

# Oysters beget shell and vice versa: generating management goals for live oysters and the associated reef to promote maximum sustainable yield of *Crassostrea virginica*

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**Abstract:** Populations of the eastern oyster (*Crassostrea virginica*) have experienced declines from overfishing and disease throughout much of its US range, though development of maximum sustainable yield (MSY) management criteria has been elusive. This is due in part to the discordance between oyster spawning stock and recruits, as the classic stock–recruitment model does not account for the requirement of shell substrate on which recruits settle. This issue was recently addressed with the development of a surface area–recruitment model, which is herein incorporated into a simulation analysis to estimate MSY-based reference points for *C. virginica* in the Delaware Bay. Simulations demonstrate that at low natural mortality, fishing mortality ( $F$ ) may be sustainable at values between 10% and 15%; however, if disease or other mortality-enhancing processes occur, the margin of error in fishing is small and may quickly lead to population and reef collapse, emphasizing a precautionary  $F < 10\%$ . The MSY-based reference points generated here provide rebuilding goals for the oyster fishery and reef management on fished and unfished reefs and the framework from which shell-planting can be incorporated and optimized in the future.

**Résumé :** Si les populations d'huîtres américaines (*Crassostrea virginica*) ont connu des déclins dus à la surpêche et aux maladies dans la majeure partie de l'aire de répartition américaine de l'espèce, l'élaboration de critères de gestion basés sur le rendement équilibré maximal (REM) demeure problématique. Cela est dû en partie à la discordance entre le stock reproducteur d'huîtres et les recrues, le modèle stock–recrutement classique ne tenant pas compte de l'exigence d'un substrat de coquilles pour l'établissement des recrues. L'élaboration récente d'un modèle reliant la superficie au recrutement tente de résoudre ce problème, et nous intégrons ce modèle à une analyse de simulation pour estimer des points de référence basés sur le REM pour *C. virginica* dans la baie du Delaware. Les simulations démontrent que, quand la mortalité naturelle est faible, la mortalité par pêche ( $F$ ) peut être durable à des valeurs entre 10 % et 15 %, mais que si des maladies ou d'autres processus qui rehaussent la mortalité ont cours, la marge d'erreur associée à la pêche est faible et pourrait rapidement mener à l'effondrement de la population et des récifs, d'où l'importance, pour une approche prudente, de valeurs de  $F < 10 \%$ . Les points de référence basés sur le REM issus de la présente étude offrent des objectifs de reconstitution pour la pêche à l'huître et la gestion des récifs exploités et non exploités, ainsi qu'un cadre à partir duquel le dépôt de coquilles peut être incorporé et optimisé. [Traduit par la Rédaction]

## Introduction

The use of biological reference points for sustainable management of commercial fisheries is well ensconced in the management of US federal fisheries, wherein achieving maximum sustainable yield (MSY) is the primary objective and biomass and fishing mortality rate at MSY ( $B_{MSY}$  and  $F_{MSY}$ , respectively) are the critical metrics. An expansive library of literature has been developed relating to the evaluation of these metrics and their proxies (e.g., Haltuch et al. 2008; Cordue 2012; Punt and Szuwalski 2012; Zhou et al. 2012; Mangel et al. 2013; Rothschild and Jiao 2013) and the advantages and limitations of their implementation (e.g., Maunder 2003; Hartill et al. 2005; O’Leary et al. 2011; Finley and Oreskes 2013). Management strategy evaluations and related modeling approaches are exemplars for consideration of management options for the implementation of these metrics (e.g., Miller et al. 2010; Stobart et al. 2013; Hennen 2015; Kjelland et al. 2015). The evolution of

reference point-based management for oysters has followed a different route than that for other stocks. This divergence is due to the relationship of the living oyster stock to the integrity of the reef (e.g., Harding et al. 2010; Southworth et al. 2010; Swannack et al. 2014; Beck and La Peyre 2015; Soniat et al. 2019) and a strong influence of the estuarine salinity gradient on population dynamics (e.g., Bergquist et al. 2006; Tolley et al. 2006; La Peyre et al. 2009, 2016; Pusack et al. 2019), which together have historically limited the application of whole-stock reference points. Unlike most management challenges for commercially fished stocks, oysters require simultaneous management of the population dynamics and the dynamics of the shell bed (Powell et al. 2012a); thus, management must inherently be area-based to compensate for the salinity-dependent physiology (Powell et al. 1998; La Peyre et al. 2009; Ascenio et al. 2016; Leonhardt et al. 2017), predator distributional patterns (Stauber 1950; Garton

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and Stickle 1980; Dekshenieks et al. 2000; Johnson and Smeed 2014), disease-induced variations in adult mortality rate (Andrews 1988; Powell et al. 1996; Bushek et al. 2012; Powell et al. 2018), and the net down-estuary flux of larvae (Narváez et al. 2012a, 2012b; Soniat et al. 2012b). Only in the ecosystem context does the management of other fisheries approach such a complex amalgam (Link et al. 2002; Zabel et al. 2003; Worm et al. 2009).

Arguably, reference point-based management of an oyster fishery began with Haskin's 40% rule (Fegley et al. 2003; Powell et al. 2018), which was historically applied to the Delaware Bay seed fishery in New Jersey and specified that fishing on a reef would cease when the volume of live oysters in a bushel of dredged material dropped to 40% of the total volume. Retrospective analysis of the period when this measure was used (approximately 1950s to 1990) showed that the fishing mortality rate rarely exceeded 5% of market abundance (Powell et al. 2008), and the annual survey time series demonstrated that this was a period of sustainable management. At the onset of Dermo disease in 1990 (Ford 1996; Bushek et al. 2012), this approach faltered and the consequent reduction in oyster abundance both voided application of the 40% rule and closed the seed fishery (Powell et al. 2008, 2009a). In the late 1990s, Klinck et al. (2001) developed the first reference point model, essentially a surplus production model that required the abundance of marketable oysters at the end of the year be no lower than the abundance present at the start of the year. The model permitted rebuilding by establishing the option of increased abundance at year's end, but defining MSY and a rebuilding goal remained elusive (Powell et al. 2009b). Nonetheless, the constant-abundance reference point brought back a period of sustainable harvest in the Delaware Bay after Dermo made the 40% rule impracticable (Powell et al. 2008). Powell et al. (2018) introduced a more sophisticated surplus production model based on that of Klinck et al. (2001) and suggested that the landings established therefrom were close to MSY under the enhanced natural mortality rate produced by Dermo disease.

The importance of shell-bed integrity to sustainable production of oysters has long been known, supported by a variety of shell addition and enhancement efforts over the last century (Woodward and Waller 1932; Smith et al. 2005; MacKenzie 2007; Harding et al. 2012). Whereas concerns over shell removal and reef degradation as a product of fishing have been well delineated (Lenihan and Peterson 1998; Powell et al. 2001; Woods et al. 2005; Beck et al. 2011), the importance of natural processes responsible for reef degradation and shell loss have only recently been acknowledged as a primary driver of shell-bed integrity. Studies suggest that rates of taphonomic degradation for oyster shell are much higher than those for most bivalve species (Powell et al. 2006, 2011a, 2011b), and the transience of oyster shell is a persistent characteristic over a range of estuarine conditions (Powell and Klinck 2007; Mann et al. 2009a; Pace et al. 2020a). As a consequence of these findings, Soniat et al. (2012a, 2014) patterned a constant shell model after the constant abundance model of Klinck et al. (2001) in which surficial shell or cultch, not oyster abundance, was conserved yearly. This was the first effort to sustainably manage the oyster reef rather than solely the living oyster stock.

In a review of reference point-based management of oyster fisheries, Powell et al. (2018) underscored the discordance between management aimed at stock sustainability and management aimed at cultch (surficial shell) sustainability. The oyster stock begets shell and vice versa; thus, the concept of sustainability applied to one does not necessarily result in management that will be sustainable to the other. The underlying challenge is the inability to explain a broodstock-recruitment relationship (Powell et al. 2008) in the classic terms of the relationship between recruitment and spawning stock biomass (Rothschild 2000; Brooks and Powers 2007; Zhou 2007; Martell et al. 2008). As recruitment has consistently been enhanced by the planting of clean shell during the appropriate time of the spawning cycle, recruitment cannot be a function solely of spawning stock biomass and larval availability. Furthermore, the enhanced

attractiveness of planted shell is impermanent. Ashton-Alcox et al. (2021) recently estimated that the degree of enhancement declined exponentially with a half-life of somewhat less than one year. This clearly demonstrates that substrate quality is substantively responsible for recruitment dynamics. This understanding has been advanced by Pace et al. (2020b), who demonstrated larval preference for settlement on live oysters and the inner surface of boxes rather than loose shell, a predilection consistent with previous observations (e.g., Soniat et al. 2004; Tamburri et al. 2008; Powell et al. 2008 and references therein). Live oysters and box interiors are the newest naturally occurring surfaces and thus can be expected to provide settlement characteristics similar to planted shell.

