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Research Articles

The effect of density on the cultivation of the native mangrove oyster *Crassostrea tulipa* (Lamarck, 1819)

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ABSTRACT. In Brazil, the cultivation of *Crassostrea tulipa* (= *C. gasar*) is gaining in importance. However, little is known about the best conditions for farming. Therefore, this study aimed to evaluate the effect of oyster density (50, 100, 200, and 400 mL of seeds/0.15 m^2; 100, 200, 300, and 400 ind/0.10 m^2 (basket area) and 30, 60, 120, and 180 ind/0.13 m^2 (lantern floor area) in nursey, juvenile and adult phase, respectively) on the growth and survival of *C. tulipa* in farm cultivation. In the nursery phase, the 50 mL density resulted in smaller oyster size, as expressed in height and height/length (H/L) ratio (1.31 ± 0.03 mm), compared to other densities, while the length and width was equal among densities. The animals' individual average weight and H/L ratio were negatively influenced by a density of 100 ind/0.10 m^2 or bigger. However, animals grown at the density of 200 ind/0.10 m^2 did not differ statistically in length or width from those grown with 100 ind/0.10 m^2. A high survival rate (≥98%) was found in the nursery and juvenile phases.

Keywords: *Crassostrea tulipa*; oyster culture; density; commercial size; hanging culture

INTRODUCTION

Crassostrea tulipa (= *C. gasar*) (Lamarck, 1819) is a tropical mangrove oyster first described to estuarine zones from Senegal to Angola (Ranson, 1948; Sandisson, 1966), with distribution, now verified by molecular markers, from Venezuela to Brazil (Lapègue *et al*., 2002; Pie *et al*., 2006; Carpenter & De Angelis, 2016), being conspecific with *C. brasiliana* (Lamarck, 1819), its synonym (Lazoski *et al*., 2011). In South America, the species predominates in the eastern Brazil ecoregion (Carranza *et al*., 2009). It is commonly associated with brackish water bordering the coast where mangroves grow, living on fallen branches, tree trunks, and mangrove roots (Caryé, 1981), but in Brazil, the species stands out for its preference for the infralittoral habitat, *i.e*., rocky coastal regions (Christo & Absher, 2006).

The species is historically associated with traditional littoral people of Africa who view this oyster as a source of protein, as well as a source of income, by the direct exploitation of its natural stock or by the cultivation of mangrove roots bearing the oysters (Gruvel, 1913; Nicklès, 1950; Ajana, 1980; Cham, 1992), and these practices continue in some localities (Ansa & Bashir, 2007; Adite *et al*., 2013; Crow & Carney, 2013).

In Brazil, *C. tulipa* has fair economic importance, and it is cultivated in tropical coastal areas where the cultivation of *C. gigas* (Thunberg, 1793) is otherwise impractical (Gomes *et al*., 2014). The preference for farming this mangrove oyster species is based on its faster growth and larger size in comparison to *C. rhizophorae* (Guilding, 1828) (Legat *et al*., 2017a), a sympatric species occurring from the US Florida coast to Uruguay (Rios, 2009). Indeed, the exploitation of these oysters in their natural stocks is one of the most recognizable traditional activities along the Brazilian coast (Wakamatsu, 1973), and it serves as a source of income in many communities (Ramos *et al*., 2013). However, in some locations, the unsustainable harvesting of mangrove oysters compromises their natural stocks, especially in the littoral zone of São Paulo

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(Mendonça & Machado, 2010) and Paraná (Westphal & Ostrenski, 2016).

C. tulipa is known for its inherent palatability (Antunes & Itô, 1968), it has potential as a species for farming (Angell, 1986). Studies proposing the development of such activity have been performed in the context of economic, health, and environmental issues arising from the new market demand (Wakamatsu, 1973; Kamara, 1982; Afinowi, 1984; Pereira & Soares, 1996).

The farming of mangrove oyster species, however, still relies, almost exclusively, on the extraction of seeds from the wild by artificial collectors (Nalesso *et al*., 2008; Gardunho *et al*., 2012; Christo *et al*., 2016; Diadhiou & Ndour, 2017; Oliveira *et al*., 2018; Funo, 2019; Tureck *et al*., 2020). The implications of utilizing such a method involve the difficulty of correct species identification, including the high polymorphism of *Crassostrea* oysters in areas of sympatric occurrence (Reece *et al*., 2008), small capacity for seeds settlement by structure (ranging from ~5.000 to ~20.000 seeds, according to Galvão *et al*., 2009) and the likelihood of different seed ages attaching to the same structure. Moreover, collecting oyster spat may prove inconsistent as the reproductive cycle of *C. tulipa* is greatly influenced by low salinity (Zabi & Le Loeuff, 1992; Paixão *et al*., 2013; Gomes *et al*., 2014). Only in recent years, as our knowledge of reproductive biology of *C. tulipa* improved (Ramos *et al*., 2013, 2014; Gomes *et al*., 2014), has the establishment of seed supplies for farming through induced spawning and broodstock selection become available.

Studies reporting on the cultivation of *C. tulipa* have been conducted along the Brazilian coastline to evaluate oyster growth in estuarine zones of Pará (Funo *et al*., 2015; Oliveira *et al*., 2018), Maranhão (Legat *et al*., 2017b), and São Paulo (Pereira *et al*., 2001; Galvão *et al*., 2009) to promote oyster cultivation. However, oyster farming based on wild seeds or adults occurs diffusely from Pará (0°38'S, 47°50'W) to Paraná (25°52'S, 48°34'W) coasts (Legat *et al*., 2008). Cultivation of *C. tulipa* thorough the central to northern littoral zone of Brazil is conducted in estuarine ecosystems, marine areas usually attributed to either extractive fishing (MPA, 2011) or other unrelated economic activities. The use of artisanal rack structure in the intertidal zone for farming is also a common practice of farmers in this region, implying lower production costs (Angell, 1986) since it is conducted by traditional family communities (Nascimento, 1990).

