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Research Article

Stochastic modeling of eastern oyster (*Crassostrea virginica*) production in a Mexican tropical coastal lagoon using alternative stocking density management schemes

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ABSTRACT. A stochastic model was developed to analyze *Crassostrea virginica* production when cultivated at three stocking densities, defined as the area occupation (50, 75, and 100%) in Nestier-type trays, using juvenile oysters with an initial size (height) of 29.40 ± 0.18 mm. A 25-week grow-out was first conducted in the Rio Lagartos lagoon, showing that final oyster size was inversely related to density ($P < 0.05$), ranging from 61.87 mm (100% density) to 68.00 mm (50% density). At the same time, mortality was negligible (lower than 1.0%). The environmental conditions in the lagoon were stable, and the oyster growth rate positively correlated with water temperature and pH. Low pH was associated with slow oyster growth, possibly as an adverse effect of acidic conditions on the oyster shell formation. The model indicated that, for an initial 100,000 oyster population, the maximum production (oyster dozens) is obtained after 20 weeks (8310 at 50% density) and 25 weeks (8250 at 75%, and 6670 at 100% density). There was a 100% probability of oysters reaching a minimum commercial size (MCS) of 60.00 mm when using the 50 and 75% densities and 80.6% when using 100%. The model estimated that, for the maximum density, extending the grow-out up to 32 weeks would allow reaching MCS with 100% probability, although this should be experimentally confirmed. The random variability of oyster production in 50 and 75% densities was minimal, while at 100% density, it was extremely high. A sensitivity analysis indicated that for 50 and 75% densities, the main stochastic elements influencing production, are related to oyster mortality, while at 100% density, they are related to oyster growth.

Keywords: *Crassostrea virginica*; stochastic model; stocking density management; water quality

INTRODUCTION

Oysters of the genus *Crassostrea* are relevant for the global fishing and aquaculture industries (Cavaleiro et al. 2019). The eastern oyster, *C. virginica*, is one of the most cultivated bivalve species in the northwest Atlantic's shallow coastal lagoons and estuaries (Poirier et al. 2019, Thomas et al. 2019). The primary aquaculture producer of eastern oysters is the USA, with 159,175 t (Van der Schatte-Olivier et al. 2020).

A critical factor for oyster farming is stocking or rearing density (Tan et al. 2023). More intense competition for food and space between individual oysters can be expected when using high densities; thus, for a given initial oyster population, increasing density implies a trade-off between reducing the number of gears required for grow-out (i.e. reducing the corresponding investment and operating costs) at the expense of slowing oyster growth (Cubillo et al. 2012, Pérez-Camacho et al. 2013), and possible increasing population mortality (Zorita et al. 2021).

Some studies have been conducted to determine the effect of stocking density for *C. virginica* when reared under different conditions. Rheault & Rice (1996) eva-

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luated oyster growth by considering different stocking densities and degrees of food limitation. Bishop & Hooper (2005) compared the growth and mortality rates of *C. virginica* and *C. ariakensis* cultivated at high and low densities during the nursery stage. Grizzle et al. (2020) evaluated the interaction between stocking density and bag mesh size on oyster growth in New Hampshire, USA. Haché & Bardon-Albaret (2021) assessed the effect of stocking density on oyster growth and shell shape when grown in floating bags in New Brunswick, Canada.

This investigation presents the results obtained from developing a production model to evaluate the effects of stocking density on the growth and survival of *C. virginica* during the grow-out phase in a Mexican coastal lagoon. In addition, stochastic elements are incorporated into the model to simulate the random variability of oyster individual size and mortality. The correlations between growth parameters and water quality variables are also analyzed. In the revised literature, no antecedents have been used in stochastic mathematical models to analyze the influence of stocking density on *C. virginica* production.

MATERIALS AND METHODS

Grow-out trial

A 174-day (September 2021-March 2022) grow-out trial was conducted to evaluate the effect of stocking density on the growth and survival of the eastern oyster in the Río Lagartos coastal lagoon in the northeast of the Yucatán Peninsula, Mexico (Fig. 1). Previously to grow-out, a 123-day nursery stage was carried out in the same lagoon using 2.40 ± 0.20 mm oyster spat produced at Centro Ostrícola Tecnológico de Tabasco (COTET) until a height (i.e. the distance between the umbo and the tip of the distal margin of the shell, hereafter referred to as "height") of 29.4 ± 0.18 mm was reached. The grow-out stage consisted of raising the oysters from that initial size to a minimum commercial size (MCS) of 60.00 mm.

An off-bottom system consisting of modules of three rigid polypropylene (58×58×7 cm) Nestier-type trays (DM Plast, Jalisco, Mexico) tied to 30 m "long lines" was used for rearing the oysters. Two trays in each module served for rearing, while the third acted as a lid and a float. Three stocking densities were tested, corresponding to 50, 75, and 100% area occupation in the trays. The experimental design was completely randomized, using three replicates for each density. Density control was adjusted monthly by decreasing the oyster population in the trays and maintaining the specified area occupancy percentages. The trays with the oysters were exposed to desiccation (air exposure) for approximately 20 to 30 min and then cleaned with a stiff hand brush to remove fouling organisms.

Data collection and processing

Oyster and water quality sampling were conducted weekly. An analog caliper (Trooper CAL-6MP, accuracy 0.02 mm) was used to measure the height of 30 oysters randomly selected from each experimental module. Dead oysters (identified as empty shells or open oysters) were counted and removed from the modules. Water temperature (°C), salinity, dissolved oxygen (mg L^{-1}), pH, and total dissolved solids (mg L^{-1}) were recorded with a portable multiparameter (YSI Pro-Plus, Ohio, USA).

