

Fertilization success in scallop aggregations: reconciling model predictions and field measurements of density effects

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Citation: Bayer, S. R., R. A. Wahle, D. C. Brady, P. A. Jumars, K. D. E. Stokesbury, and J. D. Carey. 2018. Fertilization success in scallop aggregations: reconciling model predictions and field measurements of density effects. *Ecosphere* 9(8):e02359. 10.1002/ecs2.2359

Abstract. Through sperm limitation, population density can be a critical variable in fertilization success of marine broadcast spawners. The broadcast-spawning sea scallop *Placopecten magellanicus* is a commercially important species that has rebounded in population abundance within fishing closures imposed on Georges Bank (GB) and in the Mid-Atlantic (MA). Using video surveys, we tested whether closure increased population density, degree of aggregation and body size of sea scallops. Population densities and shell heights (SHs) were consistently higher in closed areas, significantly so in the MA. Shell height was significantly greater in all closed areas. Influence of area closure on degree of aggregation was less consistent. Using observed spatial patterns of adult scallops on GB and MA and classic steady-state sperm-plume models, we modeled expected fertilization success for two spawning populations with a 10-fold difference in adult density. To test model calculations, we measured fertilization success of manipulated scallop populations of these two densities over the 2012 spawning season in the Damariscotta River tidal estuary in mid-coast Maine. Contrary to predictions, our field experiments revealed no strong effects of population density on fertilization success. We did see significant spatial autocorrelation in adult scallop abundance, however, suggesting greater aggregation at low population densities within several days of high fertilization success on our recorded peak spawning date. Small-scale behavioral adaptation that reduces nearest-neighbor distances at low population sizes may ameliorate the effect of low mean density on fertilization success. Given the exponential relationship between SH and gonad mass, the greater average SH in fishing closures on GB and the MA imply that these regions may be particularly valuable by producing substantially more larvae per capita than areas open to fishing. Positive impact of high density on fertilization success predicted by fertilization models was not borne out, however, in our field trials over a 10-fold density difference. We observed higher-than-predicted fertilization success in our low-density treatment, which may be an encouraging sign that the reproductive performance of broadcast-spawning scallops at low mean densities could be greater than expected possibly due to aggregation behavior.

Key words: Allee effects; fertilization ecology; fertilization success; fisheries; *Placopecten magellanicus*; population density effect; sea scallop.

Received 31 August 2017; revised 25 May 2018; accepted 29 May 2018. Corresponding Editor: Hunter S. Lenihan.

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INTRODUCTION

Marine organisms spanning multiple phyla broadcast gametes into the sea, where successful fertilization depends on having sufficient concentrations of viable sperm. High-density spawning aggregations can ensure high levels of fertilization success (the percentage of eggs fertilized) before gametes become diluted (Allee 1931, Levitan et al. 1992, Levitan and Young 1995, Gaudette et al. 2006). Empirical data on fertilization success in natural broadcast-spawner populations are relatively rare, however, and generally qualitative (Levitan and Sewell 1998). To date, investigators have conducted field studies on fertilization dynamics on a relatively small set of experimentally tractable, free-spawning invertebrates and fishes, including sea urchins (*Strongylocentrotus franciscanus*, Levitan et al. 1992, *Heliocidaris erythrogramma*, Styan 1997, *Strongylocentrotus droebachiensis*, Wahle and Peckham 1999), bluehead wrasse (*Thalassoma bifasciatum*, Warner et al. 1995, Petersen et al. 2001), hard corals (*Montipora digitata*, *Favites pentagona*, *Platygyra sinensis*, Oliver and Babcock 1992, *Acanthaster planci*, Babcock and Mundy 1992), soft corals (*Briareum asbestinum*, Brazeau and Lasker 1992), scallops (*Chlamys bifrons*, Styan 1998a), and sea cucumbers (*Bohadschia argus*, *Holothuria coluber*, *Actinopyga lecanora*, Babcock et al. 1992). Field and laboratory studies suggest fertilization success can be quite variable (e.g., *B. argus*: 0–96%, *H. coluber* and *A. lecanora*: 9–83%, Babcock et al. 1992, *A. planci*: 23–83%, Babcock and Mundy 1992, *S. franciscanus*: 0–82%, Levitan et al. 1992, *S. droebachiensis*: 5–60%, Wahle and Peckham 1999), frequently well below 100% at low adult densities and under conditions that promote rapid dilution of gametes.

These results support a long-standing concern that commercially exploited fishes and invertebrates with this mode of reproduction may be especially vulnerable to recruitment failure when populations are depleted (Myers et al. 1995, Petersen and Levitan 2001, Rowe et al. 2004). Aggregating behavior during the spawning season may compensate for low mean abundance. Sedentary or slowly moving broadcast spawners that form spawning aggregations, such as the abalone (*Haliotis kamtschatkana*, Seamone and Boulding 2011) and scallop (*Pecten fumatus*,

Mendo et al. 2014), may be particularly vulnerable to the effects of fishing activity that target these aggregations. Quinn et al. (1993) modeled red sea urchin (*Strongylocentrotus franciscus*) populations under different harvest strategies and suggested that the protection of high-density refuges from harvesting could protect against recruitment failure.

As a fisheries management tool, fishing closures and marine protected areas maintain a relatively natural state compared with adjacent fished areas by preserving high-density aggregations (Jennings 2000, Russ et al. 2005). Meta-analysis of spawner-recruit relationships for fishes has failed to give many examples of per-capita recruitment limited by low population sizes (depensatory effects, Liermann and Hilborn 1997). There is increasing evidence, however, suggesting that higher population densities and larger adult body sizes found in areas closed to fishing can increase reproductive performance of groundfish and invertebrate species, not only by enhancing egg production, but also by increasing spawning frequency and synchrony, per capita fertilization, and therefore larval production (Peterson et al. 1996, O'Brian and Munroe 2001, Sale et al. 2005, Orensanz et al. 2006).

The sea scallop, *Placopecten magellanicus*, is a sedentary, gonochoristic, broadcast spawner found in coastal and shelf waters of the north-west Atlantic. Sea scallop stocks in the United States have experienced unprecedented rebuilding in the last 15 yr (Stokesbury 2012, NEFSC 2014, Bethoney et al. 2016). Although key components of recruitment, such as adult gamete production (Langton et al. 1987), larval transport (Tremblay et al. 1994, Tian et al. 2009), juvenile mortality (Wong and Barbeau 2003), and patchiness (Carey et al. 2013) have been studied intensively, the recent literature reflects a growing recognition of how little empirical information is available on the role of spawning and fertilization dynamics as potentially critical factors in successful recruitment of scallops (Stokesbury and Himmelman 1993, Smith and Rago 2004, Stokesbury 2012, Harris et al. 2018).

Harvester behavior is likely very relevant to the fertilization dynamics of sea scallops. Targeting aggregations may save time and money, but it also can greatly reduce the number of effective spawning aggregations while depleting the

population. The combined effect of depletion of individual broadcast spawners and increased nearest-neighbor distances could adversely impact fertilization success (Levitan and Young 1995). As a result, persistent high-density aggregations of spawning sea scallops may be critical to the supply of larvae to areas depleted by fishing. Harris et al. (2018) examined the spatial distribution of adult scallops on Georges Bank (GB) from 1999 to 2010 and found 13 persistent, high-concentration (three to four scallops per 3.24 m²) aggregations (spatial scale of ~km²), 11 of them in areas closed to fishing. These aggregations suggest either self-recruiting and/or sink populations. Through small nearest-neighbor distances, these high-density populations could be producing high percentages of fertilized eggs.

Nearest-neighbor distances become increasingly important to fertilization success as the overall number of individuals in the aggregation decreases, as suggested from population manipulations of echinoids. Benefits of proximity alone to fertilization occur in several species of echinoid (Levitan and Young 1995, Wahle and Peckham 1999, Yund and Meidel 2003), and two species of scallop (*C. bifrons*, Styan 1998a, *P. magellanicus*, Bayer et al. 2016); in these cases, fertilization success decreased rapidly <1 m downstream of sperm release. Levitan and Young (1995) demonstrated in field experiments with the sea biscuit, *Clypeaster rosaceus*, that nearest-neighbor distances made less difference to fertilization success as aggregation size increased. Similarly, Gaudette et al. (2006) found that field aggregations of *S. droebachiensis* consisting of only a few hundred urchins did not exhibit the mass, synchronous, spawning observed in populations consisting of 100,000 + spawners, presumably because of the weakness of intraspecific cues.