The northern and southern bays of Santa Catarina Island (from 27°25'S, 48°31'W to 27°49'S, 48°34'W) are responsible for 97% of the Brazilian oyster culture coming from hatchery-produced seeds (EPAGRI, 2018; IBGE, 2019). However, only a small percentage (approximately 10%) belongs to *C. tulipa* production. Also, *C. tulipa* cultivation, in this particular area, follows the same farming steps proposed for the cultivation of *C. gigas*: floating wooden boxes for nursery, oyster basket for juveniles, and oyster lantern for final grow-out (Mizuta *et al*., 2012).

To enhance oyster production, knowledge of optimal culture density is an essential factor (Taylor *et al*., 1997), and some studies of oyster species cultivated in Brazil have reported on this metric. In Brazil, stocking density evaluation has already been conducted for *C. rhizophorae* (Maccacchero *et al*., 2005; Cardoso-Junior *et al*., 2012), *C. gigas* (Ferreira & Ferreira, 2014; Roncarati *et al*., 2017) as well as *C. tulipa* with individuals acquired from the wild (Pereira *et al*., 2001; Galvão *et al*., 2009). However, an evaluation of stocking density in the marine environment in the bays of Santa Catarina has never been performed, especially covering every phase of cultivation.

Therefore, this study aimed to evaluate the effect of oyster density on the growth and survival of *C. tulipa* cultivated at different densities at nursery, juvenile and adult phases to provide technical support for the species' production in Brazil.

MATERIALS AND METHODS

The present study was carried out at Fazenda Marinha Atlântico Sul located in Ribeirão da Ilha, Florianópolis/SC (27°44'31.29"S; 48°33'29.66"W), a representative site for *Crassostrea tulipa* cultivation, since the vast majority of farms in Brazil are located around of this site.

Environmental parameters

During the experimental period, the water temperature was recorded hourly using the Data Logger StowAway® Tidbit® sensor. Salinity was observed four times a week through a Biobrix® refractometer (Model 211). Concentrations of total particulate matter (TPM), particulate inorganic matter (PIM), and particulate organic matter (POM) were determined weekly throughout the experimental period by adopting the methodology described by Strickland & Parsons (1972).

Water samples were collected weekly at a depth of 45 cm. These samples were collected in 1 L amber bottles and stored at 4°C until laboratory analyses were performed. Then, 250 mL of water samples were filtered on 47 mm diameter Macherey-Nagel GF-3 filters, previously washed with distilled water, calcined, and weighed. At the end of each filtration, the sample filters were rinsed with ammonium formate (0.5 N) to remove the salts. TPM values were obtained after drying the filters containing samples in an oven at 60°C for 24 h. PIM values were obtained by calcining the TPM samples at 450°C for 2 h, and POM values were determined by the difference between TPM and PIM (mg L^{-1}). The index was obtained by the PIM/POM ratio.

Spawning, larviculture, and spat nursery

Spawning was performed in December of 2015, using oysters from the breeding stock of *C. tulipa* specimens from the Laboratório de Moluscos Marinhos of the Universidade Federal de Santa Catarina (LMM/UFSC). Spawning, larviculture, and spat nursery were performed as described by Silveira *et al.* (2011). Cultivation steps in grow-out farms followed Mizuta *et al.* (2012), in which, herein, the nursery phase consisted of oysters ranging from 1.5 to 20 mm in size, while, in the juvenile phase, oysters ranged from <20 to 50 mm in size.

Nursery phase

This phase of the experiment occurred from July to November 2016. Seven hundred seventeen thousand seeds retained in a 1.5 mm size mesh (mean height 2.50 ± 0.30 mm) were used to experiment. The experimental design was performed in a completely randomized block with four treatments (density of 50, 100, 200, and 400 mL seeds/0.15 m^2, respectively 11,950, 23,900, 47,800 and 95,600 seeds/0.15 m^2) in quadruplicate. Considered the best structure for oyster growth performance at this phase (Ferreira & Ferreira, 2014), the seeds were kept in floating wooden boxes measuring 92×79.5×20 cm (length×width×height) and subdivided into four compartments with an area of 0.15 m^2/compartment and volume of 0.03 m^3/compartment and covered with a mesh size of 0.710 mm. Each compartment formed an experimental unit (EU). The boxes were washed weekly with a pressurized freshwater jet.

The first sieving of seeds, by size, occurred at 42 days of cultivation, using a set of sieves with 1.5 and 3 mm mesh. The seeds were again stocked at the same densities (50, 100, 200, and 400 mL seeds/0.15 m^2) after sieving; the box was covered with 1 mm mesh. At 72 days of cultivation, the seeds were sieved again using a set of sieves with 3 and 6 mm mesh; the seeds were populated in boxes covered with 4 mm mesh, keeping the initial densities (50, 200, 200 and 400 seeds mL/EU). Final sieving, using sieves with 6 and 16 mm mesh, was carried out at 114 days of culture.

Estimates of survival (number of live seeds / initial number of seeds) and shell dimensions (n = 50 / EU / size class) were carried out with each sieving. The measurements taken were shell height (mm) and shell length (mm), using a Starrett® digital caliper (0.1 mm).