The daily growth rate of oysters was estimated as the difference between the height recorded in a given sampling and that recorded in the previous one, divided by the number of days between samplings. In addition, water quality values for successive samples were averaged to represent the prevailing conditions at each interval. An ANOVA was used to determine if there were differences in mean heights and daily growth rates among the experimental densities at the end of the grow-out trial. Previously, the normality of the data was analyzed using the Shapiro-Wilk test, and the homogeneity of variance was analyzed using Levene's test.

An ANOVA was also conducted to determine possible differences in final oyster survival among the densities. Before the ANOVA, survival percentages were transformed to Arcsine values. Statistica 6.0 (StatSoft, Inc. Tulsa, OK, USA) was used for ANOVAs, setting significance at $\alpha = 0.05$. Correlation analyses used Pearson's coefficient to determine associations between daily growth rates and water quality variables. The variables that yielded significant correlations were then used as growth rate predictors using multiple regression analyses. Statistica 6.0 (StatSoft, Inc. Tulsa, OK, USA) was used for correlation and regression analyses, setting significance at $\alpha = 0.05$.

Stochastic production model

The production model aimed to predict the number of dozen commercial oysters (i.e. 60 mm in height or higher) that could be produced considering the stocking density and the initial oyster population. The growth equation proposed by Serna-Gallo et al. (2014) was used to predict oyster height as a function of time (t):

$$h_t = H_0 + \left(H_f - H_0\right)\left[\frac{1 - k^t}{1 - k^c}\right] \quad (1)$$

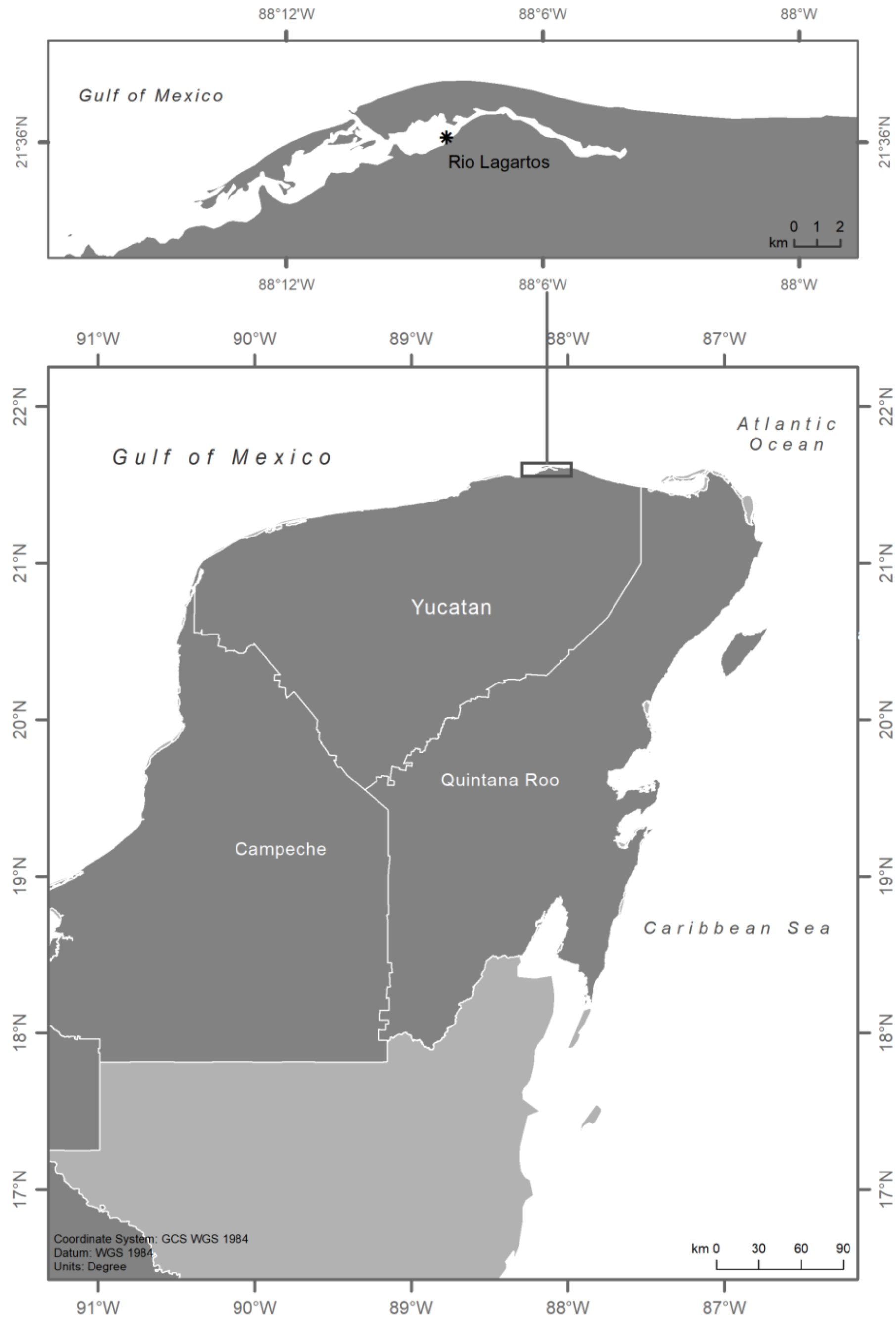

Figure 1. Location of Rio Lagartos tropical coastal lagoon in the state of Yucatan, Mexico. The grow-out site is indicated with an asterisk.

where h_t is the average shell height in t units of elapsed time, H_0 is the average initial height, Hf is the average final height, k is the rate at which the height changes from its initial value to its final value, and c is the harvesting time units.

