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Site selection for farming the oyster *Saccostrea cucullata* in a tropical coastal lagoon

Aladin Andrisoa^{a,*}, Marenjaka Masimana^b, Franck Lartaud^c, Thomas C. Stieglitz^a

^a Aix-Marseille Université, CNRS, IRD, INRAE, CEREGE, Aix-en-Provence 13545, France

^b Institut d'Enseignement Supérieur d'Anôsy, Université de Toiliara, Fort-Dauphin BP 131, 614, Madagascar

^c Sorbonne Université, Laboratoire d'Ecogéochimie des Environnements Benthiques (LECOB), Observatoire Océanologique de Banyuls, Banyuls/Mer 66650, France

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ABSTRACT

This study investigates the influence of variable environmental conditions on the growth of the natural rock oyster (hooded oyster) *Saccostrea cucullata* in the river-fed Ambinanibe coastal lagoon (Madagascar), with the objective to establish sites with optimal growth conditions for aquaculture purposes. Specimen marked with manganese were placed in cages over an approximately one-year period. The cages were installed at four sites i.e. one at the river mouth, two sites within the main lagoon and one site in an adjacent connected lagoon, which is out of river influence and considered as the control site. Multiple mark and recapture experiments were used to investigate the variations in growth rate and condition index (tissue weight/shell weight). The results show that the species overall exhibits a fast growth rate at a young age, with a gradual growth reduction with age. The hinge growth rate shows important spatial and seasonal variations in the lagoon. Oysters from the site located at the river mouth have the highest hinge growth rate ($20.5 \pm 13.6 \mu\text{m d}^{-1}$) and condition index ($4.5 \pm 2.8 \%$) while those from the control site out of river and ocean influences exhibit the lowest hinge growth rate ($7.7 \pm 4.2 \mu\text{m d}^{-1}$) and condition index ($0.7 \pm 0.6 \%$), suggesting that river freshwater inflow provides suitable environmental conditions for oyster growth and a profitable oyster farming is thus feasible. River inflow is an important external source of nutrients, providing thus a significant food source (phytoplankton), as well as suitable temperature and salinity conditions for *S. cucullata* in this lagoon. Overall, our results show that oyster market size (shell length: 40 mm) in Madagascar can be reached faster at the river-influenced site (in 8 months) in comparison with the other sites (in 1 – 1.2 years), indicating that the river-impacted site is well suitable for oyster farming.

1. Introduction

Coastal lagoons are shallow and highly dynamic transitional (brackish) water bodies, which are controlled by physical processes of both marine and terrestrial origin. These semi-enclosed ecosystems are characterized by a restricted exchange with the sea, and they are heavily dependent on watershed inputs. They are highly productive ecosystems and support numerous ecosystem services that are relied upon by coastal communities, including food provision through fish and shellfish culture (Newton et al., 2014; Cardoso-Mohedano et al., 2016). Previous studies showed that coastal lagoons are favourable sites for oyster farming (e.g. Rebelo et al., 2005; Galgani et al., 2009; Graham et al., 2020). In Madagascar, there are over hundred coastal lagoons, many of which are underutilized and could be used for aquaculture, particularly oyster

farming, thereby contributing to food security and income for local populations.

Oysters are among the commercially exploited filter feeders along the coast of Madagascar, particularly in the southeast region. During the last decades, there has been a substantial increase of oyster fishing activities related to the development of tourism and implantation of seafood collection companies in the region. Oyster fishery has hence become a major source of fishing-derived revenue for some local communities in southeast Madagascar. The natural rock oyster (hooded oyster) *Saccostrea cucullata* is the dominant oyster species in coastal lagoons in southeast Madagascar accounting for 90 % for oyster catch by artisanal fisheries. This edible species is widely distributed in the coastal zone of Indo-Pacific, Eastern Atlantic and the Mediterranean (Braley, 1984; Chowdhury et al., 2019; Tenjing, 2020). In northern Australia,

* Corresponding author.

E-mail address: andrisoa@cerege.fr (A. Andrisoa).

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Thailand, China and India, oysters *S. cucullata* are cultivated in aquaculture and are popular in local markets because of their strong iodine taste (Arkhipkin et al., 2017). In southeast Madagascar, coastal communities have exploited this species for local consumption and sale. While the *S. cucullata* fishery is an important source of income for the coastal communities, there is growing evidence suggesting the decline of catches due to increased fishing effort and habitat deterioration. For the sustainable management of this resource, the Malagasy Ministry of Fisheries and Blue Economy and local researchers decided to install an oyster farm in Ambinanibe coastal lagoon, an established practice in many locations to stabilize oyster production and reduce fishing pressure on wild populations (Lebreton et al., 2021). Successful and sustainable oyster farming largely depends on the selection of suitable sites that supports long-term growth and survival of oysters (Schulte et al., 2009; Pollack et al., 2012).

Ambinanibe coastal lagoon, located in the south-eastern coast of Madagascar, appeared to be a suitable location to develop an oyster farming because areas of relatively abundant natural oyster populations still exist (Masimana, 2019). Ambinanibe lagoon receives nutrient-rich freshwater from the Ifaho river and is connected to the Indian Ocean by a small opening. The lagoon is relatively shallow and exhibits high spatial and temporal variations in salinity. These general physical features of the lagoon are likely essential to an appraisal of its environmental suitability for oyster farming. The environmental parameters temperature and salinity are generally known to influence oyster growth (Nell and Holliday, 1988; Chávez-Villalba et al., 2005; Manuel et al., 2023). In addition, *S. cucullata* growth is influenced by variations in the quantity and quality of seston (mainly phytoplankton) and the presence of hard substrate for initial settling (Bhattacharyya et al., 2010). Recent study showed that Ambinanibe lagoon is characterized by high abundance of phytoplankton, a food source for oysters (Andrisoa et al. in review). Unlike other oyster species, little is known on the biology and ecology of *S. cucullata*, particularly in Madagascar. There are only few studies conducted on *S. cucullata* in other locations in Asia, India and Australia (Bhattacharyya et al., 2010; Chowdhury et al., 2019; Mafambissa et al., 2023). A better understanding of the environmental conditions that favour fast growth of *S. cucullata* will likely contribute to optimising farming of this species in and beyond this lagoon.

