for tow distance (Northeast Fisheries Science Center, 2010). Post-stratification (Cochran, 1977) was used to account for strata that were split by rotational area boundaries. National Oceanic and Atmospheric Administration survey data are available at www.data.gov; sea scallop survey data collected on commercial vessels by the Virginia Institute of Marine Science can be obtained by contacting David Rudders (rudders@vims.edu).

Shell heights were converted into gonad or meat weights using the relationships of Hennen and Hart (2012). Recruits on a dredge tow (~2 years old) were calculated as the number of scallops caught that were between 30 mm and the mean shell height to which a 30-mm scallop would grow in a year, using the depth- and latitude-specific growth estimates of Hart and Chute (2009). The depth and latitude covariates were used to account for the fact that scallop growth decreases with these factors in the Mid-Atlantic study area.

Statistical analysis

Mean (stratified) recruitment was calculated from survey data for each year in the three rotational areas, and the areas in the Mid-Atlantic mainly to the north of the rotational areas (referred to hereafter as simply “North”), that are not part of the rotational system (Figure 1). Recruitment was split into year classes spawned prior to the first rotational closures in 1998 (observed as 2 year olds in surveys from 1979 to 1999), and afterwards (observed in 2000–2018). We hypothesize that the initiation of rotational closures in the HCS area in 1998 would increase recruitment in the two areas immediately down-current of this area (ET and DMV) but not in HCS or the North area. Results were also examined when the transitional 1998 year class was removed from the analysis; this did not alter the results of any statistical test. Recruitment from the two periods was compared using log-transformed *t*-tests.

We also estimated Beverton–Holt stock–recruit relationships:

$$R = \frac{aB}{b + B}, \quad (1)$$

where *R* is recruitment and *B* is SSB, between recruitment in ET

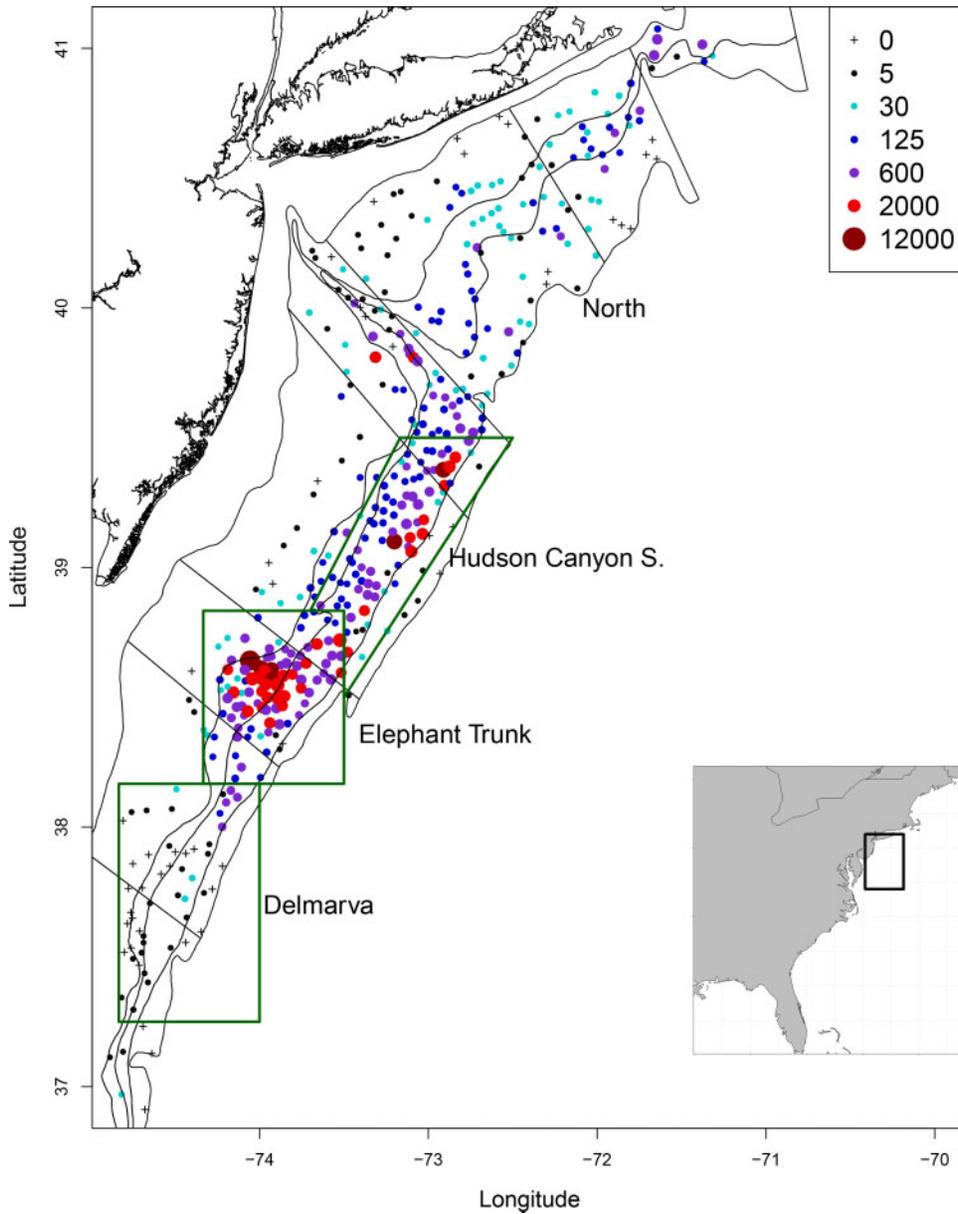


Figure 1. Sea scallop dredge survey chart in the Mid-Atlantic Bight for 2018, showing survey catches (in numbers of scallops), the three rotationally closed areas (green polygons), and survey stratum boundaries. The colours and area of the disks indicate the sizes of the catches; the legend gives the mid-point of each colour bin.

Table 1. Management status of the three rotational areas by year: open (Op) indicates that the area was open to scallop fishing, limited only by an overall days-at-sea cap for all open areas, closed (Cl) means that it was closed to all scallop fishing and reopened access (R) denotes a previously closed area that is open to limited fishing, with effectively an area-specific total allowable catch limit.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
HCS	Op/Cl	Cl	Cl	Cl/R	R	R	R	R	R	R	R/Cl	Cl	Cl	Cl/R	R	R	R/Cl	Cl/R	R	R	R
ET	Op	Op	Op	Op	Op	Op	Op/Cl	Cl	Cl	Cl/R	R	R	R	Op	Op	Cl	Cl	Cl/R ^a	R(Cl) ^a	R (Cl/R) ^a	R
DMV	Op	Op	Op	Op	Op	Op	Op	Op	Op	Op/Cl	Cl	Cl/R	R	R	R	Cl	Cl/R	R	R	R	R/Op

Closures and reopenings usually occurred between March and July, an area that was one status in the beginning of the year and another later that year is indicated using a slash. All areas were open prior to 1998.

