

# Author Manuscript

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/eap.1374](https://doi.org/10.1002/eap.1374)

This article is protected by copyright. All rights reserved

1 **Running head:** Age- and size-structured oyster IPM

2 **The demographic consequences of growing older and bigger in oyster populations**

3 Jacob L Moore<sup>1\*</sup>, Romuald N Lipcius<sup>2</sup>, Brandon Puckett<sup>3</sup>, Sebastian J Schreiber<sup>1</sup>

4 <sup>1</sup>Department of Evolution and Ecology, Center for Population Biology, One Shields Avenue,  
5 University of California, Davis, California 95616, USA. Emails: jlmoor@ucdavis.edu;  
6 sschreiber@ucdavis.edu

7 <sup>2</sup>Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester  
8 Point, Virginia 23062, USA. Email: rom@vims.edu

9 <sup>3</sup>North Carolina State University, Department of Marine, Earth & Atmospheric Sciences, Center  
10 for Marine Sciences and Technology, Morehead City, North Carolina 28557, USA. Email:  
11 brandon.puckett@ncdenr.gov

12 \*Corresponding author, jlmoor@ucdavis.edu

## ABSTRACT

13  
14 Structured population models, particularly size- or age-structured, have a long history of  
15 informing conservation and natural resource management. While size is often easier to measure  
16 than age, and is the focus of many management strategies, age-structure can have important  
17 effects on population dynamics that are not captured in size-only models. However, relatively few  
18 studies have included the simultaneous effects of both age- and size-structure. To better  
19 understand how population structure, particularly that of age and size, impacts restoration and  
20 management decisions, we developed and compared a size-structured integral projection model  
21 (IPM) and an age- and size-structured IPM, using a population of *Crassostrea gigas* oysters in the  
22 northeastern Pacific Ocean. We analyzed sensitivity of model results across values of local  
23 retention that give populations decreasing in size to populations increasing in size. We found that  
24 age- and size-structured models yielded the best fit to the demographic data and provided more  
25 reliable results about long-term demography. Elasticity analysis showed that population growth  
26 rate was most sensitive to changes in the survival of both large ( $> 175$  mm shell length) and small  
27 ( $< 75$  mm shell length) oysters, indicating that a maximum size limit, in addition to a minimum  
28 size limit, could be an effective strategy for maintaining a sustainable population. In contrast, the  
29 purely size-structured model did not detect the importance of large individuals. Finally, patterns  
30 in stable age and stable size distributions differed between populations decreasing in size due to  
31 limited local retention, and populations increasing in size due to high local retention. These  
32 patterns can be used to determine population status and restoration success. The methodology  
33 described here provides general insight into the necessity of including both age- and  
34 size-structure into modeling frameworks when using population models to inform restoration and  
35 management decisions.

37 integral projection model, *Crassostrea gigas*, age-structure, size-structure, demographic  
38 modeling, oyster demography, size-frequency distribution

Author Manuscript

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

46 Here, we focus on the role of both age- and size-structure. For many organisms, it is often easier  
47 and less destructive to measure the size of an individual, rather than age, and numerous  
48 management decisions are most directly tied to size, such as fishery catch restrictions (Punt et al.,  
49 2013). Additionally, for organisms that routinely experience fragmentation or breakage,  
50 size-structured models provide a better descriptor of demographic processes (Hughes, 1984;  
51 Hughes and Connell, 1987). Conversely, the dynamics of fluctuating populations are often best  
52 captured by including age-structure in population models (Bjornstad et al., 2004; Botsford et al.,  
53 2014), while the effectiveness of metabolic and cellular processes often decline with age,  
54 independent of size (Ivanina et al., 2008; Abele et al., 2009). Notwithstanding these distinctions,  
55 in many cases age and size are used interchangeably, with one variable serving as a predictor for  
56 the other (e.g. von Bertalanffy growth models).

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

62 vary based on the species under study, how far the population is from its steady state conditions,  
63 and the degree of correlation between size and age (see Hughes and Connell (1987), Law and  
64 Edley (1990), and references therein).

65 In many taxonomic groups, such as mollusks, crustaceans and fish, the relationship between age  
66 and size is highly variable, whereby individuals of a given age can vary greatly in size and vice  
67 versa (Lorenzen, 2016). One such globally-distributed group that exhibits substantial variation in  
68 the relationship between age and size is the Ostreidae, which includes oysters in the genera  
69 *Ostrea*, *Crassostrea* and *Saccostrea*. In these genera, survival, growth, and fecundity are both  
70 age- and size-dependent. For instance, larger females have an exponentially greater gonadal mass  
71 and egg production than smaller females, yet they can be of the same age, depending on  
72 environmental factors such as temperature (Choi et al., 1993; Kennedy et al., 1996; Cardoso et al.,  
73 2007, 2013). Mortality is also age- and size-dependent, with larger, older oysters more  
74 susceptible to diseases, whereas juveniles are much more vulnerable to predation (Kennedy et al.,  
75 1996; Anderson and Connell, 1999; Carnegie and Burreson, 2011). Age-dependent changes in  
76 oxidative stress markers and cellular defense proteins can influence the effectiveness of metabolic  
77 processes (ultimately leading to senescence and death), as well as the ability of the organism to  
78 deal with environmental stressors (Ivanina et al., 2008). Finally, in populations of oysters located  
79 in regions contaminated with heavy metals, concentrations of zinc, copper, and cadmium vary  
80 with age (Mackay et al., 1975), and long-term exposure to these metals can influence oyster  
81 metabolism and responses to environmental stressors (Luo et al., 2014). Consequently, one must  
82 model both size and age to describe population dynamics accurately.

83 In addition, oysters provide a good case study due to the current focus on oyster restoration and  
84 management. Oyster reefs have deteriorated globally due to coastal development, overfishing, and

85 pollution (Airoldi and Beck, 2007; Beck et al., 2011). Specifically, native oyster species, which  
86 are dominant ecosystem engineers that provide a suite of ecosystem services (Coen et al., 2007;  
87 Grabowski et al., 2012), have been reduced to less than 15% of their historical extent along the  
88 Pacific and Atlantic coasts of the United States (Rothschild et al., 1994; Beck et al., 2011;  
89 Zu Ermgassen et al., 2012). Major efforts are underway to restore and protect native and  
90 naturalized oyster species (Laing et al., 2006; Beck et al., 2011), and there have been successful  
91 restoration efforts in isolated cases with the eastern oyster along the mid-Atlantic coast and the  
92 Gulf of Mexico (Taylor and Bushek, 2008; Powers et al., 2009; Schulte et al., 2009; Puckett and  
93 Eggleston, 2012; Lipcius et al., 2015). Though these successes are promising, the scientific  
94 community has yet to reach agreement on the most effective means for achieving such success  
95 (Kennedy et al., 2011; but see Baggett et al. (2014) and Lipcius et al. (2015)).

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

108 monitoring restoration success (Baggett et al., 2014, 2015), vary depending upon whether  
109 populations are declining, stable, or increasing in size.