The confluence of these observations led Hemeon et al. (2020) to propose a new interpretation of the broodstock-recruitment relationship of Powell et al. (2008), where recruitment of oysters is a function of surface area quality rather than spawning stock abundance and fecundity. Hemeon et al. (2020) defined for the first time a distinct relationship between live oyster and shell abundance in establishing sustainability with potential for the development of reference point-based management goals for both the live oyster stock and shell bed. Herein is proposed a new model joining these two processes from which are derived reference points that establish MSY criteria for management of cultch quantity and stock abundance using effective surface area (ESA) as the primary metric establishing sustainability.

## Methods

### Oyster bed groups

The data on which this study is based come from the annual stock assessment surveys for the New Jersey portion of the Delaware Bay. Survey details can be found in the stock assessment workshop reports housed at the Haskin Shellfish Research Laboratory in New Jersey (<https://hsrl.rutgers.edu>; see also Powell et al. 2008 and Hemeon et al. 2020). The oyster beds in the New Jersey waters of Delaware Bay have historically been divided into regional groups based on long-term trends in mortality and productivity. The groupings used here are those used by Hemeon et al. (2020): low-mortality (LM), medium-mortality (MM), Shell Rock (SR), and high-mortality (HM) (Fig. 1).

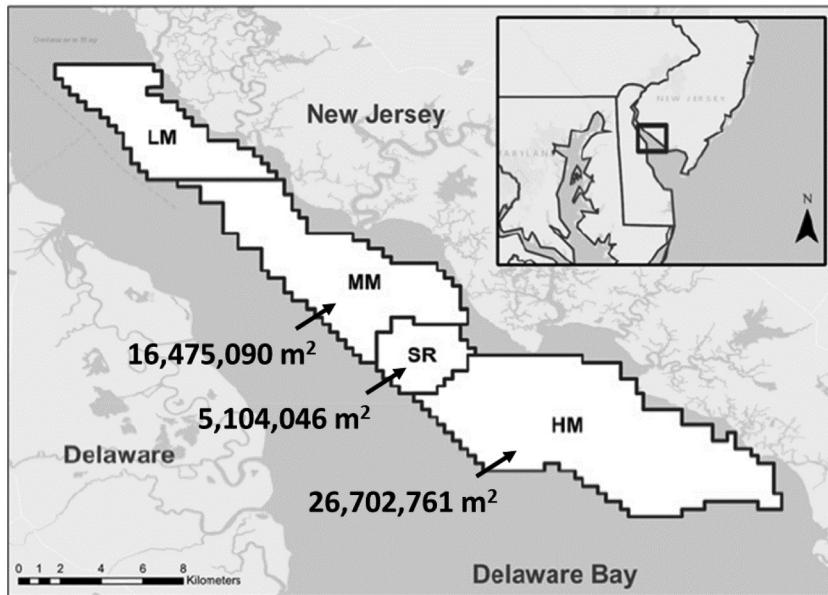
These groups rest within the salinity gradient that drives mortality and productivity (Bushek et al. 2012). The LM group was excluded from the following model simulations because recruitment in this region is limited to self-recruitment and minimal up-estuary transport of larvae, rather than available substrate for settlement (Narváez et al. 2012a, 2012b; Munroe et al. 2013, 2014; Hemeon et al. 2020). The singularity of SR, a one-bed group, originates from its high productivity. This bed sits between a region of higher predation and disease intensity (HM) and a region of slower growth and lower mortality (MM) (Kraeuter et al. 2007; Bushek et al. 2012). Bed areas for the three simulated groups are provided in Fig. 1.

Models for the MM, HM, and SR groups were developed using data collected between 1953 and 2017. To capture multiple generations of oysters, the simulated population was run for 800 months, nearly 70 years, and model output was reported at each monthly interval. In the first 200 months, only natural mortality (M) and fishing mortality (F) were causes of mortality on oyster beds. Adult mortality due to disease, henceforth termed Dermo mortality (D), was added in month 201. Fifteen thousand simulations were run for each bed group.

### Summary of population dynamics

The model uses a simple approach to population dynamics for the living oyster population based on parameterization of growth, recruitment, and mortality. Mortality is split into three components: non-disease natural mortality, disease (Dermo) mortality, and fishing

**Fig. 1.** From Hemeon et al. (2020), map of low-mortality (LM), medium-mortality (MM), Shell Rock (SR), and high-mortality (HM) oyster bed groups in the Delaware Bay. Values to the left of bed group designation are bed area in square metres ( $m^2$ ).



mortality, with size- and age-dependent selectivity for each type of mortality discussed later. “Dermo” mortality as it is defined here encompasses mortality sources that are associated with down-estuary, higher-salinity reaches of the estuary. Whereas Dermo is a primary source of mortality, other diseases such as MSX (acronym first given to the parasite *Haplosporidium nelson* for “multinucleated sphere of unknown affinity”) and predation on market size oysters are subsumed under this designation. Unlike most surplus production models, the model does not invoke a standard broodstock-recruitment relationship. Rather, the “broodstock” is specified in terms of surface area suitable for larval settlement and this “effective surface area” (Hemeon et al. 2020) is the sum of three contributing components: live oysters, boxes (dead oysters with articulated valves), and cultch (disarticulated surficial shell). This establishes a necessary relationship between the living population and the supporting reef structure required for the species’ survival. In addition, the model includes a carbonate submodel that implements the dynamics of shell addition and loss, thereby completing the feedback loop among the living population, the reef structure, and the provision of new recruits to the population. The submodel specifies carbonate ESA for the three constituent types (live animal, box, and cultch), as well as the rates of addition and loss of carbonate for each of them. The model, then, is a fully integrated population dynamics–carbonate budget model.

### Mortality

Mortality rates throughout the text and figures are specified as fractions or percentages per year, unless identified as specific rates in units of (time $^{-1}$ ). As simulations are modeled at monthly increments, annual mortality rates are adjusted to evenly distribute over 12 months. The non-disease natural mortality rate ( $M_a$ ) was based on analyses of Powell et al. (2006, 2008) and Bushek et al. (2012). Parameterization of  $M$  was consistent between bed groups and varied in a stepwise fashion according to age and length. Mortality of oysters <35 mm is elevated relative to larger individuals (Powell et al. 2008); thus, a 90% mortality was enforced on individuals below this threshold size. Mortality then stabilized between 8% and 10% mortality for oysters >35 mm until individuals reached 156 months of age (13 years). At 156 months of age, natural mortality was elevated to 50%, consistent with Powell et al. (2011c, 2012b) and Munroe et al. (2015). Maximum age was set to 240 months

(20 years) following presumptions of Mann et al. (2009b). Hereinafter, time is not included in the mathematical expressions involving mortality because mortality at age remained constant at each time step.

In each simulation, Dermo ( $D$ ) and fishing ( $F$ ) mortalities were randomly selected from rates ranging from no fishing or disease mortality to mortalities that would lead to extinction.  $F$  was selected from a range of 0% to 55% mortality per year, which was applied evenly at monthly increments and remained constant throughout the simulation until the simulation either reached the terminal month or the simulated population became extinct. Fishery selectivity followed that of the commercial fishery in Delaware Bay, fully selecting for oysters >63 mm, as only a small percentage of smaller animals were landed by the New Jersey fishery (Powell et al. 2005). Monthly fishing mortality at age was thus described by eq. 1, where  $F$  is converted from annual to monthly mortality rate,  $a$  is age in months and FS is fishery selectivity.

$$(1) \quad F_a = \frac{F}{12} \times \text{FS}_a$$

$D$  was handled in much the same way as  $F$ , though the simulation was allowed to stabilize or crash under  $F$  over a period of 200 months before  $D$  induced additional mortality on the simulated population. For each simulation,  $D$  was randomly selected from a range of 0% to 55% annual mortality rate and was fully selected for oysters >40 mm.  $D$  was constant from month 200 to 800 unless the simulated population became extinct before the terminal month. Annual Dermo mortality at age is described in the following equation, where DS is Dermo selectivity.

$$(2) \quad D_a = \frac{D}{12} \times \text{DS}_a$$

Total monthly mortality at age ( $Z_a$ ) in month 201 when natural, fishery, and Dermo mortality were all acting on the oyster population was then described by eq. 3:

$$(3) \quad Z_a = M_a + F_a + D_a$$

A separate mortality metric was calculated to account for oyster mortality that would contribute to the shell stock, initially as

**Table 1.** Parameters determined in Kraeuter et al. (2007), used here in the von Bertalanffy growth equation to determine the length at age of oysters from each region.

| Group            | $L_{\text{inf}}$ (mm) | $t_0$ (years) | $K$ (year $^{-1}$ ) |
|------------------|-----------------------|---------------|---------------------|
| Shell Rock       | 125                   | 0.2           | 0.25                |
| High-mortality   | 140                   | 0.2           | 0.23                |
| Medium-mortality | 125                   | 0.2           | 0.20                |

a box, and eventually as cultch. Since the fishery removes oysters, fished oysters do not contribute shell to the reef to support future recruitment. Only natural ( $M$ ) and Dermo ( $D$ ) mortality contribute shell to the reef. Mortality at age contributing to available shell surface area is described by eq. 4:

$$(4) \quad SM_a = M_a + D_a$$

where  $SM_a$  is mortality contributing to shell surface area of the bed.