^aA portion of ET was reopened in 2015, while the rest of the area remained closed until 2017.

or DMV and SSB in the areas up-current from ET or DMV (HCS and North areas for ET, and ET, HCS and North areas for DMV). This relationship can be alternatively parametrized using mean recruitment at zero fishing r_0 and the steepness parameter h , representing recruitment when the source population is at 20% of its un-fished level (Mace and Doonan, 1988). We estimated the parameters of this alternative parameterization using the non-linear least squares function in *R*, assuming log-normal errors, but also report estimates for the original parameters in (1). The strength of a stock–recruit relationship can be judged by the reduction in predicted recruitment at the lowest observed SSB compared to higher observed SSB, as well as examining the variance of the residuals around the predicted recruitment. To investigate the possibility that the rotational programme enhanced recruitment beyond that expected by the increased biomass alone (because of increased fertilization success), the residuals from the stock–recruit relationships were tested using one-tailed two-sample *t*-tests to determine whether the residuals tended to be higher after the rotational programme began in 1998.

We also examined the fit to the Beverton–Holt stock–recruit curve before and after the rotational programme. A stronger stock–recruit relationship since the rotational programme began would be evidence that improved fertilization success had a role in increasing recruitment. For this purpose, we fit the linearized form of the Beverton–Holt stock–recruit curve:

$$\frac{1}{R} = \alpha + \frac{\beta}{S}, \quad (2)$$

where α and β are constants (Quinn and Deriso, 1999) to the data before and after the closure using linear regressions and tested using analysis of covariance as to whether the slope has significantly increased post-closure. All statistical analyses were done using *R* version 3.4.4.

Larval transport model

A larval transport model was used to investigate whether larvae from HCS (and other areas) could settle in the down-current rotational areas (ET and DMV). Ocean circulation in the Mid-Atlantic Bight was simulated using the Regional Ocean Modeling System (ROMS, www.myroms.org; Shchepetkin and McWilliams, 2005) that has also been used to simulate larval transport for other bivalve species (e.g. Narváez *et al.*, 2012a, b; Zhang *et al.*, 2015; Zhang *et al.*, 2016). Here, an Atlantic sea scallop individual-based model (IBM) was coupled to simulated ocean dynamics calculated by ROMS.

The coupled ROMS-IBM domain covered 68–77°W and 33.8–42°N, with 13 080 cells at 5–8 km horizontal resolution and actual bathymetry with a minimum depth set to 5 m. The coupled model was forced at the sea surface by 3-hourly atmospheric data (i.e. solar radiation, winds, rain, air temperature, pressure, and moisture) obtained from the North American Regional Reanalysis dataset (<http://www.emc.ncep.noaa.gov/mmb/rrean/>). Tidal elevation and current data for the MAB were obtained from the Advanced Circulation Model (<http://adcirc.org/products/adcirc-tidal-databases/>) and input at the model domain perimeter. Daily river transport data from the US Geological Survey for seven major rivers (Connecticut, Hudson, Delaware, Susquehanna, Potomac, Choptank and James) were input into the Mid-Atlantic Bight regional model. Along the open

boundaries, the circulation model is nudged to corrected and validated tracer and momentum fields from a high-resolution (1/12°) global simulation (Wilkin and Hunter, 2013; Zhang *et al.*, 2015). A full description of the physical model can be found in Munroe *et al.* (2018). In each year, the model was run for 3 months prior to larval release to allow for adjustment of the circulation and tracer fields.

The scallop larval IBM simulates growth and swimming for Atlantic sea scallop larvae and is embedded in the circulation model so that high-frequency dynamical processes act on larval transport and dispersion. Fertilized scallop eggs are benthic and remain on the seabed for ~1 d as the embryo develops (Culliney, 1974; Tremblay *et al.*, 1994); therefore, the larval model is initialized with 1.5-day-old trochophores that enter the bottom of the water column at a size of 75 µm (Culliney, 1974).

Once the simulated larvae enter the water column, growth is simulated as a function of temperature (Munroe *et al.*, 2018, based on Hurley *et al.*, 1986, 1987; Gallagher *et al.*, 1996; Pernet *et al.*, 2003; Gouda *et al.*, 2006). Swimming and sinking rates are expressed as a function of larval size [Munroe *et al.*, 2018, based on experimental evidence from Chia *et al.* (1984), Beaumont and Barnes (1992), Gallagher *et al.* (1996)]. In combination, swimming and sinking behaviours during the veliger stage result in net larval movement that tends to be upward in temperatures less than ~16°C and downward in temperatures greater than ~16°C. Swimming and sinking behaviours depend on larval size, with larvae >240 µm tending to move downward to the seabed for settlement. Further documentation of model parameters governing swimming, sinking, and growth used to develop the model can be found in Munroe *et al.* (2018).

Scallop larvae are competent to metamorphose at shell sizes <220 µm and have been observed to settle ~35 d post-hatch, with the potential to extend larval duration by delaying metamorphosis (Culliney, 1974; Gallagher *et al.*, 1996; Pearce *et al.*, 2004). Thus, simulated larvae were assumed to settle (i.e. transition from a pelagic dispersive particle to a stationary bottom particle) when they reach a shell length of >250 µm and encounter suitable seabed habitat (defined by depth and adult distribution), after which they remain fixed at their existing horizontal location. Larvae that reach settlement size within 45 d in one of the rotational closure areas are considered “successful”. Any of the following conditions were considered to result in “unsuccessful” seeding of the rotational areas: failure to reach settlement size within 45 d, settlement outside the rotational closure areas, or larvae that leave the model domain entirely. An overview of the larval transport results over broader settlement regions can be found in Munroe *et al.* (2018).

In general, simulated larvae grew and moved as expected based on laboratory and field observations. The coupled ROMS-IBM was used to simulate physical conditions and scallop larval transport for the years 2006–2012, providing 7 years of simulated scallop larval dispersal in the Mid-Atlantic Bight supplying the rotational closed areas. Release days occurred on days 1, 6, 11, 16, 21, and 26 of May through October each year, with three release times on each of these days. About 80 000 simulated larvae were released per year (see Munroe *et al.*, 2018 for details). Within the model domain, the shelf waters shallower than 100 m were separated into the rotationally closed areas for scallops (HCS, ET, and DMV), and the “North” area outside of the closures as described above.