Restoration efforts for bay scallops (*Argopecten irradians irradians* and *Argopecten irradians concentricus*) have included increasing local populations by many orders of magnitude (Peterson et al. 1996, Tettelbach et al. 2011, 2013). Tettelbach et al. (2013) observed 11- to 32-fold increases in larval recruitment in embayments after increasing populations by two to three orders of magnitude through outplanting, and the use of lantern nets and bags. Heavily increasing local

population density has clearly been very important for bay scallop restoration efforts in near-shore seagrass beds. Self-sustaining sea scallop populations have recovered through fishing closures alone, however, and maintain lower average population densities (Stokesbury et al. 2004). When compared with bay scallops, sea scallops are also longer lived, larger, dioecious rather than hermaphroditic, and show preference for cooler waters and harder substrates.

Determining how sea scallop population density (or nearest-neighbor distance) relates to fertilization success is necessary to enhance understanding of fertilization dynamics and to inform recruitment models. Existing recruitment models for sea scallops assume that per capita fertilization success remains constant at all population densities (McGarvey et al. 1993, Smith and Rago 2004). Stokesbury et al. (2004) collected population density data from sea scallop beds using a gridded sampling approach. We evaluated this unique dataset for patterns of population aggregation and average nearest-neighbor distances inside and outside areas closed to fishing pressure. In addition, we used these observed population densities to inform our design of small-scale field population manipulations to evaluate consequences of variable spawner density on fertilization success. We know we can measure fertilization success in the field by building on laboratory-based gamete dilution experiments with *P. magellanicus* (Desrosiers et al. 1996). Expanding on these laboratory methods, we have already conducted time-integrated laboratory experiments and deployed unfertilized eggs inside manipulated dockside populations of spawning scallops (Bayer et al. 2016).

In this study, we examined the role of population density and spawner size on fertilization success for the sea scallop. First, by comparing scallop populations inside and outside area closures in the northwest Atlantic, we tested the hypotheses that closed areas are associated with higher population densities, larger shell heights (SHs), and higher degrees of aggregation. Second, we compared fertilization model predictions to field-observed spawning and fertilization rates in scallop populations spanning a 10-fold difference in population density on a defined area of seabed.

MATERIALS AND METHODS

Patterns of population density and aggregation inside and outside closed areas

Video survey data were collected by the School for Marine Science and Technology (SMAST) industry cooperative scallop survey on Georges Bank (GB) and in the Mid-Atlantic (MA). A complete description of survey methods is available in Stokesbury et al. (2004). Scallop densities were observed over 14 research cruises at 12 different locations inside and outside closures in both GB and MA regions in 2008 and 2009 as in Carey et al. (2013). Since our interest was in the density of reproductive scallops, we confined our population density estimates to scallops ≥ 60 mm in SH, the size at which they fully empty their follicles during the spawning season (Davidson and Worms 1989).

In 2008, we surveyed 932 stations on GB and 932 stations in the MA, covering an area of

approximately 8307 and 8388 km², respectively. In 2009, we surveyed 899 stations on GB and 927 stations in the MA, covering areas of approximately 8091 and 8343 km², respectively. Adjacent stations in both areas and years were separated on average by 5.6 km (Fig. 1). Four 3.24 m² quadrats, approximately 50 m apart, were sampled at each station for a total sample area of 12.94 m². Mean scallop counts from the four quadrats divided by the total quadrat area were used as the density for a station. Video was recorded along with time, depth, sediment type, number of scallops, latitude, and longitude at each station. After each survey, the video was reviewed, and a still image of each quadrat was digitized. Shell height (SH) of each scallop was measured in the still image using Image Pro Plus software (Stokesbury 2002). Stations were plotted by latitude and longitude and classified as open or closed to commercial fishing. Mean scallop

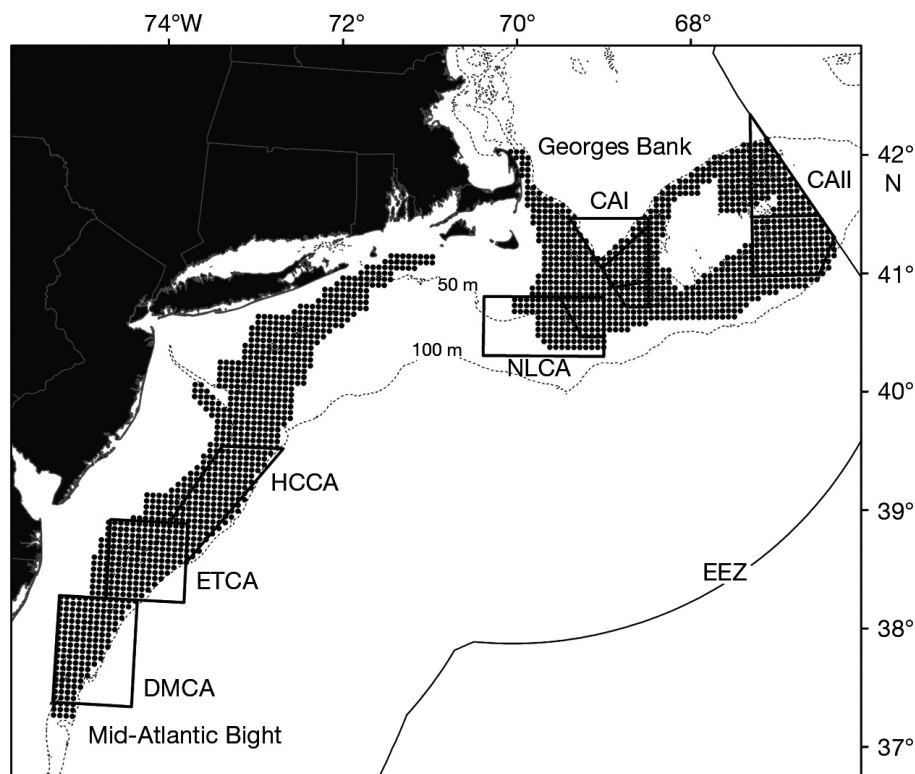


Fig. 1. Video survey station locations on a 5.6 km grid. Georges Bank closed areas are the Nantucket Lightship Closed Area (NLCA), Closed Area 1 (CA I), and Closed Area 2 (CA II). Mid-Atlantic closed areas are the Hudson Canyon Closed Area (HCCA), Elephant Trunk Closed Area (ETCA), and Delmarva Closed Area (DMCA). EEZ, exclusive economic zone (From Carey et al. 2013).

density and standard error (SE) of the mean were calculated in open and closed areas for each camera in each year (see Stokesbury et al. 2004 for details). We performed a *t* test assuming unequal variances for the effect of closed vs. open area on SH for both 2008 and 2009 for each location (GB, MA) in JMP (v.12.2.0, SAS Institute Inc., Cary, North Carolina, USA). Data were pooled across stations for year, location (GB, MA), and closure status. Since we were unable to assume equal variances, Welch's *t* test (Zar 1999) was used to compare density estimates of scallops between open and closed areas each year.

Next, we evaluated the effect of scallop density and area closure on the degree of aggregation of scallops at a site. We used the variance:mean ratio among the four quadrats sampled approximately 50 m apart at a station as our measure of aggregation at a station. Stations without scallops in any of the four quadrats were excluded from analysis. Using population density as the covariate, with the remaining data we performed ANCOVA to compare variance:mean ratios between closed and open areas (JMP v.12.1.0).

Modeling fertilization success

We used a two-dimensional, steady-state, advection–diffusion model to simulate the gamete plume produced by an individual spawner (Denny 1988, Denny and Shibata 1989). This model has been used widely in other fertilization studies (Levitan et al. 1992, Levitan and Young 1995, Claereboudt 1999, Metaxas et al. 2002). The model predicts concentrations (*C*) of sperm (sperm/mL) at positions down and cross stream (*x*, *y*, respectively) from a sperm source:

$$C(x, y) = \left(\frac{Q\bar{u}}{2\pi\alpha_y\alpha_z u_*^2 x^2} \right) \times e^{-\left(\frac{y^2 \bar{u}^2}{2\alpha_y^2 u_*^2 x^2} \right)} \quad (1)$$

where *Q* is the spawning rate (sperm/s), \bar{u} is the mean flow velocity ($\bar{u} = 0.4$ m/s based on field measurements detailed in *Fertilization assay deployments* below), α is the coefficient of turbulent sperm diffusion in seawater ($\alpha_y = 2.20$ m²/s, $\alpha_z = 1.25$ m²/s), and u_* is the friction velocity (m/s), an indicator of shear stress on the seabed. Friction velocity (u_*) was calculated from mean flow velocity using the equation that describes the profile of a turbulent flow near a boundary with a no-slip condition:

$$u_* = \frac{K\bar{u}}{\ln \left[\frac{z}{z_0} \right]} \quad (2)$$

where $K = 0.4$, the von Kármán constant, z_0 is the substrate roughness length, assumed to be 0.01 cm based on bottom type, and *z* is the height above bottom ($z = 0.05$ cm) where gametes are released. As a steady-state model, Eq. 1 predicts the average sperm concentration field assuming continuous spawning.

