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Population Structure and Growth Dynamics of the Mangrove Oyster *Crassostrea tulipa* in the Casamance Estuary (Senegal)

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Abstract

The mangrove oyster *Crassostrea tulipa* is an important ecological and fishery resource in West African estuaries, but information on its population dynamics remains limited in inverse estuarine systems. This study examines the population structure, growth, and natural mortality of *C. tulipa* in the Bliss Kassa Islands of the Casamance Estuary (southern Senegal), an environment characterized by strong spatial and seasonal variability in salinity. Oyster sampling was conducted monthly from December 2021 to November 2023 at three sites (Diogue, Hitou, and Niomoune) distributed along a downstream–upstream gradient. Water temperature and salinity were measured concurrently during each sampling campaign. Size–frequency analysis showed clear spatial differences in population structure. Diogue was dominated by small-sized individuals, indicating high recruitment and strong post-recruitment mortality, whereas Hitou exhibited a wider size range, including large oysters exceeding 70 mm. Niomoune populations were mainly composed of intermediate-sized individuals. Three overlapping cohorts were identified over the study period, suggesting continuous or multi-modal recruitment. Growth parameters were estimated from size–frequency data using the von Bertalanffy growth function. Asymptotic shell length ($L\infty$) ranged from 48.49 to 57.80 mm, and growth coefficients (K) from 0.222 to 0.367 yr^{-1}. These values indicate relatively slow growth compared with other West African populations. Natural mortality (M), estimated using Pauly's empirical model, varied between 0.565 and 0.746 yr^{-1}. M/K ratios indicated intermediate life-history strategies across sites. However, the truncated size structure observed at Diogue suggests additional mortality sources, likely related to harvesting pressure. The results highlight the combined influence of local hydrological conditions and anthropogenic pressure on the population dynamics of *C. tulipa* in the Casamance Estuary. Site-specific management measures, including minimum harvest sizes and mangrove habitat protection, are recommended to support sustainable exploitation of this resource.

Keywords: mangrove oyster, *Crassostrea tulipa*, population structure, growth, Casamance Estuary

1. Introduction

Oysters play a major ecological and socio-economic role in tropical coastal and estuarine ecosystems. By filtering large volumes of water, they contribute to water purification, organic matter recycling, and the stabilization of benthic habitats (Beck et al., 2011; Dame, 2011). They also represent an essential food and economic resource for coastal communities, particularly for women involved in harvesting and processing activities (Chuku et al. 2022; Faye et al. 2019).

In West Africa, the mangrove oyster *Crassostrea tulipa* (syn. *C. gasar*) is widely distributed along mangrove ecosystems from Senegal to Angola. This intertidal, euryhaline species primarily colonizes mangrove roots and tolerates strong fluctuations in salinity and temperature (Diadhiou et al., 2016; Ndour et al., 2021). However, natural populations are subject to intense anthropogenic pressure and pronounced environmental variability, exacerbated by climate change and habitat degradation (Mahu et al., 2022).

In the Casamance estuary, inverse estuarine conditions are seasonal, occurring mainly during the dry season, while the rainy season temporarily restores a classical estuarine gradient due to increased freshwater inputs (Descroix et al., 2020). This seasonal alternation generates strong spatio-temporal variability in salinity conditions, which can significantly influence the physiology, growth, and distribution of bivalves (Berger & Kharazova, 1997). In addition, excessive harvesting pressure can alter the demographic structure of oyster populations, often resulting in the dominance of small-sized individuals in overexploited areas (Etim and Brey 1994; Faye et al. 2019).

Despite its ecological and socio-economic importance, *C. tulipa* remains poorly studied in the Casamance Estuary, where environmental conditions vary markedly among sites. A better understanding of its growth patterns and population structure is therefore essential to assess the sustainability of its exploitation and to propose appropriate management measures.

Accordingly, this study aims to characterize the size distribution and growth parameters of *C. tulipa* across three contrasting sites in the Casamance Estuary (Diogue, Hitou, and Niomoune), by estimating the parameters of the von Bertalanffy growth model. The results will contribute to a better understanding of oyster population dynamics and support the implementation of sustainable management strategies for this resource in Senegalese estuarine ecosystems.

2. Materials and Methods

Study area

This study was conducted in the Bliss Kassa Islands, located in the central part of the estuary. The sampling sites were situated within the municipality of Kafountine, in the administrative region of Ziguinchor, southwestern Senegal (Fig. 1).

