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Eastern Oyster (*Crassostrea virginica*) nursery production in tropical coastal lagoons in Yucatán, Mexico: nonlinear regression modeling and relationships with environmental variables

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ABSTRACT. Nonlinear regression modeling was used to study the nursery production of the oyster *Crassostrea virginica* in the Celestún (CL) and Rio Lagartos (RL) lagoons in Yucatán, Mexico. Relationships between production parameters and environmental variables were also established. Spat (2.40 ± 0.20 mm) was obtained from a hatchery and reared in Nestier-type trays using an off-bottom system. Oyster cultivation took place from May 2021 to September 2021 and ended after 122–126 days when oysters reached 30.00 mm. There were no significant differences in final height (CL: 30.80 ± 0.42 mm; RL: 31.80 ± 0.65 mm; $P = 0.18$) and growth rate (CL: 0.23 ± 0.02 $\mathrm{mm \cdot d^{-1}}$; RL: 0.23 ± 0.01 $\mathrm{mm \cdot d^{-1}}$; $P = 0.98$). Final survival was 71.45% in CL and 99.40% in RL. Nonlinear regression curves were statistically satisfactory for analyzing growth and survival. Salinity (CL: 15.23 ppt; RL: 35.02 ppt), temperature (CL: 29.64 °C; RL: 31.02 °C), dissolved oxygen (CL: 4.50 $\mathrm{mg \cdot L^{-1}}$; RL: 5.04 $\mathrm{mg \cdot L^{-1}}$), pH (CL: 8.10; RL: 8.34), chlorophyll *a* (Chl *a*) (CL: 3.23 $\mathrm{mg \cdot m^{-3}}$; RL: 6.85 $\mathrm{mg \cdot m^{-3}}$), and total dissolved solids (CL: 16,101 $\mathrm{mg \cdot L^{-1}}$; RL: 34,838 $\mathrm{mg \cdot L^{-1}}$) were significantly higher in RL ($P < 0.05$). Except for Chl *a*, the environmental variables were more stable in RL than in CL ($P < 0.05$). In RL, the growth rate was positively related to salinity and pH. In CL, the growth rate slowed when salinity decreased, and the mortality rate diminished when salinity, dissolved oxygen, and total dissolved solids increased and pH decreased. Salinity was mainly responsible for the observed differences in production between lagoons. Even when temperature and salinity were high in RL, acceptable growth rate and survival were observed, possibly due to stable rearing conditions.

Key words: *Crassostrea virginica*, environmental variables, nursery, nonlinear regression models, oyster farming.

INTRODUCTION

The Eastern Oyster (*Crassostrea virginica*) has proven to be suitable for farming, mainly in the coastal waters of Canada and the United States of America (USA) (Poirier et al. 2020, Bodenstein et al. 2023). Several studies have been conducted on *C. virginica* farming, addressing issues such as alternative rearing gears (Mallet et al. 2013, Thomas et al. 2019, Grizzle et al. 2020) and the effects of desiccation and tumbling practices (Bodenstein et al. 2021).

In Mexico, *C. virginica* farming began in 2010 after a hatchery (*Centro Ostrícola Tecnológico de Tabasco*) commenced operations in the state of Tabasco with a production capacity of 40 million (M) spats per month (pers. comm., Tordecillas-Guillén 2023). Currently, 27 farms operate in Tabasco, and 12 farms operate in the state of Tamaulipas (CONAPESCA 2022). Despite the proximity of the hatchery to other states, such as Yucatán, there are no reports of commercial oyster aquaculture in other states. In addition, few antecedents are available regarding *C. virginica* farming in Yucatán. Rihani et al. (1989) reported the results of the first *C. virginica* experimental cultivation assays using juveniles from Tabasco. Cabrera-Rodríguez et al. (1997) investigated the feasibility of oyster rearing in the Rio Lagartos Lagoon. Vera and Aldana (2000) evaluated cultivating oysters in the water supply channels of a shrimp farm.

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Recent studies have focused on the influence of environmental variables on *C. virginica* growth and survival. La Peyre et al. (2013) assessed recruitment, growth, and mortality along a salinity gradient in an estuarine zone in Louisiana, USA. Rybovich et al. (2016) examined the effects of low salinity and high temperature on growth and survival. McFarland et al. (2022) evaluated osmotic limits at moderate and elevated temperatures during different life stages. Few studies have focused on *C. virginica* during the nursery stage. Among these, Bishop and Hooper (2005) compared *C. virginica* growth and mortality rates during the nursery stage. Poirier et al. (2020) tested the efficacy of a bouncing-bucket system to improve oyster shell strength and thickness.

The present study evaluated the biotechnical viability of *C. virginica* production when reared off-bottom during the nursery stage in 2 tropical lagoons in Yucatán, Mexico. In addition, the relationships between growth and survival parameters and the environmental conditions of the lagoons were analyzed. To our knowledge, this is the first study to address this topic.

Materials and methods

Study sites

Two tropical coastal lagoons in the state of Yucatán, Mexico, were used as nursery habitats: Celestún Lagoon (CL), located on the northwestern coast of the Yucatán Peninsula (20°52′11″ N, 90°22′55″ W) (Hardage et al. 2022), and Rio Lagartos (RL), located on the northern coast of the Yucatán Peninsula (21°36′21″ N, 88°09′04″ W) (Vega-Cendejas et al. 2004) (Fig. 1).

Celestún Lagoon is a karstic shallow estuary that contains limestone; freshwater entry via groundwater discharge into the lagoon varies according to the rainfall regime (Morelos-Villegas et al. 2018). Rio Lagartos is the largest coastal lagoon in Yucatán and exhibits hypersaline conditions (>40 ppt) during most of the year (Vega-Cendejas et al. 2004). The region has a well-defined weather regime with 3 seasons: dry (March to May), rainy (June to October), and windy (November to February); strong winds and temperatures below 22 °C are present during the windy season (Morelos-Villegas et al. 2018).

Nursery description

The nursery phase lasted 122 days in CL (20 May 2021 to 19 September 2021) and 126 days in RL (21 May 2021 to 24 September 2021), during which the oysters attained a mean shell height (distance between the hinge and the opposite margin) of at least 30 mm. Spat of *C. virginica* with a mean shell height of 2.4 ± 0.2 mm were obtained from the commercial hatchery *Centro Ostrícola Tecnológico de Tabasco*. Rearing was carried out in Nestier-type trays (DM Plast, Jalisco, Mexico). The oysters were stocked in plastic mesh bags (55 × 35 cm; mesh size: 0.8 mm); 5,000 individuals were stocked per bag. The bags were placed in the Nestier trays to form modules (3 vertically stacked trays per module) which were attached off-bottom to 30-m longlines. The initial oyster populations were 100,000 (CL) and 50,000 (RL) individuals.