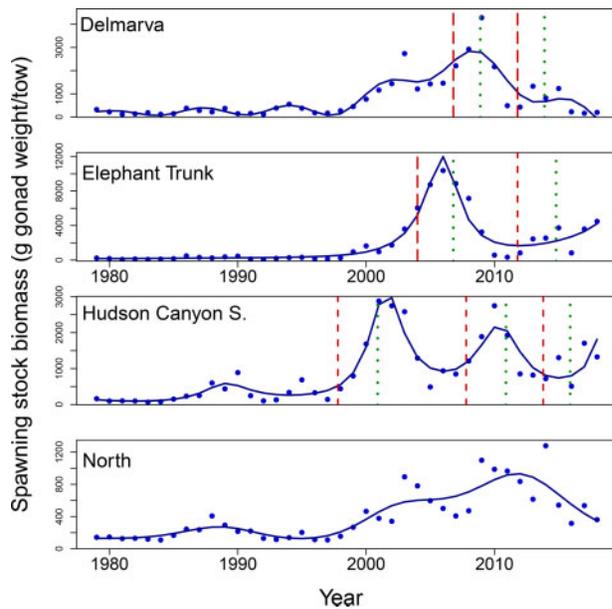


Figure 2. Dredge survey biomass per tow (filled blue circles) for, from top, the Delmarva, Elephant Trunk, Hudson Canyon South, and North areas; the solid lines are lowess smoothers. The vertical long dashed red lines indicate initiations of a closure in that area, and reopenings are shown by the short dashed green lines.

We defined model-estimated “larval connectivity” between two regions in a specified time period as the fraction of larvae released from the first region that successfully settle in the second during that time [this is a similar concept to “potential connectivity” from [Watson et al. \(2010\)](#)]. The product of larval connectivity with the (gonad) biomass in the first region is defined as the model “predicted settlement” of larvae from the first region that settle in the second region, which in turn is a predictor of recruitment in the second region. We compared the predicted settlement to recruitment observed 2 years later on the dredge survey using Pearson correlations and by using a generalized linear model (GLM) with predicted settlement as the independent variable and recruitment as the dependent variable, using a Gaussian distribution with a log link.

Results

SSB increased in all three rotational areas after their closures ([Figure 2](#)). The increases were most pronounced in HCS as well as in ET after its first closure. Mean recruitment in ET was almost seven times higher since the rotational programme began than in the years prior to this ([Table 2](#), [Figure 3](#)). Mean recruitment in DMV was over twice as high since the beginning of the rotational programme. The increases in both these areas were statistically significant. In contrast, smaller non-significant increases were observed in the North and HCS areas.

The strongest evidence for a spawner–recruit relationship is between spawners in HCS and recruits in ET ([Table 3](#), [Figure 4](#)). In this case, predicted recruitment at the low end of observed SSB was about a third of that at the higher SSBs, indicating strong recruitment limitation at low HCS SSB. The relationship between SSB in HCS and recruitment in DMV appears also to be strong. There is also some equivocal evidence for a relationship between SSB in North with recruitment in ET, as seen by the more modest

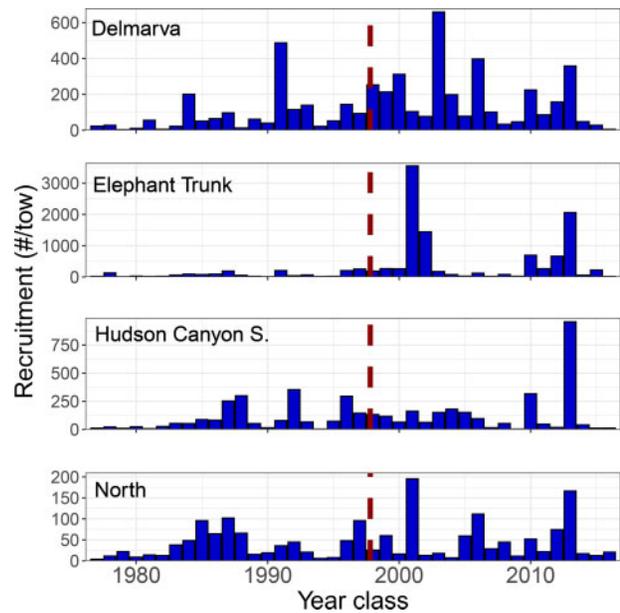


Figure 3. Estimated recruitment (number of scallops per tow) for, from top, the Delmarva, Elephant Trunk, Hudson Canyon South, and North areas. The red dashed line indicates when the rotational management programme began.

Table 2. Mean recruitment and natural logarithm of recruitment before and after implementation of the rotational management programme, together with results of two-sample *t*-tests comparing recruitment before and after the rotational programme began.

Region	Rec before	Rec after	Log rec before	Log rec after	<i>t</i>	<i>p_t</i>
DMV	82.3	178	3.79	4.7	2.43	0.01
ET	77.3	537.9	3.85	5.18	3.1	0.002
HCS	96	136.7	3.9	4.16	0.62	0.27
North	37.2	50.4	3.22	3.47	0.81	0.21

decline in predicted recruitment at lower observed SSB. However, the large residuals suggest that any stock–recruit relationship between these two areas has limited predictive abilities. The other two potential stock–recruit relationships (North-DMV and ET-DMV) are nearly flat over the observed SSB range, indicating little evidence for such a relationship.

Comparison of stock–recruit residuals from before and after the start of the rotational programme ([Table 3](#), [Figure 4](#)) indicates that mean residuals were higher in the period of rotational management in all cases, as would be expected if fertilization success improved due to the closures, but this increase was never statistically significant. Regression of the inverse of recruitment in ET or DMV with the inverse of SSB in HCS showed increased slopes in both regions after the rotational programme began, suggesting a stronger stock–recruit relationship between the areas since 1998 ([Figure 5](#)). The change in the slope was statistically significant in ET ($t = 2.26$, $p = 0.01$, one-tailed test), but not in DMV ($t = 0.47$, $p = 0.32$).

There was a strong correlation ($\rho = 0.50$) between predicted settlement of larvae in ET coming from HCS and observed recruitment for the years that the larval transport simulations were run (2006–2012) ([Figure 6](#)). This correlation is stronger than