Sampling was carried out at three sites: Diogue, Hitou, and Niomoune. All sites are located within the insular zone of the municipality, in an estuarine environment characterized by brackish waters of the Casamance River. These sites were primarily selected based on their strategic position along a salinity gradient, reflecting their increasing distance from the river mouth toward the upstream areas. Diogue is located near the estuary mouth, Hitou within the mangrove, and Niomoune further inland.

The region is characterized by a coastal South-Sudanian climate (Sagna, 2005), with a dry season from November to May and a monsoon season from June to October. The hydrographic network is dense and supports the development of extensive mangrove forests, which play a crucial role in oyster production and shoreline stabilization.

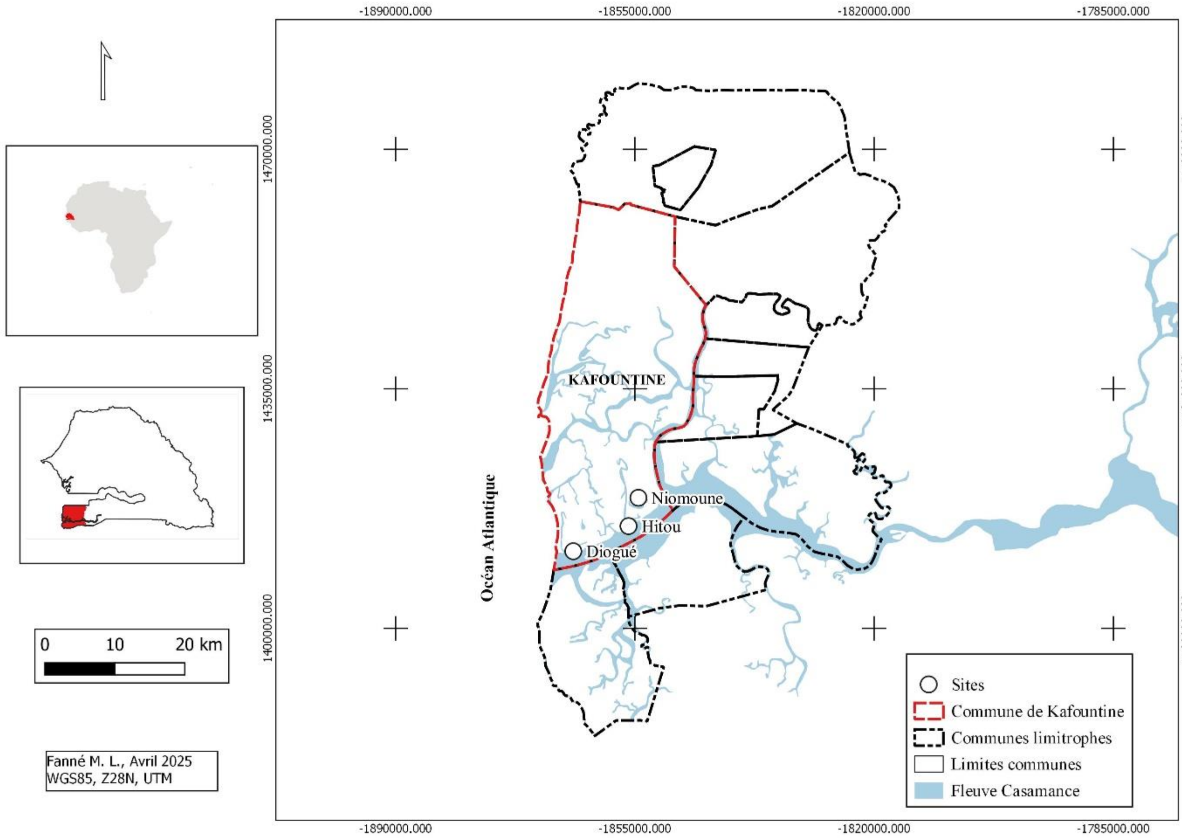

Figure 1. Location of oyster sampling sites (Diogue, Hitou, and Niomoune) in the Casamance Estuary, Senegal

Sampling protocol

At each site, three linear meters were established as sampling units, with a distance of 30 m between units to ensure spatial representativeness. Following the approach described by Diouf et al. (2009), three mangrove roots were selected for each linear meter based on their bivalve density: one root with high density, one with medium density, and one with low density. All bivalves attached to each selected root were manually collected. Subsequently, each individual was counted and measured for shell height (maximum distance from the hinge to the ventral margin) using a digital caliper with a precision of 0.01 mm. Individuals were then weighed using an electronic balance with a precision of 0.01 g. These measurements allowed the determination of size and biomass structure of oyster populations at each study site.

