

## Original Article

# Population dynamics and secondary production of *Cerastoderma edule* (Linnaeus, 1758) near its southern border: A baseline study in the Oualidia lagoon, Morocco

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**Abstract:** The edible cockle, *Cerastoderma edule* (Mollusca: Bivalvia), is a key species in many semi-enclosed coastal systems, such as lagoons and estuaries, along the northeastern Atlantic. The present study, based on a two-year sampling (2009-2010) performed at two stations (upstream and downstream), aims to explore the population dynamics and secondary production of *C. edule* in the Oualidia lagoon (Atlantic coast, Morocco). The results showed spatial and temporal variations between upstream and downstream stations. Downstream population showed higher  $L_{\infty}$  (36 mm) and a lower instantaneous growth rate ( $K = 0.83 \text{ yr}^{-1}$ ), while upstream populations exhibited a higher growth rate ( $K = 1.95 \text{ yr}^{-1}$ ) with a slightly lower  $L_{\infty}$  (32.5 mm). This disparity may be linked to differences in temperature and salinity gradients. The mortality was higher upstream ( $Z = 9.18$ ), probably due to ecological and anthropogenic stresses. Recruitment was seasonal at both sites, with temperature apparently playing a role in triggering the phenomenon. Moreover, secondary production was higher upstream, with an annual production of 96.342 gDW.m<sup>2</sup> in 2009 and 46.114 gDW.m<sup>2</sup> in 2010, highlighting optimal conditions for cockle development. These results provide baseline data for forthcoming ecological monitoring of the effects of global change, including climate change, on the fitness of the edible cockle *C. edule* in the Oualidia Lagoon, near the southern limit of the geographical distribution of the species.

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## Introduction

Marine and coastal ecosystems are not only repositories of biodiversity but also foundational to human well-being, providing an array of goods and services essential for ecological and economic sustainability (Roberts et al., 2017). These ecosystems support critical ecological processes and human livelihoods, such as fisheries, nutrient cycling, and carbon sequestration, contributing significantly to global biodiversity and climate regulation (Newton et al., 2018; Pérez-Ruzafa et al., 2019; Rodrigues-Filho et al., 2023). Nevertheless, they are among the most heavily threatened systems globally due to increasing anthropogenic pressures that can result in their degradation and loss of functionality, with cascading negative effects on their dynamics, structure, and ecological role (Halpern et al., 2008).

Considered as one of the most important marine habitats, coastal lagoons are recognized worldwide for their high productivity (Newton et al., 2018). These transitional ecosystems serve as essential nurseries for many marine species and act as buffers between terrestrial and marine environments, supporting fisheries, biodiversity, and nutrient cycling (MEA, 2005; Liqueste et al., 2016). In addition to their ecological importance, these coastal lagoon ecosystems, occupying more than 13% of the world's coastline, play an essential role in many biogeochemical processes (Sousa et al., 2013). They are particularly sensitive and vulnerable to global change, such as anthropogenic pressures, water warming, sea-level rise, salinity variations, increased pollution, and hydrological modifications (Fichez et al., 2017; Hapsari et al., 2020). All these disturbances

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can be detrimental to these environments' ecological balance and biodiversity. Such disturbances can alter species composition, impair ecosystem services, and jeopardize the resilience of these habitats, posing significant conservation challenges.

Among the diverse taxa in coastal ecosystems, bivalves are keystone species mediating critical ecological functions and supporting ecosystem stability (Taylor et al., 2018). They are a predominant component of the benthic fauna in these environments (Sousa et al., 2013). Furthermore, they are crucial for the optimal functioning of lagoons since they filter water, recycle nutrients, and offer vital habitats for several marine species (Rakotomalala et al., 2015). They also sustain significant commercial fisheries (Rowley et al., 2014). As filter-feeding organisms, bivalves contribute significantly to nutrient cycling and energy flow through their biofilter action, alleviating eutrophication pressures in nutrient-rich areas. Moreover, they have a crucial role in nutrient extraction, denitrification, and habitat change, influencing coastal benthic communities' richness and functional diversity (Ysebaert et al., 2019). Nonetheless, they face growing threats from seawater warming, ocean acidification, disease, overexploitation, and pollution, which may compromise their essential ecological roles (Zhang et al., 2022).

The edible cockle, *Cerastoderma edule*, is a prevalent bivalve mollusk that plays a key ecological and economic role. This species is found along the northeast Atlantic coast from Senegal to Norway, lives in loose intertidal sediments, and is essential as a food source for various marine organisms (Malham et al., 2012). Their impact on lagoon ecosystems remains highly significant. They have a pronounced influence on various ecological processes. Thanks to their bioturbation, these mollusks restructure sediments, adjusting the living conditions of other benthic organisms and modifying their habitat's chemical and physical properties (Hedman et al., 2011). As filter feeders, they enhance water clarity by diminishing turbidity and regulating phytoplankton biomass. They also serve a crucial function in nutrient recycling.

Cockles are an essential component of the trophic chain (Rakotomalala et al., 2015), offering habitat for many marine organisms and sustenance for predators. Through these interactions, cockles enhance lagoon stability, biodiversity, and overall ecosystem resilience (Carss et al., 2020).

Furthermore, bivalves, including cockles, serve as sentinel species, providing valuable indicators of environmental conditions and ecosystem health (Beyer et al., 2017). Establishing robust baseline data is essential for monitoring ecological dynamics and understanding the impacts of global change on bivalve populations and their habitats. These baselines enable the identification of trends, inform predictive models, and guide conservation strategies to enhance ecosystem resilience (Howard et al., 2017).

The Oualidia lagoon on Morocco's Atlantic coast represents a prime example of a vulnerable yet ecologically significant lagoon ecosystem. This site harbors substantial populations of the edible cockle, *C. edule*, and supports economic activities such as aquaculture, fisheries, tourism, and recreation, making it a critical socio-ecological system (Zourarah et al., 2007). Despite its significance, comprehensive studies on the population dynamics and ecological role of *C. edule* in this region remain scarce. The objective of this study, based on a two-year (2009-2010) monthly sampling performed at two stations (upstream and downstream of the lagoon), is to investigate, for the first time, the population dynamics and secondary production of *C. edule* in the Oualidia lagoon. The ultimate objective is to provide baseline conditions for forthcoming monitoring to understand the effects of global change on *C. edule* populations near its southern border.

