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Eutrophication and hydrodynamic confinement shape establishment patterns of the invasive Atlantic blue crab in a hypersaline coastal lagoon

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ABSTRACT

Coastal lagoons are highly vulnerable to biological invasions due to their environmental heterogeneity, hydrodynamic confinement and increasing anthropogenic disturbance. Despite the rapid expansion of the invasive Atlantic blue crab (*Callinectes sapidus*) across Mediterranean transitional ecosystems, the processes shaping its establishment remain poorly understood. Here, we investigated the long-term dynamics of *C. sapidus* in the hypersaline Mar Menor coastal lagoon (SE Spain), a eutrophication-stressed system affected by recurrent dystrophic crises and mass mortality events. Using seasonal monitoring data collected between 2018 and 2024 across shallow waters, we analysed spatio-temporal patterns in occurrence, abundance and population structure in relation to hydrodynamic confinement, connectivity and eutrophication-driven disturbances. Our results revealed a progressive but markedly non-linear trajectory, with overall increases in occurrence and abundance interrupted by abrupt declines during major dystrophic events. Hydrodynamic confinement strongly shaped population dynamics: the least confined sectors consistently supported higher recruitment and abundance increases. Shallow sectors associated with a semi-natural inlet supported the strongest evidence of population establishment, being dominated by early life stages and functioning as key recruitment and settlement areas. Size-frequency distributions revealed recurrent recruitment pulses, mainly during winter, and progressive cohort transitions, indicating sustained establishment. In contrast, the most confined sectors were dominated by larger individuals and showed limited recurrent recruitment. Overall, our findings highlight the key role of shallow habitats, hydrodynamic connectivity and disturbance regimes in shaping the establishment patterns of invasive crabs in Mediterranean coastal lagoons. They further suggest that eutrophication may act as a non-linear modulator of invasion, causing short-term population declines while potentially facilitating subsequent recolonisation and demographic expansion.

1. Introduction

Coastal lagoons are among the most productive aquatic ecosystems worldwide, playing a fundamental role in energy transfer, nutrient cycling and the maintenance of ecological integrity (Newton et al., 2018; Pérez-Ruzafa et al., 2019b). These transitional environments support high biodiversity values and provide key ecosystem services, including refuge, nursery and spawning habitats for numerous aquatic organisms (Newton et al., 2018; Pérez-Ruzafa et al., 2019b), while also sustaining socio-economic activities such as fisheries, tourism and traditional coastal uses (Pérez-Ruzafa and Marcos, 2012). However, coastal lagoons are highly vulnerable to anthropogenic disturbances, including pollution (Lillebø et al., 2015), habitat degradation (Facca et al., 2020) and climate change–related stressors (Silveira et al., 2021). These pressures can increase the susceptibility of coastal lagoons to biological invasions (Lacoste et al., 2023), with the introduction and spread of Non-native Invasive Species (NIS) accelerating in some coastal regions (González-Ortegón et al., 2020). In this context, Non-native Invasive Species (NIS) have emerged as one of the main global drivers of biodiversity loss and ecosystem change (González-Ortegón et al., 2020), particularly in transitional aquatic systems, where hydrological connectivity and intense human activity increase propagule pressure through multiple introduction pathways (Pyšek et al., 2020; Lins and Rocha, 2023).

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Among aquatic NIS, decapods are considered one of the most successful invader groups worldwide due to their high ecological plasticity, broad environmental tolerance, aggressive behaviour and prolific reproductive strategies (Rato et al., 2021). Once established, invasive decapods can affect multiple levels of ecosystem organisation through predation, competition, habitat modification and trophic restructuring (Boudreau and Worm, 2012). Their ecological impacts are often amplified in transitional ecosystems, where shallow habitats and high hydrodynamic confinement can facilitate rapid population expansion and strong interactions with native biota (Bissett et al., 2025).

One of the most successful invasive decapods currently expanding worldwide is the Atlantic blue crab *Callinectes sapidus* (hereafter, the blue crab), native to the Atlantic coasts of the Americas. This species combines broad physiological tolerance with an opportunistic omnivorous diet and marked behavioural aggressiveness, traits that favour its spread across highly contrasting environmental conditions (Clavero et al., 2022; González-Ortegón et al., 2022; Herrero-Reyes et al., 2025). Since its first record in the Mediterranean Sea, *C. sapidus* has progressively expanded throughout the basin, becoming one of the main invasive decapods in Mediterranean transitional waters (Clavero et al., 2022; Mancinelli et al., 2017; Castriota et al., 2024). The species has been associated with strong ecological and socio-economic impacts, including predation on native fauna, competition with commercially important species and alterations of trophic networks (Marchessaux et al., 2023a; Gavioli et al., 2025; Vivas et al., 2025).