#### Surface area calculations

The surface area of each individual oyster was calculated by first generating the length at age of each oyster using the von Bertalanffy growth equation:

$$(5) \quad L_a = L_{\text{inf}} \{1 - e^{-K[(a/12) - t_0]}\}$$

where  $L_a$  is length at age  $a$  in mm,  $L_{\text{inf}}$  is the asymptotic maximum length in mm,  $K$  is the growth rate per year (adjusted to a monthly growth rate), and  $t_0$  is the theoretical age at length zero. Kraeuter et al. (2007) provide values for these parameters for SR and beds in the MM and HM groups (Table 1).

Shell width was generated using the allometric equation

$$(6) \quad W_a = g \times L_a^b$$

where  $W_a$  is shell width in mm at each respective age,  $g$  is the growth constant,  $L_a$  is shell length at age  $a$ , and  $b$  is the growth rate. Parameterization for  $g$  and  $b$  were derived from Powell et al. (2016) and remained constant across bed groups, at 2.71 and 0.71, respectively.

Length and width values at age were used to generate the total surface area of each individual oyster, using the following equation from Hemeon et al. (2020):

$$(7) \quad LSA_a = L_a \times W_a \times 2 \times 0.8$$

where  $LSA_a$  is surface area of a live oyster at age  $a$  in mm $^2$ . The equation includes two constants: (1) a multiplication factor of 2 to account for the two oyster valves and (2) a shape correction factor of 0.8 to account for the ovoid shape (Kuykendall et al. 2015).  $LSA_a$  is multiplied by the numbers at age in each month ( $N_{a,t}$ ) to generate the total effective live surface area at simulation time  $t$  ( $LSA_{a,t}$ ) contributing to the surface area–recruitment relationship.

$$(8) \quad LSA_{a,t} = LSA_a \times N_{a,t}$$

The number of oysters at each age is reported for each month of simulation. A portion of these experience natural or Dermo mortality and contribute to box and eventually cultch surface area. Fished oysters are removed from the population and do not contribute to the surface area–recruitment relationship. If an oyster dies due to either natural or Dermo mortality, the recently deceased oyster first becomes a box. As a box, both the interior of the shell and the exterior can be used for settlement, and the box effective surface area is calculated using eq. 9:

$$(9) \quad BSA_{a,t} = LSA_{a,t-1} \times (1 - e^{-SM_a}) \times 2 \times 0.8 \times C_{b'}$$

$BSA_{a,t}$  is box surface area at age  $a$  (corresponding to the age of the oyster at death) in mm $^2$ , calculated by accumulating the shell

**Table 2.** Correction factors for box and cultch in the three modeled groups.

| Group            | Box correction ( $C_{b'}$ ) | Cultch correction ( $C_c$ ) |
|------------------|-----------------------------|-----------------------------|
| Shell Rock       | 0.73                        | 0.40                        |
| High-mortality   | 0.72                        | 0.21                        |
| Medium-mortality | 0.675                       | 0.53                        |

from  $LSA_{a,t}$  that died from natural or Dermo mortality ( $SM_a$ ), then multiplying by two to account for the interior and exterior surface area of the shell, and finally multiplying by a correction factor for boxes,  $C_{b'}$ . Because not all surface area is equally conducive to recruitment, Hemeon et al. (2020) developed correction factors for box and cultch surface area ( $C_b$  and  $C_c$ ) scaled to LSA. Two box correction factors are specified to respectively represent the inside and outside of boxes, as the inside is generally cleaner and more attractive to larval settlement. These two values are summarized, averaging the  $C_b$  and  $C_c$  values to obtain the box correction factor used here,  $C_{b'}$  (Table 2).

The accumulation of boxes is also traced through the simulation as oysters die, creating new boxes, while old boxes disarticulate. The total box surface area contributing to the surface area–recruitment relationship is then calculated for each month of simulation using eq. 10:

$$(10) \quad BSA_t = \sum (BSA_{a,t}) + (BSA_{t-1} \times e^{-\lambda_b})$$

where  $BSA_t$  is total box effective surface area in mm $^2$  at time  $t$ , calculated as the sum of new  $BSA_{a,t}$  and the BSA from simulation time ( $t - 1$ ) that has not disarticulated by time  $t$ , the disarticulation rate being  $\lambda_b$ . The disarticulation rate was generated from Ford et al. (2006), which estimated the half-life of boxes in the Delaware Bay at four and a half months. Limited information is available on the influence of salinity and other environmental factors on disarticulation rates; thus, the rate was set as constant across regions. This value is similar to that used by Pace et al. (2020a) and Damiano and Wilberg (2019), but faster than that used by Christmas et al. (1997).

As boxes disarticulate, the disarticulated valves are added to the cultch effective surface area, calculated using eq. 11:

$$(11) \quad CSA_t = [BSA_{t-1} \times (1 - e^{-\lambda_b}) \times C_c / C_{b'}] + (CSA_{t-1} \times e^{-\lambda_c}) - [(LSA_t + BSA_t) \times 0.18]$$

where cultch effective surface area  $CSA_t$  in mm $^2$  at time  $t$  comprises newly disarticulated boxes adjusted by the cultch correction factor ( $C_c$ ), and cultch from simulation time  $t - 1$  that has not decayed, according to decay rate  $\lambda_c$ . The decay rate of cultch ( $\lambda_c$ ) across regions was set to a 2.5-year half-life, consistent with Powell et al. (2006), Mann et al. (2009a), and Pace et al. (2020a). Values in Powell et al. (2006) cover a relatively wide range of half-lives, and the value used herein is at the lower end of that range, but within reasonable estimates of an average condition.

Finally, cultch volume has historically been difficult to quantify from survey observations, as it is infrequently culled from live oyster and boxes that are collected in surveys. The Delaware Bay survey estimated that attached cultch accounted for 18% of the reported live oyster and box volume. Thus, cultch surface area was debited by 18% of the live oyster and box surface area in these simulations with expectation that this surface area was not accounted for in survey estimates of cultch weight. An important presumption is that this underestimate would routinely be found in survey datasets, as shell is rarely culled from live oysters or boxes when cultch weights are recorded.

The total ESA at time  $t$  is generated by the following equation:

**Table 3.** Hemeon et al. (2020) parameters of the adjusted Beverton–Holt shell surface area–recruitment curve for the three simulated oyster bed groups.

| Group            | $a_R$ | $b_R$ | X (axis shift, in ha) |
|------------------|-------|-------|-----------------------|
| Shell Rock       | 0.73  | 0.40  | 211                   |
| High-mortality   | 0.725 | 0.21  | 275                   |
| Medium-mortality | 0.675 | 0.53  | 876                   |

$$(12) \quad \text{ESA}_t (\text{ha}) = \text{LSA}_t + \text{BSA}_t + \text{CSA}_t \times 10^{-10} (\text{mm}^2)$$

where  $\text{LSA}_t$ ,  $\text{BSA}_t$ , and  $\text{CSA}_t$  are summed and converted from  $\text{mm}^2$  to hectares (ha). This surface area is then available at time  $t$  to oyster recruits.

### Surface area–recruitment

The number of recruits was determined in each month of simulation using a modified Beverton–Holt stock–recruitment curve, where instead of using spawning stock biomass to generate recruitment, the ESA available to newly recruiting oysters determined year-class success. This process is described in the following equation taken from Hemeon et al. (2020):

$$(13) \quad R_t = \frac{a_R(\text{ESA}_t - X)}{1 + b_R(\text{ESA}_t - X)}$$

where  $R_t$  is the number of recruits at time  $t$ ,  $\text{ESA}_t$  is total effective surface area at time  $t$ , and  $a_R$ ,  $b_R$ , and  $X$  are model parameters (Table 3). To force the shell surface area–recruit relationship to go through or near zero, an  $X$ -axis shift ( $X$ ) was developed by Hemeon et al. (2020) and is subtracted by  $\text{ESA}_t$  to determine the number of recruits, effectively inserting the analogue of an Allee effect.

### Model spin-up

The initial number of live oysters at age (LAA) was generated using the natural mortality rate ( $M_a$ ) to distribute the starting population number ( $N_{\text{zero}}$ ) across the 240 age classes. Values of  $N_{\text{zero}}$  at each bed group were somewhat arbitrarily selected between two and six billion oysters, values meant to ensure the population came to a stabilization point within the first 1000 months of simulation. The eventual point of stabilization did not vary based on values of  $N_{\text{zero}}$  and instead was determined by population dynamics of the bed group. Equilibrium surface area values for live oyster, box, and cultch components in month 1000 then fed into the next phase of spin-up.