## Materials and Methods

**Study site:** The Oualidia coastal lagoon is situated along Morocco's Atlantic coastline at coordinates (34°47'N, 6°13'W) (Fig. 1). Covering an area of 3.5 km<sup>2</sup>, it stretches to a maximum width of 0.5 km and a length of 7 km. A 2-meter-deep and 150-meter-wide arm between the lagoon and the ocean ensures water exchange. The tides are semi-diurnal, with water

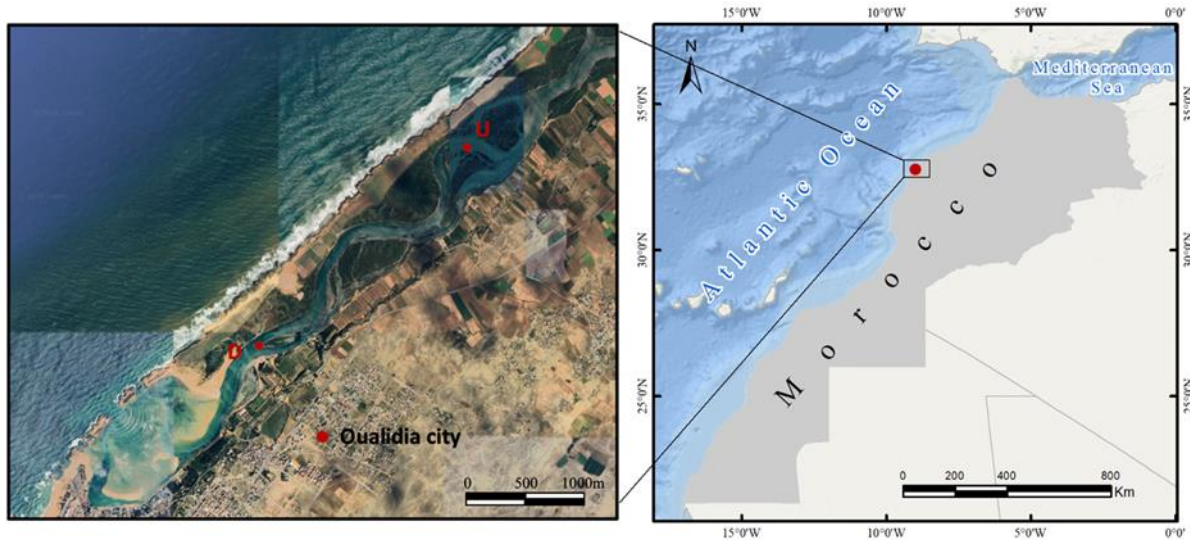


Figure 1. Situation of the two sampling stations in the Oualidia lagoon (Morocco): D: Downstream, and U: Upstream (Source: Image © 2024 Google, Airbus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO, TerraMetrics).

levels varying between 0.8 and 3.6 meters depending on the cycle (Hilmi et al., 2005). The lagoon's water temperature ranges from 16.1 to 21.1°C, and salinity fluctuates throughout the year between 20 and 35 during low tides and 30 to 36 during high tides (Makaoui et al., 2018). The lagoon's sedimentology is dominated by fine sands, with an average grain size of 260  $\mu\text{m}$ . The sedimentology of the lagoon influences biodiversity by playing a key role in the distribution of benthic organisms. Indeed, the lagoon is home to a wide variety of benthic species, contributing to the site's ecological richness (Maanan et al., 2014). However, the lagoon is under much human strain, mainly from tourism, aquaculture, and increasing urbanization (Maanan et al., 2014). These human activities increase the lagoon's vulnerability, impacting sediment dynamics and water quality, changing habitat structure, and lowering biodiversity (Tlig et al., 2023).

**Data collection:** Cockles were sampled monthly at two stations, upstream (U) and downstream (D) of the lagoon (Fig. 1), over two years from January 2009 to December 2010. Every month, six 0.25 m<sup>2</sup> quadrats, each with a depth of 10 cm, were collected and filtered through a sieve with a 1 mm mesh size at each station. Shell lengths were measured and rounded to the nearest millimeter using a vernier caliper. FISAT software was used to identify the cohorts, applying the

modal progression analysis method described by Bhattacharya (1967) and Gayanilo et al. (2005). When groups had a separation index greater than 2, they were considered distinct cohorts. Mean abundance values (Ind.m<sup>-2</sup>) were calculated monthly.

#### Populations parameters

**Von Bertalanffy Growth Parameters:** FiSAT II software was used to process the size frequency data (Gayanilo et al., 2005). The von Bertalanffy growth model, the most widely used to evaluate growth, was adopted to calculate the parameters of the Von Bertalanffy Growth Formula (VBGF), namely asymptotic length ( $L_{\infty}$ ) and growth coefficient ( $K$ , an<sup>-1</sup>) through the ELEFAN-I method (Pauly and David, 1981). In this formula,  $L_t = L_{\infty} (1 - \exp^{-k(t-t_0)})$ ,  $L_t$  denotes the anticipated length at age  $t$ ,  $L_{\infty}$  represents the asymptotic average length (the mean maximum length attained by an individual),  $k$  signifies the body growth rate coefficient (indicating the rate at which  $L_{\infty}$  is approached), and  $t_0$  is biologically irrelevant as  $L = 0$  is non-existent (Ogle et al., 2015).

The  $\Phi$  growth performance index enables inter-site and inter-species comparisons, particularly with benthic macroinvertebrates.  $L_{\infty}$  and  $K$  estimates were used to calculate this index based on Pauly and Munro's (1984) equation of  $\Phi' = \log(K) + 2\log(L_{\infty})$ . The theoretical maximum age ( $T_{max}$ ) for each population was calculated using the Michaelson and

Neves (1995) formula of  $T_{max} = (\ln(L_{\infty}) + Kt_0)/K$ .

**Mortality and exploitation rate:** The instantaneous mortality rate (Z, per year) was estimated using the length-converted catch curve (LCCC) method across a two-year span, with intervals marked by recruitment periods. Based on the mean size distribution of *C. edule* cockles, the empirical equation integrating the parameters of the Von Bertalanffy Growth Function (VBGF) and the mean water temperature was used.

The data fit was assessed using FiSAT software, which produced Z and the 95% confidence intervals surrounding the value. Pauly's (1980) empirical relationship of  $\text{Log}_{10} M = -0.0066 - 0.279 \text{Log}_{10} L_{\infty} + 0.6543 + \text{Log}_{10} K + 0.4634 \text{Log}_{10} T$  was used to compute natural mortality (M). The mean annual habitat temperature in Oualidia during the study period is denoted by T, whereas  $L_{\infty}$  is expressed in millimeters.

Following the determination of Z and M, fishing mortality (F,  $\text{yr}^{-1}$ ) was calculated using the formula  $F = Z - M$ , where Z stands for overall mortality, F for fishing mortality, and M for natural mortality. The Gulland (1971) formula of  $E = F/Z = F / (M+F)$  was used to determine the exploitation rate (E).

**Recruitment:** The FiSAT method uses VBGF parameters to rebuild recruitment pulses from a time series of length-frequency data, thereby determining the annual number of pulses and the relative strength of each pulse (Pauly, 1983; Moreau and Cuende, 1991). NORMSEP (Pauly and Caddy, 1985) was used to determine the normal distribution (%) of the recruitment pattern using FiSAT.

**Biomass and production:** From 2009 to 2010, 40 cockles of different sizes were harvested each month. To measure the "dry weight of the flesh", the soft part was removed and dried for 24 hours at 60°C. The length-weight relationship obtained for Oualidia was as  $\text{Log}_{10} W = 2.9084 \times \text{Log}_{10} L - 4.9564$  ( $r^2=0.63$ ), where W represents shell weight (g dry weight (gDW)), and L represents shell length (mm).