Juvenile phase

From the total number of seeds obtained in the nursery phase, 16,000 seeds were taken randomly and placed in 0.10 m^2 baskets; four attached trays formed a set. The experimental design at this stage was completely randomized. Four culture densities of 100, 200, 300, and 400 ind/0.10 m^2 (basket) were evaluated with 16 replicates/treatment.

The juvenile phase was concluded after 48 days of cultivation, and the fouling was removed using a freshwater pressurized jet, and oysters were individually scraped for cleaning. The survival rate was calculated, and the animals' total live weight from each experimental unit was measured using the Shimadzu® precision digital scale (Model UX4200H - 0.0001 g). Biometry was performed with the aid of a Starrett® digital caliper (0.1 mm), using measurements of shell height (mm), shell length (mm), and shell width (mm).

Grow-out phase

The grow-out phase was carried out from January to October 2017. A total of 6,240 oysters from the juvenile phase were used. The animals were distributed in lanterns with a 24 mm mesh opening, containing five floors with an area of 0.13 m^2. Measurements of total live weight (g) of each experimental unit were accomplished using the Shimadzu® precision digital scale.

The experimental design was completely randomized, and the densities tested were 30, 60, 120, and 180 ind/0.13 m^2 (lantern floor) with 16 replications/treatment. Management of the experimental units was carried out monthly, consisting of washing using a high-pressure freshwater jet and an individual scraping of oysters with a cleaver to remove fouling before the evaluations.

At the tenth month of culture, survival (%), shell height, length, and width (mm) (n = 30 ind/replicate) were carried out. The measurements were taken according to Galtsoff (1964), using an analog caliper. The oysters' weight was taken using the Shimadzu® digital precision scale. All oysters in different size classes (<60, ≥60 to <80, and ≥80 mm) were evaluated using an analog caliper. The measurements were taken according to Galtsoff (1964).

Statistical analysis

Survival and growth data (height, length, height/length ratio (H/L), width, individual average weight) were submitted to the normality (Shapiro-Wilk), and homoscedasticity of variances (Levene) tests. Subsequently, ANOVA was applied. When a difference between the averages of treatments was found, Tukey's test was applied at a significance level of 5%. All analyses were performed using the SAS® program (SAS, 2003).

RESULTS

Environmental parameters

The lowest salinity mean was observed at the end of January 2017 (26 ± 1.41) and the highest was detected in September 2017 (35.80 ± 0.45), with a mean of 32.85 ± 2.15. The lowest average temperature was recorded in August 2016 (16.82 ± 0.71ºC), and the highest in February 2017 (28.67 ± 0.64ºC); the overall mean was 21.81 ± 3.13ºC (Fig. 1).

Throughout the experimental period, TPM, PIM, and POM values showed their lowest and highest mean values, respectively, in June 2017 and November 2016. TPM's average values ranged from 25.98 ± 6.34 to 84.76 ± 6.65 mg L^{-1} with an overall mean of 54.67 ± 14.43 mg L^{-1}. For PIM, the averages varied from 19.55 ± 4.13 to 67.35 ± 5.33 mg L^{-1} with a general mean of 39.66 ± 9.83 mg L^{-1}, while POM averages varied (Fig. 2) from 6.43 ± 2.66 to 17.41 ± 5.33 mg L^{-1} with an overall mean of 10.42 ± 2.93 mg L^{-1}. The average values of the PIM/POM ratio showed an overall mean of 4.61 ± 1.73, while the minimum and maximum values encountered for this parameter ranged from 1.31 to 10.64.

Nursery phase

The first evaluation carried out at 42 days of cultivation demonstrated significant differences among the densities for height in the seeds retained in the 3 mm mesh (Fig. 3). Seeds grown at densities of 400 mL/0.15 m^2 had the highest mean height of 6.15 ± 0.14 mm, while those grown at a density of 50 mL/0.15 m^2 presented the lowest mean of 4.99 ± 0.18 mm, with no differences for mean length. H/L values were higher in seeds retained at 3 mm mesh grown at a density of 400 mL/0.15 m^2 (1.22 ± 0.03), reflecting their high height value (Fig. 3). Seeds retained at 1.5 mm mesh exhibited similar growth ($P > 0.05$) for all densities tested (Fig. 3).

In the second evaluation, at 72 days of cultivation, seeds surpassed the 3 mm size category since they were all retained at the 6 mm mesh size category. The higher values of height come from seeds grown at a density of 400 mL/0.15 m^2 (13.92 ± 0.63 mm) and 200 mL/0.15 m^2 (12.78 ± 0.23 mm), showing a significant difference between them and from each other. Likewise, the average length and H/L ratio of seeds retained at the 6 mm mesh size after sifting was higher at a density of 400 mL/0.15 m^2 (11.56 ± 0.20 and 1.20 ± 0.04, respectively). It should be noted that the density of 200 mL/0.15 m^2 treatment did not differ from seeds grown at densities of 50 mL/0.15 m^2 and 100 mL/0.15 m^2 ($P > 0.05$) (Fig. 3).

In the third and final evaluation carried out at 114 days of cultivation, the seeds retained in the 6 mm mesh did not exhibit significant differences in any other attribute besides length, in which the density of 400 mL/0.15 m^2 showed the lowest values differing from 100 mL/0.15 m^2 (Fig. 4). For the seeds retained in the 16 mm mesh, differences were only noted in height, and the H/L ratio between seeds cultivated at 50 mL/0.15 m^2, in that seeds of this treatment was more rounded than the seeds cultivated at the lowest density (Fig. 4).

