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The functional relationships between seagrass beds and their associated bivalves in the Algerian Basin (El Mellah Lagoon) in relation to climate variation

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Abstract

This paper presents the first study examining the relationship between angiosperms, their associated bivalves, and environmental conditions, with the aim of assessing the health of the El Mellah lagoon. The study was conducted monthly throughout 2019 at three stations selected for their continental and marine influences. The seagrass beds exhibit remarkable abundance, with biomass reaching up to 1313.32 ± 132.73 g DW m^{-2} in September. The biomass of *Zostera noltei* is positively correlated with temperature, while that of *Ruppia maritima* is positively correlated with salinity. Bivalve density in El Mellah follows the variation in seagrass bed biomass. The densities of the native bivalve *Loripes orbiculatus* and the invasive species *Arcuatula senhousia* increase with both the aboveground and belowground biomass of *Z. noltei*, as well as with temperature. This suggests the existence of a tripartite mutualism between seagrass beds, lucinid bivalves, and their sulphide oxidising gill symbionts. These findings highlight the importance of investigating the factors influencing the mutualistic relationship between seagrasses and lucinid bivalves in the El Mellah lagoon, not only to improve the long-term success of seagrass restoration but also to strengthen their resilience to climate change.

Keywords: Coastal lagoon; *Zostera noltei*; *Ruppia maritima*; climate change; invasive species; biodiversity; El Mellah Lagoon; Algeria.

Introduction

Submerged macrophytes, which include both macroalgae and angiosperms, are aquatic organisms. They account for around 40% of primary production in coastal areas (Charpy-Roubaud & Sournia, 1990; Le Fur, 2018). Forming vast meadows in many coastal lagoons (Agostini *et al*., 2003; Le Fur *et al*., 2018), they play a significant role in influencing various chemical and physical processes while contributing to the structuring of lagoon ecosystem habitats (Jeppesen *et al*., 2012; Le Fur *et al*., 2018). Due to their ability to modify their environment and control the availability of resources for themselves and other organisms, they are referred to as engineering organisms (Jones, Lawton & Shachak, 1997; Le Fur *et al*., 2018; Bertrin *et al*., 2019). In coastal lagoons, these plants play a vital role in influencing biogeochemical cycles (Plus *et al*., 2003; Bertrin *et al*., 2019).

The distribution of seagrass meadows, like that of most aquatic plants, is influenced by various natural biotic and abiotic factors. These include the physiological characteristics of each species, grazing by consumers, climatic variations, water salinity, current and wave intensity, and light exposure (Koch, 2001; Lee *et al*., 2007; Le Fur *et al*., 2018). Seagrass meadows are among the most valuable ecosystems in terms of their ecological importance and the services they provide. They provide habitat, contribute to primary productivity (i.e. carbon storage), stabilise sediments, filter water, participate in the nutrient cycle, and offer coastal protection (Costanza *et al*., 1997; Hemminga & Duarte, 2000; Terrados & Borum, 2004; Orth *et al*., 2006; Le Fur *et al*., 2018). Furthermore, seagrass meadows capture and store approximately 12% of the total carbon present in the oceans, thereby playing a significant role in regulating the global carbon cycle (Terrados & Borum, 2004). Seagrass beds are also frequently used as biological indicators of ecosystem health owing to their sensitivity and vital ecological function (Montefalcone, 2009; Do, 2012).

The development of human activities in the catchment areas of coastal lagoons has resulted in increased nutrient and chemical contaminant inputs, such as urban wastewater, wastewater treatment plant effluents, and agricultural run-off (Barnes, 1980; Castel *et al*., 1996; Kennish & Paerl, 2010; Munaron *et al*., 2012; Le Fur *et al*., 2018). This increase in nutrients has affected Mediterranean lagoons since the mid-20th century, causing eutrophication and significant changes in primary producers (Le Fur *et al*., 2019). Despite their ecological and societal importance, seagrass meadows are experiencing a rapid global decline, with an estimated annual loss of 2–5% of their surface area (Duarte *et al*., 2009; Waycott *et al*., 2009; Le Fur *et al*., 2018). Since the 1980s, this loss has amounted to over 33,000 km^2 (Green & Short, 2003).

Seagrass meadows play a fundamental role in determining the diversity, abundance, and richness of bivalve assemblages by providing essential habitats. In this context, the ecosystem services provided by these meadows are of particular importance (Lebreton *et al*., 2012; Nordlund & Gullström, 2013; Syukur *et al*., 2021). However, the service capacity of seagrasses can vary significantly depending on the specific species and the characteristics of the marine ecosystem (Nordlund *et al*., 2016; Syukur *et al*., 2021).

Bivalves support primary producers, including seagrasses, and play a crucial role in modulating the impacts of anthropogenic pressure and global climate change (Chin *et al*., 2020; Syukur *et al*., 2021). Conversely, environmental disturbances, particularly those driven by human activities, can disrupt facilitative interactions, with potential consequences for ecosystem functioning. For instance, studies have demonstrated that global changes can impair mutualisms by altering the phenology of the species involved, such as the relationship between plants and their pollinators (Memmott *et al*., 2007; Sanmartí *et al*., 2018).

The Algerian coastline extends for 2,148 km. Lagoon coastal ecosystems are largely absent along extensive sections of this coastline. Additionally, shellfish farming in the lagoon has remained unexploited since the late 1990s due to the mass mortality of *Mytilus galloprovincialis* (Lamarck, 1819) mussels and *Magallana gigas* (Thunberg, 1793) oysters (Benmarce, 2012). Recurrent fires reduce vegetation and increase the risk of erosion, which could lead to lagoon infilling and increased sedimentation (Kherifi & Bousnoubra, 2012; Melouah, 2013). Furthermore, previous studies on the composition of angiosperm communities in El Mellah lagoon are insufficient to provide a detailed understanding, underscoring the need for further investigation.