The number of oysters allocated from  $N_{\text{zero}}$  to age-class 1 represented the base number of recruits ( $R_0$ ) for the first 1000 months of spin-up. The number of oysters from ages 2 to 240 were calculated following the equation:

$$(14) \quad N_{a,t} = N_{a-1,t-1} \times e^{-M_{a-1}}$$

where the number of live animals at age  $a$  at time  $t$  is equal to the number of live animals from age  $a - 1$  at time  $t - 1$  that survived natural mortality associated with age  $a - 1$ . Mortality is also the only mechanism for death in the following 1000 months of spin-up from  $t = 1001$  to  $t = 2000$ . LAA<sub>1000</sub> informed on the population size and age distribution for the second spin-up, and LSA<sub>1000</sub>, BSA<sub>1000</sub>, and CSA<sub>1000</sub> were used to calculate the ESA contributing to oyster recruitment at time 1000. With this, from time 1001 to 1999,  $R_t$  was generated using the surface area–recruitment relationship described in eq. 13.

### Simulating fishing and Dermo mortality

For the following simulated time, the clock resets and results from spin-up  $t = 2000$  are now the initial population for a simulation beginning at  $t = 1$ . For the first 200 months of simulation, the bed groups face only natural and fishing mortalities, allowing

the population to come to a new equilibrium with fishing mortality before Dermo mortality begins acting on the population.  $\text{ESA}_{t=1}$  from the model spin-up generates the number of recruits (age = 1), and number of oysters at ages 2–240 are generated from the following equation:

$$(15) \quad N_{a(2-240),t(1-200)} = N_{a-1,t-1} \times e^{-Z_{a-1}}$$

where  $Z_a$  (see eq. 3) is the total mortality, with Dermo mortality ( $D_a$ ) set to zero. Over the course of 200 months, the amount and distribution of live, box, and cultch surface area either stabilizes and comes into equilibrium with the higher total mortality rate or the simulated population experiences extinction from fishing mortality.

At  $t = 201$ ,  $D$  is added to total mortality, and the simulation is allowed to continue to  $t = 800$ , where, again, the population has either experienced extinction from a combination of  $F$  and  $D$  or is sustained to the terminal month,  $t = 800$ . Populations that survived to  $t = 800$ , or approximately 70 years, were described as maintaining sustainable levels of fishing and Dermo mortality. In addition to levels of  $F$  and  $D$ , other relevant statistics to describe the theoretically sustainable populations including type, amount, and ratio of surface area, as well as catch, were extracted from  $t = 800$ .

### Threshold metrics

Three metrics were assessed for each region to determine population thresholds that sustained fishing pressure through gradients of Dermo mortality. These metrics represent thresholds that oyster fishery managers can use to evaluate the current status of a region and suggest fishery regulations, stock biomass, and  $F$  relative to  $F_{\text{MSY}}$  and  $B_{\text{MSY}}$ . They also provide the option for setting rebuilding targets and threshold control points for  $B$  and  $F$  leading to fishery closure. The first metric is number of live oysters· $\text{m}^{-2}$  larger than 63 mm, the size of full fishery selectivity in Delaware Bay (Powell et al. 2005). The oyster fishery is managed primarily by the number of bushels landed (1 bushel  $\sim 36.4 \text{ L}$ ), each bushel having a known range of market size individuals (Powell et al. 2005), regardless of biomass. At time  $t = 800$ , live oysters  $>63 \text{ mm}$  were tallied, and this value was divided by the total region area (Fig. 1) to generate density as number of market size oysters· $\text{m}^{-2}$ .

Mass of cultch· $\text{m}^{-2}$  was the second threshold to describe sustainable population characteristics. In  $t = 800$ , cultch surface area, in hectares was converted to  $\text{kg} \cdot \text{m}^{-2}$  using the following equation:

$$(16) \quad \text{Cultch}_{\text{KG}} = (\text{CSA}) \times \frac{0.69 \text{ kg}}{0.111 \text{ m}^2}$$

where the constant 0.69 kg per  $0.111 \text{ m}^2$  (Kuykendall et al. 2015; Hemeon et al. 2020) is used to convert effective CSA from area ( $\text{m}^2$ ) to mass (kg). This is done largely to create a more realistic comparison with field data collected on oyster beds, as surface area is a metric rarely recorded in historical data. Finally, mass of cultch is divided by bed group area ( $\text{m}^2$ ) and used to determine sustainability thresholds for cultch mass across the range of fishing and Dermo mortality levels.

Finally, the ratio of live surface area to total ESA at  $t = 800$  was reported. This metric is analogous to the original 40% rule of Haskin that produced sustainable harvests for several decades prior to the onset of Dermo disease in Delaware Bay (Powell et al. 2008), in that it compares a volume-based ratio of box and cultch surface area to that available from live oysters. For scale, the total ESA is also reported.

### Model verification

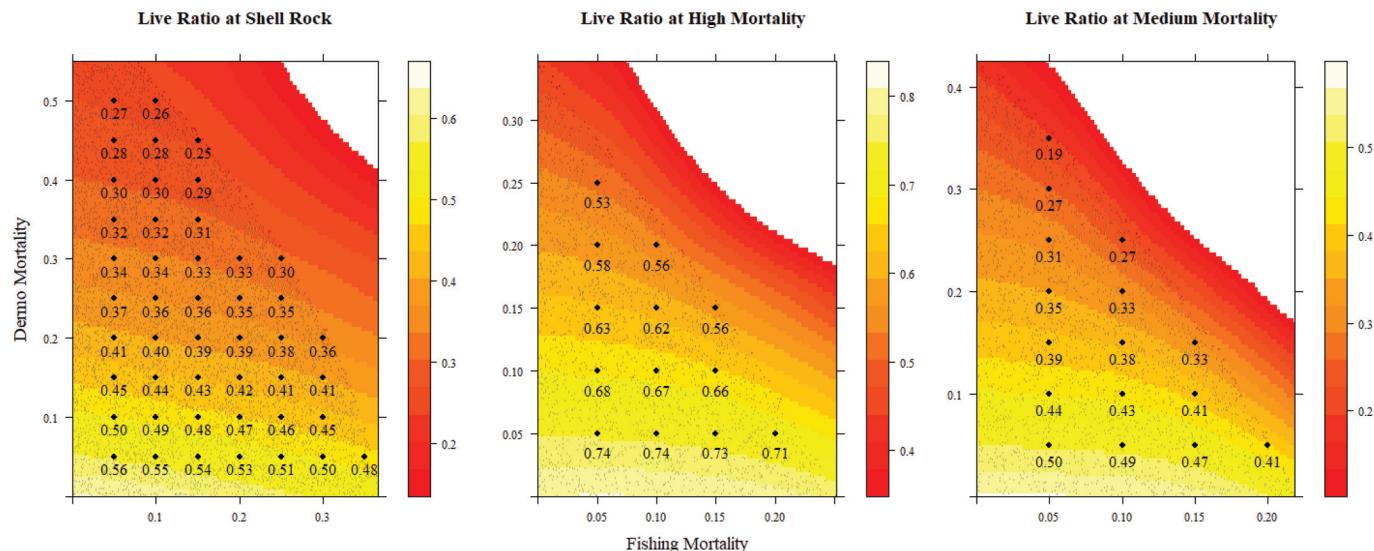
Simulations for each bed group were verified against fall survey data for Delaware Bay oyster beds collected annually since 1953 (Fegley et al. 2003; Powell et al. 2008; Ashton-Alcox et al. 2018). Estimates for total number of live oysters, number of boxes, and volume of cultch are recorded in the survey and were subsequently

**Table 4.** Comparison of Delaware Bay survey observations of effective surface area (ESA; in hectares) at Shell Rock, high-mortality, and medium-mortality oyster beds to effective surface area (ESA) estimated during model spin-up and at  $t = 800$ .

| Group            | ESA <sub>1970s</sub> |      |           | ESA <sub>2000s</sub>   |      |     | ESA <sub>t=800</sub> |      |
|------------------|----------------------|------|-----------|------------------------|------|-----|----------------------|------|
|                  | Mean                 | SD   | Range     | ESA <sub>spin-up</sub> | Mean | SD  | Range                |      |
| Shell Rock       | 1006                 | 321  | 669–1773  | 1326                   | 464  | 209 | 222–869              | 633  |
| High-mortality   | 2893                 | 2735 | 1044–8595 | 2365                   | 531  | 180 | 355–826              | 788  |
| Medium-mortality | 3551                 | 2120 | 1771–8144 | 3419                   | 1682 | 673 | 886–2735             | 1095 |

Note: Values at  $t = 800$  represent ESA coincident with Dermo and fishing mortalities at 10%.

