The demographic consequences of growing older and bigger in oyster populations

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Abstract. Structured population models, particularly size- or age-structured, have a long history of informing conservation and natural resource management. While size is often easier to measure than age and is the focus of many management strategies, agestructure can have important effects on population dynamics that are not captured in size-only models. However, relatively few studies have included the simultaneous effects of both age- and size-structure. To better understand how population structure, particularly that of age and size, impacts restoration and management decisions, we developed and compared a size-structured integral projection model (IPM) and an age- and size-structured IPM, using a population of Crassostrea gigas oysters in the northeastern Pacific Ocean. We analyzed sensitivity of model results across values of local retention that give populations decreasing in size to populations increasing in size. We found that age- and sizestructured models yielded the best fit to the demographic data and provided more reliable results about long-term demography. Elasticity analysis showed that population growth rate was most sensitive to changes in the survival of both large (>175 mm shell length) and small (<75 mm shell length) oysters, indicating that a maximum size limit, in addition to a minimum size limit, could be an effective strategy for maintaining a sustainable population. In contrast, the purely size-structured model did not detect the importance of large individuals. Finally, patterns in stable age and stable size distributions differed between populations decreasing in size due to limited local retention and populations increasing in size due to high local retention. These patterns can be used to determine population status and restoration success. The methodology described here provides general insight into the necessity of including both age- and size-structure into modeling frameworks when using population models to inform restoration and management decisions.

Key words: age-structure; Crassostrea gigas; demographic modeling; integral projection model; oyster demography; size-frequency distribution; size-structure.

INTRODUCTION

Structured population models have a long history of informing conservation and natural resource management (e.g., Crouse et al. 1987). This is due to the often direct link between state-specific transition rates and management actions that can allow researchers to evaluate the relative efficacy of alternative management choices (Beissinger and Westphal 1998). These structured population models take various forms and can include discretely structured traits, such as age, stage, or gender, and continuously structured traits, such as size.

We focus on the role of both age- and size-structure. For many organisms, it is often easier and less destructive to measure the size of an individual, rather than age, and numerous management decisions are most directly tied to size, such as fishery catch restrictions (Punt et al. 2013). Additionally, for organisms that routinely experience fragmentation or breakage, size-structured models provide a better descriptor of demographic processes (Hughes 1984, Hughes and Connell 1987). Conversely, the dynamics of fluctuating populations are often best captured by including age-structure in population models (Bjornstad et al. 2004, Botsford et al. 2014), while the effectiveness of metabolic and cellular processes often decline with age, independent of size (Ivanina et al. 2008, Abele et al. 2009). Notwithstanding these distinctions, in many cases age and size are used interchangeably, with one variable serving as a predictor for the other (e.g., von Bertalanffy growth models).

Far less common are studies that include both age- and size-structure simultaneously. Although age and size may be correlated, there are often independent and interactive effects of age and size. For example, Hughes and Connell (1987) and Babcock (1991) both found that age- and size-structure were necessary to model the demography of several coral species. The relative importance of

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age-dependence and size-dependence on demographic rates has been shown to vary based on the species under study, how far the population is from its steady state conditions, and the degree of correlation between size and age (see Hughes and Connell 1987, Law and Edley 1990, and references therein).

In many taxonomic groups, such as mollusks, crustaceans, and fish, the relationship between age and size is highly variable, whereby individuals of a given age can vary greatly in size and vice versa (Lorenzen 2016). One such globally distributed group that exhibits substantial variation in the relationship between age and size is the Ostreidae, which includes ovsters in the genera Ostrea, Crassostrea, and Saccostrea. In these genera, survival, growth, and fecundity are both age- and size-dependent. For instance, larger females have an exponentially greater gonadal mass and egg production than smaller females, yet they can be of the same age, depending on environmental factors such as temperature (Choi et al. 1993, Kennedy et al. 1996, Cardoso et al. 2007, 2013). Mortality is also age- and size-dependent, with larger, older oysters more susceptible to diseases, whereas juveniles are much more vulnerable to predation (Kennedy et al. 1996, Anderson and Connell 1999, Carnegie and Burreson 2011). Age-dependent changes in oxidative stress markers and cellular defense proteins can influence the effectiveness of metabolic processes (ultimately leading to senescence and death), as well as the ability of the organism to deal with environmental stressors (Ivanina et al. 2008). Finally, in populations of oysters located in regions contaminated with heavy metals, concentrations of zinc, copper, and cadmium vary with age (Mackay et al. 1975), and long-term exposure to these metals can influence oyster metabolism and responses to environmental stressors (Luo et al. 2014). Consequently, one must model both size and age to describe population dynamics accurately.