Additionally, seagrass beds, which are an important component of coastal ecosystems, have experienced an alarming global decline in recent decades, leading to significant biodiversity loss (Waycott *et al*., 2009; van der Heide *et al*., 2012). This deterioration is likely to be exacerbated by the accelerating rate of global climate change observed this century, which will significantly impact the Earth's oceans and potentially have severe consequences for seagrass beds (Duarte *et al*., 2008; Do, 2012). Therefore, in light of these factors, our study aimed to assess the environmental status of the El Mellah lagoon for the first time by examining the relationship between angiosperms, their associated bivalves, and environmental conditions.

Materials and Methods

Study site and location of stations

El Mellah lagoon (36.89290° N, 8.32623° E) is the only shallow brackish coastal lagoon in Algeria. It has a maximum depth of 6.4 m and an average depth of 2.7 m and is located in the far north-eastern region of the country, within the El-Kala National Park, which is recognised as a UNESCO biosphere reserve (Hamza *et al*., 2022). El Mellah is situated in the Algerian sub-basin on the southern shore of the Mediterranean Sea (Fig. 1). The 865-hectare lagoon has a single 900-metre-long, 10- to 20-metre-wide natural inlet in the north. It is characterised by limited water exchange with the open sea (Cataudella *et al*., 2015).

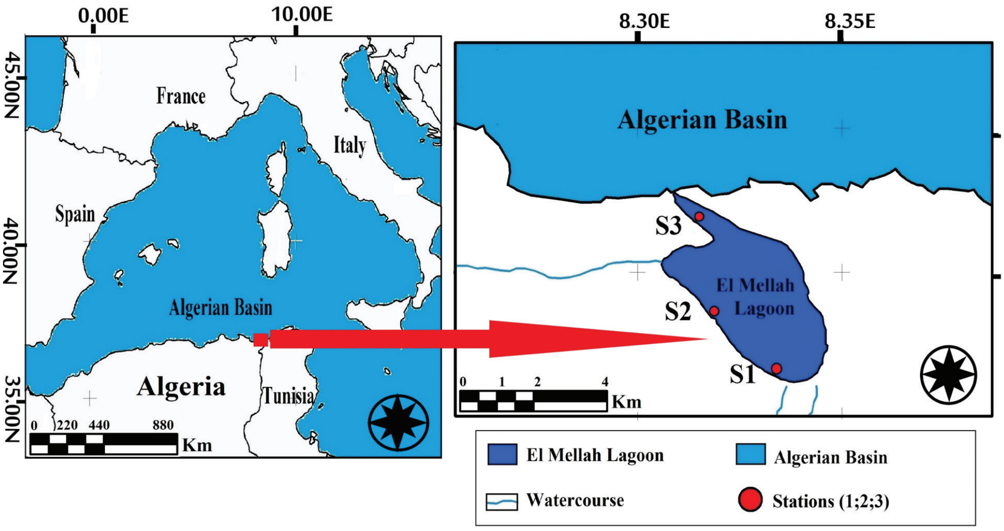

Fig. 1: The study area is located in the Mediterranean Sea. The sampling stations are situated in El Mellah Lagoon on the southern coast of the Algerian Basin in Algeria (Station 1: 36.87722° N, 8.33083° E; Station 2: 36.88722° N, 8.31444° E; Station 3: 36.90944° N, 8.31444° E) (Hamza *et al*., 2022).

Sampling of benthic assemblages

Triplicate sediment cores were collected manually each month in the shallow subtidal zone (at depths of 0.3 to 0.5 m) from three representative stations with heterogeneous seagrass meadows. Benthic sampling was destructive and involved the use of manual cores (n = 3) with a diameter of 19 cm and an area of 0.028 m², which were pushed vertically through the vegetation and sediment. Physico-chemical parameters, including salinity, pH, temperature, and dissolved oxygen, were measured in situ each month at all sampling sites using a multi-parameter HANA HI9829 probe (Hamza *et al*., 2022).

The samples were immediately transferred to the laboratory and carefully washed with tap water to remove any remaining organic debris and sediment. Macrophytes and bivalves were then carefully sorted and identified at both functional and species levels. The macrophytes were separated into leaf and root–rhizome fractions, which were dried at 60° C for 24 hours to estimate dry biomass. Biomass was calculated by normalising the dry weight (DW) measured within a 0.028 m² sampling area to a standard surface of 1 m². The final values are expressed as g DW m^{-2}.

The density of bivalves was determined by extrapolating the number of individuals recorded within the 0.028 m² sampling area to a standard surface of 1 m². The results are expressed as the number of individuals per square metre (ind. m^{-2}). All data are presented as the mean ± standard error of the mean (SEM). The specimens were identified by examining their shells at the MARBEC (Marine Biodiversity, Exploitation and Conservation) laboratory at the University of Montpellier, in accordance with the reference provided by the World Register of Marine Species (WoRMS).

Statistical analysis

The data are presented as means (± SD) in the tables and figures. Principal component analysis (PCA) was carried out using version 7.5.2 of the XLSTAT-Pro software to relate the distribution patterns of angiosperm leaf and root biomass and benthic bivalve density to environmental variables. Furthermore, Canonical Correspondence Analysis (CCA) was performed to link species abundances to environmental variables (Ter Braak, 1986).

Results

Taxonomic identification of seagrasses and their associated bivalves

During the 2019 study period, the inventory of the benthic angiosperm flora in the El Mellah lagoon identified three species of Magnoliopsida. These species include *Zostera noltei* (Hornemann, 1832), *Ruppia maritima* (Linnaeus, 1753), and *Ruppia cirrhosa* (Petagna) Grande, 1918. The inventory of the benthic malacofauna in the El Mellah lagoon led to the identification of five bivalve species belonging to five different families: Cardiidae, Semelidae, Veneridae, Lucinidae, and Mytilidae. These species include *Cerastoderma glaucum* (Bruguière, 1789), *Abra ovata* (Philippi, 1836), *Ruditapes decussatus* (Linnaeus, 1758), and *Loripes orbiculatus* (Poli, 1795) (Table 1). Additionally, a new species from the Mytilidae family, *Arcuatula senhousia* (Benson, 1842), was recorded for the first time in the El Mellah lagoon in June 2019. This invasive species was more abundant than the other four species and played a dominant role in the benthic community of this shallow coastal ecosystem (Table 1).