**Fig. 2.** Heat map showing contours of the ratio of live oyster surface area to total effective surface area at Shell Rock (left), the high-mortality beds (center), and the medium-mortality beds (right). All x axes are fishing mortality ( $F$ ) as fractions of the marketable stock, and all y axes are Dermo mortality ( $D$ ) as fractions of the stock. Dots indicate individual simulations of  $F$  and  $D$  that reached  $t = 800$ . Colour bars indicating values of the ratio contour are shown to the right of individual graphs.



converted to ESA in Hemeon et al. (2020). They are used for verification here. Box and cultch surface area were adjusted according to the correction factors in Table 2. The oyster population in Delaware Bay in the 1970s is considered to have been near carrying capacity (Powell et al. 2009a, 2012a) and fishing mortality was consistently  $\leq 5\%$  of the stock. The range of observed total ESA from 1970–1979 in addition to the mean and standard deviation of ESA during this period, was compared to the terminal month of spin-up values from each regional model. During the 2000s, Delaware Bay oyster populations had declined due primarily to Dermo mortality, and the range, mean, and standard deviation of observed ESA from 2000–2009 were compared to the terminal month ( $t = 800$ ) of each region model for simulations with  $F = 10\%$  and  $D = 10\%$ . These are reasonable estimates of Dermo and fishing mortalities to represent this period in the Delaware Bay (Powell et al. 2012b, 2018).

## Results

### Model verification

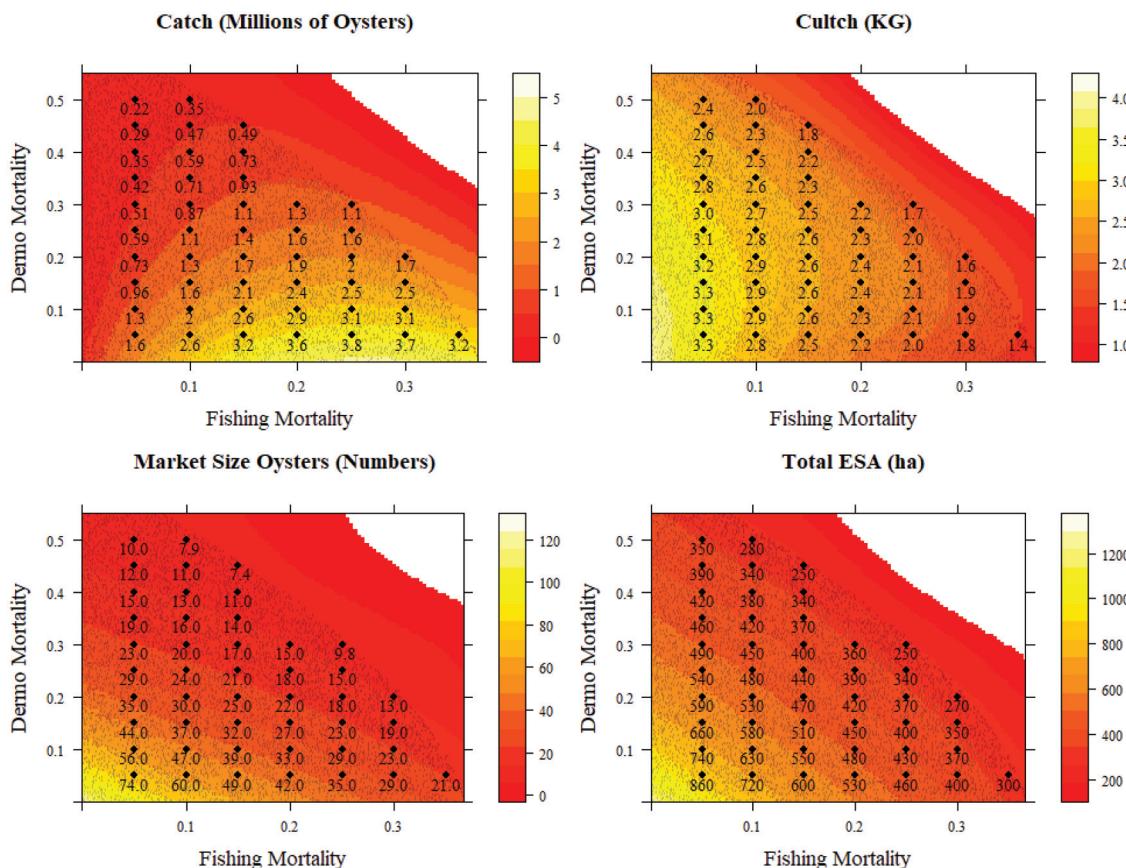
Across model regions, spin-up and terminal month ESA values were well-within empirical ESA observations (Table 4). SR is the smallest bed group and predictably had the lowest standard deviation during both the 1970s and 2000s, though model estimates were still within the first standard deviation of the mean within both periods. HM beds demonstrated a large range in ESA during the 1970s, and the ESA after spin-up was just below the mean, well-within the range of observed values. The range of ESA contracted substantially during the 2000s when fishing and Dermo

mortalities were in effect, and the model simulation for HM beds with  $F = 10\%$  and  $D = 10\%$  captured this decrease well, generating a terminal ESA of 788 ha, above the mean though within the range of observed values. MM ESA also varied considerably during the 1970s, though spin-up values fell near the mean. ESA at  $t = 800$  was 1095 ha, within the first standard deviation of the mean during the 2000s.

### Ratio of live shell to total shell

Simulations of SR were the most resilient to varying Dermo and fishing mortalities, with simulated populations only becoming extinct when Dermo and fishing mortalities were most elevated. The ratio of LSA to total ESA at SR ranged from 25% at the highest mortality rates to 56% at the lowest imposed mortality (Fig. 2). Whereas the decline in the ratio of live-to-total ESA was relatively linear with Dermo and fishing mortalities at SR, the HM and MM regions demonstrated an increased rate of decline in this ratio with elevated fishing mortality. At HM, the live-to-total ESA ratio ranges from 53% to 74%, declining by approximately 1% with each 1% increase in Dermo mortality, though ratios remain stable through 10% fishing mortality. At  $D = 15\%$ , an increase in  $F$  from 5% to 10% results in a reduction in live ratio of only 1%, while further increase in  $F$  from 10% to 15% reduces ratio of live-to-total ESA by 6%, demonstrating an accelerating decline in ratio with increased fishing mortality. MM beds exhibit a similar trend, though the range of the ratio of live-to-total ESA is lower, from 19% to 50%. Again, MM beds experience a 1% decline in this ratio with each 1% increase in Dermo mortality, though the ratio is relatively stable with fishing mortality up to 10%, at which point

**Fig. 3.** Heat map showing contours of catch in numbers (top left), kilograms of cultch·m<sup>-2</sup> (top right), number of market size oysters (>63 mm)·m<sup>-2</sup> (bottom left), and total effective surface area (ESA, bottom right) for Shell Rock. Dots indicate individual simulations of F and D that reached  $t = 800$ . Colour bars indicating values of the z-axis contour are shown to the right of individual graphs.



declines in live ratio increase and eventually lead to extinction. Fishing much above 20%, even in the absence of Dermo, results in extinction of the MM bed.

## Shell Rock

SR was able to sustain higher levels of fishing mortality across a range of Dermo mortality rates than either HM or MM. The threshold for extinction was  $F = 36\%$  and  $D = 55\%$  (Fig. 3). Catch peaked at 3.8 million landed oysters per month at  $F = 25\%$  when  $D = 5\%$ . As Dermo increased, fishing at this level reduced overall catch by around half a million oysters with each 5% increase in Dermo mortality. At  $D$  up to 20%, fishing at  $F = 25\%$  also generated the greatest catch for this level of disease, though the increase was minimal compared to if the population were fished more cautiously at  $F = 20\%$ . Once Dermo reached 25%, fishing at  $F = 20\%$  maintains or declines total landed catch and risks extinction if Dermo mortality is greater than expected or fishing at  $F = 20\%$  is improperly implemented. Consistent with a total natural mortality rate of 18%–20% (Powell et al. 2018),  $D = 10\%$  was used to develop threshold metrics of cultch  $\text{kg} \cdot \text{m}^{-2}$ , number of market size oysters ( $>63 \text{ mm}$ ) $\cdot \text{m}^{-2}$  (hereinafter referred to as  $\text{oysters} \cdot \text{m}^{-2}$ ) and total ESA. At  $D = 10\%$ , catch is maximized at  $F = 25\%$  and SR would require  $2.1 \text{ kg} \cdot \text{m}^{-2}$  of cultch,  $29 \text{ oysters} \cdot \text{m}^{-2}$ , and 430 ha of ESA to sustain this level of catch. Note that cultch mass has much greater sensitivity to  $F$  than to  $D$  because fishing mortality removes shell from the stock, while Dermo mortality continues to contribute shell. Oysters $\cdot \text{m}^{-2}$  and ESA respond more evenly to both  $F$  and  $D$  because both sources of mortality result in death.