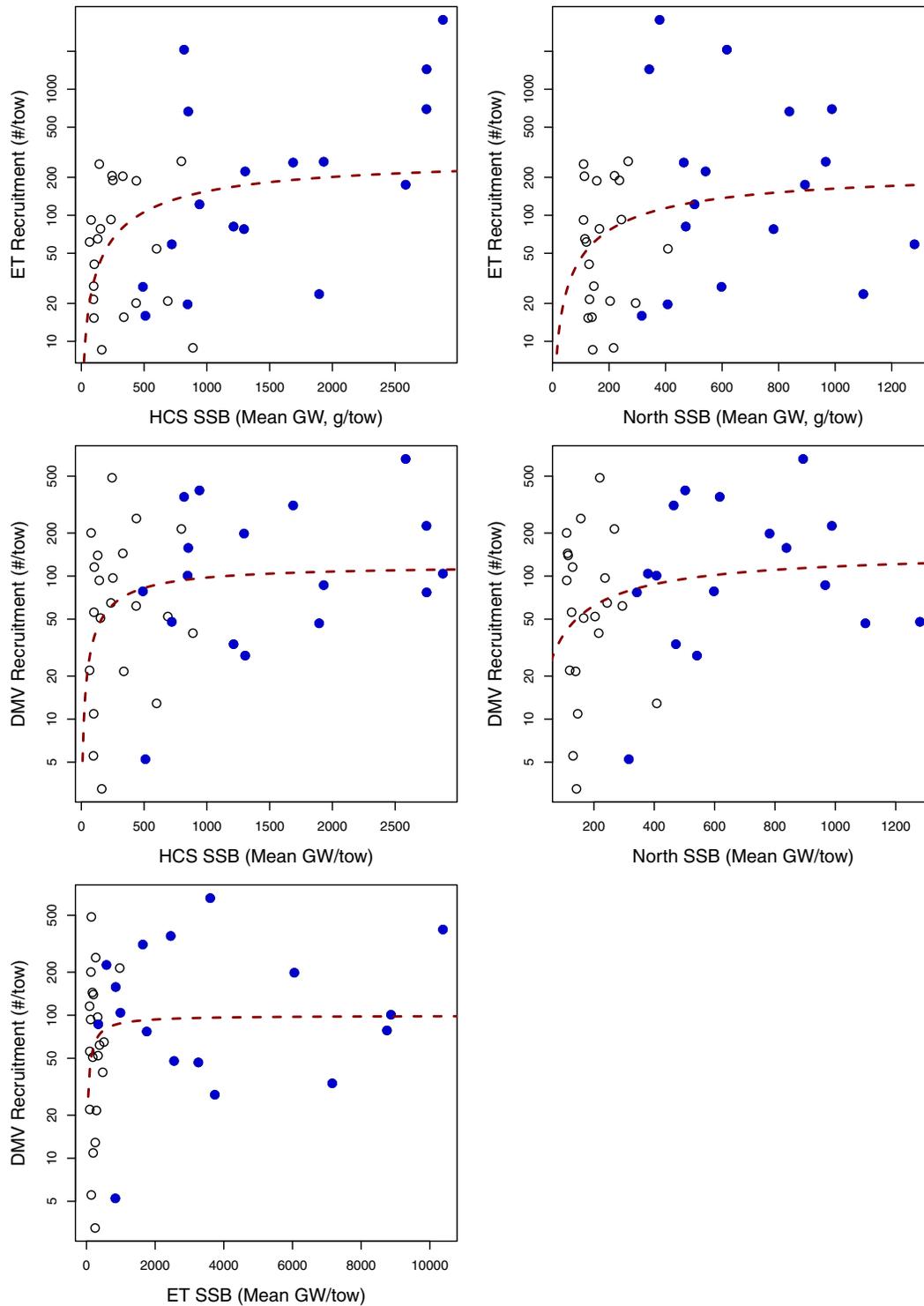


Figure 4. Stock–recruit plots for recruitment in Elephant Trunk and Delmarva, based on SSB in the North, Hudson Canyon South, and (for Delmarva) Elephant Trunk areas. The open circles represent year classes prior to 1998, and the filled circles are year classes after that date.

either between larval connectivity and recruitment ($\rho = 0.19$) or between (gonad-based) biomass and recruitment ($\rho = 0.39$) alone. The GLM between predicted settlement from HCS and ET recruitment showed a positive relationship but was not quite

statistically significant ($t = 1.8, p = 0.07$), which is not surprising given the limited number of data points.

The correlation between DMV recruitment and predicted settlement from HCS was smaller ($\rho = 0.12$) than that in ET.

Connectivity alone had a higher correlation ($\rho = 0.35$) to recruitment than predicted settlement, and the correlation between HCS biomass to DMV recruitment was actually slightly negative during those 7 years ($\rho = -0.10$). The GLM showed a slightly positive but not significant ($t = 0.21$, $p = 0.39$) relationship between predicted settlement from HCS and DMV recruitment.

Discussion

Large changes in biomass were observed in all three rotational areas after the implementation of the rotational programme in 1998. In the years leading up to this time, the sea scallop fishery was severely overfished (Hart and Rago, 2006), making for a strong contrast between the period after the rotational closures, where fishing mortality was zero or low. In HCS, the increases after 1998 appear to be mainly a direct result of reduced (or in some years zero) fishing mortalities. In particular, a strong 2-year-old year class in this area in 1998 was allowed to grow unfished until 2001, resulting in an order of magnitude increase in biomass. In contrast, previous strong year classes in this area were quickly fished out.

Table 3. Estimated stock–recruit parameters for recruitment in ET and DMV, with SSB in North, HCS, and (for DMV only) ET.

Stock–recruit	A	b	r_0	H	t	p_t
HCS-ET	291	878	262	0.71	0.47	0.32
HCS-DMV	120	226	112	0.80	0.6	0.23
North-ET	287	589	287	0.78	1.2	0.11
North-DMV	144	263	135	0.80	0.8	0.45
ET-DMV	99	135	95	0.85	1	0.16

The parameters a and b are as in (1), r_0 is recruitment at zero fishing, and h is the steepness parameter. Two-sample t -tests on the stock–recruit residuals are also shown that evaluate the effects of the rotational programme beyond increases in SSB alone.

Biomass in the other two rotational areas (ET and DMV) began increasing after 1998, even before these areas were themselves closed, due to a combination of increased recruitment and decreased fishing mortality, as effort control measures began to be effective (Hart and Rago, 2006). Biomass in ET increased about 30-fold from 1998 to its peak in 2006, mainly from the very large 2001 year class that was protected by the closure of the ET starting in July 2004. Although biomass in DMV increased during the first 10 years of the rotational programme, it has been decreasing since then, potentially due to temperature increases in this area (Wallace et al., 2018). Some increases in biomass were also seen in the North area, which was not part of the rotational programme, mainly due to the reductions in fishing effort.

Strikingly large increases in recruitment in ET were observed after closure of HCS in 1998. Scallop recruitment in ET was never strong prior to this date, but afterwards this area became the most productive scallop grounds in the Mid-Atlantic. Not only were there 2 year classes (2001 and 2013) of unprecedented size, but 8 year classes since 1999 in this area had recruitment greater than the maximum observed between 1979 and 1999. Moreover, many of the years since 1999 for which recruitment in ET was poor (e.g. 2005–2009) correspond to periods of reduced biomass in HCS due to the reopening of HCS to fishing (see Figures 2 and 3). The correlation between SSB in HCS and recruitment in ET, together with the model-based evidence of larval connectivity in many years between HCS and ET, strongly suggests a causative link, i.e. larval spillover, between the increased SSB in HCS due in large part to the rotational programme, and the subsequent increases in recruitment in ET. A similar, albeit weaker, relationship was present between SSB in HCS and recruitment in DMV, that is also consistent with model-based connectivity estimates.