Chemical marking technique is a good alternative to estimate oyster growth rate. Chemical marking techniques such as fluorochromes (Thébault et al., 2006; Sato-Okoshi et al., 2010; Andrisoa et al., 2019), strontium (Fujikura et al., 2003) and manganese (Langlet et al., 2006; Lartaud et al., 2010; Huyghe et al., 2019) have been widely used to

investigate the growth rate of calcifying organisms in coastal ecosystems. Experimental enrichment with these chemicals on living bivalves creates bright artificial growth lines that can be revealed using microscopy. Because incorporation of such chemical elements into calcite lattice is fast (1 – 4 hours), chemical marking methods provide high-resolution chronologic framework, crucial for growth rate measurement of fast growing species (Lartaud et al., 2010). In this study, we investigate the variations in growth rate using manganese (Mn^{2+}) marking technique and assess their condition index (tissue dry weight/shell dry weight). This study will provide essential information for the installation of oyster farm in Ambinanibe lagoon.

2. Materials and methods

2.1. Study area

Ambinanibe lagoon is located on the south-eastern coast of Madagascar (Fig. 1). The study region is characterized by humid subtropical (warm-humid) climate condition with a wet season from November to April and a dry season from May to October. The highest monthly precipitation is observed in January (340 mm) and lowest in October (10 mm). The region is characterized by a strong north-westerly winds, regularly exceeding 10 m s^{-1} , particularly during the dry season. Ambinanibe lagoon has a surface area of ca. 1000 ha and a mean water depth of 2.1 m. It is connected with the Indian Ocean by a small opening in the coastal sand spit, which is temporary closed during the dry season but open during the wet season (Fig. 1). Ambinanibe lagoon receives freshwater inputs mainly from the Ifaho river draining a relatively large catchment dominated by agriculture (80,000 ha). The Ifaho river flow fluctuates considerably during seasons with a mean flow of $68.6\text{ m}^3\text{ s}^{-1}$ in the wet season and $9.4\text{ m}^3\text{ s}^{-1}$ in the dry season (Andrisoa et al. in review). The main lagoon is connected to a smaller lagoon by a small stream of 3 km length (Fig. 1). This secondary lagoon is located far from both river and ocean influences and thus constitutes a suitable control site for our study. This lagoon has a surface area of 740 ha and mean water depth of 2.4 m. Four different locations were selected to compare the growth of *S. cucullata*. The sites St1, St2 and St3 are located in the main lagoon while the site St4 is in the second lagoon (Fig. 1). St1 is located at the mouth of the Ifaho river and therefore referred as river-influenced site, and the site St4 is considered the control site.

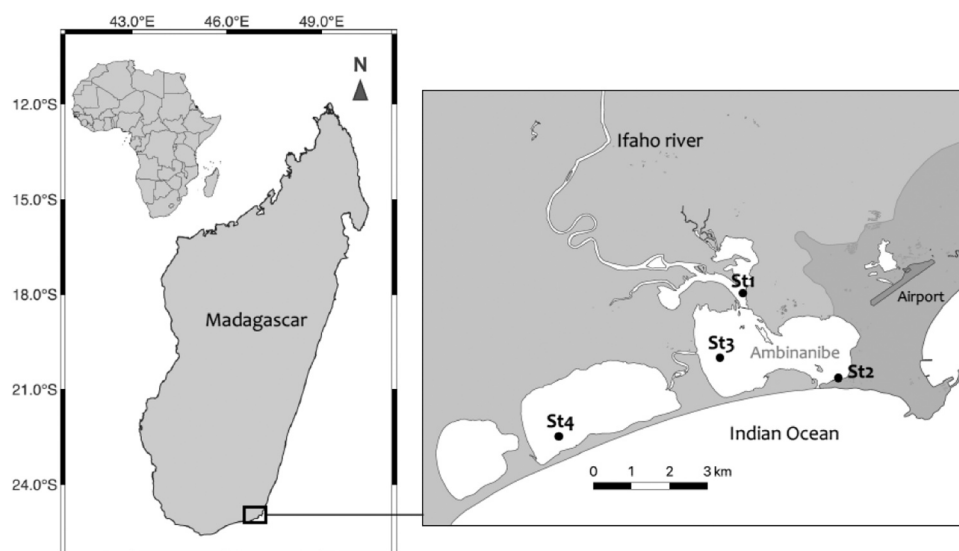


Fig. 1. : Map showing the location of the four study sites (St1, St2, St3 and St4) in Ambinanibe lagoon in southwest Madagascar.

2.2. Field experiment and sample preparation

At each site, 87–90 oysters naturally present in the lagoon were collected on 01 May 2022, at the beginning of the dry season (Table 1). Shell length of each individual were measured with a stainless caliper and the body weight measured with a digital balance. Shell length represents the maximum distance between the hinge to the posterior margin of the valve. At each location, oysters were marked by immersion for 2 h in 20 L lagoon water containing 90 mg L⁻¹ of manganese chloride tetrahydrate (MnCl₂, 4H₂O), similarly to the method described in Lartaud et al. (2010). The Mn²⁺ marking is a commonly used method to study the growth rate of various calcifying species such as oyster as it serves as temporal point of reference (Langlet et al., 2006; Doldan et al., 2018; Huyghe et al., 2019). After shell marking, the Mn²⁺-marked oysters were returned to their original location by placing them in cages (66 × 27 × 16 cm). Cages were installed at 30–100 cm from the bottom, experiencing different environmental conditions. The marking process was repeated on 05 September 2022 and 24 April 2023. The Mn²⁺-marked oysters were sampled on 05 September 2022, 03–20 December 2022, 24 April 2023 and 10 June 2023 (Table 1). For each occasion, five individuals from each site were sampled for analysis in the laboratory and oyster mortality was monitored. New cages were installed at St3 on 05/09/2022 and at St1 on 24/04/2023 as the older cages were stolen (Table 1).

In the laboratory, oyster samples were cleaned to remove all epibionts and other attached organisms. The shell length was measured along the maximum growth axis using a caliper. The shells were carefully opened to avoid any damage, and tissues removed. The shells and tissue of each individual were dried at 60°C overnight and weighed separately using a digital balance. The dry left shell valve of each oyster was cut along the maximum growth axis through the middle of the hinge region to the ventral shell margin with a Buehler Isomet low-speed saw, using a 0.5 mm thick diamond wafering blade. The hinge length was also measured using a caliper. The section was mounted on a glass slide using Epoxy Araldite 2020 resin. A thin section (0.8 mm) of shell was cut along the maximum growth axis, ground with 80, 180, 400, and 800 SiC grit, polished with 3, 1 and 0.3 mm Al₂O₃ powder and rinsed with deionized water. Using this protocol, 65 shells were prepared for cathodoluminescence analysis.