Although the expansion and ecological impacts of *C. sapidus* have been increasingly documented across Mediterranean transitional ecosystems (e.g. (Clavero et al., 2022; Mancinelli et al., 2017)), existing studies have primarily focused on distribution patterns, trophic ecology, interactions with fisheries or environmental drivers of abundance (Clavero et al., 2022; Herrero-Reyes et al., 2025; Gavioli et al., 2025; Cicala et al., 2025). However, spatial and temporal dynamics underlying population establishment of the blue crab remain poorly understood (Mancinelli et al., 2017). This knowledge gap is particularly relevant in coastal lagoons, where strong environmental heterogeneity, hydrodynamic confinement and disturbance-driven habitat changes can influence invasion trajectories and establishment success. In these systems, shallow habitats may play an important ecological role during establishment processes, acting simultaneously as refuge areas, recruitment zones and spatial corridors for population expansion (Herrero-Reyes et al., 2025). Consequently, population metrics derived from them may provide a particularly sensitive proxy for tracking invasion dynamics and demographic structure, potentially capturing ecological responses that are often overlooked by fishery-derived datasets, which are primarily focused on adult individuals. This role may become especially important under disturbance scenarios. For instance, in coastal lagoons affected by recurrent hypoxia and dystrophic crises, shallow habitats frequently act as ecological refuges concentrating mobile fauna during disturbance events (Zamora-Lopez et al., 2023; Guerrero-Gomez et al., 2024). Under such conditions, these habitats may not only buffer environmental stress but also facilitate the persistence, demographic consolidation and spatial expansion of opportunistic invasive species.

Within this context, the Mar Menor coastal lagoon (SE Spain) constitutes an exceptional study system to investigate invasion dynamics in transitional waters. As one of the largest hypersaline coastal lagoons in the Mediterranean basin, the Mar Menor combines strong hydrodynamic confinement, marked habitat heterogeneity and human pressures (Pérez Ruzafa et al., 2005; Pérez-Ruzafa et al., 2020). Over recent decades, the system has undergone profound ecological degradation associated with chronic eutrophication processes, leading to recurrent hypoxic crises and large-scale dystrophic events (Pérez-Ruzafa et al., 2019a; Álvarez-Rogel et al., 2020; Zamora-López et al., 2026). These disturbances have not only deeply changed macrozoobenthic and fish communities (Sala-Mirete et al., 2025; Zamora-López et al., 2025), but also altered habitat structure and ecosystem functioning, particularly in deeper areas, while shallow habitats have increasingly acted as refuge zones during disturbance events (Zamora-Lopez et al., 2023; Guerrero-Gómez et al., 2025). Such environmental instability provides a unique opportunity to examine how mobile invasive species respond to habitat change processes within a confined coastal lagoon.

Within the Mar Menor lagoon, the occurrence of *C. sapidus* was documented for the first time in 2004 (Giménez-Casalduero et al., 2016), but evidence of sustained occurrence has only been reported since 2016 onwards (Vivas et al., 2025). Previous studies conducted in the lagoon have described aspects related to the species' trophic ecology, reproductive biology and potential ecological impacts (Herrero-Reyes et al., 2025; Vivas et al., 2025). However, spatio-temporal dynamics underlying the colonisation process within the lagoon remain largely unknown, particularly regarding the use of shallow habitats under a scenario of eutrophication-driven environmental instability. These environments have been shown to be important nursery and refuge areas for juveniles and recruits of *C. sapidus*, as well as relevant feeding habitats for adults (Beck et al., 2001; Hines et al., 2007; Gavioli et al., 2026a; Ortega-Jimenez et al., 2025). Consequently, these are strategic areas which provide a sensitive ecological proxy for evaluating population expansion, habitat use and establishment patterns within the lagoon.

In this study, we investigated the colonisation and establishment trajectories of *C. sapidus* across shallow habitats of the Mar Menor coastal lagoon by using data from a long-term (2018-2024) monitoring programme. More specifically, our objectives were to: (i) assess spatial and temporal patterns underlying the colonisation process of *C. sapidus* in the lagoon; and (ii) analyse temporal changes of the population structure occupying shallow habitats. By integrating long-term biological monitoring with spatial and environmental information, this study provides new insights into how hydrodynamic confinement and eutrophication shape the establishment patterns of invasive crabs in hypersaline coastal lagoons. We hypothesised that critical eutrophication-driven disturbances, particularly hypoxic events, would negatively affect *C. sapidus* populations and potentially slow its expansion within the Mar Menor. We further expected these effects to be spatially heterogeneous, with stronger impacts in highly confined areas and more subdued responses in sectors with greater hydrodynamic renewal.