Relationship between seagrass meadow, associated bivalves communities, and environmental factors

As shown in Figure 2, the PCA indicates that the first two factorial axes account for 50.24% of the total variance. Along the horizontal axis (F1), two groups of observations can be distinguished. The first, located in the positive part of the F1 axis, comprises temperature, pH, aboveground and belowground biomass of *Z. noltei*, as well as the density of *L. orbiculatus* and *A. senhousia*. This group is mainly characterized by positive correlations: between temperature and both the aboveground and belowground biomass of *Z. noltei* (r = 0.38 and r = 0.41,

Table 1. Taxonomic list of malacofauna associated with seagrass beds collected in the El Mellah Lagoon during 2019.

Class	Order	Family	Species	Authors	St 1	St 2	St 3	Total (N)
Bivalvia	Cardiida	Cardiidae	*Cerastoderma glaucum*	(Bruguière, 1789)	15	14	17	46
		Semelidae	*Abra ovata*	(Philippi, 1836)	4	14	18	36
	Venerida	Veneridae	*Ruditapes decussatus*	(Linnaeus, 1758)	15	2	11	28
	Lucinida	Lucinidae	*Loripes orbiculatus*	(Poli, 1795)	109	50	86	245
	Mytilida	Mytilidae	*Arcuatula senhousia*	(Benson, 1842)	427	422	94	943

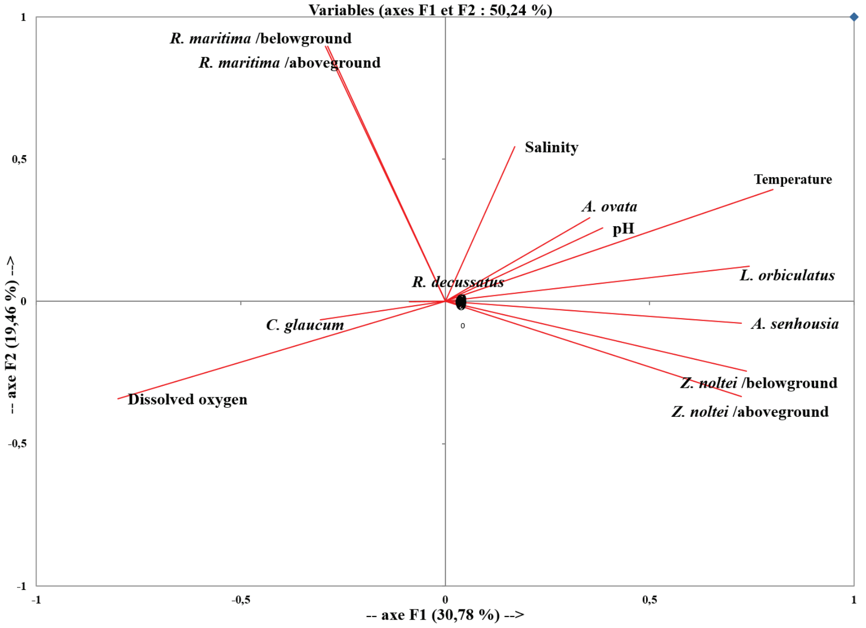

Fig. 2: Graphical representation of the F1–F2 projection plane of the principal component analysis (PCA), performed on the following variables: temperature, salinity, pH, dissolved oxygen, aboveground biomass, belowground biomass, and the density of benthic bivalves (*C. glaucum*, *A. ovata*, *R. decussatus*, *L. orbiculatus*, and *A. senhousia*). Data were collected at three stations in the El Mellah Lagoon in 2019.

respectively); between temperature and the density of *A. ovata*, *L. orbiculatus*, and *A. senhousia* (r = 0.31, r = 0.57, and r = 0.60, respectively); between the aboveground and belowground biomass of *Z. noltei* and the density of *L. orbiculatus* (r = 0.44 and r = 0.69, respectively); and between the aboveground and belowground biomass of *Z. noltei* and the density of *A. senhousia* (r = 0.55 and r = 0.39, respectively). In the negative part of the F1 axis, a second group (G2) is formed by the aboveground and belowground biomass of *R. maritima*, which are positively correlated (r = 0.32; r = 0.30) (Fig. 2).

Trajectory of bivalves density as a function of angiosperm biomass

Figure 3A shows that the density of associated bivalves varies with angiosperm biomass. It increases as angiosperm biomass increases, particularly during summer, especially in June, when the highest bivalve density values were recorded (1,619 ± 623.8, 1,286 ± 251 and 1,178 ± 272.5 ind. m^{-2}), corresponding to angiosperm biomass values (559 ± 231.5, 673.4 ± 97.7 and 595.5 ± 143.8 g DW m^{-2}) at stations 1, 2, and 3, respectively (Fig. 3A).

We observed that the density of *A. senhousia* varies considerably in relation to the aboveground and belowground biomass of *Z. noltei* rather than *R. maritima* (Fig. 3B and 3C). *A. senhousia* reached maximum densities of 1321 ± 475.6 ind. m^{-2} (station 1), 1071 ± 125.4 ind. m^{-2} (station 2), and 892 ± 119.1 ind. m^{-2} (station 3) in June, when significant increases in aboveground biomass (304.16 ± 131.9 g DW m^{-2}, 341.7 ± 71.4 g DW m^{-2}, 109.6 ± 24.6 g DW m^{-2}) and belowground biomass (221.9 ± 66.1 g DW m^{-2}, 331.6 ± 26.3 g DW m^{-2}, 1153 ± 50.9 g DW m^{-2}) of *Z. noltei* were recorded at stations 1, 2, and 3, respectively.

At stations 1 and 2, located farther from the channel, a decrease in the density of *A. senhousia* was observed after July, reaching minimum values of 262 ± 105.8 ind. m^{-2} at station 1 and 500 ± 123.7 ind. m^{-2} at station 2 in December. This decline was accompanied by a decrease in the aboveground biomass of *Z. noltei* (89.1 ± 12.9 g DW m^{-2}, 34.5 ± 8.9 g DW m^{-2}) and in the belowground biomass (208.1 ± 51.3 g DW m^{-2}, 127.3 ± 29.7 g DW m^{-2}) at stations 1 and 2, respectively. At station 3, which was dominated by *R. maritima* and located near the channel, the total disappearance of *A. senhousia* was observed after July (Fig. 3B and 3C).