Using the mass-specific growth rate approach (Brey, 2001), the total annual production (P) of *C. edule* was determined based on the size-mass

relationship, the size-frequency distribution was derived from pooled samples, and the VBGF parameters as follows:  $P = \sum N_i M_i G_i$ , where P denotes production ( $\text{gDW} \cdot \text{m}^{-2} \cdot \text{an}^{-1}$ ),  $N_i$  refers to the average number of cockles in length class I ( $\text{Ind} \cdot \text{m}^{-2}$ ),  $M_i$  is the mean dry weight of individuals in length class i (gDW), and  $G_i$  represents the mass-specific growth rate ( $\text{yr}^{-1}$ ) that calculated using the formula of  $G_i = bK((L_{\infty}/L_i)-1)$ , where  $L_i$  (mm) is the average shell length in class i, K, and  $L_{\infty}$  are the VBGF parameters, and b is the particular constant of the size-mass relationship, obtained from the formula of  $\text{Log}_{10} W = b \text{Log}_{10} L + c$ . The formula for calculating mean annual biomass B was  $B = \sum N_i M_i$  ( $\text{gDWm}^{-2}$ ). Annual cockle population ratios P/B ( $\text{yr}^{-1}$ ) were determined by squaring total annual production P and mean annual biomass B.

**Statistical analysis:** A student's t-test was used to compare mean lengths and growth characteristics (K,  $L_{\infty}$ ) between the two sampling stations and years. Before using the t-test, the data's normality and the variances' homogeneity were evaluated to guarantee the validity of the test results. The ANOVA (Analysis of Variance) was used to examine variations in population dynamics at various dates and stations. The two-sample Welch's t-test was developed when the assumptions of equality of variances were not satisfied due to the potential heterogeneity of variances, especially when comparing mean lengths between zones and different years. R statistical software was used for all statistical tests, and a significance level 0.05 was applied.

## Results

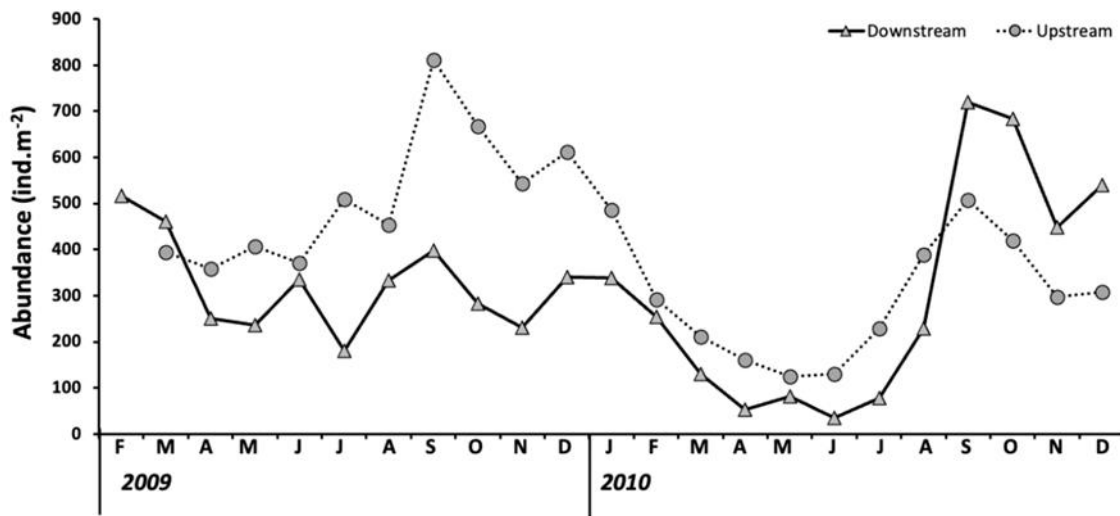
**Abundance:** A total of 24,635 individuals of *C. edule* were sampled: including 11,621 at the downstream station and 13,014 at the upstream station. Seasonal variation was observed at both stations, marked by increased cockle abundance and summer peaks (Fig. 2). The average downstream density and upstream density in 2009 were 325 ( $\pm 14.30$ ) and 598 ( $\pm 15.50$ )  $\text{Ind} \cdot \text{m}^{-2}$ , respectively. Downstream cockle density peaked in September at 811.33 ( $\pm 27.46$ )  $\text{Ind} \cdot \text{m}^{-2}$ , then declined significantly by almost 25% by the end of the

Table 1. Summary of shell length structures of *Cerastoderma edule* in the sampling stations (Downstream vs Upstream) of the Oualidia lagoon.

Sampling area	Min	Max	Mode	Mean	SD
Downstream	1	32	22	17.45340	6.951504
Upstream	1	31	22	15.7239	6.676972

Table 2. Summary of comparative statistical tests performed on the shell length of *Cerastoderma edule* in the Oualidia lagoon.

Test	Comparison	p-value
t-test	Downstream Vs Upstream	< 0.001
t-test	Downstream 2009 Vs 2010	< 0.001
t-test	Upstream 2009 Vs 2010	< 0.001
ANOVA	Downstream Vs Upstream by date	Site: < 0.001 / Date: < 0.001

Figure 2. Monthly abundance (Ind.m<sup>-2</sup>) of *Cerastoderma edule* at upstream and downstream sites in the Oualidia Lagoon, 2009-2010.

year. A similar peak, measuring 398 ( $\pm 14.78$ ) Ind.m<sup>-2</sup>, was recorded upstream in September. In 2010, summer peaks were recorded with abundances of 299.27 ( $\pm 12.01$ ) Ind.m<sup>-2</sup> downstream and 296.11 ( $\pm 9.77$ ) Ind.m<sup>-2</sup> upstream. However, these peaks were marginally lower than those observed in 2009, indicating inter-annual and inter-site variability.

**Shell length:** The results showed significant differences in lengths between the upstream and downstream sites (Fig. 3). Cockles in the downstream area had an average length of 17.45 mm ( $\pm 6.95$ ), with minimum and maximum values of 1 and 32 mm, respectively, and a mode of 22 mm. In the upstream area, lengths were slightly smaller, with an average of 15.72 mm ( $\pm 6.68$ ), minimum and maximum values of 1 and 31 mm, respectively, and a mode of 22 mm (Table 1). The means for each site upstream and downstream, as well as across years, differed

significantly ( $P < 0.001$ ) (Table 2).

**Recruitment:** The structure of the cockle recruitment pattern at Oualidia revealed a clear seasonal aspect to cockle development (Fig. 4). The first cohort's recruitment at the downstream zone started in June 2009, while the second cohort's recruitment started in May 2010. Recruitment in the upstream zone routinely started in July for the two successive cohorts. Temperatures appeared to be rising in tandem with this recruitment period; they were 19.8°C in June 2009, 22°C in July 2009, 19.9°C in May 2010, and 20.2°C in July 2010.

**Growth parameters:** The results revealed distinct growth patterns between downstream and upstream populations of *C. edule* in the lagoon (Table 3). Downstream, the most accurate values ( $R_n = 0.143$ ) showed an asymptotic length ( $L_\infty$ ) of 36 mm and an instantaneous growth rate ( $K$ ) of 0.83 per year, with a

Table 3. Parameters of the Von Bertalanffy growth function for *Cerastoderma edule*.  $L_{\infty}$ : asymptotic length; K: growth rate;  $t_0$ : theoretical age at which length equals zero, lifespan;  $\Phi'$ : growth performance index.