2. Methods

2.1. Study area

The Mar Menor is one of the largest hypersaline coastal lagoons in the Mediterranean basin, covering an area of approximately 136.5 km^2. It is located in southeastern Spain (western Mediterranean) and partially separated from the Mediterranean Sea by a narrow sandy barrier, which extends for about 21 km (Pérez Ruzafa et al., 2005). Water temperature in the lagoon shows strong seasonal variability, ranging from approximately 9–10 °C in winter to 30–35 °C in summer (Pérez-Ruzafa et al., 2020). Salinity values currently fluctuate between 42 and 46 PSU (Álvarez-Rogel et al., 2020), remaining consistently higher than those of the adjacent Mediterranean Sea (Vargas-Yáñez et al., 2017). The lagoon has an average depth of approximately 4.5 m and benthic habitats of the lagoon are mainly dominated by sandy and muddy substrate, with sporadic rocky areas (Pérez Ruzafa et al., 2005). Sandy bottoms, which are mainly found in shallower areas, are dominated by scattered patches of the marine phanerogam *Cymodocea nodosa*. In contrast, muddy bottoms are dominated by the macroalga *Caulerpa prolifera*, leading into monospecific or mixed meadows with *C. nodosa* (Pérez-Ruzafa et al., 2012). The lagoon is connected to the Mediterranean through three inlets that differ markedly in origin, morphology and hydrodynamic characteristics (Table 1). The northern channel, hereafter *Encañizadas inlet*, is the main natural connection with the Mediterranean Sea and it is represented by a large intertidal area dominated by extensive shallow habitats. The central connection, called *Estacio inlet*, is an artificial deep channel dredged in the 70s to allow navigation of small vessels, and it

Table 1
Physical and hydrodynamic characterization of the three inlets connecting the Mar Menor coastal lagoon with the Mediterranean Sea. Minimum and maximum values have been gathered from Pérez-Ruzafa et al. (Pérez Ruzafa et al., 2005), CARM (CARM, 2016), López-Castejón (López Castejón, 2017), Erena et al. (2020) and Gilabert et al. (2023). Some physical characteristics, such as depth, may vary temporarily.

Feature \ Inlet	Encañizadas	Estacio	Marchamalo
Origin	Natural	Artificial	Artificial
Channel	Multiple	Unique	Unique
Average length (km)	1.5	1.5	0.7
Max width (m)	110	39	25.5
Minimum - Maximum hydrodynamic flow from Mar Menor to Mediterranean (m^3/s)	≈ 0-5 (min) ≈ 15 (max)	≈ 20-50 (min) ≈ 150 (max)	≈ 0-5 (min) ≈ 40 (max)
Minimum - Maximum hydrodynamic flow from Mediterranean to Mar Menor (m^3/s)	≈ 0-5 (min) ≈ 10-15 (max)	≈ 20-50 (min) ≈ 200-220 (max)	≈ 0-5 (min) ≈ 25-30 (max)
Depth (m)	0.2-1.4	3.5-5	0.4-2
Bottom	Mix of unvegetated – vegetated cover in sandy-muddy substrates	Sandy and rocky	Sandy

constitutes the deepest and most stable inlet. Finally, the *Marchamalo inlet* is located on the southern side of the lagoon, and it is an artificial shallow channel that provides a limited water exchange with the Mediterranean Sea (García-Ayllón and Miralles, 2014; García-Oliva et al., 2018).

The Mar Menor exhibits high biological productivity and supports significant ecological and socio-economic values (León and Bellido, 2016). This importance is reflected in the wide range of protection figures assigned to the lagoon at regional, national and international levels, such as Site of Community Importance (SCI) and a Special Protection Area for Birds (SPA), both within the European Natura 2000 network, or RAMSAR wetland. Furthermore, this coastal lagoon has been the first European ecosystem to be granted legal personality (Jones, 2022). Despite this extensive legal protection, the lagoon is currently subjected to multiple anthropogenic pressures that compromise its ecological integrity. Owing to the expansion of intensive agriculture in the adjacent watershed over recent decades, increased nutrient inputs into the lagoon have triggered recurrent eutrophic episodes (Pérez-Ruzafa et al., 2019a; Álvarez-Rogel et al., 2020).

