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Unveiling seasonal variability in *Crassostrea tulipa* larval dispersal in Gulf of Guinea coastal waters: foundations for sustainable shellfish farming

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The coastal zone of the Gulf of Guinea holds significant natural potential for the production of the mangrove oyster *Crassostrea tulipa*. This study assessed the larval dispersal of *C. tulipa* in the Benin's coastal lagoon. Oyster larvae were sampled monthly from January to December 2023 in three traditional oyster production areas (Ahouandji, Dégouè, and Djondji) using a 50 µm mesh plankton net. The larvae samples collected, were analyzed under a light microscope, and the different larval stages (D-, veliger, and pediveliger larvae) of *C. tulipa* were identified and counted. The results show a major larvae abundance period extending from November to April, with maximum density occurring in March and/or April, depending on the site. A secondary phase of larvae abundance production was observed from May to July, although it was characterized by a very low presence of advanced larval stages (pediveliger). A dominance of D- and veliger larvae was noted in the Djondji area, whereas pediveliger larvae were more prevalent in the Ahouandji production zone. The highest cumulative number of larvae (56,220.0) was recorded in the Djondji area, compared to 35,586.7 in Dégouè and 36,160.0 in Ahouandji. In terms of larval survival, the lowest rate (0.1%) was observed in Djondji, compared to 0.2% in Ahouandji and 0.4% in Dégouè. Therefore, the high larval abundance observed in the Djondji production area does not necessarily reflect favorable survival conditions for larvae. The production areas of Ahouandji and Dégouè may offer more favorable environments for larval development. These results provide valuable data that

can be used to improve oyster farming and management in Benin's coastal waters.

KEYWORDS

coastal lagoon, larval dynamics, oysters, *Crassostrea tulipa*, oyster farming

1 Introduction

Larval dispersal and availability, as well as recruitment, are fundamental processes in the dynamics of marine populations, particularly in bivalve molluscs such as the oysters (Theuerkauf et al., 2021). Ecologically adapted to dynamic coastal environments, these species play a key role in the functioning of these ecosystems, contributing significantly to global fisheries production (Toupoint et al., 2016; Androuin et al., 2021). Oysters are benthic macroinvertebrates belonging to the class of Bivalvia and exhibit a benthopelagic life cycle characterized by a relatively long larval phase (Thorson, 1950; Doinsing and Ransangan, 2022). Like annelids, polychaetes and crustaceans, bivalve molluscs constitute an important part of benthic macrofauna due to their diversity, abundance and the essential ecological functions, including bioturbation and their role as intermediate trophic links (Dimitriadis et al., 2014; Barbier, 2016; Politi et al., 2019).

The dynamic of the population of these organisms, particularly that of oysters, depends largely on the success of larval dispersal and the transition from the pelagic to the benthic phase (Olafsson et al., 1994; Pedersen et al., 2008; Pineda et al., 2010; Androuin et al., 2021). This process ensures population renewal (Cowen and Sponaugle, 2009) and contributes to spatial structuring by enabling colonization of diverse habitats (Adams et al., 2014). The connectivity established through larval dispersal between different habitats is crucial for the survival of metapopulations, as it maintains genetic diversity and supports low-performing patches that cannot produce sufficient larvae (Powers et al., 2023). Green et al. (2015) demonstrated that this demographic connectivity across habitats is also a critical parameter in the design of marine reserves due to its implications for the resilience and persistence of populations following disturbance.

The dispersal of larvae is influenced by various abiotic factors, such as temperature, salinity, hydrodynamics and substrate type and availability, biotic factors including competition and predation, as well as intrinsic variables related to the larvae themselves (Androuin et al., 2021). Manuel et al. (2023) demonstrated that salinity and larval age influence the swimming behavior of *Crassostrea gigas*, while Marcelino et al. (2023) revealed the combined effect of temperature and salinity on the survival of *Saccostrea cucullata* larvae. Hydrodynamic conditions (Tedford-

Callahan et al., 2025) and substrate quality also play a significant role in the success of metamorphosis (Chuku et al., 2020). The viability, abundance and cohort structure of the larvae influence their capacity to disperse, settle and metamorphose on favorable substrates (Androuin et al., 2021).

Oysters (*Crassostrea tulipa*) have significant socio-economic value for local populations in the Gulf of Guinea region. Chuku et al. (2022) estimated that shellfish fisheries, which are largely dominated by mangrove oyster harvesting, generate over 300 million USD in annual revenue in Gulf of Guinea countries, with more than 570,000 households directly dependent on this fishery. However, despite the socio-economic importance of oyster fisheries for local populations in the Gulf of Guinea region and the favorable ecological potential of the area, oyster farming remains predominantly traditional and relies primarily on hand-harvesting. Due to the lack of a sub-regional management policy for oyster fishing, oysters are subject to intensive and unregulated harvesting in estuaries and lagoons (Adite et al., 2013). As a result, the natural stock is exposed to the risks of overexploitation. Additionally, pollution and climate change also impact oyster populations (Mahu et al., 2022). It is therefore necessary to sustain the natural oyster stocks through management measures, primarily by promoting *C. tulipa* farming in the Gulf of Guinea region. In recent years, research efforts have been made to improve understanding of this species ecology, focusing on substrate selection for spat collection, demographic aspects and growth experiments (Adite et al., 2013; Chuku et al., 2020; Chuku and Osei, 2020; Chuku et al., 2022; Mahu et al., 2022; Chuku et al., 2023; Bunting et al., 2024). Unfortunately, data on the reproduction of *C. tulipa* in its natural habitat remains poorly documented.

Assessing the spatial and temporal variability of oyster reproduction in the natural environment requires data on spat collection, spawning, and larval dispersal in the environment (Bernard, 2011). Spat recruitment tends to be high in areas where larvae are abundant (Christo et al., 2021). Data on larval distribution are therefore crucial to manage efficiently the spat collection and the oyster farming (Pineda et al., 2010; Ubertini et al., 2017; Oliveira et al., 2024). The present study provides the first data on the availability of *C. tulipa* larvae in the coastal waters of the Gulf of Guinea. It aimed to assess the spawning dynamics and larval distribution of *C. tulipa* in the coastal lagoon of Benin with regard to environmental conditions.

2 Materials and methods

2.1 Study area

This study was conducted in the coastal lagoon of Benin. The lagoon is located between meridians 1°48' and 2°16' East, and parallels 6°16' and 6°20' North and covers an area of 55 km². It stretches almost parallel to the Atlantic Ocean for approximately 60 km, from Grand-Popo to Togbin. The Grand-Popo coastal lagoon receives water from the Mono River and Lake Ahémé, and discharges into the sea through the “BOUCHE DU ROY” outlet near the village of Avlo-Plage, and more recently through Djondji mouth (Viaho, 2014).

The region has a subequatorial climate, with two rainy seasons (April to July; mid-September to October) and two dry seasons (December to March; mid-August to mid-September). Annual average rainfall is approximately 1385.3 mm (Oyede, 2023), and ambient temperatures range from 25 °C to 27.7 °C. The vegetation is highly diverse but dominated by mangrove species such as *Rhizophora racemosa* and *Avicennia africana*. These mangrove ecosystems serve as spawning and refuge areas for many aquatic species and are therefore characterized by high biodiversity (Sinsin et al., 2018). With their dense and submerged root networks, they provide extensive surfaces for the settlement of *C. tulipa* oyster. Fishing is the primary livelihood for communities along the lagoon. These activities include mainly oyster harvesting and traditional oyster farming, primarily carried out by women.

2.2 Sampling design

As part of this study, the coastal lagoon was divided into three sectors, each representing a major oyster (*C. tulipa*) production area. This subdivision was based on traditional oyster production areas in the region, specifically the villages of Ahouandji, Dégouè, and Djondji. In each production area, three sampling stations were established (Figure 1), taking into account parameters such as biotope characteristics, presence or absence of mangroves, and land use along the lagoon banks.