We scaled up the individual plume model to a population using densities informed by dive surveys at our field sites in the Damariscotta River (see description below) to evaluate how predicted mean fertilization would be expected to change in population densities similar to those observed in fishery surveys. Scallop density and fertilization success were interpolated using inverse-distance weighting (IDW) in MATLAB (R 2015b, MathWorks, Natick, Massachusetts, USA). For modeling purposes, we assumed IDW to be the best interpolating method because scallops are assumed to clump at a spatial resolution of 1–5 m² (Stokesbury and Himmelman 1993). Using population density maps with interpolation between assay quadrats, we back-calculated the mean number of scallops present for both low- and high-density patches for each of our six SCUBA survey dates (17, 26 July 2012; 3, 8, 16 August 2012; 11 September 2012). We then developed probability distributions by seeding 30 × 30 m (model mesh size of 0.1 × 0.1 m) simulated plots with male scallops only and applying the steady-state sperm advection–diffusion model (Eq. 1). The sperm plume emanating from the aggregation was modeled over a 70 × 70 m area that included the 30 × 30 m simulated plots.

Male spawning rate, *Q*, was estimated in the laboratory and peaked at 10⁸ sperm/s (Bayer et al., unpublished). Empirical data suggest that within 1 m the concentration of sperm (sperm/mL) downstream from an individual spawning male should fall to a level that results in near-zero-percent fertilization (*Chlamys bifrons*, Styan 1998a, *Strongylocentrotus droebachiensis*, Gaudette et al. 2006). We therefore are interested in the effect of surrounding males on fertilization success, especially if these areas fall within 1 m of a fertilization assay station.

The fertilization ratio (F) is the proportion of available eggs fertilized and was calculated as follows:

$$F = 1 - e^{(-C_{stf} u_s C \Delta t)} \quad (3)$$

where C_{stf} (m^2) is the available surface area of an egg. Based on experiments conducted by Vogel et al. (1982) on the sea urchin *Paracentrotus lividus*, this value is assumed to be 1–3% of the surface area of an egg. More than 100 spermatozoa per egg were needed to achieve a fertilization success >95%, and the authors concluded that only 1% of the egg surface is available for fertilization or only 1% of spermatozoa are able to fertilize (Vogel et al. 1982). The diameter of scallop eggs is assumed to be 70 μm (Culliney 1974, Desrosiers et al. 1996). Because the value of C (sperm/mL) is derived from a steady-state equation, we assume that Δt is equivalent to the viable half-life of sperm estimated to be 9 min at 16°C at a concentration of 10^6 sperm/mL (Bayer et al. 2016). Distribution of females and eggs were not addressed in this particular model.

Fertilization experiments in experimental scallop populations

Methods for collecting broodstock and inducing spawning are described in Appendix S1. Two experimental populations of sexually mature scallops ($SH \geq 80$ mm) were established at selected locations (near $\sim 43.9^\circ N$, $\sim 69.5^\circ W$, 1 km apart) in the Damariscotta River estuary (23 km long \times ~ 1 km wide; Leonard et al. 1998) in 2012. Initial reconnaissance by SCUBA divers ensured that the sites had suitable bottom (coarse sand/mud) and flow conditions unperturbed by large features (>1 m) on the seabed for at least 50 m upstream and downstream. Scallops were

naturally sparse at both sites, and all previously existing scallops were cleared from each site prior to the start of the experiment (July 2012) to ensure no background effect on sperm supply at our monitoring positions.

Each population was established on a 30×30 m ($900 m^2$) area of the seabed at 10–15 m depth. This area was a manageable scale to service by diver—large enough for the aggregation to remain intact and stationary over the course of the spawning season, yet small enough to be surveyed by four divers in one or two dives. Divers staked off boundaries on the seabed to facilitate subsequent dive surveys. A 3×3 array of nine fertilization assay stations was established on the $900 m^2$ scallop patch. As a distance control, we situated another row of three stations 50 m away in both the upstream and downstream directions perpendicular to the axis of tidal flow for a total of 15 stations at each site (Fig. 2). Station positions were stored with GPS and marked with buoys at the surface.

To simulate the lower and higher end of observed average densities on commercial scallop grounds (Stokesbury et al. 2004), we created two populations by stocking the high-density site with 900 scallops (1.0 scallop/ m^2) and the low-density site with 90 scallops (0.1 scallop/ m^2). To simulate natural conditions, both sites had equal male : female ratios (Smith and Rago 2004), so that male densities were 0.5 and 0.05 individuals/ m^2 , respectively. Females were included in the populations to mimic natural conditions and in case the presence of females facilitates male spawning. Shell height and sex were recorded prior to release into each experimental plot. We tagged each individual with a plastic, numbered label affixed

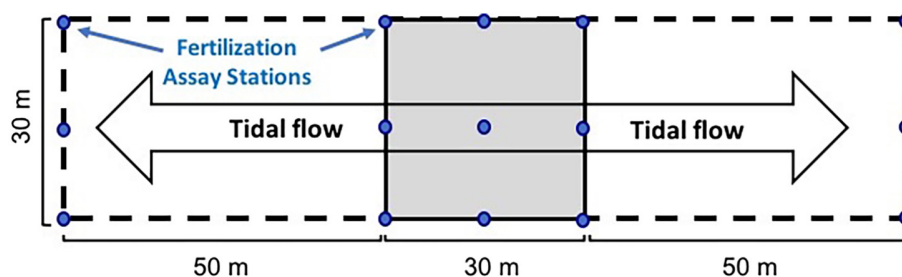


Fig. 2. Array of 15 fertilization assay stations (filled blue circles) located outside and inside the experimental scallop population (gray filled box) oriented along the direction of tidal flow in the Damariscotta River estuary.

with underwater epoxy to its top valve. Based on laboratory observations, the tag did not hinder spawning or movement. Temperature was recorded at both sites using Onset HOBO temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA).

Population dive surveys

During the scallop spawning season, we conducted SCUBA surveys on six dates (17, 26 July 2012; 3, 8, 16 August 2012; 11 September 2012). Dive surveys served to record deviations from the initial population density that resulted from movement and natural mortality during the study. Divers used transect tapes to divide the 30 × 30 m area into seven rows 5 m apart. Each row was further divided into 15 two-meter intervals. Divers counted scallops within a 2 × 2 m (4 m²) quadrat centered on four or five randomly selected points along each row for a total of up to 35 quadrats (= 7 rows × 5 quadrats) per survey. From these data, we conducted spatial autocorrelation analysis using Moran's Index (*I*) to test for statistically significant clustering of adults. Moran's *I* ranges from +1 (highly aggregated: densities in adjacent cells highly positively correlated) to -1 (uniformly dispersed: densities in adjacent cells inversely correlated) with 0 autocorrelation representing random dispersion (Jumars et al. 1977, Blanchard 1990). We used Moran's *I* to detect whether clumping of adults was statistically significant and changed over the spawning season. We tested for significant departures from a Moran's Index of 0 using code developed in R (3.3.1 GUI 1.68, R Core Team 2016).

Gonadosomatic indices and spawning season

To monitor onset and progression of the spawning season during our field experiment, we recorded changes in the gonadosomatic index (GSI) of both experimental populations. Starting in July 2012, at two-week intervals, we dissected a subsample of at least 10 males and 10 females randomly drawn from dive surveys. They were replaced with 10 males and 10 females from our broodstock populations. The GSI is the ratio of wet gonadal mass to the total wet body mass without the shell (Langton et al. 1987, Parsons et al. 1992, Bayer et al. 2016). Tissue was blotted with paper towels before measurements.

Fertilization assay deployments

At each fertilization assay station, we deployed fertilization chambers (15 mm inner diameter × 70 mm height; see Bayer et al. 2016 for details) when eggs were available from broodstock in the lab on 11 dates (18, 19, 20, 23, 25, 27, 28 July 2012; 2, 4, 8, 14 August 2012) during the spawning season. Deployments ended when the GSI began to decline, and it became difficult to induce scallops to spawn enough eggs for all fertilization assay stations in our field experiments. Eggs ≥8 h after spawning were not used, as the viable half-life of eggs is between 8 and 24 h (Bayer et al. 2016). Chambers were loaded with 0.5 mL of concentrated eggs (~2000–5000 by number) in the laboratory, filled with water in which the females had been spawned, and their screw caps were carefully applied under water to avoid bubbles within the chamber. Chambers were kept in small coolers of 10°C, ultraviolet-sterilized, aged seawater during transport into the field. Once in the field, fertilization chambers were fastened to a cement block over the side of the boat under water where they were carefully checked for bubbles before deployment at each of the 15 sites at both high- and low-density treatments. After 24 h, chambers were retrieved, and each was carefully flushed with aged seawater, filtered and fixed in 4% buffered formalin, and scored for developmental stage.