2.3. Environmental parameters

Water temperature was measured hourly with ONSET HOBO loggers UA-002–64 installed with the cages. During each marking experiment, salinity and dissolved oxygen concentrations were measured with a pre-calibrated WTW Multiparameter probe (Multi 3430 probes with a precision of ± 0.5 %). During three sampling campaigns (April 2022, September 2022 and April 2023), lagoon water samples (100–300 mL) for chlorophyll-*a* and phaeopigment concentrations were collected and filtered through a pre-combusted 25 mm GF/F filters of 0.7 μm nominal pore size. Chlorophyll-*a* and phaeopigment samples were not collected for December 2022 and June 2023 because the sampling equipment was not available onsite. Filters were wrapped in aluminium foil and kept frozen at –20°C. Chlorophyll-*a* and phaeopigment concentrations were determined by fluorometry using the methanol extraction procedure (Raimbault et al., 1988). The proportion of chlorophyll-*a* to the sum of chlorophyll-*a* and phaeopigments, known as Pigment Ration Index (PRI) was also estimated as proxy of phytodetritus degradation (Bourgeois et al., 2011).

2.4. Condition index

The condition index (CI) i.e. the ratio between the flesh (tissue) dry weight and the shell dry weight is commonly used to assess the health and the quality of bivalves for scientific and commercial purposes (e.g. Barraza-Guardado et al., 2008; Bhattacharyya et al., 2010; Yildiz et al., 2011). It is particularly important in quality assessment and in the marketing value of oysters – the higher the CI, the higher the commercial value.

$$CI = \frac{\text{Tissue dry weight}}{\text{Shell dry weight}} * 100 \quad (1)$$

2.5. Cathodoluminescence analysis

The cathodoluminescence (CL) phenomenon results from the interactions between a light-emitting centre (impurity or chemical element) and an electron gun (Machel et al., 1991; Pagel et al., 2000; Lartaud et al., 2010). The shell of *S. cucullata* consists of calcite and when exposed to an electron beam, pure calcite presents a weak dark-blue luminescence (intrinsic luminescence). In calcite, CL emission

Table 1

Dates of Mn²⁺ marking of the oyster shells on each site together with shell length Mean ± SD (Min-Max) and number (*n*). The number of oysters on 01/05/2022 represents the number of oysters placed in the cages at the beginning of the experiments. St1, St2, St3 and St4 represent the four study sites. New cages were installed at St3 on 05/09/2022 and at St1 on 24/04/2023 due to sample loss. Asterisk (*) indicates new cage installation and Mn²⁺ marking.

Date of Mn ²⁺ marking / collection	Sites	Immersion duration (days)	Number of collected oysters (<i>n</i>)	Mortality (%)	Oyster shell length (mm) Mean ± SD (Min-Max)	Number of oysters with visible Mn ²⁺ mark
01/05/2022	St1	0	88	-	61 ± 12 (39–90)	-
	St2	0	88	-	61 ± 14 (32–90)	-
	St3	0	90	-	62 ± 12 (22–91)	-
	St4	0	87	-	61 ± 13 (34–90)	-
05/09/2022	St1	127	5	0	66 ± 4 (62–70)	5
	St2	127	5	3.5	69 ± 16 (51–94)	5
	St3*	0	114	0	58 ± 13 (30–88)	-
	St4	127	5	0	59 ± 10 (43–68)	5
3–20/12/2022	St1	-	-	-	-	-
	St2	216	5	1.4	72 ± 13 (53–83)	3
	St3	106	5	6.14	58 ± 14 (43–79)	4
	St4	231	5	4.4	54 ± 9 (41–65)	4
24/04/2023	St1*	0	56	-	68 ± 14 (47–101)	-
	St2	358	5	1.6	71 ± 13 (55–87)	5
	St3	231	5	1.0	65 ± 21 (36–88)	5
	St4	358	5	6.6	60 ± 12 (41–70)	5
10/06/2023	St1	47	5	0	68 ± 6 (60–76)	4
	St2	405	5	0	76 ± 16 (52–92)	5
	St3	278	5	0	67 ± 14 (48–85)	3
	St4	405	5	3.2	50 ± 9 (40–62)	1

(ca. 620 nm) principally results from the presence of Mn^{2+} trapped into the lattice during mineral growth (Rafélis et al., 2000). CL emission was observed with a cold cathode (Cathodyne NewTec, 12 kV and 190 μ A under a pressure of 80 mTorr) coupled with an optical microscope (LEICA DM 2700 M) on the hinge section, because this area contains an ontogenetic record of both oyster's hinge growth and environmental conditions experienced during their life (Fig. 2a and b) (Kirby et al., 1998; Lartaud et al., 2010; Huyghe et al., 2019). A numerical IDS uEye (UI388) camera was used for luminescence image acquisition with a constant exposure time of 6 s. Growth analyses were carried out on mounted photographs using image processing software Image Composite Editor. Image J software was used to measure the distance between two Mn^{2+} markings, allowing the estimation of growth rate of oyster during two Mn^{2+} marking periods (Fig. 2).

The shell Mn^{2+} marking allowed to transform CL spectra along a growth profile into a calendar profile (Huyghe et al., 2019). The parameters of the Von Bertalanffy growth equation was estimated using the least square method for non-linear regression analysis described in Motulsky and Ransnas (1987) with R software.

$$L_t = L_{\infty}(1 - \exp^{-K(t-t_0)}) \quad (2)$$

where L_t is the hinge shell length (mm) at time t (in years); L_{∞} is the maximum hinge shell length (mm); K represents the growth coefficient (year^{-1}); and t_0 (in years) is the setting size. The shell mean growth rate was estimated using the linear relationship between the hinge and the shell length measured in this study.