We also observed that the density of *L. orbiculatus* increased significantly in relation to the aboveground and belowground biomass of *Z. noltei*, but not in relation to *R. maritima* (Fig. 3D and 3E). The lowest densities of *L. orbiculatus* were recorded when *Z. noltei* biomass was lowest in the lagoon, specifically during February, March, April, and May, when biomass was below 160 g DW m^{-2}.

A significant increase in *L. orbiculatus* density was recorded from 35.71 ± 20.62 ind. m^{-2} in May to 238.09 ± 103.78 ind. m^{-2} in June. This increase occurred simultaneously with a significant rise in both aboveground and belowground biomass of *Z. noltei* at the three stations from May to June. Maximum densities of *L. orbiculatus* of 309.52 ± 83.33 ind. m^{-2} (station 1), 202.38 ± 66.28 ind. m^{-2} (station 2), and 285.71 ± 71.43 ind. m^{-2} (station 3) were recorded when hypogeal biomass of *Z. noltei* reached peak values of 710.71 ± 127.86 g DW m^{-2} (September), 390.00 ± 109.19 g DW m^{-2} (September), and 164.87 ± 33.75 g DW m^{-2} (August), respectively (Fig. 3D and 3E).

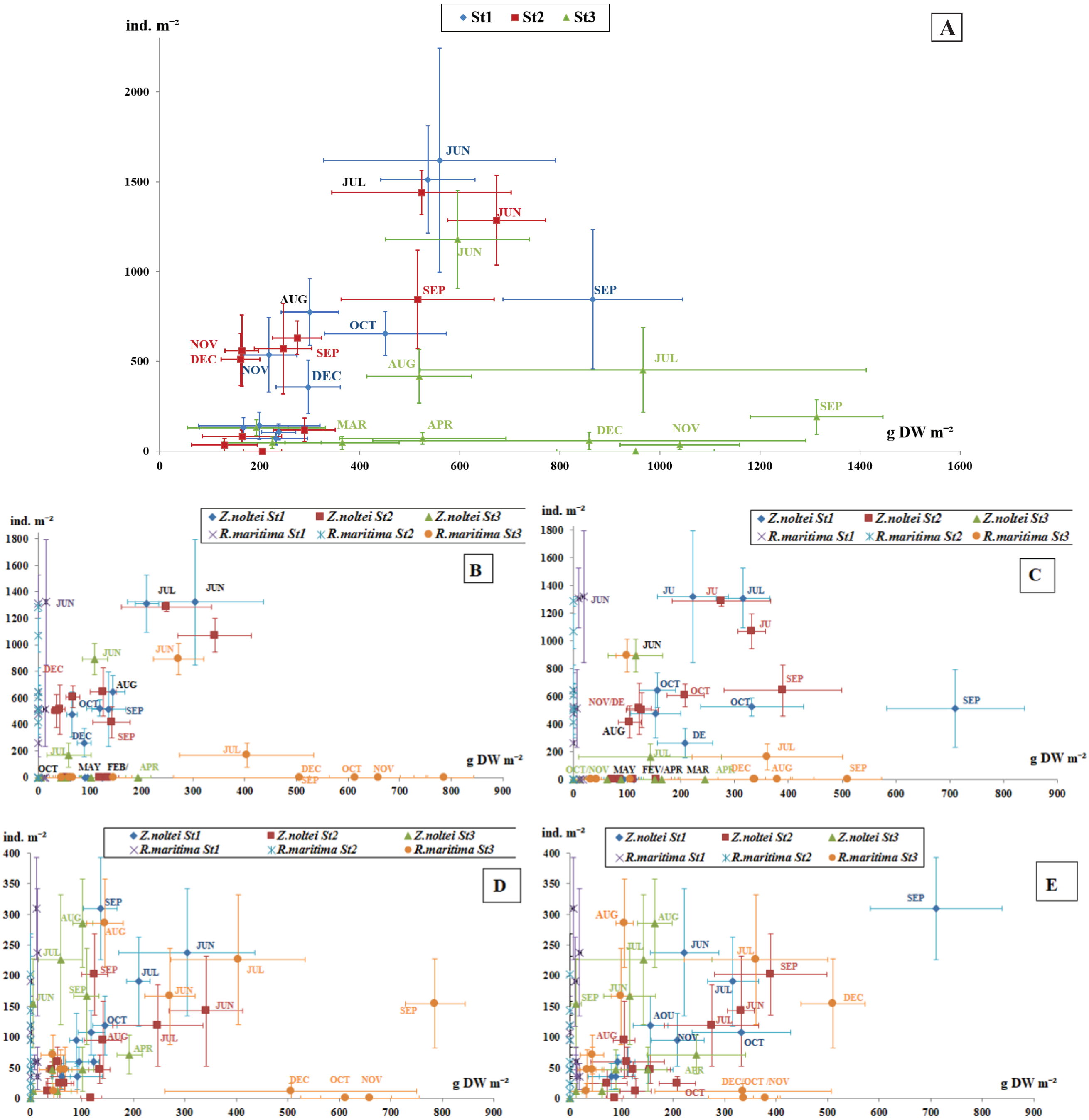

Fig. 3: **A.** Trajectory of benthic bivalve density (ind. m⁻²) in relation to angiosperm biomass (g DW m⁻²) during 2019 in the El Mellah Lagoon (mean ± SEM).
B-C. Density of *Arcuatula senhousia* (ind. m⁻²) as a function of the aboveground and belowground biomass (g DW m⁻²) of *Zostera noltei* and *Ruppia maritima* during 2019 in the El Mellah Lagoon (mean ± SEM).
D-E. Density trajectory of *Loripes orbiculatus* (ind. m⁻²) as a function of the aboveground and belowground biomass of *Z. noltei* and *R. maritima* (g DW m⁻²) during 2019 in the El Mellah Lagoon.