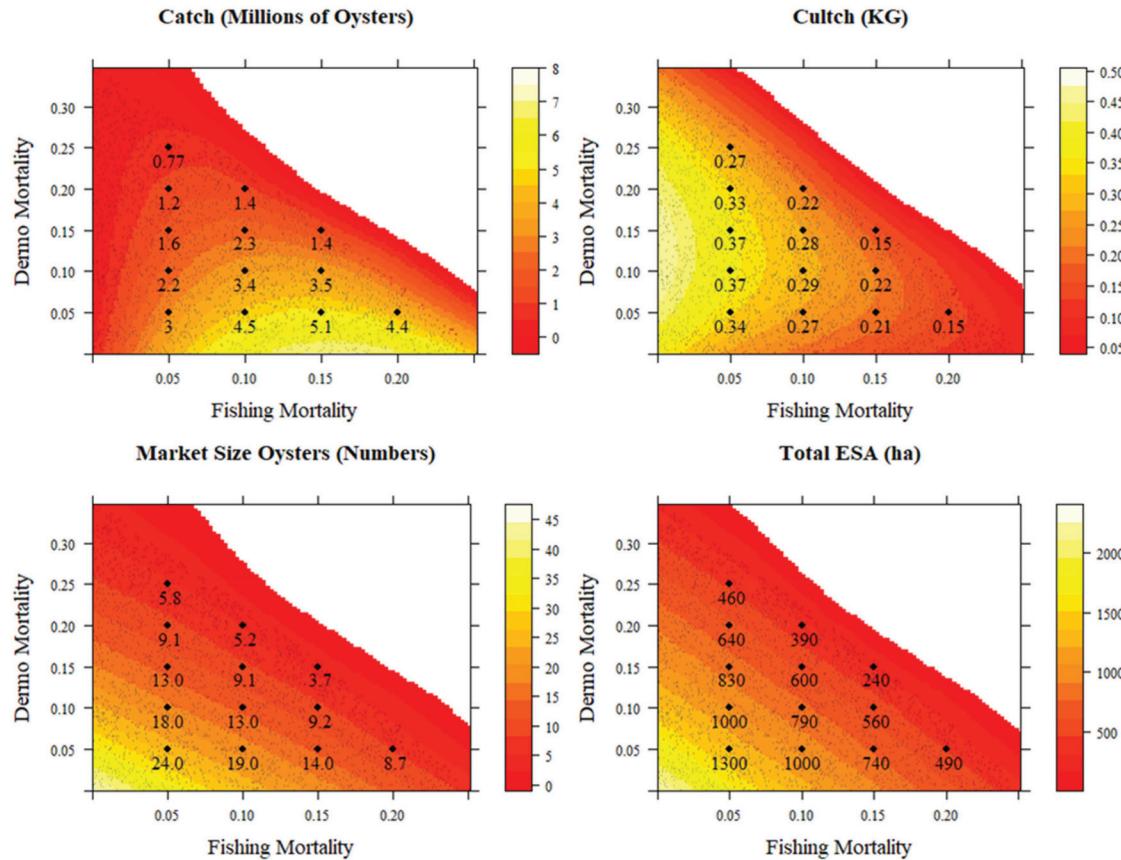
## High-mortality

The threshold of extinction in the HM group was a total fishing and Dermo mortality of around 35%, though simulations were more sensitive to fishing than Dermo (Fig. 4; note that  $x$ - and  $y$ -axis scales vary across heat maps in Figs. 3–5). Whereas simulated populations remained viable with Dermo as high as 35%, fishing mortality above 24%, independent of Dermo mortality, resulted in extinction. At  $F = 24\%$ , catch declined substantially from the maximum of 5.1 million oysters at  $F = 15\%$ . Following the analysis used for SR,  $D = 10\%$  was used to develop threshold metrics. In this case, catch is maximized at  $F = 15\%$ , landing 3.5 million oysters. At HM, however, population stability is far more precarious, and an increase of  $F$  from 15% to 20% at  $D = 10\%$  results in extinction, whereas a reduction in fishing mortality from 15% to 10% results only in a modest decline in catch from 3.5 to 3.4 million oysters. At  $D = 10\%$  and  $F = 15\%$ , HM sustains 0.22 cultch  $\text{kg} \cdot \text{m}^{-2}$ , 9 oysters  $\text{m}^{-2}$ , and 560 ha of ESA. The volatility of catch, cultch, and number of oysters over a wide range of  $D$  and  $F$ , relative to SR, emphasizes the sensitivity of the HM bed group to variations in exploitation rate.

## Medium-mortality

The MM region was far more sensitive to fishing than Dermo mortality (Fig. 5). When  $F = 0\%$ , Dermo mortality as high as 42% maintained a population to  $t = 800$ , while independent of  $D$ , fishing mortality above 23% resulted in extinction. Maximum catch at MM occurred at lower fishing rates than both HM and SR, at 4.5 million oysters with  $F = 10\%$  and  $D = 5\%$ . Despite low  $D$ , catch declines above and below  $F = 10\%$ . Following SR and HM,  $D = 0.10$  was used to develop threshold metrics. Catch at  $D = 10\%$  is

**Fig. 4.** Heat map showing contours of catch in numbers (top left), kilograms of cultch·m<sup>-2</sup> (top right), number of market size oysters (>63 mm)·m<sup>-2</sup> (bottom left), and total effective surface area (ESA, bottom right) for high-mortality region. Dots indicate individual simulations of  $F$  and  $D$  that reached  $t = 800$ . Colour bars indicating values of the z-axis contour are shown to the right of individual graphs.



maximized at  $F = 10\%$ , landing three million oysters, with 1.9 cultch kg·m<sup>-2</sup>, 23 oysters·m<sup>-2</sup>, and 1100 ha of ESA.

## Discussion

### Perspective

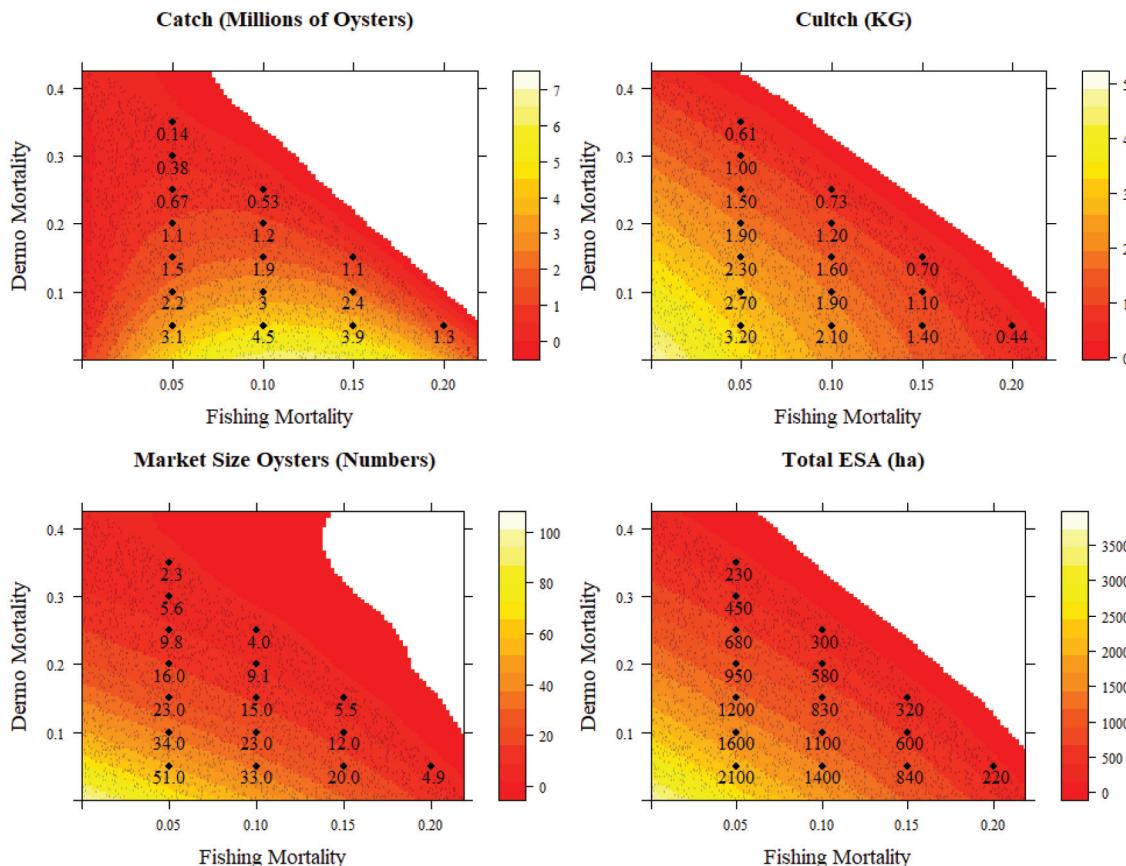
The importance of the eastern oyster and its reef in the ecology, biodiversity, nutrient cycling, and provision of other ecosystem services in estuaries is well described (Peterson et al. 2003; Coen et al. 2007; Booth and Heck 2009; Grabowski et al. 2012; Gedan et al. 2014; Kritzer et al. 2016; McCoy et al. 2017; McAfee and Bishop 2019), though sustainable management of this important resource has been rare (Hargis and Haven 1988; Jackson et al. 2001; Mann and Powell 2007; Camp et al. 2015). An exception was the 40% rule in the Delaware Bay, which successfully used supporting science to implement a simple reference point-based management strategy (Hargis and Haven 1988; Jackson et al. 2001; Mann and Powell 2007; Camp et al. 2015). Though successful for many decades, this management strategy proved inadequate upon the onset of Dermo in the 1990s. Declines in populations of eastern oysters have been thoroughly characterized (Rothschild et al. 1994; Beck et al. 2009; Zu Ermgassen et al. 2012; Powell et al. 2018), and some considerable portion of the decline over the last few decades is owed to Dermo disease, which unduly impacts adult mortality rates with biased emphasis on adult oysters (Powell et al. 2013; Harding et al. 2013). Dermo increases the mortality rate, but the oyster cannot respond by increasing production of larvae (Powell et al. 2009a). Accordingly, population abundance must decline, even in unfished populations (Powell et al. 1996, 2018). The concomitant decline in surplus production imperils

the stock if fishing is not carefully managed (Powell et al. 2009b, 2018).