There were two types of stochasticity sources potentially affecting h_t values. One is associated with the random variability in parameters H_f and k, which could vary among production cycles, and the second one is the variability that, for a given constant set of H_f and k values, h_t may show along the grow-out period. In other words, there is no reason to assume that, for a given set of H_f and k values, the oyster height calculated at different times of the rearing period should be precisely the same in every production cycle.

The first type of stochasticity was incorporated as follows. A nonlinear regression procedure was used to fit Equation 1 separately to data sets corresponding to the three replicates of each stocking density, thus resulting in nine deterministic estimates of H_f and k. Such estimates and linear regression were used to make the parameters dependent on stocking density (sd). Accordingly:

$$H_f = 72.27 - 0.112\ sd \quad (2)$$

$$k = 0.987 + 0.000028\ sd \quad (3)$$

The envelope method proposed by Vose (2000) was used to incorporate random variability in H_f and k. Accordingly, the residual errors of H_f and k values resulting from fitting Equations 2-3 (eH_f and ek) were used to predict their stochastic values (H_{fs} and k_s) as:

$$H_{fs} = H_f + eH_f \quad (4)$$

$$eH_f = \text{PERT}\ (-0.49, -0.07, 0.77) \quad (5)$$

$$k_s = k + ek \quad (6)$$

$$ek = \text{PERT}\ (-0.0011, 8.01\text{E-}05, 0.0008) \quad (7)$$

where the residual errors are calculated as PERT distributions defined by their minimum, most likely, and maximum values (within parentheses). The stochastic values of the growth parameters calculated with Equations 4 and 6 were then used in Equation 1 to predict height, thus incorporating the first source of stochasticity (h_{ts1}).

The envelope method was also used to incorporate the second type of stochasticity in h_t. Accordingly, the residual error values of h_t (eh_t) resulting from fitting Equation 1 to the replicate densities data sets were used to define their distribution as:

$$eh_t = \text{PERT}\ (-3.50, 3.50, 0.18) \quad (8)$$

Finally, the calculation of height incorporating the two sources of random variability ($ht_{s1,2}$) was accomplished according to:

$$ht_{s1,2} = h_{ts1} + eh_t \quad (9)$$

On the other hand, the percentage of surviving oysters during the rearing period (n_t) was calculated using the negative exponential equation:

$$n_t = N_0 exp^{(-zt)} \quad (10)$$

where N_0 is the initial percentage (100%), t is time, and z is the mortality rate, estimated using a nonlinear regression procedure for each density replicate. Accordingly, fitting Equation 1 resulted in nine deterministic z estimates.

Similar to h_t, two stochasticity sources were considered to affect n_t. One source was the random variability of z, and the second source was that, for a given z value, the survival percentages calculated for the different times of the rearing period are not precisely the same in every oyster production cycle.

A quadratic equation served to calculate z depending on the stocking density as follows:

$$z = -7.28\text{E-}05 + 2.32\text{E-}06\ sd - 1.49\text{E-}08\ sd^2 \quad (11)$$

The stochastic value of z (z_s) was then calculated using the envelope method, and a PERT distribution of the error residual z values (ez) was obtained from fitting Equation 12 to the nine z estimates.

Accordingly:

$$z_s = z + ez \quad (12)$$

$$ez = \text{PERT}\ (-6.39\text{E-}06, -2.61\text{E-}07, 7.43\text{E-}06) \quad (13)$$

The stochastic values of z in Equation 13 were then used in Equation 11 to predict survival, thus incorporating the first source of stochasticity (n_{ts1}).

The envelope method was used to incorporate the second n_t stochasticity source. Accordingly, the residual error values of n_t (en_t) resulting from fitting Equation 11 to survival data from each density replicate allowed defining their distribution as:

$$en_t = \text{PERT}\ (-0.108, -0.002, 0.071) \quad (14)$$

Finally, the calculation of survivors incorporating the two random variability sources ($n_{ts1,2}$) was carried out as follows:

$$n_{ts1,2} = n_{ts1} + en_t \quad (15)$$

Nonlinear and linear regression analyses were conducted using GraphPad Prism 10 (GraphPad Software, San Diego, California, USA) and Statistica 6.0 (StatSoft, Inc. Tulsa, OK, USA), rendering significant ($P < 0.05$). D'Agostino-Pearson and Shapiro-Wilk tests showed that the residuals were normally distributed. PERT distributions rather than normal distributions served to calculate residuals and limit their values to the minimum and maximum empirically determined with the experimental trial, thus avoiding extreme theoretical values that could be obtained using normal distributions. Oyster dozens were used as a practical unit to measure production because it is preferred for commercialization. They were calculated straightforwardly using $n_{ts1,2}$ from Equation 15 for the cases when $ht_{s1,2}$ in Equation 9 was equal to or greater than 60 mm.

The stochastic production model was implemented as a Monte Carlo simulation model, and the production was calculated for an initial population of 100,000 oysters for each density. A sensitivity analysis was conducted to determine the contribution of the different sources of stochasticity in the model to the random variation of oyster production. The Monte Carlo simulation and the sensitivity analysis were accomplished using @Risk 8.4 (Palisade, Ithaca, NY, USA).

RESULTS

The final height of oysters and their growth rate were significantly and inversely related to stocking density (P = 1.81E-06). The statistical result was the same for both variables because the growth rate is a function of final height, and the initial height and the grow-out period were identical for every stocking rate. On the other hand, the oyster survival rate was high and remained above 99% in all treatments (Table 1).

