Extreme population densities reduce reproductive effort of Atlantic sea scallops in high-density recruitment events

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ABSTRACT: The Atlantic sea scallop *Placopecten magellanicus* supports one of the most valuable federal fisheries in the USA, with annual ex-vessel values of US$400–600 million since 2010. Among other strategies, the fishery utilizes rotational area management to protect juvenile sea scallops, increasing yield per recruit and spawning potential. While generally successful, area management was challenged by 2 extremely high-density recruitment events. Juveniles at both study sites, the Nantucket Lightship Closed Area and the Elephant Trunk portion of the Mid-Atlantic Access Area, persisted at high densities (up to 39 and 5 sea scallops m^{-2}, respectively) and initially exhibited poor growth, yield, and gamete production. The effect of sea scallop population density on reproduction was investigated through quarterly sampling from May 2018 through January 2020 in low-, medium-, and high-density strata. Reproductive effort, i.e. the proportion of energy devoted to gamete production, was quantified to investigate differences in energy allocation across density, depth, shell height, reproductive stage, and sex. Reproductive activity was limited in the Nantucket Lightship high-density stratum, where the percentage of sea scallops staged as mature or spawning reached 50% during only 1 of 7 sampling trips, compared to 4–6 sampling trips in other strata. Population density was a significant predictor of reproductive effort, with a 28% reduction in reproductive effort from the highest densities to more typical densities. These results illustrate the complexities of managing fisheries for heterogeneous populations of sessile benthic invertebrates. Negative density-dependent effects should be monitored and accounted for in future extreme recruitment events.

KEY WORDS: *Placopecten magellanicus* · Reproduction · Reproductive effort · Population density · Density-dependent effects · Spatial fisheries management · Recruitment

1. INTRODUCTION

Wild-capture fisheries are an important source of employment and nutrition for communities worldwide. Global demand for seafood has steadily increased over the past 40 yr (Kidane & Brækkan 2021) and is projected to double by 2050 (Naylor et al. 2021). Over this same period, landings from wild-capture fisheries have plateaued, and there is a need for novel and adaptive fisheries management strategies to improve yields and resource sustainability.

One tool rising in popularity is the implementation of marine protected areas and other forms of spatial management (Botsford et al. 2009, Rassweiler et al. 2012, Di Lorenzo et al. 2016). Depending on management goals, spatial management strategies can be designed to protect biodiversity and habitat (Bradshaw et al. 2001, Howarth et al. 2015a), improve the stability of fisheries yields or populations (Hopf et al. 2019), allow for resource recovery (Bloor et al. 2021), reduce bycatch of sensitive species (Watson et al. 2009), or improve larval production (Hart et al. 2020),

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with demonstrated successes in some goals and promising projections in others.

In marine fisheries, the impact of spatial management strategies on yield depends on fishing mortality (Hart 2006), larval connectivity and dispersal (Lipcius et al. 2008, Botsford et al. 2009, Davies et al. 2015, Hart et al. 2020), the movement of juveniles and adults (Botsford et al. 2009), the size of protected or closed areas (Walters 2000), and the presence and intensity of density-dependent effects (Sánchez Lizaso et al. 2000, Gårdmark et al. 2006). Spatial management strategies for sessile invertebrates often aim to elevate population densities of target species, which can increase the prevalence of negative density-dependent effects, including food limitation (Olafsson 1986), parasitism (Rudders et al. 2023), predation (Shank et al. 2012), and disease prevalence (Stokesbury et al. 2019). Density-dependent effects can ultimately impact growth (Côté et al. 1993, Gascoigne et al. 2005, Gårdmark et al. 2006, Turra et al. 2014, van der Geest et al. 2019), gamete production (Wahle & Peckham 1999), and mortality (Andresen et al. 2014, Hart & Chang 2022) at the individual level, altering the growth and size of the target population. Understanding the impact of density-dependent effects on outcomes from spatial management strategies is critical for their successful implementation in fisheries management.

The Atlantic sea scallop *Placopecten magellanicus* serves as a useful case study in considering impacts of density-dependent effects on rotational area management in a large-scale fishery. Sea scallops support a major fishery on the east coast of the USA, where over 19 000 t of adductor muscle meats valued at US\$670 million were landed in 2021 (NOAA Fisheries 2022). Though currently one of the most valuable single-species fisheries in the USA, the fishery experienced extreme variations in landings from the 1950s to the early 2000s. Historically, most catches were supported by strong incoming year classes harvested far below maximum yield per recruit (Hart & Rago 2006). Recent management measures for the sea scallop fishery, including limits on permits and effort (days at sea), gear and crew restrictions, and a system of rotational area management, have helped to stabilize landings and improve resource sustainability (Hart 2003, Hart & Rago 2006).

The sea scallop spatial management strategy is uniquely designed to be responsive to changing resource conditions. Annual resource surveys identify dense aggregations of 1 to 2 yr old juvenile sea scallops, which are then protected from fishing pressure for 2 to 3 yr in closed areas (NEFMC 2003, O'Keefe &

NEFMC Scallop PDT 2022). Both growth and yield increase rapidly in early years (Hart & Chute 2009, Sarro & Stokesbury 2009, Hennen & Hart 2012), and protecting juveniles increases yield per recruit and reduces the risk of growth overfishing (Hart 2003). Closed areas also allow sea scallops to spawn multiple times before they are susceptible to harvest by the fishery. Sea scallops can produce gametes at age 2, but production is low until age 4, after which it increases rapidly (MacDonald & Thompson 1985, Langton et al. 1987). Sea scallops are broadcast spawners with external fertilization, and fertilization success is generally positively correlated with higher adult population densities in broadcast spawning invertebrates (Levitan 1991, Levitan et al. 1992, Levitan & Young 1995, Wahle & Peckham 1999, Styan & Butler 2000, Lundquist & Botsford 2011, Bayer et al. 2016). The formation and persistence of dense sea scallop aggregations within closed areas may improve fertilization rates (Bayer et al. 2016) and reduce the risk of recruitment overfishing (Hart 2003), although high fertilization success has been observed in sea scallops even at low population densities (Bayer et al. 2018). The sea scallop rotational area strategy is considered fully adaptive, and the boundaries and existence of closed areas can be adjusted on a yearly basis in response to updated data on growth, yield, or reproductive potential. Outside of the closed areas, the sea scallop fishery is managed through allocations of 'days at sea' which are fished on open bottom.