Measurement of environmental parameters

In parallel with oyster sampling, environmental parameters (water temperature and salinity) were measured during each sampling campaign. Temperature and salinity were recorded using a calibrated portable multiparameter probe.

Estimation of growth parameters

Growth of *Crassostrea tulipa* was analyzed based on size–frequency data collected between

December 2021 and November 2023. Monthly shell height distributions were used to identify modal progressions over time and to describe population growth patterns. Growth parameters were estimated using the von Bertalanffy growth function (VBGF), which is widely applied to marine bivalves to describe asymptotic growth trajectories:

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

where L_t is the shell height at theoretical age t, L_∞ is the asymptotic shell height, K is the growth coefficient describing the rate at which shell size approaches L_∞ and t_0 is the theoretical age at which shell size is zero.

Growth parameters were derived from size–frequency distributions following a modal progression approach, under the assumption that successive modes represent cohorts growing through time. The estimation focused on fitting the VBGF to the observed displacement of modal size classes rather than on directly observed ages. Consequently, the age variable (t) represents a theoretical, model-derived time scale, and not an observed biological age. The von Bertalanffy growth parameters (L_∞, K, t_0) were calculated in R using the vbFuns function implemented in the *FSA* package (Ogle, 2018), which provides analytical tools for fitting and manipulating VBGF-based growth models. Derived parameters included the growth performance index (Φ′) (Pauly & Munro, 1984), calculated as:

$$\Phi' = \log_{10} K + 2.\log_{10}(L_{inf}) \quad (2)$$

to allow standardized comparisons of growth performance among sites. Theoretical maximum age was estimated from the VBGF parameters as:

$$t_{max} \approx \frac{3}{K} \quad (3)$$

and should be interpreted as an index of potential longevity derived from growth parameters, rather than as a directly observed lifespan.

Estimation of natural mortality (M)

Annual natural mortality (M) was estimated using the empirical relationship proposed by Pauly (1980). This approach is widely applied in fisheries and invertebrate population studies when direct age-based mortality estimates are not available. The equation used is expressed as:

$$\log_{10} M = -0.0066 - 0.279 \log_{10}(L\infty) + 0.06543 \log_{10}(K) + 0.463 \log_{10}(T) \quad (4)$$

Where M is the annual natural mortality rate ($year^{-1}$), L∞ is the asymptotic length estimated from the von Bertalanffy growth model, is the growth coefficient ($year^{-1}$), T is the mean annual water temperature (°C).

Calculation of the M/K ratio

The M/K ratio was calculated for each site as an indicator of the population's life-history strategy and biological resilience. This ratio provides a synthetic measure of the balance between natural mortality and growth rate and enables comparisons of population renewal potential among sites. M/K values were interpreted according to threshold ranges commonly reported for exploited bivalve species (Beverton & Holt, 2008; Pauly, 1980). with values < 1.5 indicating a slow life-history strategy, values between 1.5 and 2.5 reflecting an intermediate strategy, and values > 2.5 characterizing an opportunistic life-history strategy.

Data analysis

All statistical analyses were performed using the R software environment (R Core Team, 2022). Temperature and salinity values were compared among the different sampling sites. Mean values, as well as minimum and maximum ranges, were calculated for each site. Data normality and homogeneity of variances were tested prior to analysis. Subsequently, a one-way analysis of variance (ANOVA) was conducted to assess significant differences among sites. When significant differences were detected, a Tukey post hoc test was applied to identify pairwise differences between sites. Individuals sampled at each site were grouped into 10-mm size classes (shell height) in order to establish size-frequency distributions for each locality. Relative abundances (%) per size class were calculated to allow standardized comparisons among sites. Kruskal–Wallis tests, followed by Dunn's post hoc tests with Bonferroni correction, were used to statistically compare mean shell heights among sites when parametric assumptions were not met.

3. Results

Environmental parameters

For temperature, the highest mean value was recorded at Diogue (29.19 °C), followed by Hitou (28.64 °C) and Niomoune (28.41 °C). One-way ANOVA revealed a highly significant difference among sites ($F = 80.42$, $p < 0.001$). Tukey's post hoc test indicated that the mean temperature at Diogue was significantly higher than those observed at Hitou and Niomoune ($p < 0.001$). The range of variation, calculated as the difference between maximum and minimum values, was 13.5 °C at both Diogue (22.0–35.5 °C) and Hitou (22.0–35.5 °C). At Niomoune, the temperature range was lower, reaching 10.0 °C (23.0–33.0 °C). Regarding salinity, the highest mean value was observed at Niomoune (30.6), followed by Hitou (29.7) and Diogue (29.5). Tukey's test showed that Diogue differed significantly from Niomoune ($p < 0.001$), but not from Hitou ($p = 0.076$, Table 2). Salinity ranges were 14.5 at Diogue (21.0–35.5), 21.5 at Hitou (16.5–38.0), and 22.5 at Niomoune (16.0–38.5).