Larval sampling was carried out monthly over a one-year period from January to December 2023. At each of the three sampling stations in each production area, 0.2 cubic meters (m³) of lagoon water were collected in a bucket and filtered through a 50 µm mesh plankton net with a collector at the end. After filtration, the plankton concentrate was reduced to a final volume of 0.00019 m³ and fully preserved in 4% formalin for subsequent analysis. Thus, three samples were collected per production area each month throughout the study period.

2.3 Identification and enumeration of *C. tulipa* larvae

In the laboratory, six “1 × 10⁻⁶ m³” samples were taken for independent observations under the microscope (KERN ODC Version 1.0 01/201). Before each was taken, the sample was

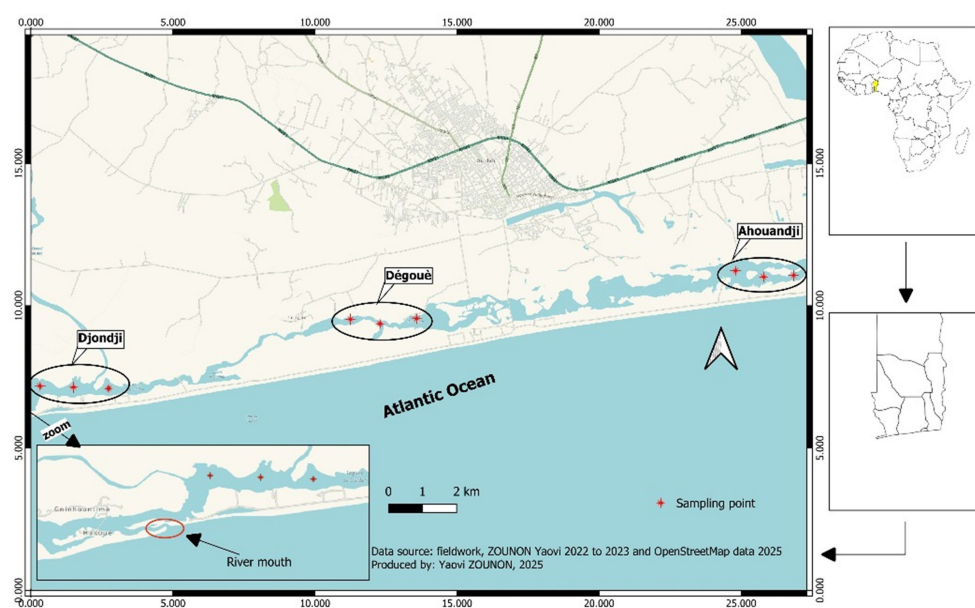


FIGURE 1
Map of the sampling stations.

mixed by hand to ensure its contents were homogeneous. Larvae and their developmental stages were identified and counted with the aid of the Sedgewick-Rafter cell. Counts were recorded separately for each larval stage. A total volume of $6 \times 10^{-6} \text{ m}^3$ (V_p), which was taken from the 0.00019 m^3 (V_r) of water that was recovered and preserved in the field after filtering, 0.2 m^3 (V_f).

The larval density (D_s) was calculated using the following formula:

$$\frac{n}{V_p} \times \frac{V_r}{V_f}$$

n = Total number of larvae counted in the analyzed aliquots.

V_p = Total volume of the analyzed aliquots (m^3).

V_r = Volume of the sample recovered after filtration (m^3).

V_f = Total volume of water filtered (m^3).

2.4 Descriptors of larval dynamics

To describe larval dynamics throughout the year 2023, five Descriptors were computed to characterize the larval cohort across the study sites. These Descriptors cover three main categories: abundance, survival and persistence. The Descriptors are summarized in Table 1.

2.4.1 Abundance

Four abundance-related Descriptors were calculated for each larval stage: the mean, median, maximum, and the total number of larvae (the product of density and filtered volume at each date and station), all expressed in individuals per cubic meter (ind.m^{-3}), except for the last one (the total number of larvae), which is

expressed as ind. These values provide an overview of larval presence and density throughout the sampling period.

2.4.2 Survival and persistence

A survival rate was computed as a proxy for larval survival, based on the ratio of cumulative densities of pediveliger larvae to D-larvae, following Bernard (2011). This ratio is expressed as a percentage (%). Additionally, the presence duration of pediveliger larvae was calculated as the proportion of sampling dates where they were detected, relative to the total number of sampling events. This provides an indication of larval persistence in the water column.

1.5 Measurement of physico-chemical parameters of the coastal lagoon waters. Environmental factors strongly influence the reproduction and development of oysters of (Hawkins et al. 2013; Paixao et al. 2013; Mahu et al., 2022). In this study, salinity (ppt), temperature ($^{\circ}\text{C}$), pH, dissolved oxygen (mg/L), and water transparency (cm) were measured *in situ* at sampling stations during each field campaign. For each sampling event, these parameters were measured once at each station using a multi-parameter probe (Aquaread AP-700 & AP-800), and transparency was assessed with a Secchi disk.

2.5 Data analysis

Larval density data are presented as mean $\pm$ standard deviation. Non-parametric Kruskal-Wallis tests were used to compare mean larval density for each stage (D_s) between collection sectors and months, as the assumptions of homoscedasticity and normality were not met. Environmental variables are represented as boxplots. Multiple Factor Analysis (MFA) was performed to jointly analyze

TABLE 1 Summary of descriptors of larval dynamics used to characterize *Crassostrea tulipa* larval assemblages.

Descriptor number	Definition	Equation	Unit	Remark
Descriptor 1	Mean larval density by stage and production area	$\bar{D}_s = (1/n) \sum D_{s,i}$	ind.m^{-3}	Allows comparison of mean abundance levels between sites and larval stages
Descriptor 2	Median larval density by stage and production area	$\text{Median}(D_s)$	ind.m^{-3}	Less sensitive to extreme values, summarizes distribution
Descriptor 3	Total number of larvae counted	$N_s = \sum (D_{s,i} \cdot V_e)$	ind	Reflects the relative contribution of each stage over the study period
Descriptor 4	Survival index	$SI = (\sum \text{Pedi-veliger} / \sum \text{D-larvae}) \times 100$	%	A proxy of larval survival, to be interpreted with caution (not absolute survival)
Descriptor 5	Duration of pediveliger presence	$\text{Duration} = (n_{\text{obs}} / n_{\text{total}}) \times 100$	%	Percentage of sampling campaigns in which pediveliger larvae were detected

$D_{s,i}$: density of larval stages (D-larvae, umbo-veliger, or pediveliger) measured at sampling event i (ind.m^{-3}).

$\bar{D}_s$: mean density of larval stages across all sampling dates.

N_s : Total number of larvae counted of stages across all sampling dates.

V_e : Volume of water filtered at each date and at each station.

SI (Survival Index): ratio of cumulative pediveliger density to cumulative D-larvae density.

Duration of pedi-veliger larvae: percentage of sampling campaigns in which pediveliger larvae were detected, with n_{obs} = number of campaigns with pediveliger occurrence, and n_{total} = total number of sampling campaigns.

environmental variables (temperature, salinity, transparency) and a reduced set of larval indices (mean density, maximum density, survival index, duration of presence). This approach allowed us to visualize relationships between larval dynamics and environmental conditions across sampling dates and sites. Quantitative variables are represented using a correlation circle. Individuals are displayed in plots with ellipses corresponding to the monitored months or sectors. R version 4.3.0 was used for all the analyses.

3 Results

3.1 Larval dynamics of the coastal lagoon waters

The evolution of the average density of each larval stage and the total density s is presented in [Tables 2–4](#). The total density for each sampling site is summarized [Figure 2](#).