## 110 METHODS

### 111 *Model*

112 Age- and size-based IPMs describe a population where  $n_a(x,t)dx$  is the number of individuals  
113 aged  $a$  in the size range  $[x, x + dx]$  at time  $t$ . We consider  $n_a(t)$  to include both male and female  
114 oysters. Though there is some evidence that growth rate differs between males and females  
115 (Baghurst and Mitchell, 2002), for simplicity we consider the two sexes to have equal growth  
116 rates. Individuals transition between sizes and ages according to an age-specific projection kernel  
117  $K_a(y,x)$ , which describes the infinitesimal contribution of size  $x$  individuals of age  $a$  to size  $y$   
118 individuals of age  $a + 1$ . The projection kernel  $K_a$  is here expressed as  
119  $K_a(y,x) = S_a(x)[G_a(y,x) + F_a(y,x)]$ , where  $S_a(x)$  is the annual survival probability of individuals  
120 of size  $x$  and age  $a$ ,  $G_a(y,x)dy$  is the infinitesimal probability of surviving individuals of size  $x$   
121 and age  $a$  growing to size  $y$  and age  $a + 1$ , and  $F_a(y,x)dy$  is the expected number of offspring of  
122 size  $y$  produced by surviving individuals of size  $x$  and age  $a$ . In the most general form, the  
123 dynamics of the population are expressed as

$$n_1(y, t + 1) = \sum_{a=2}^A \int_0^L S_a(x) F_a(y, x) n_a(x, t) dx, \quad (1)$$

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

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



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

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

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

$$F_a(y, x) = z(y) \int_0^L [G_a(x', x) f_a(x')] dx'. \quad (3)$$

148 We estimated kernels for survival, growth, and fecundity using data collected from *C. gigas*  
149 populations in the Pacific Northwest (Stick, 2011). A full description of the rearing procedure is  
150 given in Stick (2011), which we summarize as follows. Juvenile oysters were bred from adults at  
151 the Molluscan Broodstock Program (MBP) hatchery (Hatfield Marine Science Center, Newport  
152 OR). Adults were crossed to maximize phenotypic and genetic variance. Juveniles were  
153 transferred at 80 days of age to growout units held under flow-through raceway conditions at the  
154 MBP facility for an additional 50-75 days. When oysters reached approximately 30 mm in length,  
155 at an average age of 140 days and weight of 2.4 g, they were randomly assigned in pairs to each  
156 of 120 pearl oyster panel net pockets and planted subtidally at two locations in Yaquina Bay, OR.  
157 Shell length (measured from anterior hinge to posterior shell margin) and survival were recorded  
158 for a total of 1,440 oysters in October 2005, May 2006, February 2007, and January 2008.  
159 Although the data were not collected in exact one-year intervals, we assumed that census  
160 occurred at approximately the same point in the oyster life cycle each year. Additional data on the  
161 relationship between dry tissue weight, size, and number of eggs was obtained from Kang et al.  
162 (2003) and Ren et al. (2003). As oysters are protandric hermaphrodites, with most individuals  
163 born male and becoming female later in life, we obtained size-specific sex ratios from Buroker  
164 (1983).

165

*Statistical fitting*

166 *Growth kernel.*—Past applications of IPMs typically estimate the growth kernel for a given age,  $a$ ,  
167 by fitting a linear regression of size at time  $t + 1$  against size at time  $t$ , assuming that for each size  
168  $x$  the probability distribution of growth into size  $y$  is normally distributed (Easterling et al., 2000).  
169 However, as the size of an oyster (measured as shell length) will not decrease in size between

170 years, regardless of whether the nutrient requirements of the oyster are met, we instead estimated,  
171 for a given age, the log change in size from time  $t$  to  $t + 1$  using the size at time  $t$ . This  
172 methodology ensures that growth is positive, and is thus more realistic for our application. We  
173 compared the fit of this kernel to the traditional normally distributed growth kernel using AICc  
174 criteria (Anderson, 2007). For both model types, we tested whether including only size, only age,  
175 both age and size, or the interaction between age and size led to a better fit. Since we are  
176 evaluating the use of IPMs, not matrix models, and since most oyster management decisions are  
177 based on size, rather than age, we did not evaluate the results of an age-only model. For  
178 simplicity, all models assume that variance is constant across all ages and sizes.

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

183 *Fecundity kernel.*—We estimated the total number of eggs produced,  $h(x')$ , using a linear  
184 regression of log egg number against parent size at time  $t$ , using the pre-spawning relationship  
185 between shell length and dry tissue weight obtained from Ren et al. (2003), and the relationship  
186 between dry tissue weight and total number of eggs obtained from Kang et al. (2003). Individual  
187 oysters are likely to switch from male to female as they grow older and larger. We thus estimated  
188 the proportion of female oysters at each size,  $v(x)$ , by fitting a linear regression using data  
189 obtained from Buroker (1983). Local retention ( $p$ ), the fraction of eggs that survive from  
190 fertilization to the successful settlement and establishment of the larvae, is composed of  
191 fertilization success, survival during the pelagic larval stage, the probability of larvae  
192 encountering suitable settlement substrate, and the probability of successful metamorphosis. In

193 marine environments, these values are notoriously difficult to estimate (Cowen and Sponaugle,  
194 2009). Past structured models of marine invertebrates have approximated these values by applying  
195 relationships obtained from other species (e.g., Levitan (1991)'s estimate of density-dependent  
196 fertilization success for urchins is widely applied), fitting models to data and selecting recruitment  
197 values that provide the best fit, or examining patterns under varying assumptions of recruit  
198 origination (e.g. Gotelli, 1991; Dudas et al., 2007; Yau et al., 2014; Puckett and Eggleston, 2016).  
199 Here, we explored population dynamics using a range of values for  $p$ , chosen such that 1) the  
200 amount of local retention was insufficient to sustain the population, causing the population to  
201 decrease in size; 2) the amount of local retention was sufficient for population persistence, but not  
202 growth; or 3) the amount of local retention was sufficient to sustain the population, causing the  
203 population to increase in size. Finally, we estimated the distribution of larval sizes at the time of  
204 census,  $z(y)$ , using a normal distribution. We obtained this distribution using the mean and  
205 standard deviation of oyster sizes at the first time step of collected data (age  $\approx$  150 days).

### 206 *Model analysis*

207 Evaluating the IPM, we calculated the long-term population growth rate, reproductive values, and  
208 stable age and size distributions. The dominant eigenvalue of the integral operator,  $\lambda$ , describes  
209 the long-term population growth rate. If  $\lambda < 1$  the population is decreasing, while if  $\lambda > 1$  the  
210 population is increasing. The dominant left and right normalized eigenfunctions describe the  
211 reproductive values and the stable distributions across all sizes and ages, respectively.  
212 Reproductive values give an indication of the lifetime contribution of an individual in a particular  
213 age and size class to the population size in future generations, and stable distributions give the  
214 long-term size and age distribution of oysters within the population. We also computed the  
215 elasticity of  $\lambda$  to determine how proportional changes in the contribution of size  $x$  to size  $y$

216 individuals of a particular age (through either survival or fecundity) lead to proportional changes  
217 in  $\lambda$  (Caswell, 2006; Ellner and Rees, 2006). To assess the importance of including age-structure  
218 in the IPM, we compared model results from an IPM that includes both age- and size-structure to  
219 results from an IPM that includes only size-structure.

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

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

## 225 RESULTS

### 226 *Statistical fits*

227 Within the data set, oyster size ranged from 10.2 mm to 169.0 mm, while oyster ages ranged from  
228 147 days to 2.7 years. In the implementation of the IPM we extrapolated both size and age past  
229 the minimum and maximum values in the data, with size ranging from  $L = 0$  to  $L = 300$  mm and  
230 age from  $A = 0$  to  $A = 15$  years. This allowed us to capture maximum sizes generated by the  
231 model (Appendix S1). While *C. gigas* oysters can live longer than 15 years, if the maximum size  
232 and age are set sufficiently high ( $\geq 250$  mm and  $\geq 10$  years, respectively), qualitative model  
233 output is not highly sensitive to the maximum size or age chosen (see Appendix S2).

234 The growth model that included age, size, and the interaction between age and size provided the  
235 best fit (lowest AICc; Appendix S3), suggesting that all of these parameters are important for  
236 modeling growth. Additionally, all models that forced growth to be positive were selected by  
237 AICc criteria over the commonly used models that allowed for both positive and negative growth.