Current understandings of sea scallop growth (Hart & Chute 2009), yield (Sarro & Stokesbury 2009, Hennen & Hart 2012), and reproduction (MacDonald & Thompson 1985) underpin the mathematical formulations used in stock assessment and subsequent management decisions. The sea scallop resource is currently assessed as a single stock divided into 2 resource subunits, Georges Bank (including Nantucket Shoals) and the Mid-Atlantic Bight (Fig. 1), due to differences in oceanographic conditions that impact biological parameters (NEFSC 2018). Georges Bank is a raised bank with depths less than 30 m at the center to over 300 m at the bank edge. The dominant oceanographic feature is a year-round, clockwise gyre between the central, well-mixed portion of the bank and the seasonally stratified outer bank (Mavor & Bisagni 2001). The Mid-Atlantic Bight encompasses the continental shelf region bounded by Cape Hatteras to the south and Cape Cod to the north. The dominant current in this region is an alongshelf southwestward flow (Lentz 2008), and seasonal stratification produces large spring phytoplankton blooms. Sea scallops grow to larger shell heights on Georges Bank than in the
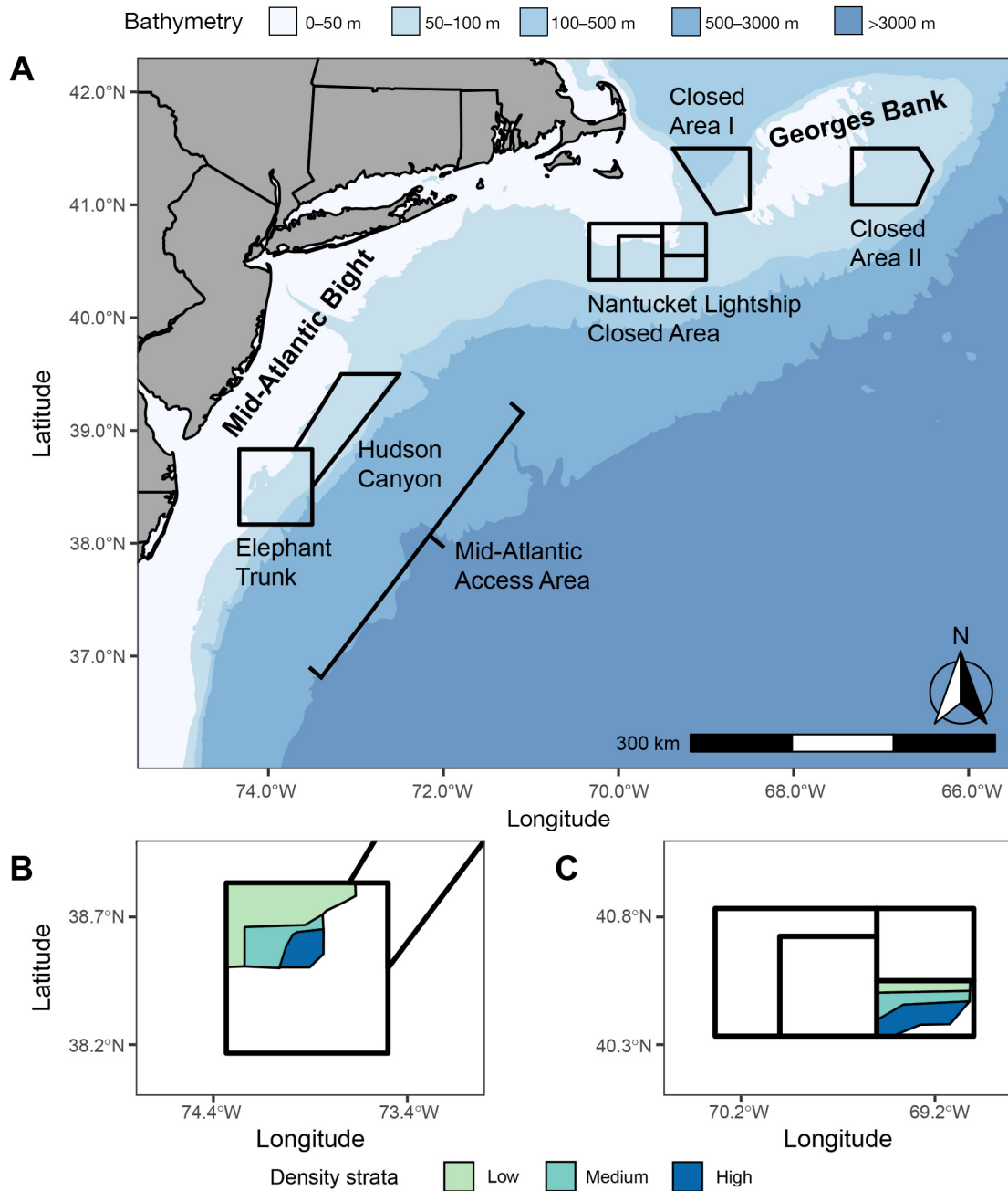
Fig. 1. (A) Study region with 2018 sea scallop access area boundaries and resource sub-units, (B) Elephant Trunk sea scallop density stratification, and (C) Nantucket Lightship sea scallop density stratification. Mean population densities were 0.02, 0.30, and 0.69 sea scallops m^{-2} in the Elephant Trunk low-, medium-, and high-density strata and 0.02, 0.35, and 19.21 sea scallops m^{-2} in the Nantucket Lightship low-, medium-, and high-density strata, respectively

Mid-Atlantic Bight, although shell heights decline with depth in both areas (Hart & Chute 2009). Yield varies by sub-unit and with depth and latitude (Hennen & Hart 2012). Sea scallops in the Mid-Atlantic Bight typically experience 2 spawning events a year (Schmitzer et al. 1991). Sea scallops on Georges Bank historically experienced a single spawning event in the fall (Almeida et al. 1994), but a spring spawning event is becoming more common (Dibacco et al. 1995, Thompson et al. 2014), likely due to warming winter temperatures. These biological attributes are used to parameterize forward-projecting size-based models (NEFSC 2018). A catch-at-size analysis model is used to estimate past fishing mortality, biomass, and

recruitment (Appendix A6 of NEFSC 2018), and the Scallop Area Management Simulator (SAMS) model is used to evaluate the impacts of opening and closing rotational areas by modeling the population and fishery at a fine spatial scale (Appendix A7 of NEFSC 2018). Conditions that deviate from typical conditions can complicate the assessment and management process by introducing uncertainties that make accurate projections of sea scallop biomass challenging.

In 2013, resource assessment surveys identified high numbers of juvenile sea scallops from the 2012 year class along the Southern Flank of Georges Bank extending west into the Nantucket Lightship Closed Area, with the highest densities in the southern portion of the Nantucket Lightship at depths between 60 and 90 m (Fig. 1, NEFMC 2014). This is not an area where sea scallop recruitment has historically been high, particularly at such elevated densities (NEFSC 2018). In 2014, resource surveys identified a second high-density recruitment event from the 2013 year class in the Mid-Atlantic Bight, with the highest densities in the Elephant Trunk portion of the Mid-Atlantic Access Area (NEFMC 2015), which is typically a productive sea scallop habitat. These recruitment events had the highest densities of juveniles since routine resource surveys began in 1979 (Hart & Rago 2006, NEFSC 2020). The 2012 year class on Georges Bank was 1.5 times higher than the previous largest recruitment event in 2001, with the 2013 year class in the Mid-Atlantic Bight more than double that of 2001 (NEFSC 2020). Sea scallops in both aggregations persisted at high population densities, initially demonstrating growth and gamete production below expectations (NEFMC 2018) and higher rates of natural mortality (Hart & Chang 2022), likely due to density-dependent predation on juvenile sea scallops by *Cancer* spp. crabs (Hart & Shank 2011). In response, a number of management options were considered through the New England Fishery Management Council (NEFMC) process, including (1) transplanting sea scallops to more productive areas, (2) allowing targeted harvesting of sea scallops to decrease abundance and potentially increase growth and yield, and (3) protecting sea scallops as spawning reserves with the assumption that high densities would support high fertilization efficiencies when spawning occurred (NEFMC 2019a,b).

Choosing an optimal management action to respond to poor growth and low gamete production is complicated by the complex relationship between population density, environmental conditions, and reproductive processes. Elevated population densities can reduce individual gamete production (Levitan 1991, Wahle &

Peckham 1999, Tettelbach et al. 2011, Hasegawa et al. 2014) in marine invertebrates, likely through resource limitation. Sea scallops experience a reduction in gamete production (MacDonald & Thompson 1986, Hennen & Hart 2012) and reproductive effort (MacDonald et al. 1987, Barber et al. 1988) with increasing depth, which was used as a proxy for food availability by MacDonald & Thompson (1986) and MacDonald et al. (1987). Increased food availability has been linked to increased larval production in bivalves (Beekey & Karlson 2003) but may only be an important driver below a certain threshold (Shriver et al. 2002). Reductions in individual gamete production may be mitigated by improved fertilization efficiencies at high population densities (Levitan et al. 1992, Wahle & Peckham 1999, Bayer et al. 2016) or through physical aggregation at low population densities (Lundquist & Botsford 2011, Bayer et al. 2018). The interplay between population density, environmental factors, gamete production, individual behavior, and fertilization efficiency is complicated, with varied impacts on gamete and larval production at the population level.

To investigate the effect of population density on sea scallop reproduction, we sampled the extreme recruitment events in the Elephant Trunk and Nantucket Lightship areas and analyzed our samples for (1) density-dependent effects on reproductive effort and (2) differences in response between recruitment events. We employed reproductive effort as a proxy for the investment in gamete production compared to somatic processes, hypothesizing that reproductive effort will be lower in sea scallops in high-density aggregations than low-density aggregations due to the presence of negative density-dependent effects on reproduction. The outcomes of this study will contribute to spatial management discussions and inform resource managers about the potential utility of extreme recruitment events as spawning reserves.

2. MATERIALS AND METHODS

2.1. Study areas

Sea scallop aggregations from the extremely high-density recruitment events in the Elephant Trunk and the Nantucket Lightship areas were identified based on results from the 2017 annual resource assessment survey data (NEFSC 2018). Both areas were stratified into low (<1 sea scallop m^{-2}), medium (1–2 sea scallops m^{-2}), and high (>2 sea scallops m^{-2}) density strata (Fig. 1) to ensure sampling effort was distributed across the full range of population densities in both

study areas. For reference, sea scallops can be viably fished at about 0.25 sea scallops m^{-2}, while densities greater than 2 sea scallops m^{-2} are exceptionally high for the resource (D. R. Hart pers. comm.). The 2018 SAMS area boundaries were used as strata boundaries when possible to provide relevant data for real-time management decisions. Observed population densities were often lower than the strata definitions due to the lag between the 2017 surveys and the start of sampling in summer 2018, patchiness of wild sea scallop beds, and fishery removals in both areas (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m746p067_supp.pdf).