3.1.1 Case of the Ahouandji production area

Larval densities varied significantly from month to month for each larval stage at Ahouandji. D-larvae show an overall trend of two periods of abundance throughout the year. A large period of abundance covers the period from January to May, with peaks in March and April, followed by a smaller period of abundance from May to July, with a drop in density in June. The other months of the year are characterized by low abundance of D-larvae in the coastal lagoon waters at Ahouandji. November has the lowest larval density (423.3 ind/m³). Veliger larvae also showed a similar trend, with a large period of abundance from January to May, peaking only in March. From June to August, the density of veliger larvae in the lagoon waters at Ahouandji was less consistent and lower than in the beginning of the year, with a peak in August. The month with the lowest density was December, in which no veliger larvae were observed (0.0 ind/m³).

As for pedi-veliger larvae, they showed a single large period of abundance early in the year, in March and April, with a peak in March. For the rest of the year, their abundance in the lagoon waters at Ahouandji was relatively low. Pedi-veliger larvae were not observed in the coastal lagoon waters at Ahouandji in December, September, October, or January (0.0 ind/m³ for each of these months).

3.1.2 Case of the Dégouè production area

As at Ahouandji, densities vary significantly from month to month for each larval stage at Dégouè. An abundance of D-larvae was observed at Dégouè early in the year, covering the period from December to April, with peaks in February and March (8286.7 ind/m³ and 3956.7 ind/m³, respectively). Larval density then decreased in May and June, before another, but smaller, peak of abundance in July (2113.3 ind/m³). The larval density drastically dropped in the coastal lagoon waters from September to November.

A similar trend was observed for veliger larvae in this production area, which saw an increase in density starting in

TABLE 2 Evolution of larval densities by larval stage over time at Ahouandji.

Density(ind/m ³)	Month	Larvae stage	Production area
1323.3 ^c	Jan	D-larvae	AH
1163.3 ^{ab}	Jan	veliger	AH
0.0 ^c	Jan	pedi-veliger	AH
1636.7 ^{bc}	Feb	D-larvae	AH
1106.7 ^{abc}	Feb	veliger	AH
106.7 ^{bc}	Feb	pedi-veliger	AH
8076.7 ^a	March	D-larvae	AH
4380.0 ^a	March	veliger	AH
7126.7 ^a	March	pedi-veliger	AH
2693.3 ^{ab}	April	D-larvae	AH
846.7 ^{abcd}	April	veliger	AH
213.3 ^{ab}	April	pedi-veliger	AH
1216.7 ^c	May	D-larvae	AH
373.3 ^{bcde}	May	veliger	AH
53.3 ^{bc}	May	pedi-veliger	AH
530.0 ^d	June	D-larvae	AH
266.7 ^{def}	June	veliger	AH
53.3 ^{bc}	June	pedi-veliger	AH
1320.0 ^c	July	D-larvae	AH
160.0 ^{ef}	July	veliger	AH
160.0 ^{abc}	July	pedi-veliger	AH
2056.7 ^{ab}	Aug	D-larvae	AH
950.0 ^{abcde}	Aug	veliger	AH
160.0 ^{ab}	Aug	pedi-veliger	AH
583.3 ^d	Sept	D-larvae	AH
213.3 ^{def}	Sept	veliger	AH
0.0 ^c	Sept	pedi-veliger	AH
476.7 ^d	Oct	D-larvae	AH
320.0 ^{cdef}	Oct	veliger	AH
0.0 ^c	Oct	pedi-veliger	AH
423.3 ^d	Nov	D-larvae	AH
213.3 ^{def}	Nov	veliger	AH
370.0 ^{abc}	Nov	pedi-veliger	AH
633.3 ^d	Dec	D-larvae	AH
0.0 ^f	Dec	veliger	AH
0.0 ^c	Dec	pedi-veliger	AH

The letter groupings (a, ab, cd...) indicate significance groups derived from the Kruskal-Wallis tests. Groups assigned different letters are significantly different.

TABLE 3 Evolution of larval densities by larval stage over time at Dégouè.

Density (ind/m ³)	Month	Larvae stage	Production area
3746.7 ^{abc}	Jan	D-larvae	DG
2110.0 ^a	Jan	veliger	DG
0.0 ^c	Jan	pedi-veliger	DG
8286.7 ^a	Feb	D-larvae	DG
1270 ^{ab}	Feb	veliger	DG
53.3 ^{bc}	Feb	pedi-veliger	DG
3956.7 ^{ab}	March	D-larvae	DG
1900.0 ^a	March	veliger	DG
2480.0 ^a	March	pedi-veliger	DG
2270.0 ^{bcd}	April	D-larvae	DG
1000.0 ^{ab}	April	veliger	DG
423.3 ^{ab}	April	pedi-veliger	DG
1266.7 ^{de}	May	D-larvae	DG
686.67 ^{bc}	May	veliger	DG
0.0 ^c	May	pedi-veliger	DG
686.7 ^{ef}	June	D-larvae	DG
320.0 ^{cd}	June	veliger	DG
106.7 ^{abc}	June	pedi-veliger	DG
2113.3 ^{cd}	July	D-larvae	DG
1316.7 ^{ab}	July	veliger	DG
263.3 ^{abc}	July	pedi-veliger	DG
1106.7 ^{de}	Aug	D-larvae	DG
106.7 ^{cd}	Aug	veliger	DG
106.7 ^{bc}	Aug	pedi-veliger	DG
213.3 ^f	Sept	D-larvae	DG
106.7 ^d	Sept	veliger	DG
106.7 ^{bc}	Sept	pedi-veliger	DG
266.7 ^f	Oct	D-larvae	DG
160.0 ^d	Oct	veliger	DG
0.0 ^c	Oct	pedi-veliger	DG
316.7 ^f	Nov	D-larvae	DG
266.7 ^{cd}	Nov	veliger	DG
106.7 ^{abc}	Nov	pedi-veliger	DG
2426.7 ^{bcd}	Dec	D-larvae	DG
2426.7 ^{bcd}	Dec	D-larvae	DG
106.7 ^{abc}	Dec	pedi-veliger	DG

The letter groupings (a, ab, cd...) indicate significance groups derived from the Kruskal-Wallis tests. Groups assigned different letters are significantly different.

TABLE 4 Evolution of larval densities by larval stage over time at Djondji.

Density (ind/m ³)	Month	Larvae stage	Production area
7336.7 ^a	Jan	D-larvae	DJ
2640.0 ^{ab}	Jan	veliger	DJ
106.7 ^c	Jan	pedi-veliger	DJ
8286.7 ^a	Feb	D-larvae	DJ
1846.7 ^{abc}	Feb	veliger	DJ
0.0 ^c	Feb	pedi-veliger	DJ
6333.3 ^{ab}	March	D-larvae	DJ
1900.0 ^{abc}	March	veliger	DJ
2060.0 ^{ab}	March	pedi-veliger	DJ
9920.0 ^a	April	D-larvae	DJ
4643.3 ^a	April	veliger	DJ
2850.0 ^a	April	pedi-veliger	DJ
1263.3 ^c	May	D-larvae	DJ
1056.7 ^{bc}	May	veliger	DJ
106.7 ^{bc}	May	pedi-veliger	DJ
106.7 ^d	June	D-larvae	DJ
0.0 ^d	June	veliger	DJ
0.0 ^c	June	pedi-veliger	DJ
1266.7 ^c	July	D-larvae	DJ
106.7 ^d	July	veliger	DJ
0.0 ^c	July	pedi-veliger	DJ
160.0 ^d	Aug	D-larvae	DJ
106.7 ^d	Aug	veliger	DJ
0.0 ^c	Aug	pedi-veliger	DJ
160.0 ^d	Sept	D-larvae	DJ
106.7 ^d	Sept	veliger	DJ
106.7 ^c	Sept	pedi-veliger	DJ
316.7 ^d	Oct	D-larvae	DJ
53.3 ^d	Oct	veliger	DJ
0.0 ^c	Oct	pedi-veliger	DJ
213.3 ^d	Nov	D-larvae	DJ
160.0 ^d	Nov	veliger	DJ
0.0 ^c	Nov	pedi-veliger	DJ
2113.3 ^{bc}	Dec	D-larvae	DJ
1056.7 ^c	Dec	veliger	DJ
106.7 ^c	Dec	pedi-veliger	DJ

The letter groupings (a, ab, cd...) indicate significance groups derived from the Kruskal-Wallis tests. Groups assigned different letters are significantly different.