In addition, oysters provide a good case study due to the current focus on oyster restoration and management. Oyster reefs have deteriorated globally due to coastal development, overfishing, and pollution (Airoldi and Beck 2007, Beck et al. 2011). Specifically, native oyster species, which are dominant ecosystem engineers that provide a suite of ecosystem services (Coen et al. 2007, Grabowski et al. 2012), have been reduced to less than 15% of their historical extent along the Pacific and Atlantic coasts of the USA (Rothschild et al. 1994, Beck et al. 2011, Zu Ermgassen et al. 2012). Major efforts are underway to restore and protect native and naturalized oyster species (Laing et al. 2006, Beck et al. 2011), and there have been successful restoration efforts in isolated cases with the eastern oyster along the mid-Atlantic coast and the Gulf of Mexico (Taylor and Bushek 2008, Powers et al. 2009, Schulte et al. 2009, Puckett and Eggleston 2012, Lipcius et al. 2015). Though these successes are promising, the scientific community has yet to reach agreement on the most effective means for achieving such success (Kennedy et al. 2011, but see Baggett et al. 2014 and Lipcius et al. 2015).

We use the Pacific oyster, Crassostrea gigas, as a model species to investigate population structure. Specifically, we develop an integral projection model (IPM) that allows for the simultaneous inclusion of both discrete age structure and continuous size-structure (Easterling et al. 2000, Ellner and Rees 2006, Coulson 2012, Merow et al. 2014, Rees et al. 2014, Ellner et al. 2016). We use this model to address several important questions. First, we assess whether predictions of long-term demography vary depending upon whether only size, or both age and size, are included as structuring variables. Second, while IPMs have most often been applied to size-structured terrestrial populations in which the size of an organism can both increase (e.g., through growth) or decrease (e.g., through starvation), the size of an oyster is often measured along the hard shell structure, which usually does not decrease in size. We fit the IPM with a growth kernel that only allows for positive growth and investigate the consequences of describing growth in this way. Finally, we explore how the long-term size-distributions, recently proposed as a means of monitoring restoration success (Baggett et al. 2014, 2015), vary depending upon whether populations are declining, stable, or increasing in size.

METHODS

Model

Age- and size-based IPMs describe a population where $n_a(x,t)dx$ is the number of individuals aged a in the size range [x, x + dx] at time t. We consider $n_a(x,t)$ to include both male and female oysters. Though there is some evidence that growth rate differs between males and females (Baghurst and Mitchell 2002), for simplicity we consider the two sexes to have equal growth rates. Individuals transition between sizes and ages according to three age-specific demographic functions: $S_a(x), G_a(y,x)$ and $F_a(y,x)$. $S_a(x)$ is the annual survival probability of individuals of size x and age a, $G_a(y,x)dy$ is the probability of surviving individuals of size x and age a growing to within a range of sizes [y, y+dy], and age a + 1, and $F_a(y,x)dy$ is the expected number of offspring within a range of sizes [y, y+dy] produced by surviving individuals of size x and age a. In the most general form, the dynamics of the population are expressed as

$$n_{1}(y,t+1) = \sum_{a=2}^{A} \int_{0}^{L} S_{a}(x)F_{a}(y,x)n_{a}(x,t)dx,$$
(1)

$$n_{a+1}(y,t+1) = \int_0^{\infty} S_a(x)G_a(y,x)n_a(x,t)dx,$$
 (2)

where L is the maximum size of an individual, and A is the maximum age of an individual. By setting a maximum size for individuals, there is the possibility that large individuals can grow past this upper limit and be "evicted" from the population (Williams et al. 2012). This



FIG. 1. Modeled life cycle of *Crassostrea gigas*. Census occurs immediately following summer recruitment. Oysters then must survive and grow for the majority of the year prior to reproduction. Following reproduction, new oyster recruits experience a separate growth and survival event before joining existing oysters immediately prior to the next census.

phenomenon artificially increases the mortality of the larger size classes and lowers the population growth rate. To avoid this issue, a discrete size class is added to the model for individuals of size x > L. The kernels for survival and fecundity of this discrete class are set equal to kernels for individuals of size x = L (Easterling et al. 2000, Williams et al. 2012).

In Oregon, *C. gigas* populations reproduce once during the summer months (Lannan et al. 1980). Thus, we modeled the census as occurring immediately following summer recruitment (Fig. 1). We assumed that oysters must first survive and grow throughout the majority of the year prior to reproduction. Following reproduction, larvae experience growth and mortality prior to the census. We consider a single, closed population with no external recruitment; all new oyster recruits are a result of local retention of larvae.