2.2. Sample collection

Quarterly sampling was conducted from May 2018 through January 2020 in the Elephant Trunk and Nantucket Lightship areas to ensure all reproductive stages were adequately represented in data analysis (Table 1). Sampling trips planned for spring 2020 in both areas were cancelled due to the COVID-19 pandemic. During each trip, 7 stations were randomly assigned to each of the 3 population density strata for a total of 21 stations per sampling period. Due to low catch rates of sea scallops in the low-density strata in both areas, up to 2 additional random stations were completed when catches were less than the target sample size.

Sampling was conducted with a standard Northeast Fisheries Science Center (NEFSC) 2.4 m sea scallop

survey dredge, as has been used to survey the resource since 1979 (NEFSC 2018). The survey dredge is equipped with 5 cm rings, a 10 cm diamond twine top, and a 3.8 cm diamond mesh liner. The dredge was towed for 15 min with a towing speed of approximately 7−7.75 km h^{-1} and a tow wire scope-to-depth ratio of 3:1. High-resolution navigational logging equipment was used to accurately determine and record vessel position. A Star-Oddi™ DST sensor was affixed to the dredge to record dredge tilt angle and depth. Synchronous time stamps on both the navigational log and DST sensor were used to estimate the linear distance for each tow, and area swept was calculated using the width of the sampling dredge.

Sampling of scallop catch was conducted as in DuPaul & Kirkley (1995), which has been utilized during all sea scallop surveys since 2005 (Rudders et al. 2020). At each station, all sea scallops were placed in traditional 1 bushel (~45 l) sea scallop baskets to quantify total catch. Depending on catch volume, the entire catch or a sub-sample was individually measured to the nearest millimeter from the umbo to the shell margin to determine shell height. Thirty sea scallops were dissected from each station across the range of represented shell heights, and the adductor muscle, gonad, and viscera (digestive gland, gills, and mantle) were weighed separately with a Marel™ M2200 motion compensating scale to the nearest 0.01 g wet weight.

For each dissected individual, the sex and reproductive stage were determined through gross examination (Table 2; see Figs. S2 & S3 for images). Sea

Table 1. Sampling trip information for all sampling periods. Dates are given as mo/yr or mo/d/yr

Sampling period	Study area	Vessel name	Stations	Sail date	Land date
05/2018	Elephant Trunk	'Italian Princess'	21	05/19/2018	05/29/2018
07/2018	Nantucket Lightship	'Celtic'	22	07/12/2018	07/18/2018
08/2018	Elephant Trunk	'Anticipation'	21	08/30/2018	09/01/2018
10/2018	Nantucket Lightship	'Santa Isabel'	23	10/30/2018	10/31/2018
11/2018	Elephant Trunk	'Anticipation'	22	11/30/2018	12/01/2018
01/2019	Nantucket Lightship	'Queen of Peace'	22	01/03/2019	01/05/2019
02/2019	Elephant Trunk	'Anticipation'	21	02/19/2019	02/28/2019
05/2019	Nantucket Lightship	'Queen of Peace'	21	05/02/2019	05/04/2019
05/2019[a]	Elephant Trunk	'Italian Princess'	12	05/10/2019	05/18/2019
05/2019[a]	Elephant Trunk	'Carolina Capes II'	7	05/22/2019	06/02/2019
07/2019	Nantucket Lightship	'Socatean'	22	07/24/2019	07/31/2019
08/2019	Elephant Trunk	'Anticipation'	21	08/12/2019	08/15/2019
11/2019	Nantucket Lightship	'Santa Isabel'	23	11/04/2019	11/05/2019
01/2020	Elephant Trunk	'Norreen Marie'	21	01/09/2020	01/10/2020
01/2020	Nantucket Lightship	'Queen of Peace'	22	01/21/2020	01/23/2020

[a]Indicates Mid-Atlantic resource survey trips completed in 05/2019 in the Elephant Trunk study area. These 2 trips are considered 1 sampling event

Table 2. Descriptions of reproductive stages assigned at sea through gross examination (adapted from Davidson & Worms 1989)

Stage	Female	Male
Resting	Gonad flaccid and watery to the touch; no visible gametes; very faint pink in color, difficult to distinguish from a male gonad	Gonad flaccid and watery to the touch; no visible gametes; very faint white in color, difficult to distinguish from a female gonad
Rebuilding	Gonad watery to firm to the touch; pink or red oocytes visible with space between; intestinal loop visible but fading	Gonad watery to firm to the touch; cloudy white sex cells visible; intestinal loop visible but fading
Mature	Gonad turgid, round, and very firm to the touch; no open space visible; oocytes bright pink to red in color; intestinal loop cannot be seen unless it is near the gonad wall	Gonad turgid, round, and very firm to the touch; no open space visible; off-white to cream in color; intestinal loop cannot be seen unless it is near the gonad wall
Spawning	Gonad firm but not fully extended; some open space visible, though areas with oocytes are tightly packed; oocytes can vary from bright pink or red to light pink in color	Gonad firm but not fully extended; some open space visible, though areas with oocytes are tightly packed; gonad may look translucent depending on spawning progress
Spent	Gonad flaccid and somewhat watery to the touch; may have few remaining solitary oocytes	Gonad flaccid and somewhat watery to the touch; may have remaining areas of white sex cells
Unknown	Gonad flaccid or watery to the touch; no visible gametes; clear in color; typically impossible to distinguish from a male gonad	Gonad flaccid or watery to the touch; no visible gametes; clear in color; typically impossible to distinguish from a female gonad

scallops with very small gonads and no identifiable sex characteristics were classified as 'unknown' sex and undefined reproductive stage.

2.3. Reproductive effort

Reproductive effort was used as a proxy for the proportion of energy invested in reproduction relative to growth and other somatic processes (Bayne & Newell 1983, MacDonald et al. 1987). This metric was used to assess differences in sea scallop energy partitioning between study areas and population density strata as it offers an integrated metric for investigating potential energetic limitations rather than analyzing each tissue separately. Reproductive effort was defined as:

$$\text{Reproductive Effort} = \frac{P_r}{P_r + P_g} \qquad (1)$$

where P_r represents gamete production (gonad wet weight) and P_g represents somatic production (adductor muscle wet weight plus viscera wet weight). This metric has also been referred to as gonadosomatic index or gonadal index. We use the term reproductive effort here to highlight its use to investigate differences in energy investment. Reproductive effort was calculated individually for each dissected sea scallop from the gonad, adductor muscle, and viscera wet weights collected during at-sea sampling.

2.4. Population density

Prior to data analysis, absolute population density (sea scallops m^{-2}) was calculated for each sampling station to include density in models as a continuous predictor:

$$\text{Population Density} = \frac{\text{TotalNumber}/q}{\text{Area Swept}} \qquad (2)$$

The total number of sea scallops collected at each station was calculated by expanding the number of sea scallops in the measured sub-sample by the total catch volume. To account for reduced survey dredge efficiency (q) above 2 sea scallops m^{-2}, a reduced q of 0.13 was used to scale the relative number of sea scallops in the Nantucket Lightship high-density stratum (NEFSC 2018). The reduced q was determined using paired dredge and optical tows (NEFSC 2018, Rudders et al. 2019). The standard q of 0.40 for soft bottom was applied to all other strata in both study areas consistent with stock assessment methods for this species (NEFSC 2018, Miller et al. 2019).

2.5. Modeling the effect of environmental and individual conditions on reproductive effort

The relationship between reproductive effort and several individual and station-level predictor variables was investigated using generalized additive mixed

models (GAMMs) and generalized linear mixed models (GLMMs). Generalized models were selected due to the non-normality of the response variable, and GAMMs were included to investigate the potential for non-linearity in density-dependent effects (D. Hart pers. comm.). Reproductive effort data consist of proportions bounded by 0 and 1, so beta regression with the logit link function was selected for model development (Kieschnick & McCullough 2003, Ferrari & Cribari-Neto 2004). Multiple fixed effect predictors were considered in the GAMMs and GLMMs: shell height (mm), average depth at a station (m), sea scallop population density (ind. m^{-2}), sex, study area, an interaction term of density and study area, and an interaction term of shell height, depth, and study area. Reproductive stage was included as a fixed effect in all models to account for seasonal variations in gonad and adductor muscle weights over the spawning cycle (Schmitzer et al. 1991, Sarro & Stokesbury 2009, Thompson et al. 2014). Sampling station was included as a random effect in all models to account for correlations between sea scallops caught at the same station (Pinheiro & Bates 2000).