In addition, the hinge growth rate from different sites were compared using commonly used indices of growth performance: the phi-prime index (φ') and the index P, calculated from the Von Bertalanffy growth parameters K and L_{∞} (Brey, 1999; Ragonese et al., 2012; Legat et al., 2017):

$$\varphi' = \log_{10}(K) + 2 * \log_{10}(L_{\infty}) \quad (3)$$

$$P = \log_{10}(K * L_{\infty}) \quad (4)$$

2.6. Statistical analysis

Data normality and homogeneity of variances were tested with Shapiro-Wilk and Levene's test, respectively. Two-way ANOVA was applied to assess the spatial and seasonal variability in hinge growth rate using the car R package. Kruskal-Wallis test was applied to assess the variability in condition indices between sites. All statistical analyses were performed using R software (v4.1.2; R Core Team, 2021).

To assess the environmental parameters controlling the growth rate

and the condition index of oysters, a Principal Components Analysis (PCA) was applied using the Factoextra R package. The PCA was performed based on daily growth rate, condition index (CI), salinity, temperature, dissolved oxygen, chlorophyll-*a*, phaeopigments and the Pigment Ration Index (PRI).

3. Results

3.1. Environmental parameters

The precipitation in the region is seasonally variable with highest precipitation in January (340 mm) and lowest in October (10 mm) (Fig. 3a). The main environmental parameters at the four study sites are summarized in Table 2. The sites St1, St2 and St3, located in the main lagoon, exhibited overall variable and higher salinity values in comparison with the site St4. Highest salinity values were recorded at St2 (located near the lagoon – ocean connection) in April 2022 (21.4 ± 18.0), September 2022 (17.0 ± 7.3) and April 2023 (21.7 ± 15.9). The salinity was overall lower in September compared to those of April for all sites. No important differences were reported between different sites for temperature (Table 2). However, the daily temperature indicated lower values between May and August ($19.9 - 24.4$ °C), then the values increased gradually and reached higher temperature between November and April ($25.4 - 30.5$ °C), corresponding to the wet season (Fig. 3b). Dissolved oxygen concentrations were not considerably different between sites (Table 2). The four study sites were overall well oxygenated, with oxygen concentrations close to saturation during the three campaigns. The site St1 had the highest concentrations of photosynthetic pigments (i.e., chlorophyll-*a* and phaeopigments) during the three sampling campaigns while the site St4 exhibited the lowest concentrations. The PRI values were lowest at the site St1 in comparison with the other sites, with 46.1 and 58.8 % of the pigments were degraded in April and September 2022, respectively (Table 2).

3.2. Growth rate and condition Index

Overall, the oyster *S. cucullata* in this study exhibited low mortality rate (Table 1). The hinge growth rates varied between sites (two-way ANOVA: $F_{3,58} = 11.71$, $p < 0.0001$) and St1 exhibited the highest growth rate for all seasons while the lowest growth rate was observed at St4 (Fig. 4). Growth rates from the three sites located in the main lagoon (St1, St2 and St2) exhibited overall high inter-individual variability while St4 exhibited relatively low inter-individual variability in growth rates (Fig. 5). For the entire study period, the mean hinge growth rates from sampled oysters were $20.5 \pm 13.6 \mu\text{m d}^{-1}$ ($n = 9$) at St1, $10.5 \pm$

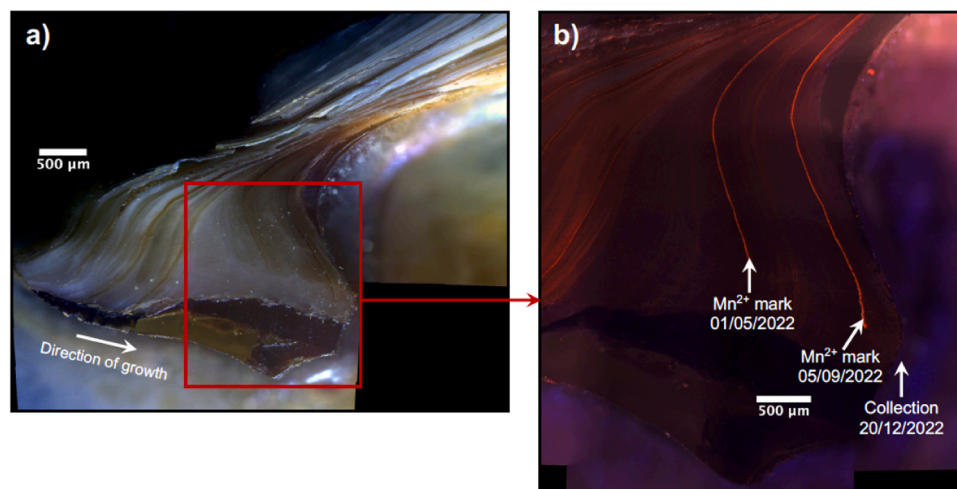


Fig. 2. : Observation of the oyster hinge section under (a) transmitted light and (b) cathodoluminescence showing the Mn^{2+} marking lines.