Sampling area	K	$L_{\infty}$	Predicted extreme length	$t_0$	$\Phi'$	Rn
Downstream	0.83	36	32.59 (31.34 - 33.83)	-0.3201	3.032	0.143
Upstream	1.95	32.5	31.59 (30.60 - 32.59)	-0.1337	3.314	0.128

Table 4. Mortality parameters of *Cerastoderma edule* collected from Oualidia Lagoon.

Sampling area	M	F	Z	E
Downstream	1.27671	2.82	4.1	0.69
Upstream	2.29721	6.88	9.18	0.75

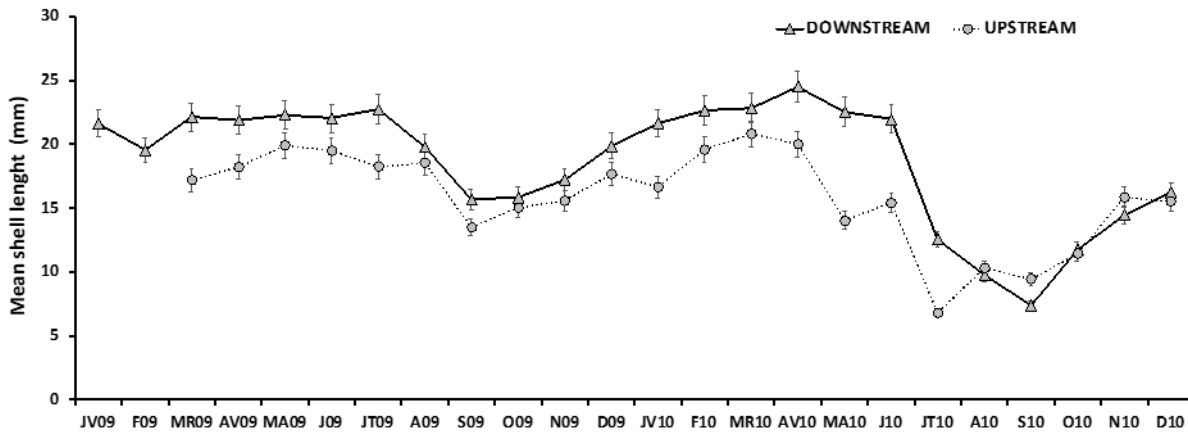


Figure 3. Monthly mean shell length (mm) of *Cerastoderma edule* at the upstream and downstream stations of the Oualidia lagoon.

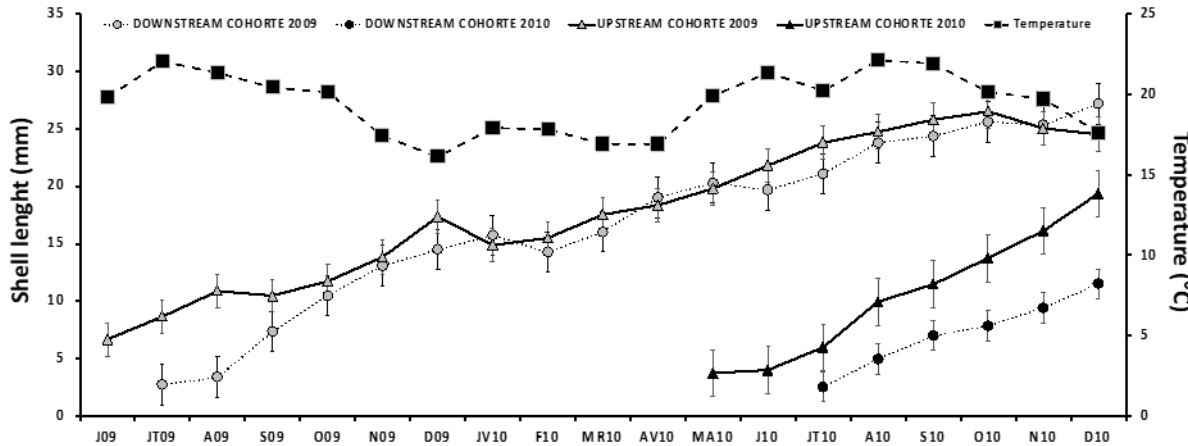


Figure 4. Mean length (mm  $\pm$  1 standard deviation) of the different *Cerastoderma edule* cohorts, identified by modal progression analysis, upstream and downstream of the Oualidia lagoon and evolution of the monthly mean temperature ( $^{\circ}$ C).

predicted extreme length of 32.59 mm (CI: 31.34 - 33.83 mm), with a  $t_0$  estimated at -0.3201 years, and a  $\Phi'$  value of 3.032. Conversely, upstream populations exhibited a higher growth rate ( $K = 1.95 \text{ yr}^{-1}$ ) with a slightly lower  $L_{\infty}$  of 32.5 mm. The predicted extreme length was 31.59 mm (CI: 30.60-32.59 mm), with  $t_0$  estimated at -0.1337 years and  $\Phi'$  at 3.314. These

results were further supported by  $Rn = 0.128$ .

Figures 5 and 6 illustrate the length frequency distribution and the overlaid growth curves estimated with ELEFAN-I for *C. edule* populations located upstream and downstream, respectively. Comparing growth curves between the two zones revealed significant temporal differences in recruitment, likely

Table 5. Annual Biomass, Production, and P/B Ratios of *Cerastoderma edule* in the Oualidia Lagoon.

Site	Period	Biomass	Production	P/B
Downstream	Feb 2009 - Dec 2009	27,856	38,158	1,370
	Jan 2010 - Dec 2010	13,742	26,138	1,902
Upstream	Mar 2009 - Dec 2009	30,561	96,342	3,152
	Jan 2010 - Dec 2010	13,046	46,114	3,535