The significant strengthening of the stock–recruit relationship between HCS and ET after the initiation of the rotational programme is most likely due to improved fertilization success in HCS after the closures, although there conceivably could be other

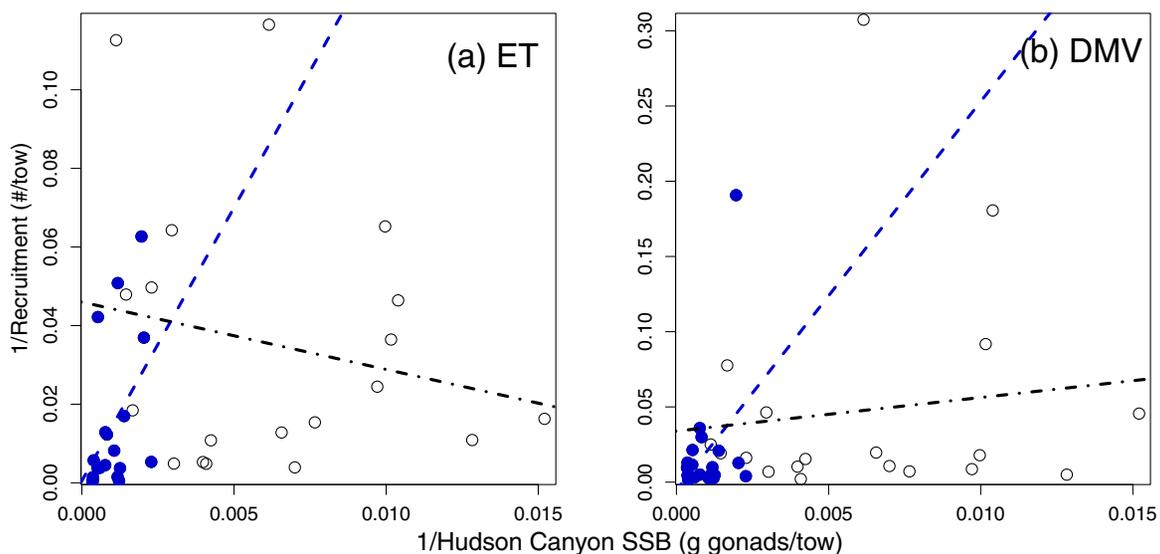


Figure 5. Plot of 1/recruitment in (a) ET and (b) DMV vs. 1/gonad biomass in HCS. Open circles indicate year classes spawned prior to the rotation programme, whereas year classes spawned afterwards are indicated by blue-filled circles. The lines are regressions for the period before rotation (black dashed-dotted lines) and afterwards (blue dashed lines).

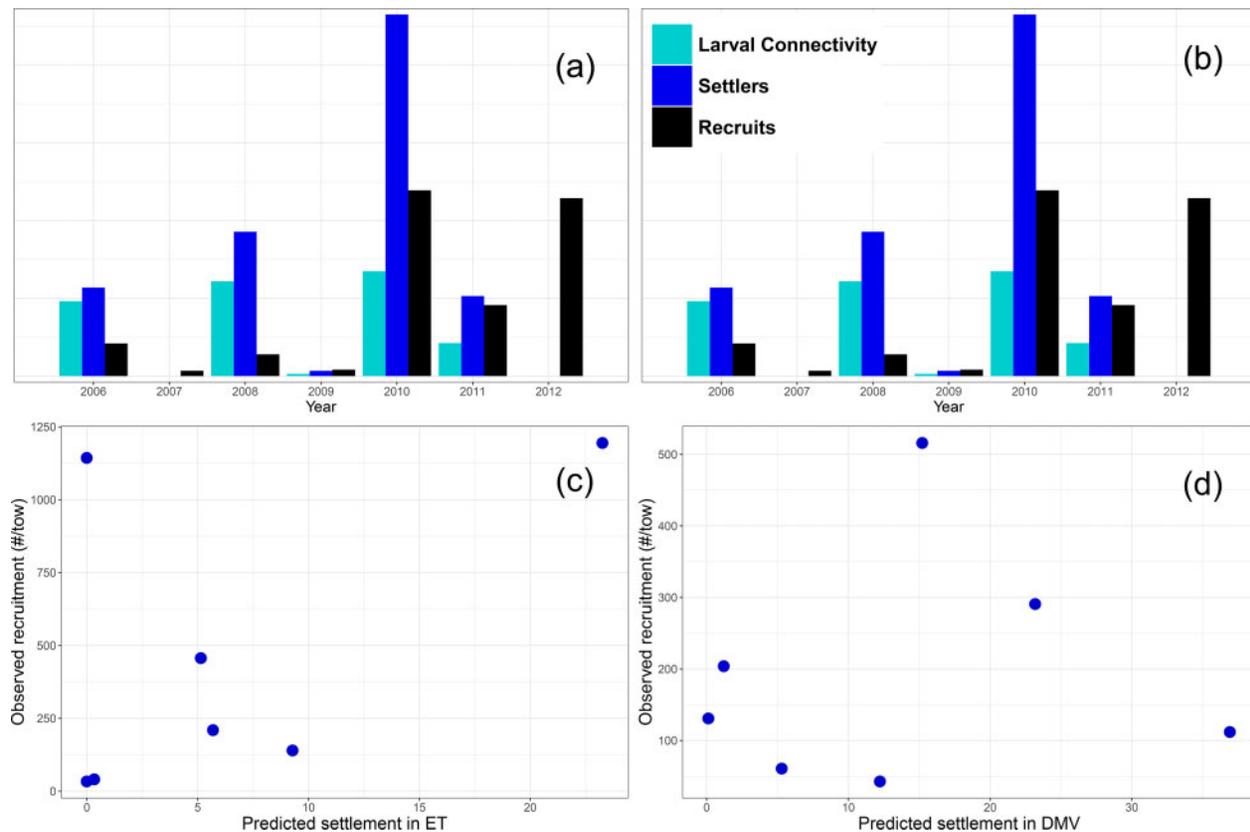


Figure 6. Top: barplots of model-estimated larval connectivity and predicted settlement from HCS to (a) ET and (b) DMV, together with observed recruitment, for the years 2006–2012. All three quantities were normalized by dividing by their maximum over the time period. Bottom: relationship between observed recruitment and predicted settlement of larvae originating in HCS for (c) ET and (d) DMV.

explanations (e.g. improved larval connectivity that coincided with the rotational programme). The positive residuals in the stock–recruit relationships after 1998 also are suggestive of a reduced Allee effect; even though none of these were statistically significant, it is unlikely that all five of the fits would have positive residuals simply by chance.