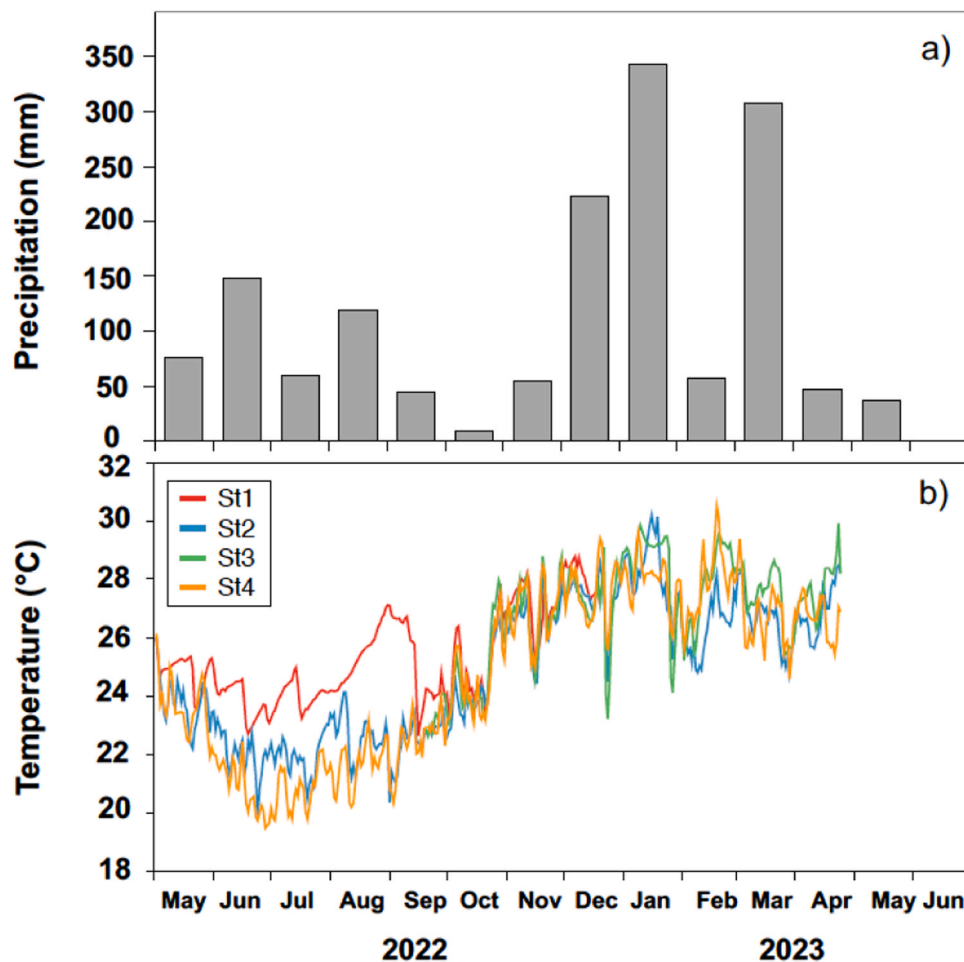


Fig. 3. : The variations in (a) monthly precipitation and (b) daily water temperature. Precipitation data were provided by ASECNA from nearby airport. St1, St2, St3 and St4 represent the four study sites.

Table 2

The main environmental parameters (mean \pm SD) in the four study sites (St1, St2, St3 and St4) in April 2022, September 2022 and April 2023.

Sampling period	Site	Salinity	Temp (°C)	DO (mg L ⁻¹)	Chl-a (µg L ⁻¹)	Phaeopigments (µg L ⁻¹)	PRI (%)
April 2022	St1	16.1 \pm 14.1	24.5 \pm 1.1	6.9 \pm 0.6	1.52	1.30	53.9
	St2	21.4 \pm 18.0	23.9 \pm 0.2	7.6 \pm 0.6	0.60	0.30	66.7
	St3	20.3 \pm 17.1	24.7 \pm 0.5	7.6 \pm 0.3	0.87	0.33	72.5
	St4	7.2	24.1	9.8	-	-	-
September 2022	St1	10.6 \pm 2.4	23.1 \pm 1.7	8.4 \pm 0.3	0.87	1.24	41.2
	St2	17.0 \pm 7.3	21.9 \pm 1.8	8.9 \pm 0.4	0.97	0.67	59.1
	St3	10.9 \pm 2.3	22.4 \pm 1.3	8.5 \pm 0.3	0.44	0.18	71.0
	St4	10.4 \pm 0.3	22.8 \pm 1.0	8.6 \pm 0.0	0.35	0.18	66.0
April 2023	St1	19.8 \pm 14.3	30.0 \pm 2.7	7.6 \pm 0.5	-	-	-
	St2	21.7 \pm 15.9	25.9 \pm 1.5	8.4 \pm 0.6	-	-	-
	St3	21.4 \pm 11.3	26.6 \pm 2.7	8.2 \pm 0.3	-	-	-
	St4	9.0 \pm 0.4	25.8 \pm 1.0	9.1 \pm 0.4	-	-	-

5.0 $\mu\text{m d}^{-1}$ ($n = 27$) at St2, 12.0 \pm 8.1 $\mu\text{m d}^{-1}$ ($n = 13$) at St3 and 7.7 \pm 4.2 $\mu\text{m d}^{-1}$ ($n = 22$) at St4 (Fig. 5). Furthermore, the mean hinge growth rates varied significantly between seasons (two-way ANOVA: $F_{3,58} = 9.15$, $p < 0.0001$) (Fig. 4). Highest hinge growth rates were reported between 24/04/2023 and 10/06/2023 while lowest growth rates were recorded between 20/12/2022 and 24/04/2023 (Fig. 4).

Similar to growth rates, condition indices were significantly different between the four study sites (Kruskal-Wallis: $Chi\ square = 27.61$, $p < 0.0001$). The site St1 exhibited the highest condition index (4.50 \pm 2.82 %) while St4 showed the lowest index (0.72 \pm 0.55 %) (Fig. 5). The condition indices were 3.60 \pm 3.11 % at St2 and 3.24 \pm 2.00 % at St3.

High inter-individual variability in condition indices was also observed from the three sites located in the main lagoon (St1, St2 and St3) whereas condition index at St4 exhibited low inter-individual variability (Fig. 5).

3.3. Growth model of *S. cucullata* shells

A significant correlation between oyster shell and hinge length is observed (Fig. 6), allowing for the calculation of shell length from hinge growth measurements. From this relationship, mean shell growth rates in this study were calculated to be 104.7 $\mu\text{m d}^{-1}$ (3.1 mm month⁻¹) at

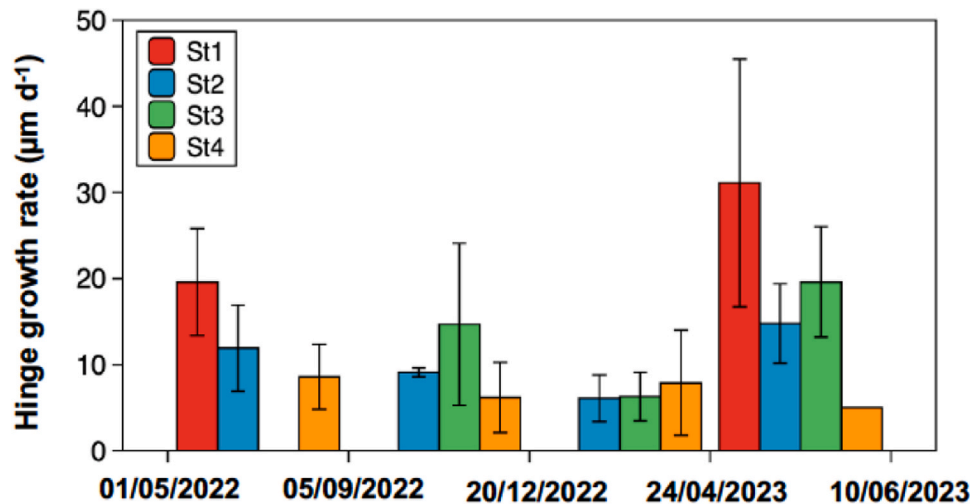


Fig. 4. : The mean hinge growth rate at the four study sites (St1, St2, St3 and St4) between two consecutive Mn²⁺ markings. The vertical bars represent the standard deviation.