The most substantive scientific failure in supporting management throughout periods of decline has been the failure to understand the impermanence of oyster shell. A primary factor influencing the observed historical degradation of reefs was likely an imbalance between carbonate addition and loss, inescapably leading to loss of reef area that amplified with the emergence of Dermo (Smith et al. 2005; Mann and Powell 2007; Mann et al. 2009a; Powell et al. 2012a). Mann and Powell (2007) and Powell and Klinck (2007) raised this issue as an urgent challenge to management and restoration, and Soniat et al. (2012a) preferred a focus on cultch management as a primary assessment tool to achieve sustainability. None of these offered a way to link the population dynamics of the oyster with the carbonate budget sustaining the reef, however, and subsequently, Powell et al. (2018) was unable to provide a solution.

A key to this problem came from a proposed link between recruitment and ESA (Hemeon et al. 2020), rather than the classic dependency of recruitment on spawning stock biomass or fecundity. This linkage stems from a wealth of previous observational, experimental, and practical evidence of the importance of “clean” shell for recruitment enhancement (Ashton-Alcox et al. 2021), including the preference by oyster larvae to settle on new shell, be it the living animal, new boxes, or planted shell (Pace et al. 2020a). Live oysters produce both recruits and the habitat necessary for them to settle, whether from inherent provision of new live shell or through death providing boxes and cultch. ESA supports settlement of recruits that contribute both to the live population and to

**Fig. 5.** Heat map showing contours of catch in numbers (top left), kilograms of cultch·m<sup>-2</sup> (top right), number of market size oysters (>63 mm)·m<sup>-2</sup> (bottom left), and total effective surface area (ESA, bottom right) for the medium-mortality region. Dots indicate individual simulations of F and D that reached  $t = 800$ . Colour bars indicating values of the z-axis contour are shown to the right of individual graphs.



its habitat, first while alive, and ultimately by death as their shell continues to be part of the reef. This feedback loop between live oysters and ESA defines the integrated role of population dynamics and the carbonate budget to support surplus production and a sustainable fishery. Simulations presented herein define the ambit of sustainability for the oyster-reef system, including characteristics leading to MSY and conditions leading to population (and reef) extinction.

#### States of sustainability

In these simulations, oyster bed groups consistently remained sustainable with Dermo mortality rates as high as 25% (total natural and disease mortalities ~35%). These values are higher than sustainable fishing mortality rates, likely because the population and reef can withstand greater Dermo mortality than fishing mortality as Dermo mortality continues to contribute shell to the oyster bed, whereas fishing does not. Fishing mortality removes live shell surface area and ultimately box and cultch surface area, thereby preventing the contribution of shell to the ESA-recruitment relationship. Consequently, susceptibility to fishing mortality was more variable across bed groups.

The SR population was able to withstand the greatest fishing mortality without experiencing extinction before the terminal month. SR sits in an ideal region of the Delaware Bay that averages 15‰ salinity, a situation where salinity is not so high as to unduly increase adult mortality, nor too low to restrain growth rate or larval availability. Thus, growth and recruitment rates are high on SR and mortality rates tend to be lower than those on the more saline HM beds (Powell et al. 2008). Moreover, the value of cultch as ESA is relatively high (Table 2), and the decline in live-to-total

ESA ratio is not confounded by fishing mortality, instead remaining relatively linear with offsetting declines in Dermo mortality and increased fishing (Fig. 2). These advantages foster resiliency not observed in either the HM or MM regions. Sustainable fishing mortality was restricted to far lower values on the MM and HM beds, with catch maximized between  $F = 10\%$  to  $F = 15\%$ , above which catch declined. Interestingly, maximum catch associated with  $D = 10\%$  was similar across bed groups, ranging between three and four million oysters per month, despite bed-group-specific fishing mortality associated with maximized catch at  $D = 10\%$ . This equivalency, however, disregards the vast area of the HM region in comparison to the smaller MM region and smaller-still SR. The productivity per unit area necessary to support a similar catch is very different among regions. The balance between productivity and bed area, with area highest in the HM region balancing the lowest per-m<sup>2</sup> productivity, reiterates the importance in dynamics of larval supply, cultch quality, and adult mortality in determining spatial variability in reef productivity.

However, the model assumes constant adherence to the ESA-recruitment model without error, which is likely to allow for greater sustained fishing mortality and catch than would be observed in true stock assessments. In reality, oyster recruitment is highly variable (Austin et al. 1996; Powell et al. 2008; Mann et al. 2009a), with increased variability at regions that are farther up-estuary as events that transport larvae up-estuary (thereby contributing recruits) are infrequent while up-estuary beds contribute larvae down-bay as part of the typical down-bay larval drift. Model simulations did not invoke uncertainty in the recruitment-ESA relationship described in Hemeon et al. (2020).

Given the narrow window of conditions leading to sustainability at MSY as shown in Figs. 3–5, precautionary management maintaining fishing mortality rate below  $F_{MSY}$  would appear prudent.

Furthermore, whereas each simulation was run for 800 months, or about 70 years, some simulations with Dermo and fishing mortalities near extinction levels continued to decline slowly but did not reach extinction within the simulated time allotment. Though the time series could have been extended, 70 years captures 10+ generations of oysters (see Kraeuter et al. 2007 for typical age ranges), greater than the minimum 1–2 generations suggested by Punt et al. (2016). These marginal simulations serve to capture the boundaries of fishing mortality and Dermo mortality that can be sustained by an oyster population for a time, but these bounds are unlikely to sustain the population long-term given natural stochasticity in population dynamics.

### Reference points

These simulations confirm the urgency of maintaining a low  $F$  under conditions of a natural mortality rate above ~10%, arguably the historical pre-disease rate for at least some estuarine regions. Powell et al. (2018) proffered a  $F_{MSY} \sim 6\%$ , near the level that has proven sustainable in Delaware Bay (Powell et al. 2009a, 2009b) and well below historical catch levels in most oyster fisheries (e.g., Jordan et al. 2002; Jordan and Coakley 2004; Wilberg et al. 2013; Pine et al. 2015). The present set of simulations, based for the first time on an integrated model that projects sustainability of both the stock and the shell bed, reinforces the requirement of maintaining a low  $F$  with natural mortality rates that are above 10% per year to limit the otherwise inexorable decline in the shell base that eventually results in reef demise. Simulations show, however, that at low natural mortality ( $D = 0\%$ ), sustainable  $F$  rises from lower rates into the range of 10%–15% per year in the MM and HM regions. Survey data from the initial years of the Delaware Bay time series, prior to the introduction of MSX, show that  $F$  at 20%–25% resulted in population collapse (Powell et al. 2008), consistent with the results of these simulations.

The present model establishes a mechanism to identify analogues to the commonly used reference points of today,  $B_{MSY}$  and  $F_{MSY}$ . Given a rate of Dermo mortality, MSY is specified in terms of the stock size (numbers·m<sup>-2</sup>) and fishing mortality ( $F$ ). These effectively represent  $B_{MSY}$  (actually  $N_{MSY}$ , as biomass is a poor measure of oyster landings due to variable condition index; Soniat et al. 1989; Rheault and Rice 1996; Powell et al. 2016) and  $F_{MSY}$  at the point of highest catch yielding a sustainable stock. Finally, total ESA (live + box + cultch) represents a reference point for the sustainability of the reef, designated here as  $E_{MSY}$ , which includes the requirement to sustainably manage the shell bed. Simulations show that  $E_{MSY}$  represents a unique balance of available cultch, stock abundance, and the rate of box formation generated by natural mortality. Modern MSY-based reference points generally accept the Schaefer model of surplus production, wherein the biomass at MSY (where surplus production is maximized) is approximately one-half of carrying capacity (Maunder 2003; Mangel et al. 2013; Powell et al. 2018). The premise is primarily an outcome of the relationship of broodstock to recruitment (Brooks and Powers 2007; Brooks 2013; Punt et al. 2013). Removal of the classic broodstock-recruitment relationship in the present model might be expected to jeopardize the primary basis for MSY, the parabolic shape of the surplus production to spawning stock biomass relationship. Interestingly, the parabolic form remains, likely due to the large influence of live animals on ESA and the requirement of live animals to support cultch ESA. Thus, the original rationale for modern-day reference points is retained and the analogy with  $F_{MSY}$  and  $B_{MSY}$  uncompromised, while the third necessary reference point,  $E_{MSY}$ , is incorporated.