During grow-out, the average water temperature was 28.88 ± 0.79°C, ranging from 24.70 to 33.00°C. The mean salinity was 35.16 ± 0.24, ranging from 34.20 to 36.40. The mean dissolved oxygen was 4.87 ± 1.48 mg L^{-1} with a minimum of 4.10 mg L^{-1} and a maximum of 5.80 mg L^{-1}. The average pH was 8.27 ± 0.11, while the total dissolved solids was 34,580 ± 216 mg L^{-1} (Fig. 2). The correlation analysis between growth rates and water quality variables indicated a significant positive correlation between growth rates with temperature and pH. The equations that significantly relate the growth rate with both variables are shown in Table 2.

The growth model (Eq. 1) proposed by Serna-Gallo (2014) adequately fitted the oyster growth data at the three densities with significant results (P = 1.05E-14, P = 5.98 E-14, P = 1.82 E-06, respectively) (Fig. 3).

The results obtained with the stochastic production model showed that starting with field-nursed juveniles 29.40 ± 0.18 mm in height size, the use of the lowest density (50%) allows obtaining MCS (i.e. 60 mm) after 13 weeks, followed by a rapid increase in the number of dozens until week 19 when production stabilizes until the end of the fattening period (Fig. 4). When using the intermediate density (75%), the negative impact of increasing density on the growth rate of oysters results in MCS after 15 weeks and stabilization of dozens of oyster numbers after 23 weeks (Fig. 4). With 100% density, MCS are attained after 19 weeks; however, no stabilization phase in the number of dozens is observed by the end of the grow-out (Fig. 4). According to the model, the maximum number of dozens is obtained after 20 weeks (50% density) and 25 weeks (75 and 100% density).

The production model was used to predict, by interpolation, the potential results that could be obtained by stocking densities other than those used for the experimental trial (Fig. 5). The results indicate that marketable oyster production drastically diminishes for densities higher than 75% because the experimental grow-out duration (25 weeks) allows reaching MCS only a percentage of the times the grow-out is carried out. In contrast, using densities lower than 75% guarantees oysters reach the marketable size every time the grow-out is conducted, with optimum harvesting times lower than 25 weeks.

The production model was also used to explore, by extrapolation, whether the production could be improved by extending the growth-out duration up to 33 weeks for densities higher than 75% (Fig. 6). The results of such extrapolation showed that yields using 100% density could be increased from 6667 to 8315 (i.e. 25%) dozens by extending the rearing to 32 weeks when oysters reach MCS every time the grow-out is carried out. In the case of the 75% density, the extrapolation did not indicate that further production improvement could be expected by extending the grow-out beyond 25 weeks (Fig. 6).

The results of the Monte Carlo simulation indicated that, when using the 50% density, there is a 95% probability of producing between 8287 and 8331 dozen oysters after 20 weeks of grow-out, with an average production of 8311 dozen (Fig. 7a). For the 75% stocking density, there is a 95% probability of producing from 8229.5 to 8284 dozen oysters by the end of the grow-out (25 weeks), with an average production of 8257 dozen (Fig. 7b).

Using the highest density (100%) resulted in a 95% probability of either not producing at all or producing up to 8316 dozen, with a mean production of 6667 (Fig. 7c). There was a 19.4% probability of not producing because that was the percentage of the times the grow-out does not lead to reaching the MCS (Fig. 8).

Table 1. Mean values (± standard error) of final height, daily growth rate, and survival of *C. virginica* reared at different stocking densities. Values with different letters indicate significant differences.

Stocking density (% area occupation)	Final height (mm)	Daily growth rate (mm d^{-1})	Survival (%)
50	68.00 ± 0.52[a]	0.222 ± 0.04[a]	99.58[a]
75	65.30 ± 0.53[b]	0.207 ± 0.04[b]	99.25[a]
100	61.87 ± 0.60[c]	0.187 ± 0.03[c]	99.52[a]

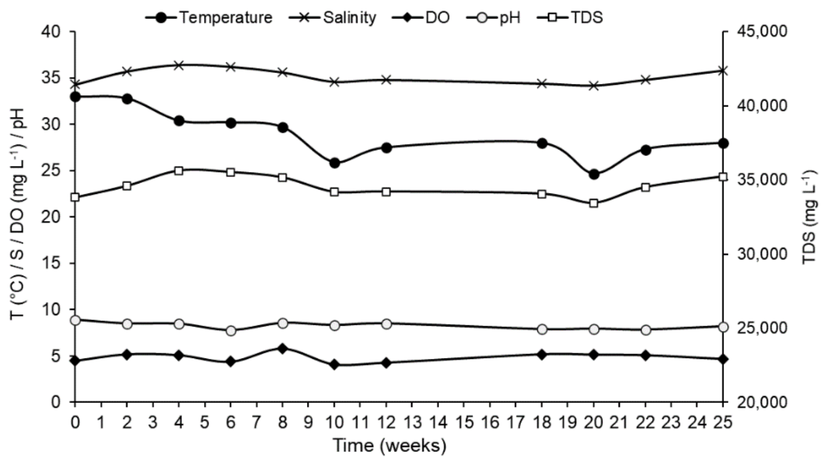

Figure 2. Variation of temperature (T), salinity (S), dissolved oxygen (DO), pH, and total dissolved solids (TDS) during grow-out of *C. virginica* in the Rio Lagartos coastal lagoon, Yucatan, Mexico.

Table 2. Regression equations relating oyster growth rate (GR) to water temperature (T) and pH.

Stocking density (%)	Equation
50	GR = -2.45 + 0.0315 T + 0.218 pH
75	GR = -2.49 + 0.0261 T + 0.239 pH
100	GR = -2.17 + 0.0166 T + 0.231 pH

The sensitivity analysis showed that, when using 50 and 75% densities, the random variability of the mortality rate (*e*z in Eq.13) and the percentage of surviving oysters during the rearing period (en_t in Eq. 14) are the most influential stochasticity sources affecting oyster production (Table 3). On the other hand, the random variability of oyster height during the rearing period (en_t in Eq. 8) and the final height of the oysters (eH_f in Eq.5) are the primary sources influencing oyster production at the maximum density of 100% (Table 3). The "mapped regression coefficients" values indicate the number of oyster dozens that either increase or decrease per standard deviation of each source.