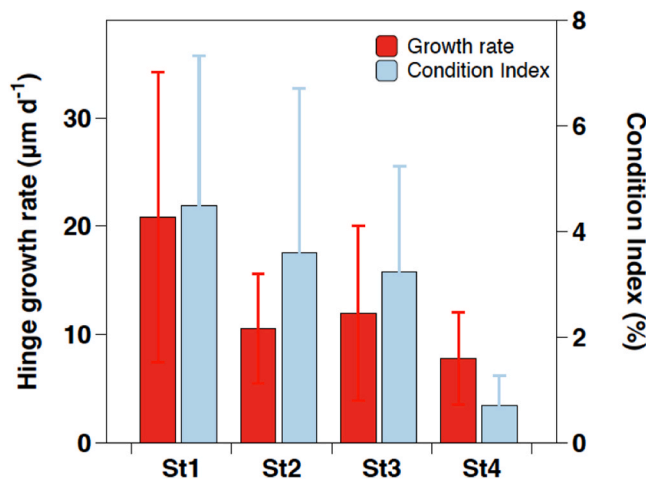


Fig. 5. : Mean (\pm SD) hinge growth rates and condition indices at the four study sites (St1, St2, St3 and St4).

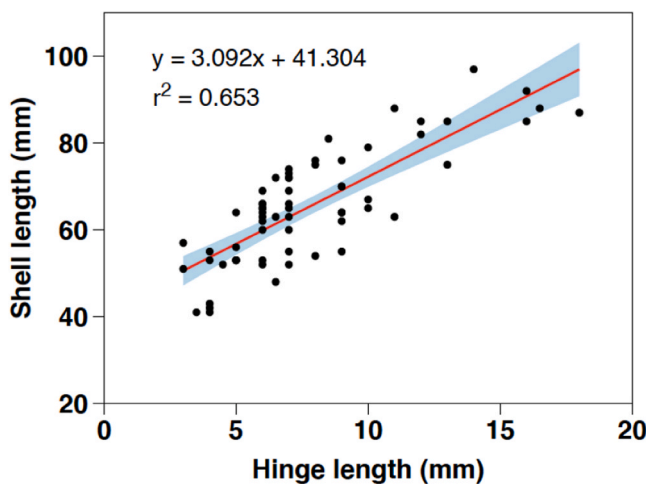


Fig. 6. : Linear relationship measured between hinge and shell length of *S. cucullata* from Ambinanibe lagoon. Shaded area represents the 95 % confidence interval.

St1, 73.8 $\mu\text{m d}^{-1}$ (2.2 mm month⁻¹) at St2, 78.5 $\mu\text{m d}^{-1}$ (2.4 mm month⁻¹) at St3 and 65.1 $\mu\text{m d}^{-1}$ (1.9 mm month⁻¹) at St4 (Table 3).

Overall, the growth rates at the four study sites exhibited a similar pattern (Fig. 7). As commonly observed for oyster species, the growth rates of *S. cucullata* in this study were marked by a fast growth at a younger age and a decrease in growth as the oysters approach their maximum size. The Von Bertalanffy growth models showed higher hinge growth rate from oyster installed at St1 ($K = 1.79, L_{\infty} = 5.32$), followed by those from St3 ($K = 1.21, L_{\infty} = 4.67$) and from St2 ($K = 1.31, L_{\infty} = 4.19$) (Table 3; Fig. 7a). Oysters from St4 showed the lowest hinge growth rate ($K = 1.31, L_{\infty} = 3.47$). The shell growth curves followed similar pattern as the hinge growth curves (Fig. 7b). The shell curves indicated that 8-months-old *S. cucullata* attain market size (40 mm) at St1 while the market size was reached at the age of 1 year at St2 and St3 and at the age of 1.2 years at St4 (Fig. 7

b). In addition, the growth performance indices at the site St1 ($\varphi' = 1.70, P = 0.98$) were the highest among the study sites while those at St4 were the lowest ($\varphi' = 1.20, P = 0.66$) (Table 3).

3.4. Relationship between environmental parameters and oyster growth

To determine the environmental parameters governing the growth of *S. cucullata*, we analysed the relationship between growth rate, condition index (CI), salinity, temperature, dissolved oxygen (DO), chlorophyll-*a*, phaeopigments and PRI for the four study sites combined using a principal component analysis (PCA) (Fig. 8). This analysis showed significant positive correlations of growth rate with water temperature ($r = 0.939$), chlorophyll-*a* ($r = 0.949$) and phaeopigments ($r = 0.955$) (Fig. 8). Conversely, significant negative correlations were observed of growth rate with dissolved oxygen concentration ($r = -0.939$) and PRI ($r = -0.800$). Similar to the growth rate, the condition index exhibited significant positive correlations with chlorophyll-*a* ($r = 0.928$), phaeopigments ($r = 0.755$) and salinity ($r = 0.792$) (Fig. 8). In contrast, significant negative correlations were observed between condition index and dissolved oxygen concentration ($r = -0.945$).

4. Discussion

4.1. Growth of *S. cucullata*

Similar to previous studies of the widely distributed oyster *Magallana gigas* (formerly *Crassostrea gigas*) (Langlet et al., 2006; Lartaud et al., 2010), this study on *S. cucullata* confirms that growth measurements made on the hinge are an appropriate tool to estimate oyster shell

Table 3

Measured hinge growth rate, estimated shell growth rate, the Von Bertalanffy growth parameters and the growth performance indices from the four study sites (St1, St2, St3 and St4). Shell growth rates were estimated from the linear relationship between the hinge and the shell length.