To model the fecundity kernel conditioned on survival, $F_a(y,x)$, we consider oysters that first survive and grow from size x to their final end-of-year size x' before reproducing. During reproduction, the total number of larvae produced for a given age class, $f_a(x')$, is equal to the number of eggs produced that survive and successfully establish. We estimated this function as a product of three terms (1) the proportion of size x individuals in the population that are female, v(x'); (2) the total number of eggs produced, h(x'), which we assume is dependent upon the size, but not the age, of the parent; and (3) the fraction of eggs produced that survive and join the census population, p (i.e., local retention). Thus, $f_a(x') = v(x')h(x')p$. The sizes of the newly recruited oysters are assumed to be normally distributed with density z(y). Thus, the overall fecundity kernel can be expressed as

$$F_{a}(y,x) = z(y) \int_{0}^{L} [G_{a}(x',x)f_{a}(x')]dx'.$$
(3)

Data

We estimated kernels for survival and growth using data collected from C. gigas populations in the Pacific Northwest (Stick 2011). A full description of the rearing procedure is given in Stick (2011), which we summarize as follows. Juvenile oysters were bred from adults at the Molluscan Broodstock Program (MBP) hatchery (Hatfield Marine Science Center, Newport, Oregon, USA). Adults were crossed to maximize phenotypic and genetic variance. Juveniles were transferred at 80 d of age to growout units held under flow-through raceway conditions at the MBP facility for an additional 50-75 d. When oysters reached approximately 30 mm in length, at an average age of 140 d and weight of 2.4 g, they were randomly assigned in pairs to each of 120 pearl oyster panel net pockets and planted subtidally at two locations in Yaquina Bay, Oregon, USA. Shell length (measured from anterior hinge to posterior shell margin) and survival were recorded for a total of 1,440 oysters in October 2005, May 2006, February 2007, and January 2008. Although the data were not collected in exact 1-yr intervals, we assumed that census occurred at approximately the same point in the oyster life cycle each year. To estimate the fecundity kernel, data on the relationship between dry tissue weight, size, and number of eggs was obtained from Kang et al. (2003) and Ren et al. (2003). As oysters are protandric hermaphrodites, with most individuals born male and becoming female later in life, we obtained size-specific sex ratios from Buroker (1983).

Statistical fitting

Growth kernel.—Past applications of IPMs typically estimate the growth kernel for a given age, a, by fitting a linear regression of size at time t + 1 against size at time t, assuming that for each size x the probability

distribution of growth into size y is normally distributed (Easterling et al. 2000). However, as the size of an oyster (measured as shell length) will not decrease in size between years, regardless of whether the nutrient requirements of the ovster are met, we instead estimated, for a given age, the log change in size from time t to t + 1using the size at time t. This methodology ensures that growth is positive, and is thus more realistic for our application. We compared the fit of this kernel to the traditional normally distributed growth kernel using Akaike's information criterion corrected for small sample size (AIC_c) (Anderson 2008). For both model types, we tested whether including only size, only age, both age and size, or the interaction between age and size led to a better fit. Since we are evaluating the use of IPMs, not matrix models, and since most oyster management decisions are based on size, rather than age, we did not evaluate the results of an age-only model. For simplicity, all models assume that variance is constant across all ages and sizes.

Survival kernel.—For established individuals, we fit the survival kernel, $S_a(x)$, using logistic regression of survival between years. As with the growth kernel, we compared models that included only size, only age, both age and size, and the interaction between age and size using AIC_c criteria, but did not include an age-only model in model analysis.

Fecundity kernel.-We estimated the total number of eggs produced, h(x'), using a linear regression of log egg number against parent size at time t, using the prespawning relationship between shell length and dry tissue weight obtained from Ren et al. (2003) and the relationship between dry tissue weight and total number of eggs obtained from Kang et al. (2003). Individual oysters are likely to switch from male to female as they grow older and larger. We thus estimated the proportion of female oysters at each size, v(x'), by fitting a linear regression using data obtained from Buroker (1983). Local retention (*p*), the fraction of eggs that survive from fertilization to the successful settlement and establishment of the larvae, is composed of fertilization success, survival during the pelagic larval stage, the probability of larvae encountering suitable settlement substrate, and the probability of successful metamorphosis. In marine environments, these values are notoriously difficult to estimate (Cowen and Sponaugle 2009). Past structured models of marine invertebrates have approximated these values by applying relationships obtained from other species (e.g., Levitan's (1991) estimate of densitydependent fertilization success for urchins is widely applied), fitting models to data and selecting recruitment values that provide the best fit, or examining patterns under varying assumptions of recruit origination (e.g., Gotelli 1991, Dudas et al. 2007, Yau et al. 2014, Puckett and Eggleston 2016). We explored population dynamics using a range of values for p, chosen such that (1) the amount of local retention was insufficient to sustain the population, causing the population to decrease in size; (2) the amount of local retention was sufficient for population persistence, but not growth; or (3) the amount of local retention was sufficient to sustain the population, causing the population to increase in size. Finally, we estimated the distribution of larval sizes at the time of census, z(y), using a normal distribution. We obtained this distribution using the mean and standard deviation of oyster sizes at the first time step of collected data (age ≈ 150 d).