The starting GAMM included smoothing terms for the interaction between population density and study area and the interaction between shell height, depth, and study area to investigate the potential for non-linearity in density-dependent effects. Both thin-plate regression splines and cubic regression splines were evaluated in initial models, but no differences in modeled relationships were observed. Thin-plate regression splines were used for all models presented here because they do not require the specification of knot placement, allowing for more flexibility in modeled relationships, and allow models to be compared using conventional hypothesis testing (Wood 2003). Smoothing terms were allowed to behave non-monotonically. The global GAMM was:

$$\text{Reproductive Effort}_{ijklm} \sim \text{Beta}(\mu, \phi) \qquad (3)$$

$$\text{E}(\text{Reproductive Effort}_{ijklm}) = \mu \qquad (4)$$

$$\text{var}\left(\text{Reproductive Effort}_{ijklm}\right) = \frac{\mu(1-\mu)}{1+\phi} \qquad (5)$$

$$\mu = \text{inv.logit}\Big(\beta_0 + \alpha_{\text{Stage}_j} + \tau_{\text{Sex}_k} + s\big(\text{Density} \times \delta_{\text{Area}}\big)_{il}$$
$$+ s\big(\text{Shell Height} \times \text{Depth} \times \delta_{\text{Area}}\big)_{il}$$
$$+ \gamma_{\text{Station}_m}\Big) \qquad (6)$$

where β_0 is the model intercept and μ is the mean reproductive effort of a sea scallop from sample i of shell height, density, and depth. α_{Stage_j} is the parameter estimate of reproductive stage j, τ_{Sex_k} is the parameter estimate of sex k, δ_{Area_l} is the parameter estimate from study

area l, and $\gamma_{\text{Station}_m}$ is the random effect of station m. Reproductive effort is modeled as a beta distribution where the expectation (E) and variance (var) are described by parameters μ (mean reproductive effort) and ϕ. The parameter ϕ is estimated during fitting along with the smoothing parameters and the random effect of station m is normally distributed with a mean of 0 and a variance of σ^2 ($\gamma_{\text{Station}_m} \sim N[0,\sigma^2]$). Main effect terms for all interaction variables were included in models with interaction terms. Where smoothing terms were removed in subsequent GAMMs and GLMMs, shell height and depth were transformed using a natural logarithm to account for more rapid increases in reproductive effort at smaller shell heights (MacDonald et al. 1987) and to facilitate depth comparisons with Hennen & Hart (2012). In models without smoothing terms, population density was square root transformed, as reproductive effort is not expected to continue declining at a constant rate once population densities are already extreme.

2.6. Model selection and validation

Candidate models were developed with a manual backward selection procedure where non-significant predictors were sequentially removed from the model. Interaction and smoothing terms were sequentially removed to evaluate the statistically supported level of complexity and non-linearity in modeled relationships. Models were compared with Akaike's information criterion (AIC), and the model with the lowest AIC was selected as the preferred model (Burnham & Anderson 2002). Models with an AIC within 2 units of the lowest AIC (AIC$_{\text{min}}$) were considered equally plausible as preferred models (Bolker 2008). Due to model complexity, the Bayesian information criterion (BIC) was used as a secondary support in model comparisons.

The appropriateness of model specification was graphically assessed for all preferred models (those within 2 units of AIC$_{\text{min}}$) with residual diagnostics including a Q-Q plot, residuals against the linear predictor, residuals against fitted model values, and residuals against all explanatory variables. Where the appropriateness of model specification was consistent between preferred models, the most parsimonious model was selected for interpretation. Due to the small sampling areas, collinearity was assessed *a priori* with Pearson's correlation coefficients (r) and *a posteriori* with generalized variance inflation factors, which account for varying numbers of parameters between continuous and factor variables (Fox & Monette 1992).

All statistical analyses were completed in R Statistical Software (v4.3.0, R Core Team 2021). Both GAMMs and GLMMs were fitted with maximum likelihood using the 'mgcv' R package (v1.9.0, Wood 2017) to facilitate model comparison using AIC. Post hoc comparisons between categorical factor levels were conducted using the single-step method with the 'glht' function in the 'multcomp' R package (v1.4.25, Hothorn et al. 2008).

3. RESULTS

In total, 4067 sea scallops from 155 sampling stations in the Nantucket Lightship and 3978 sea scallops from 146 sampling stations in the Elephant Trunk were evaluated to investigate the effect of population density on reproductive effort (Table 3, Fig. 2). Sample depths ranged from 37–59 m in the Elephant Trunk and 48–83 m in the Nantucket Lightship. Population densities ranged from 0 to 5.3 sea scallops m^{-2} in the Elephant Trunk and from 0.001 to 39.0 sea scallops m^{-2} in the Nantucket Lightship, although 85% of stations had fewer than 5 sea scallops m^{-2}. The high-density stratum of the Nantucket Lightship was the exception, with a mean population density of 19.2 sea scallops m^{-2} and only 8% of stations below 5 sea scallops m^{-2}. Across all 7 sampling periods, shell heights and adductor muscle, gonad, and viscera weights were lower in the high-density stratum in the Nantucket Lightship than in the medium or low-density strata in this area, although these values were relatively consistent between density strata in the Elephant Trunk (Tables S1 & S2). There was strong overlap in shell height and tissue weight data across density strata in the Elephant Trunk, but sea scallops in the Nantucket Lightship were more separated by density strata. Tissue weight and shell height data for sea scallops staged as mature in each study area are provided in Fig. 3 as an example. For a 100 mm sea scallop, the average mature gonad weight was 5.68, 5.66, and 5.58 g in the Elephant Trunk low-, medium-, and high-density strata and 7.73, 6.00, and 3.83 g in the Nantucket Lightship low-, medium-, and high-density strata, respectively.

3.1. Reproductive activity

Overall, sea scallops in the Nantucket Lightship exhibited reduced reproductive activity, especially in the high-density stratum, compared to sea scallops in the Elephant Trunk. The percentage of sea scallops staged as mature or spawning in the Nantucket Lightship high-density stratum reached 50% during only 1 of the 7 sampling trips (Fig. 4), while the low- and medium-density Nantucket Lightship strata crossed this threshold on 4 out of 7 sampling trips. In the Elephant Trunk, over 50% of sea scallops were reproductively active on 5 (low-density strata) or 6 (medium- and high-density strata) out of 7 sampling trips. The number of sea scallops staged as unknown sex and undefined reproductive stage was 9 times higher in the Nantucket Lightship (n = 295) than the Elephant Trunk (n = 31). In the Nantucket Lightship, 85% of these small, potentially immature sea scallops were collected in the high-density stratum, with the majority collected in 2018 and early 2019. Sea scallops in the Elephant Trunk were staged as mature or spawning more frequently than in the Nantucket Lightship, and the percentage of sea scallops staged as spawning or mature in the Elephant Trunk was similar between density strata.

3.2. Reproductive effort analysis

Twelve candidate GAMMs and GLMMs were developed to analyze the effect of population density and other individual and station-level predictors of

Table 3. Mean, standard error (SE), and range of density of sea scallops and average depth at a station by study areas and density strata. Population density in each stratum was variable during sampling due to the patchiness of sea scallop beds and fishing activity in both areas