238 Overall, growth trajectories also differed between growth models. In models that allowed for  
239 negative growth, individuals were unable to reach large sizes, and on average decreased in size  
240 approximately 42% of the time (Appendix S1), a phenomenon never observed in the data. In  
241 models that forced growth to be positive, there was a positive relationship between the size of an  
242 oyster and the log change in size between years in the two youngest age classes. For the older age  
243 classes, this relationship became negative (Figure 2A). This leads to larger oysters becoming  
244 more likely to experience little to no growth between years, compared to smaller oysters of the  
245 same age (Figure 2B). Note that, at small sizes ( $< 50$  mm), the growth model predicts that older  
246 oysters can grow upwards of 150 mm in a single year. This is biologically unrealistic, and is an  
247 artifact of the statistical extrapolation. As there is a very low chance that in the model an oyster  
248 older than  $\approx 3$  years will be smaller than 100 mm, this effect had little impact on model results. A  
249 second artifact, due to the need to extrapolate the growth of oysters past age 3, was the substantial  
250 difference in growth of an age 1 oyster and an age 15 oyster at large sizes ( $> 200$ mm). Again, as  
251 it is unlikely that an age 1 oyster will be  $> 100$  mm, this effect had little impact on the results.

252 Similar to growth, oyster survival was dependent upon size, age, and the interaction between age  
253 and size (Appendix S3). Above a threshold of approximately 80 mm, oysters had a high  
254 probability of survival, regardless of age (Figure 2C). For older individuals below this size  
255 threshold, survival increased sharply with size, whereas for younger oysters, the increase was  
256 more gradual.

257 The proportion of females in the population increased sigmoidally as a function of size (Figure  
258 3A). For simplicity, we fit this data using a piecewise linear function, as model results were not  
259 highly sensitive to the specific function used. Log number of eggs increased linearly as a function  
260 of female size (Figure 3B), while the size of new recruits was normally distributed (mean = 30.6

261 mm,  $sd = 6.4$  mm; Figure 3C).

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

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

#### 270 *Model analysis*

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

278 In a declining population with limited local retention and  $\lambda < 1$ , the stable size and age  
279 distributions from the age- and size-structured model were unimodal and skewed to larger sizes  
280 and older ages (Figure 4D, E). Most individuals in the population were between 150-250 mm and  
281  $\geq 10$  years of age. When  $\lambda \approx 1$ , the stable size distribution shifted toward smaller sizes and  
282 became bimodal, with peaks at approximately 40 mm and 200 mm. Individuals were distributed

283 roughly equally across all age classes. In a growing population with high local retention and  
284  $\lambda > 1$ , the stable size distribution was nearly unimodal and skewed to smaller sizes. Most  
285 individuals were approximately 40 mm and  $< 4$  years old. The slightly smaller peak to the right  
286 of the primary mode was likely due to the ample numbers of oysters in the second age class.

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

292 The survival of younger oysters had a higher elasticity than that of older oysters in the age- and  
293 size-structured model, with this difference becoming more pronounced with high local retention  
294 and  $\lambda > 1$  (Figure 5A). Across sizes, survival of the smallest and the largest oysters had the  
295 highest elasticity (Figure 5B), while only changes in the fecundity of oysters approximately  
296 150-250 mm had an impact on  $\lambda$  (Figure 5E). However, the fecundity of older individuals had a  
297 higher elasticity than that of younger oysters (Figure 5D). As local retention increased and  $\lambda$   
298 increased from 0.5 to 1.5, the fecundity of the younger ages became more important. Relative  
299 changes in growth and survival across all ages and sizes had a greater impact on  $\lambda$  than changes  
300 in fecundity (Figure 5).

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



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

## 315 DISCUSSION

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

323 For the age- and size-structured model, most individuals were large and old in declining  
324 populations, whereas most individuals were small and young in populations with positive  
325 population growth. Intuitively, in declining populations with low local retention, few juveniles are  
326 added to the population. As such, size distributions are skewed towards the older, larger sizes.  
327 Alternatively, for populations with high local retention leading to positive growth, there is a  
328 substantial influx of small juveniles each year. This leads to the right-skewed stable size and age

329 distributions when  $\lambda > 1$ . Finally, the joint age- and size-structure was required to detect the  
330 importance, measured by elasticity, of both small and large individuals to population growth.  
331 With the size-only model, elasticity analysis indicated that survival of the smaller individuals was  
332 most important to population growth.

333 The differences in results between the size-only model and the age- and size-structured model  
334 likely arose due to the differences in individual growth rate at large sizes. In the size-only model,  
335 individual growth rate continued to increase as individuals grew, rather than declining to no  
336 growth, as with the age- and size-structured model. Biologically, continued increases in  
337 individual growth rate as size increases makes little sense for organisms such as oysters  
338 characterized by indeterminate growth. Moreover, in the size-only model there was no maximum  
339 age at which all individuals die. When local retention was low, this led to a majority of  
340 individuals growing beyond the set maximum size and entering the discrete size class of sizes  
341  $> 300$  mm. The accumulation of individuals in that size class was not evident in the age- and  
342 size-structured model.

343 Model results from the age- and size-structured model are supported by population patterns  
344 observed in wild *Crassostrea spp.* populations. For example, in three *C. gigas* populations along  
345 the west European coast (Cardoso et al., 2007), the distribution of sizes within each age class  
346 matches that predicted by the model. In the Lower Saxony Wadden Sea, Germany, populations of  
347 *C. gigas* experiencing significant increases in population size have size distributions characterized  
348 by a major peak in the smaller ( $> 55$  mm) sizes, with some populations also exhibiting a smaller  
349 peak in size ranges between 55 – 100 mm (Schmidt et al., 2008). These size distributions are  
350 fairly consistent across the three years of the study, and match IPM predictions for populations  
351 experiencing positive population growth. Other populations of *C. gigas* in the North Wadden

352 along the coast of Denmark and Germany also exhibit right skewed distributions when population  
353 densities are increasing (Diederich et al., 2005). In these populations, however, size distribution  
354 are more variable over the ten years of the study due to inconsistent recruitment. In upper  
355 Chesapeake Bay, where recruitment is limited, *C. virginica* populations outplanted as juveniles  
356 become dominated by large, old oysters after 2-4 years due to extremely low recruitment in the  
357 years subsequent to the outplant (Paynter et al., 2010). These populations eventually go locally  
358 extinct without further transplants of young juveniles. In lower Chesapeake Bay, where  
359 recruitment is not limiting, persisting populations of *C. virginica* with multiple year classes are  
360 characterized by two major peaks, one for younger, smaller oysters up to 2 years old, and a  
361 second one of larger oysters ranging in age from 3-6 years old (Schulte et al., 2009; Lipcius et al.,  
362 2015). This pattern was also observed in *C. virginia* populations located in no-take reserves in  
363 North Carolina where recruitment was not limiting (Puckett and Eggleston, 2012, 2016).

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

373 In a recent review, Baggett et al. (2015) proposed size-frequency distributions as a “universal  
374 metric” for monitoring oyster restoration success. Our results support this proposal, and indicate

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

390 To assess restoration success, it is necessary to monitor changes in the size distribution of a  
391 population over time to differentiate between stable population patterns, and transient dynamics  
392 or patterns that emerge as a result of external recruitment (e.g. Diederich et al., 2005). Model  
393 results showed that, in a closed population started with a few small, young individuals, patterns in  
394 population size structure approached the stable distribution in as little as 5 years if the population  
395 was doing well ( $\lambda > 1$ ). However, model simulations required 10-15 years to distinguish between  
396 stable ( $\lambda \approx 1$ ) and declining ( $\lambda < 1$ ) populations (Appendix S5). Post-restoration is often  
397 characterized by distributions skewed towards small individuals. Our results indicate that, in a

398 closed population, subsequent monitoring over at least 5 years will inform if the distribution  
399 remains skewed toward small individuals, indicating possible population persistence, or becomes  
400 skewed toward larger individuals, indicating insufficient local retention and necessitating  
401 additional intervention. However, it is important to recognize that if the population is open, size  
402 distributions could be misleading, as even a sink population could exhibit a bimodal distribution  
403 given sufficient amounts of external recruitment. If this is the case, then additional data is needed  
404 to assess persistence of local populations, as well as the entire metapopulation.