DISCUSSION

The results of this study show an inverse relationship between stocking density and oyster growth. In contrast, the survival of oyster populations (field-nursed juveniles 29.4 ± 0.18 mm in height size) was minimally affected. Oysters reared at the highest stocking density showed a significantly slower growth rate than those reared at the lowest. In agreement with these results, Grizzle et al. (2020) observed that eastern oysters grown in bags with the highest density also showed significantly lower final shell height than oysters grown at a lower density. Rheault & Rice (1996) reported that higher initial stocking densities (5 kg eastern oysters per bag) at grow-out had smaller increases in wet weight and condition index than in lower densities bags (1 kg oysters). Haché & Bardon-Albaret (2021) found the same growth and density trend for eastern oysters with an initial height above 35 mm, except juvenile oysters with an initial height between 20 and 35 mm, for which the highest growth was obtained at intermediate densities.

Studies reporting the effect of stocking density on *C. virginica* survival are scarce. Adams et al. (1995) report that stocking density did not affect oyster survival, averaging 31%. Bishop & Hooper (2005) observed mortalities below 2% in an experimental six-day nursery stage, but the effect of stocking density on oyster survival was unclear. In this study, the overall mean survival rate was above 99% for all densities, indicating the excellent response and tolerance of *C. virginica* to the water environmental conditions prevailing in the Rio Lagartos lagoon.

The *C. virginica* growth rates obtained in this investigation are difficult to compare with those reported by other authors due to differences in initial size, farming practices, gears used, and environmental conditions. Frequently, the growth rates in height are not reported directly and must be calculated from the reported initial and final sizes and the duration of the period analyzed. Growth rates of approximately 0.13 mm d^{-1} are usually reported with extreme values ranging from 0.03 to 0.32 mm d^{-1} (Grabowski et al. 2004, Thomas et al. 2019, Haché & Bardon-Albaret

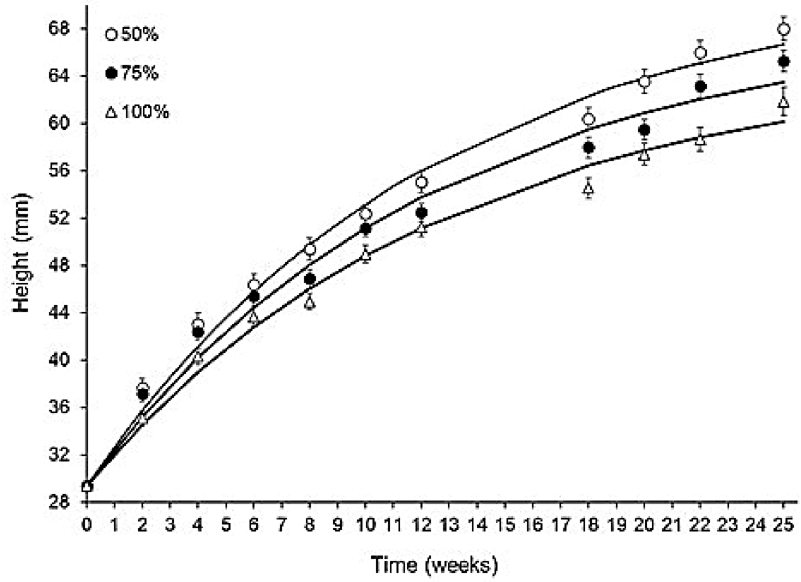

Figure 3. Growth curves fitted to *C. virginica* mean height values reared at different stocking densities (as percentage area occupation in "Nestier" trays) in the coastal lagoon of Rio Lagartos, Yucatan, Mexico.

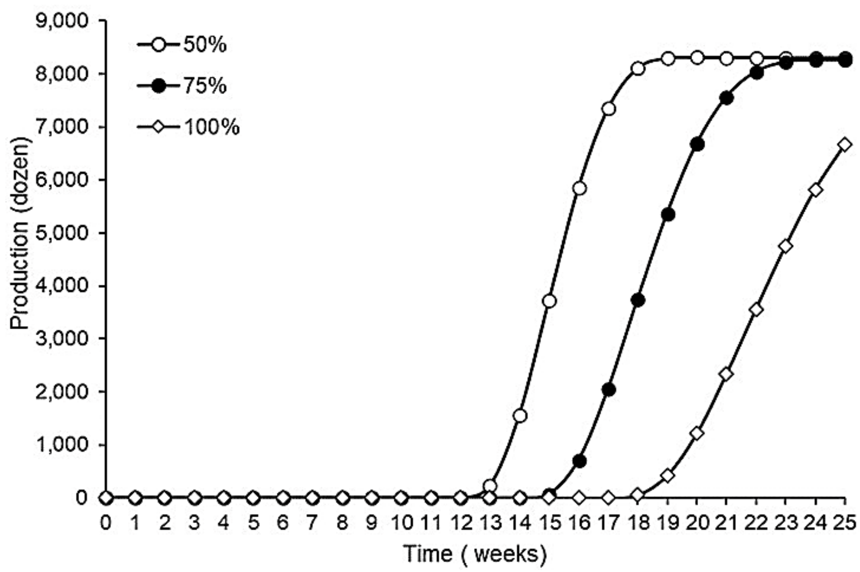

Figure 4. Production (in dozens) of commercial *C. virginica* grown at different densities (as percentages of area occupation) in the coastal lagoon of Rio Lagartos, Yucatan, Mexico.