During this eutrophic scenario two major dystrophic disturbances occurred, triggering large-scale animal mass mortality events (MMEs) in the lagoon. The first event occurred in late 2019, following an episode of extreme rainfall that caused the massive input of freshwater, sediments and organic matter into the lagoon. This abrupt disturbance promoted strong water column stratification, limiting vertical mixing and causing rapid oxygen depletion in deeper waters. Under these conditions, anaerobic decomposition processes intensified, favouring the accumulation of toxic compounds, particularly sulphides (Álvarez-Rogel et al., 2020; Ruiz-Fernández et al., 2020). The resulting euxinic conditions affected more than 70% of the lagoon's surface and caused severe mortality of fish and benthic invertebrates, particularly in habitats deeper than 2 m (Guerrero-Gomez et al., 2024; Ruiz-Fernández et al., 2020). A second and more gradual episode took place in mid-2021, when new oxygen depletion events led to another faunal MMEs, although spatially more restricted than the 2019 event (Zamora-López et al., 2026). Despite differing in the immediate triggering mechanisms, this second episode similarly resulted in extensive hypoxic to anoxic conditions and caused widespread mortality across multiple animal groups (Zamora-López et al., 2025; García-Onsurbe et al., 2024). Altogether, these two dystrophic episodes represented major disturbance pulses during the study period, profoundly altering habitat availability and faunal organisation within the lagoon (Sala-Mirete et al., 2025; Zamora-López et al., 2025). Accordingly, the study period was divided into three temporal phases: (1) the Pre-MMEs period, which included surveys conducted before the mass mortality events (2018-2019); (2) the MMEs period, which encompassed the years characterised by critical dystrophic events (2020-2021); and (3) the Post-MMEs period, which included surveys conducted during a slight lagoon recovery process after MMEs (2022-2024). This temporal approach allows for evaluating the subsequent spatial and demographic dynamics of *C. sapidus* under post-MMEs environmental conditions.

2.2. Field surveys

Sampling was conducted in shallow nearshore waters of the Mar Menor lagoon (<1.5 m depth). A total of 18 sampling sectors were established along the entire perimeter of the lagoon shoreline (Fig. 1), providing representative coverage of the main shallow-water habitats. Surveyed areas included both vegetated and unvegetated substrates, including bottoms dominated by monospecific or mixed meadows of *Cymodocea nodosa* and/or *Caulerpa prolifera*, as well as sandy and muddy substrates. Sampling locations were selected to ensure consistency with previous long-term ecological monitoring studies conducted in the shallow waters of the lagoon (Zamora-Lopez et al., 2023; Guerrero-Gomez et al., 2024; Zamora-López et al., 2025; Guerrero-Gómez et al., 2025).

For analytical purposes, sampling sectors were classified according to two complementary criteria: hydrodynamic confinement and type of coastline (natural or urbanised areas) (Fig. 1). Hydrodynamic confinement refers to the average time that a given volume of water remains in a given sector within a lagoon, and it is classified here in three confinement levels following García-Oliva et al. (2018): low (Confinement 1; < 300 days), intermediate (Confinement 2; 300–350 days), and high (Confinement 3; > 350 days). In parallel, shorelines were classified according to their degree of naturality as either natural or urbanised areas (Zamora-Lopez et al., 2023; Guerrero-Gómez et al., 2025). In addition, the role of the inlets connecting the lagoon —*Encañizadas, Estacio* and *Marchamalo*— to the adjacent Mediterranean was also investigated. For this purpose, the sectors with the greatest influence from each of these inlets were identified based on their geographical proximity to them, and these were defined as the representative units for these channels in subsequent analyses.

We conducted seasonal surveys at each sampling sector over a seven-year period, from 2018 to 2024. Sampling was carried out using a beach seine net with an effective catching length of 8 m (total length 10 m; 2 mm mesh size), operated manually by two technicians positioned at each end of the net. Trawling was performed along predefined 20-m length transects, ensuring that the sampled area was fully enclosed against the shoreline. At each sector, three replicates were conducted along a 20 m stretch of shoreline. Hence, a total surface area of 480 m^2 was surveyed per sampling sector (3 replicates x 160 m^2 per replicate). However, some scheduled replicates could not be completed due to specific constraints in the field. As a result, 1494 valid sampling replicates were finally included in the analyses. This sampling procedure has been successfully applied in previous studies targeting *C. sapidus* and other swimming crabs (Castriota et al., 2024; Gavioli et al., 2026b; Bellchambers and de Lestang, 2005).