405 Once there is information about whether a population is increasing or decreasing, one must then  
406 understand which individuals are most important to the growth of that population, and on which  
407 ages or sizes efforts should focus to have the greatest positive impact on the population growth  
408 rate. Patterns in elasticity can be used to inform these decisions. Our results indicate that, for the  
409 modeled population of *C. gigas*, increasing the survival of both small (< 50 mm) and very large  
410 (> 175 mm) oysters had the greatest impact on  $\lambda$ . This suggests several strategies to assist  
411 protected or harvested oyster populations. For example, by enhancing the abundance of  
412 broodstock (large oysters) in source habitats (*sensu* Lipcius et al., 2011; Puckett and Eggleston,  
413 2016), one could achieve the dual objective of increasing abundance of very small and very large  
414 oysters, since in subsequent years the offspring of the broodstock would recruit throughout the  
415 metapopulation and consequently increase recruitment of young, small oysters (Lipcius et al.,  
416 2008, 2015). Additionally, instead of only establishing a minimum size limit to protect small and  
417 intermediate sizes, as is often done, our results suggest that an additional maximum size limit to  
418 harvest would be beneficial.

419 Finally, our results show that growth kernels that restrict growth to be positive between years  
420 produced a better fit relative to more commonly used growth kernels allowing for reduction in

421 size with age. Many sessile marine organisms, such as oysters, grow by forming a calcified,  
422 protective shell. As such, fitting growth kernels by performing a standard least squares linear  
423 regression of size at time  $t + 1$  against size at time  $t$  is not appropriate, as it allows for organisms  
424 to decrease in size between time steps. This indicates the importance of developing appropriate  
425 models of individual growth for the focal organism.

#### 426 *Limitations and challenges*

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

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

444 accurate, realistic results, such as examining sensitivities of key response variables to  
445 sub-sampling of the collected data.

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

450 Another challenge of applying IPMs to marine systems is in obtaining an accurate estimate of  
451 recruitment. This parameter can be difficult to estimate, particularly for broadcast spawners, and  
452 can display a high degree of spatial and temporal heterogeneity (Cowen and Sponaugle, 2009).  
453 However, even when this parameter is unknown or highly uncertain, our results show that  
454 investigating patterns in population structure over a range of recruitment scenarios can provide  
455 insight into the current state (e.g., decreasing, stable, increasing) of a population. Our model  
456 assumes a closed population, whereby recruitment occurs via local retention of larvae and not  
457 from immigration via connectivity from external larval sources. This assumption is reasonable  
458 when local retention is high relative to connectivity because recruitment is driven by local  
459 reproduction (Figueira, 2009; Carson et al., 2011; Puckett and Eggleston, 2016). However, when  
460 local retention is low relative to external recruitment, accounting for this external recruitment is  
461 important as it can affect size and age distributions, as well as management strategies (Yau et al.,  
462 2014). Acquisition of this necessary data, which likely involves temporal variability in  
463 recruitment, and incorporating these features in our models, is a key challenge for the future.

464 Finally, additional factors that are relevant to oyster populations could be incorporated into the  
465 IPM, including size-specific susceptibility to disease, size-specific harvest and size limits, and  
466 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.

## ACKNOWLEDGMENTS

Support for J.L. Moore was provided by an NSF Graduate Research Fellowship, award number DGE-0940903, and an NSF GK-12 Fellowship under DGE grant #0841297 to S.L. Williams and B. Ludaescher. Support for R.N. Lipcius was provided by NSF award DMS-1313093 and NOAA Chesapeake Bay Office award NA13NMF4570205. Support for B. Puckett was provided by NSF award OCE 1155628 and NC Sea Grant award 14-HCE-9. Support for S.J. Schreiber and J.L. Moore was provided by NSF Grants DMS-1022639 and DMS-1313418. *Crassostrea gigas* growth and mortality data were provided by David Stick and Chris Langdon at the Hatfield Marine Science Center, in concert with the Oregon State University Molluscan Broodstock Program.



## Literature Cited

- 487
- 488 D Abele, T Brey, and E Philipp. Bivalve models of aging and the determination of molluscan  
489 lifespans. *Experimental Gerontology*, 44:307–315, 2009.
- 490 L Airoidi and MW Beck. Loss, status and trends for coastal marine habitats of Europe.  
491 *Oceanography and Marine Biology: An Annual Review*, 45:345–405, 2007.
- 492 DR Anderson. *Model based inference in the life sciences: a primer on evidence*. Springer  
493 Science & Business Media, 2007.
- 494 MJ Anderson and SD Connell. Predation by fish on intertidal oysters. *Marine Ecology Progress  
495 Series*, 187:203–211, 1999.
- 496 RC Babcock. Comparative demography of three species of scleractinian corals using age- and  
497 size-dependent classifications. *Ecological Monographs*, 61(3):225–244, 1991.
- 498 LP Baggett, SP Powers, R Brumbaugh, LD Coen, B DeAngelis, J Greene, B Hancock, and  
499 S Morlock. *Oyster habitat restoration monitoring and assessment handbook*. The Nature  
500 Conservancy, 2014.
- 501 LP Baggett, SP Powers, RD Brumbaugh, LD Coen, BM DeAngelis, JK Greene, BT Hancock,  
502 SM Morlock, BL Allen, DL Breitburg, D Bushek, JH Grabowski, RE Grizzle, ED Grosholz,  
503 MK La Peyre, MW Luckenbach, KA McGraw, MF Piehler, SR Westby, and PSE  
504 zu Ermgassen. Guidelines for evaluating performance of oyster habitat restoration. *Restoration  
505 Ecology*, 2015. doi: 10.1111/rec.12262.
- 506 BC Baghurst and JG Mitchell. Sex-specific growth and condition of the Pacific oyster  
507 (*Crassostrea gigas* Thunberg). *Aquaculture Research*, 33:1253–1263, 2002.

508 MW Beck, RD Brumbaugh, L Airoidi, A Carranza, LD Coen, C Crawford, O Defeo, GJ Edgar,  
509 B Hancock, MC Kay, S Hunter, MW Luckenbach, CL Toropova, and GG Zhang. Oyster reefs  
510 at risk and recommendations for conservation, restoration, and management. *BioScience*, 61  
511 (2):107–116, 2011.

512 SR Beissinger and MI Westphal. On the use of demographic models of population viability in  
513 endangered species management. *The Journal of Wildlife Management*, 62(3):821–841, 1998.

514 ON Bjornstad, RM Nisbet, and J-M Fromentin. Trends and cohort resonant effects in  
515 age-structured populations. *Journal of Animal Ecology*, 73(6):1157–1167, 2004.

516 Ben Bolker and R Development Core Team. *bbmle: Tools for general maximum likelihood*  
517 *estimation*, 2014. URL <https://CRAN.R-project.org/package=bbmle>. R package version  
518 1.0.17.

519 LW Botsford, MD Holland, JC Field, and A Hastings. Cohort resonance: a significant component  
520 of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of*  
521 *Marine Science*, 71(8):2158–2170, 2014.

522 JF Bruno, SP Ellner, I Vu, K Kim, and CD Harvell. Impacts of aspergillosis on sea fan coral  
523 demography: modeling a moving target. *Ecological Monographs*, 81(1):123–139, 2011.

524 NE Buroker. Sexuality with respect to shell length and group size in the Japanese oyster  
525 *Crassostrea gigas*. *Malacologia*, 23(2):271–279, 1983.

526 JF Cardoso, D Langlet, JF Loff, AR Martins, JI Witte, PT Santos, and HW van der Veer. Spatial  
527 variability in growth and reproduction of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793)  
528 along the west European coast. *Journal of Sea Research*, 57(4):303–315, 2007.

529 JF Cardoso, N Peralta, JP Machado, and HW van der Veer. Growth and reproductive investment  
530 of introduced pacific oysters *Crassostrea gigas* in southern european waters. *Estuarine, Coastal  
531 and Shelf Science*, 118:24–30, 2013.