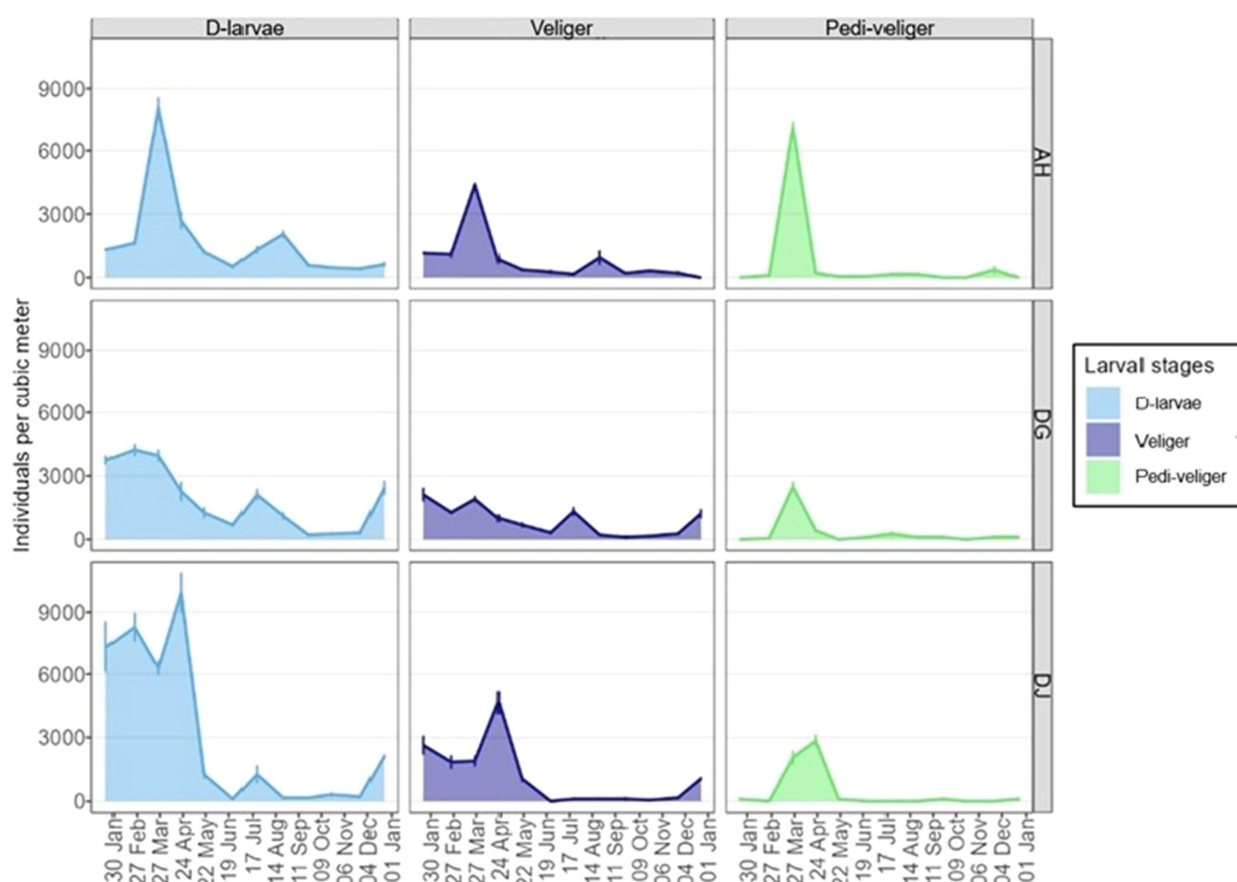


FIGURE 2
Larval dynamics by stage, over time and by oyster production areas (ind. m^{-3}).

December, with abundance peaks in January (2110.0 ind/ m^3) and March (1900.0 ind/ m^3). Their density then decreased from April onwards, before rising again with a peak in July (1316.7 ind/ m^3), although still lower in amplitude than those observed in January and March. The months with the lowest larval abundance were August, September, and October (106.7 ind/ m^3 /month).

As for pedi-veliger larvae, a similar pattern was observed, with a peak in March (2480.0 ind/ m^3). For the rest of the year, their density remained relatively low.

3.1.3 Case of the Djondji production area

The evolution of larval density at Djondji followed almost the same trend observed in the production areas of Ahouandji and Dégouè. D- and veliger larvae showed high abundance early in the year, with a peak in April (9920.0 ind/ m^3 for D-larvae and 4643.3 ind/ m^3 for veliger). Their densities relatively decreased for the rest of the year, with a complete absence of Umbo-veliger larvae in June.

Pedi-veliger larvae also showed a high abundance early in the year in the coastal lagoon waters at Djondji, with a peak in April (2850.0 ind/ m^3), before stabilizing for the remainder of the year with a declining trend. Pedi-veliger larvae were absent from the coastal lagoon waters at Djondji in February, June, July, August, October, and November.

3.2 Descriptors of larval dynamics

3.2.1 Mean density per larval stage

The average larval densities per stage and per production area in the coastal lagoon waters obtained during this study are presented in Table 5 as descriptor 1.

A total average of 2251 ± 25 D- larvae was obtained in the coastal lagoon waters during this study. The highest average value of D- larvae was recorded in the Djondji production area (3123 ± 106 larvae), followed by the Dégouè production area (1883 ± 43 larvae). The lowest average value of D- larvae was found in the Ahouandji production area (1748 ± 59 larvae).

For veliger larvae, a total average of 951 ± 11 larvae was recorded in the lagoon waters. As with the D- larvae, the same trend was observed. The highest average value (1140 ± 42 larvae) was found in the Djondji production area. It was followed by the Dégouè production area (880 ± 21 larvae). The lowest average value for veliger larvae was observed in the Ahouandji production area (833 ± 33 larvae).

For pedi-veliger larvae, a total average of 481 ± 12 larvae was recorded in the lagoon waters. The highest average value in the coastal lagoon was observed in the Ahouandji production area (687 ± 55 larvae), followed by the Djondji production area ($445 \pm$ larvae).