Model analysis

Evaluating the IPM, we calculated the long-term population growth rate, reproductive values, and stable age and size distributions. The dominant eigenvalue of the integral operator, λ , describes the long-term population growth rate. If $\lambda < 1$ the population is decreasing, while if $\lambda > 1$ the population is increasing. The dominant left and right normalized eigenfunctions describe the reproductive values and the stable distributions across all sizes and ages, respectively. Reproductive values give an indication of the lifetime contribution of an individual in a particular age and size class to the population size in future generations, and stable distributions give the longterm size and age distribution of oysters within the population. We also computed the elasticity of λ to determine how proportional changes in the contribution of size x to size y individuals of a particular age (through either survival or fecundity) lead to proportional changes in λ (Caswell 2006, Ellner and Rees 2006). To assess the importance of including age-structure in the IPM, we compared model results from an IPM that includes both age- and size-structure to results from an IPM that includes only size-structure.

To approximate the integral operators, we used the midpoint rule with 300 equally sized bins from size 0 to 300 mm, for each age class from 0 to 15 yr. As noted previously, we also included an extra discrete size class to account for individuals growing outside the range of the integration limits.

Model implementation and data analysis were conducted in R (Bolker and R Core Team 2014, R Core Team 2015).

RESULTS

Statistical fits

Within the data set, oyster size ranged from 10.2 to 169.0 mm, while oyster ages ranged from 147 d to 2.7 yr. In the implementation of the IPM, we extrapolated both size and age past the minimum and maximum values in the data, with size ranging from L = 0 to L = 300 mm and age from A = 0 to A = 15 yr. This allowed us to capture maximum sizes generated by the model (Appendix S1). While *C. gigas* oysters can live longer than 15 yr, if



FIG. 2. Age- and size-dependent growth and survival functions. Statistical fitting of (A, B) age- and size-dependent growth and (C) survival functions. (A) Growth functions are fit using linear regression on the log change in size against size and age. (B) Growth functions are translated to generate the age-dependent relationship between size at time t + 1 and size at time t. The dotted (black) diagonal line is the 1:1 line. Note that, at small sizes (<50 mm), the growth model predicts that older oysters can grow upwards of 150 mm in a single year, and that at large sizes (>200 mm), there is a large difference in the growth of young and old oysters. This result is an artifact of the statistical extrapolation, and has little impact on model results. (C) Survival functions are fit using logistic regression of survival between time points. All functions are extrapolated past the collected data (black and gray points) to the minimum and maximum sizes. Parameters of the models are given in Table 1.

the maximum size and age are set sufficiently high (\geq 250 mm and \geq 10 yr, respectively), qualitative model output is not highly sensitive to the maximum size or age chosen (see Appendix S2).

The growth model that included age, size, and the interaction between age and size provided the best fit (lowest AIC_c; Appendix S3), suggesting that all of these parameters are important for modeling growth. Additionally, all models that forced growth to be positive were selected by AIC_c criteria over the commonly used models that allowed for both positive and negative growth. Overall, growth trajectories also differed between growth models. In models that allowed for negative growth, individuals were unable to reach large sizes and on average decreased in size approximately 42% of the time (Appendix S1), a phenomenon never observed in the data. In models that forced growth to be positive, there was a positive relationship between the size of an oyster and the log change in size between years in the two youngest age classes. For the older age classes, this relationship became negative (Fig. 2A). This leads to larger ovsters becoming more likely to experience little to no growth between years, compared to smaller oysters of the same age (Fig. 2B). Note that, at small sizes (<50 mm), the growth model predicts that older oysters can grow upwards of 150 mm in a single year. This is biologically unrealistic and is an artifact of the statistical extrapolation. As there is a very low chance that in the model an oyster older than ≈ 3 yr will be smaller than 100 mm, this effect had little impact on model results. A second artifact, due to the need to extrapolate the growth of oysters past age 3, was the substantial difference in growth of an age 1 oyster and an age 15 oyster at large sizes (>200 mm). Again, as it is unlikely that an age 1 oyster will be >100 mm, this effect had little impact on the results.

Similar to growth, oyster survival was dependent upon size, age, and the interaction between age and size

Table 1.	Age- and	1 size-dep	pendent	demogra	iphic f	unctio	ns.
Statistical	models	and par	ameter	estimate	s for a	age- a	ınd
size-struct	ured mo	dels used	to de	scribe C	rassosti	rea gi	gas
demograp	bhy.						