Trajectory of angiosperm biomass and associated bivalve density in relation to physicochemical characteristics

In the F1-F2 factorial plane, canonical correspondence analysis (CCA) clearly divided the communities (96.66%). This division is reflected in the formation of three distinct groups (Fig. 4). Axis I accounted for 69.49% of the total variability, while Axis II accounted for 27.18%. The first group consists of three bivalve species (*A. ovata, L. orbiculatus* and *A. senhousia*) and one flowering plant (*Z. noltei*). The abundance of this group is influenced by temperature. A positive correlation was observed between the abundance of these species and temperature, and they did not show a particular affinity for a specific location.

The second group comprises only the seagrass *R. maritima*. This species is positively correlated with salinity and is primarily found in the northern part of the lagoon (station 3). The third group includes two bivalve

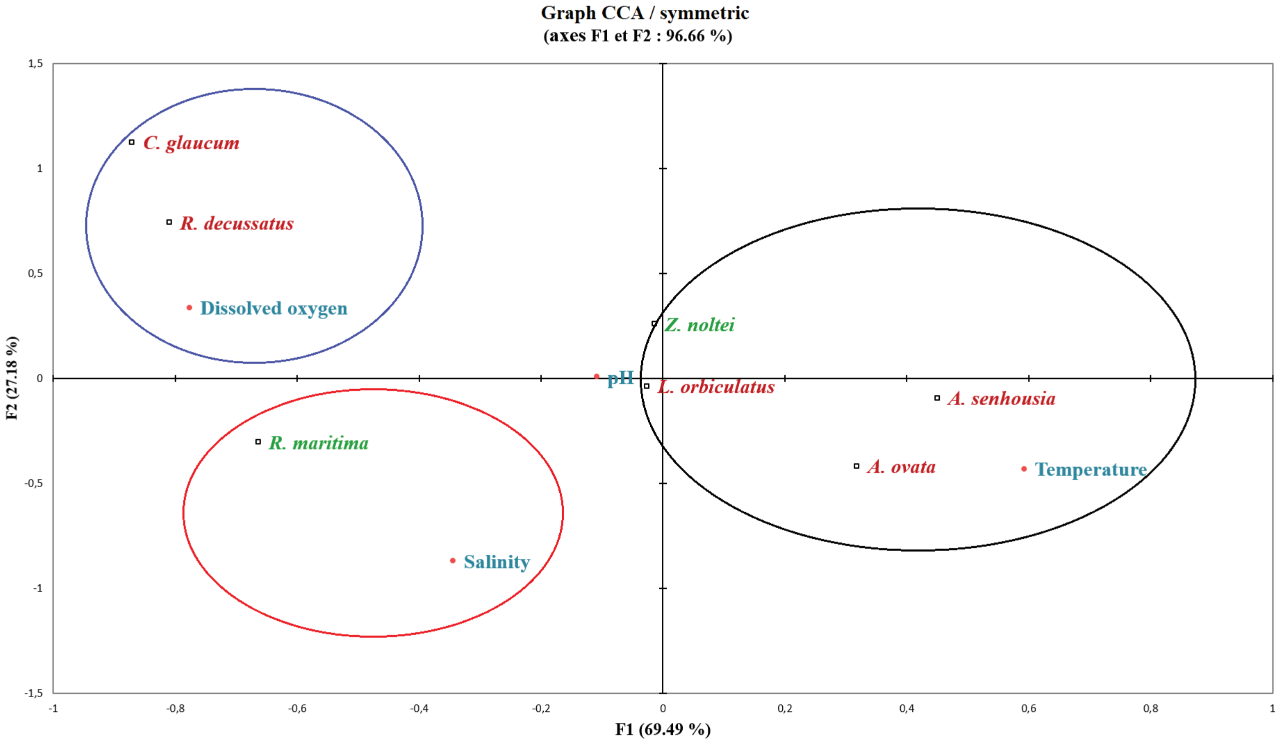

Fig. 4: Results of the Canonical Correspondence Analysis (CCA) showing the relationships between environmental variables (temperature, salinity, pH, and dissolved oxygen), angiosperm biomass (*Z. noltei* and *R. maritima*), and the density of benthic bivalves (*C. glaucum*, *A. ovata*, *R. decussatus*, *L. orbiculatus*, and *A. senhousia*) at three stations in the El Mellah Lagoon in 2019.

species (*C. glaucum* and *R. decussatus*), whose density is influenced by dissolved oxygen. This relationship was observed at all three lagoon stations (Fig. 4).

The spatio-temporal variation in the density of *A. senhousia* as a function of temperature highlights the seasonal effect on its dynamics (Fig. 5A). An increase in the density of *A. senhousia* was observed in association with rising summer temperatures. Maximum densities of *A. senhousia* were recorded at 1,619 ± 623.8 ind. m^{-2} (station 1), 1,286 ± 251 ind. m^{-2} (station 2), and 1,178 ± 272.5 ind. m^{-2} (station 3). These peak values occurred in June, when the temperature exceeded 28° C for the first time in the El Mellah lagoon (Fig. 5A). After July, a decrease in water temperature in El Mellah was accompanied by a decline in *A. senhousia* density (Fig. 5A).

In El Mellah, the density of *L. orbiculatus* also increased with temperature, particularly during summer (Fig. 5B). Maximum densities of *L. orbiculatus* of 309.52 ± 83.33 ind. m^{-2} (station 1), 202.38 ± 66.28 ind. m^{-2} (station 2), and 285.71 ± 71.43 ind. m^{-2} (station 3) were recorded in August and September, when temperatures exceeded 26° C (Fig. 5B). Fig. 5C summarises the spatio-temporal variation in the density of *Abra ovata* as a function of temperature. Following a marked increase in temperature above 28° C, *A. ovata* appeared at all three stations in June. The maximum density of *A. ovata*, 119.04 ± 66.28 ind. m^{-2}, was recorded at station 3 near the channel in August, when the temperature reached 26.1° C (Fig. 5C).