Table 1. Mean, minimum, and maximum values of temperature and salinity at the Diogue, Hitou, and Niomoune sites

Site	Temperature			Salinity		
	Mean	Min	Max	Mean	Min	Max
Diogue	29.19	22	35.5	29.5	21	35.5
Hitou	28.64	22	35.5	29.7	16.5	38
Niomoune	28.41	23	33	30.6	16	38.5

Table 2. Statistical comparison of temperature and salinity among sampling sites in the Casamance estuary (one-way ANOVA followed by Tukey HSD post-hoc test)

Parameter	Comparison	Mean difference	Test statistic	df	p-value
Temperature	Overall ANOVA	—	F = 80.42	2	$< 2 \times 10^{-16}$
	Hitou – Diogue	-0.549	—	—	< 0.0001
	Niomoune – Diogue	-0.786	—	—	< 0.0001
	Niomoune – Hitou	-0.237	—	—	7.0×10^{-6}
Salinity	Overall ANOVA	—	F = 152.3	2	$< 2 \times 10^{-16}$
	Hitou – Diogue	0.229	—	—	0.0757
	Niomoune – Diogue	1.134	—	—	< 0.0001
	Niomoune – Hitou	0.905	—	—	< 0.0001

Size structure

Comparison of size structures among the three studied sites revealed distinct demographic profiles. At Diogue, the size structure was dominated by small and medium-sized individuals, with a strong representation in the 20-30 mm and 30-40 mm size classes, and a notable contribution of the 10-20 mm class. This site exhibited the highest proportion of young individuals among the three sites. Oysters larger than 60 mm were almost absent. In contrast, Hitou was characterized by a broader size structure ranging from 20 mm to more than 80 mm. High abundances were observed in the 30-40 mm, 40-50 mm, and 50-60 mm size classes. Hitou was the only site where large individuals (60-70 mm and 70-80 mm) were recorded. The Niomoune site showed a strong concentration of individuals in the 30-40 mm and 40-50 mm size classes, with a pronounced peak in the 40-50 mm class. Statistical analysis of individual shell sizes revealed a significant difference among sites (Kruskal–Wallis test, $p < 0.001$). Dunn's post hoc tests with Bonferroni correction indicated that oyster sizes at Diogue were significantly smaller than those observed at Hitou and Niomoune, whereas no significant difference was detected between Hitou and Niomoune ($p > 0.05$).