532 RB Carnegie and EM Burreson. Declining impact of an introduced pathogen: *Haplosporidium*  
533 *nelsoni* in the oyster *Crassostrea virginica* in Chesapeake Bay. *Marine Ecology Progress  
534 Series*, 432:1–15, 2011.

535 HS Carson, GS Cook, PC Lopez-Duarte, and LA Levin. Evaluating the importance of  
536 demographic connectivity in a marine metapopulation. *Ecology*, 92:1972–1984, 2011.

537 H Caswell. *Matrix Population Models*. Sinauer Associates, Inc., 2 edition, 2006.

538 K-S Choi, DH Lewis, EN Powell, and SM Ray. Quantitative measurement of reproductive output  
539 in the American oyster, *Crassostrea virginica* (Gmelin), using an enzyme-linked  
540 immunosorbent assay (ELISA). *Aquaculture and Fisheries Management*, 24:299–322, 1993.

541 LD Coen, RD Brumbaugh, D Bushek, R Grizzle, MW Luckenbach, MH Posey, SP Powers, and  
542 SG Tolley. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*,  
543 341:303–307, 2007.

544 T Coulson. Integral projections models, their construction and use in posing hypotheses in  
545 ecology. *Oikos*, 121(9):1337–1350, 2012.

546 RK Cowen and S Sponaugle. Larval dispersal and marine population connectivity. *Annual  
547 Review of Marine Science*, 1(1):443–466, 2009.

548 DT Crouse, LB Crowder, H Caswell, N Oct, and T Crouse. A stage-based population model for  
549 loggerhead sea turtles and implications for conservation. *Ecology*, 68(5):1412–1423, 1987.

550 S Diederich, G Nehls, JEE van Beusekom, and K Reise. Introduced Pacific oysters (*Crassostrea*  
551 *gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgoland*  
552 *Marine Research*, 59:97–106, 2005.

553 SE Dudas, JF Dower, and BR Anholt. Invasion dynamics of the varnish clam (*Nuttallia*  
554 *obscurata*): a matrix demographic modeling approach. *Ecology*, 88(8):2084–2093, 2007.

555 MR Easterling, SP Ellner, and PM Dixon. Size-specific sensitivity: applying a new structured  
556 population model. *Ecology*, 81(3):694–708, 2000.

557 PJ Edmunds, SC Burgess, HM Putnam, ML Baskett, L Bramanti, NS Fabina, X Han, MP Lesser,  
558 JS Madin, CB Wall, DM Yost, and RD Gates. Evaluating the causal basis of ecological success  
559 within the scleractinia: an integral projection model approach. *Marine Biology*, 161(12):  
560 2719–2734, 2014.

561 SP Ellner and M Rees. Integral projection models for species with complex demography. *The*  
562 *American Naturalist*, 167(3):410–428, 2006.

563 WF Figueira. Connectivity or demography: defining sources and sinks in coral reef fish  
564 metapopulations. *Ecological Modelling*, 220:1126–1137, 2009.

565 NJ Gotelli. Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology*,  
566 72(2):457–467, 1991.

567 JH Grabowski, RD Brumbaugh, RF Conrad, G Andrew, JJ Opaluch, CH Peterson, MF Piehler,  
568 SP Powers, and AR Smyth. Economic valuation of ecosystem services provided by oyster  
569 reefs. *BioScience*, 62(10):900–909, 2012.

570 TP Hughes. Population dynamics based on individual size rather than age: a general model with a  
571 reef coral example. *The American Naturalist*, 123(6):778–795, 1984.

572 TP Hughes and JH Connell. Dynamics based on size or age? a reef-coral analysis. *The American*  
573 *Naturalist*, 129(6):818–829, 1987.

574 AV Ivanina, IM Sokolova, and AA Sukhotin. Oxidative stress and expression of chaperones in  
575 aging mollusks. *Comparative Biochemistry and Physiology, Part B*, 150:35–61, 2008.

576 S-G Kang, K-W Choi, AA Bulgakov, Y Kim, and S-Y Kim. Enzyme-linked immunosorbent  
577 assay (ELISA) used in quantification of reproductive output in the pacific oyster, *Crassostrea*  
578 *gigas*, in Korea. *Journal of Experimental Marine Biology and Ecology*, 282:1–21, 2003.

579 VS Kennedy, RIE Newell, and AF Eble. *The Eastern Oyster*. University of Maryland Sea Grant  
580 Publications, 2 edition, 1996.

581 VS Kennedy, DL Breitburg, MC Christman, MW Luckenbach, K Paynter, J Kramer, KG Sellner,  
582 J Dew-Baxter, C Keller, and R Mann. Lessons learned from efforts to restore oyster population  
583 in Virginia and Maryland. *Journal of Shellfish Research*, 30:1–13, 2011.

584 I Laing, P Walker, and F Areal. Return of the native—is European oyster (*Ostrea edulis*) stock  
585 restoration in the UK feasible? *Aquatic Living Resources*, 19(03):283–287, 2006.

586 JE Lannan, Robinson A, and WP Breese. Broodstock management of *Crassostrea gigas* II:  
587 Broodstock conditioning to maximize larval survival. *Aquaculture*, 21:337–345, 1980.

588 R Law and MT Edley. Dynamics of populations with age- and size-dependent vital rates.  
589 *Ecology*, 71(5):1863–1870, 1990.

590 DR Levitan. Influence of body size and population density on fertilization success and  
591 reproductive output in a free-spawning invertebrate. *Biological Bulletin*, 181(2):261–268, 1991.

592 RN Lipcius, DB Eggleston, SJ Schreiber, RD Seitz, J Shen, M Sisson, WT Stockhausen, and  
593 HV Wang. Importance of metapopulation connectivity to restocking and restoration of marine  
594 species. *Reviews in Fisheries Science*, 16(1-3):101–110, 2008.

595 RN Lipcius, GM Ralph, J Liu, V Hill, AT Morzillo, JA Wiens, et al. Evidence of source-sink  
596 dynamics in marine and estuarine species. *Sources, sinks and sustainability*, pages 361–381,  
597 2011.

598 RN Lipcius, RP Burke, DN McCulloch, SJ Schreiber, DM Schulte, RD Seitz, and J Shen.  
599 Overcoming restoration paradigms: value of the historical record and metapopulation dynamics  
600 in native oyster restoration. *Frontiers in Marine Science*, 2:65, 2015.

601 K Lorenzen. Toward a new paradigm for growth modeling in fisheries stock assessments:  
602 Embracing plasticity and its consequences. *Fisheries Research*, 2016. In Press.

603 L Luo, C Ke, X Guo, B Shi, and M Huang. Metal accumulation and differentially expressed  
604 proteins in gill of oyster (*Crassostrea hongkongensis*) exposed to long-term heavy  
605 metal-contaminated estuary. *Fish & Shellfish Immunology*, 38:318–329, 2014.

606 NJ Mackay, RJ Williams, JL Kacprzac, MN Kazacos, AJ Collins, and EH Auty. Heavy metals in  
607 cultivated oysters (*Crassostrea commercialis* = *Saccostrea cucullata*) from the estuaries of  
608 New South Wales. *Australian Journal of Marine & Freshwater Research*, 26:31–46, 1975.

609 JS Madin, TP Hughes, and SR Connolly. Calcification, storm damage and population resilience  
610 of tabular corals under climate change. *PLOS ONE*, 7(10):e46637, 2012.

611 C Merow, JP Dahlgren, JE Metcalf, DZ Childs, MEK Evans, E Jongejans, S Record, M Rees,  
612 R Salguero-Gomez, and SM McMahon. Advancing population ecology with integral  
613 projection models: a practical guide. *Methods in Ecology and Evolution*, 5:99–110, 2014.

614 EW North, DM King, J Xu, RR Hood, RIE Newell, K Paynter, ML Kellogg, MK Liddel, and  
615 DF Boesch. Linking optimization and ecological models in a decision support tool for oyster  
616 restoration and management. *Ecological Applications*, 20(3):851–866, 2010.