2021). Cabrera-Rodríguez et al. (1997) used 22.50-32.05 mm wild oyster seeds and Nestier boxes for a grow-out trial in Rio Lagartos and obtained growth rates of 0.05 and 0.14 mm d^{-1}. The growth rates observed in this study ranged from 0.19 to 0.22 mm d^{-1} and can be considered relatively high compared with those previously reported.

Oysters are recognized as organisms that tolerate a wide range of environmental conditions (Shumway 1996). The eastern oyster is a eurytopic species with a wide latitudinal distribution in the Atlantic Ocean (Casas et al. 2017). However, oysters' tolerance to extreme conditions that exceed their optimal ranges for growth and survival varies geographically and is highly dependent on exposure time (Marshall et al. 2021, McFarland et al. 2022).

The optimum water temperature for the growth of *C. virginica* is generally considered to be 20 to 30°C

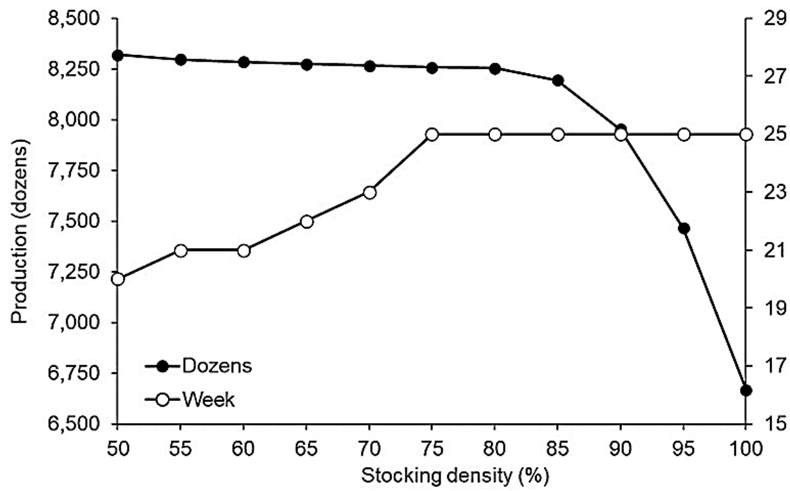

Figure 5. Production of marketable oysters (in dozens) and optimum harvesting time using alternative rearing densities. For densities other than those tested in the experimental trial, the projections are made by model interpolation.

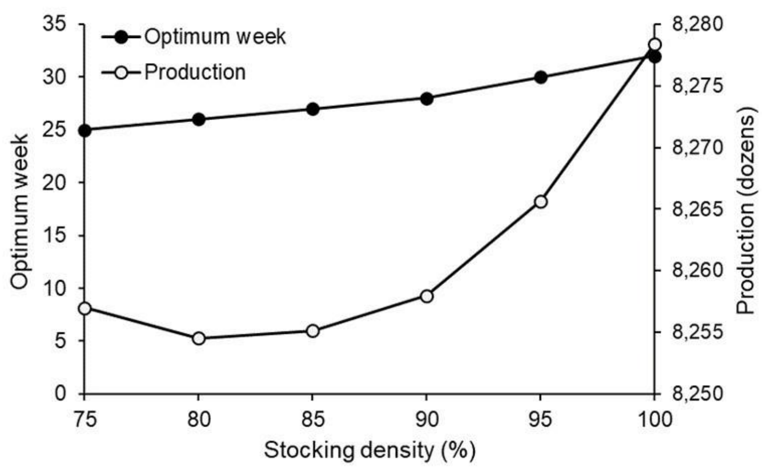

Figure 6. Results of extrapolating the oyster grow-out to 33 weeks. The time when production is maximized (optimum week) and the corresponding yields for each theoretical stocking density are indicated.

(Heilmayer et al. 2008), although a more recent report indicates 15 to 25°C (Sehlinger et al. 2019). Harding (2007) noted that the most significant increases in oyster height occurred during months with higher temperatures (27-28°C). Similarly, Lowe et al. (2017) found that growth rates of juvenile oysters were maximized at a temperature of 27.8°C but were reduced at temperatures above 30°C. In this study, a positive relationship was observed between growth rates and water temperature, and the highest growth rates were observed at the warmest temperatures (30 to 33°C), exceeding the values generally indicated as optimal for the species.

The optimum salinity range for *C. virginica* is 14-28; a minimum of 10 is required for growth (Shumway 1996). However, wild oyster populations in the lower Laguna Madre (Gulf of Mexico) grow adequately in a salinity range of 32 to 42 (Shumway 1996). Marshall et al. (2021) found differences in salinity tolerance in different oyster populations from the Gulf of Mexico, observing that the progeny of wild broodstock oysters from the Upper Laguna Madre were able to tolerate the highest experimental salinities (38.0 and 44.0) under controlled laboratory conditions. During the grow-out trial conducted for this study, the range of salinity levels was between 34.2 and 36.4.