Demographic process	Model		
Growth	$\hat{y} = 2.961(0.047) + 0.18(0.027)a$ + 0.005(0.001)x - 0.002(0.0004)ax		
	standard deviation about the growth curve, $\sigma = 0.402 (0.005)$		
Survival	logit(s) = 4.003(0.395) - 0.016(0.010)a - 1.625(0.223)x + 0.018(0.004)ax		
Sex ratio	v(x') = 0.0311(0.050) + 0.0044(0.0004)x'		
Fecundity (number of eggs)	h(x') = 12.568(0.601) + 0.053(0.006)x'		
Distribution of larval size	Gaussian with mean = 30.575, variance = 40.73		
Local retention	$\begin{split} \lambda &= 0.506; \ p = 2.44 \times 10^{-15} \\ \lambda &= 1.003; \ p = 1.00 \times 10^{-11} \\ \lambda &= 1.499; \ p = 3.97 \times 10^{-10} \end{split}$		

Notes: All models are functions of age, a, and/or size, x. Values in parentheses are standard errors of parameter estimates. Predicted values for growth (\hat{y}) are the log change in size given current age and size. Models and parameter estimates for the size-only model are given in Appendix S4.

(Appendix S3). Above a threshold of approximately 80 mm, oysters had a high probability of survival, regardless of age (Fig. 2C). For older individuals below this size threshold, survival increased sharply with size, whereas for younger oysters, the increase was more gradual.

The proportion of females in the population increased sigmoidally as a function of size (Fig. 3A). For simplicity, we fit this data using a piecewise linear function, as model results were not highly sensitive to the specific function



FIG. 3. Fecundity functions. (A) The proportion of females as a function of size (adapted from Buroker 1983). For simplicity we fit the data using a linear function, as model results are not sensitive to the function used. (B) The log number of eggs produced as a function of parent size (from Kang et al. 2003, Ren et al. 2003). (C) The distribution of offspring size, fit to the first time step of the *C. gigas* dataset (shown grouped in size bins of 5 mm). Parameters of all model fits are given in Table 1.

used. Log number of eggs increased linearly as a function of female size (Fig. 3B), while the size of new recruits was normally distributed (mean = 30.6 mm, SD = 6.4 mm; Fig. 3C).

In the age- and size-structured model, setting local retention, p, to 2.44×10^{-15} , 1.00×10^{-11} , and 3.97×10^{-10} yielded long-term population growth rates $\lambda = 0.506$, $\lambda = 1.003$, and $\lambda = 1.499$, respectively. In the size-only model, setting p to 3.74×10^{-13} and 6.68×10^{-12} yielded $\lambda = 1.009$ and $\lambda = 1.508$, respectively. For all values of $p \ge 0$, the population growth rate λ was greater than 0.9 in the size-only model. As such, for the size-only model we did not evaluate the case when $\lambda = 0.5$.

Final models and parameter estimates for growth, survival, and fecundity are given in Table 1 for the age- and size-structured model, and in Appendix S4 for the size-only model.

Model analysis

In the age- and size-structured model, for all values of λ larger oysters had higher reproductive values than smaller oysters, while younger oysters had higher reproductive values than older ones (Fig. 4A, B). The difference in reproductive values between the youngest and oldest oysters was greatest when local retention and λ were low. When age was excluded from the model, the difference in reproductive values between the smallest and largest oysters was greatest when local retention and λ were high. For $\lambda > 1$ the largest individuals had the highest reproductive value, while when $\lambda \approx 1$ the values were more evenly distributed across all size classes (Fig. 4C).

In a declining population with limited local retention and $\lambda < 1$, the stable size and age distributions from the age- and size-structured model were unimodal and skewed to larger sizes and older ages (Fig. 4D, E). Most individuals in the population were between 150 and 250 mm and ≥ 10 yr of age. When $\lambda \approx 1$, the stable size distribution shifted toward smaller sizes and became bimodal, with peaks at approximately 40 and 200 mm. Individuals were distributed roughly equally across all age classes. In a growing population with high local retention and $\lambda > 1$, the stable size distribution was nearly unimodal and skewed to smaller sizes. Most individuals were approximately 40 mm and <4 yr old. The slightly smaller peak to the right of the primary mode was likely due to the ample numbers of oysters in the second age class.

When age was excluded from the statistical fitting and only size included in the IPM, much of the information about the value of larger oyster sizes was lost. For instance, in the size only model, the stable size distribution was unimodal with a major peak at small sizes, whereas the age- and size-structured model produced size distributions skewed toward larger oysters as λ decreased (Fig. 4E vs. F).