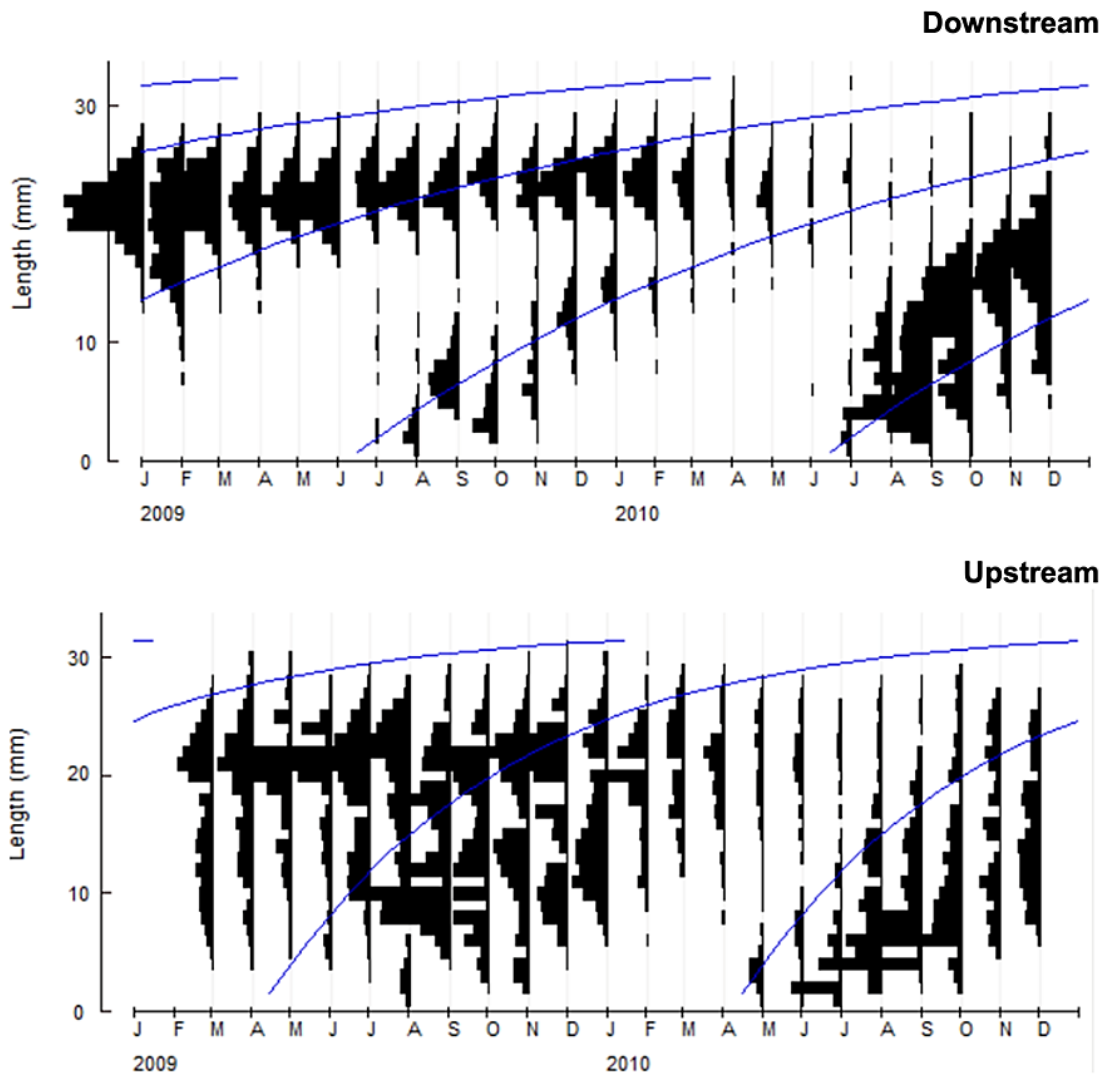


Figure 5. Growth curves at Oualidia's upstream (down) and downstream (top), which were created using the VBGF parameters as established by ELEFAN I and fitted to the population's length-frequency data.

attributable to local factors. In the downstream area, summer recruitment was observed in June and July, while in the upstream area, it occurred in April and May. Recruitment periods generally remained consistent from year to year in both zones.

**Mortality and exploitation rate:** There were notable variations in mortality rates between the upstream and downstream zones (Table 4, Fig. 7). Total mortality (Z) was 4.10 downstream, suggesting a moderate

pressure on mortality, and 9.18 upstream, almost twice as high as that downstream, indicating a significant pressure on mortality. Compared to upstream, which reported significantly higher natural mortality rates ( $M = 2.29721$ ) than downstream areas, which had a comparatively small natural mortality rate ( $M = 1.27671$ ). The rates of fishing-induced mortality (F), which ranged from 2.82 downstream to 6.88 upstream, showed notable variation. Overfishing is suggested by



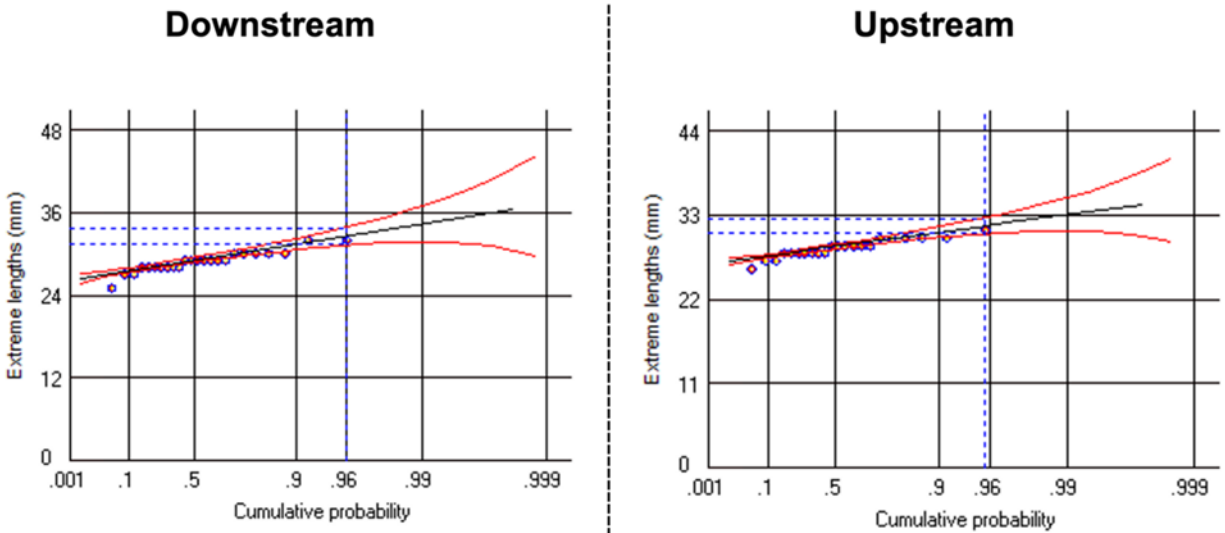


Figure 6. Predicted extreme length at Oualidia lagoon; downstream (left) and upstream (right).