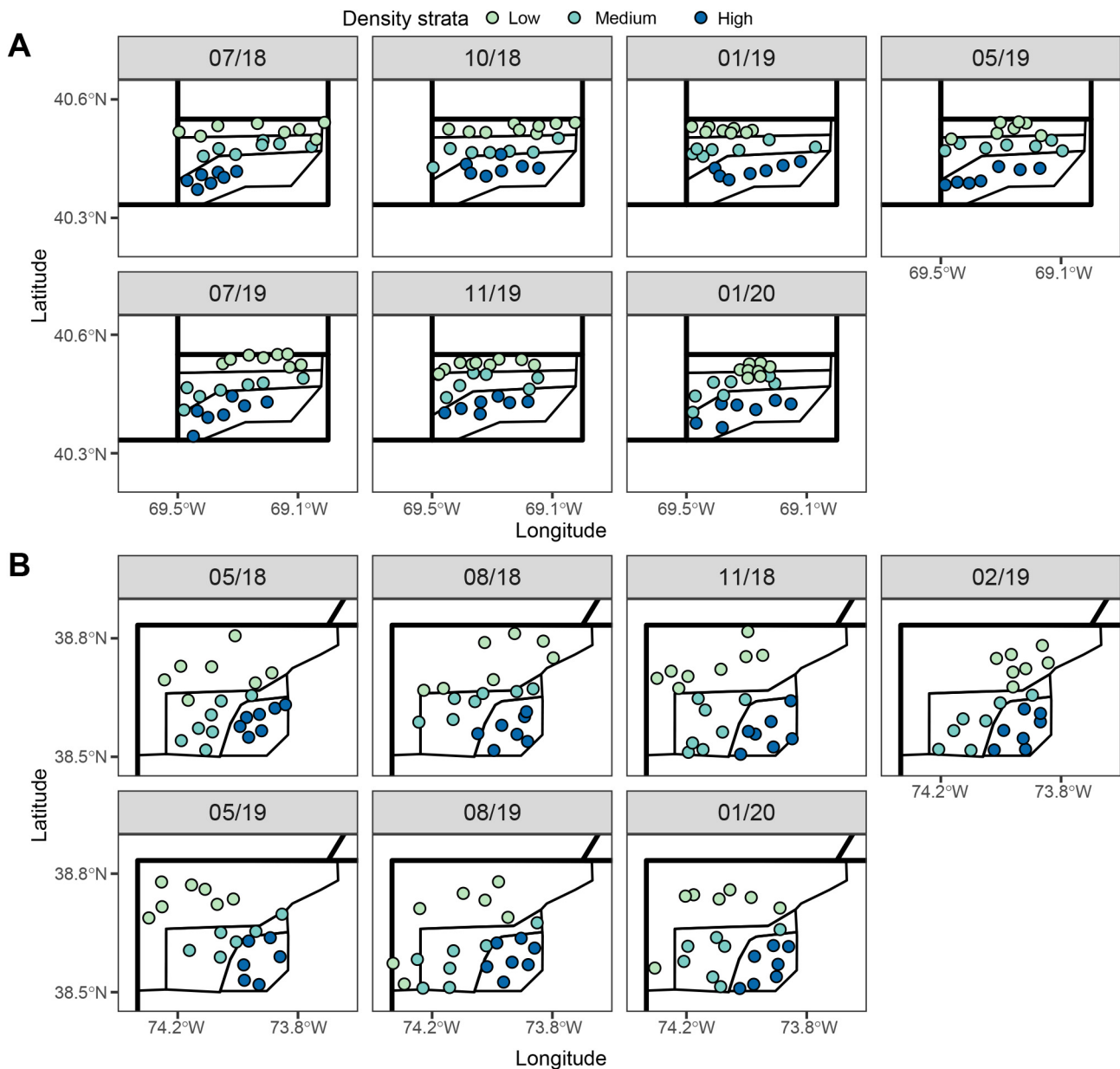| Study area	Density Strata	Density (sea scallops m^{-2})			Depth (m)		
		Mean	SE	Range	Mean	SE	Range
Nantucket Lightship	Low	0.02	0.00	0.001–0.10	65.0	0.96	50.1–78.4
	Medium	0.35	0.11	0.01–3.76	68.8	0.94	53.1–79.1
	High	19.21	1.14	2.35–38.98	72.5	1.04	48.3–83.3
Elephant Trunk	Low	0.06	0.01	0–0.37	44.2	0.49	36.6–51.1
	Medium	0.30	0.12	0.005–5.26	49.7	0.46	42.1–54.9
	High	0.69	0.10	0.01–2.72	52.1	0.50	45.7–59.2

Fig. 2. Location of sampling stations in the (A) Nantucket Lightship and (B) Elephant Trunk across all sampling periods (May 2018 to January 2020). Mean population densities are given in Fig. 1

reproductive effort (Table 4). Three of the models (R_5, R_6, and R_7) were within 2 units of AIC_{min} and were considered equally plausible as preferred models. Model diagnostics indicated that model specification was appropriate, with all 3 models meeting all relevant assumptions. Pearson's correlation coefficients (r) initially indicated moderate collinearity between continuous predictors (r = −0.61 for population density and shell height, r = 0.51 for population density and depth, and r = −0.35 for shell height and depth), but generalized variance inflation factors <2 indicated a lack of collinearity between all predictors in the preferred models (Fox & Monette 1992). The only difference between preferred models R_5 and R_6 is the modeled relationship between population density and reproductive effort, with a smoothing term in R_5 and a square root transformation in R_6. Model R_7 uses the same transformation as R_6 but includes an interaction between population density and study area. Model R_6 was chosen for interpretation due to principles of parsimony. Comparing models using BIC instead of AIC did not change the selection of preferred models.
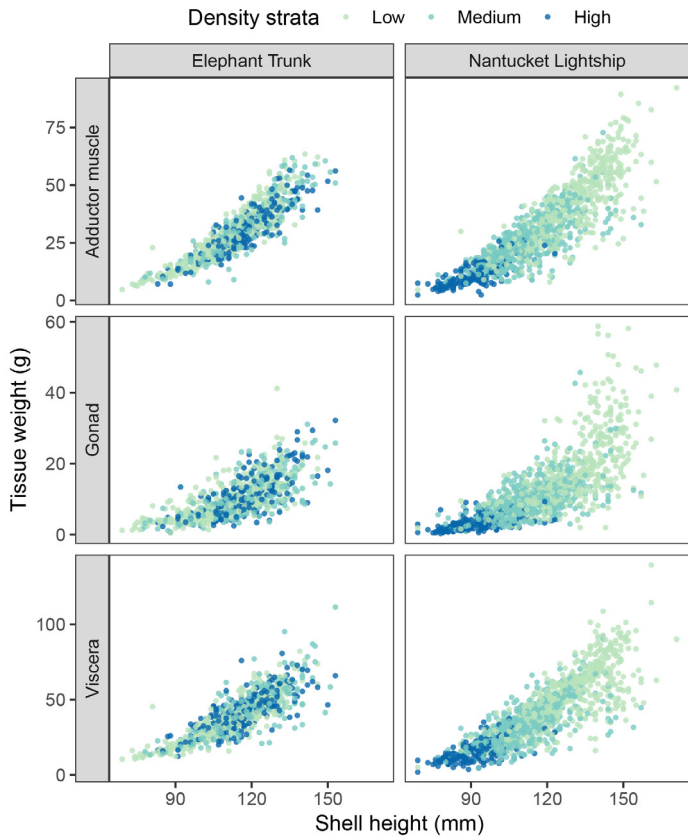
Fig. 3. Shell heights (mm) and adductor muscle, gonad, and viscera weights (g) of sea scallops staged as mature during at-sea surveys. Mean population densities are given in Fig. 1

Fixed effect predictors in model R_6 include sex, reproductive stage, population density, and an interaction between shell height and study area (Table 5), which collectively explained 61% of model deviance. Depth was not found to be a significant predictor of reproductive effort, and an interaction between study area and shell height was supported over an interaction between study area and population density. Reproductive stage was included in all models to explain variation in reproductive effort over the spawning cycle, and estimated coefficients followed expected patterns (Table 5). Both male and unknown sexes had positive effects on mean reproductive effort compared to female sea scallops, although the multiple comparisons test indicated that only male and female sexes were significantly different from each other (Fig. 5). Population density exhibited a negative effect on mean reproductive effort, with the rate of this decline slowing at more extreme population densities (Fig. 5A). Shell height and study area exhibited a significant interaction effect, with mean reproductive effort increasing more rapidly with increasing shell height in the Elephant Trunk than in the Nantucket Lightship (Fig. 5B). In both study areas, shell height had a positive effect on mean reproductive effort, with larger sea scallops devoting more energy to reproduction on average. In
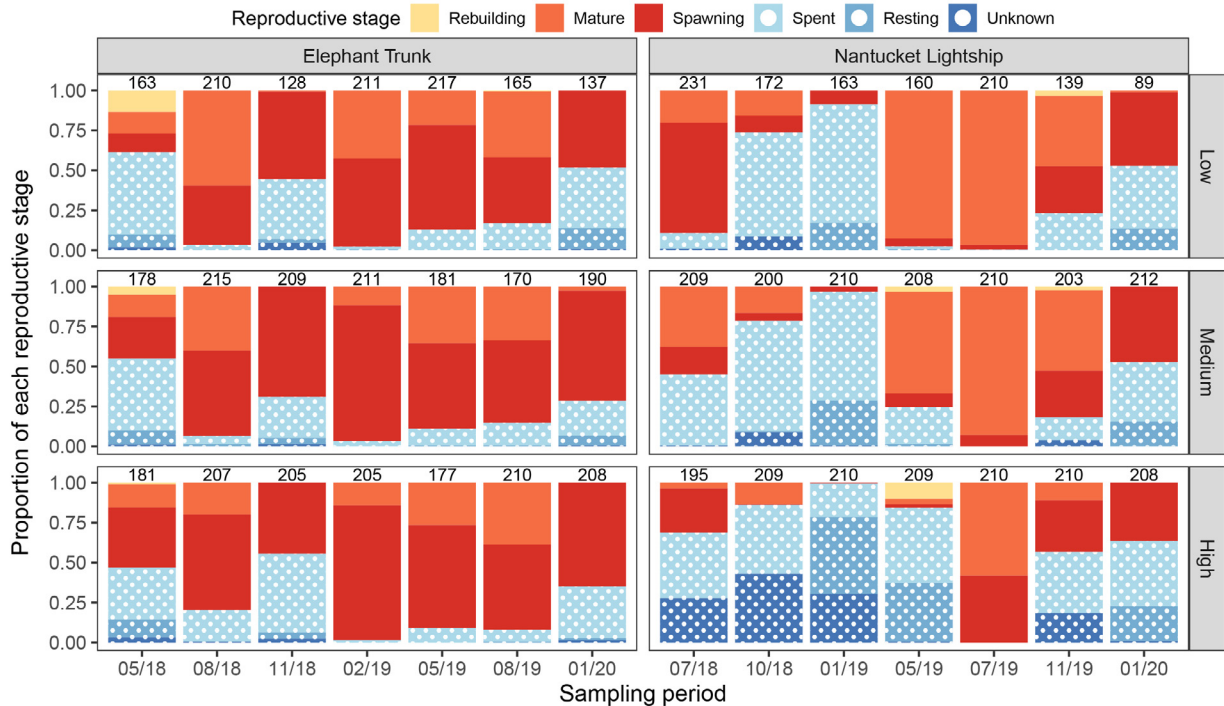