Juvenile phase

The cultivated oyster growth results at a different density per basket exhibited a particular pattern in which oysters appeared longer and wider with individual average weight most directly affected by decreasing density in cultivation (Fig. 5). More specifically, oysters cultivated at 100 ind/0.10 m^2 presented the highest values of individual average weight and a more rounded conformation, as corroborated by the lowest H/L ratio values, in comparison to any other treatment. The survival rate of oysters cultivated at 400 ind/0.10 m^2 was higher, though all other density treatments' survival rate reached at least 98% (Fig. 5).

The growth of oysters in the juvenile phase occurred primarily in height and length. Height and length in late cultivated juvenile oysters (Fig. 5) ranged from 50.51 ± 3.77 to 52.54 ± 3.16 mm and 34.24 ± 3.39 to 39.38 ± 2.66 mm, respectively, while in seeds retained at 16 mm mesh (Fig. 4), values varied from 26.78 ± 0.74 to 28.69 ± 0.74 mm in height and 20.15 ± 0.67 to 20.50 ± 0.26 mm in length. For width, though, values were similar, as indicated by seeds retained at the 16 mm mesh (Fig. 4), varying from 9.68 ± 1.84 to 10.94 ± 2.75 mm, while juvenile oysters (Fig. 5) varied from 9.34 ± 0.87 to 10.38 ± 0.92 mm.

Differences were perceived at different densities of cultivation. As density increased, the length of oysters and individual average weight decreased. The lowest density of 100 ind/0.10 m^2 showed 39.38 ± 2.66 mm in length and an individual average weight of 12.78 ± 1.45 g, while the highest density of 400 ind/0.10 m^2 showed the lowest values for both parameters (34.24 ± 3.39 mm length and 8.56 ± 1.56 g, respectively) (Fig. 5). Higher density treatment (400 ind/0.10 m^2) also showed a small H/L ratio (1.48 ± 0.13) when compared with small density treatment (100 ind/0.10 m^2 and H/L

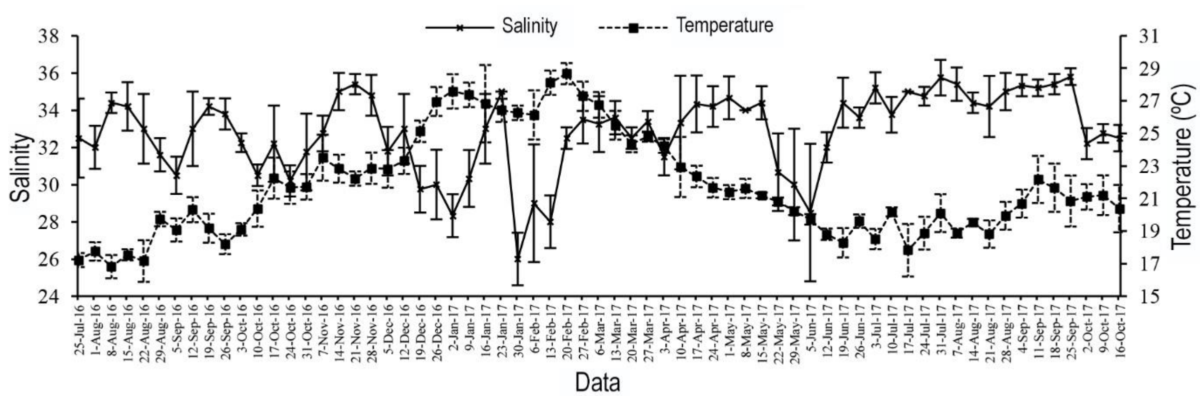

Figure 1. Salinity and temperature (ºC) of water during the experimental period. The bar represents the standard deviation.

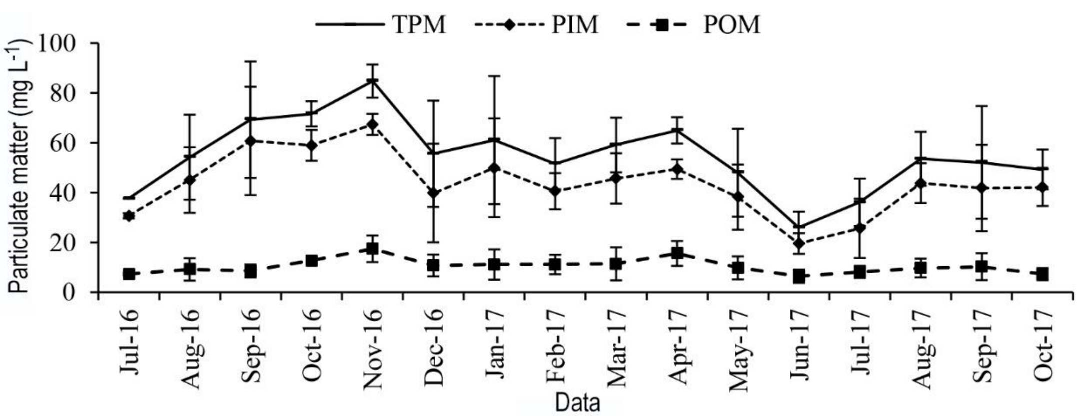

Figure 2. Total (TPM), inorganic (PIM), and organic (POM) particulate matter during the experimental period. The bar represents the standard deviation.

1.31 ± 0.07), implicating narrower juveniles. The survival rate in this phase-maintained value greater than 98% in all treatments; however, survival and density 100 was statistically higher.

Final grow-out

During the final phase of cultivation, in higher density, height and H/L ratio of individuals exhibited higher values, while length showed lower values, except the 30 ind/0.13 m^2 treatment, which did not differ significantly from those of other treatments (Fig. 5). The cultivated oysters' width showed similar values among treatments, varying from 26.54 ± 0.97 to 28.40 ± 1.39 mm, a significant growth compared to the previous cultivation phase, forming a cupped-shape shell.