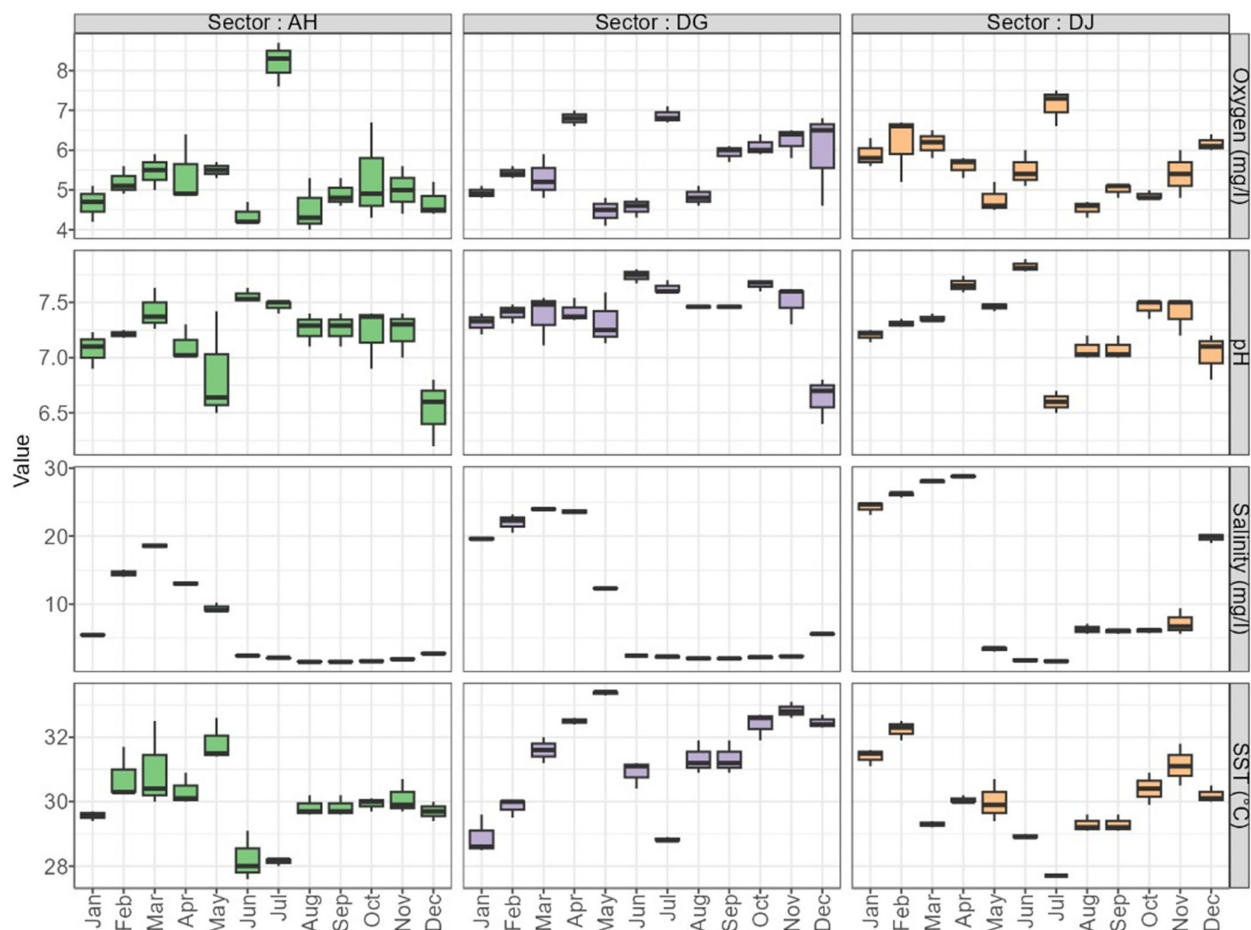


FIGURE 3

Evolution of the physio-chemical parameters of the coastal lagoon waters in the different oyster production areas.

The Dégoué production area had the lowest average value of pedi-veliger larvae ($313 \pm \text{larvae}$).

Overall, a total average of 3555 ± 45 larvae was recorded in the coastal lagoon waters during this study. The Djondji production area presented the highest total average of *C. tulipa* oyster larvae (4685 ± 163 larvae), followed by the Ahouandji production area (3013 ± 145 larvae). The Dégoué production area, which also had a notable value, had the lowest total average of larvae (2966 ± 75 larvae).

3.2.2 Median density per larval stage

The median values of larval density by stage and production area in the coastal lagoon waters obtained during this study are presented in Table 5 as descriptor 2.

A total median value of 2251 ± 25 D- larvae was recorded in the coastal lagoon waters during this study. The highest median value of D- larvae was observed in the Dégoué production area (1425 ± 43 larvae), followed by the Ahouandji production area (1190 ± 59 larvae). The lowest median value of D- larvae was found in the Djondji production area (1105 ± 106 larvae). For veliger larvae, a total median value of 951 ± 11 larvae was recorded in the lagoon waters. The highest median value (710 ± 21 larvae) was found in the lagoon waters of the Dégoué production area. It was followed by the Djondji production

area (475 ± 42 larvae). The lowest median value of veliger larvae was found in the Ahouandji production area (320 ± 33 larvae). For pedi-veliger larvae, a total median value of 481 ± 12 larvae was recorded in the lagoon waters. In the three production areas, the median value for pedi-veliger larvae in the coastal lagoon waters was zero.

Overall, a median value of 3555 ± 45 larvae was recorded in the coastal lagoon waters. The Dégoué production area had the highest total median value of *C. tulipa* oyster larvae (2375 ± 75 larvae), followed by the Djondji production area (2060 ± 163 larvae). The Ahouandji production area had the lowest total median value of larvae (1190 ± 145 larvae).

3.2.3 Total number of individuals counted by larval stage

Descriptor 3 (Table 5) provides information on the total number of larvae counted by larval stage in the coastal lagoon waters across the different production areas of the oyster *C. tulipa*. In the Ahouandji production area, a total of 23,524 larvae were counted, including 12,582 D- larvae, 5996 veliger larvae, and 4946 Pedi-veliger larvae during the study period. In the Dégoué production area, a total of 22,146 larvae were recorded, including 13,556 D-, 6338 veliger, and 2252 Pedi-veliger larvae.

TABLE 5 Larval descriptors by stage and production area.

Sector	Larvae stage	Descriptor 1		Descriptor 2		Descriptor 3	Descriptor 4	Descriptor 5
		Mean	SD	Mediane	SD	Sum	Survival (%)	Percentage of observations of pedi-velyger larvae
AH	D-larvae	1747.5	58.7	1190.0	58.7	12582	0.4	66.7
	Veliger	832.8	33.1	320.0	33.1	5996		
	pedi-veliger	686.9	55.2	0.0	55.2	4946		
	Total_Larve	3013.3	145.0	1190.0	145.0	23524		
DG	D-larvae	1882.8	43.0	1425.0	43.0	13556	0.2	75.0
	velyger	880.3	21.2	710.0	21.2	6338		
	pedi-veliger	312.8	19.5	0.0	19.5	2252		
	Total_Larvae	2965.6	74.5	2375.0	74.5	22146		
DJ	D-larvae	3123.1	106.2	1105.0	106.2	20206	0.1	50.0
	Velyger	1139.7	41.6	475.0	41.6	7826		
	pedi-veliger	444.7	27.1	0.0	27.1	3202		
	Total_Larvae	4685.0	162.5	2060.0	162.5	31234		
Lagoon	D-larvae	2251.1	25.2	2251.1	25.2	46344	0.2	91.7
	velyger	950.9	11.0	950.9	11.0	20160		
	pedi-veliger	481.5	12.4	481.5	12.4	10400		
	Total_Larvae	3554.6	44.5	3554.6	44.5	76904		

In the Djondji production area, a total of 31,234 larvae were counted, comprising 20,206 D-, 7826 veliger, and 3202 Pedi-veliger larvae. Considering the entire lagoon, a total of 76904 larvae were recorded, including 46,344 D-, 20,160 veliger, and 10,400 Pedi-veliger larvae.

3.2.4 Larval survival = ratio of pedi-veliger to D-veliger densities (sum of pedi-veliger/sum of D-veliger)

Descriptor 4 (Table 5) provides an estimate of the survival rate of *C. tulipa* larvae in the coastal lagoon waters of Benin, expressed as the ratio between the number of pedi-veliger and D- larvae.

The larval survival rate, calculated as the density ratio between Pedi-veliger and D-veliger larvae, was 0.4 in the Ahouandji production area. In Dégouè, the ratio was 0.2. In the Djondji production area, a ratio of 0.1 was obtained. Considering the entire lagoon, the overall larval survival ratio was 0.2.

3.2.5 Presence duration of pedi-veliger larvae in the environment (percentage of sampling campaigns in which pedi-veliger larvae were recorded)

Descriptor 5 (Table 5) indicates the percentage of sampling campaigns during which Pedi-veliger larvae were observed in the coastal lagoon waters of Benin.