Fig. 4. Frequency of sea scallops in each reproductive stage across sampling periods (May 2018 to January 2020), study areas, and density strata. The numbers above the bars indicate the number of sea scallops staged in each sampling period and density stratum

Table 4. Candidate generalized additive mixed models (GAMMs) and generalized linear mixed models (GLMMs) analyzing sea scallop reproductive effort based on environmental and individual conditions. Model structure, Akaike's information criterion (AIC), and ΔAIC (the difference between the AIC of a given model and the model with the lowest AIC) are provided. For GLMMs, we include k, the number of fixed effect parameters in the model including the intercept and theta. For GAMMs, k is an estimate that includes the number of fixed effect parameters, including the intercept and theta, and the effective degrees of freedom (edf) for smoothing terms. Interaction terms are indicated by the form (Shell height × Depth × Area); all main effects were included in models with interactions. Models with at least 1 smoothing term are checked (✓) in the GAMM column. Model R_6 (in **bold**) was selected for interpretation

Model	Model structure	k	AIC	ΔAIC	GAMM
R_1	Stage + Sex + s(Density × Area) + s(Shell height × Depth × Area)	18.6	−34492.0	14.8	✓
R_2	Stage + Sex + s(Density × Area) + s(Shell height × Area) + ln(Depth)	15.5	−34451.5	55.3	✓
R_3	Stage + Sex + s(Density × Area) + s(Shell height × Area)	14.0	−34497.9	8.9	✓
R_4	Stage + Sex + s(Density) + s(Shell height × Area)	15.8	−34499.4	7.4	✓
R_5	Stage + Sex + s(Density) + ln(Shell height) × Area	15.8	−34506.6	0.3	✓
R_6	**Stage + Sex + sqrt(Density) + ln(Shell height) × Area**	**13**	**−34506.9**	**0**	
R_7	Stage + Sex + sqrt(Density × Area) + ln(Shell height × Area)	14	−34506.6	0.3	
R_8	Stage + Sex + ln(Shell height) × Area	12	−34492.1	14.7	
R_9	Stage + Sex + ln(Shell height) + Area	11	−34473.3	33.5	
R_{10}	Stage + Sex + ln(Shell height)	10	−34471.6	35.2	
R_{11}	Stage + Sex	9	−34358.3	148.6	
R_{12}	Stage	7	−33888.4	618.5	

Table 5. Parameter estimates and standard errors (SE) for the preferred model R_6 in logit space. Significant p-values are **bolded**. Details on model structure are available in Table 4

Parameter	Estimate	SE	Z	p
Intercept	−4.650	0.224	−20.793	**<0.001**
$Stage_{Mature}$	0.218	0.044	4.968	**<0.001**
$Stage_{Spawning}$	0.078	0.044	1.785	0.074
$Stage_{Spent}$	−0.222	0.044	−5.099	**<0.001**
$Stage_{Resting}$	−0.361	0.048	−7.584	**<0.001**
$Stage_{Unknown}$	−0.444	0.099	−4.482	**<0.001**
Sex_{Male}	0.165	0.007	22.216	**<0.001**
$Sex_{Unknown}$	0.154	0.091	1.691	0.091
sqrt(Density)	−0.069	0.010	−7.001	**<0.001**
ln(Shell height)	0.512	0.046	11.109	**<0.001**
$Area_{Nantucket\ Lightship}$	1.477	0.327	4.518	**<0.001**
ln(Shell Height) × $Area_{Nantucket\ Lightship}$	−0.317	0.069	−4.620	**<0.001**

tucket Lightship (Fig. 4). Despite being well past the typical age of maturity (which generally occurs at 2 yr old and 35−75 mm shell height; MacDonald & Thompson 1985, Langton et al. 1987), 7% of sea scallops sampled in the Nantucket Lightship had no observable gamete development. For mature sea scallops, mean reproductive effort decreased by 28% with an increase in population density from 1 to 39 sea scallops m^{-2} (Fig. 5A). These results suggest the influence of negative density-dependent effects on reproduction in sea scallops in extremely high-density recruitment events.

examining the effects of study area, shell height, and density together, the lowest reproductive effort is expected in small sea scallops at high population densities in the Nantucket Lightship (Figs. 5 & 6).

4. DISCUSSION

Our study shows an effect of population density on reproductive effort in sea scallops. We observed a lower frequency of sea scallops engaged in gamete production (mature and spawning reproductive stages) at extreme population densities in the Nan-