As in Bayer et al. (2016), we conducted parallel control assays to assure that eggs were viable and uncontaminated with sperm. To assess egg viability in these longer-term, 24-h trials, we fertilized a sample of eggs with a saturating dose of sperm and set it aside to incubate for the duration of the trial at ambient water temperature. The criterion for successful fertilization in this experiment included the blastula and all subsequent stages of embryonic development. Although earlier stages were present in these trials, we considered the blastula the most conservative measure of fertilization success given occasional presence of earlier stages observed in our sperm-free controls. For all samples, we subtracted the percentage of developed blastulae in controls from the experimental values observed in the field for that trial before statistical analysis of the field results. We also recorded our controls for each deployment and the relative effect of the correction on

calculated means for stations within the density treatments (Appendix S2: Table S1).

The proportion of fertilized eggs (f) that were scored as blastula stage or more advanced were logit-transformed ($\log f/[1 - f]$) as recommended by Warton and Hui (2011) to improve normality. We tested for a difference between density treatments with Welch's t test on the logit-transformed fertilization values. We then performed an ANOVA with location (inside/outside scallop population) and density as fixed factors. We ran ANCOVA with density (high/low) and fertilization assay station as fixed factors and date as a continuous covariate. All these statistics were performed using JMP (v.12.2.0). We analyzed spatial autocorrelation on fertilization assay stations through the spawning season (see previous methods for Moran's Index on population surveys).

To evaluate the flow to inform our model simulations, we deployed a SeaHorse Tilt Current Meter (Dr. Vitalii Sheremet, University of Rhode Island, Kingston, Rhode Island, USA) on the study sites in the Damariscotta River estuary on 16 December 2012. These deployments were four weeks long, intended to capture the range of tidal flow at the sites over a full spring-neap tidal cycle. The SeaHorse captures the flow of the first meter above the bottom. These deployments were not concurrent with the fertilization experiment. The resulting information was used to inform the fertilization model.

RESULTS

Patterns of population density and aggregation inside and outside closed areas

The density of mature scallops was consistently higher inside fishing closures than inside fished areas for both years and both GB and MA (Table 1). On GB densities ranged from 1.3 to 2.0 times higher in closed than in open areas. In the MA, densities were 2.3–5.2 times higher in closed areas. Given the variability in quadrat counts, these differences were statistically significant only in the MA (Table 2).

Scallops tended to be larger in closed than open areas. Compared to fished areas, shell height (SH) of scallops in closed areas averaged ~20 mm larger in GB and ~2–10 mm larger in MA (Table 3). Shell heights were greater inside closed areas both on GB and in the MA (GB:

Table 1. Video surveys of *Placopecten magellanicus* populations in open and closed areas.

Year and area	Fishing	n	D	SE	V	M	$V:M$	
2008	GB	Open	521	0.07	0.01	2.8	0.6	4.4
		Closed	411	0.09	0.01	4.0	0.7	5.5
	MA	Open	516	0.05	0.00	1.2	0.5	2.6
		Closed	416	0.26	0.03	36.4	2.3	15.6
2009	GB	Open	523	0.09	0.02	14.2	1.1	13.3
		Closed	376	0.18	0.02	19.5	1.8	11.0
	MA	Open	501	0.08	0.01	2.3	0.8	2.7
		Closed	426	0.18	0.02	12.2	2.0	6.1

Notes: Data collected by camera surveys on Georges Bank (GB) and Mid-Atlantic (MA). Year, area, fishing type (open/closed), number of stations (n), scallop density (D , scallops/m²), density standard error (SE, scallops/m²), mean (M , scallops/quadrat), and variance (V , scallops/quadrat) and variance:mean ratio ($V:M$) of scallops ≥ 60 mm shell height in the 3.24 m² quadrats.

Table 2. Welch's t test on the effect of open and closed areas on scallop (>60 mm) densities (scallops/m²) for Georges Bank (GB) and the Mid-Atlantic (MA) from video surveys.

Year	Area	t ratio	df	P value	Mean difference (n/m^2)
2008	GB	0.51	771	0.306	0.023
	MA	2.06	492	0.020	0.210
2009	GB	0.94	720	0.173	0.087
	MA	1.91	571	0.028	0.102

Notes: Reporting t ratio, degrees of freedom (df), P value, and mean difference between open and closed area (closed–open) scallop densities (scallops/m²). Significant P values (<0.05) are in bold face.

Table 3. Area, year, number of scallops (n), and shell height (SH, mm) \pm standard error (mm) for closed and open areas to fishing from video surveys.

Area and year	Closed n	Closed SH	Open n	Open SH	
GB	2008	924	101 \pm 35	410	82 \pm 25
	2009	760	100 \pm 33	751	79 \pm 25
	MA	2008	1184	92 \pm 26	328
	2009	905	95 \pm 20	429	92 \pm 19

Notes: GB, Georges Bank; MA, Mid-Atlantic.

Welch's t test allowing for unequal variances $t = -6.06$, $df = 1347$, $P < 0.001$, MA: ANOVA $F = 249.22$, $df = 2065$, $P < 0.0001$, Fig. 3). Levene's test revealed significantly different

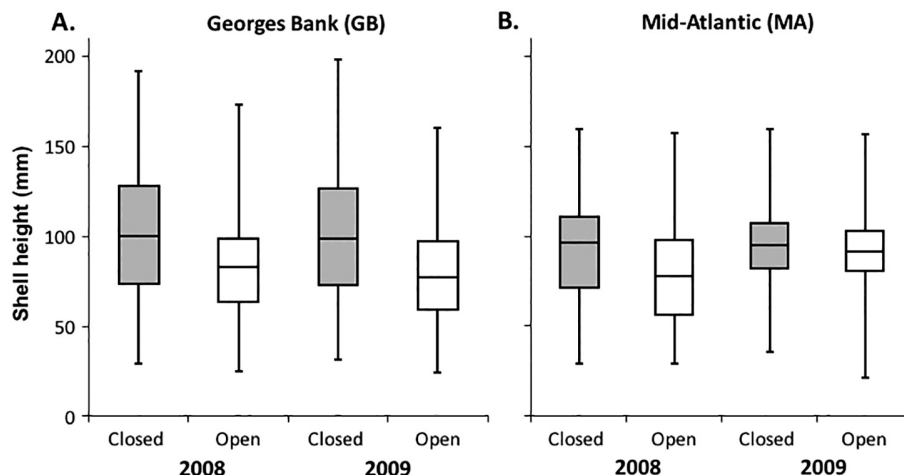


Fig. 3. Minimum, maximum, first quartile, median, and third quartile shell heights (mm) for (A) Georges Bank, (B) Mid-Atlantic of closed (filled boxes) and open (empty boxes) areas in 2008 and 2009.

variances in SH between open and closed areas for GB ($F = 135.07$, $df = 1$, $P < 0.0001$), but not for MA ($F = 0.27$, $df = 1$, $P = 0.60$).

The degree of aggregation of adult scallops (variance:mean ratios of all stations with scallops) was higher in closed areas than in open areas except for GB in 2009 (Table 1). Significance of closure and population density effects was mixed (Table 4, Fig. 4). In GB during 2008, closure status had no significant independent effect, but population density and the interaction of closure status and density were significant (Closure: $F = 34.8$, $df = 1$, $P = < 0.001$; Closure \times density: $F = 5.97$, $df = 1$, $P = 0.015$; Table 4). In 2009, neither closure nor density nor their interaction significantly influenced variance:mean ratios (Table 4). In MA during 2008, closure status and the interaction between closure and density had a significant to marginally significant (Closure: $F = 4.46$, $df = 1$, $P = 0.035$; Closure \times density: $F = 3.73$, $df = 1$, $P = 0.05$) influence on variance:mean values, but density effects on their own were not significant (Table 4). In 2009, closure status and population density effects were both significant (Density: $F = 5.02$, $df = 1$, $P = 0.026$; Closure: $F = 12.6$, $df = 1$, $P < 0.001$), but their interaction was not (Table 4).

Experimental scallop population: Changes in density and dispersion over time

Scallops within our two experimental plots in the Damariscotta River maintained a 10-fold

Table 4. ANCOVA table for variance:mean ratios for open vs. closed areas with population density of scallops ≥ 60 mm shell height as a covariate.