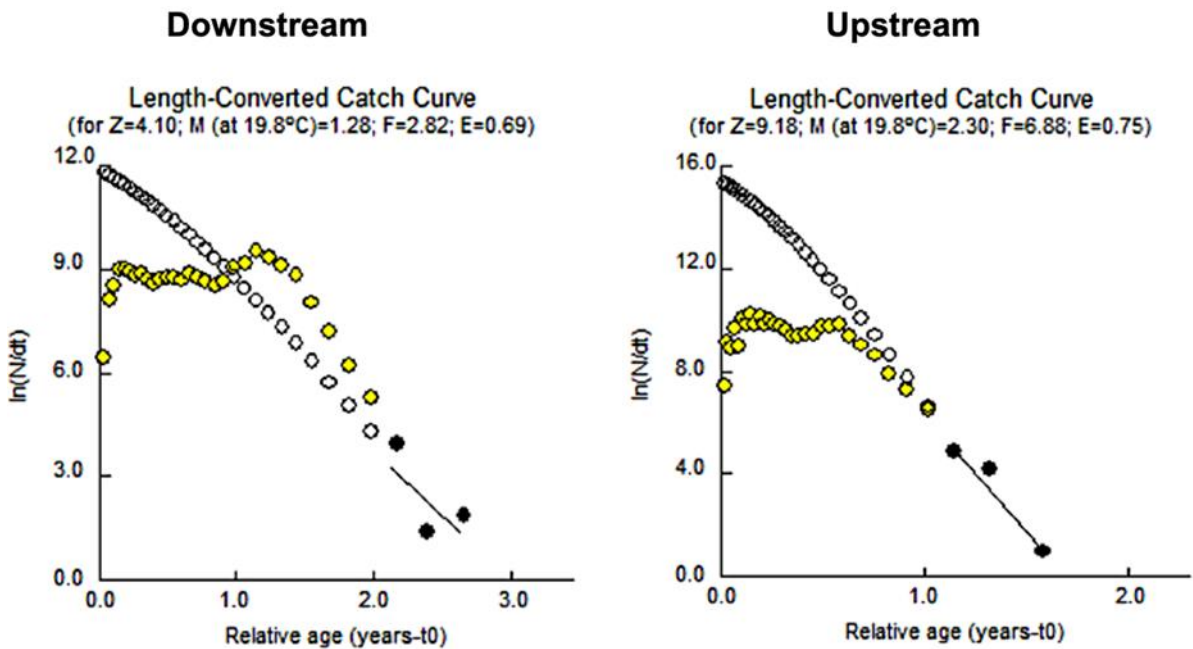


Figure 7. Length-converted catch curve at Oualidia, showing upstream (right) and downstream (left) locations. The descending slope (●) was used to determine the instantaneous mortality rate (Z) for *Cerastoderma edule*.

the higher-than-normal exploitation rates (E) for both zones, with a stronger effect of fishing activities on overall mortality shown upstream. The exploitation rates (E) were calculated at 0.69 downstream and 0.75 upstream to emphasize further the varying effects of fishing operations on the overall mortality in these zones. These data indicate a high fishing demand, with slightly higher effort and more damage observed upstream than downstream.

**Secondary production and productivity:** The results showed higher productivity upstream

compared to downstream of the lagoon (Table 5, Figs. 8, 9). Indeed, in 2009, average biomass reached 30.56 gDW.m<sup>-2</sup>, with an annual production of 96.34 gDW.m<sup>-2</sup>, corresponding to a production to biomass ratio (P/B) of 3.15 yr<sup>-1</sup>. In 2010, although biomass decreased slightly to 13.04 gDW.m<sup>-2</sup>, production remained relatively high at 46.11 gDW.m<sup>-2</sup>. yr<sup>-1</sup>, with a P/B ratio increased to 3.53 yr<sup>-1</sup>. In contrast to upstream, downstream showed lower levels of biomass and production. In 2009, biomass did not exceed 27.856 gDW.m<sup>-2</sup>, and production was 38.158



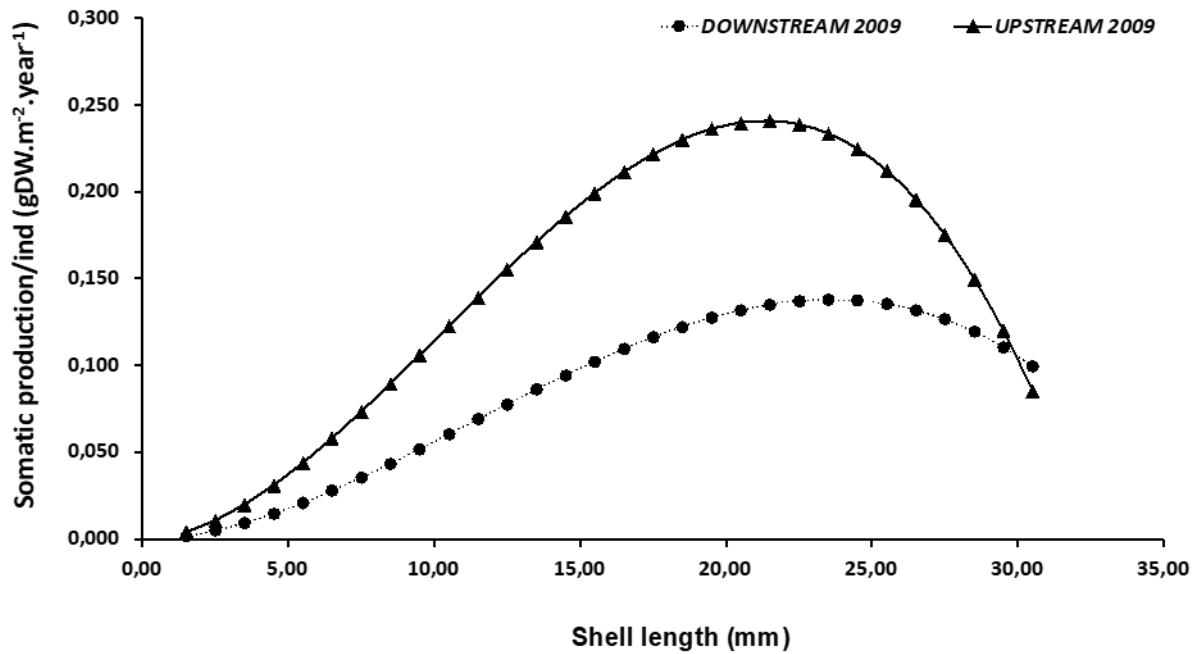


Figure 8. Annual somatic production (gDW.m<sup>-2</sup>.yr<sup>-1</sup>) per individual for the *Cerastoderma edule* population at Oualidia.

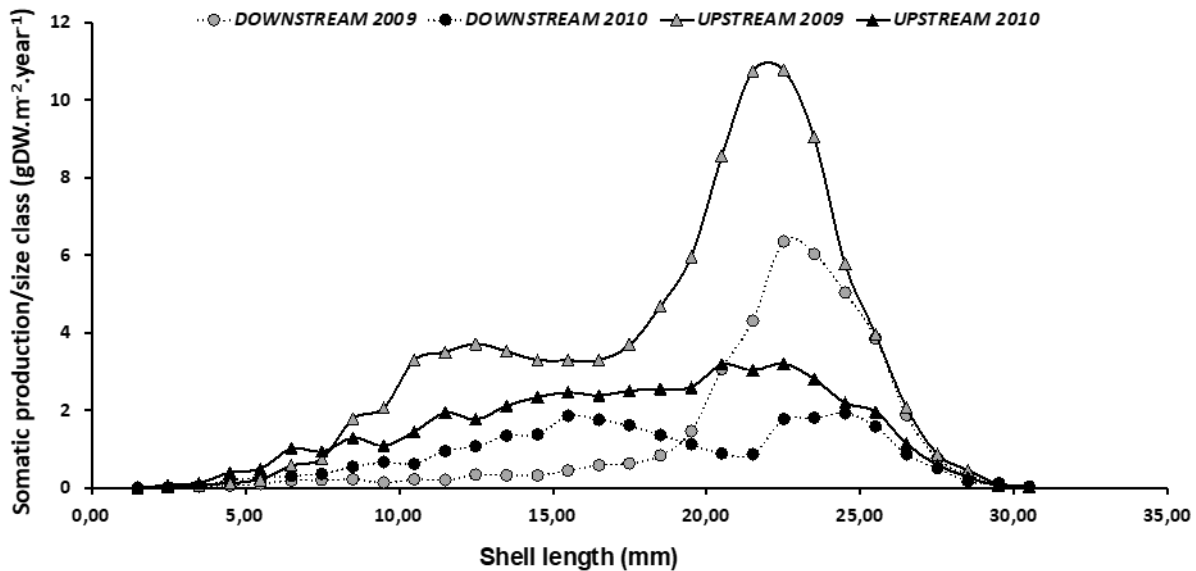


Figure 9. Annual somatic production distribution (gDW.m<sup>-2</sup>.yr<sup>-1</sup>) by shell length class (mm) for the *Cerastoderma edule* population at Oualidia.