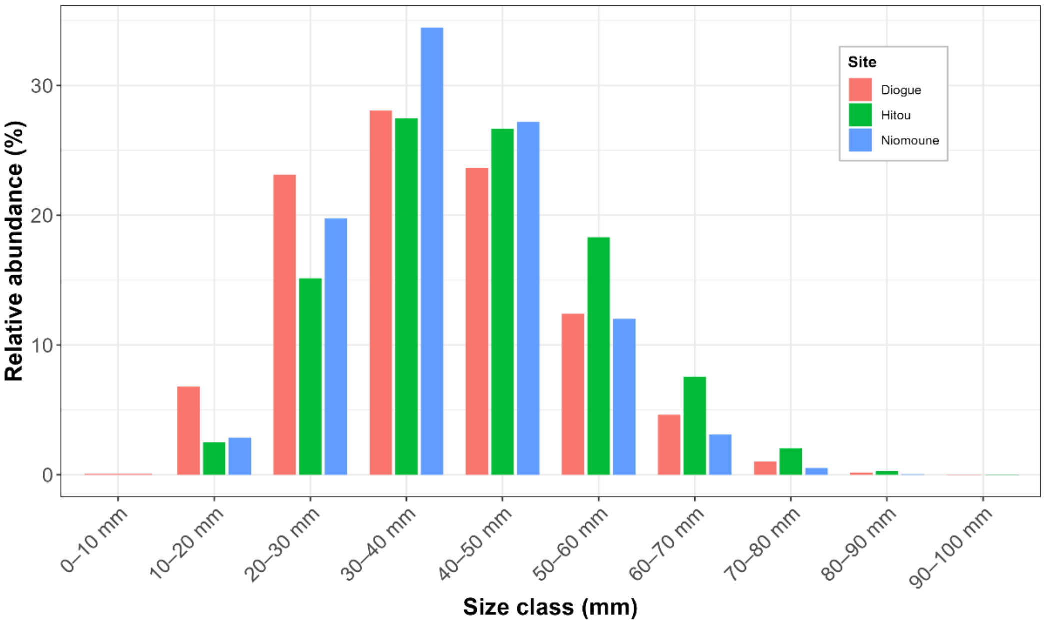

Figure 2. Relative size structure of bivalve population across three sampling sites in the Casamance estuary: Diogue, Hitou, and Niomoune. Relative abundance (%) of individuals is shown by size classes (10-mm intervals), ranging from 0 to 100 mm

Three overlapping cohorts were identified in the size-frequency distributions of the studied population between December 2021 and November 2023. From December 2021 to approximately July 2022, the population exhibited a predominantly unimodal distribution, with the first cohort progressively shifting from smaller size classes (30-40 mm) toward larger classes (50-60 mm). From August 2022 onward, the size distribution became bimodal, reflecting the persistence of cohort 1 in the larger size classes (≥ 60 mm) and the emergence of a second cohort in the smaller size classes (20-30 mm). This bimodal pattern persisted through the end of 2022 and into early 2023. By mid-2023, particularly between May and August, a new recruitment event was observed, leading to the formation of a third cohort (10-20 mm), while cohorts 1 and 2 occupied intermediate and larger size classes, respectively. Between September and November 2023, the size-frequency distributions clearly indicated the presence of three distinct cohorts, with the youngest individuals concentrated in the 10-20 mm size class, an intermediate cohort around 30-40 mm, and older individuals exceeding 50