Mean values of the individual average weight of oysters cultured at 30 and 60 ind/0.13 m^2 (87.91 ± 9.48 and 87.70 ± 9.95 g, respectively) showed the lowest values when compared to oysters cultured at a density of 120 (91.06 ± 7.62 g) and 180 (90.32 ± 6.17 g) ind/0.13 m^2. Also, differences were noted between oysters grown at densities of 180 and 120, and densities of both 30 and 60 ind/0.13 m^2 (Fig. 5).

Size class after ten months of cultivation

The survival rate was 75.06 ± 4.38% (Fig. 5), considering the performance growth of oysters at 120 ind/0.13 m^2, showing that 54.88 ± 5.88 individuals reached the height of ≥80mm, providing a total of 5.177 ± 0.439 kg of oysters. As for the oysters, the height of which ranged from ≥60 to <80 mm, 25.38 ± 2.06 individuals provided a total of 1.391 ± 0.222 kg (Fig. 6).

Superior results were also found in the performance growth of oysters at a density of 180 ind/0.13 m^2 in that these oysters had a survival rate of 76.53 ± 7.28%, among which 63.17 ± 3.38 individuals reached a height of ≥80 mm, providing 5.813 ± 0.169 kg. Oysters with a height ranging from ≥60 to <80 mm at this density totaled 54.50 ± 1.95 individuals with a total weight of 2.977 ± 0.230 kg of oysters suitable for commercialization (Fig. 6). Other density treatments showed lower results in both the number and weight of oysters (Fig. 6) and the lowest rates of survival (Fig. 5).

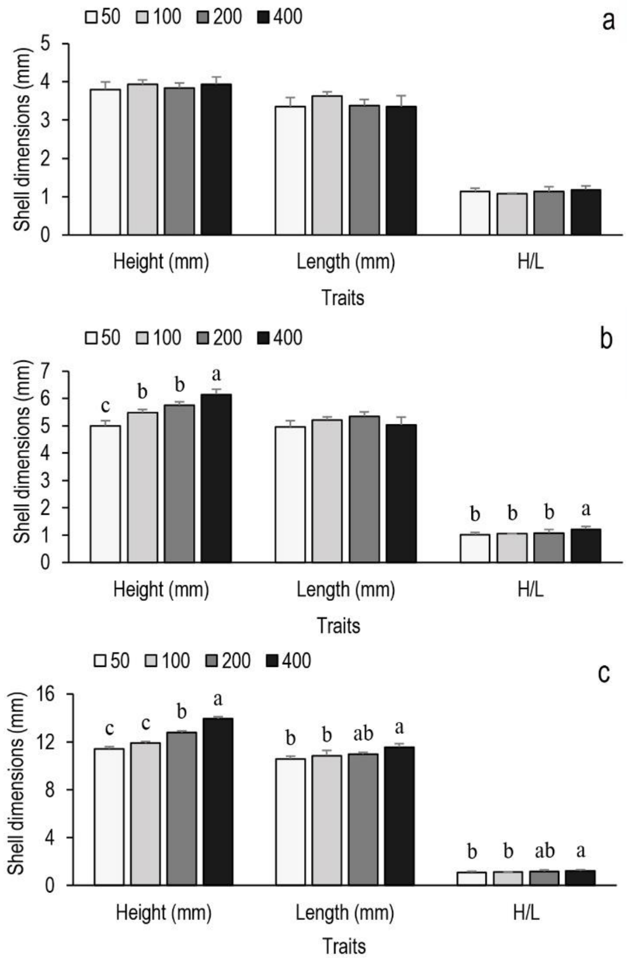

Figure 3. Mean ± standard deviation of height (mm), length (mm), height/length ratio (H/L), and width (mm) of *Crassostrea tulipa* oyster seeds after a), b) 42 and c) 72 days of nursery culture in the field in different density treatments. Figure shows seeds retained at a) 1.5 mm mesh, b) 3 mm mesh, c) 6 mm mesh. Density treatments are 50, 100, 200, and 400 mL of oyster seeds/0.15 m^2. Least square means with different letters in the column were significantly different ($P < 0.05$) by Tukey's test.

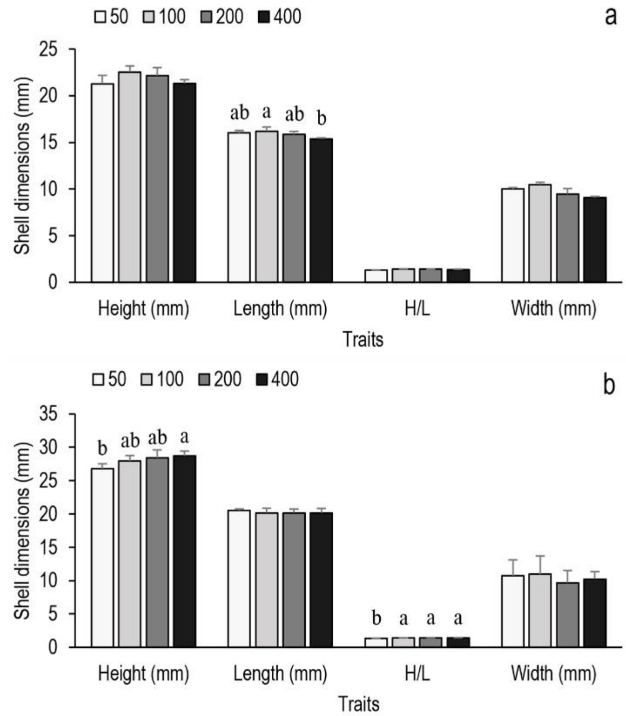

Figure 4. Mean ± standard deviation of height (mm), length (mm), height/length ratio (H/L), and width (mm) of *Crassostrea tulipa* oyster seeds after 114 days of nursery culture in the field in different density treatments. a) Shows seeds retained at 6 mm mesh, and b) shows seeds retained at 16 mm mesh. Density treatments are 50, 100, 200, and 400 mL of oyster seeds/0.15 m^2. Least square means with different letters in the column were significantly different ($P < 0.05$) by Tukey's test.