During the study period, the Dégouè production area exhibited the highest observation rate of pedi-veliger larvae, with 75% of

sampling campaigns recording their presence. This was followed by the Ahouandji area, with a 66.67% observation rate. The Djondji production area showed the lowest rate, with only 50% of sampling campaigns detecting pedi-veliger larvae. At the scale of the entire lagoon, the observation rate of pedi-veliger larvae in the water column was 91.67%.

3.3 Influence of environmental parameters on larval abundance in the coastal lagoon waters

3.3.1 Physico-chemical parameters of coastal lagoon waters in oyster production areas

The variation in physico-chemical parameters of the coastal lagoon waters in the oyster production areas during the study period is shown in the graphs in Figure 3.

The physicochemical parameters measured in the coastal lagoon waters during this study vary from one area to another and depending on the period.

Dissolved oxygen ranged from 4.37 mg/L to 8.2 mg/L, with an average of 5.27 ± 0.03 mg/L in the coastal lagoon waters at Ahouandji. In the Dégouè production area, dissolved oxygen fluctuated between 4.47 mg/L and 6.87 mg/L, with an average of 5.62 ± 0.02 mg/L. At Djondji, dissolved oxygen ranged from 4.53 mg/L to 7.13 mg/L, with an average of 5.6 ± 0.02 mg/L. The highest value (8.2 mg/L) was recorded in July (specify the zone), while the lowest value (4.37 mg/L) was measured in June.

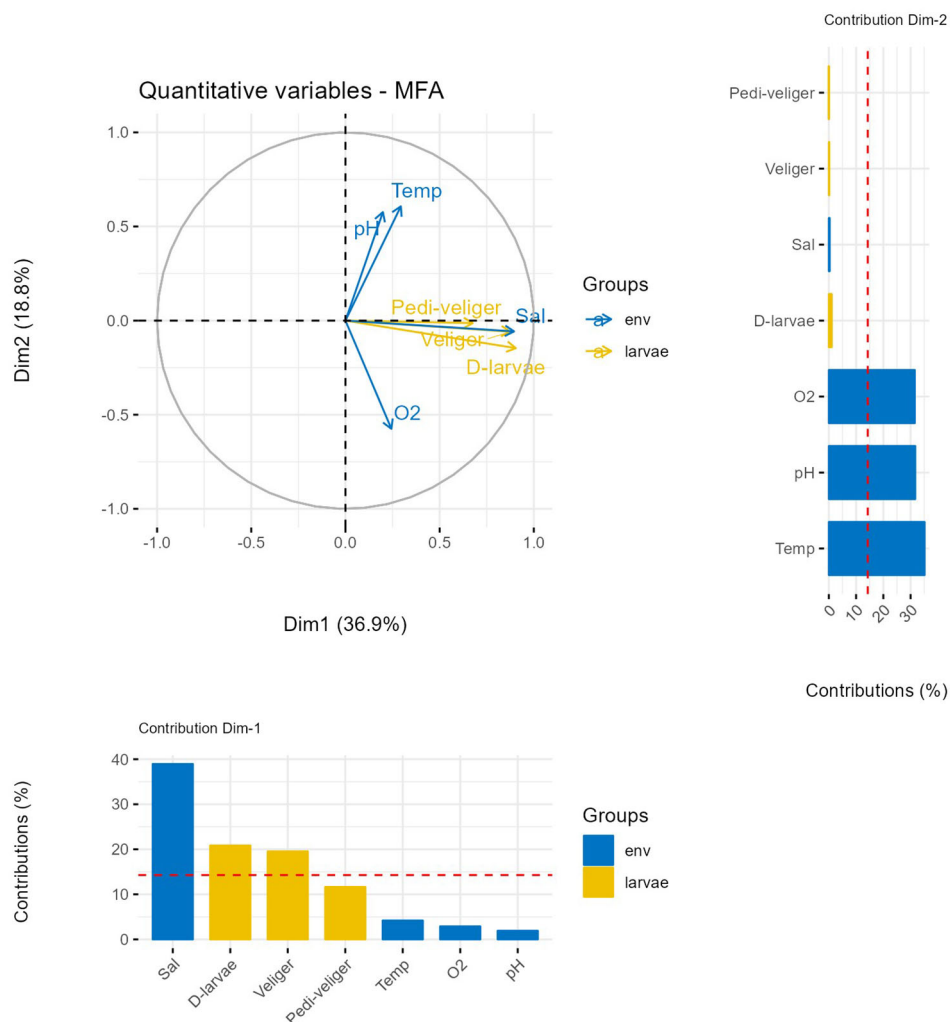


FIGURE 4
MFA (Multiple Factor Analysis) conducted on the quantitative data (larval density) and environmental variables.

The pH values measured ranged from 6.53 to 7.56, with an average of 7.18 ± 0.01 in the Ahouandji production area At Dégouè, the pH of the lagoon waters fluctuated between 6.63 and 7.74, with an average of 7.41 ± 0.01 . In the Djondji production area, the pH values measured during this study ranged from 6.6 to 7.83, with an average of 7.29 ± 0.01 . The lowest pH value (6.53) was observed in December, while the highest value (7.83) was recorded in June.

During the study period, the salinity of the coastal lagoon waters ranged from 1.53 to 14.53 g/L with an average of 6.25 ± 0.164 g/L in the Ahouandji production area. At Dégouè, it fluctuated between 2.2 g/L and 23.97 g/L, with an average of 10.02 ± 0.26 g/L. In the Djondji production area, the salinity values measured ranged from 1.6 g/L to 28.03 g/L, with an average of 13.27 ± 0.30 g/L. The highest value (28.03 g/L) was recorded in March, while the lowest value (1.53 g/L) was measured in August.

The temperature of the coastal lagoon waters was relatively homogeneous during the study period. It ranged from 28.23°C to 31.83°C, with an average of 29.94 ± 0.03 °C in Ahouandji production area. In Dégouè production area, it ranged from 28.9°C to 33.37°C, with an average of 31.36 ± 0.04 °C. In the Djondji production area, the

temperature values measured in the coastal lagoon waters ranged from 27.7°C to 32.23°C, with an average of 29.99 ± 0.034 °C. The lowest temperature value (27.7°C) was recorded in July, while the highest temperature value (33.37°C) was recorded in May.

During the study period, transparency values measured in the coastal lagoon waters in the Ahouandji production area ranged from 0.51 m to 1.71 m, with an average of 0.71 ± 0.35 m. In the Dégouè production zone, transparency ranged from 0.38 m to 2.08 m, with an average of 1.67 ± 0.62 m. In the Djondji production area, transparency values measured in the coastal lagoon waters ranged from 0.20 m to 1.92 m, with an average of 1.75 ± 0.93 m. The lowest transparency value (0.20 m) was recorded in May, while the highest value (2.08 m) was recorded in April.