Year and area	Source	df	MS	F	P value
2008 GB	Density	1	19.2	34.8	<0.001
	Closure status	1	0.07	0.12	0.73
	Closure \times density	1	3.29	5.97	0.015
	Error	282	0.55	–	–
2008 MA	Density	1	0.09	0.25	0.62
	Closure status	1	1.59	4.46	0.035
	Closure \times density	1	1.33	3.73	0.05
	Error	432	0.36	–	–
2009 GB	Density	1	97.3	1.32	0.25
	Closure status	1	6.17	0.08	0.77
	Closure \times density	1	2.71	0.04	0.85
	Error	309	73.3	–	–
2009 MA	Density	1	38.6	5.02	0.026
	Closure status	1	96.8	12.6	<0.001
	Closure \times density	1	0.37	0.05	0.83
	Error	437	8.06	–	–

Notes: Tests are by year and area, Georges Bank (GB), and the Mid-Atlantic (MA). Reporting source, degrees of freedom (df), mean square (MS), F value, and P values. Significant P values ($P < 0.05$) are bolded.

difference in density, although numbers declined by about one-third over the course of the season from the initial density (both sexes) of 1 and 0.1 scallops/m² in the two density treatments, respectively. In both populations scallops formed aggregations that changed in shape and size over

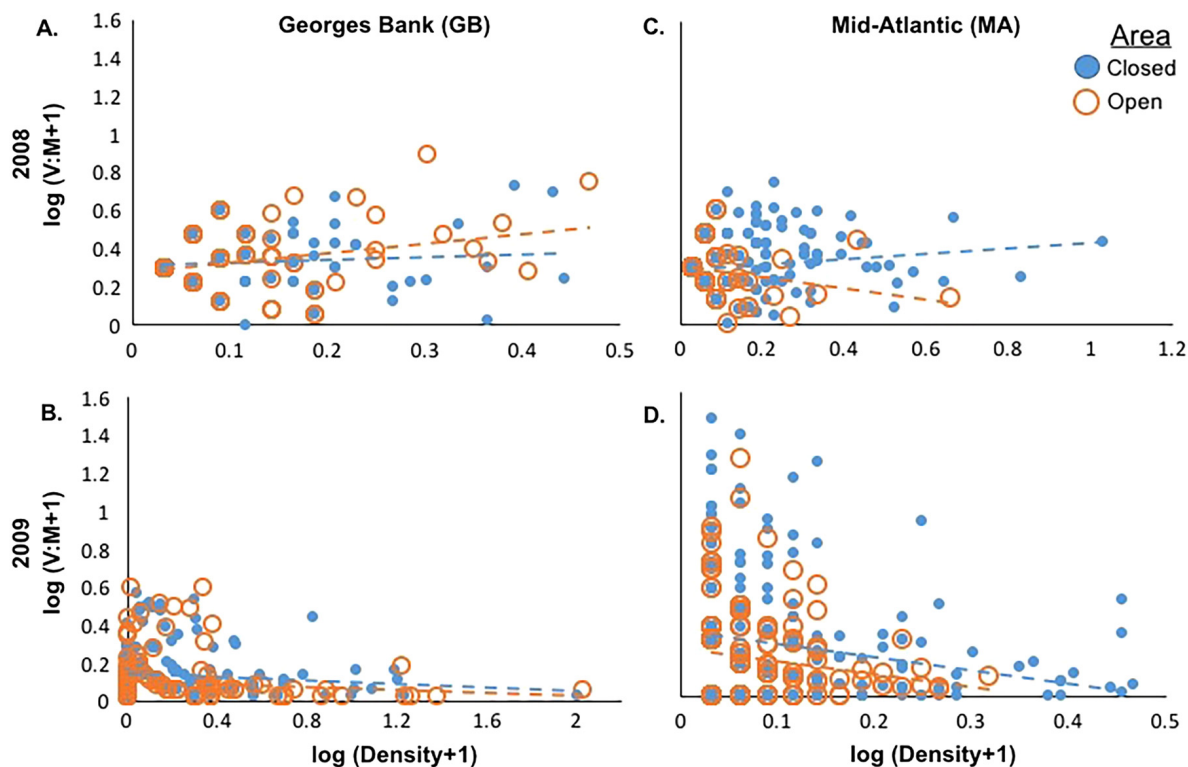


Fig. 4. Log-transformed variance:mean ($V:M$) and density data from Georges Bank in (A) 2008 and (B) 2009, and Mid-Atlantic in (C) 2008 and (D) 2009 video surveys of all stations with nonzero abundances in both closed (blue, filled marker) and open (orange, unfilled marker) sites, with corresponding trend lines (dashed).

several weeks (Fig. 5A). By calculating Moran's Index we detected statistically significant ($P < 0.05$) clumping among adults during the spawning season on three of the six sampling dates in the high-density treatment (8 August, 16 August, 11 September) and two of the six dates in the low-density treatment (26 July, 8 August Table 5). July 26 was only three days after peak fertilization success was recorded in both populations (July 23, Fig. 6); however, there was significant ($MI = -0.02$, $z = 0.42$, $P = 0.02$) spatial autocorrelation in the low-density site but not in the high-density site ($MI = 0.05$, $z = 0.08$, $P = 0.34$; Table 5).

At both locations, maximum velocities measured within 0.1–0.3 m of the seabed over full spring-neap tidal cycles ranged from 0.2 to 0.4 m/s. Residual bottom flow was northward, and residual surface flow was southward, in a classical estuarine circulation. We used the maximum northward (upstream) flow rate of

0.4 m/s to inform our model and calculate u^* using Eq. 2.

Modeled fertilization potential of scallop populations

Mean model-predicted fertilization success from population density surveys was approximately four times greater in the high than the low population density, with similar standard deviations (mean \pm SDs: high, $27\% \pm 8\%$; low, $7\% \pm 7\%$). Unsurprisingly, simulated population densities showed distinct localized areas of high fertilization success near clusters of individuals, particularly in the low-density simulation (Fig. 5B). At steady state, a large fertilization "footprint" extended several meters northward of the simulated population, but encompassed nearly 100% of the individuals. (Fig. 5B). Fertilization success was always at or near 100% within a few centimeters of individual males in the simulations, but diminished to 50% at ~ 1 m