The increases in biomass in HCS since 1998 is reflective of the strong contrast between the overfished conditions that occurred prior to 1998 (Hart and Rago, 2006) and the closures and relatively light fishing that occurred afterwards. There would have likely been some increases in recruitment in ET and DMV had there been only fishing effort reduction without the rotational system. However, both the stock–recruit curves (Figure 4) and the evidence for increased fertilization success since 1998 suggest that the increases in recruitment would have been less than what was observed under rotation. Perhaps most importantly, rotation of the HCS area likely increased yield per recruit and hence yield in the HCS area itself (Hart, 2003), in addition to the spillover of recruitment into the down-current areas.

It might also be asked whether a permanent closure (or marine reserve) in HCS would have been superior to the rotational closures in terms of fishery yield. It is possible, and perhaps probable, that such a permanent closure would have further increased down-current recruitment, particularly in years (e.g. 2004–2008) where fishing considerably reduced HCS biomass. However, in order for a permanent closure to increase total landings, the increased spillover must be sufficient to make up for the loss of

landings that occurred since 1998 in HCS, which totalled over 30 000 t meats from 2001 to 2018. Based on the landings in the three rotational areas after 2000, a full closure of HCS would increase yield over rotation only if the additional spillover induced landings in ET and DMV that were over 41% greater than that under the rotational programme. This would require recruitment to be at least 41% higher with a permanent closure than under rotation, and perhaps more, if strong year classes suffer density-dependent natural mortality as observations suggest (Hart and Shank, 2011). However, the stock–recruit relationships of HCS with ET and DMV (Figure 4) were generally close to saturation during the period of rotational management, making an increase in that magnitude unlikely.

Besides larval supply, environmental factors play a role in recruitment dynamics. In particular, very large year classes are typically associated with both high larval supply and environmental conditions favouring good post-settlement survival. For example, the large 2013 year class was strongest in ET but was widespread across the entire Mid-Atlantic scallop grounds. Predation on juvenile scallops, particularly by the sea star *Astropecten americanus* and *Cancer* spp. crabs, is also an important factor affecting recruitment (Hart, 2006; Hart and Shank, 2011; Shank *et al.*, 2012).

Model-estimated larval connectivity between HCS and DMV was stronger than that from HCS to ET, but the observed relationship between HCS biomass and DMV recruitment was weaker. Because DMV is close to the southern boundary of the

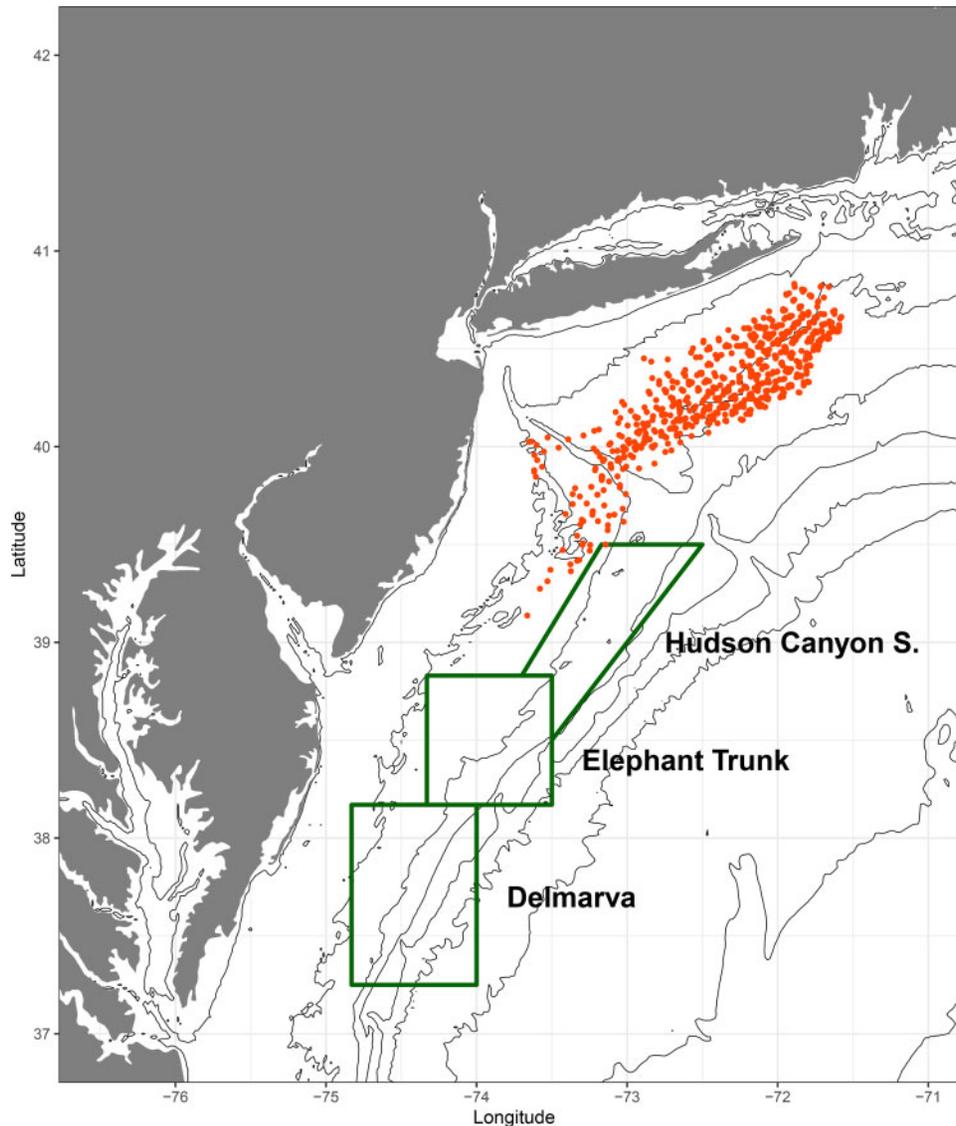


Figure 7. Release points of larvae in 2012 that settled in the Elephant Trunk area, based on the larval transport model.

scallops' range, environmental factors such as high temperatures and predator abundance may exert stronger control on recruitment than larval supply. In contrast, both bottom temperatures and *A. americanus* abundances are lower in ET compared to DMV (Hart, 2006; Shank *et al.*, 2012), suggesting that larval supply has a greater influence on recruitment in ET.

For six of the 7 years for which larval transport was modelled, the model predicted settlement in ET from HCS correlated reasonably well with observed recruitment. The one exception was the 2012 year class, where strong recruitment was observed despite no larval connectivity between ET and HCS. That year class was unusual in that it was almost exclusively observed in the shallower portions of ET. In contrast, other strong year classes in this area, including 2001, 2010 and 2013, had much broader depth distributions. We examined model output that included larval releases from areas outside the closed areas and found the larval transport model predicted settlement to ET from portions of the North area, in particular northwest of HCS and off of Long Island (Figure 7). SSB in the North area was at its maximum in

2012, further suggesting that it was the source of the ET recruitment for this year, rather than HCS.