Figures 6A and 6B summarise the spatio-temporal evolution of the aboveground and belowground biomass of *Z. noltei* as a function of temperature. The aboveground and belowground biomass of *Z. noltei* increases during the summer period, when temperature reaches its maximum value (> 28° C). This indicates a clear seasonal effect on biomass dynamics. The lowest aboveground and belowground biomass of *Z. noltei* was observed when lagoon temperature was below 21° C, particularly in December, February, March, April, and May. Maximum aboveground biomass (304.16 ± 131.98 g DW m^{-2}) and maximum belowground biomass (710.71 ± 127.86 g DW m^{-2}) were recorded in June and September, respectively, at the southern end of the lagoon (station 1), where the herbaceous cover is dominated by *Z. noltei* (Fig. 6A and 6B).

In contrast, the aboveground and belowground biomass of *R. maritima* increased when salinity reached its maximum value (> 27 PSU) in the northern part of the lagoon (station 3), where this species dominates the angiosperm community. The lowest aboveground and belowground biomass of *Z. noltei* was observed when salinity was below 20 PSU in the lagoon during February, March, April, and May. Maximum aboveground biomass (786.19 ± 58.06 g DW m^{-2}) and belowground biomass (510.23 ± 62.05 g DW m^{-2}) of *R. maritima* were recorded in September at station 3, when salinity reached 27 PSU (Fig. 6C and 6D).

Discussion and Conclusion

Marine angiosperms colonise almost all intertidal and subtidal coastal environments worldwide (Green & Short, 2003). They generally attain high biomass in the environments they colonise. In El Mellah, the biomass

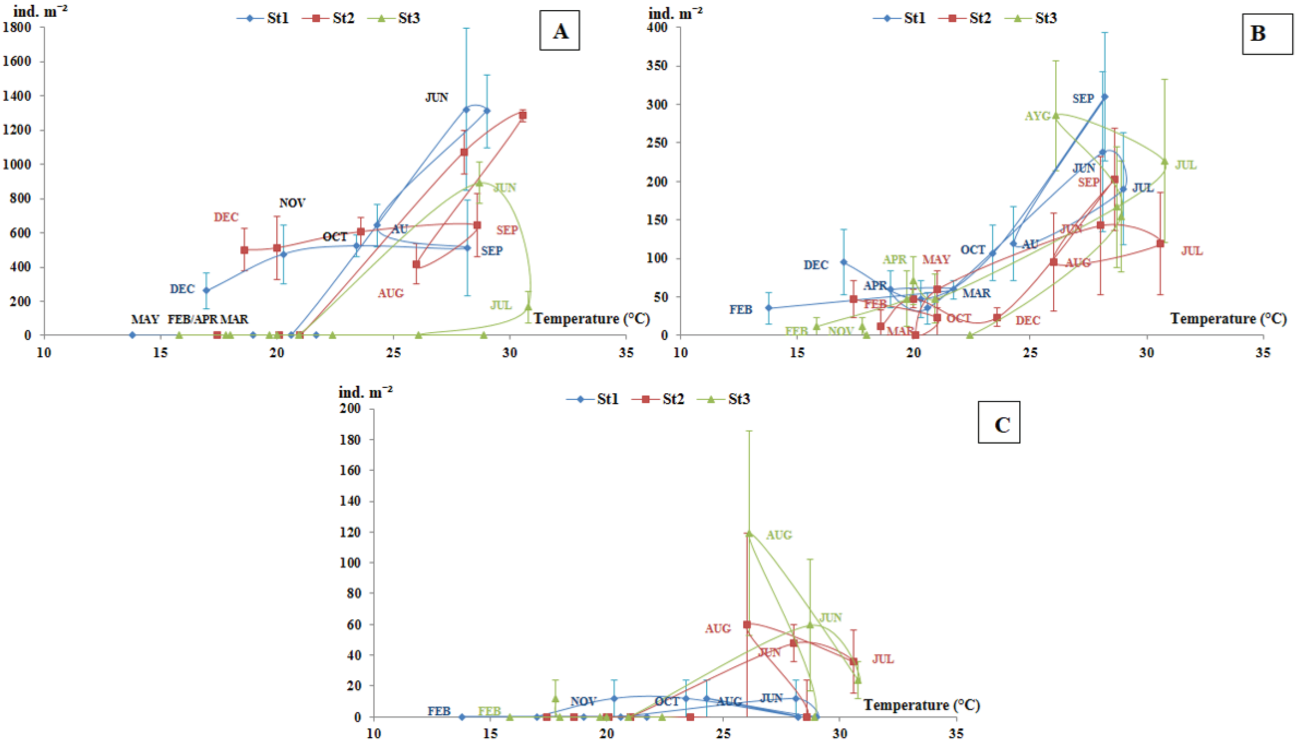

***Fig. 5:* A.** Density trajectory of *A. senhousia* (ind. m⁻²) as a function of temperature (°C). **B.** Density trajectory of *L. orbiculatus* (ind. m⁻²) as a function of temperature (°C). **C.** Density trajectory of *A. ovata* (ind. m⁻²) as a function of temperature (°C) during 2019 in the El Mellah lagoon (mean ± SEM).