The survival of younger oysters had a higher elasticity than that of older oysters in the age- and size-structured model, with this difference becoming more pronounced with high local retention and $\lambda > 1$ (Fig. 5A). Across sizes, survival of the smallest and the largest oysters had the highest elasticity (Fig. 5B), while only changes in the fecundity of oysters approximately 150–250 mm had an impact on λ (Fig. 5E). However, the fecundity of older individuals had a higher elasticity than that of younger oysters (Fig. 5D). As local retention increased and λ increased from 0.5 to 1.5, the fecundity of the younger ages became more important. Relative changes in growth and survival across all ages and sizes had a greater impact on λ than changes in fecundity (Fig. 5).

There were large differences in elasticity between the ageand size-structured model and the size-only model. The peaks at larger sizes in the size-specific survival elasticities of the age- and size-structured model were absent in the size-only model (Fig. 5C), whereas size-specific fecundity elasticities of the size-only model never peaked, but only increased monotonically with size (Fig. 5F).



FIG. 4. IPM model output. Model output for $\lambda = 0.5$ (black line and points), $\lambda \approx 1.0$ (dark gray line and points), and $\lambda = 1.5$ (light gray line and points). (A) Age-specific reproductive values for the age- and size-structured model. (B) Size-specific reproductive values for the age- and size-structured model. (C) Reproductive values for the size-only model. For (A–C), reproductive values for each λ are scaled such that the sum of all values = 1. (D) Stable age distributions for the age- and size-structured model. (E) Stable size distributions for the age- and size-structured model. (F) Stable age distributions for the age- and size-only model. For the size-only model, that $\lambda \approx 1$, and $\lambda = 1.5$ approximately 62.17%, and 1.81%, respectively, of the population is contained in the discrete size class of individuals greater than 300 mm (not shown on graph). Additionally, for the size-only model it was not possible to simulate a population with $\lambda = 0.5$. As such, only relationships for $\lambda \approx 1$ and $\lambda = 1.5$ are shown.

Finally, for the size-only model the population growth rate λ was greater than 0.9 for all values of $p \ge 0$. At large sizes, survival of oysters increased to almost 100%, while the mean change in size between time steps continued to increase as oysters got larger, rather than decreasing to 0 (Appendix S4). As such, when λ was low most oysters were in the discrete size class of oysters ≥ 300 mm (62.2% when $\lambda \approx 1$). Because these individuals have a high probability of survival, the long-term population growth rate will still be close to 1, even in the absence of successful recruitment. If we assume that all oysters die after reaching the maximum size, a long-term population growth rate of $\lambda = 0.5$ is possible. Even in this case, however, model output failed to capture the peaks at larger sizes that were observed in the age- and size-structured model.

DISCUSSION

We found substantive differences in the importance of large and small oysters to population dynamics between an IPM using age- and size-structured and one using only size-structure. In general, the importance of large oysters to population dynamics was clear from the age- and sizestructured model, but absent from the size-structured model. In addition, the age- and size-structured model yielded differences in size distributions between growing populations with high local retention and declining population with low local retention that were not apparent in the size-only model.

For the age- and size-structured model, most individuals were large and old in declining populations, whereas most individuals were small and young in populations with positive population growth. Intuitively, in declining populations with low local retention, few juveniles are added to the population. As such, size distributions are skewed towards the older, larger sizes. Alternatively, for populations with high local retention leading to positive growth, there is a substantial influx of small juveniles each year. This leads to the rightskewed stable size and age distributions when $\lambda > 1$. Finally, the joint age- and size-structure was required to detect the importance, measured by elasticity, of both small and large individuals to population growth. With the size-only model, elasticity analysis indicated that survival of the smaller individuals was most important to population growth.

The differences in results between the size-only model and the age- and size-structured model likely arose due



FIG. 5. IPM elasticity analysis. Elasticity analysis for when $\lambda = 0.5$ (black line and points), $\lambda \approx 1.0$ (dark gray line and points), (A) Age-specific survival elasticities for the age- and size-structured model. (B) Size-specific survival elasticities for the age- and size-structured model. (C) Size-specific survival elasticities for the size-only model. (D) Age-specific fecundity elasticities for the age- and size-structured model. (E) Size-specific fecundity elasticities for the age- and size-structured model. (E) Size-specific fecundity elasticities for the age- and size-structured model. (E) Size-specific fecundity elasticities for the age- and size-structured model. (E) Size-specific fecundity elasticities for the age- and size-structured model. (F) Size-specific fecundity elasticities for the age- and size-structured model. For the size-only model, it was not possible to simulate a population with $\lambda = 0.5$. As such, only relationships for $\lambda \approx 1$ and $\lambda = 1.5$ are shown.

to the differences in individual growth rate at large sizes. In the size-only model, individual growth rate continued to increase as individuals grew, rather than declining to no growth, as with the age- and size-structured model. Biologically, continued increases in individual growth rate as size increases makes little sense for organisms such as oysters characterized by indeterminate growth. Moreover, in the size-only model there was no maximum age at which all individuals die. When local retention was low, this led to a majority of individuals growing beyond the set maximum size and entering the discrete size class of sizes >300 mm. The accumulation of individuals in that size class was not evident in the age- and size-structured model.