Stock–recruit relationships often appear to be weak or non-existent (e.g. Szuwalski *et al.*, 2015). Although there are likely many causes of this, one contributing factor is that the “stocks” are typically assumed to be closed populations, whereas they are often in reality metapopulations. In this study, we explicitly recognized the metapopulation structure of sea scallops in the Mid-Atlantic Bight and took it into account when constructing stock–recruit curves. This, in combination with the strong contrast in SSB and relatively precise survey data, helped reveal the striking stock–recruit patterns.

The goal of the sea scallop rotational management programme was to increase yield per recruit by delaying the capture of the scallops until they were closer to an optimal size (Hart, 2003; New England Fishery Management Council, 2003). However, it was recognized that rotation might also improve recruitment by increasing SSB and reducing potential Allee effects compared to non-spatial management at the same effort levels (Hart, 2003). We have presented evidence that the closure of HCS has indeed

increased recruitment downstream of the HCS rotational area. The combination of improved yield per recruit and recruitment indicates that the rotational system has been successful and should be continued.

Acknowledgements

We thank Julia Levin and Hernan Arango for guidance and expertise regarding the ROMS model, Zhiren Wang for conducting the coupled simulations, and the NEFSC Ecosystem Surveys Branch for collecting the NEFSC dredge survey data. We also thank Russell Brown and two anonymous reviewers for constructive comments on drafts of this article.

Funding

This work was supported by an NOAA Fisheries and the Environment (FATE) grant, with funds provided through NOAA/CINAR (NA09OAR4320129) (Subaward A101070, WHOI project 37022909). DM was also partially supported by the USDA National Institute of Food and Agriculture Hatch project (1002345), through the New Jersey Agricultural Experiment Station, Hatch project (NJ32115).

References

- Bayer, S. R., Wahle, R. A., Jumars, P. A., and Brady, D. C. 2016. Measuring scallop fertilization success in the field: chamber design and tests. *Marine Ecology Progress Series*, 551: 141–154.
- Beaumont, A. R., and Barnes, D. A. 1992. Aspects of veliger larval growth and byssus drifting of the spat of *Pecten maximus* and *Aequipecten (Chlamys) opercularis*. *ICES Journal of Marine Science*, 49: 417–423.
- Botsford, L. W. 1993. Rotating spatial harvest of a benthic invertebrate, the red sea urchin, *Strongylocentrotus franciscanus*. In *Proceedings of the International Symposium on Management Strategies of Exploited Fish Populations*, 1993. Alaska Sea Grant College Program, University of Alaska.
- Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B., Largier, J., O'Farrell, M. R., Ralston, S. *et al.* 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*, 19: 69–95.
- Caddy, J. F. 1975. Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. *Journal of the Fisheries Board of Canada*, 32: 1305–1328.
- Chia, F. S., Buckland-Nicks, J., and Young, C. M. 1984. Locomotion of marine invertebrate larvae: a review. *Canadian Journal of Zoology*, 62: 1205–1222.
- Claereboudt, M. 1999. Fertilization success in spatially distributed populations of benthic free-spawners: a simulation model. *Ecological Modelling*, 121: 221–233.
- Claudet, J., and Guidetti, P. 2010. Improving assessments of marine protected areas. *Aquatic Conservation: marine and Freshwater Ecosystems*, 20: 239–242.
- Cochran, W. G. 1977. *Sampling Techniques*, 3rd edn. Wiley, New York.
- Cohen, P. J., and Foale, S. J. 2013. Sustaining small-scale fisheries with periodically harvested marine reserves. *Marine Policy*, 37: 278–287.
- Crowder, L. B., Lyman, S. J., Figueira, W. F., and Priddy, J. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science*, 66: 799–820.
- Culliney, J. L. 1974. Larval development of the giant scallop *Placopecten magellanicus* (Gmelin). *The Biological Bulletin*, 147: 321–332.
- Gaines, S. D., Gaylord, B., and Largier, J. L. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications*, 13: 32–46.
- Gallager, S. M., Manuel, J. L., Manning, D. A., and O'Dor, R. 1996. Ontogenetic changes in the vertical distribution of giant scallop larvae, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of light, food, and temperature stratification. *Marine Biology*, 124: 679–692.
- Goetze, J. S., Claudet, J., Januchowski-Hartley, F., Langlois, T. J., Wilson, S. K., White, C., Weeks, R. *et al.* 2018. Demonstrating multiple benefits from periodically harvested fisheries closures. *Journal of Applied Ecology*, 55: 1102–1113.
- Gouda, R., Kenchington, E., Hatcher, B., and Vercaemer, B. 2006. Effects of locally-isolated micro-phytoplankton diets on growth and survival of sea scallop (*Placopecten magellanicus*) larvae. *Aquaculture*, 259: 169–180.
- Hart, D. R. 2001. Individual-based yield-per-recruit analysis, with an application to the Atlantic sea scallop, *Placopecten magellanicus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2351–2358.
- Hart, D. R. 2003. Yield-and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*). *Fishery Bulletin*, 101: 44–57.
- Hart, D. R. 2006a. When do marine reserves increase fishery yield? *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 1445–1449.
- Hart, D. R. 2006b. Effects of sea stars and crabs on sea scallop *Placopecten magellanicus* recruitment in the Mid-Atlantic Bight (USA). *Marine Ecology Progress Series*, 306: 209–221.
- Hart, D. R., and Chute, A. S. 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 Journal of Marine Science*, 66: 2165–2175.
- Hart, D. R., and Rago, P. J. 2006. Long-term dynamics of US Atlantic Sea scallop *Placopecten magellanicus* populations. *North American Journal of Fisheries Management*, 26: 490
- Hart, D. R., and Shank, B. V. 2011. Mortality of sea scallops *Placopecten magellanicus* in the Mid-Atlantic Bight: Comment on Stokesbury. 2011. *Marine Ecology Progress Series*, 443: 293–297.
- Hennen, D. R., and Hart, D. R. 2012. Shell height-to-weight relationships for Atlantic sea scallops (*Placopecten magellanicus*) in offshore US waters. *Journal of Shellfish Research*, 31: 1133–1145.
- Hurley, G. V., Tremblay, M. J., and Couturier, C. 1986. Daily Growth Increments in the Shells of Larval Sea Scallops (*Placopecten magellanicus*). Northwest Atlantic Fisheries Organization (NAFO) Science Council Research Document, 86/99 11 pp.
- Hurley, G. V., Tremblay, M. J., and Couturier, C. 1987. Age estimation of sea scallop larvae (*Placopecten magellanicus*) from daily growth lines on shells. *Journal of Northwest Atlantic Fishery Science*, 7: 123–129.
- Jensen, O. P., Branch, T. A., and Hilborn, R. 2012. Marine fisheries as ecological experiments. *Theoretical Ecology*, 5: 3–22.
- Leviton, D. R., Sewell, M. A., and Chia, F. S. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology*, 73: 248–254.
- Leviton, D. R., and Petersen, C. 1995. Sperm limitation in the sea. *Trends in Ecology and Evolution*, 10: 228–231.
- Lipcius, R. N., Eggleston, D. B., Schreiber, S. J., Seitz, R. D., Shen, J., Sisson, M., Stockhausen, W. T. *et al.* 2008. Importance of metapopulation connectivity to restocking and restoration of marine species. *Reviews in Fisheries Science*, 16: 101–110.
- Mace, P. M., and Doonan, I. J. 1988. A Generalised Bioeconomic Model for Fish Population Dynamics. New Zealand Fishery Assessment Research Document 88/4, Fisheries Research Centre, MAFFish, POB 297, Wellington, NZ.