4.1. Impacts on reproductive effort and activity

The impact of extreme population densities was evident in the number of sea scallops of unknown sex and undefined reproductive stage sampled in the Nantucket Lightship. Sea scallops from this high-density recruitment event were 6 yr old when sampling started (R. Mann & D. B. Rudders unpubl.), 4 yr older than the typical age of maturity (MacDonald & Thompson 1985, NEFSC 2018), yet had no observable gamete production. Sea scallops in the Nantucket Lightship high-density stratum also lagged behind their low- and medium-density counterparts in gamete
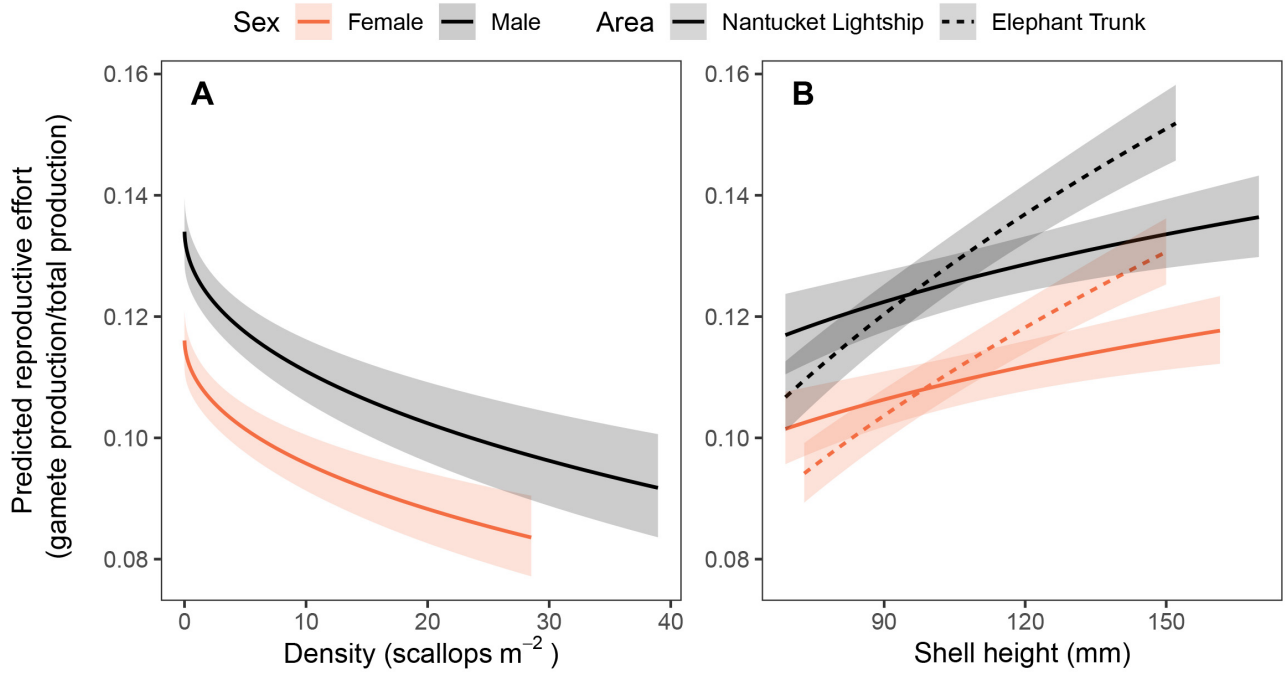
Fig. 5. Modeled effects of (A) population density, (B) the interaction between shell height and study area, and sex on predicted reproductive effort for a mature sea scallop. Model outputs are from preferred model R_6 (Tables 4 & 5). Bands show 95% confidence intervals
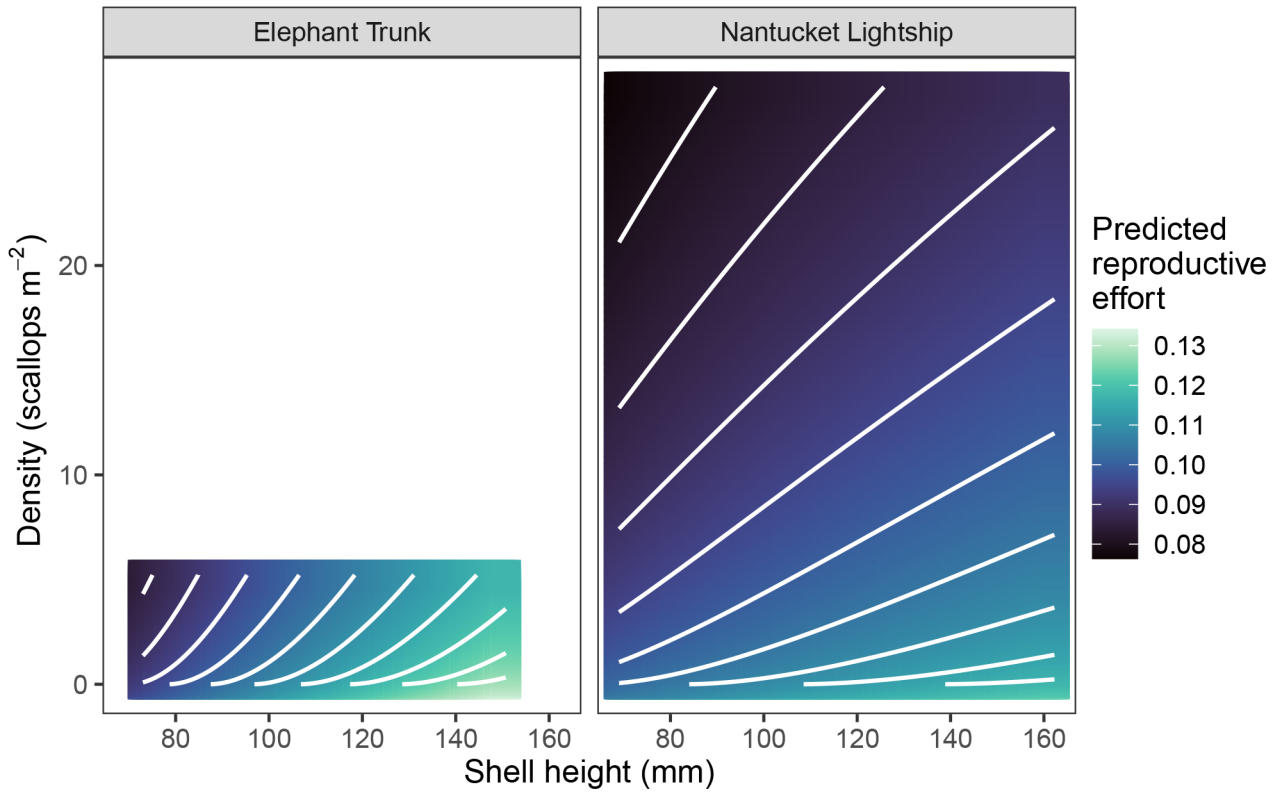

Fig. 6. Modeled effects of population density, shell height, and study area on predicted reproductive effort for a mature female sea scallop. Model outputs are from preferred model R_6 (Tables 4 & 5). White lines indicate constant predicted reproductive effort for interpretation purposes

production in both 2018 and 2019. This is most clearly demonstrated in the July 2018 and May 2019 sampling events (Fig. 4). Fewer sea scallops were staged as mature or spawning in the Nantucket Lightship than the Elephant Trunk, but this may be due to differences in spawning frequency between areas. Sea scallops in the Mid-Atlantic Bight, including the Elephant Trunk, typically experience a spring and fall spawning event each year (Schmitzer et al. 1991), while sea scallops on Georges Bank and surrounds, including the Nantucket Lightship, may not always experience a spring spawning event (Dibacco et al. 1995, Thompson et al. 2014). Few individuals in either area were staged as resting or rebuilding, suggesting that a defined resting period between gametogenic cycles may be rare, as has been previously noted in the Mid-Atlantic Bight (Schmitzer et al. 1991) and Bay of Fundy (Beninger 1987), or indicate bias in stage determination during at-sea data collection.

Male sea scallops were predicted to have higher mean reproductive effort than females in this study. This is contrary to the current understanding of evolutionary stable strategies for gamete production, which predict that investment should be equal between sexes in broadcast spawners or, where there is a bias, that females should invest more heavily (Parker et al. 2018). Data are limited from other mollusks, but this taxon appears to deviate somewhat from these predictions with a bias toward higher male investment (Parker et al. 2018). Possible explanations include a higher energetic cost of eggs than sperm (see Hayward & Gillooly 2011 for a review across taxa) or that males may start producing gametes earlier than females in some mollusk species (Parker et al. 2018). The present study contributes an additional example of higher male investment in gamete production in a bivalve mollusk. Caution should be exercised in interpreting higher investment as an increase in released sperm quantity, however, as larger males did not release more sperm than smaller males in an induced spawning event with 2 species of scallops (*Chlamys bifrons* and *C. asperrima*; Styan & Butler 2003). Styan & Butler (2003) suggested that instead of releasing more sperm per spawning event, larger males may spawn more often over the course of a spawning season, but this has yet to be documented.

Sea scallop population density was an important factor in predicting reproductive effort, even when accounting for differences in shell heights between the 2 study areas and across the full range of population densities sampled in this study. Density-dependent effects can also reduce growth and body size at elevated densities (Gascoigne et al. 2005, Gårdmark et al. 2006,

Turra et al. 2014, van der Geest et al. 2019), suggesting that the estimated impacts on reproductive effort presented here are conservative. Importantly, the present study was not a controlled experiment, and population density was calculated for each station at the time of sampling. The random stratified approach to station allocation precluded the tracking of population density at each station over the duration of the study period. Population density may be more meaningful as a time-lagged covariate because gamete development takes place over multiple months (Schmitzer et al. 1991, Thompson et al. 2014). Future work with experimental populations could help clarify the temporal importance of population density in energy allocation to gamete production.

Previous work with sea scallops and king scallops *Pecten maximus* at varying population densities has focused on differences in growth and tissue weights in closed areas protected from fishing pressure (Beukers-Stewart et al. 2005, Kaiser et al. 2007, Hart & Chute 2009, Hennen & Hart 2012, Hold et al. 2013, Howarth et al. 2015b). Our study differs in that it was designed to examine the effects of extreme population densities within high-density recruitment events, rather than the impacts of fishing protection, but general comparisons are possible. At more moderate population densities, sea scallops in closed areas have exhibited increased growth, adductor muscle weight, and gonad weight due to sustained protection (Hart & Chute 2009, Hennen & Hart 2012). Even within closed areas, king scallops in the Isle of Man and the UK are generally found at much lower population densities, up to 0.07 scallops m^{-2} in the UK (Howarth et al. 2015b) and 0.2 scallops m^{-2} in the Isle of Man (Beukers-Stewart et al. 2005, Hold et al. 2013), but protected king scallops exhibited significant increases in exploitable and reproductive potential. King and sea scallops in these studies are likely below a threshold at which density-dependent effects of resource limitation become relevant. Density-dependent effects may also be exacerbated by resource perturbations or the presence of additional resource constraints. For Manila clams *Ruditapes philippinarum*, density-dependent effects on condition index and fecundity were only detected in an area of high juvenile density following a major recruitment event (Hasegawa et al. 2014). Eastern Bering Sea snow crabs *Chionoecetes opilio* declined precipitously following observation of historic juvenile population densities in 2015 (Szuwalski et al. 2023). Warmer water temperatures from a marine heatwave increased the caloric requirements of crabs during this period of elevated population density, likely exacerbating impacts on food availability and

increasing mortality rates (Szuwalski et al. 2023). Reproductive investment may also be a particularly sensitive metric to elevated population densities in marine bivalves. In bay scallop *Argopecten irradians irradians* restoration, there were no differences in growth or mortality between 3 stocking densities, but gonad dry weights were consistently reduced at the highest stocking density (Tettelbach et al. 2011).