The model also derives sustainability in terms of the ratio of live to total ESA. This augurs back to the first reference point used for oysters, the 40% rule implemented by Haskin for the

New Jersey oyster beds of Delaware bay. This reference point is a volume-based reference point and, thus, inherently ratio-based. The opportunity is thus presented to use a simple ratio derived during surveys to evaluate both stock and reef status, advocated by Mann et al. (2009a) and Soniat et al. (2019). This ratio may provide an approach for setting stock status in cases where survey time series data are insufficient. The challenge of managing data poor stocks is well described (Cope 2013; Dowling et al. 2015; Newman et al. 2015) and often imperils evaluation of oyster fisheries wherein short survey time series or insufficient data are collected to represent the status of both the living stock and the reef.

### Area management

Area management is essential for oysters due to the strong influence of the salinity gradient on growth, recruitment, and mortality, though it is challenging to accomplish, as all metrics used to evaluate stock status must be local. Growth rate and mortality are inherently local, but recruitment in its classic form (broodstock-recruitment) is evaluated for either the whole stock or within a connected component of the stock, though the region of connectivity is often hard to judge (Narváez et al. 2012a, 2012b; Munroe et al. 2013, 2014). The new formulation overcomes this impediment, as ESA is inherently local. Accordingly, area-based reference points can now be routinely obtained, as all necessary metrics are locally derived.

The formulations of Hemeon et al. (2020) show that ESA values for its components (live oysters, boxes, and cultch) vary along the salinity gradient. Generally, the value of cultch as a source of ESA increases up-estuary, to the extent that cultch ESA is nearly as valuable as box or live ESA in low salinities but offers very poor substrate at high salinities. Given the estuarine influence, the question becomes the degree to which a location can be assigned to one of the regions defined by Hemeon et al. (2020). One possible option, given a data-poor condition, is to use natural mortality ( $D + M$ ) as a key decision tool if data resources are not sufficient to generate a formal ESA-recruitment relationship.

### Application to shell planting

This model provides information about sustainable cultch mass, numbers of oysters, and the sustainable ratio of live oyster-to-total ESA. Shell-planting, though not included here, could be incorporated into the model as well. The dynamics of shell-planting are important to understand, as this shell enters the population as new shell that is ideal for the enhancement of larval oyster settling (Ashton-Alcox et al. 2021). The enhancement factor of planted shell decreases with a half-life similar to the disarticulation rate of boxes, the inner valves of which are similarly attractive to larval settlement. Cultch quantity at MSY and the ratio of live oyster-to-total surface area are useful metrics to quantify the influence of shell-planting efforts that have had variable success throughout the continental US (Abbe 1988; Mann and Powell 2007; Powers et al. 2009; Kennedy et al. 2011; Harding et al. 2012). Although mass of cultch matters, and cultch can be planted, how this mass relates to the ratio of live oyster-to-total surface area is infrequently assessed (though see Ashton-Alcox et al. 2021). Differences in the stability of the ratio of live oyster-to-total surface area among regions coincide with sensitivity to fishing mortality, emphasizing the need to carefully evaluate outcomes to provide best results from finite funds supporting recruitment enhancement programs.

Smothering an oyster bed with healthy cultch that overwhelms the relevance of live surface area would seem to be detrimental, especially as the value of new cultch decays over the initial years but remains as part of the shell bed for years beyond that. Complementary to shell planting, transplanting oysters from one region to another is another method of reef rehabilitation that has proven effective in the Delaware Bay (Ashton-Alcox et al. 2013)

and has expanded to the use of hatchery seed in other areas (Carlsson et al. 2008; Kennedy et al. 2011). Transplanting not only provides increased oyster abundance but also encourages recruitment through the provision of the most effective ESA, live oyster shell. Incorporating both shell-planting and transplanting into simulation analyses may help determine optimal levels of both enhancement methods to support cultch mass, maintain the ratio of live oyster-to-total surface area, and subsequently sustain an increased fishing effort.

### Precautionary comments

The simulations considered here have used the relationships between ESA and recruitment obtained by Hemeon et al. (2020) for Delaware Bay. The degree to which these relationships vary beyond the Delaware Bay is unknown. For example, oysters in the Gulf of Mexico have a higher frequency of spawning (Ingle 1951; Hopkins 1954; Hayes and Menzel 1981; Hofmann et al. 1992; Choi et al. 1994), and it is likely that recruitment rate per ESA may be higher. This represents a critical uncertainty in exporting this model to regions differing substantively in oyster recruitment dynamics.

The relationship between ESA and recruitment in each of the three regions simulated herein contains what is basically an Allee effect, the magnitude of which is likely to vary given regionally explicit recruitment dynamics (Kraeuter et al. 2005; Moore et al. 2018; Aalto et al. 2019). The Allee effect specifies that at a certain nonzero value of ESA, recruitment ceases, the population subsequently goes extinct, and over sufficient time, the cultch degrades and the reef itself dies. The low value of degraded cultch in providing ESA strongly suggests that a practical extinction point likely does exist. The Hemeon et al. (2020) dataset does not include low ESA values because Delaware Bay has been managed under successful reference points for more than half a century, so the ESA-recruitment relationship at low ESA remains obscure. These simulations focus attention on the incidence of mass mortality events in oyster populations (Munroe et al. 2013; Cheng et al. 2016; Grizzle et al. 2018; Gledhill et al. 2020; Pace et al. 2020a, 2020b) and the implications for recovery when a primary source of ESA, live oysters, no longer contributes to the ESA on the reef.

Finally, this model rests on a well-established, multi-decadal time series from Delaware Bay that permits detailed estimates of ESA, ranges of natural and fishing mortalities, and related metrics. Some of the model parameters are much less well constrained. That oyster shell has a relatively short half-life in comparison to other molluscan shells, save for mussels, is well established (Pace et al. 2020a); however, the range of values for the specific rate of shell loss is relatively large. Understanding the mechanisms that influence the rate of shell loss is a critical component in describing the carbonate budget of a reef and should receive focused research (Frérotte et al. 1983; Waldbusser et al. 2011). The disarticulation rate for boxes is also uncertain, resting on a very small sample size that identifies a relatively wide range of box half-lives (Christmas et al. 1997; Pace et al. 2020a; as inferred from Ford et al. 2006), yet boxes provide an important source of ESA. As boxes are also used for the direct measurement of mortality rate (Ford et al. 2006; Powell et al. 2008; Vølstad et al. 2008; Summerhayes et al. 2009; Doering et al. 2021), well-constrained estimates of disarticulation rates are urgently needed. Parameterization of the box disarticulation rates used conforms with observations from direct measurements and time series data for Delaware Bay. Alternate rates are likely to be required for application under other estuarine conditions. An additional poorly constrained parameter is the degree of survivorship from settlement to yearling age, with an important source of uncertainty being the tendency for the recruit index to be measured after substantive post-settlement mortality has occurred (e.g., Hopkins 1954; Newell et al. 2000).

### Conclusions

Achieving sustainability has been elusive in managing the eastern oyster fishery throughout much of its range. The world-wide demise of oyster reefs suggests that the eastern oyster is not an unusual case. Underlying this management predicament is the assumed applicability of standard approaches to managing any commercial species. The oyster is unique in temperate estuaries, however, in requiring a supporting physical structure that it itself creates. Thus, sustainable management of the stock in the absence of proper management of the critical substrate upon which it depends and creates is inherently impossible over the long term. The tendency for the shell loss rate to be slower than the turnover rate of the oyster population generates an illusion of permanence that in fact does not exist. The challenge has been to develop reference points that permit specification of rebuilding goals, optimal yield, and threshold control rules, which include the necessary provision of a sustainable shell bed. The present model propounds a resolution to this dilemma in defining recruitment in terms of characteristics of the habitat as well as the stock. One of the singular revelations is the importance of the living populations not just to provide larvae for the coming generation but to provide habitat for settlement. Two corollaries are of immediate concern. The first is that maintaining the shell bed demands a population density and this coincident with a fishing mortality rate well below that typical of an animal with a 10- to 20-year lifespan. The fishing mortality rate must be maintained well below 15% per year. The second is the likely presence of an Allee-like effect, in which a condition can be achieved where the reef continues to exist for a time, but recovery of the population is no longer a feasible option without external intervention in the form of reef rehabilitation efforts. Thus, precautionary management is critical as the cost of restoration and the time required for rebuilding involve much more than the need for one good recruitment event or one round of shell-planting. The left-skewed relationship among  $F$ ,  $M$ , and surplus production, in which the decline in surplus production occurs much more rapidly at  $F > F_{MSY}$  than at  $F < F_{MSY}$  spotlights the need for routine and substantive precautionary management. What is argued here is that the science base for sustainable management is now present and can be implemented under strong reference-point criteria and that doing so can provide a cost-efficient option for restoring the eastern oyster across its range.

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