- Munroe, D. M., Klinck, J. M., Hofmann, E. E., and Powell, E. N. 2014. A modelling study of the role of marine protected areas in metapopulation genetic connectivity in Delaware Bay oysters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 645–666.
- Munroe, D. M., Haidvogel, D., Caracappa, J. C., Klinck, J. M., Powell, E. N., Hofmann, E. E., Shank, B. V. *et al.* 2018. Modeling larval dispersal and connectivity for Atlantic sea scallop (*Placopecten magellanicus*) in the Middle Atlantic Bight. *Fisheries Research*, 208: 7–15.
- Narváez, D. A., Klinck, J. M., Powell, E. N., Hofmann, E. E., Wilkin, J., and Haidvogel, D. B. 2012a. Modeling the dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. *Journal of Marine Research*, 70: 381–409.
- Narváez, D. A., Klinck, J. M., Powell, E. N., Hofmann, E. E., Wilkin, J., and Haidvogel, D. B. 2012b. Circulation and behavior controls on dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. *Journal of Marine Research*, 70: 411–413.
- Narváez, D. A., Munroe, D. M., Hofmann, E. E., Klinck, J. M., Powell, E. N., Mann, R., and Curchitser, E. 2015. Long-term dynamics in Atlantic surfclam (*Spisula solidissima*) populations: the role of bottom water temperature. *Journal of Marine Systems*, 141: 136–148.
- New England Fishery Management Council. 2003. Final Amendment 10 to the Atlantic Sea Scallop Fishery Management Plan and Supplemental Environmental Impact Statement to the Sea Scallop Fishery Management Plan. New England Fishery Management Council, Newburyport, MA. <https://www.nefmc.org/library/amendment-10-1>.
- Northeast Fisheries Science Center. 2010. 50th Northeast Regional Stock Assessment Workshop (50th SAW) Assessment Report. US Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc, 10–17. 844 pp. <https://www.nefsc.noaa.gov/publications/crd/crd1017/> (last accessed 4 June 2020).
- Pearce, C. M., Manuel, J. L., Gallager, S. M., Manning, D. A., O’Dor, R. K., and Bourget, E. 2004. Depth and timing of settlement of veligers from different populations of giant scallop, *Placopecten magellanicus* (Gmelin), in thermally stratified mesocosms. *Journal of Experimental Marine Biology and Ecology*, 312: 187–214.
- Pernet, F., Tremblay, R., and Bourget, E. 2003. Biochemical indicator of sea scallop (*Placopecten magellanicus*) quality based on lipid class composition. Part II: larval growth, competency and settlement. *Journal of Shellfish Research*, 22: 377–388.
- Plagányi, É. E., Skewes, T., Murphy, N., Pascual, R., and Fischer, M. 2015. Crop rotations in the sea: increasing returns and reducing risk of collapse in sea cucumber fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, 112: 6760–6765.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York and Oxford. 542 pp.
- Serchuk, F. M., and Wigley, S. E. 1986. Evaluation of USA and Canadian research vessel surveys for sea scallops (*Placopecten magellanicus*) on Georges Bank. *Journal of Northwest Atlantic Fishery Science*, 7: 1–13.
- Shank, B. V., Hart, D. R., and Friedland, K. D. 2012. Post-settlement predation by sea stars and crabs on the sea scallop in the Mid-Atlantic Bight. *Marine Ecology Progress Series*, 468: 161–177.
- Shchepetkin, A. F., and McWilliams, J. C. 2005. The Regional Ocean Modeling System: a split-explicit, free-surface, topography-following coordinate oceanic model. *Ocean Modelling*, 9: 347–404.
- Smith, S. J., and Rago, P. 2004. Biological reference points for sea scallops (*Placopecten magellanicus*): the benefits and costs of being nearly sessile. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1338–1354.
- Smith, S. J., Sameoto, J. A., and Brown, C. J. 2017. Setting biological reference points for sea scallops (*Placopecten magellanicus*) allowing for the spatial distribution of productivity and fishing effort. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 650–667.
- Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A., and Hilborn, R. 2015. Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, 16: 633–648.
- Tremblay, M. J., Loder, M. W., Werner, F. E., Naimie, C. E., Page, F. H., and Sinclair, M. M. 1994. Drift of sea scallop larvae *Placopecten magellanicus* on Georges Bank: a model study of the roles of mean advection, larval behavior and larval origin. *Deep Sea Research Part II: Topical Studies in Oceanography*, 41: 7–49.
- Truesdell, S. B., Hart, D. R., and Chen, Y. 2016. Effects of spatial heterogeneity in growth and fishing effort on yield-per-recruit models: an application to the US Atlantic sea scallop fishery. *ICES Journal of Marine Science*, 73: 1062–1073.
- Wallace, E. J., Looney, L. B., and Gong, D. 2018. Multi-decadal trends and variability in temperature and salinity in the Mid-Atlantic Bight, Georges Bank, and Gulf of Maine. *Journal of Marine Research*, 76: 163–215.
- Watson, J. R., Mitarai, S., Siegel, D. A., Caselle, J. E., Dong, C., and McWilliams, J. C. 2010. Realized and potential larval connectivity in the Southern California Bight. *Marine Ecology Progress Series*, 401: 31–48.
- Weinberg, J. R. 2005. Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean temperature. *ICES Journal of Marine Science*, 62: 1444–1453.
- Wilkin, J., and Hunter, E. 2013. An assessment of the skill of real-time models of Middle Atlantic Bight continental shelf circulation. *Journal of Geophysical Research: Oceans*, 118: 2919–2933.
- Zhang, X., Haidvogel, D., Powell, E., Klinck, J., Mann, R., Castruccio, F., and Munroe, D. 2015. Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: model development, larval dispersal and metapopulation connectivity. *Estuarine Coastal and Shelf Science*, 153: 38–53.
- Zhang, X., Munroe, D., Haidvogel, D., and Powell, E. N. 2016. Atlantic surfclam connectivity within the Middle Atlantic Bight: mechanisms underlying variation in larval transport and settlement. *Estuarine, Coastal and Shelf Science*, 173: 65–78.

Handling editor: David M. Kaplan