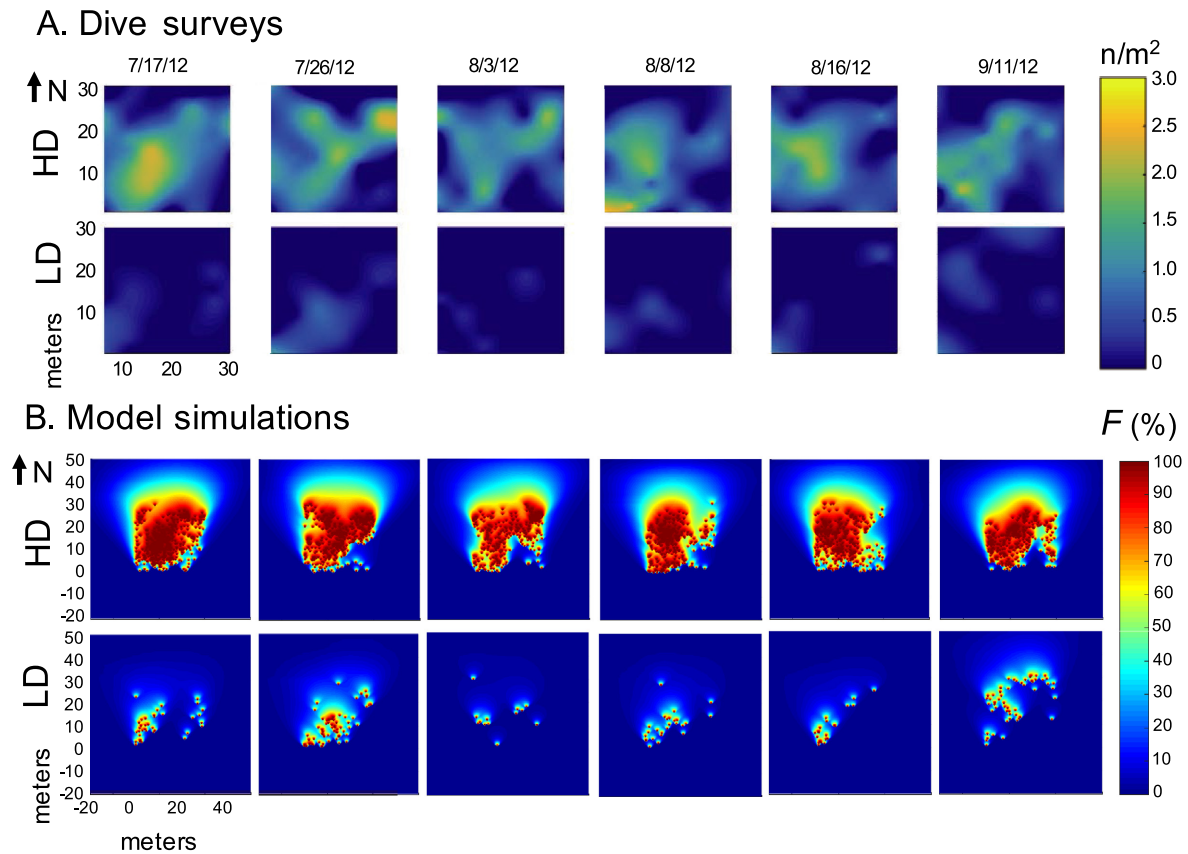


Fig. 5. (A) Spatial patterns of interpolated scallop population densities (n/m^2) in 30×30 m experimental plots during the July – August 2012 spawning season and (B) modeled fertilization success (F) based on Claerebout (1999) with overall flow ($\bar{u} = 0.4$ m/s) direction upstream (north) on a 70×70 m plot where the origin coordinates represent the southeastern corner of the 30×30 m plot in (A). Color bar indicates percentage of eggs fertilized.

Table 5. Data from adult scallop population dive surveys (2×2 m quadrats) for low and high densities during the July – August 2012 spawning season.

Site	Date	D	$V:M$	MI	EI	z score	SD	P	n
High density	17 July 2012	0.69	2.25	0.03	-0.04	0.31	0.04	0.06	28
	26 July 2012	0.63	2.50	-0.02	-0.04	0.08	0.04	0.34	28
	3 August 2012	0.62	2.12	0.02	-0.03	0.28	0.03	0.06	35
	8 August 2012	0.71	2.12	0.13	-0.03	0.87	0.04	<0.01	34
	16 August 2012	0.67	1.86	0.11	-0.03	0.79	0.03	<0.01	35
	11 September 2012	0.67	2.01	0.03	-0.03	0.35	0.03	0.03	35
Low density	17 July 2012	0.05	0.85	-0.07	-0.04	-0.17	0.04	0.81	28
	26 July 2012	0.12	1.51	0.05	-0.04	0.42	0.04	0.02	28
	3 August 2012	0.04	0.88	-0.05	-0.03	-0.12	0.03	0.76	35
	8 August 2012	0.06	1.31	0.04	-0.03	0.41	0.03	0.01	35
	16 August 2012	0.05	1.52	0.02	-0.03	0.29	0.04	0.07	30
	7 September 2012	0.06	1.19	0.01	-0.03	0.25	0.03	0.08	35

Notes: Reported variables are site, date, population density (D , scallops/ m^2), variance:mean ratios ($V:M$), Moran's Index (MI), expected values (EI), standard deviation (SD), z score, P value, and sample size (n). Statistically significant P values ($P < 0.05$) are bolded.

distance in the low population density, and at ~ 7 m in the high population density simulation.

Observed fertilization success in field assays

Contrary to the simulations, fertilization success was not consistently higher in the high-density population (6A). There was no significant difference in fertilization success (Fig. 6A) when comparing assay stations inside manipulated positions to assay stations placed outside (Fig. 2). For each date and population, mean fertilization across all assay stations was no higher than $\sim 40\%$ (Fig. 6A), although on occasion, we observed individual chambers with $\sim 100\%$ fertilization. Statistical analysis revealed no significant effect of density, location (inside vs. outside population), or their interaction (Table 6A) on logit-transformed fertilization values. The highest mean fertilization success for both sites was recorded on 23 July (Fig. 6A). It coincided with a slight decline in male, but not female, gonadal

indices (Fig. 6B) and occurred after a 1°C decrease in temperature (Fig. 6C, D). Our ANCOVA on logit-transformed fertilization values showed no significant effect of density, assay station location, their interaction, or date (Table 6B). Welch's t test showed no statistically significant difference in fertilization success between density treatments ($10.5\% \pm 1.5$ SE in low density; $9.8\% \pm 1.3$ SE in high density) for 2012 (Table 6C). Moran's Index showed no evidence of clumping affecting the spatial pattern of fertilization rates in either of the density treatments during the spawning season (Appendix S3: Table S1).

Temperature and gonadosomatic indices

At the onset of the fertilization assays, temperatures were 13°C , rose to 18°C by mid-August, and dipped to 15°C by the beginning of September. Two large ($\sim 1^\circ\text{C}$) drops in temperature occurred at the end of July and beginning of September (Fig. 6C, D). Gonadosomatic indices

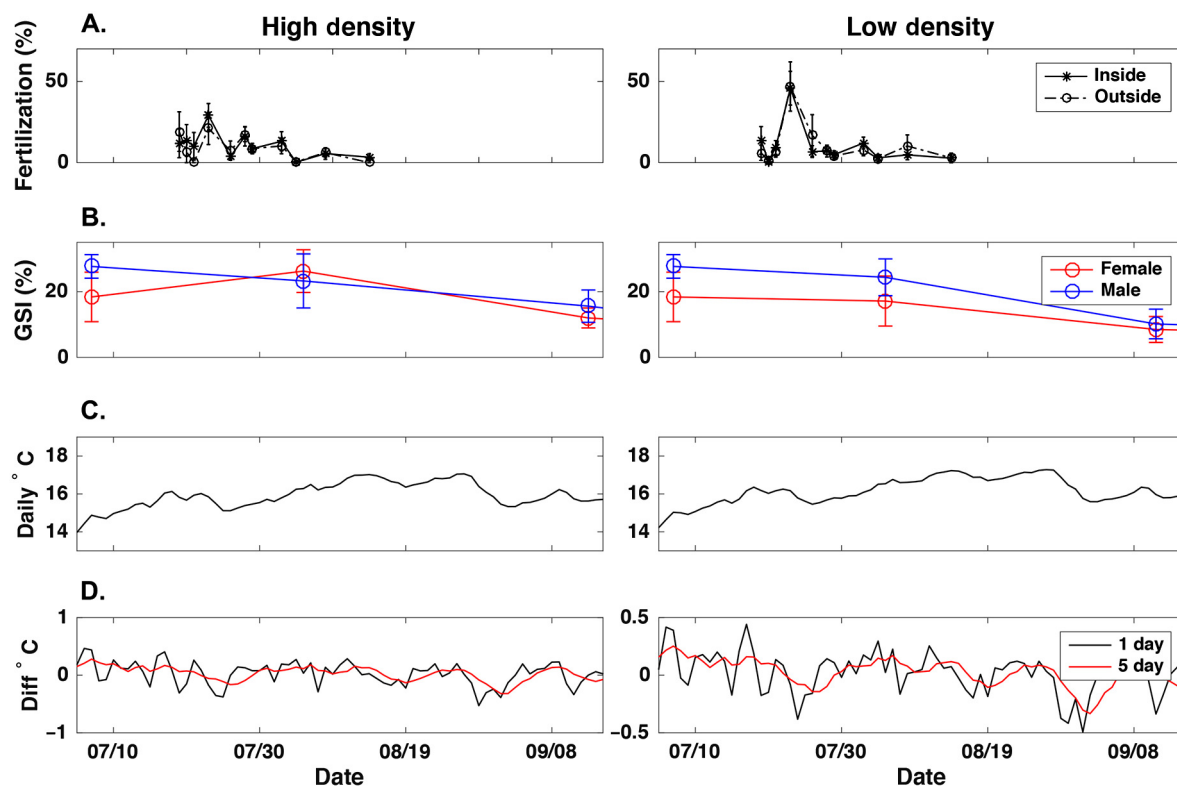


Fig. 6. Time series of (A) mean (± 1 standard deviation) fertilization success, (B) gonadosomatic indices (GSI), (C) daily temperatures, (D) 1 and 5 d moving averages of temperature change on the experimental scallop populations between July and September 2012.

Table 6. Statistical analysis of 2012 fertilization assay station data (fertilization success, *f*) using density (high-density plot vs. low-density plot) and inside vs. outside treatment as categorical variables.