Study sites	Number of shells	Measured mean hinge growth rate ($\mu\text{m d}^{-1}$)	Estimated mean shell growth rate ($\mu\text{m d}^{-1}$)	K	L_{∞} (mm)	ϕ'	P
St1	9	20.5	104.7	1.79	5.32	1.70	0.98
St2	27	10.5	73.8	1.31	4.19	1.36	0.74
St3	13	12.0	78.5	1.21	4.67	1.42	0.75
St4	22	7.7	65.1	1.31	3.47	1.20	0.66

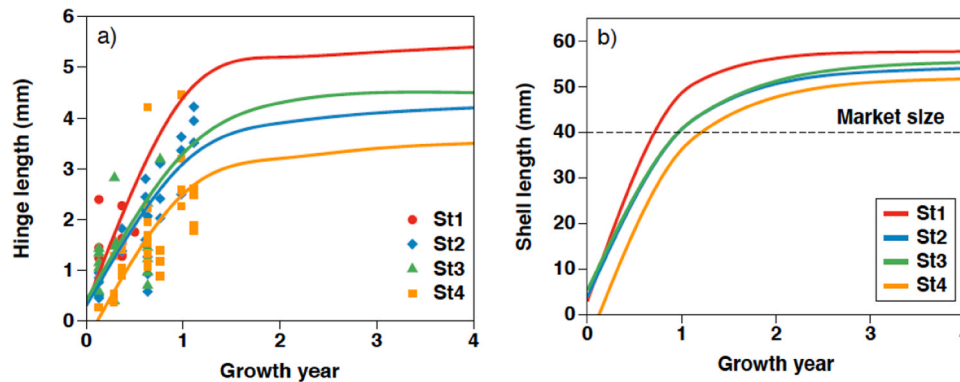


Fig. 7. : (a) Size-at-age and Von Bertalanffy growth model for oyster hinge at St1 ($K = 1.79, L_{\infty} = 5.32$), St2 ($K = 1.31, L_{\infty} = 4.19$), St3 ($K = 1.21, L_{\infty} = 4.67$) and St4 ($K = 1.31, L_{\infty} = 3.47$) and (b) growth model for oyster shell at St1 ($K = 1.79, L_{\infty} = 56.75$), St2 ($K = 1.31, L_{\infty} = 54.25$), St3 ($K = 1.21, L_{\infty} = 55.73$) and St4 ($K = 1.31, L_{\infty} = 52.02$). St1, St2, St3 and St4 represent the four study sites.

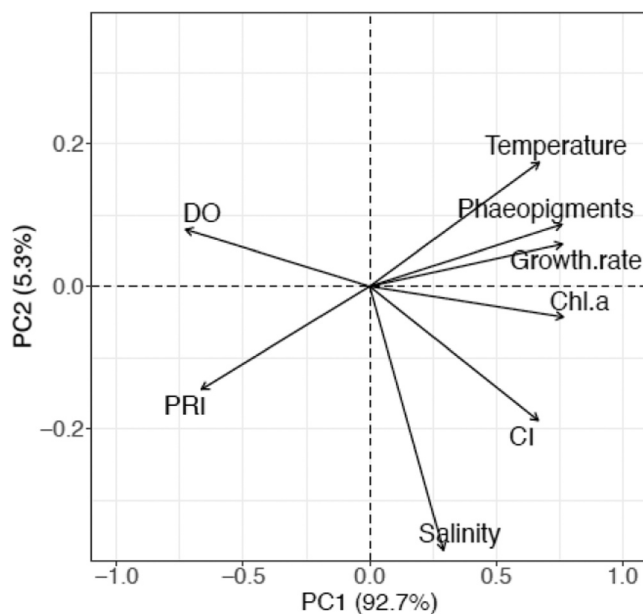


Fig. 8. : Principal component analysis for oyster samples from the four study sites. The relationships between mean hinge growth rate, condition index, salinity, water temperature, dissolved oxygen, chlorophyll-a, phaeopigments and PRI were tested.

growth rate. The seasonal variations in hinge growth rates observed in this study are consistent with seasonal growth reported from *S. cucullata* elsewhere (Krishnakumari et al., 1990; Arkhipkin et al., 2017; Chowdhury et al., 2019), as well as those of other oyster species such as *Ostrea edulis* (Richardson et al., 1993), *Crassostrea virginica* (Kraeuter et al., 2007) or *Magallana gigas* (Huyghe et al., 2019). In temperate regions, growth of oysters practically ceases during cold winter months (Richardson et al., 1993; Huyghe et al., 2019). In tropical regions, although variation in water temperatures is relatively small (e.g. 19.5 –

30.5 °C in this study and 26.5 – 32.7 °C in Pakhmode et al. 2021), tropical *S. cucullata* shows periodical growth of their shells.

Estimated shell growth rate ($65.1 \mu\text{m d}^{-1}$ (1.9 mm month⁻¹; St4) - $104.7 \mu\text{m d}^{-1}$ (3.1 mm month⁻¹; St1); Table 3) are comparable to those reported for the same species from the Mumbai coast, India, ranging between 88.2 and $102.8 \mu\text{m d}^{-1}$ (Krishnakumari et al., 1990) and the Sundarbans ($110 \mu\text{m d}^{-1}$; Bhattacharyya et al., 2010). Growth is relatively fast during early life stages, with a subsequent gradual reduction in growth rate (Fig. 7), similar to observations on the same species in Bangladesh (Chowdhury et al., 2019) and in central-east Atlantic (Arkhipkin et al., 2017). Growth rates are overall higher than in temperate regions, e.g. 2-year-old oysters attain 47.7 – 56.2 mm shell length in Ambinanibe lagoon versus 40 mm in Ascension Island (central-east Atlantic), (Arkhipkin et al., 2017). Whilst sizes of adult *S. cucullata* are generally smaller than those of commercial *Magallana gigas* (Harding and Mann, 2006; Cardoso et al., 2007), the ability of rock oysters *S. cucullata* to survive high temperatures in the tropics as well as their specific taste make them popular in artisanal fisheries and aquaculture in tropical areas of the Indo-West Pacific (Nell, 2001; Arkhipkin et al., 2017).

4.2. Drivers of oyster growth

The highest growth rates, condition indices and growth performance indices were observed at the site most influenced by river inflow (St1), similar to findings on other oysters (e.g., Lebreton et al., 2021). This freshwater inflow represents a key process controlling environmental factors such as salinity, temperature, dissolved oxygen, chlorophyll-a and phaeopigments.