617 KT Paynter, V Politano, HA Lane, SM Allen, and D Meritt. Growth rates and prevalence of  
618 *Perkinsus marinus* in restored oyster population in Maryland. *Journal of Shellfish Research*, 29  
619 (2):309–317, 2010.

620 SP Powers, CH Peterson, JH Grabowski, HS Lenihan, et al. Success of constructed oyster reefs in  
621 no-harvest sanctuaries: implications for restoration. *Marine Ecology Progress Series*, 389:  
622 159–170, 2009.

623 BJ Puckett and DB Eggleston. Oyster demographics in a network of no-take reserves:  
624 recruitment, growth, survival, and density dependence. *Marine and Coastal Fisheries*, 4(1):  
625 605–627, 2012.

626 BJ Puckett and DB Eggleston. Metapopulation dynamics guide marine reserve design:  
627 importance of connectivity, demographics, and stock enhancement. In Press, 2016.

628 AE Punt, T Huang, and MN Maunder. Review of integrated size-structured models for stock  
629 assessment of hard-to-age crustacean and mollusc species. *ICES Journal of Marine Science:*  
630 *Journal du Conseil*, 70(1):16–33, 2013.

631 R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for  
632 Statistical Computing, Vienna, Austria, 2015. URL <https://www.R-project.org/>.

- 633 M Rees, DZ Childs, and SP Ellner. Building integral projection models: a user's guide. *Journal*  
634 *of Animal Ecology*, 83:528–545, 2014.
- 635 JS Ren, ID Marsden, AH Ross, and DR Schiel. Seasonal variation in the reproductive activity and  
636 biochemical composition of the Pacific oyster (*Crassostrea gigas*). *New Zealand Journal of*  
637 *Marine and Freshwater Research*, 37:171–182, 2003.
- 638 BJ Rothschild, JS Ault, P Gouilletquer, and M Heral. Decline of the Chesapeake Bay oyster  
639 population: a century of habitat destruction and overfishing. *Marine Ecology Progress Series*,  
640 111:29–39, 1994.
- 641 A Schmidt, Wehrmann A, and Dittmann S. Population dynamics of the invasive Pacific oyster  
642 *Crassostrea gigas* during the early stages of an outbreak in the Wadden Sea (Germany).  
643 *Helgoland Marine Research*, 62:367–376, 2008.
- 644 DM Schulte, RP Burke, and RN Lipcius. Unprecedented restoration of a native oyster  
645 metapopulation. *Science*, 325:1124–1128, 2009.
- 646 DA Stick. *Identification of optimal broodstock for Pacific Northwest oysters*. PhD thesis, Oregon  
647 State University, 2011.
- 648 J Taylor and D Bushek. Intertidal oyster reefs can persist and function in a temperate north  
649 american atlantic estuary. *Marine Ecology Press Series*, 361:301, 2008.
- 650 JL Williams, TEX Miller, and SP Ellner. Avoiding unintentional eviction from integral projection  
651 models. *Ecology*, 93(9):2008–2014, 2012.
- 652 AJ Yau, HS Lenihan, and BE Kendall. Fishery management priorities vary with self-recruitment  
653 in sedentary marine populations. *Ecological Applications*, 24(6):1490–1504, 2014.



654 PSE Zu Ermgassen, MD Spalding, B Blake, LD Coen, B Dumbauld, S Geiger, JH Grabowski,  
655 R Grizzle, M Luckenbach, K McGraw, W Rodney, JL Ruesink, SP Powers, and R Brumbaugh.  
656 Historical ecology with real numbers: past and present extent and biomass of an imperilled  
657 estuarine habitat. *Proceedings of the Royal Society B: Biological Sciences*, 279(1742):  
658 3393–3400, 2012.

Author Manuscript

DESCRIPTION OF SUPPORTING INFORMATION

659

660 Appendix S1. **Maximum age and size of individuals.** Includes a figure showing the results of  
661 individual growth trajectories using both lognormal growth fitting and normal growth fitting.

662 Appendix S2. **Sensitivity of model output to maximum age and size.** Includes figures showing  
663 differences in reproductive values, stable age and size distributions, and elasticities for different  
664 values of maximum size and maximum age.

665 Appendix S3. **Model comparisons for growth and survival functions.** Includes AICc  
666 comparisons of different growth and survival models.

667 Appendix S4. **Size-only demographic functions.** Includes a figure and table showing statistical  
668 fits used for the size-only model.

669 Appendix S5. **Time to stable size distribution.** Includes figures showing how long the age- and  
670 size-structured IPM, when started with a single individual at age 1, take to reach the stable size  
671 distribution.

672 Metadata S1. **Description of data and code.** Provides a brief description of all code and data  
673 required to run the simulations and generate the figures in the manuscript.

Table 1: **Age- and size-dependent demographic functions.** Statistical models and parameter estimates for age- and size-structured models used to describe *Crassostrea gigas* demography.

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	$\text{logit}(s) = 4.003(0.395) - 0.016(0.010)a - 1.625(0.223)x + 0.018(0.004)ax$
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
Recruitment success	$\lambda = 0.506: p = 2.44 \times 10^{-15}$ $\lambda = 1.003: p = 1.00 \times 10^{-11}$ $\lambda = 1.499: p = 3.97 \times 10^{-10}$

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.

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

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

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

697 **Figure 4. IPM model output.** Model output for  $\lambda = 0.5$  (black line and points),  $\lambda \approx 1.0$  (dark

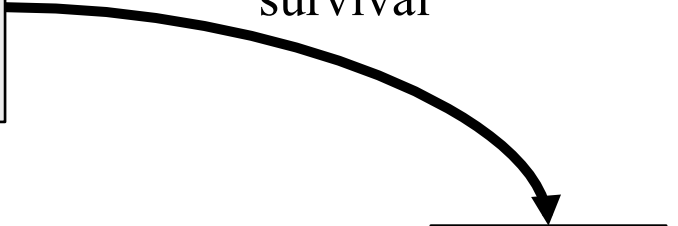
698 gray line and points), and  $\lambda = 1.5$  (light gray line and points). A) Age-specific reproductive  
699 values for the age- and size-structured model. B) Size-specific reproductive values for the age-  
700 and size-structured model. C) Reproductive values for the size-only model. For (A)-(C),  
701 reproductive values for each  $\lambda$  are scaled such that the sum of all values = 1. D) Stable age  
702 distributions for the age- and size-structured model. E) Stable size distributions for the age- and  
703 size-structured model. F) Stable size distributions for the size-only model. For the size-only  
704 model, when  $\lambda \approx 1$ , and  $\lambda = 1.5$  approximately 62.17%, and 1.81%, respectively, of the  
705 population is contained in the discrete size class of individuals greater than 300 mm (not shown  
706 on graph). Additionally, for the size-only model it was not possible to simulate a population with  
707  $\lambda = 0.5$ . As such, only relationships for  $\lambda \approx 1$  and  $\lambda = 1.5$  are shown.