gDW.m<sup>-2</sup>.yr<sup>-1</sup>, giving a P/B ratio of 1.37 yr<sup>-1</sup>. In 2010, biomass declined to 13.742 gDW.m<sup>-2</sup> and production did not exceed 26.138 gDW.m<sup>-2</sup>.yr<sup>-1</sup>, with a slightly improved P/B ratio of 1.90 yr<sup>-1</sup>.

## Discussions

**Recruitment:** Assessing recruitment is essential for understanding bivalve population dynamics (Borsa and Millet, 1992). Cockle recruitment at Oualidia Lagoon showed a clear seasonal pattern, occurring

once a year, in June or July. For the 2009 cohort, recruitment in the downstream zone began in June, while the second cohort started in May. By contrast, recruitment systematically began in July for the two upstream cohorts. This seasonality of recruitment underscores the significance of water temperature as a determining factor in the life cycle of *C. edule* in the Oualidia Lagoon. Temperatures aligned with these recruitment periods: 19.8°C in June 2009, 22°C in July 2009, 19.9°C in May 2010, and 20.2°C in July

2010. These temperatures are well above the recruitment thresholds identified at 13°C (Boyden, 1971) and are important for recruitment success (Beukema and Dekker, 2005, 2014). Recruitment at higher temperatures is linked to optimal conditions for newly settled cockles, including better food quality and quantity. According to Ducrotoy et al. (1991), a sharp increase in temperature acts as a stimulus for *C. edule* recruitment. However, our observations showed a more complex picture. In June 2009, 19.8°C coincided with the start of downstream recruitment. Although significant, this increase did not trigger immediate upstream recruitment. In 2010, the first summer temperature peak occurred in May (19.9°C). This sudden increase was synchronous with upstream recruitment, whereas downstream recruitment did not occur until July. These observations show that while temperature may play a role in recruitment, it is not the only determining factor. This finding aligns with a study by de Montaudouin et al. (2021), where recruitment was not always strongly correlated with temperature (De Montaudouin et al., 2021).

**Growth:** This study significantly contributes to understanding *C. edule* population dynamics in a lagoon ecosystem. The results highlight substantial differences in growth parameters between upstream and downstream cockle populations, with a significantly higher growth rate ( $K$ ) upstream ( $1.95 \text{ yr}^{-1}$ ) compared to downstream ( $0.83 \text{ yr}^{-1}$ ) and a slightly lower asymptotic length ( $L_{\infty}$ ) upstream (32.5 mm vs. 36 mm downstream). These findings are key to understanding the adaptive strategies of *C. edule* in the face of intra-site environmental variation. Spatial variations in growth rates and asymptotic sizes between upstream and downstream can be attributed to different environmental factors prevailing at each position. Upstream environmental conditions such as lighter currents and better availability of food resources could favor faster growth rates. Indeed, Navarro et al. (1992) reported that food concentration in suspension accounts for as much as 87% of the variation observed in cockle growth (Navarro et al., 1992). They respond to shifts in the quantity and quality of available food (Navarro et al., 2016). Earlier

studies support this finding and appear to align with the dynamic energy budget (DEB) theory, which proposes that food quantity and quality exert the most significant positive impact on growth, with temperature as a secondary factor (Van Der Meer et al., 2014). Other studies propose that growth rates may be impacted by a rise in water temperature, which could enhance food availability and consequently support cockle growth (Beukema et al., 2017).

Temperature measurements upstream (27.5°C) are higher than those downstream (25°C), highlighting temperature as a key factor in promoting growth. This suggests that the influence of climate change on cockle populations could be complex and, at times, contradictory. On the other hand, other environmental stressors, such as salinity, affect growth. Salinity can fluctuate significantly inside a lagoon, affecting cockle physiology and diminishing their eating capacity (Gonçalves et al., 2017). It is, therefore, clear that temperature and salinity can significantly affect cockle population dynamics. Exceeding tolerance thresholds can have adverse consequences (Wither et al., 2012). At Oualidia, water salinity remains close to oceanic waters, with a mean annual salinity of 36.5 (Orbi et al., 2008), and follows a desalination gradient from downstream to upstream (Bennouna et al., 2000). The lower salinity upstream could explain the smaller size of *C. edule* cockles observed in this zone. Indeed, low salinity causes cockles to close their valves, feed less, and consequently have reduced energy available for growth (Domínguez et al., 2020). This reduction in growth is highlighted by the observations in the current study, where upstream populations show a slightly lower asymptotic length ( $L_{\infty}$ ) (32.5 mm) compared to those downstream (36 mm). On the other hand, where salinity is higher and more stable, cockles benefit from favorable conditions for growth downstream. However, very high salinity can cause biochemical alterations in cockles (Magalhães et al., 2018). In this study, downstream populations show a greater asymptotic length but a lower growth rate ( $K = 0.83 \text{ yr}^{-1}$ ) than upstream populations ( $K = 1.95 \text{ yr}^{-1}$ ). This phenomenon can be attributed to the moderate biochemical stress caused by the high salinity, which

slows the growth rate despite the greater potential size.

Numerous studies have identified population density as a key factor influencing cockle growth, with higher densities often leading to slower growth rates. Cockle density values were close upstream and downstream, at 299.27 and 296.11 Ind.m<sup>-2</sup>, respectively. These densities remain below the thresholds observed in previous studies, where significant impacts on cockle growth have been reported. Jensen (1992), in the Wadden Sea, showed that cockles in areas of high density (>2500 Ind.m<sup>-2</sup>) were smaller in size. De Montaudouin and Bachelet (1996) have shown in the Arcachon Basin that growth rates decrease with increasing density, sometimes to the point of constancy (De Montaudouin and Bachelet, 1996). This suggests that the density of cockle populations at Oualidia is probably not a determining factor in the slowdown of their growth downstream, as smaller sizes upstream. On the other hand, warming seawater facilitates the transmission of trematode parasites (De Montaudouin et al., 2016).