The oysters were transferred to larger plastic bags (55 × 55 cm; mesh size: 1.35 mm) after reaching a shell height of >10 mm. When the oysters attained a shell height of >20 mm, they were removed from the bags and placed directly into the trays, using 50% of the bottom area until the end of the trials. This protocol increased the modules to a maximum of 42 at CL and 18 at RL. Fouling organisms were removed from the bags and trays each week by scrubbing with a stiff hand brush.

Data collection and processing

Samples of 30 individual oysters were randomly selected every 7–14 days to measure shell height using a dial caliper (505-730 D15TX; Mitutoyo, Kanagawa, Japan) (precision: 0.02 mm). The dead oysters (identified as empty shells or gaping oysters) were counted and removed from the bags or trays each week. Temperature (°C), salinity (ppt), dissolved oxygen ($mg \cdot L^{-1}$), pH, and total dissolved solids ($mg \cdot L^{-1}$) were recorded using a handheld multimeter (Pro-Plus; Yellow Spring Instruments, Yellow Springs, USA). Chlorophyll *a* data were obtained from the Giovanni platform of the National Aeronautics and Space Administration (NASA, 2022).

Daily growth and mortality rates were calculated for the periods between successive sampling dates as the differences in height and survival (%) divided by the number of days between sampling dates. The values of environmental variables corresponding to the successive sampling dates were averaged to represent the prevailing conditions.

Growth and survival analyses

Equations (1) and (2) were used to analyze oyster growth as a function of time (t). Equation (1) is the curve proposed by Estrada-Pérez et al. (2018):

$$h_t = H_i + Bt + C\,sin(2\pi t/L + S) \quad , \quad (1)$$

where h_t is mean height, H_i is the initial mean height, b is the growth rate, C is the amplitude of height variation (deviation) around a linear growth trend, L is the length of the period between minima or maxima deviations, and S is a time adjustment parameter. Equation (2) was proposed by Serna-Gallo et al. (2014):

$$h_t = H_0 + (H_f - H_0)\left[\tfrac{1-k^t}{1-k^c}\right] \quad , \quad (2)$$

where h_t is mean height, H_0 is the initial mean height, H_f is the mean height at the end of the nursery stage, k is a parameter representing the rate at which the height changes from its

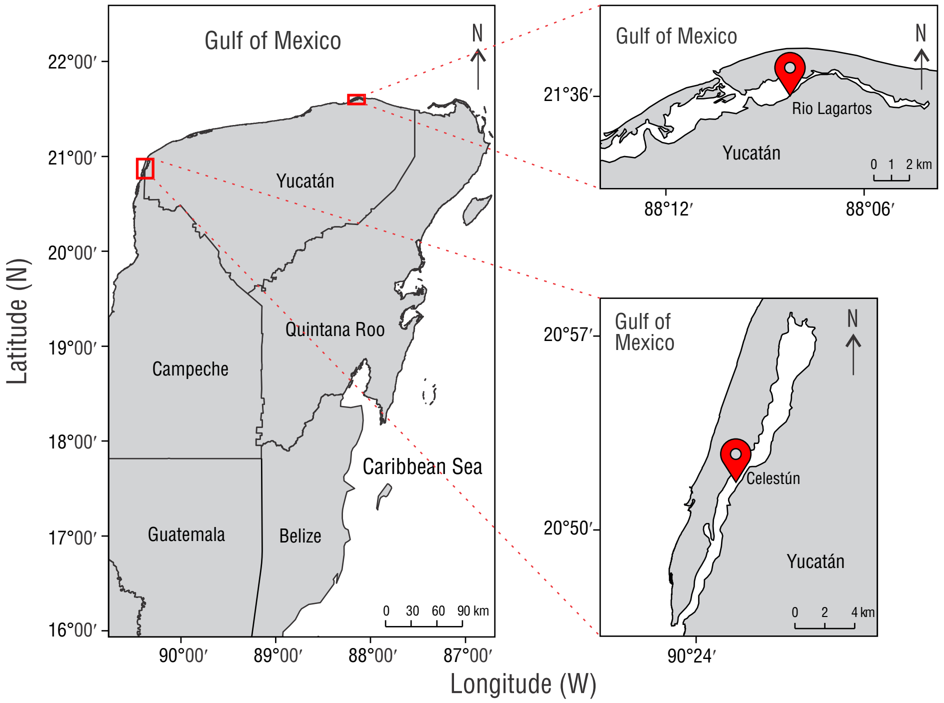

Figure 1. Study sites in the state of Yucatán, Mexico. Oysters were reared in the tropical coastal lagoons of Celestún (CL) and Rio Lagartos (RL). Cultivation sites are indicated with marker pins (📍).

initial value to its final value, t is elapsed time units, and c is the time units elapsed at the end of the rearing period.

Oyster survival in CL was analyzed as a function of time (t), using the following model:

$$S_t = S_i exp^{(-A+Bt)t} \quad , \quad (3)$$

where S_t is the percentage of survivors, S_i is the initial survival of the stock (i.e., 100%), A is the initial instantaneous mortality rate, and B is the rate at which the instantaneous mortality rate increases. Oyster mortality in RL was negligible; thus, statistical analysis was not required.

Environmental variables and relationships with growth and mortality rates

The mean values of the environmental variables were compared to test differences in environmental rearing conditions between the lagoons. The relative stability of the environmental conditions within and between the lagoons was analyzed by comparing the coefficient of variation (i.e., ratio of standard deviation to the variable mean). Subsequently, linear regression analyses were conducted to evaluate possible relationships between environmental variables and growth and mortality rates.

A relationship was established between the coefficients of variation of oyster height (CV_h) and salinity (CV_s) in CL:

$$CV_h = CV_0 exp^{(-G \cdot CVs)} \quad , \quad (4)$$

where CV_0 is the coefficient of variation of the growth rate when the coefficient of variation of salinity is zero, and G is the instantaneous rate at which CV_h changes as a function of CV_s.

Statistical analyses

Equations (1), (2), (3), and (4) were estimated using nonlinear regression fitting methods. Equations (1) and (2) were fitted to the height data collected in both lagoons; the best fit was determined using the Akaike information criterion (AIC). D' Agostino–Pearson and Shapiro–Wilk tests were used to assess the normality of the regression residuals. The lack of fit of the model and parameter skewness were also tested. Parameter skewness was measured using the Hougaard index (h-index) and compared with the index values recommended by Ratkowsky (1983). Accordingly, h-index absolute values were categorized as follows: ideal (<0.10) (almost linear), adequate (0.10–0.25), noticeably skewed (0.25–1.00), and considerably skewed (>1).

The final mean oyster heights of the lagoons were compared with a one-way analysis of variance (ANOVA), considering that the difference in the nursery length between the sites was negligible (i.e., 3.2%). A repeated measures ANOVA was used to compare the growth rate values and environmental variables of the lagoons. Data normality was evaluated with the Shapiro–Wilk test before conducting the analyses. A non-parametric Mann–Whitney test was used when the data were not normally distributed. The coefficients of variation of the environmental variables were compared using the method proposed by Forkman (2009). Statistica v. 6.1 (StatSoft, Inc., Tulsa, USA), GraphPad Prism v. 9.0 (GraphPad Software, San Diego, USA), and MedCalc Statistical Software v. 20.218 (MedCalc Software Ltd., Ostend, Belgium) were used to conduct the statistical analyses. Significance was evaluated at $\alpha = 0.05$.