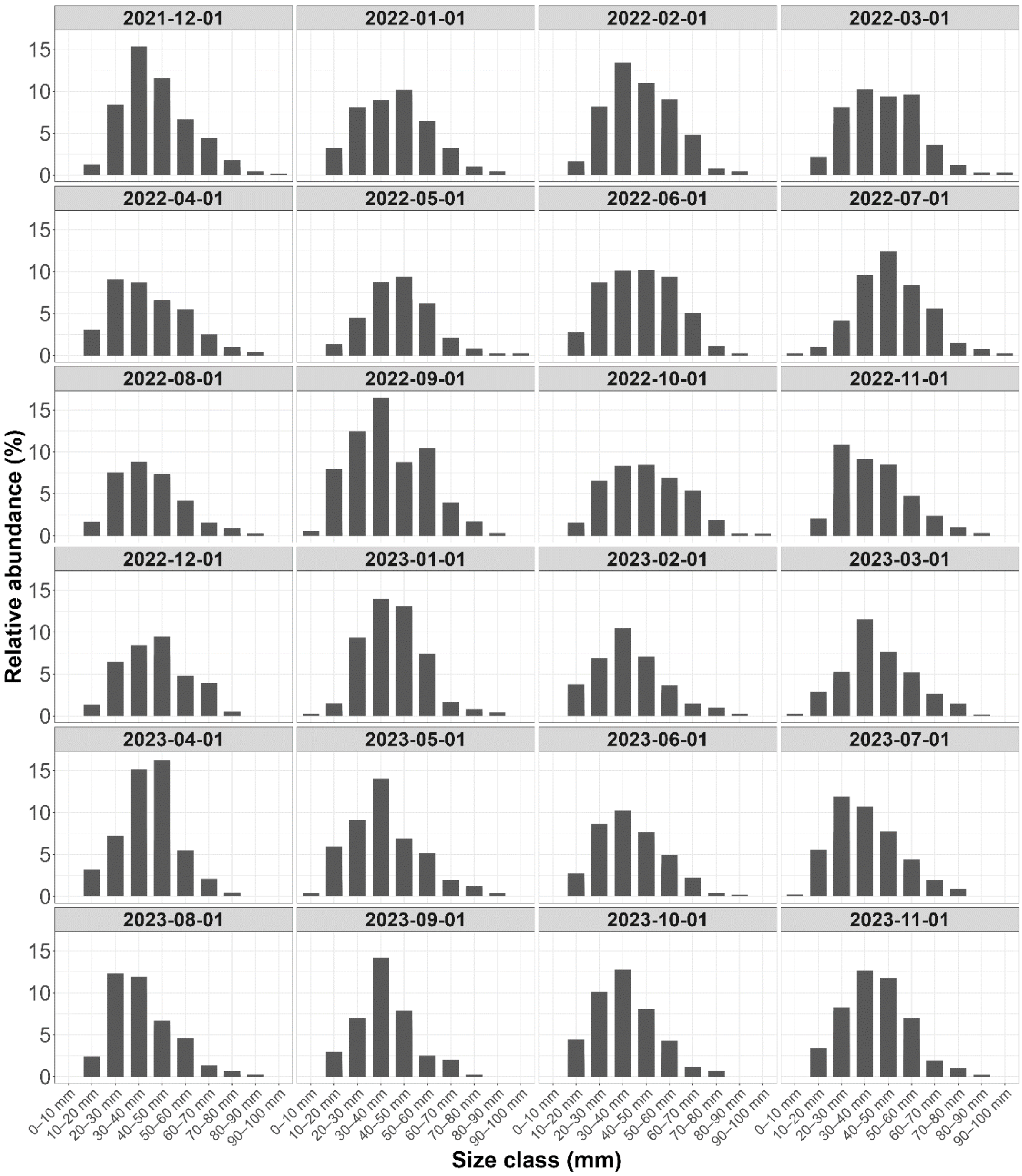

Figure 3. Monthly size-class distribution (mm) and relative abundance (%) of the bivalve population from December 2021 to November 2023 for all sites combined

Growth parameters

Figure 4 illustrates the growth curves of individuals as a function of age, modeled using the von Bertalanffy growth parameters estimated for each site. Marked differences were observed among the three localities. The population from Hitou exhibited the fastest growth, with shell lengths consistently greater than those observed at the other sites across all ages. At the age of 5 years, individuals reached a shell length of approximately 55 mm. This site was characterized by the highest growth parameters, with an asymptotic length of $L\infty$ = 57.80 mm and a growth coefficient $K = 0.367$ yr⁻¹ (Table 3). The growth curve associated with Diogue showed intermediate growth, with individuals reaching approximately 45 mm at 5 years of age. The estimated parameters for this site were $L\infty = 55.08$ mm and $K = 0.238$ yr^{-1} (Table 3). In contrast, the Niomoune population exhibited the smallest sizes at equivalent ages. At 5 years, individual shell length remained below 40 mm. This site displayed the lowest growth performance, with $L\infty = 48.49$ mm and $K = 0.222$ yr^{-1}.

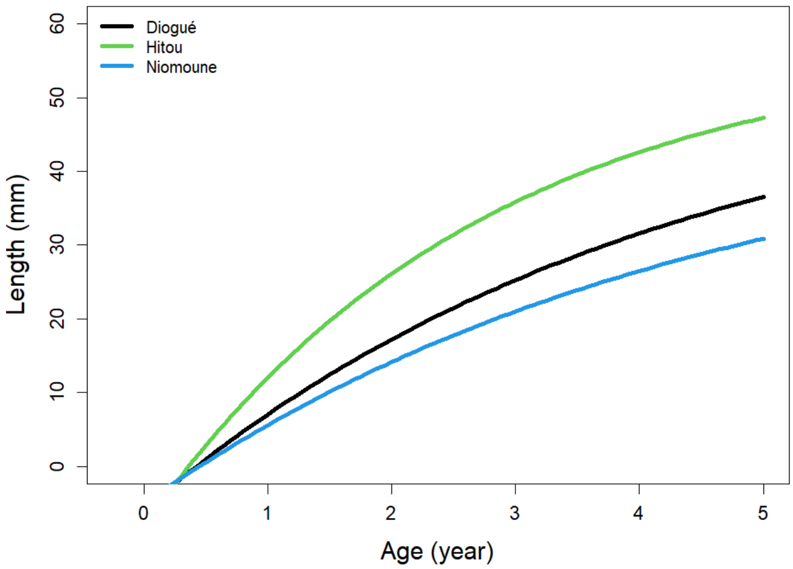

Figure 4. Illustrates the predicted growth trajectories of oysters at the three study sites

Natural Mortality and M/K ratio

Estimates of natural mortality (M) varied among sites (Table 3). The highest value was recorded at Hitou (M = 0.746 yr^{-1}), followed by Diogue (M = 0.570 yr^{-1}), while the lowest value was observed at Niomoune (M = 0.565 yr^{-1}). When combined with site-specific growth coefficients (K), M/K ratios also differed among localities (Table 3). M/K values ranged from approximately 2.03 to 2.39 across the study area. The highest M/K ratio was observed at Diogue (M/K = 2.39), whereas lower values were recorded at Hitou (M/K = 2.03) and Niomoune.