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

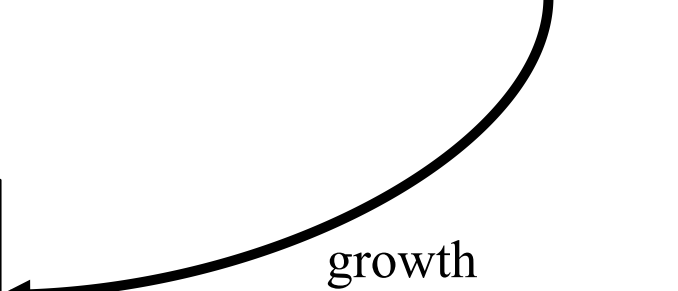
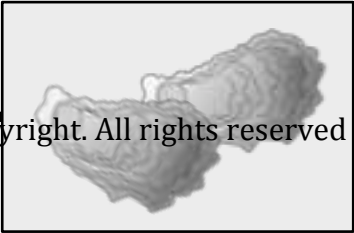
growth & survival of  
new recruits



survival

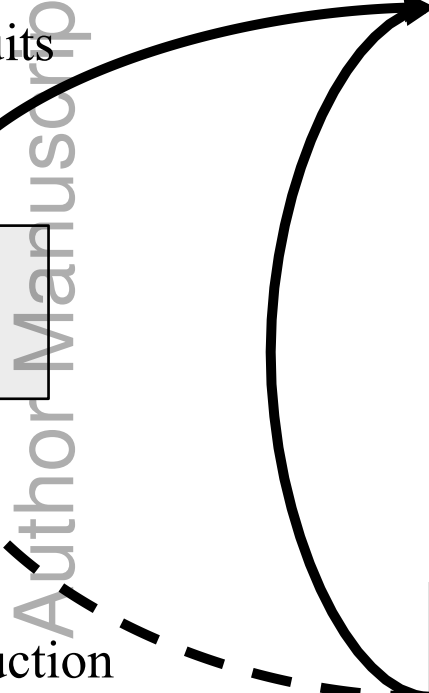
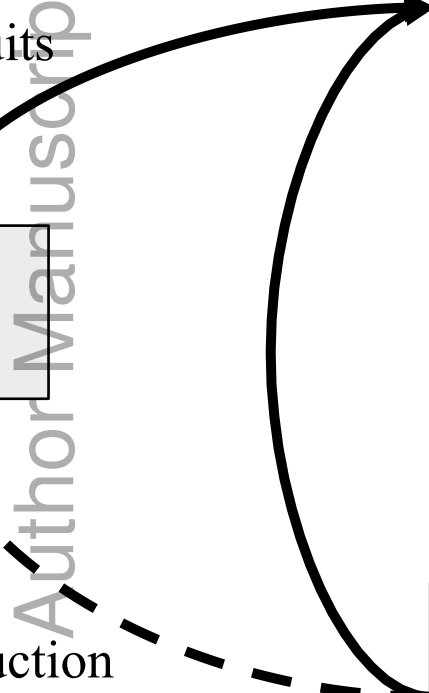


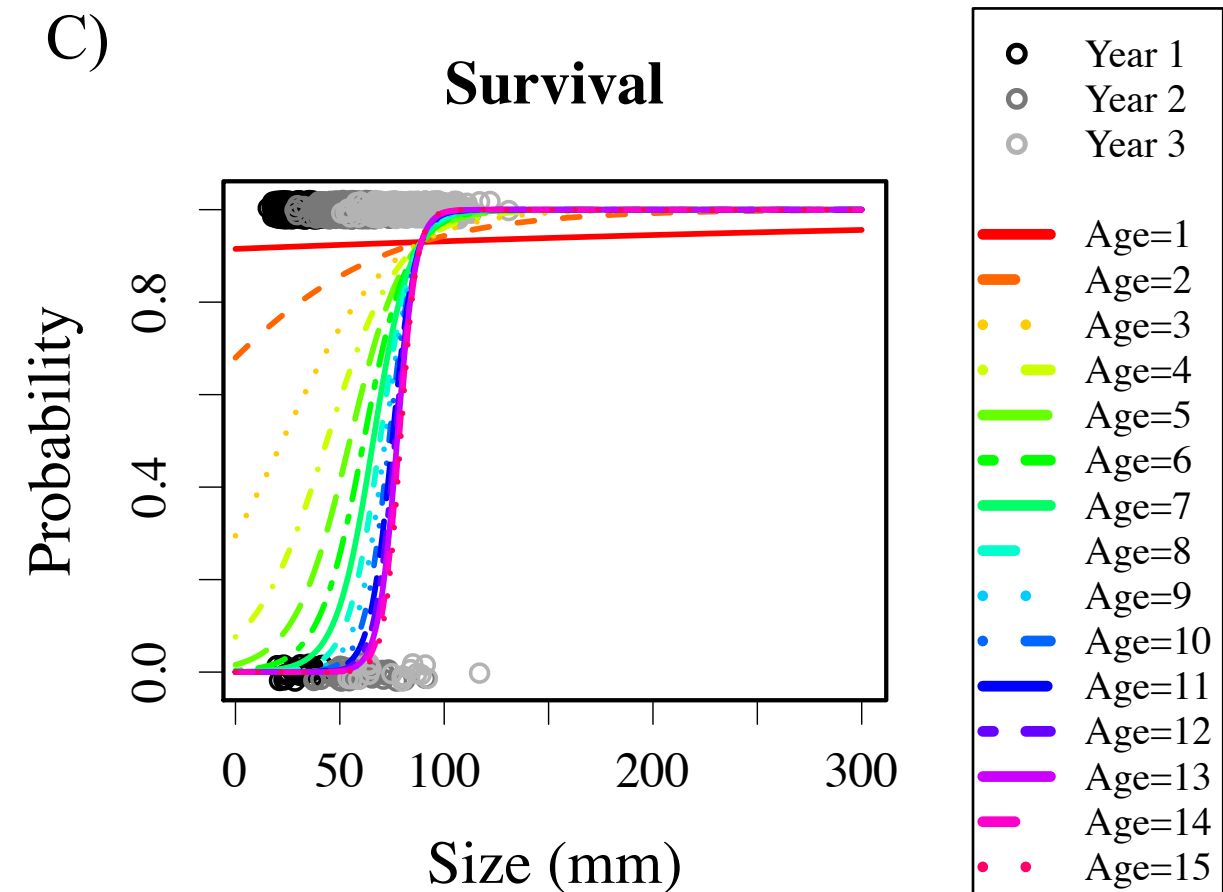
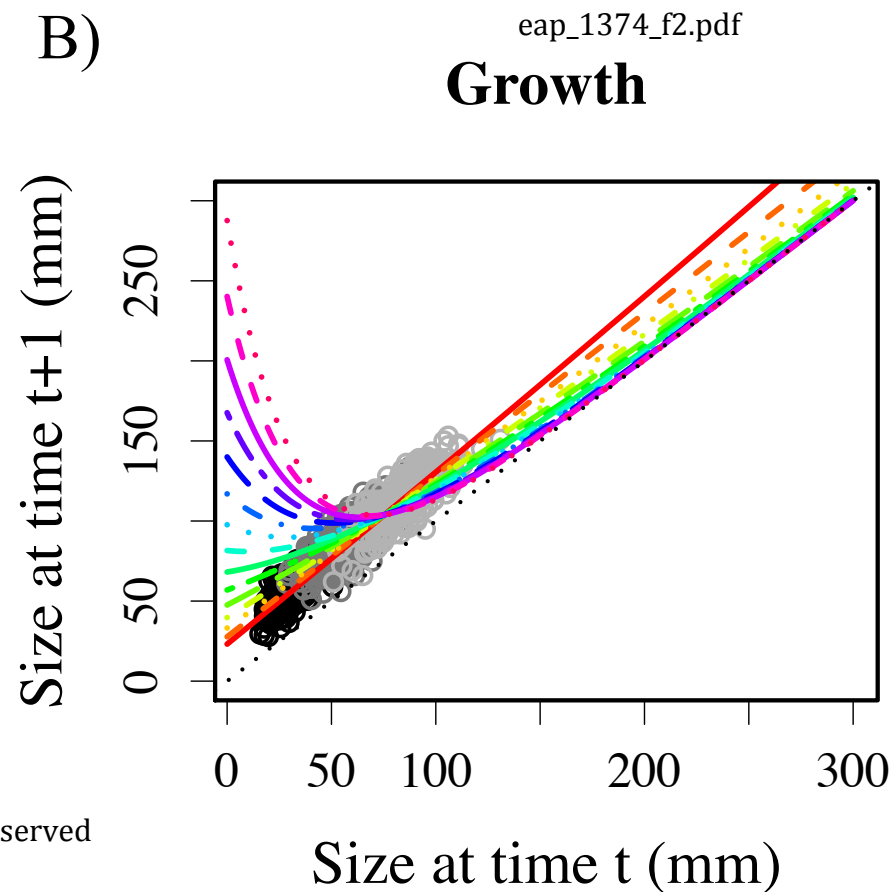
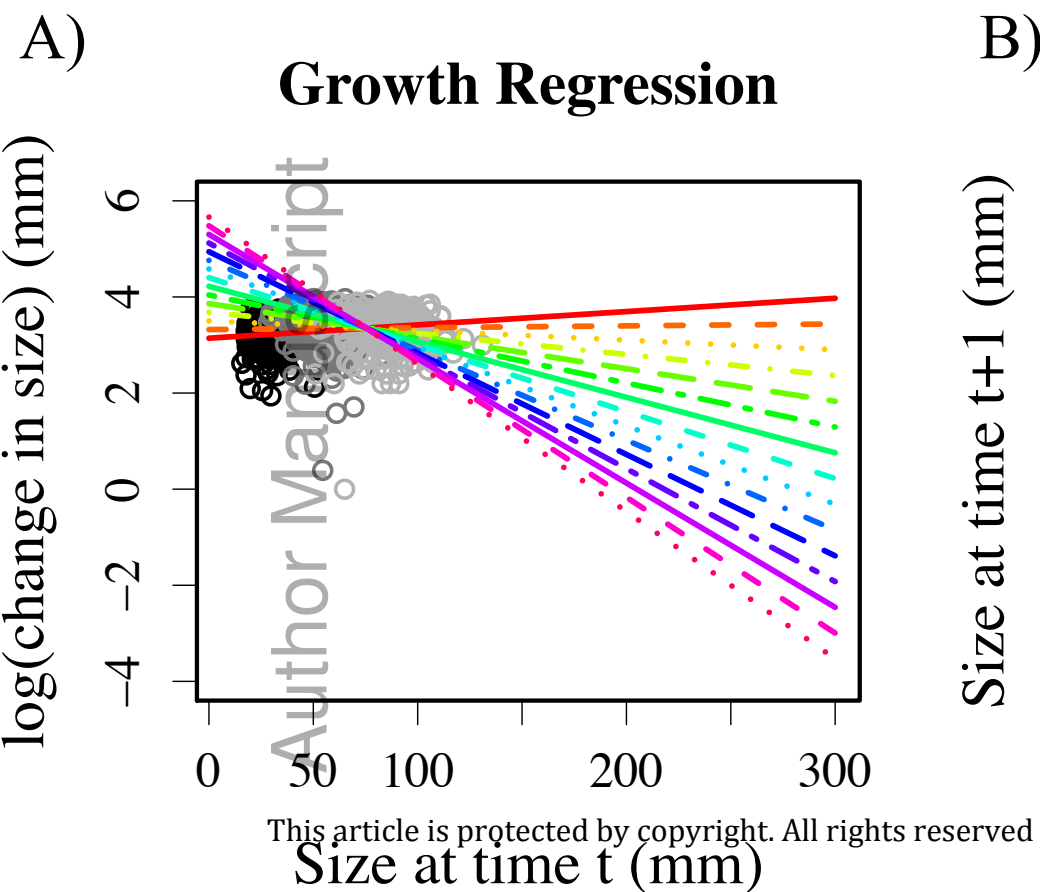
growth