In the Oualidia lagoon, temperatures are high throughout the year. In summer, water temperatures can vary from 16°C at high tide to 20°C at low tide in the central part of the lagoon, while in winter, they can rise from 12.5°C at low tide to 16°C at high tide (Makaoui et al., 2018). The possibility of transmission of digenean trematodes is, therefore, high in the lagoon (Alfeddy et al., 2024). Trematodes can have a detrimental effect on cockle growth, as metacercarial infestations force cockles to devote part of their energy to defense against parasites, thus reducing the energy available for growth (Thieltges, 2006). Therefore, it would be relevant to examine the distribution of trematodes between upstream and downstream to assess their impact on cockles, as some trematode species are more detrimental than others (Longshaw and Malham, 2013).

Wegeberg and Jensen (2003) state that a longer immersion time and a higher feed rate would result in greater growth. This may seem contradictory to our observations, where upstream cockles, potentially benefiting from a longer immersion time, show a higher growth rate but a lower asymptotic length.

Although our results show differences in growth between upstream and downstream populations, they also highlight the importance of local factors in determining growth rates and growth performance of *C. edule* populations in lagoon systems. The various factors influencing cockle growth are likely to interact in different ways, either working against each other, enhancing each other, or having a combined effect, depending on the specific environmental context.

**Mortality:** Mortality rates of *C. edule* cockles in the Oualidia Lagoon showed significant differences between the upstream (U) and downstream (D) zones, with  $Z = 9.18$  and  $M = 2.29721$  for the upstream and  $Z = 4.1$  and  $M = 1.27671$  for the downstream. These results not only demonstrated a much higher mortality rate upstream but also highlighted the impact of the different ecological conditions between these two habitats on cockle survival and raised important questions about the ecological and anthropogenic pressures that can affect these populations. A combination of extrinsic and intrinsic factors could help explain the increase in upstream mortality. As noted by El Asri et al. (2015), temperature variations between upstream (27.5°C) and downstream (25°C) provide a plausible explanation. According to previous research, such as that carried out in the Arcachon basin (Guillou and Tartu, 1994) and Galicia (Gonzalez and Perez Camacho, 1984), temperature variations could lead to increased mortality in juvenile cockles. In Oualidia, this temperature sensitivity was particularly important, as temperature variations could reflect the different ecological pressures between the two zones.

Salinity in the Oualidia lagoon did not appear to be a direct limiting factor for cockle survival due to the euryhaline nature of the cockle, which can tolerate wide variations in salinity, ranging from 18 to 40 (De Montaudouin et al., 2021), with an optimum around 30 to 35 (Kingston, 1974), and critical lethal thresholds of 10 (Verdelhos et al., 2015). Salinity in the lagoon varied between 20 to 36 (Makaoui et al., 2018), well above the lethal threshold for *C. edule* cockles. This range of salinity, influenced by both marine and freshwater inputs, suggests that other

environmental or anthropogenic factors may play a greater role in observed cockle mortality in the context of the Oualidia lagoon. Although overall salinity in the lagoon was generally adequate for cockle survival, local and/or temporal variations could create stressful situations for cockles upstream, explaining the higher natural mortality values. Upstream, relatively low salinities due to freshwater influx could induce valve closure in cockles, reducing their feeding ability (Domínguez et al., 2020) and increasing their vulnerability to pathogens (e.g., parasites).

The significant presence of digenetic trematodes in Oualidia cockle populations underscores the potential role of parasitism in regulating populations of these bivalves (Alfeddy et al., 2024). The four main parasitic trematodes (*Himasthla quissetensis*, *H. interrupta*, *Curtuteria arguinae*, and *Gymnophallus minutus*) showed different infestation patterns, suggesting a complex interaction between parasite load and local environmental conditions. These parasites use the cockle of *C. edule* as an intermediate host. Several studies have already highlighted the role of parasitism, in particular the correlation between cockle size and trematode infestation, in cockle mortality. These studies underlined the importance of biotic interactions, including predation and parasitism, on cockle mortality and highlighted the importance of these factors in cockle population dynamics. Episodes of significant increases in infestation intensity demonstrated the influence of parasitic infection events, leading to so-called parasite-dependent mortality.

**Productivity and secondary production:** Estimating a species' production and productivity is necessary to analyse its ecological role in an ecosystem (Casagrande and Boudouresque, 2005). Over two years, from 2009 to 2010, the productivity and secondary production of *C. edule* populations in the Oualidia lagoon were evaluated in this study. Productivity was significantly higher upstream than downstream. In 2009, the average upstream biomass was 30.56 gDW.m<sup>-2</sup>, with an annual production of 96.342 gDW.m<sup>-2</sup> and a P/B ratio of 3.15 gDW.m<sup>-2</sup>.

However, downstream biomass was 27.85 gDW.m<sup>-2</sup>, with an annual production of 38.15 gDW.m<sup>-2</sup> and a P/B ratio of 1.37 yr<sup>-1</sup>. Seasonal variability is also apparent. In 2010, upstream biomass decreased to 13.04 gDW.m<sup>-2</sup>, but production reached 46.11 gDW.m<sup>-2</sup> with a P/B ratio of 3.53 yr<sup>-1</sup>, indicating greater efficiency in converting biomass to production despite lower total biomass. Downstream, biomass decreased to 13.74 gDW.m<sup>-2</sup> and production to 26.13 gDW.m<sup>-2</sup>, with a P/B ratio of 1.90 yr<sup>-1</sup>. Multiple factors influence productivity, such as habitat conditions, population structure, stability, and growth rates (Casagrande and Boudouresque, 2005; Verdelhos et al., 2015). Within the same environment, these variables will result in varying productivity among populations and even for various sampling locations (Casagrande and Boudouresque, 2005).

The variations observed in the lagoon may, therefore, be responsible for this disparity in productivity. Water temperature, salinity, and nutrient availability directly affect the growth and reproduction of *C. edule* cockles (Domínguez et al., 2023). Upstream, if higher temperatures and low salinity are combined with better food availability, they can provide optimal conditions for production (Gosling, 2015). These factors may explain the higher growth rate at this station. At Oualidia, chlorophyll concentrations vary seasonally and can impact production by directly influencing food availability. Doukilo et al. (2022) describe maximum chlorophyll concentrations in May (5.37 µg/L). This peak in food resources coincides with the upstream cockle recruitment period, which promotes the rapid growth of young cohorts, contributing to the higher production levels observed in this zone compared to downstream. However, minimum concentrations observed in November (0.09 µg/L) (Doukilo et al., 2022) could affect downstream productivity generally by affecting nutrient availability. The P/B ratio values align with those reported in other studies in similar ecosystems. The relatively high values upstream (3.53 yr<sup>-1</sup> in 2010) indicate that this population is more productive and reflects optimal conditions upstream compared to downstream, where conditions are less

favorable.

## Conclusions

This study has revealed significant variations in population dynamics and *C. edule* production between the upstream and downstream zones of the Oualidia Lagoon. There appears to be no single determining factor influencing population dynamics at Oualidia. Several factors contribute to these disparities, including temperature, salinity, and food availability, parasitism, and fishing. These biotic and abiotic factors interact to create variation in population parameters within the same site at two different stations. The Oualidia Lagoon requires constant monitoring to understand better and manage the cumulative impacts of anthropogenic and natural stressors.

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