Model results from the age- and size-structured model are supported by population patterns observed in wild *Crassostrea* spp. populations. For example, in three *C. gigas* populations along the west European coast (Cardoso et al. 2007), the distribution of sizes within each age class matches that predicted by the model. In the Lower Saxony Wadden Sea, Germany, populations of *C. gigas* experiencing significant increases in population size have size distributions characterized by a major peak in the smaller (>55 mm) sizes, with some populations also exhibiting a smaller peak in size ranges between 55 and 100 mm (Schmidt et al. 2008). These size distributions are fairly consistent across the 3 yr of the study and match IPM predictions for populations experiencing positive population growth. Other populations of C. gigas in the North Wadden along the coast of Denmark and Germany also exhibit right skewed distributions when population densities are increasing (Diederich et al. 2005). In these populations, however, size distribution are more variable over the 10 yr of the study due to inconsistent recruitment. In upper Chesapeake Bay, where recruitment is limited, C. virginica populations outplanted as juveniles become dominated by large, old oysters after 2-4 yr due to extremely low recruitment in the years subsequent to the outplant (Paynter et al. 2010). These populations eventually go locally extinct without further transplants of young juveniles. In lower Chesapeake Bay, where recruitment is not limiting, persisting populations of C. virginica with multiple year classes are characterized by two major peaks, one for younger, smaller oysters up to 2 yr old, and a second one of larger oysters ranging in age from 3 to 6 yr old (Schulte et al. 2009, Lipcius et al. 2015). This pattern was also observed in C. virginia populations located in no-take

reserves in North Carolina where recruitment was not limiting (Puckett and Eggleston 2012, 2016).

Importantly, these examples represent populations in which recruitment occurs through a combination of local retention and larval subsidies from external sources, though in many cases the precise source of new recruits is unknown. Our model assumes a closed population with recruitment only occurring through local retention. However, due to the way in which we used p, the amount of local retention, as a tuning parameter to yield populations with various population growth rates, we expect that qualitative stable age and size distribution would not differ significantly if we were to incorporate a mix of local and external recruitment, though implications for management strategies might vary if one is considering a single closed population.

In a recent review, Baggett et al. (2015) proposed sizefrequency distributions as a universal metric for monitoring oyster restoration success. Our results support this proposal and indicate that certain patterns in size distributions can point to populations in need of restoration or can be indicative of restoration success or failure. If populations exhibit a skewed distribution with most individuals found in the larger, older age groups, this could point to a declining, recruitment-limited population, in which case restoration efforts should focus on broodstock enhancement and incorporating metapopulation dynamics to identify optimal locations for restoration and increased management protection (e.g., marine reserves; Lipcius et al. 2008, North et al. 2010, Lipcius et al. 2015, Puckett and Eggleston 2016). If a bimodal size distribution is observed, this could indicate a population with $\lambda \approx 1$, in which case monitoring, and perhaps limited restoration, are sufficient. Finally, if populations exhibit a skewed distribution with substantial numbers of individuals in the smaller, younger age groups, as well as abundant adults, this could point to a successful population with sufficient recruitment and broodstock (Schulte et al. 2009, Lipcius et al. 2015). Such locations where populations are increasing in abundance may be ideal candidates for additional habitat restoration to expand the footprint of successful populations to ensure habitat limitation is not the bottleneck preventing population recovery.

To assess restoration success, it is necessary to monitor changes in the size distribution of a population over time to differentiate between stable population patterns and transient dynamics or patterns that emerge as a result of external recruitment (e.g., Diederich et al. 2005). Model results showed that, in a closed population started with a few small, young individuals, patterns in population size structure approached the stable distribution in as little as 5 yr if the population was doing well ($\lambda > 1$). However, model simulations required 10–15 yr to distinguish between stable ($\lambda \approx 1$) and declining ($\lambda < 1$) populations (Appendix S5). Post-restoration is often characterized by distributions skewed towards small individuals. Our results indicate that, in a closed population, subsequent monitoring over at least 5 yr will inform if the distribution remains skewed toward small individuals, indicating possible population persistence, or becomes skewed toward larger individuals, indicating insufficient local retention and necessitating additional intervention. However, it is important to recognize that if the population is open, size distributions could be misleading, as even a sink population could exhibit a bimodal distribution given sufficient amounts of external recruitment. If this is the case, then additional data is needed to assess persistence of local populations, as well as the entire metapopulation.