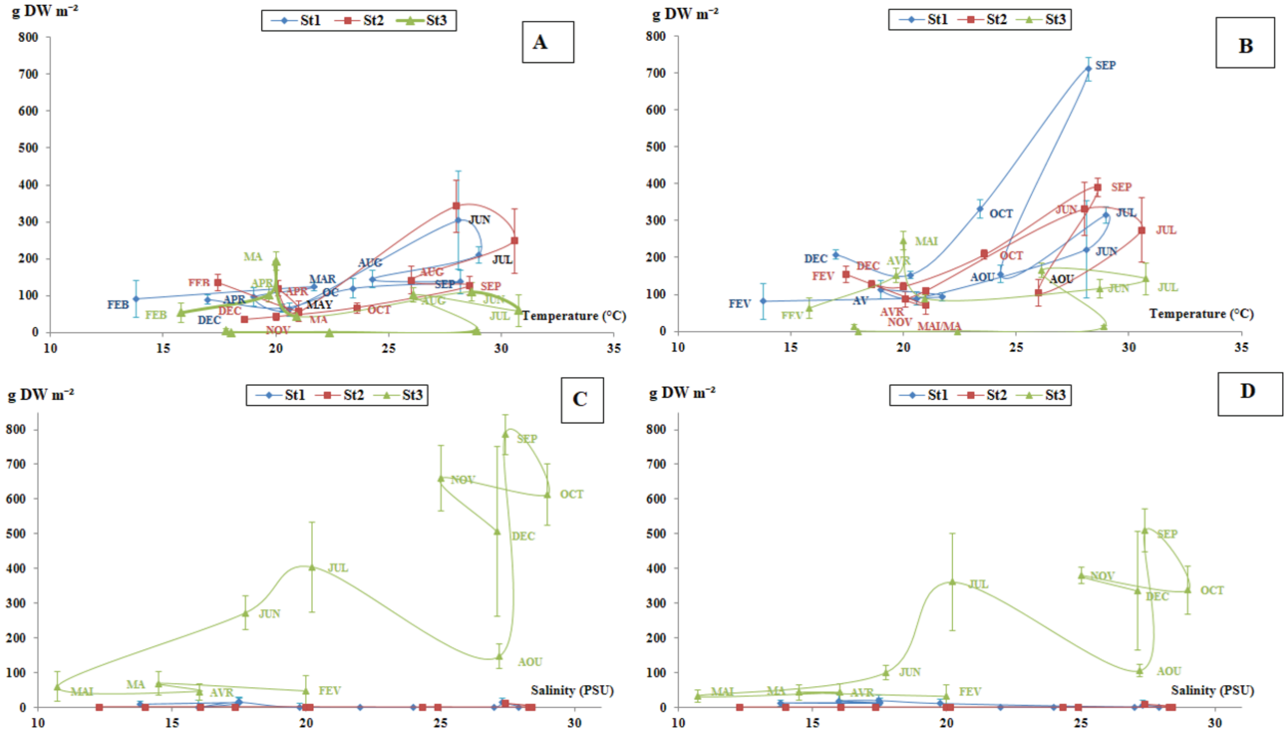

***Fig. 6:* A-B.** Aboveground and belowground biomass trajectories of *Z. noltei* (g DW m⁻²) as a function of temperature (°C) during 2019 in the El Mellah lagoon (mean ± SEM). **C-D.** Aboveground and belowground biomass trajectories of *R. maritima* (g DW m⁻²) as a function of temperature (°C) during 2019 in the El Mellah lagoon (mean ± SEM).

of this community can reach 1,313.32 ± 132.73 g DW m⁻² in August (Fig. 3A). The development of seagrass beds influences the health of cockle populations by affecting their growth, abundance, and recruitment (Do *et al*., 2011). According to Melouah (2013), El Mellah is the least diverse bivalve site among Mediterranean lagoons. This is attributed to the physicochemical characteristics of the environment: the channel connecting the lagoon to the sea is winding and narrow, leading to rapid clogging and significantly restricting water exchange between the lagoon and the adjacent coast. Consequently, the El Mellah lagoon experiences high confinement, which contributes to its low biological diversity (Draredja, 2007). We therefore suggest that this decline may also be associated with the regression of *R. maritima* in the lagoon, given its recognised ecological importance.

In line with the findings of Refes (1994), it has been reported that the primary habitat of most young clams and juvenile cockles is within seagrass beds (Melouah, 2013). The decline may also be attributed to multiple factors, including intense predation by crabs and sea bream and competition between clams and cockles for food resources (Melouah, 2013). The higher abundance of lucinids in vegetated areas compared to bare areas (Van der Geest *et al*., 2020) is linked to the crucial role of lucinid bivalves in seagrass beds. These bivalves form a mutually beneficial relationship with seagrasses, which provide a suitable habitat and oxygen through their roots. In return, members of the Lucinidae family harbour chemosynthetic symbionts that enable them to oxidise sulphide, a process essential for their survival (Van der Heide *et al*., 2012; Cardini *et al*., 2019).

During our study, we observed an increase in *L. orbiculatus* density in relation to the aboveground and belowground biomass of *Z. noltei*, but not *R. maritima* (Fig. 3D and 3E). These findings are consistent with those of Van der Geest *et al*. (2020), who identified a positive correlation solely between the aboveground biomass of *Zostera* sp. and the density of *L. orbiculatus* in Thau. In their study, no correlation was observed with hypogeal biomass. In comparison, El Mellah exhibits a higher abundance of *Z. noltei* than Thau, with an aboveground biomass of 251 ± 45.71 g DW m^{-2} and a belowground biomass of 258 ± 16.84 g DW m^{-2} (Fig. 3D and 3E). In contrast, Thau displays an aboveground biomass of 74.0 ± 12.1 g DW m^{-2} and a belowground biomass of 134.3 ± 31.2 g DW m^{-2} during late spring (Van der Geest *et al*., 2020).

The positive correlation observed between the aboveground biomass of *Z. noltei* and the density of *L. orbiculatus* in El Mellah may be explained by the fact that the strength of the tripartite mutualism depends directly on the association between aboveground seagrass biomass and oxygen release induced by root photosynthesis. In addition, the indirect relationship between aboveground seagrass biomass and the trapping of organic matter may contribute to higher sulphide production in sediments (Van der Geest *et al*., 2020). Furthermore, this observation may be linked to the substantial amounts of NH_4^+ excreted by *L. orbiculatus*. The form of nitrogen supplied by *L. orbiculatus*, which is preferred by the plant, may also contribute to the productivity of these blue carbon ecosystems (Alexandre *et al*., 2015; Cardini *et al*., 2019).

Widespread recognition of invasive species as a major driver of biodiversity loss in the Mediterranean region has increased in recent decades. These species have the capacity to disrupt various components of marine and other aquatic ecosystems (Galil, 2007; Otero *et al*., 2013). In June 2019, the Asian mussel *Arcuatula senhousia* (Benson, 1842) was documented for the first time in the El Mellah lagoon, with maximum densities of 1321 ± 475.6 ind. m^{-2} at station 1, 1071.428 ± 36 ind. m^{-2} at station 2, and 893 ± 119 ind. m^{-2} at station 3 (Fig. 5). This non-native bivalve has frequently been reported alongside eelgrass meadows (*Zostera* spp.) in regions where it has been introduced, including the Solent, San Francisco Bay, and San Diego Bay (Cohen, 2005; Kushner & Hovel, 2006; Watson *et al*., 2021).