3.3.2 Relationship between environmental parameters and the presence of different larval stages in the coastal lagoon waters of Benin

The results of the MFA (Multiple Factor Analysis) conducted on the quantitative data (larval density) and environmental variables (Figure 4) showed a positive correlation between the

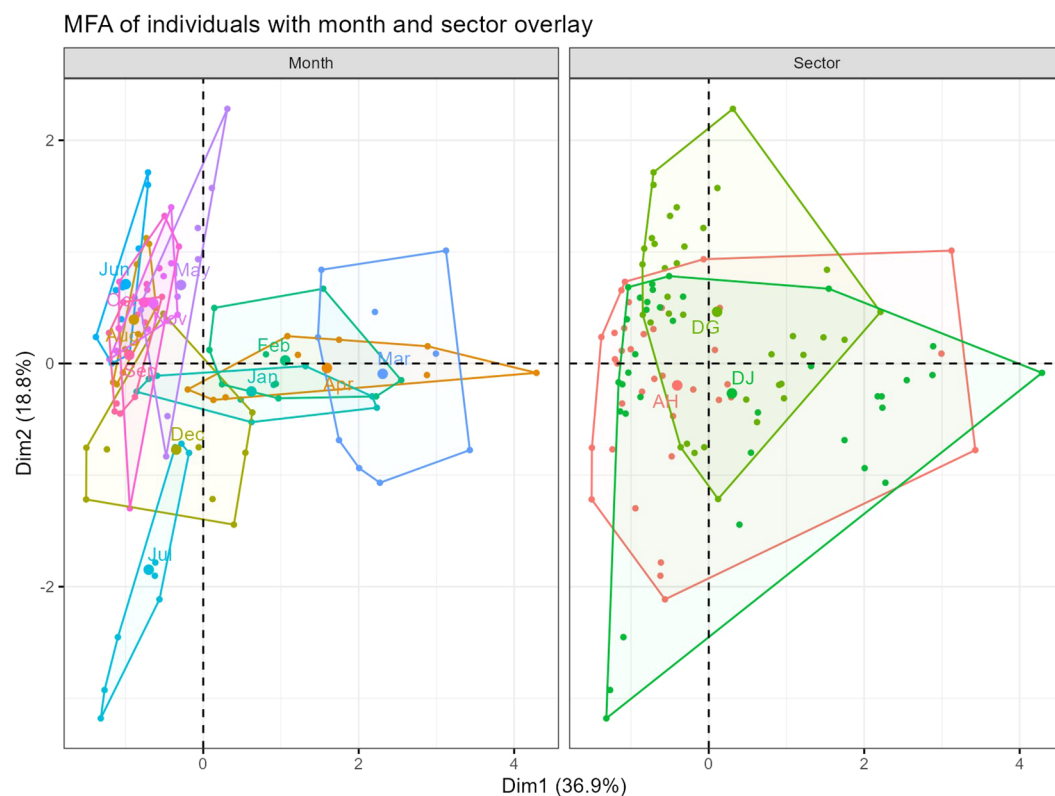


FIGURE 5
MFA: Representation of ellipses based on months or sectors.

increase in salinity and the presence as well as the abundance of the three larval stages of the oyster *C. tulipa* in the coastal lagoon waters of Benin.

A representation of the ellipses based on the months or sectors (Figure 5) showed that the months of January, February, March, and April were similar in terms of larval density, with a slight distinction in the month of March. These months were positioned opposite to the other months of the year, where the larval density appeared to be similar, except for the month of July, which stood out from the two groups. Considering the production areas (sectors), the evolution of larval density appears to be similar across the three production areas considered in this study, with minor specificities for each zone.

Some photos of larvae observed during this study are presented in Figure 6.

4 Discussion

4.1 Larval dynamics in the coastal lagoon waters

The density of *C. tulipa* oyster larvae showed significant variation over time during this study. The results show two periods of abundance for D- and veliger larvae across the three

lagoon production areas. The first period of abundance occurs at the beginning of the year, starting as early as December and extending through April, with peak abundance observed in March or April, depending on the production area. This can be explained by the fact that this period coincides largely with the dry season in southern Benin. Chuku et al. (2023) noted a predominance of *C. tulipa* oyster spat in the coastal waters of the Gulf of Guinea along the Ghanaian coast during the dry season. During this period, environmental parameters recorded in the coastal lagoon waters show high salinity values in the three production areas, reaching up to 28.03 g/L in Djondji zone, 23.97 g/L in Dégouè area, and 14.53 g/L in Ahouandji area. Several studies have demonstrated the effect of salinity on oyster reproduction.

Indeed, a sudden change in the salinity or temperature of the water creates thermal or salinity stress, which acts as a trigger for reproduction in oysters (Bernard, 2011). This is exactly what was observed in the lagoon waters during this study, where an increase in salinity was noted during this period. From December to February, the salinity of the lagoon waters increased from 16.4 ± 0.90 to 26.1 ± 0.86 ‰; from 6.23 ± 0.63 to 22 ± 3.421 ‰, and from 5.03 ± 0.14 to 14.53 ‰ respectively at Djondji, Dégouè, and Ahouandji.

Regarding the pediveliger larvae, they were abundant in the lagoon waters only during the early months of the year, with a peak in March or April depending on the production area. Unlike the D-

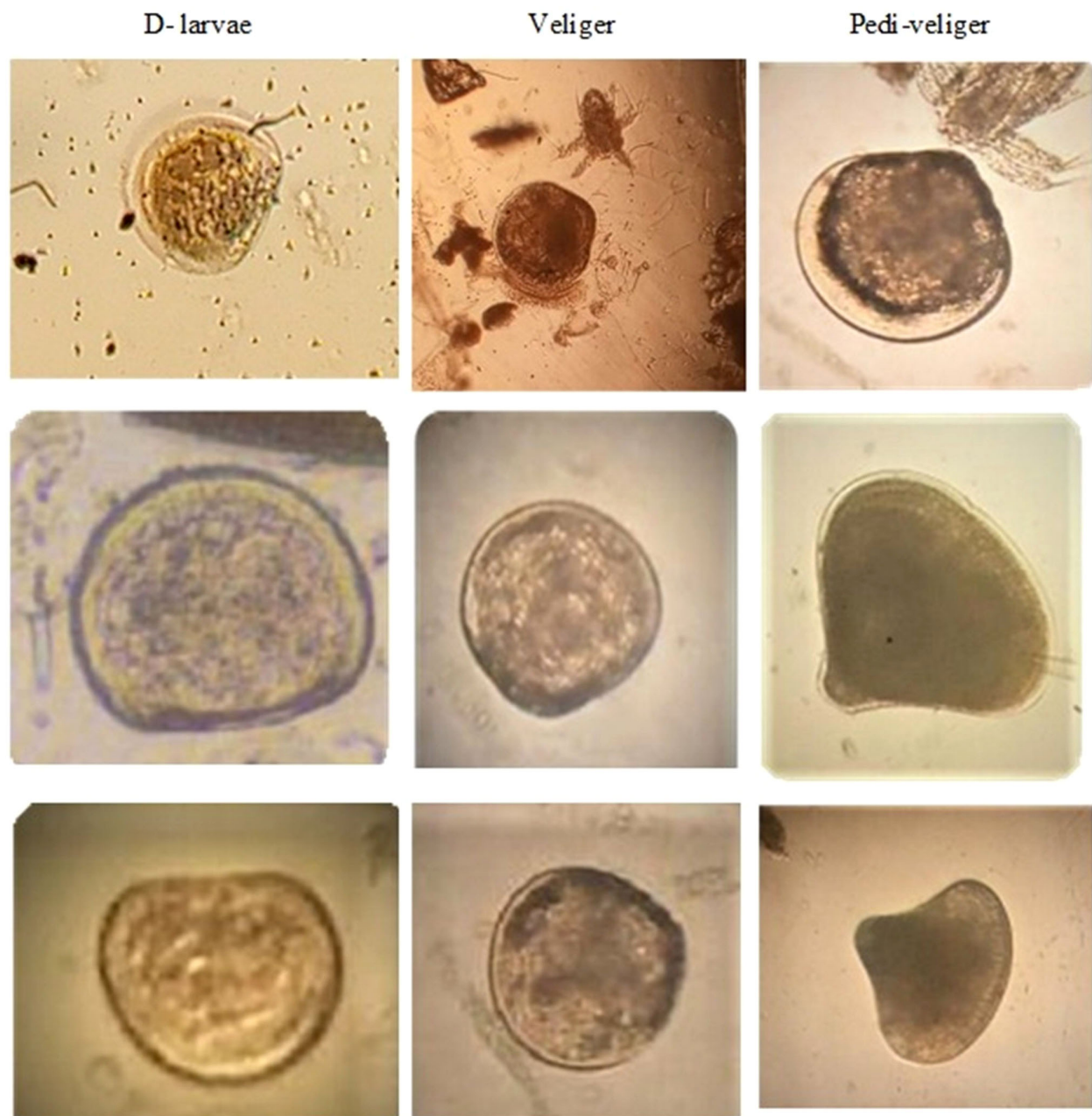


FIGURE 6
Some photos of mangrove oyster larvae *C. tulipa* in the Coastal lagoon.