Table 3. Von Bertalanffy growth parameters for individuals from the three study sites

Site	$L\infty$ (mm)	K (yr^{-1})	t_0	Phi	M (yr^{-1})	t_{max} (yr)	M/K
Diogue	55.081	0.238	0.424	2.859	0.570	13	2.39
Hitou	57.797	0.367	0.362	3.089	0.746	9	2.03
Niomoune	48.492	0.222	0.448	2.719	0.565	14	2.55

4. Discussion

This study revealed significant differences in temperature and salinity among the three study sites during the sampling period. Maximum temperatures were recorded at Diogue, located downstream in the estuary, whereas Niomoune, situated upstream, exhibited the highest salinity levels. These patterns illustrate the intrinsic dynamics of West African estuaries, where marine influence interacts with terrestrial inputs and seasonal evaporation processes (Pages & Citeau, 1990; Sagna, 2005). In so-called "inverse" estuarine systems such as the Casamance and the Sine Saloum, marked differences occur, with salinity increasing upstream, particularly during the dry season (Descroix et al., 2020). As emphasized by Gosling (2015), these environmental factors strongly affect bivalve growth, reproduction, and mortality rates.

Population structure varied considerably among sites. Diogue was characterized by active recruitment and the early harvesting of larger individuals, suggesting a dominance of younger cohorts. In contrast, Hitou displayed a broader size distribution, including individuals exceeding 70 mm, indicative of favorable conditions for growth and long-term survival. Niomoune was dominated by intermediate-sized individuals (40-50 mm), which may reflect either selective harvesting of larger oysters or environmental constraints limiting longevity. Similar patterns have been reported for *Crassostrea gasar* in Benin and Nigeria, where oyster size structure reflects both local salinity regimes and fishing pressure (Adite et al. 2013; Agboola et al. 2021; Faye et al. 2019). The presence of three overlapping cohorts suggests multimodal reproduction and near-continuous recruitment, as reported for several tropical oyster species inhabiting West African lagoons and estuaries (Diadhiou et al., 2016; Etim & Brey, 1994). This reproductive strategy contrasts sharply with that of temperate species such as *C. gigas*, which exhibit more strictly seasonal spawning patterns (Chavez-Villalba et al., 2003). Growth indicators revealed significant disparities among sites. At Hitou, growth rates were higher and asymptotic size greater than at the other two sites, reflecting more favorable environmental conditions, likely linked to higher food availability and the relative abiotic stability provided by mangrove habitats (Alongi, 2009; Dame, 2011). Growth and mortality parameters of *Crassostrea tulipa* in the Casamance Estuary highlighted pronounced spatial variability, reflecting heterogeneity in environmental conditions among sites. The estimated values of $L\infty$ (48.5-57.8 mm) and K (0.222-0.367 yr^{-1}) indicate relatively slow growth compared with values reported for the same species in other West African regions. In Gambia and Ghana, Abdallah (2022) reported asymptotic shell sizes ranging from 107 to 130 mm and growth coefficients (K) between 0.52 and 0.90 yr^{-1}, with maximum ages of 3 to 6 years. These differences suggest that Casamance oysters attain smaller sizes but over longer lifespans when expressed as theoretical maximum ages derived from growth models (up to 14 years at Niomoune)**.** These maximum ages should be interpreted strictly as theoretical values derived from the von Bertalanffy growth function, rather than as directly observed biological longevities. This pattern of slower growth and increased longevity may be associated with responses to environmentally constraining conditions, particularly high and seasonally variable salinities (Etim & Brey, 1994; Goulletquer et al., 1998). The fastest growth was observed at Hitou ($L\infty = 57.8$ mm; $K = 0.367$ yr^{-1}), accompanied by a higher growth performance index ($\Phi' = 3.09$) than at the other sites. This trend suggests more favorable trophic and hydrological conditions, probably associated with mangrove stability and enhanced food availability (Alongi, 2009; Dame, 2011). Conversely, the slow growth observed at Niomoune ($K = 0.222$ yr^{-1}) appears to be linked to osmotic stress induced by high salinity levels, confirming previous findings that energy allocation to growth decreases under hyperhaline conditions (Berger &

Kharazova, 1997; Shumway, 1977). Similar trends have been described for *C. gasar* in estuaries of Guinea-Bissau and Senegal, where reduced growth rates are associated with elevated salinities.