RESULTS

The final height of the oysters did not differ significantly between sites (CL: 30.80 ± 0.42 mm; RL: 31.80 ± 0.65; $P = 0.18$). The daily growth rate also did not differ significantly between sites (CL: 0.23 ± 0.02 $\text{mm}\cdot\text{d}^{-1}$ [6.98 $\text{mm}\cdot\text{month}^{-1}$]; RL: 0.23 ± 0.01 $\text{mm}\cdot\text{d}^{-1}$ [6.99 $\text{mm}\cdot\text{month}^{-1}$]; $P = 0.98$).

According to the AIC, the Estrada-Perez et al. (2018) model showed a better fit to the oyster growth observed in CL, while the Serna-Gallo et al. (2014) equation resulted in a better fit for the RL data (Table 1). It is worth noting that the Estrada-Perez et al. (2018) model showed erratic behavior when fitting growth data for RL, yielding unrealistic values of 130 days for parameter L (the length of the period between minimum or maximum height deviations), which is longer than the nursery period. Erratic behavior was also evident by the negative growth rate values (parameter B).

The variation in the growth rate observed in CL (Fig. 2, Table 2) throughout the nursery phase was adequately described by the model of Estrada-Pérez et al. (2018). The growth model proposed by Serna-Gallo (2014) adequately described oyster growth in RL (Fig. 2, Table 2). Final oyster survival was 71.45% in CL. In RL, mortality was negligible, and survival was as high as 99.40%. The survival model (Eq. 3) adequately described the mortality observed in CL (Fig. 3, Table 3).

The values of environmental variables recorded in the lagoons during the nursery phase are shown in Figures 4 and 5. Except for mean dissolved oxygen, which was not significantly different between sites, the values of the environmental variables were significantly higher in RL (Supplementary Material Table S1). The coefficients of variation of the environmental variables showed that CL was more unstable in terms of salinity and total dissolved solids, while Chl *a* was more unstable in RL (Supplementary Material Table S1). When compared within each lagoon, salinity (CL) and Chl *a* (RL) were significantly more unstable than the rest of the variables, while temperature was the most stable variable in both lagoons (Supplementary Material Table S2).

No significant relationships were detected between the growth rate and environmental variables in CL. Nevertheless, 4 periods were identified where oyster height increased or stabilized, which corresponded to periods when salinity was relatively stable (periods I and III) or decreasing (periods II and IV), respectively (Fig. 6). The coefficients of variation during the periods were used to estimate the relative variability of height and salinity. Low CV values indicated high stability, while high values corresponded to periods when the variables were unstable (i.e., when height increased or salinity decreased). A significant and inverse relationship between the CV values of both variables was determined by fitting Eq. (4) (Fig. 7). The results from the regression analysis were: $CV_0 = 2.16 \pm 0.61$, $P = 0.07$, and h-index = 1.23; $G = 7.46 \pm 1.47$, $P = 0.04$, and h-index = –1.61 (regression: $P = 0.01$; normality: $P = 0.75$; lack of fit: $P > 0.99$). Thus, oyster growth slowed down as salinity decreased.

The results from the linear regression analyses showed that in CL, the mortality rate was inversely related to salinity, dissolved oxygen, and total dissolved solids and positively related to pH. In contrast, in RL, the growth rate was positively related to salinity and pH (Table 4). The slope values in the equations indicated a change in the growth and mortality rates per unitary change in the corresponding environmental variable. For example, an increase (or decrease) of 1 ppt in salinity corresponded to an increase (or decrease) in the daily mortality rate in CL of 0.051%.

DISCUSSION

The coastal lagoons analyzed in the present study showed substantial differences in environmental conditions that are relevant for the nursery production of *C. virginica*. Noticeable differences were observed in the magnitude, relative stability, and dynamics of the environmental variables between the lagoons. Unstable salinity caused an oscillating oyster growth pattern in CL. At the same time, higher general stability favored more consistent growth in RL (Fig. 2). Oyster height was greater in CL during most of the rearing period, although by the end of the nursery phase, mean height was similar in both lagoons. Despite the difference in growth patterns, the daily growth rates and final heights did not differ significantly. In contrast, a substantial difference was observed in oyster survival; the prevailing conditions in CL were more unfavorable than in RL.

The main factors determining oyster rearing conditions were the water exchange regimes between the lagoons, sea, and groundwater sources. Celestún Lagoon is a shallow estuary with freshwater contributions from groundwater and

Table 1. Fitting performance of equations (1) and (2) to oyster growth data by study site. Lower values of the Akaike Information Criterion (AIC) indicate better performance.

Site	Model	AIC
Celestún	Serna Gallo et al. (2014)	–18.47
	Estrada-Pérez et al. (2018)	–22.7
Rio Lagartos	Serna Gallo et al. (2014)	–39.95
	Estrada-Pérez et al. (2018)	–39.15

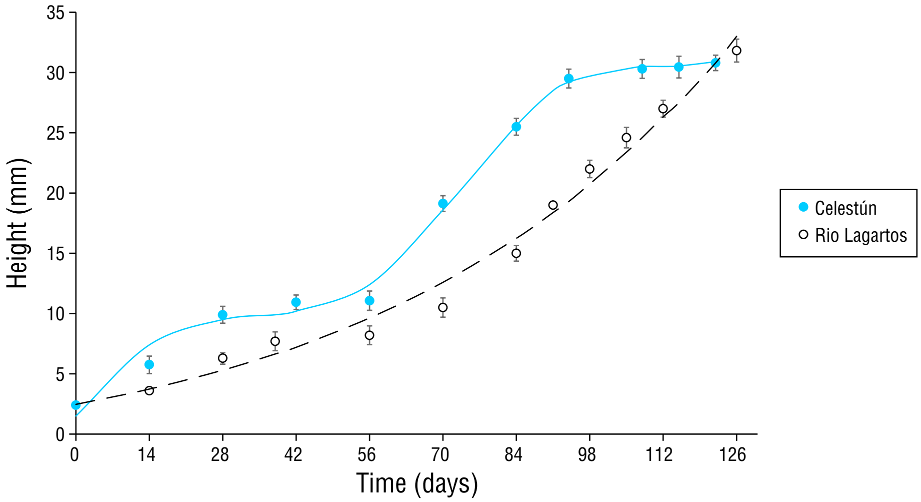

Figure 2. Growth models fitted using Eq. (1) and Eq. (2) to the mean height data of *Crassostrea virginica* reared off-bottom during the nursery stage in the coastal lagoons of Celestún (CL) and Rio Lagartos (RL), respectively. The vertical bars indicate standard error (height).