Mean reproductive effort increased with increasing shell height, which is expected, as sea scallops devote relatively more energy toward reproductive than somatic processes as they grow (MacDonald & Thompson 1985, MacDonald et al. 1987, Hennen & Hart 2012). However, the slope of the relationship between reproductive effort and shell height differed by study area. The increase in reproductive effort with shell height had a shallower slope in the Nantucket Lightship than in the Elephant Trunk, indicating a smaller increase in reproductive effort as sea scallops in the Nantucket Lightship reach larger sizes. This shallower rate of increase may suggest a difference in resource limitation (e.g. food availability or quality) or energy requirements between these 2 regions.

The Elephant Trunk and Nantucket Lightship both fall in regions with generally high phytoplankton production (Mouw & Yoder 2005, Ma & Smith 2022), but the southern, deep portion of the Nantucket Lightship, where the highest sea scallop densities were found, is generally considered atypical habitat at depth (NEFSC 2018). Bottom shear stresses are elevated in this area, with a high frequency of sediment movement (Dalyander et al. 2013). Optical surveys of the Nantucket Lightship showed that these scallops were typically covered with a layer of sediment (D. Hart pers. comm.). Sea scallops are considered opportunistic filter feeders with high retention efficiency for particles above 5 µm (Grant et al. 1997). A wide variety of particles, including phytoplankton, detritus, and bacteria, have been found in gut contents, which vary with depth in the Gulf of Maine (Shumway et al. 1987). Sea scallops can adjust their clearance rate to facilitate pre-ingestion sorting with the labial palps to increase ingestion of high-quality food particles (MacDonald & Ward 1994, Bacon et al. 1998, MacDonald & Ward 2009). However, their ability to reject poor-quality particles is impacted when there is a high concentration of low-quality particles (Bacon et al. 1998, MacDonald et al. 1998), as may occur during periods of intense sediment resuspension. Challenges selecting high-quality particles or a general lack of food availability, compounded by the extremely high population densities in the Nantucket Lightship, could have left these sea scallops with a smaller pool of energy to partition between reproductive and somatic processes than those in the Elephant Trunk.

Depth was not found to be a significant predictor of reproductive effort in this study, which is contrary to previous work that used depth as a proxy for the effect of food availability on reproductive effort (MacDonald et al. 1987, Barber et al. 1988). Barber et al. (1988) investigated a much more extreme density range (13–20 m compared to 170–180 m) in the Gulf of Maine, while MacDonald et al. (1987) compared 2 depths (10 and 31 m) at one site in Newfoundland. Hennen & Hart (2012) reported a decrease in adductor muscle, gonad, and whole tissue weights with increasing depth but did not compare energy allocation between tissues. Hennen & Hart (2012) also evaluated stations across the Mid-Atlantic Bight and Georges Bank, covering a much wider spatial area than the present study. Depth was likely confounded by our study areas, as the depth ranges were relatively limited (Nantucket Lightship: 48–83 m, Elephant Trunk: 37–59 m), with low overlap between study areas. Any differences in food availability between study areas were likely captured in the interaction between shell height and study area, discussed above. The relationship between depth and food availability for sea scallops should be investigated over a greater spatial range to better facilitate conclusions on the impact of depth on reproductive processes.

4.2. Implications for reproductive output

The reduction in mean reproductive effort at extreme population densities indicates that sea scallops are investing less energy into gamete production. Lower energy inputs likely indicate fewer viable gametes are being developed at extreme population densities. However, our calculation of reproductive effort did not directly investigate gamete development, production, or viability. More research focused specifically on gamete development and fecundity is needed to fully characterize the effect of population density on gamete production in sea scallops, particularly as higher rates of oocyte resorption have been documented for sea scallops in potentially energetically limited populations (Barber et al. 1988).

A decline in reproductive effort at extreme population densities may be mitigated by increased fertilization efficiencies in these areas. Broadcast spawners are generally assumed to benefit from higher population densities due to improved fertilization efficiencies, which can result in high production of larvae

even if the fecundity of individual animals is depressed (Levitan 1991, Wahle & Peckham 1999). The behavior of spawning individuals can also influence the relationship between population density and fertilization success. At higher population densities, Australian scallops *P. fumatus* exhibited increases in aggregation and decreases in nearest-neighbor distances, potentially leading to increased success in oocyte fertilization (Mendo et al. 2014). Aggregation at low densities may also improve fertilization success beyond that expected from a random distribution (Lundquist & Botsford 2011, Bayer et al. 2018). For sea scallops hung in nets from docks, there was a significant difference in fertilization rates across a 30-fold difference in density, with higher densities having fertilization rates 2—10 times higher than the low- or medium-density treatments (Bayer et al. 2016). However, in a population manipulation experiment with sea scallops across a 10-fold change in density (from 0.1 to 1 sea scallops m^{-2}), there was no significant difference in fertilization rates between density treatments, though aggregation in the low-density population may have mitigated these effects (Bayer et al. 2018). In comparison, in the Nantucket Lightship, this study observed a 950-fold difference in density from the mean density of the low-density stratum (0.02 sea scallops m^{-2}) to the mean density of the high-density stratum (19.2 sea scallops m^{-2}). The extreme range in sea scallop population densities in these study areas makes it difficult to assess any mitigation of reduced reproductive effort by increased fertilization efficiencies. Estimates of fertilization efficiency across a broader range of population density and examination of aggregation during spawning would help refine our understanding of impacts on total larval production at extreme population densities.

The reproductive contribution of high-density sea scallop aggregations is also impacted by the path of larvae released in these areas. Larvae that settle in unsuitable or unproductive habitat contribute little to the future of the population. In the Mid-Atlantic Bight, a general northeast to southwest current pattern contributes to 'downstream' larval connectivity (Munroe et al. 2018, Hart et al. 2020). This suggests that larvae released in the Elephant Trunk are likely to recruit south of Delaware Bay in a portion of the resource that has been declining in both sea scallop health and population density (Rudders & Roman 2020) and is projected to become unsuitable sea scallop habitat with ocean warming (Zang et al. 2023). Larvae spawned on Georges Bank are largely retained by the tidal-mixing-front recirculation (Tian et al. 2009), with the degree of larval retention or advec-

tion influenced by the strength of recirculation. Larvae spawned in the Nantucket Lightship are not a major source to scallop beds on Georges Bank (Davies et al. 2015), as they are consistently advected away (Tian et al. 2009). Connectivity between sea scallop populations on Georges Bank and the Mid-Atlantic Bight is thought to be limited (Chen et al. 2021), so the benefit of a large spawning aggregation in this area is unlikely to provide a benefit to the overall resource. Larval connectivity between regions is highly variable between years (Tian et al. 2009, Owen & Rawson 2013, Munroe et al. 2018, Hart et al. 2020, Chen et al. 2021), which introduces additional difficulties in designing short-lived access areas around high-density aggregations.

4.3. Management implications

A major management strategy of the sea scallop fishery is protecting high-density aggregations of juvenile sea scallops to leverage rapid increases in growth, yield, and reproductive output in early years. This study suggests that the presence of density-dependent effects may influence the expected outcomes from managing extremely high-density recruitment events with rotational area management. One proposed option for managing high-density recruitment events is to protect them as spawning reserves due to the assumed increase in fertilization efficiency at higher sea scallop population densities. However, the uncertainty around how fertilization rates differ across an extreme range of sea scallop population density, coupled with declines in reproductive effort, indicates that care must be taken with implementing this strategy. The likely trajectory of larvae from high-density aggregations and the suitability of the likely settlement habitat should be considered when developing rotational area closures with a goal of increasing larval production or recruitment. Offshore wind lease areas, which are increasingly being developed on the US east coast, may provide an opportunity to further test these assumptions given that they are likely to operate as de facto spawning reserves with limited fishing disturbance. Monitoring high-density sea scallop aggregations to evaluate potential impacts from resource limitation is recommended to aid in adaptive management decisions, and it may be useful to identify a threshold population density above which alternative management strategies are considered.

Broadly, this study provides evidence of a negative density-dependent effect operating within a spatial

area management strategy for a major benthic invertebrate fishery. Though the results are species-specific, they suggest care should be taken with predicting individual and population responses to closed area protection, particularly with extremely high population densities of sessile or limited-mobility species. Further investigation is warranted into the prevalence and intensity of density-dependent effects on wild populations managed through protected area strategies.

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