The growth performance index (Φ′) estimated in this study was lower than values reported for the Gulf of Guinea (1.8–2.1; Osei et al. 2021), even when accounting for differences in measurement scales (cm vs. mm). These lower values suggest reduced productivity in the Casamance Estuary, likely resulting from more variable trophic conditions and harvesting pressure targeting larger individuals, particularly at Diogue. Natural mortality rates (M = 0.565-0.746 yr^{-1}) were lower than those reported for Ghana and Gambia (1.57-2.26 yr^{-1}; Abdallah 2022), consistent with the observed slower growth and increased longevity of Casamance oysters as inferred from VBGF-derived parameters. However, it should be noted that Pauly's empirical model was originally developed for fish stocks and assumes relatively stable environmental conditions. In highly variable tropical estuaries such as the Casamance system, mortality estimates derived from this model should therefore be interpreted cautiously and considered as approximations rather than precise estimates. Nevertheless, the higher mortality observed at Hitou indicates rapid population turnover, a characteristic feature of bivalves inhabiting productive but environmentally variable systems (Amaral & Paula, 2010; Pauly, 1980). The number of cohorts identified further supports the occurrence of multimodal reproduction and near-continuous recruitment, a pattern previously described for *C. tulipa* and other tropical oyster species (Chuku et al., 2022). This reproductive strategy contrasts strongly with that of temperate oysters such as *C. gigas*, which display strictly seasonal reproduction (Chavez-Villalba et al., 2003).

Overall, these results demonstrate that the population dynamics of *C. tulipa* in the Casamance Estuary are strongly influenced by local hydrological conditions and anthropogenic pressures. The slower growth rates and smaller asymptotic sizes observed relative to other West African populations likely reflect the combined effects of hyperhaline stress and overexploitation. To ensure the sustainability of this resource, the implementation of appropriate management measures is essential, including the establishment of minimum harvest sizes, the protection of ecologically valuable mangrove habitats, and spatio-temporal monitoring of abiotic parameters. Such approaches have proven effective in enhancing oyster population resilience in other West African estuaries (Adite et al. 2013; Faye et al. 2019).

The M/K ratio was not used as a direct indicator of fishing mortality or exploitation rate (E). Instead, stock status was evaluated using an integrative framework combining growth parameters (K, L∞, Φ′), natural mortality (M), the M/K ratio, and the observed size structure (King, 2007; Pauly, 1980). Discrepancies among these indicators were interpreted as evidence of additional mortality sources, including fishing pressure and/or local environmental constraints. At Diogue, growth parameters and the M/K ratio indicate an intermediate life-history strategy; however, the population exhibited a strongly truncated size structure dominated by juveniles and lacking large individuals. Such patterns are commonly associated with elevated post-recruitment mortality in exploited stocks (Beverton & Holt, 2008; Froese, 2004), suggesting the influence of additional mortality pressures beyond natural processes. In contrast, the Hitou population showed consistency between life-history indicators and demographic structure. The presence of large individuals and a continuous size distribution reflect a balance between growth and natural mortality, consistent with a moderate exploitation regime and adequate reproductive biomass (Beverton & Holt, 2008; King, 2007). Overall, although M/K values suggest comparable intrinsic resilience between sites, only Hitou displays a size structure consistent with this potential, whereas the divergence observed at Diogue points to stronger local anthropogenic and/or environmental pressures

5. Conclusion

This study provides new insights into the population structure and growth dynamics of the mangrove oyster *Crassostrea tulipa* in the Bliss Kassa Islands of the Casamance Estuary. Marked spatial differences in environmental conditions, particularly salinity and temperature, were reflected in contrasting size structures, growth parameters, and mortality rates among sites. The observed patterns indicate that *C. tulipa* populations in the Casamance exhibit relatively slow growth and small asymptotic sizes compared with other West African regions, but over longer theoretical lifespans, highlighting an adaptive response to environmentally constraining and highly variable estuarine conditions.

Overall, the results emphasize the strong influence of local hydrological regimes and anthropogenic pressures on oyster population dynamics. These findings underline the need for site-specific management strategies, including the establishment of minimum harvest sizes, the protection of mangrove habitats, and the continued monitoring of environmental parameters, to ensure the long-term sustainability of this key socio-ecological resource in Senegalese estuarine ecosystems.

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Author contributions

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Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Informed consent

Obtained.

Ethics approval

The Publication Ethics Committee of the Macrothink Institute.

The journal's policies adhere to the Core Practices established by the Committee on Publication Ethics (COPE).

Provenance and peer review

Not commissioned; externally double-blind peer reviewed.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Data sharing statement

No additional data are available.

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