Table 2. Regression analysis results using Eq. (1) and Eq. (2) for growth (height) and survival of *Crassostrea virginica* reared off-bottom during the nursery stage in the Celestún and Rio Lagartos lagoons, Mexico. SE = standard error.

Equations and parameters	Estimate ± SE	P	Skewness (h-index)
Eq. (1)			
H_i	0.48 ± 0.69	0.51	–8.68E^{-04}
B	0.27 ± 0.01	1.30E^{-07}	0.02
C	3.20 ± 0.51	7.98E^{-04}	0.01
L	76.93 ± 3.52	5.99E^{-07}	0.19
S	0.32 ± 0.27	0.28	0.08
Eq. (2)			
H_0	2.62 ± 0.79	0.01	–0.06
H_f	34.21 ± 1.69	1.40E^{-10}	0.03
k	1.02 ± 0.002	1.00E^{-10}	0.06
Equation	**Regression (P)**	**Normality (P)**	**Lack of fit (P)**
Eq. (1)	1.80E^{-08}	0.30	0.91
Eq. (2)	2.55E^{-11}	0.26	0.18

rainwater (Stalker et al. 2014), while RL is a long and hypersaline estuary (>35 ppt) with minimum freshwater contributions (Vega-Cendejas et al. 2004).

Published references of *C. virginica* growth rates during the nursery stage are scarce. Bishop and Hooper (2005) used upwellers to study growth during nursery rearing, allowing for a growth rate of 6.80 mm·month^{-1} to be estimated. A growth rate of 6.60 mm·month^{-1} has also been reported for the nursery stage using "Australian-type" cages (pers. comm., Tordecillas-Guillén 2023). These growth rate estimates are similar to those obtained in this study (6.96 mm·month^{-1} and 7.00 mm·month^{-1}).

The optimal water temperature for *C. virginica* ranges from 20 °C to 32 °C (Lowe et al. 2017). Overall, the temperature values observed in this study were adequate in both lagoons, with the mean value in RL (31.02 °C) nearing the maximum tolerable limit. Information on tolerable and optimal salinity levels for *C. virginica* is abundant, particularly regarding its wild populations. Tolerable limits range from 10 ppt to 30 ppt, while values within approximately 15–23 ppt are usually considered optimal (Shumway 1996). In the present study, salinity levels of 15.23 ppt were observed in CL, nearing the minimum acceptable limit. In contrast, salinities higher than those considered adequate were observed in RL (35.02 ppt).

Dissolved oxygen higher than 3.00 mg·L^{-1} is recommended for *C. virginica* (Baker and Mann 1992, Coxe et al. 2023). Acceptable dissolved oxygen levels were observed in the present study, except for CL, where an unacceptably low concentration (2.95 mg·L^{-1}; Fig. 4) was recorded at the end of the trial, although this situation prevailed for a short period and did not lead to hypoxic conditions (i.e., <2 mg·L^{-1}, Coxe et al. 2023). The pH values recorded in the present study (8.10 and 8.30) were within limits considered adequate for *C. virginica* embryos, larvae, and spat (i.e., 6.80–8.80) (Calabrese and Davis 1966, Beniash et al. 2010). According to Snyder et al. (2017), the ideal chlorophyll concentration for *C. virginica* farming is 3–10 mg·m^{-3}. According to this ranking, the mean concentrations of Chl *a* in the present study were ideal (3.23 mg·m^{-3} in CL and 6.85 mg·m^{-3} in RL). No recommended values of

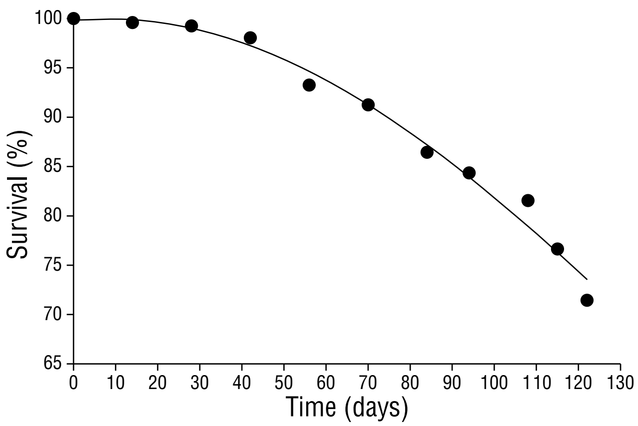

Figure 3. Survival curve, Eq. (3), fitted to survival percentage data during the nursery stage of *Crassostrea virginica* reared in an off-bottom system in the coastal lagoon of Celestún (CL). No estimates of the standard error were available because survival values corresponded to single counts.

Table 3. Regression analysis results using Eq. (3) for survival of *Crassostrea virginica* reared off-bottom during the nursery stage in the Celestún Lagoon, Mexico. SE = standard error.

Parameters	Estimate ± SE	P	Skewness (h-index)
S_i	99.71 ± 0.01	5.9753E^{-18}	0.71E^{-2}
A	$4.47\text{E}^{-04} \pm 0.40$	0.40	0.81E^{-2}
B	$2.42\text{E}^{-05} \pm 2.48\text{E}^{-04}$	2.48E^{-04}	-0.65E^{-2}

Regression, $P = 2.00\text{E}^{-15}$; Normality, $P = 0.35$; Lack of fit, $P = 0.52$.

total dissolved solids for *C. virginica* were found in the reviewed literature.

The salinity tolerance limits of the *C. virginica* may vary depending on the magnitude and duration of exposures to extreme conditions (McFarland et al. 2013) or sudden changes in salinity (McFarland et al. 2022). In response to extreme changes in salinity, oysters close their valves and seal themselves within their shells to avoid osmotic stress (Rybovich et al. 2016); consequently, oysters stop feeding, and growth rates decrease (Lavaud et al. 2017). In CL, salinity abruptly changed from 24 ppt to 11 ppt from day 28 to day 56 and from 19 ppt to 5.40 ppt from day 98 to day 122 (Fig. 6). During those periods, the growth rate decreased from 0.35 $\text{mm}\cdot\text{d}^{-1}$ to 0.01 $\text{mm}\cdot\text{d}^{-1}$ and from 0.33 $\text{mm}\cdot\text{d}^{-1}$ to 0.03 $\text{mm}\cdot\text{d}^{-1}$. As has been reported by other authors, the growth decreases in this study were most likely due to limited filtration due to the shell being closed. This situation resulted in a pattern in which the growth rate decreased during intervals related to sudden changes in salinity. Later, when salinity stabilized, the growth rate increased again. The decreases and increases in the growth rate observed in CL can thus be attributed to successive periods of stress and no-stress associated with periods of unstable and stable salinity, respectively.