The open ocean's typical pH values range from 7.8 to 8.2 (Beniash et al. 2011). Low pH levels are associated with elevated CO_2 levels (hypercapnia) and seawater acidification, which is thought to affect calcifying marine organisms (Clements et al. 2021). The effect of pH on oyster growth, mortality, and reproduction as an indicator of ocean acidification is of great interest (Boulais et al. 2017). In laboratory experi-

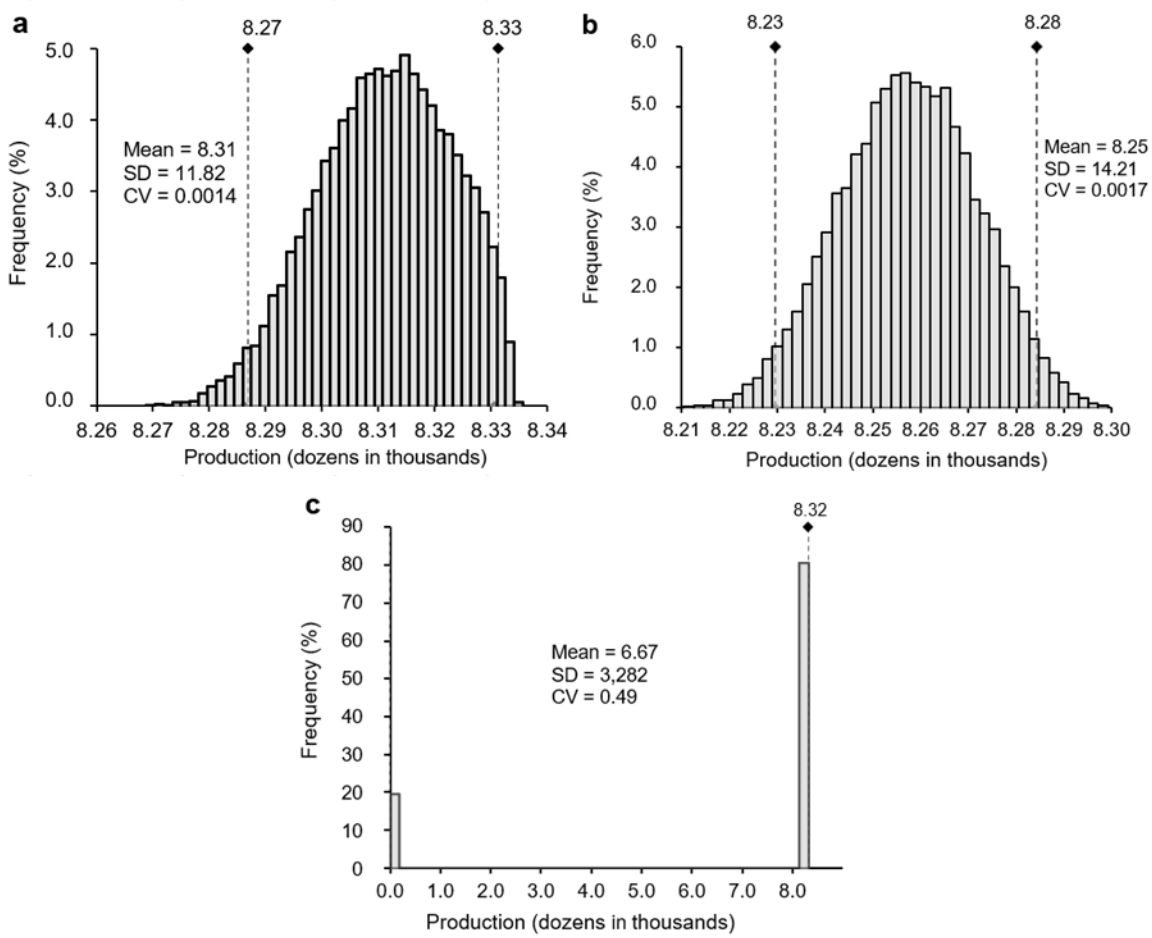

Figure 7. Output probability distributions of oyster production. Yields correspond to a) 50% density after 20 weeks, b) 75% density after 25 weeks, and c) 100% density after 25 weeks. The values corresponding to the dashed lines indicate the 95% probability intervals. SD: standard deviation, and CV: coefficient of variation.

ments, Beniash et al. (2011) showed that high levels of CO_2 concentration (pH ~7.5, pCO_2 ~3500 µatm) inhibited shell and soft body growth of experimental juvenile oysters *C. virginica*, compared with organisms under control conditions (pH ~8.2, pCO_2 ~380 µatm). This investigation showed a positive relationship between growth rates and pH, which ranged between 7.90 and 8.90. Therefore, the reduced growth rates observed at low pH values could result from a negative effect on the formation of the oyster shell, as explained by the authors referred to above.

Recent research has indicated that juvenile oysters, *C. virginica*, exhibit higher tolerance levels to extreme environmental conditions when exposed to gradual changes in temperature or salinity, as opposed to abrupt shifts in environmental factors. McFarland et al. (2022) showed that gradual changes in salinity favor the eastern oyster survival and also found that juvenile oysters at high salinities (20-35) had high survival at 25°C (≥98%) and 30°C (82%). Cassis et al. (2011) mention that oysters have better growth and survival rates when temperature fluctuations are relatively small. Likewise, the tolerance of the eastern oyster to extreme environmental conditions will also depend on the time of exposure (Rybovich et al. 2016). La Peyre et al. (2013) indicate that high mortality of oysters occurs during long periods of high seawater temperature and low salinity.

Rio Lagartos is a shallow coastal lagoon characterized by high salinity (>34) (Dávila-Jiménez et al. 2019), a considerable evaporation rate, and little freshwater input from rain and groundwater (Vega-Cendejas & Hernández de Santillana 2004). The results of this investigation indicate that environmental water conditions were very stable, with no abrupt shifts during grow-out, thus most likely favoring *C. virginica* growth and survival.