Test	Source	df	MS	stat	P value
A. ANOVA	Density	1	0.34	$F = 0.56$	0.46
	Inside/outside	1	0.97	$F = 1.58$	0.21
	Density \times inside/outside	1	0.16	$F = 0.26$	0.61
	Error	317	194.6	–	–
B. ANCOVA	Density	1	0.24	$F = 0.39$	0.54
	Date	1	0.80	$F = 1.31$	0.25
	Assay location	14	10.6	$F = 1.24$	0.25
	Density \times assay location	14	6.77	$F = 0.79$	0.68
	Error	290	196.0	–	–
C. Welch's <i>t</i> test	–	314	–	$t = 0.44$	0.51

Notes: Shown are (A) ANOVA, (B) ANCOVA using date as a covariate, (C) Welch's *t* test between density treatments for 2012 fertilization assay stations.

started at ~30% for males, ~20% for females (Fig. 6B). While there was a gradual drop in GSI for both males and females over the summer, it was not until the beginning of September that the mean GSI substantially to ~10%, indicating the probable end of the spawning season for the majority of the population.

DISCUSSION

Large fishing closures along the eastern United States have created scallop grounds with higher densities and larger scallops than in adjacent open areas. Higher densities (2–5 \times those in open areas, Table 1) and larger body sizes (Table 3) together should increase mean egg production. For the difference in mean shell height (~90 mm vs. ~80 mm, Table 3), mean estimated seasonal egg production would increase from 21.75 to 34.25 million eggs per female (McGarvey et al. 1992). Assuming a sex ratio of 1:1 (Stokesbury et al. 2016), the higher density in closed areas, when multiplied across the total survey area for each year, would result in 6–32 $\times 10^{15}$ more eggs released in the closed areas for GB and MA areas combined (~8000 km²). Our model simulations, using observations from field surveys, predicted a fourfold increase in fertilization success with one order of magnitude increase in adult density. Using field manipulations of density, however, we did not detect a significant difference in fertilization success despite a 10-fold difference in density. Even without a difference in fertilization success between open and closed areas, the predicted increase in

reproductive output (6–32 $\times 10^{15}$ more eggs) of closed areas would greatly affect the larval supply of offshore sea scallops.

Reproductive benefits of area closures

Scallop populations closed to fishing in the MA consistently had higher densities than those open to fishing in 2008 and 2009. Population densities in closed areas on GB, despite having higher densities, were not significantly different, however, from open areas. A high-density recruitment event observed in the South Channel (an area open to fishing) in 2008 (Bethoney et al. 2016) may be a possible explanation. By the time of the survey in 2009, a large percentage of these newly recruited scallops had grown to sizes ≥ 60 mm. Despite this recruitment event, however, the average SH of *Placopecten magellanicus* was ~20% greater in closed areas than in open areas, suggesting greater reproductive potential of scallops within closed areas. Similarly, Beukers-Stewart et al. (2005) found more large (≥ 130 mm SH) scallops (*Pecten maximus*) inside closed areas (71% of scallops) than in fished areas (34% of scallops) near the Isle of Mann. Scallops exhibit an exponential relationship between SH and gonad size (Langton et al. 1987), and therefore, larger individuals contribute disproportionately more larvae to the population per capita.

Variance:mean ratios in scallop densities in closed areas were always significantly higher except on GB in 2009. Statistical analysis of this ratio indicates that closure status was a strong predictor of aggregation in the MA, but not necessarily on GB (Table 4). It is possible that the

MA closed areas targeted prime scallop habitat, whereas on GB scallop habitat quality was more uniformly distributed across open and closed areas (Stokesbury et al. 2004). Density was an important covariate, as well as its interaction with fishing area type on GB in 2008, but not in 2009, the decoupling possibly due to the previously mentioned recruitment event in 2008. Density was a significant variable in the MA in 2009. This observation is consistent with closure effects on king scallops (Beukers-Stewart et al. 2005). Our observations could also have been affected by how recently some sites were closed and by regional variation in habitat. These two variables significantly influenced aggregation size in the Australian green-lipped abalone, *Haliotis laevis* (Shepherd and Partington 1995).

Comparison of experimental scallop populations with video surveys

Average scallop population densities in open areas ranged from 0.05 to 0.09 scallops/m² (Table 1), which fell within densities in our low-density experimental scallop population (0.04–0.12 scallops/m², Table 5). However, ranges of average densities observed in closed areas (0.09–0.26 scallops/m², Table 1) were less than those in our high-density experimental scallop population (0.62–0.71 scallops/m², Table 5). Densities in our high-density experimental population, however, were only three to six times greater than those in closed areas; less than one order of magnitude. Given the lack of significant difference in measured fertilization success across a density range of 0.04–0.71 scallops/m², we expect that populations observed in the video surveys would have similar averages of fertilization success. This result differs starkly from studies on bay scallop population restoration efforts. To achieve increased larval recruitment in bay scallops, outplanting densities (94.4–128 scallops/m², 117–468 individuals per bag) were several orders of magnitude greater than natural population densities (0.4–0.15 scallops/m²; Tettelbach et al. 2011). Our results suggest that at the low population densities we observed, sea scallops may be able to recover better from exploitation than bay scallops. Recovery of sea scallop populations from closures on GB supports this idea (Stokesbury 2012, NEFSC 2014). We do not know what happens to fertilization success

below our study densities, however, nor what a mass mortality event or disease may do to population dynamics.

Modeled vs. observed fertilization dynamics in experimental scallop populations

Fertilization success in our field experiment did not match results from our simulated populations. We generally observed lower fertilization success within the domain of our 30 × 30 m experimental plots than predicted by the model, whereas outside the plots we often measured higher-than-predicted fertilization success. In the field, we recorded a range of fertilization values on par with other broadcast-spawning species (i.e., seastars, Metaxas et al. 2002, abalone, Babcock and Keesing 1999, solitary ascidians, Marshall 2002). Many of these studies found distance from sperm source to significantly affect fertilization success and thus predicted that increasing average density should increase average fertilization success. Our spatial autocorrelation analysis of fertilization success collected in the field indicated no statistically significant clustering of fertilization success values and thus no discernible effect of distance for any date during our experiment.

The effect of polyspermy on fertilization success at high spawner densities is another potential explanation for the disparity between model predictions and field results. Bayer et al. (2016) observed a decrease in fertilization success of *P. magellanicus* at high sperm concentrations in laboratory dilution series that is most likely attributed to polyspermy (Styan 1998b). Marshall (2002) observed high sperm concentrations associated with decreased fertilization success in the broadcast spawning, solitary ascidian *Pyura stolonifera*, suggesting a strong effect of polyspermy. However, these observations were made in tidal pools which often have low rates of flow. Sea scallops experience high flow velocities that cause rapid sperm advection and dilution in their preferred habitat (Harris et al. 2018), therefore, it seems unlikely that polyspermy is reducing fertilization success in the field.

Temporal patterns of spawning in experimental scallop populations

We observed that for both population density treatments, higher fertilization success occurred early in the season while scallops were losing

gonadal mass, presumably as a result of spawning. We also observed that while the high-density population did not clump significantly in July, it did in late August (Table 5). The observed July–August spawn is unusual, but perhaps not surprising given that 2012 had a record ocean heat wave (Mills et al. 2013, Chen et al. 2014). Scallops typically spawn in late August and September in mid-coast Maine (Langton et al. 1987, Barber et al. 1988). Many scallop species (including *P. magellanicus*) spawn multiple times in a season; having an initial small spawn followed by a much larger event 2–4 weeks later (*P. magellanicus*, Parsons 1994, *Chlamys opercularis*, Taylor and Venn 1979, *Amusium japonicum balloti*, Dredge 1981, *Chlamys islandica*, Sundet and Lee 1984, *Pecten alba*, Sause et al. 1987, *P. maximus*, Paulet et al. 1988). Large changes in temperature are known to trigger sea scallop spawning in Canadian waters (Bonardelli et al. 1996). In early September, we recorded a large (~1°C) drop in temperature that we have previously associated with scallop spawning in mid-coast Maine (Bayer et al. 2016). It is possible that there was a second, larger, unobserved spawn in the high-density population during September 2012 associated with this temperature drop.

Asynchronous spawning

Another factor that could explain our lower-than-expected fertilization rates inside the boundaries of our experimental plot is asynchronous spawning. Average fertilization rates can change dramatically if only a fraction of the population spawns at any given time (Claereboudt 1999). Our field results for both density treatments, however, were on a par with the model-estimated, averaged fertilization rates for the low-population density treatment. For example, in two sympatric scallop species, Styan and Butler (2003a) observed asynchronous spawning *Chlamys bifrons* and *Chlamys asperrima*, and differences in spawning phenology between sexes.

Population genetic models predict sex-specific differences in spawning patterns. These models suggest that female broadcast spawners optimize conditions for their offspring and therefore are expected to have a monomorphic spawning behavior (Olito et al. 2017). During our experiments, we have verified this expectation with female sea scallops in the laboratory (Bayer,

unpub.). The same models predict polymorphic spawning phenologies in males due to sperm competition (Bode and Marshall 2007, Olito et al. 2015, 2017, Parker et al. 2018). Body size-specific spawning patterns may also come into play. For example, Styan and Butler (2003b) reported that larger male scallops spawned more frequently but in smaller quantities than small ones.