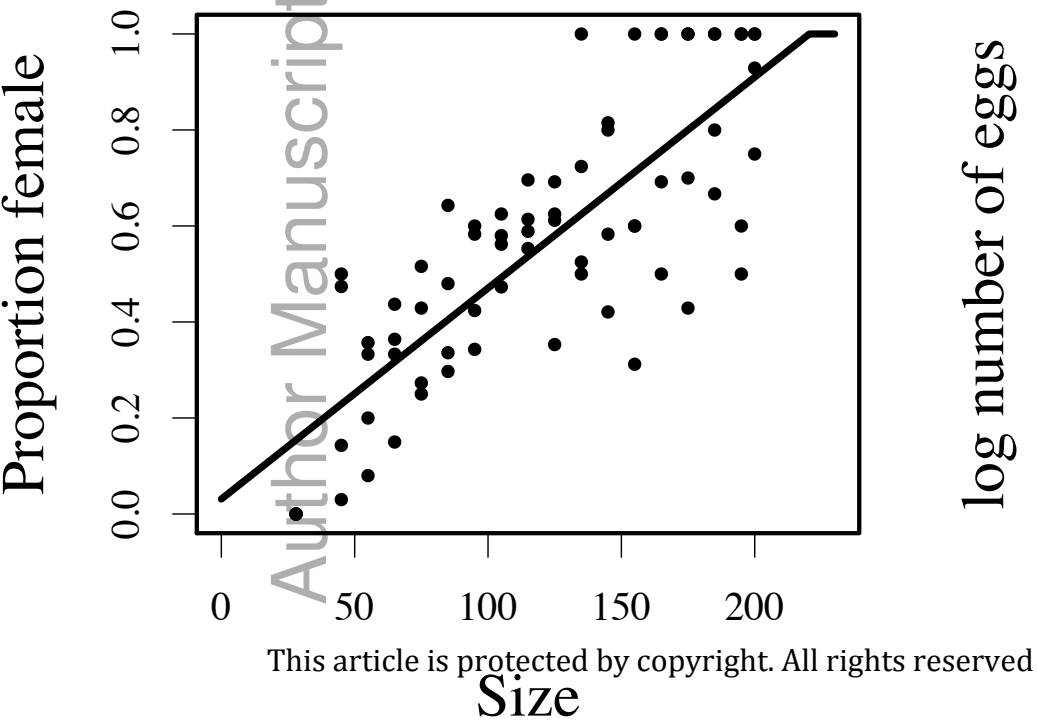
reproduction

This article is protected by copyright. All rights reserved

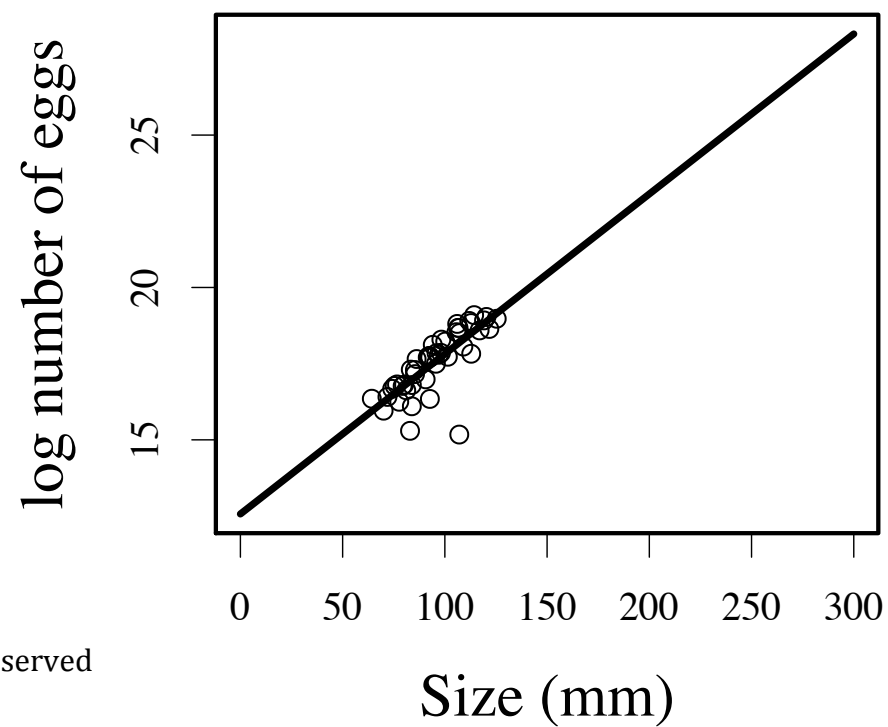




A)

**Sex Ratio**

B)

**Number of Offspring**

C)

**Offspring Size**