Several studies have indicated that low salinity negatively affects the survival of oyster species. According to Maeda-Martinez et al. (2023), environmental fluctuations, particularly salinity in the range of 32 ppt to 13.6 ppt and high temperatures (>34 °C), caused mortality in farms of *Crassostrea corteziensis*. Low salinities impair the survival rate of *C. virginica* at any life stage (La Peyre et al. 2013, Leonhardt et al. 2017). The synergistic effects of salinity and temperature are probably the most important for *C. virginica* (Heilmayer et al. 2008). Low salinities (<15 ppt) and high water temperatures (>30 °C) have been shown to increase oyster mortality significantly (McFarland et al. 2022). In agreement with those studies, mortality in this study increased in CL after ~42 days (Fig. 3) when salinity fell to 15 ppt, and the temperature was close to 30 °C (Fig. 4).

The nursery phase in CL was conducted during the rainy season, a dynamic period with massive freshwater inputs due to rainfall and groundwater entering the lagoon. According to Herrera-Silveira and Ramírez-Ramírez (1998), CL is characterized by low salinity (2.10–3.70 ppt) and low dissolved oxygen concentrations (<1 $\text{mg}\cdot\text{L}^{-1}$) during this period, which may explain the negative relationships between the mortality rate and salinity and dissolved oxygen found in the lagoon. The role of pH in oyster mortality is unclear, and the significant relationship obtained for CL may have resulted from correlations between pH and other environmental variables.

Direct evidence of the ability of *C. virginica* to filter, ingest, and assimilate marine bacteria has been published (Crosby et al. 1990). Detritus and bacteria are food sources for *C. virginica*, although phytoplankton, nanozooplankton, non-cellulosic particulates, and dissolved organic matter are also required (Landon and Newell 1990). In the present investigation, Chl *a* was significantly higher in RL than in CL. However, no direct relationship was established between oyster growth and mortality rates with the Chl *a* concentration in either site. Moreover, no significant differences were detected in final oyster height and daily growth rates between the lagoons at the end of the nursery stage. Thus, it is likely that the difference in food availability associated with Chl *a* in both sites was compensated by the availability of other food sources.

Piyathilaka et al. (2012) found a positive relationship between the growth rate of *Crassostrea madrasensis* and total dissolved solids. The authors argued that dissolved solids were indicative of food abundance, as oysters feed on phytoplankton, detritus from sediment, bacteria, and dead phytoplankton and zooplankton. We found no evidence of dissolved solids influencing oyster growth. However, a possible positive effect on survival was observed in CL, where higher dissolved solids were associated with better survival. However, this result must be taken cautiously, as a positive correlation may exist between salinity and total dissolved

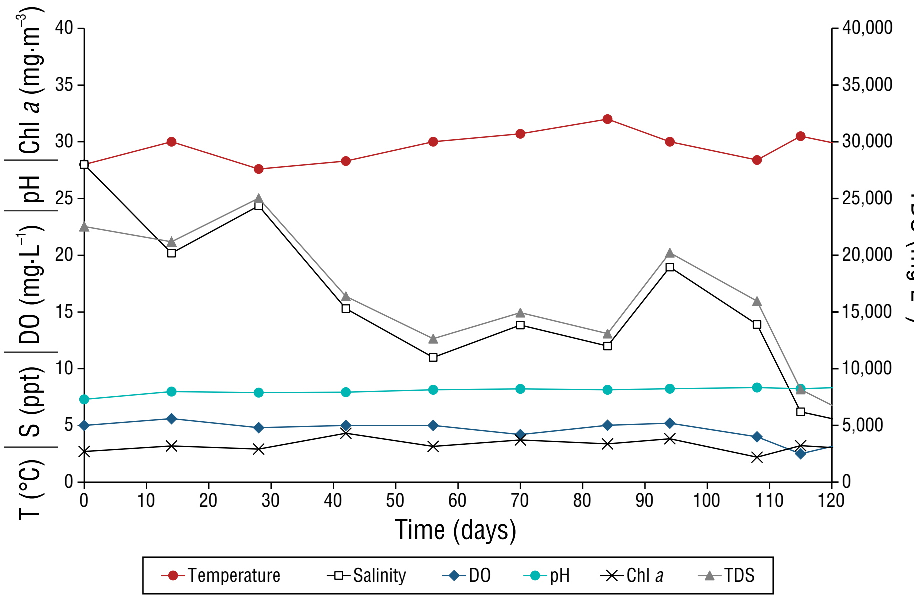

Figure 4. Temperature (T), salinity (S), dissolved oxygen (DO), pH, chlorophyll *a* (Chl *a*) concentration, and total dissolved solids (TDS) during the nursery stage of *Crassostrea virginica* reared in an off-bottom system in the coastal lagoon of Celestún (CL).

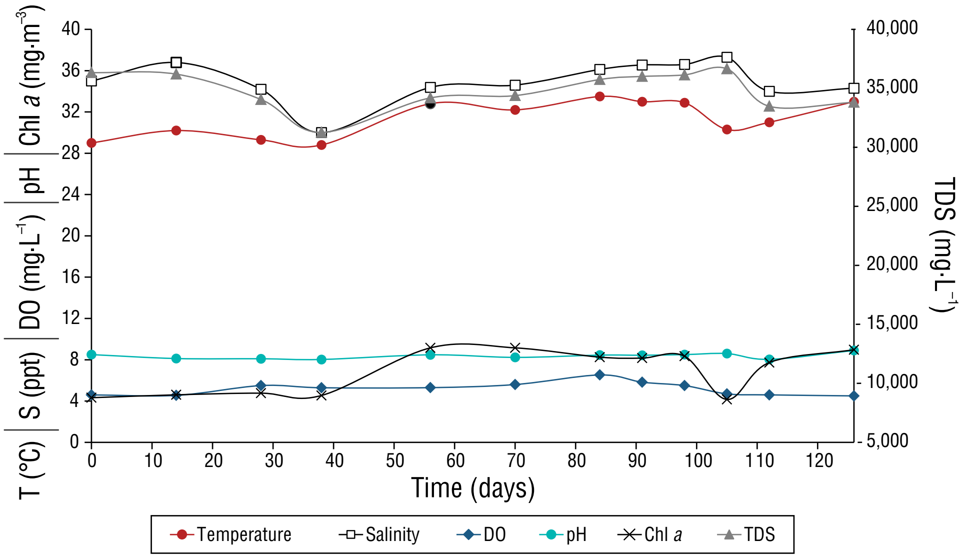

Figure 5. Temperature (T), salinity (S), dissolved oxygen (DO), pH, chlorophyll *a* (Chl *a*) concentration, and total dissolved solids (TDS) during the nursery stage of *Crassostrea virginica* reared in an off-bottom system in the coastal lagoon of Rio Lagartos (RL).

solids (Boyd 2020, Adjovu et al. 2023). Thus, total dissolved solids may appear to affect survival merely because this variable is correlated with salinity, with the latter being the actual cause influencing survival. To summarize, low salinity, low dissolved oxygen, and possibly low food availability in CL could increase oyster mortality, particularly at the end of the nursery stage.