Reconciling experimental scallop population results with previous research

Our previous research demonstrated a significant effect of scallop abundance on fertilization success (Bayer et al. 2016). In this study, we did not observe an effect of a 10-fold difference in scallop density (90 vs. 900 per 30 m² plot) on fertilization success. Our previous dockside experiment (high density = 60 individuals per dock, low density = 2 individuals per dock) simulated a 30-fold difference in scallop density with a much smaller number of scallops (Bayer et al. 2016). It is possible that the greater difference in density and smaller total number of spawners in the dockside experiment explains the disparity. The difference in population densities applied in Bayer et al. (2016) maybe be more relevant to restoration efforts where populations are being artificially restocked at several orders of magnitude in population density (Tettelbach et al. 2011, 2013) instead of recovering from fishing pressure through natural population growth.

Several other possibilities exist, however, for the difference between studies. Although we used laboratory controls to make conservative estimates of fertilization success in the field, there is still the possibility of sperm contamination from upstream scallop populations. Some broadcast spawners have demonstrated remarkable sperm longevity (Johnson and Yund 2004) and that could be the case for *P. magellanicus* in field conditions. Styan (1997) found relatively high levels of fertilization (17%) 400 cm downstream of spawning male sea urchins (*H. erythrogramma*), supporting the notion that some broadcast spawners (including crown-of-thorns starfish *Acanthaster planci*, Babcock et al. 1994) have high levels of fertilization several meters downstream. If this were true for *P. magellanicus*, it could contribute to our observed results of no significant difference in fertilization success between populations. We used lantern nets in

our previous study to contain scallops and maintain population abundance (Bayer et al. 2016). This may have isolated a component Allee effect that does not manifest as a demographic Allee, or compensatory, effect (Stephens et al. 1999, Gascoigne and Lipcius 2004, Kramer et al. 2009) at the range of nearest-neighbor distances used in this study or in a more natural environment. Scallops in lantern nets could not move, and close proximity to males likely was of inordinate importance because of the tendency of eggs to sink.

Aggregation behavior

Within a few days of our observed highest fertilization values (23 July), there was significant spatial autocorrelation of scallop abundance within the low-density site but not the high-density site (Table 5). Decreased nearest-neighbor distances allow scallops to detect neurosecretions that regulate spawning synchrony (Barber and Blake 2006) and are important for high fertilization success in small populations (Levitan and Young 1995). An increase in spawning synchrony in low-density populations, however, may mitigate the adverse effect of low-population density on fertilization success. Despite limited replication, our data suggest that scallops may be able to compensate for Allee effects in small populations and at low densities by aggregating (Stokesbury and Himmelman 1993). This line of research deserves further investigation not only in scallops but other ecologically and commercially important sedentary broadcast spawners.

The importance of spatial scale

Deciding on the appropriate spatial and temporal scale at which to conduct a field study is a perennial challenge in ecological science (Stommel 1963, Haury et al. 1978, Steele 1978, Levin 1992). Here, we made observations across several critical scales. Our video surveys on scallop fishing grounds ranged from a few meters (between quadrats) to several kilometers (between survey stations) and over months and years. Our field experiments were far more spatially constrained by diving logistics than the video population surveys on GB and the MA, but they were designed with the intent to be relevant to the probable effective dispersal distance of scallop sperm over their viable half-lives.

We also needed to simplify the physical dynamics of the Damariscotta tidal estuary for our sperm advection–diffusion model. Due to the tidal nature of the estuary, the average velocity we used in the model does not capture how the ebb and flow of tides would spread gametes over our study area. We artificially constrained eggs in chambers to compare measured F to modeled F values more easily. Naturally released eggs may move through varying sperm concentrations, resulting in different fertilization frequencies than observed in our study. Interpretations of our results are restricted to the scales at which they were measured. Most importantly, our study revealed that simply scaling up an individual model for sperm advection, diffusion, and fertilization success did not capture the variability we and others (Levitan and Young 1995) have observed at the scale of a small spawning population over one reproductive season.

Suggested model improvements

Given the difference between the model and the field experiments, it may be that this particular model is a poor fit for the fertilization dynamics of *P. magellanicus* and possibly other broadcast spawners. A more simplistic model excluding hydrodynamics (Lundquist and Botsford 2004) may have provided a better average, but would not have addressed the surprising lack of difference between treatments we observed in our empirical fertilization data.

Our fertilization assay stations showed no statistically significant spatial patterns (Appendix S3: Table S1), likely reflecting extensive physical mixing and flow variability typical of this tidal estuary. The steady-state modeled assumes steady flow at a given location and does not account for the variation in direction and velocity observed in a tidal system, nor does it account for the pulsed nature of spawning in most free spawners. In Eq. 3, the fertilization ratio, F , does not decrease very much, if at all, with increasing \bar{u} at a given sperm concentration (c) (Appendix S4: Fig. S1). This insensitivity results from the multiplicative effect of shear velocity (u^*) on sperm–egg encounters in the equation for F (Eq. 3). Under low flow, increases in shear can positively affect fertilization success, whereas high flows decrease residence time and the probability of sperm–egg interaction (Babcock et al. 1994, Zimmer and Riffell 2011).

Excessive shear has been shown to inhibit fertilization in other broadcasting species (e.g., *Strongylocentrotus purpuratus*, Mead and Denny 1995, *Haliotis rufescens*, Zimmer and Riffell 2011). In laboratory experiments, Riffell and Zimmer (2007) discovered that fertilization success decreased at shears $>1.0 \text{ s}^{-1}$ ($u^* = 0.001 \text{ m/s}$) for *H. rufescens* gametes.

Polyspermy is another potential factor that we have previously mentioned, and other authors have incorporated it into their models (Styan 1998b, Parker et al. 2018). The Styan (1998b) model matched very well with fertilization curves of the two sympatric species *C. bifrons* and *C. asperrima* (Styan and Butler 2000). Incorporation of polyspermy dynamics into the model could create an average F in high-density populations that is closer in value to the low-density population, thus producing model results similar to those observed in our experiment.

Another element to consider for future fertilization models is sperm swimming behavior. Across three phyla (oyster, *Crassostrea gigas*; polychaete, *Galeolaria caespitosa*; fish, *Gasterosteus acleatus*), sperm often accumulate against surfaces (Falkenberg et al. 2016); in situ this behavior could potentially result in sperm accumulation at the seabed. Scallop eggs are negatively buoyant, so downward sperm swimming may also be an adaptive behavior that could not be captured in our dockside experiments. These dynamics, and how they influence fertilization success at an ecological scale, may be worth further exploration.

CONCLUSIONS

Although we observed no strong effects of population density on fertilization success over a range of densities observed in the northwest Atlantic, our field experiments suggest that nearest-neighbor distances may be important to fertilization success at small population sizes. By aggregating, small scallop populations may be able to produce higher per capita fertilization rates than predicted by models currently in use. If average fertilization success remains high across a wide range of population densities, larval production will largely depend on spawner abundance and body size. Given the exponential relationship between shell height (SH) and gonad size, the greater average SH in fishing closures in

the northwest Atlantic implies that these regions produce more larvae per capita than open areas. Our observations of (1) greater average SH in closed areas, and (2) high fertilization success observed at relatively low population densities in field experiments, are encouraging signs regarding the effectiveness of protecting broadcast spawners through marine protected areas and fishing closures.

ACKNOWLEDGMENTS

This article is dedicated to the late Andy Mays, a fisherman whose moral support and help collecting scallops made this project possible. This work was supported by NOAA Scallop Research Set Aside grant NA11NMF4540025 awarded to R. Wahle, P. Jumars, K. Stokesbury, J. Gaudette and M. Sieracki. In addition, S. Bayer was supported by the National Science Foundation Graduate Research Fellowship Program, a University of Maine Janet Waldron Scholarship and School of Marine Sciences Research Assistantship. This activity was also supported by the National Science Foundation award no. IIA-1355457 to Maine EPSCoR at the University of Maine. We thank C. Bergeron, J. Gaudette, and P. Jekielek for aiding with both field and flume experiments and project development, and N. Oppenheim, A. Umstead, I. Vega, and J. Rosa for their assistance in experimental deployment and SCUBA support. We also thank the late Dave Mason who helped design and construct our many fertilization assay chambers. C. Petersen and R. Steneck provided constructive advice on experimental design and feedback on this manuscript. We thank S. Morello for his help with R programming, N.D. Bethoney for help with video survey and GIS data analysis, and T. Young-Bayer for his edits.

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