and veliger larvae, pediveliger larvae were relatively scarce during the second period of larval abundance. This suggests that the D- and veliger larvae from the second spawning event did not reach maturity. This could be explained by unfavorable environmental conditions, particularly related to the low salinity of lagoon waters during that period. Several studies have shown that *Crassostrea* larvae fail to reach maturity when water salinity is too low. [McFarland et al. \(2022\)](#) demonstrated that *Crassostrea virginica* larvae are vulnerable when exposed to salinities below 10 ppt. However, the survival of larvae of the same oyster species can be

strongly influenced by the origin of the broodstock. Thus, the larval pool of a single estuary contains abundant genetic variation for survival at different salinities, partly due to functional genetic differences between source reefs ([Eierman and Hare, 2013](#)).

To ensure the sustainability of oyster farming, it is crucial to identify the zones and periods that are most favorable for oyster reproduction. This enables the establishment of strategic spat collection areas or integrated hatcheries in zones with optimal salinity conditions during critical reproductive periods ([Phei Fang et al., 2016](#)). Based on the larval dynamics of *C. tulipa* in the coastal

lagoon waters of Benin, a spat collection calendar targeting the main dry season (December to April) as the key collection period would support the development of sustainable, productive oyster farming in these waters.

4.2 Larval descriptors

The highest overall mean density of *C. tulipa* larvae in the lagoon was recorded in Djondji production zone. This indicates a high intensity of oyster reproduction in this area, linked to the high salinities recorded there. This can be explained by the very close position of Djondji to the mouth of the “Bouche du Roi,” where the coastal lagoon is connected to the Atlantic Ocean.

The predominance of D- and veliger larvae in Djondji and Dégouè observed during this study is thus justified, as Dégouè is the second closest site to the estuary after Djondji. As observed in this study, during the salinization and low-water periods, a decreasing salinity gradient forms from the points closest to the mouths to those farther away in the lagoon systems of the Gulf of Guinea. This is due to the strong influx of marine waters during this season (Wognin et al., 2005; Honfo et al., 2024).

Unlike D and veliger larvae, pedi-veliger larvae were more predominant in Ahouandji production area. This predominance of Pedi-veliger larvae in Ahouandji may be explained by optimal environmental conditions for oyster larval development, particularly water salinity that is neither too high nor too low during this period (Phei Fang et al., 2016). This predominance may also be due to the lower anthropogenic pressure observed in the Ahouandji area during the study period, compared to Djondji and Dégouè, which are within the perimeter of major road construction and sand dredging operations undertaken by the Beninese government. Indeed, human activities can affect water quality and larval distribution (Wall et al., 2005; Williams et al., 2024).

Descriptors 3 and 4, which concern respectively the total number of larvae counted by stage and larval survival in the coastal waters, confirm the spatial heterogeneity in distribution and highlight the survival of *C. tulipa* larvae in the lagoon. The Djondji area, despite showing the highest larval abundance (56,220 larvae), is characterized by a low survival rate (0.14), indicating a predominance of early larval stages in this area, which may serve as a temporary aggregation area without providing favorable conditions for further larval development (Cowen and Sponaugle, 2009). In contrast, the combination of relatively high larval abundance and the highest survival rate (0.4) observed at Ahouandji suggests a potentially more stable or less disturbed environment for larval development (Williams et al., 2024), thus supporting the predominance of Pedi-veliger larvae observed in this area, as previously discussed.

The results of Descriptor 5, which corresponds to the percentage of observations of Pedi-veliger larvae, indicate that the Dégouè area, despite having a lower total abundance compared to Djondji, shows a higher observation percentage of pedi-veliger larvae (75%). This suggests that these larvae, although fewer in number, are more consistently present over time, indicating stable

environmental conditions that favor their development. Ahouandji follows with 66.7%, while Djondji has the lowest frequency (50%), supporting the hypothesis of a transit area or an area where larvae face developmental constraints. The regular presence of pedi-veliger larvae throughout the sampling campaigns can be explained by a prolonged larval residence time, which is an indicator of stable environmental conditions that support development (Pouvreau, 2009).

These calculated Descriptors reveal that the Djondji production area is a “source area” that plays an important role in maintaining larval flow to other areas (Ahouandji and Dégouè), where the conditions are favorable for the larvae to mature. In the context of implementing a policy for the sustainable management of the natural stock of *C. tulipa* oysters and promoting oyster farming in the waters of Benin’s coastal lagoon, it could thus serve as a buffer zone. However, this would require strict regulation of human activities during breeding periods (Smyth et al., 2023; Pouvreau, 2009). The results of the MFA (Multi-Factor Analysis) conducted on larval densities and environmental variables show a positive correlation between increasing salinity and the presence as well as the abundance of the three larval stages of the oyster *C. tulipa* in the coastal waters of Benin. This confirms that salinity is a key environmental factor influencing the emission and distribution of *C. Tulipa* larvae in the coastal waters of Benin. Several studies have already reported the strong recruitment of *C. Tulipa* oyster spat in the coastal waters of the Gulf of Guinea (Diadhiou, 1995; Chuku et al., 2023).

5 Conclusion

The objective of this study was to assess the larval dispersal dynamics of the oyster *C. tulipa* in the coastal waters of Benin and to describe the associated environmental conditions. The study indicates that a significant spawning event with high larval production episode occurred from December to April in the coastal waters of Benin. Although Djondji area stands out as the best area in terms of larval abundance, it was observed that the Dégouè and Ahouandji areas offer better conditions for larval maturation, with a predominance and regular observation of advanced larval stages (Pedi-veliger larvae) in these zones. Djondji area, due to its position relative to the mouth, could serve as a larval transfer area towards optimal areas for larval maturation and development. A second spawning event episode occurred in July, but it was short-lived, and the environmental conditions (low salinity) likely did not allow for larval development, as evidenced by the near absence of Pedi-veliger larvae in the lagoon waters during this period. Salinity appears to be a major trigger for oyster reproduction in these waters.

This study therefore provides detailed information on the seasonal and spatial patterns of larval abundance in the coastal lagoon waters of Benin. This information can be used to plan spat collection and grow-out periods in order to optimize natural recruitment as part of a sustainable management policy for the natural stocks of *C. tulipa*, as well as to encourage oyster farming in Beninese waters.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors upon request.

Ethics statement

The animal study protocol was approved by the Ethics Committee of the Ministry of Higher Education and Scientific Research and the Ministry of Agriculture, Livestock, and Fisheries of the Republic of Benin (Protocol code: law No 2014-19, approved on 2014 Aug 7), and complied with Directive 2010/63/EU of the European Parliament on the protection of animals used for scientific purposes. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

YZ: Investigation, Methodology, Software, Conceptualization, Writing – review & editing, Formal Analysis, Writing – original draft. DA: Conceptualization, Writing – review & editing, Investigation, Methodology. PB: Writing – review & editing, Methodology, Formal Analysis, Conceptualization. SW: Writing – review & editing, Methodology, Investigation, Conceptualization. TG: Methodology, Investigation, Conceptualization, Writing – review & editing. FM-R: Writing – review & editing, Supervision, Conceptualization, Methodology. MV-Y: Methodology, Supervision, Conceptualization, Writing – review & editing. MG: Methodology, Supervision, Conceptualization, Writing – review & editing. ZS: Methodology, Supervision, Conceptualization, Writing – review & editing.

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