In RL, faster growth rates were associated with high temperature and pH values. Temperature increases within acceptable limits promote oyster growth (Lowe et al. 2017), and seawater acidification appears to affect calcifying marine organisms (Clements et al. 2021). Beniash et al. (2010) showed that pH values of ~7.50 inhibited the shell and soft body growth of *C. virginica* when compared with control organisms growing under pH conditions of ~8.20. Thus, the inferior growth results obtained in RL at low pH may be due to an adverse effect on calcification when conditions in the lagoon were more acidic.

According to Rybovich et al. (2016), *C. virginica* can survive extended periods of low salinity (<5 ppt) at low

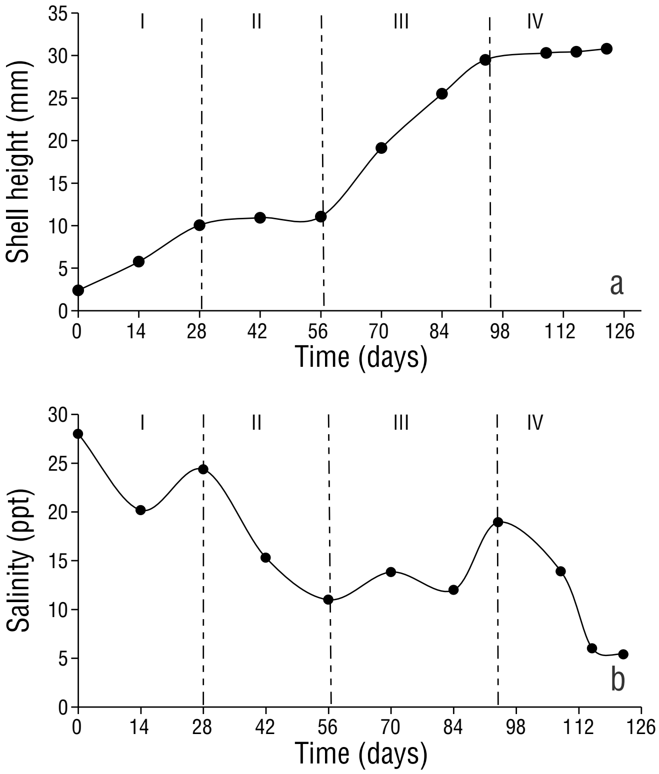

Figure 6. Periods when oyster growth increased (I and III) or stabilized (II and IV), which were associated with stable or unstable (decreasing) salinity values, respectively, during the nursery stage of *Crassostrea virginica* reared in an off-bottom system in the coastal lagoon of Celestún (CL).

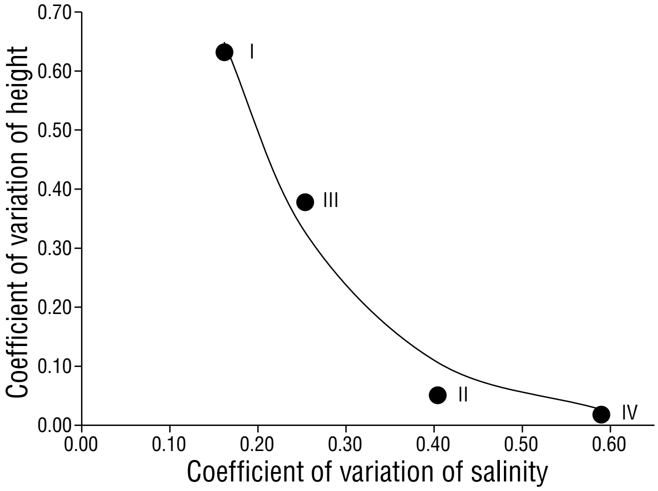

Figure 7. Relationship between the coefficients of variation of oyster height and salinity during the nursery stage of *Crassostrea virginica* reared in an off-bottom system in the coastal lagoon of Celestún (CL). Roman numerals indicate the periods when oyster growth increased (I and III) or stabilized (II and IV), which were associated with stable or unstable (decreasing) salinity values, respectively.

Table 4. Linear regression equations relating mortality rate (MR) and growth rate (GR) to environmental variables. S = salinity; DO = dissolved oxygen; TDS = total dissolved solids.

Site	Equation	*P*
Celestún	MR = –0.051 S + 1.107	0.001
	MR = –0.386 DO + 1.11	$3.75E^{-05}$
	MR = 1.043 pH – 8.11	0.034
	MR = –6.08 TDS + 1.31	$7.97E^{-04}$
Rio Lagartos	GR = 0.065 S – 1.99	0.045
	GR = 0.75 pH – 5.95	0.032

temperatures (<15 °C) but not elevated temperatures (>25 °C). On the other hand, Lowe et al. (2017) reported the deleterious effects of high temperature (>30 °C) and low salinity (<5 ppt). The authors also noted that the combination of high water temperature (>30 °C) and high salinity (>15 ppt) resulted in even higher oyster mortality. In contrast to those results, salinity and temperature in RL were high (31.02 °C and 35.02 ppt), but oyster mortality was negligible (lower than 1.0%), and survival was higher than in CL, where salinity was generally lower. Thus, even when the conditions are not those commonly reported as suitable for *C. virginica* production, high environmental stability (mainly in salinity, as seen in RL) may compensate for suboptimal rearing conditions.

Recent studies have shown that the hypoxia and salinity tolerance of *C. virginica* varies among populations in the Gulf of Mexico. For instance, Coxe et al. (2023) showed that distinct populations might be better adapted to tolerate extended periods of hypoxia during summer. Marshall et al. (2021) tested the salinity tolerance of oyster progeny from wild broodstock collected from estuaries with different mean salinities (7.40–35.50 ppt). They found that the progeny were better able to tolerate the salinity levels of the estuary where the corresponding broodstock was collected.

The spat used for this study was produced from a cultivated broodstock maintained in an estuary with a mean salinity of 18 ppt; the spat was then acclimated to a salinity of 24 ppt in the hatchery. The potentially high plasticity of the broodstock may have contributed to the excellent performance observed at high salinities and temperatures in this study, particularly in RL, although further studies are required to evaluate this possibility.

The modeling approach used in the present study helped us analyze and understand the dynamics of oyster nursery production and its relationships with the environmental variables of notably different lagoons. The growth and survival nonlinear regression models, namely Eq. (1), Eq. (2), and Eq. (3), proved to be statistically adequate for describing the shell height and survival of the oysters grown in both lagoons. It is worth noting that the model used to describe oyster survival in CL assumed that the mortality rate increased over time, thus accounting for the worsening environmental conditions in the lagoon as the nursery phase progressed.