DISCUSSION

For most density treatments throughout all farm phases, the cultivation of *Crassostrea tulipa* presented good performance. All four densities provide satisfactory results for nursery phase cultivation, even though some differences are significant among shell dimensions, as individuals reached suitable size for the juvenile phase of cultivation (at least 20 mm height). Most parameters evaluated in oyster growth maintained similar values for the juvenile phase except for width and individual average weight where treatments of 100 and 200 ind/0.10 m^2 exhibited the highest values. As for the grow-out phase, a density of 120 ind/0.13 m^2 seems ideal for acquiring most commercial oysters with heavier individual average weight.

The attempt to cultivate *C. tulipa* in marine areas seems quite diffuse in the literature. Cayré (1981) reports that mangrove oysters placed in cages and cultivated in a marine environment presented initial mortality of 16%, but the specimens' growth was higher, and the specimens acquired better palatability than those cultivated in the mangrove. Lopes *et al.* (2013) showed that *C. tulipa* seeds cultivated in Santa Catarina for a year exhibited a higher initial growth, until the 240th day of cultivation, in the marine site compared to the estuarine site [marine oysters with a mean of 31.5 ± 6.6 height × 25.6 ± 4.5 length mm and estuarine oysters with 27.0 ± 13.2 height × 22.6 ± 10.2 length mm]. The same study also demonstrated that oysters in the estuarine site surpassed, in mean shell height and length, oysters cultivated in the marine site in the last four months of cultivation, with 75.86% of oysters reaching height values of at least 50 mm, in comparison to 42.92% of oysters in the marine site (Lopes

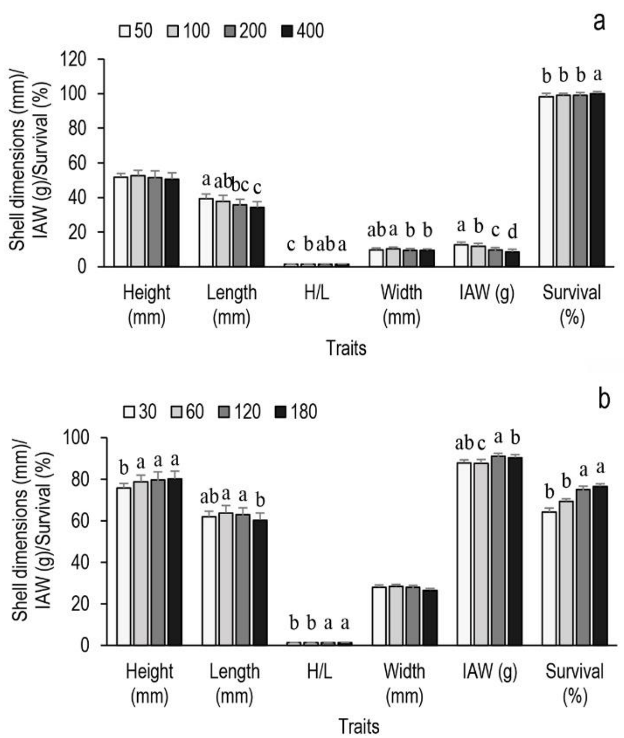

Figure 5. Mean ± standard deviation of height (mm), length (mm), height/length ratio (H/L), width (mm), individual average weight (IAW) (g), and survival (%) at a) the intermediate culture and b) after 10 months of final grow-out cultivation in different density treatments. Density treatments of 50, 100, 200, and 400 represent the number of oysters/0.10 m^2 culture and density treatments of 30, 60, 120, and 180 represent the number of oysters/0.13 m^2, respectively, in figures a and b. Least square means with different letters in the column were significantly different ($P < 0.05$) by Tukey's test.

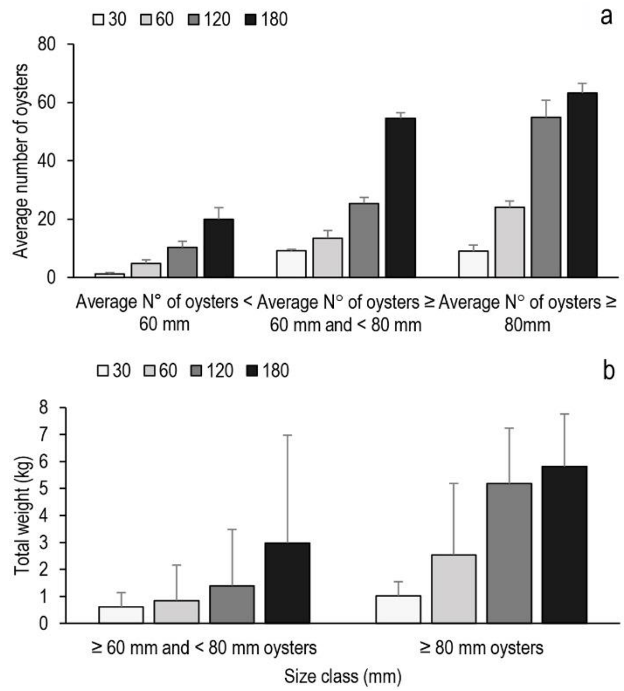

Figure 6. Mean ± standard deviation of a) number of oysters and b) weight by size class after 10 months of final grow-out cultivation in different density treatments. Density treatments of 30, 60, 120, and 180 represent the number of oysters/0.13 m^2.