In El Mellah, specimens of *A. senhousia* were found attached to the leaves and rhizomes of *Z. noltei* (Hamza *et al*., 2022). Our analysis at station 2 revealed a direct correlation between the density of *A. senhousia* and the biomass of *Z. noltei*, including both aboveground and belowground components (Fig. 3B and 3C). This positive relationship suggests that increasing abundance of *A. senhousia* could potentially contribute to a decline in *Zostera* spp. populations within this ecosystem. This interpretation is supported by observations from San Diego Bay, where high densities of *A. senhousia* (15,000 ind. m^{-2}) were reported to hinder the growth and expansion of *Z. marina* (Reusch & Williams, 1998).

Over the last few decades, coastal ecosystems, particularly seagrass beds, have experienced a marked global decline in condition, leading to substantial biodiversity loss (Waycott *et al*., 2009; van der Heide *et al*., 2012). Numerous studies worldwide have documented changes in the distribution and abundance of seagrasses (Young & Kirkman, 1975; Quammen & Onuf, 1993; Short & Neckles, 1999). The dynamics of benthic macroorganisms, such as macrophytes, bivalves, and macroalgae, are influenced by abiotic factors including temperature, salinity, pH, and dissolved oxygen. The effect of each factor varies among organisms (Vélez & Epifanio, 1981; Short & Neckles, 1999).

Investigations into the physicochemical characteristics of the El Mellah Lagoon revealed both temporal and spatial variability. In Mediterranean lagoons, the distribution of benthic macrophytes is primarily influenced by two key factors: salinity and the trophic state of the water column (Le Fur, 2018). In El Mellah, the observed change in seagrass bed distribution compared to previous studies is likely linked to salinity fluctuations over recent decades. Canonical correspondence analysis (CCA) at El Mellah revealed that temperature and salinity significantly influence the abundance of *Zostera noltei* and *Ruppia maritima*, respectively (Fig. 4). *Z. noltei* abundance was positively correlated with temperature, whereas *R. maritima* abundance was positively correlated with salinity (Fig. 6).

Temperature changes may also affect the distribution and abundance of seagrass beds by directly influencing flowering (De Cock, 1981; Short & Neckles, 1999) and seed germination (Harrison, 1982; Phillips *et al*., 1983; Short & Neckles, 1999). Studies have shown that seed germination of *Z. marina* and *Z. noltei* increases significantly when temperatures rise from 10° C to 30° C (Hootsmans *et al*., 1987; Short & Neckles, 1999). This may account for the observed positive correlation between *Z. noltei* biomass (both aboveground and belowground) and temperature (Fig. 6A and 6B) at *Z. noltei*-dominated stations.

Changes in environmental conditions, such as temperature, eutrophication, light availability, water movement, and basin drying, can significantly affect the biomass and productivity of *R. maritima* (Congdon & McComb, 1979; Mannino *et al*., 2015). In addition, changes in salinity can influence the photosynthetic rates of submerged angiosperms (Lirman *et al*., 2008). However, *R. maritima* is considered the submerged angiosperm with the highest known salinity tolerance (Kantrud, 1991). Seagrass germination is influenced by the interaction between salinity and temperature. In *Ruppia maritima*, for example, seeds germinate successfully at 43.4 PSU and 28° C; however, germination rates decrease at high temperatures combined with low salinity (below 3.5 PSU) (Kantrud, 1991; Tyler-Walters & d'Avack, 2015). This may explain the positive correlation between the aboveground and belowground biomass of *R. maritima* and salinity observed north of El Mellah (Fig. 6C and 6D).

On the other hand, temperature plays an important role in the regulation and reproduction of bivalves (Vélez & Epifanio, 1981). Canonical correspondence analysis (CCA) revealed that temperature significantly influences the density of *A. ovata*, *L. orbiculatus* and *A. senhousia* at El Mellah (Fig. 4). Previous studies by van der Heide *et al*. (2012) suggested that the intensity of the mutualism between seagrasses and lucinids may also be affected by temperature. We observed a significant increase in the density of *L. orbiculatus* with rising temperature at all three stations in El Mellah (Fig. 5B). We also observed a positive correlation between the aboveground and belowground biomass of *Z. noltei* and temperature (Fig. 6A and 6B). These results emphasise the role of temperature in the relationship between *L. orbiculatus* and *Z. noltei* in this ecosystem, as anaerobic decomposition of organic matter and sulphide production are closely linked to temperature (Van der Geest *et al*., 2020).

The invasive mussel *A. senhousia* demonstrates a notable capacity to tolerate diverse environmental conditions and to survive and adapt to temperatures between 1 and 31° C (Cohen, 2005; Zenetos, 2016; Hamza *et al*., 2022). According to Inoue & Yamamuro (2000), a minimum water temperature of 22.5° C is required for reproduction. In the El Mellah ecosystem, where water temperatures fluctuated between 15.7 and 30° C from June to September, exceeding the 22.5 °C threshold, conditions were favourable for the reproductive period of *A. senhousia* during this time (Hamza *et al*., 2022). Our study also identified a positive correlation between mussel density and temperature at each station (Fig. 6A), indicating the influence of temperature on the proliferation of *A. senhousia* in El Mellah.

These findings highlight the importance of investigating the factors influencing the mutualistic relationship between seagrasses and Lucinidae in the El Mellah lagoon. Such research is necessary to improve the long-term success of seagrass restoration projects and strengthen their resilience to climate change. Comprehensive studies and continuous monitoring are also essential to evaluate the impact of environmental changes on the lagoon's benthic community. These investigations will contribute to a better understanding of the effects of environmental disturbances and support the development of appropriate conservation and restoration strategies to protect ecosystem integrity.

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