CONCLUSIONS

The present study has shown that nursey production of *C. virginica* is technically feasible in the tropical coastal lagoons of CL and RL in Mexico. The results indicate that even when the environmental conditions are not optimal, rearing oysters under relatively stable conditions (RL) may be preferable to rearing oysters under more unstable conditions (CL). Further research should focus on the tolerance of *C. virginica* to the stressful conditions associated with genetic and physiological characteristics of the oyster populations in the southern Gulf of Mexico and the Caribbean Sea. The economic feasibility of nursery production in CL and RL should also be investigated.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3447/420421092.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: AHLL (main); Data curation: MEDM (main); Formal analysis: AHLL (main), MEDM (supporting); Funding acquisition: MAVM (main); Investigation: MEDM (main); Methodology: AHLL (main), MEDM (supporting); Project administration: MAVM (main); Resources: MAVM (main); Software: AHLL (main), MEDM (supporting); Supervision: AHF; Validation: AHLL (main), MEDM (supporting); Visualization: MEDM (main); Writing–original draft: AHL (main), MEDM (main) Writing–review & editing: AHL (main), MEDM (main), AHF (supporting), MAVM (supporting).

Data availability

The data for this study are not available.

Use of AI tools

The authors did not employ any AI tools in this work.

REFERENCES

Adjovu E, Stephen H, James D, Ahmad S. 2023. Measurement of total dissolved solids and total suspended solids in water systems: A Review of the Issues, Conventional, and Remote Sensing Techniques. Remote Sens. 15(14):3534. https://doi.org/10.3390/rs15143534

Baker SM, Mann R. 1992. Effects of hypoxia and anoxia on larval settlement, juvenile growth, and juvenile survival of the oyster *Crassostrea virginica*. Biol Bull. 182(2):265-269. https://doi.org/10.2307/1542120

Beniash E, Ivanina A, Lieb NS, Kurochkin I, Sokolova IM. 2010. Elevated level of carbon dioxide affects metabolism and shell formation in oysters *Crassostrea virginica*. Mar Ecol Prog Ser. 419:95-108. https://doi.org/10.3354/meps08841

Bishop MJ, Hooper P. 2005. Flow, stocking density and treatment against *Polydora* spp.: Influences on nursery growth and mortality of the oysters *Crassostrea virginica* and *C. ariakensis*. Aquaculture. 246(1-4):251-261. https://doi.org/10.1016/j.aquaculture.2005.01.021

Bodenstein S, Walton WC, Steury TD. 2021. Effect of farming practices on growth and mortality rates in triploid and diploid eastern oysters *Crassostrea virginica*. Aquacult Environ Interact. 13:33-40. https://doi.org/10.3354/aei00387

Bodenstein S, Callam BR, Walton WC, Rikard SF, Tiersch TR, La Peyre JF. 2023. Survival and growth of triploid eastern oysters, *Crassostrea virginica*, produced from wild diploids collected from low-salinity areas. Aquaculture. 564:739032. https://doi.org/10.1016/j.aquaculture.2022.739032

Boyd CE. 2020. Dissolved Solids. In: Boyd CE (ed.), Water Quality: An Introduction. Cham (Switzerland): Springer. p. 83-118. https://doi.org/10.1007/978-3-030-23335-8_5

Cabrera-Rodríguez P, Aldana D, Brulé T, Amador E. 1997. Culture of the American oyster, *Crassostrea virginica* (Gmelin 1971) in Rio Lagartos, Yucatán, México. Aquac Res. 28(8):611-619. https://doi.org/10.1046/j.1365-2109.1997.00902.x

Calabrese AF, Davis H. 1966. The pH tolerance of embryos and larvae of *Mercenaria mercenaria* and *Crassostrea virginica*. Bio Bull. 131(3):427-436. https://doi.org/10.2307/1539982

Clements JC, Carver CE, Mallet MA, Comeau LA, Mallet AL. 2021. CO_2-induced low pH in an eastern oyster (*Crassostrea virginica*) hatchery positively affects reproductive development and larval survival but negatively affects larval shape and size, with no intergenerational linkages. ICES J Mar Sci. 78(1):349-359. https://doi.org/10.1093/icesjms/fsaa089

[CONAPESCA] Comisión Nacional de Pesca y Acuacultura. 2022. Títulos acuícolas otorgados: CONAPESCA; [accessed 2022 Oct 27]. https://acuasesor.conapesca.gob.mx/transparencia_permisos.php

Coxe N, Casas SM, Marshall DA, La Peyre MK, Kelly MW, La Peyre JF. 2023. Differential hypoxia tolerance of eastern oysters from the northern Gulf of Mexico at elevated temperature. J Exp Mar Bio Ecol. 559:151840. https://doi.org/10.1016/j.jembe.2022.151840

Crosby M, Newell R, Langdon C. 1990. Bacterial mediation in the utilization of carbon and nitrogen from detrital complexes by *Crassostrea virginica*. Limnol Oceanogr. 35(3):625-639. https://doi.org/10.4319/LO.1990.35.3.0625

Estrada-Pérez N, Hernández-Llamas A, Ruiz-Velazco M. 2018. Stochastic modelling of aquaponic production of tilapia (*Oreochromis niloticus*) with lettuce (*Lactuca sativa*) and cucumber (*Cucumis sativus*). Aquac Res. 49(12):3723-3734. https://doi.org/10.1111/are.13840

Forkman J. 2009. Estimator and tests for common coefficients of variation in normal distributions. Commun Stat-Theory Methods. 38(2):233-251. https://dx.doi.org/10.1080/03610920802187448

Grizzle R, Ward K, Burdick D, Payne A, Berlinsky D. 2020. Eastern Oyster *Crassostrea virginica* growth and mortality in New Hampshire (USA) using off-bottom farm gear. N Am J Aquac. 82(2):132-142. https://doi.org/10.1002/naaq.10135

Hardage K, Street J, Herrera-Silveira JA. 2022. Late Holocene environmental change in Celestún Lagoon, Yucatán, Mexico. J Paleolimnol. 67:131-162. https://doi.org/10.1007/s10933-021-00227-4

Heilmayer O, Digialleonardo J, Qian L, Roesijadi G. 2008. Stress tolerance of a subtropical *Crassostrea virginica* population to the combined effects of temperature and salinity. Estuar Coast Shelf Sci. 79(1):179-185. https://doi.org/10.1016/j.ecss.2008.03.022

Herrera-Silveira JA, Ramírez-Ramírez J. 1998. Salinity and nutrients in the coastal lagoons of Yucatan, Mexico. SIL Proc. 1922-2010. 26(3):1473-1478. https://doi.org/10.1080/03680770.1995.11900971

La Peyre MK, Eberlin BS, Soniat TM, La Peyre JF. 2013. Differences in extreme low salinity timing and duration differentially affect eastern oyster (*Crassostrea virginica*) size class growth and mortality in Breton Sound, LA. Estuar Coast Shelf Sci. 135:146-157. https://doi.org/10.1016/j.ecss.2013.10.001

Langdon C, Newell R. 1990. Utilization of detritus and bacteria as food source by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. Mar Ecol Prog Ser. 58:299-310. https://doi.org/10.3354/meps058299