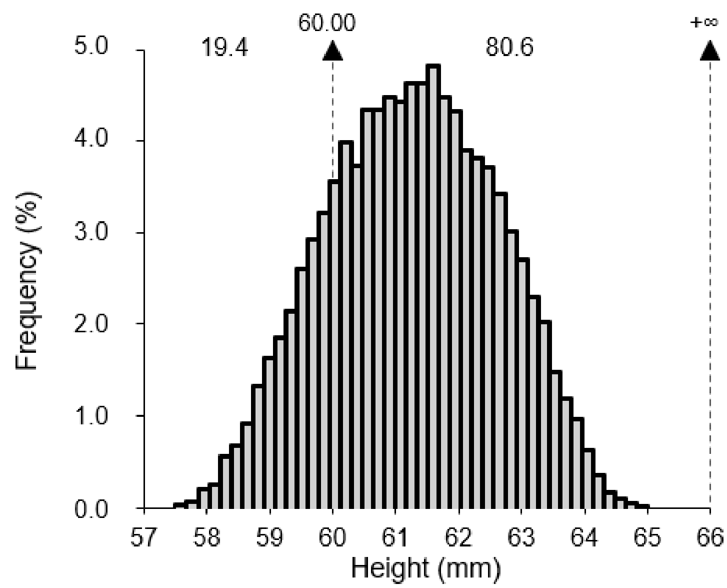

Figure 8. Output probability distribution of oyster height when reared at 100% density after 25 weeks. The percentage at the left of the dashed line indicates the probability of oysters attaining the minimum commercial size (60 mm).

Table 3. Sensitivity analysis of commercial oyster dozen production to stochasticity sources in the production model. The sources are hierarchically ranked from most to least important according to the absolute value of "mapped" regression coefficients (MRC).

Stocking density (% area occupation)					
50		75		100	
Source	MRC	Source	MRC	Source	MRC
ez (Eq. 14)	-8.69	*ez* (Eq. 13)	-11.43	eh_t (Eq. 8)	2282.04
en_t (Eq. 15)	7.89	en_t (Eq. 14)	8.39	eH_f (Eq. 5)	385.12

Studies evaluating the effects of environmental factors on the growth and mortality of *C. virginica* agree that optimal ranges are challenging to define and that tolerance limits vary for each population (Marshall et al. 2021). In this regard, Lowe et al. (2017) note that the mortality and growth patterns of oysters evaluated from different populations show significant differences in temperature and salinity tolerance, suggesting that the organisms are adapted to the local conditions of their preferred location. Further studies are required to determine whether such tolerance contributes to the excellent production results obtained in this study despite some environmental conditions not being reported as optimal.

The modeling approach used in this report was adequate to comprehensively evaluate the effect of stocking density on *C. virginica* production. Overall, the model indicates that oyster growth, rather than survival, is the main factor affecting the dynamic of oyster production. As expected, faster oyster growth at the lowest density results in reaching MCS and harvesting earlier than in the other densities (Fig. 4). Although the optimum harvesting time at 50 and 75% densities differ, the maximum productions in both densities are very similar because the oyster mortality over time is negligible. However, using 100% density results in lower yield after 25 weeks because such grow-out length allows oysters to attain MCS only 80.4% of the time (Fig. 4).

Projecting results for densities other than those studied experimentally show that for densities higher than 75%, the increasing percentages of the times the grow-out does not allow reaching the MCS results in progressively lower yields (Fig. 5). Moreover, oyster production at those densities is maximized by harvesting after 25 weeks, thus evidencing that the length of the experimental trial does not suffice for oysters attaining MCS every time the grow-out is performed. Projecting production for grow-out periods longer than 25 weeks showed that production using

100% density could be similar to those obtained with 50 and 75% only by extending the grow-out period up to 32 weeks when there is the certainty of oysters reaching MCS every occasion rearing is carried out.

Both interpolations and extrapolations were accomplished using Equations 2-3 to predict growth parameters as a function of stocking density. The projections are robust considering that the regression analysis results estimating the equations' coefficients were excellent regarding significance and residuals normality and homoscedasticity. However, a new experimental trial lasting at least 33 weeks is necessary to confirm the yields predicted by extrapolation.

The Monte Carlo simulation showed that the random variability of oyster production in 50 and 100% densities was minimal, as indicated by very low standard deviation and coefficient of variation values (Fig. 7). For 95% probability intervals, the range between the minimum and maximum dozen numbers were 44 and 55 dozens, scarcely representing 0.53 and 0.66% of the mean yields. In contrast, the random variability of production when rearing oysters at 100% density was extremely high, ranging from 0.0 (no production) to 8316 dozens (i.e. 124.7% of the mean yield) (Fig 7).

The shape of output probability distributions of yields obtained for the three densities are dissimilar (Fig. 7). According to the data collected during the experimental trial, in two of three replicates of 50% density, no dead oyster was observed until week 12. Such high survival causes the distribution obtained for the 50% density to be truncated on the right side because there were many cases when, merely by chance, survival approached or reached (but not surpassed) 100%. This situation was not observed for the 75% density distribution because harvesting is accomplished later than 50% density, thus causing higher oyster mortality and no cases when 100% survival occurred. On the other hand, the possibility of not producing at all when using 100% density (because MCS is not reached) results in a bimodal distribution associated with the two potential scenarios.

The results from the sensitivity analysis coincide with the above explanations regarding the random variability of oyster production. According to the analysis for 50 and 75% densities, the main stochastic elements influencing production are the ones related to oyster populations; however, given that oyster mortality is minimal, their influence is meager, as indicated by low regression coefficient values. In contrast, a different scenario was observed when analyzing the 100% density, where the dominant stochastic elements influencing production are those affecting oyster growth. In this case, however, the regression coefficient values indicate a remarkably intense influence of growth on production. To summarize, the results in this study indicate that recruitment to the commercial category is critical to determine drastically different *C. virginica* production scenarios.

CONCLUSION

The stochastic production model prepared for this investigation helped gain insight into the production dynamics of the eastern oyster *C. virginica* when reared at alternative stocking densities and identify potential scenarios for improving farming practices for the species. The production model can be directly used as a part of a bioeconomic model to determine, in future research, the optimum density management from an economic perspective.

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