et al., 2013). Legat *et al*. (2017b) cultivated *C. tulipa* for 300 days in Santa Catarina (south of Brazil), in marine and estuarine sites, and two estuarine sites in Maranhão state (north of Brazil). Results of this study showed that the estuarine site of Santa Catarina presented the best growth performance (final height of 71.96 ± 8.05 mm), followed by the marine site (55.31 ± 6.05 mm), while in Maranhão estuarine sites, oysters did not reach a minimum of 50 mm in height.

Such previous promising results reflect the wide optimum tolerance range of *C. tulipa* for either hypersaline or hyposaline waters for extended periods (10-45 g L^{-1}, Funo *et al*., 2015; Horodesky *et al*., 2019), which makes *C. tulipa* a proper species to farm in most coastal areas of Brazil.

Our study aimed to verify proper density thorough all steps of cultivating *C. tulipa* since the arrival of seeds in nursery structures to adult commercialization in grow-out farms located in marine areas. Analyses of the best stocking rate in oyster farming give information for organizing resources and establishing proper labor dynamics to minimize inputs and maximize the highest outputs (Shang, 1981; Asche *et al*., 2009). Such information contributes to spatial planning at the regional level to avoid environmental and production risks (Alleway *et al*., 2016).

Previous studies have attributed higher oyster growth rates to low-density treatments, which enhances the value of individual oysters per cultivated unit as cultivation becomes limited per area (Holliday *et al*., 1993; Mgaya & Mercer, 1995; Alunno-Bruscia *et al*., 2001; Cardoso-Junior *et al*., 2012; Marshall & Dunham, 2013; Azevedo *et al*., 2015; Roncarati *et al*., 2017). Additionally, overstocking situations usually drive cultivations toward a fragile state, mostly expressed in terms of increased time to marketable size and irregular growth (Beland, 1987), increased mortality, and, sometimes, individuals exhibiting morphological deformities or clumps (Galtsoff, 1964).

For nursery cultivation of oysters, however, growth in the height of seeds and H/L ratio was significantly higher at more dense treatment, even though any density treatment evaluated could satisfy the cultivation of *C. tulipa*. Independent of density treatment, seed shape varied from round to oval, and 100% of individuals, at the 72nd day of cultivation, surpassed 10×10 mm size, a referential seed index utilized to evaluate the performance of nursery farm cultivation through seed sifting in Santa Catarina state (Ferreira *et al*., 2011). A similar pattern was also found for Sambaqui at the 63rd day of cultivation, in which 95.3% of *C. tulipa* seeds surpassed 10 mm in height and length (Tureck *et al*., 2014).

The stocking density effect in nursery phase cultivation of *C. tulipa* was either null or insignificant for densities tested, as even the differences among them did not implicate less oyster yield or quality of seeds. Although such pattern of results is uncommon, other studies demonstrated the lack of negative density effect in *C. gigas* cultivated in floating boxes in the same region, in which different density treatments of 50 or 200 mL/0.13 m² seeds gave a yield similar to seeds retained at ≥3.0 mm mesh nets (Ferreira & Ferreira, 2014). Besides, Galvão *et al.* (2009) showed that seed growth in nursery cultivation of *Crassostrea* sp. at either 150 or 450 ind/0.13 m^2 (lantern floor) in the Cananéia Estuary (25ºS, 48ºW) performed essentially the same. Therefore, the range of densities in our study and the study mentioned above were not wide enough to evince a more significant effect.

Higher density treatments could reduce the velocity of water current inside the cultivation system, thus enabling a more efficient filtering process, since current velocity is inversely related to feeding rate and growth (Cole *et al.*, 1992; Honkoop & Bayne, 2002), although a continuous water flow is essential in maintaining the availability of food in culture systems (Wilson-Ormond *et al.*, 1997). Food availability in the study site was enough to maintain the densest treatment's growth rate, and food depletion, if it occurred, did not exhibit concerning aspects of oyster growth, shape, or survival. Additionally, a high density of oysters may increase water flux activity in the experimental units (EU) caused by bivalves' feeding pump currents (Nikora *et al.*, 2002; Bayne, 2017). Additionally, oysters can physiologically compensate for a low quality and small quantity of food, expressed in increased clearance rate by functional changes in particle capture efficiency (Ward & Shumway, 2004) and reduced pseudofaeces production (Bayne, 1993).

The balance between the amount of PIM and POM in seston determines whether bivalves efficiently establish a positive energy balance (Wallace & Reinsnes, 1985; Hawkins *et al.*, 2002). At large PIM portions, the quality of seston decreases as POM becomes either unavailable for absorption or does not fairly compensate energy used for selective filtering (Velasco & Navarro, 2003; Bayne, 2017). Tureck *et al.* (2014) showed a better yield of *C. tulipa* seeds in marine sites compared to estuarine sites, even though estuarine sites had more available POM (10.53 ± 1.68 mg L^{-1} *vs*. 3.59 ± 0.14 mg L^{-1}) and lower PIM/POM ratio (101.47 ± 1.54/10.53 ± 1.68 *vs*. 55.87 ± 6.59/3.59 ± 0.14) than marine sites at similar temperature conditions, implying that salinity may influence the filtration rate. Local marine farming conditions at the study site are characterized by more available POM (6.43 ± 2.66 to 17.41 ± 5.33 mg L^{-1}) with variable PIM values (19.55 ± 4.13 to 67.35 ± 5.33 mg L^{-1}). With similar POM values, our initial yield of seeds at the 72nd day of plant-out performed like that of Tureck *et al.* (2014), culturing marine species after 63 days and reporting the vast majority of seeds with a height greater than 10 mm. This result suggests that seston utilization and related growth are less related to seasonal food and temperature fluctuations and more related to a wide range of physiologically regulated feeding and digestion (Riisgård, 2001; Ward & Shumway, 2004).