Water temperature, food supply (chlorophyll-a and phaeopigments) and salinity are the most important environmental factors affecting growth (Fig. 8). Several studies have documented the role of water temperature to modulate oyster growth in coastal systems (Brown, 1988; Barraza-Guardado et al., 2008; Benjamin et al., 2009; Huyghe et al., 2019). In oysters, the rate of food acquisition and oxygen consumption (metabolic loss) depend on water temperature (Barraza-Guardado et al., 2008). Previous studies reported optimum temperature

ranges between 25 and 32 °C for *S. cucullata* (Chowdhury et al., 2019; Pakhmode et al., 2021; Marcelino et al., 2023), in agreement with the water temperature observed in this study (19.5 – 30.5 °C; Fig. 3b), particularly at the site influenced by river inflow (22.6 – 28.8 °C). Whilst in temperate regions low winter temperature can result in a cessation of shell growth during winter months (e.g. Kirby et al., 1998; Huyghe et al., 2019), only a reduction and not cessation of growth is observed in tropical settings.

Chlorophyll-*a* and phaeopigment concentrations indicate the abundance of phytoplankton which are the primary food source the filter-feeding oysters (Loret et al., 2000; Tomaru et al., 2002). It is well recognized that oyster growth rate generally increases with increasing phytoplankton abundance (Brown, 1988; Barraza-Guardado et al., 2008; Benjamin et al., 2009; Grangere et al., 2009). Higher growth rate and condition index at the river-impacted site (St1) is thus likely due to overall higher chlorophyll-*a* and phaeopigment concentrations (Table 2), supported by high nutrient input from Ifaho river, as also reported in other coastal lagoons (Carlier et al., 2007; Andrisoa et al., 2019). Typically, higher currents are desirable because they increase delivery of food to the oysters, improve water quality, and disperse biodeposits (Campbell and Hall, 2019). Conversely, lower growth rate and condition index at the site away from river influence (St4) is likely attributable to lower phytoplankton abundance due to lack of river-derived nutrient supply. Low PRI at the river-impacted site indicate dominance of degraded pigments at this site in comparison with the other site, as commonly reported in river delta (e.g. Bourgeois et al., 2011). Furthermore, our results show that chlorophyll-*a* and phaeopigment concentrations are both positively correlated with water temperature, as also observed in other studies (e.g. Trombetta et al., 2019; Fernández-González et al., 2022). However, it is possible that phytoplankton abundance and temperature act independently on oyster shell growth and further investigation is needed to elucidate their respective impact on oyster growth. In addition, the salinity ranges from the three sites located in the main lagoon (St1, St2 and St3) between 10.6 and 21.7 (Table 3) are consistent with the tolerable salinity range of *S. cucullata* from 9 to 27 (Pinto and Wignarajah, 1980; Chowdhury et al., 2019). Whilst dissolved oxygen concentration generally affect the physiology of bivalves (Coxe et al., 2023), oyster species are relatively tolerant to hypoxia, especially at elevated temperature (Shumway and Koehn, 1982; Baker and Mann, 1992; Coxe et al., 2023). Overall high dissolved oxygen concentrations in this study (close to saturation; Table 2) suggest good lagoon water quality and are indicative of good lagoon ecological condition (Debska et al., 2021), and no significant effect of DO on growth parameters is expected.

Heavy rainfall events may also have impacts on the growth of *S. cucullata*. This study shows that lowest growth rates were observed between 20/12/2022 and 24/04/2023, which coincides with the period of significant rainfall events (Fig. 3a). Extensive deforestation, use of fire for clearing and hydrologic modifications in Madagascar may increase sediment flux in coastal zones (Grossman et al., 2020; Wu et al., 2020). Strong river flows during heavy rainfall events induce a significant increase in sedimentation, which likely affect oyster recruitment and growth (Hofmann et al., 1994). Increased sedimentation and suspended materials from resuspension may result in reduced food filtration in oysters, caused by clogging of gill system, and therefore in growth rate (Solomon et al., 2014). It should be noted, however, that oysters can feed in turbid environments, but are less efficient and produce significant amounts of pseudofaeces, which affects gill sorting (Urban and Kirchner, 1992; Ward et al., 1998). Sedimentation is also an important factor in oyster recruitment, since increased sedimentation can result in loss of available substrate for settlement from clays sediment particles and abrasion of new recruits by larger grains (Wall et al., 2005).

4.3. Aquaculture site selection

The river-impacted site has the highest growth rates and condition

index among the study sites, demonstrating that river inflow provides suitable environmental conditions for oyster growth by enhancing the abundance of phytoplankton which is the main food source for *S. cucullata*, as well as providing an optimum salinity range for oyster growth. Overall, Ambinanibe lagoon appears to be a good location for aquaculture projects given the overall high growth performance of the investigated species. The Von Bertalanffy growth curves generated in this study provide means of optimising (a) farm site selection and (b) harvest timing. 8-months-old *S. cucullata* in Ambinanibe lagoon attain market size (40 mm) at St1 while the market size can only be reached in 1 year at St2 and St3 and 1.2 years at St4 (Fig. 7b). Such information is important to oyster farmers not only to select the optimum site, but also to determine the date of collection of oysters. Another factor that requires consideration is the season for introducing spat into the lagoon. As our results showed that lower growth rates occur during wet season (Fig. 4), a strategy could be to introduce spat after the wet season and profit from increased temperature and food availability (phytoplankton abundance) driven by river inflow (Chávez-Villalba et al., 2005). However, the river could also be an important source of contaminants (e.g. heavy metals, pesticides) (Buisson et al., 2008; Senez-Mello et al., 2020), and further investigations are required from a food safety perspective.

The condition index is frequently used in bivalve aquaculture as a rapid measure of ecophysiological state and considered a powerful economic indicator of market products, nutritive state and optimal harvesting schedules (Orban et al., 2002). Overall, the river-dominated site St1 constitutes thus a suitable location to optimise oyster growth rate, at highest quality and market value products when compared to the other parts of the lagoon, and based on this investigation, is the site most suitable for the ongoing installation of an oyster farm in Ambinanibe lagoon.

CRediT authorship contribution statement

Marenjaka Masimana: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Aladin Andrisoa:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Conceptualization. **Thomas C. Stieglitz:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Franck Lartaud:** Writing – review & editing, Writing – original draft, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Aladin Andrisoa reports financial support was provided by French National Research Institute for Sustainable Development. Thomas C. Stieglitz reports financial support was provided by French National Research Institute for Sustainable Development. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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