Lavaud R, La Peyre MK, Casas SM, Bacher C, La Peyre JF. 2017. Integrating the effects of salinity on the physiology of the eastern oyster, *Crassostrea virginica*, in the northern Gulf of Mexico through a Dynamic Energy Budget model. Ecol Model. 363:221-233. https://doi.org/10.1016/j.ecolmodel.2017.09.003

Leonhardt JM, Casas S, Supan JE, La Peyre JF. 2017. Stock assessment for eastern oyster seed production and field grow-out in Louisiana. Aquaculture. 466:9-19. https://doi.org/10.1016/j.aquaculture.2016.09.034

Lowe MR, Sehlinger T, Soniat TM, La Peyre MK. 2017. Interactive effects of water temperature and salinity on growth and mortality of eastern oysters, *Crassostrea virginica*: a meta-analysis using 40 years of monitoring data. J Shellfish Res. 36(3):683-697. https://doi.org/10.2983/035.036.0318

Maeda-Martínez AN, García-Murillo AG, Espinosa-Chaurand D, Garza-Torres R, García-Morales R. 2023. Growth, survival, and morphometric relationships of *Crassostrea corteziensis* cultivated during the nursery stage in oyster bags at different tidal levels, in Boca de Camichín, Nayarit, Mexico = Crecimiento, supervivencia y relaciones morfométricas de *Crassostrea corteziensis* cultivado en costales ostrícolas durante la etapa de preengorda, a diferentes niveles de marea en Boca de Camichín, Nayarit, México. Cienc Mar. 49:3388. https://doi.org/10.7773/cm.y2023.3388

Mallet A, Carver C, Doiron S, Thériault MH. 2013. Growth performance of eastern oysters *Crassostrea virginica* in Atlantic Canada: effect of the culture gear. Aquaculture. 396-399:1-7. https://doi.org/10.1016/j.aquaculture.2013.02.019

Marshall DA, Casas SM, Walton WC, Rikard FS, Palmer TA, Breaux N, La Peyre MK, Beseres J, Kelly M, La Peyre JF. 2021. Divergence in salinity tolerance of northern Gulf of Mexico eastern oysters under field and laboratory exposure. Conserv Physiol. 9(1):coab065. https://doi.org/10.1093/conphys/coab065

McFarland K, Donaghy L, Volety A. 2013. Effect of acute salinity changes on hemolymph osmolality and clearance rate of the non-native mussel, *Perna viridis*, and the native oyster, *Crassostrea virginica*, in Southwest Florida. Aquat Invasions. 8(3):299-310. http://dx.doi.org/10.3391/ai.2013.8.3.06

McFarland K, Vignier J, Standen E, Volety AK. 2022. Synergistic effects of salinity and temperature on the eastern oyster *Crassostrea virginica* throughout the lifespan. Mar Ecol Prog Ser. 700:111-124. https://doi.org/10.3354/meps14178

Morelos-Villegas AD, Condal A, Ardisson PL. 2018. Spatial heterogeneity and seasonal structure of physical factors and benthic species in a tropical coastal lagoon, Celestun, Yucatan Peninsula. Reg Stud Mar Sci. 22:136-146. https://doi.org/10.1016/j.rsma.2018.06.008

[NASA] National Aeronautics and Space Administration. 2022. Giovanni platform: NASA; [accessed 2024 April 25]. https://giovanni.gsfc.nasa.gov/giovanni

Piyathilaka M, Hettiarachchi M, Wanninayake W. 2012. Growth and health status of cultured edible oyster, *Crassostrea madrasensis* (Preston) in the Panadura estuary, Sri Lanka. J Natn Sci Found Sri Lanka. 40(3):201-210. http://dx.doi.org/10.4038/jnsfsr.v40i3.4694

Poirier LA, Clements JC, Sonier R, Lanteigne L, Nadeau A, Comeau LA. 2020. Testing the efficacy of bouncing-bucket nursery systems for enhancing shell strength and thickness in on-bottom cultured Eastern oysters (*Crassostrea virginica*). Aquacult Eng. 90:102101. https://doi.org/10.1016/j.aquaeng.2020.102101

Ratkowsky DA. 1983. Non-linear Regression Modeling: A Unified Practical Approach. New York: Marcel Dekker. 276 p.

Rihani VA, Torres R, Peraza J, Mendoza I, Domínguez F. 1989. Información Básica de la Actividad Pesquera en Yucatán, 1988. First edition. México: Gobierno del Estado de Yucatán. 59 p.

Rybovich M, La Peyre MK, Hall SG, La Peyre JF. 2016. Increased temperatures combined with lowered salinities differentially impact oyster size class growth and mortality. J Shellfish Res. 35(1):101-113.
https://doi.org/10.2983/035.035.0112

Serna-Gallo I, Ruiz-Velazco JMJ, Acosta-Salmón H, Peña-Messina E, Torres-Zepeda G, Saucedo PE. 2014. Growth and reproduction patterns of the winged pearl oyster, *Pteria sterna*, cultivated in tropical environments of Mexico: Implications for pearl farming = Patrones de crecimiento y reproducción de la concha nácar, *Pteria sterna*, cultivada en un ambiente tropical de México: Implicaciones para el cultivo de perlas. Cienc Mar. 40(2):75-88.
https://doi.org/10.7773/cm.v40i2.2393

Shumway SE. 1996. Natural environmental factors. In: Kennedy VS, Newell RIE, Eble AF (eds.), The Eastern Oyster, *Crassostrea virginica*. College Park (USA): Maryland Sea Grant College. p. 467-513.

Snyder J, Boss E, Weatherbee R, Thomas AC, Brady D, Newell C. 2017. Oyster aquaculture site selection using Landsat 8-derived sea surface temperature, turbidity, and chlorophyll *a*. Front Mar Sci. 4:190.
https://doi.org/10.3389/fmars.2017.00190

Stalker JC, Price RM, Rivera-Monroy VH, Herrera-Silveira J, Morales-Ojeda S, Benítez JA, Parra-Parra D. 2014. Hydrologic dynamics of a subtropical estuary using geochemical tracers, Celestún, Yucatan, Mexico. Est Coast. 37:1376-1387.
https://doi.org/10.1007/s12237-014-9778-5

Thomas L, Allen SK, Plough LV. 2019. The effect of aquaculture gear on the growth and shape of the oyster *Crassostrea virginica* during a “finishing period” in Chesapeake Bay, USA. Aquaculture. 508:1-9.
https://doi.org/10.1016/j.aquaculture.2019.03.061

Vega-Cendejas MaE, Hernández M. 2004. Fish community structure and dynamics in a coastal hypersaline lagoon: Rio Lagartos, Yucatán, Mexico. Estuar Coast Shelf Sci. 60(2):285-299.
https://doi.org/10.1016/j.ecss.2004.01.005

Vera DA, Aldana DA. 2000. Crecimiento y sobre vivencia de semillas del ostión: *Crassostrea virginica* en una granja camaronícola en Yucatán, México. Rev Biol Trop. 48:1-17.