The filtration rate of *C. tulipa* maintains a constant maximum activity at salinity variation of 35 to 18.3 with lower salinity values implicating less food uptake (Sutton *et al.*, 2012). During farm cultivation, salinity ranged from 26 ± 1.41 to 35.80 ± 0.45, which indicates a good site for maximum filtration rate for species production.

Cultivation at the juvenile phase displayed a different growth pattern from those at nursery and final phases. Although significant differences were verified at some density treatments, the width of oysters maintained nearly the same values of seeds retained in 16 mm mesh at 114 days of cultivation. Rapid growth occurred especially in height and length and may be characteristic at this phase. In just 48 days of cultivation, most *C. tulipa* individuals reached 50 mm in all densities, values comparable to *C. gigas* cultivation at this phase, the cultivation period of which lasted from 60 to 450 days (Mizuta *et al.*, 2012).

The final phase is defined as the period of final growth with adults' fattening process for commercialization. Usually, at the end of this cultivation phase, oysters must acquire conditions for their commercialization, during which the weight of meat comes into play (Lawrence & Scott, 1982) since deshelling is a typical food process. However, in Brazil, shelled oysters are sold by the dozen, and quality is determined by oyster height and length, even if this means buying an oyster with a large shell and little flesh (Lopes *et al.*, 2013). Oyster yield, as evaluated in the present work, reflects Brazilian market conditions.

Low survival of oysters at the final stage of cultivation is quite expected, but not for lower density treatments (30 and 60 ind/0.13 m^2) compared to higher densities since the competition's effect is decreased (Holliday *et al.*, 1993). Mainly, Sabry & Magalhães (2005) found a similar survival rate percentage in *C. rhizophorae* oysters cultivated at 40 ind/0.13 m^2, even though correctly managing individuals. Some studies indicate that biofouling encrustation in oysters is intensified at low densities (Adams *et al.*, 1994; Dunham & Marshall, 2012), as verified in *C. tulipa* cultivated in a Cananéia estuary (Pereira *et al.*, 2001) and for the same *C. tulipa* specimens presented in this study (Lehner *et al.*, 2019). Under these conditions, the total surface area exposed to biofouling colonization is higher, mostly when individuals are distributed in different sizes, thus creating more irregular colonization (Gutiérrez *et al.*, 2003). Biofouling has various harmful effects, including competition for food and space, physical disruption to opening and closing of valves, and stress, precursors for increased mortality (Adams *et al.*, 2011; Fitridge *et al.*, 2012).

Evaluating the total amount of oysters of marketable quality per time spent in cultivation provides a real glimpse into the most profitable density treatments. Oysters' marketability is first based on the weight of individuals since it directly reflects their meat weight (Quayle & Newkirk, 1989). The size of oysters measures another basis of marketability. However, the size considered ideal for commercializing mangrove oysters varies. Nascimento *et al.* (1980) indicate that the ideal commercial size of *C. rhizophorae* is approximately 70 mm in height. Pereira *et al.* (2003) considered a commercially minimum size of 50 mm in height for *C. tulipa* cultivated for one year in a natural environment. Here, we consider at least two marketable types of oysters based on size: oysters with a height between 60-80 mm and oysters with height >80 mm with correspondingly higher meat and market appeal.

Legat *et al.* (2017b) observed that 95.6 and 24.1% of *C. tulipa* oyster's growth above 60 mm in height at eight months of cultivation, in São Francisco do Sul estuary and Sambaqui farm (southern region), respectively, although the average individual weight of each oyster did not exceed 70 g. As for our results, all treatments showed a mean height of oysters above 70 mm and individual average weight of oysters with values exceeding 80 g at 10 months of cultivation. These experiments indicate that it is possible to obtain *C. tulipa* oysters in commercial size in a relatively short period of cultivation from marine farms.

In Brazil, apart from the present study, growth evaluation of native mangrove oysters has already been performed, *e.g.*, Pereira *et al.* (2001) and, more recently, Lopes *et al.* (2013) and Legat *et al.* (2017b). Growth of mangrove oysters here and in these studies was lower than the growth of *C. gigas* in Santa Catarina as the Pacific oyster takes from 8 to 13 months of cultivation to grow from seeds to a commercial oyster size between 70 and 120 mm in height (Mizuta *et al*., 2012).

It should be noted that *C. gigas* is adapted to low water temperature, limiting and restricting its production, most notably in the summer and in areas where tropical conditions prevail, and the average temperature of the water is high, making the cultivation of *C. gigas* impractical (Poli, 2004; Gomes *et al.*, 2014). In this sense, the production of *C. tulipa* appears to be an alternative species, as it has adapted to warmer regions and distributed in both tropical and subtropical climates. In both quantity and quality of meat, it is important to note that *C. tulipa* is very good, surpassing *C. gigas*, mainly in the meat quality, which can satisfactorily meet commercial demand.

The data obtained in the present research demonstrate remarkable growth and survival of *C. tulipa* and its potential for bringing subsidies to cultivate native oysters of great importance for economic development.

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