Once there is information about whether a population is increasing or decreasing, one must then understand which individuals are most important to the growth of that population, and on which ages or sizes efforts should focus to have the greatest positive impact on the population growth rate. Patterns in elasticity can be used to inform these decisions. Our results indicate that, for the modeled population of C. gigas, increasing the survival of both small (<50 mm) and very large (>175 mm) oysters had the greatest impact on λ . This suggests several strategies to assist protected or harvested oyster populations. For example, by enhancing the abundance of broodstock (large oysters) in source habitats (sensu Lipcius and Ralph 2011, Puckett and Eggleston 2016), one could achieve the dual objective of increasing abundance of very small and very large oysters, since in subsequent years the offspring of the broodstock would recruit throughout the metapopulation and consequently increase recruitment of young, small oysters (Lipcius et al. 2008, 2015). Additionally, instead of only establishing a minimum size limit to protect small and intermediate sizes, as is often done, our results suggest that an additional maximum size limit to harvest would be beneficial.

Finally, our results show that growth kernels that restrict growth to be positive between years produced a better fit relative to more commonly used growth kernels allowing for reduction in size with age. Many sessile marine organisms, such as oysters, grow by forming a calcified, protective shell. As such, fitting growth kernels by performing a standard least squares linear regression of size at time t + 1 against size at time t is not appropriate, as it allows for organisms to decrease in size between time steps. This indicates the importance of developing appropriate models of individual growth for the focal organism.

Limitations and challenges

While IPMs have been applied extensively to terrestrial plants and mammals, only a handful of examples exist of IPMs applied to a marine system (Bruno et al. 2011, Madin et al. 2012, Edmunds et al. 2014, Yau et al. 2014). Our results further demonstrate that IPMs can be a powerful tool for modeling population dynamics of marine species. However, several challenges remain.

First, long-term datasets must be developed that include trait-specific information on individuals (not just cohorts) through time. The size-only model and the ageand size-structured model produced similar results across a narrow size range (10-100 mm length) and for which data were available. Past a size of 100 mm, the results of the two models became disparate. Consequently, emphasis should be on acquisition of data across the full size and age range of a focal species, not just on the early years, although the necessary number of years of data collection will vary from species to species. For C. gigas populations, our analysis suggests that 4 yr of data produces informative patterns. However, we had to extrapolate the statistical demographic kernels upwards of 7 yr and 140 mm length, so the specifics of the results should be interpreted with caution. Additional years of data are likely necessary to better tease apart the age- or sizedependence of different vital rates and to accurately inform on-the-ground decisions about specific populations. Given these limitations, we also need methods to assess how much data is needed to yield accurate, realistic results, such as examining sensitivities of key response variables to sub-sampling of the collected data.

Due to our limited dataset, we were not able to parameterize an age-only model for comparison. Future work could utilize an extended dataset that contained enough years of data to fit an age-only model and assess whether this model is able to capture important patterns in the population, or if the model including both age and size is still essential.

Another challenge of applying IPMs to marine systems is in obtaining an accurate estimate of recruitment. This parameter can be difficult to estimate, particularly for broadcast spawners, and can display a high degree of spatial and temporal heterogeneity (Cowen and Sponaugle 2009). However, even when this parameter is unknown or highly uncertain, our results show that investigating patterns in population structure over a range of recruitment scenarios can provide insight into the current state (e.g., decreasing, stable, increasing) of a population. Our model assumes a closed population, whereby recruitment occurs via local retention of larvae and not from immigration via connectivity from external larval sources. This assumption is reasonable when local retention is high relative to connectivity because recruitment is driven by local reproduction (Figueira 2009, Carson et al. 2011, Puckett and Eggleston 2016). However, when local retention is low relative to external recruitment, accounting for this external recruitment is important as it can affect size and age distributions, as well as management strategies (Yau et al. 2014). Acquisition of this necessary data, which likely involves temporal variability in recruitment, and incorporating these features in our models, is a key challenge for the future.

Finally, additional factors that are relevant to oyster populations could be incorporated into the IPM, including size-specific susceptibility to disease, size-specific harvest and size limits, and temporal variability in harvest.

CONCLUSION

Using demographic data from a population of the Pacific oyster, *C. gigas*, in Oregon, our modeling analysis demonstrates the utility of IPMs for understanding the relative importance of including age- and size-structure for understanding population dynamics. We show that simultaneous inclusion of both age and size, as well as limiting growth to positive changes, is necessary to parameterize an IPM of *C. gigas* population dynamics. This type of modeling framework can also be used to assist with management decisions involving restoration and conservation of sensitive and important marine species. However, more long-term datasets are needed that include both age- and size-dependent information on population demographic rates for this tool to be truly effective.

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