Data on occurrence and abundance of blue crabs were recorded during all surveys. Additionally, from 2021 onwards, the carapace width (CW, maximum length between lateral spines) for all blue crabs captured was recorded by using a calliper, and sex was also determined based on abdominal morphology. Measured crabs were classified into three size operational classes for subsequent analyses and interpretation, following Vivas et al. (2025): recruits (CW < 50 mm), juveniles (50 mm ≤ CW < 94 mm), and adults (CW ≥ 94 mm). The same CW thresholds were applied to both males and females.

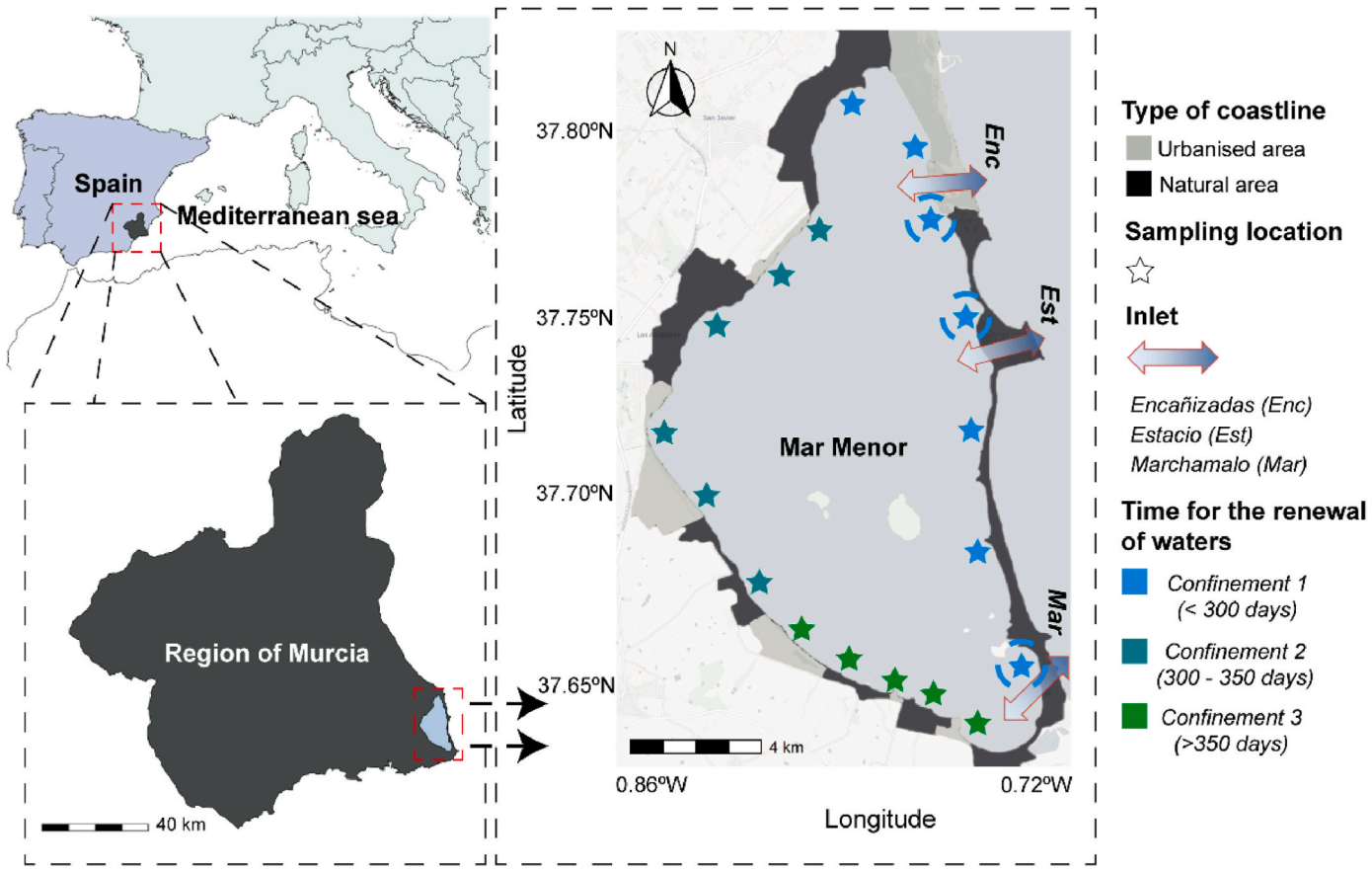


Fig. 1. Location of the Mar Menor coastal lagoon within the western Mediterranean Sea and the Region of Murcia (Spain), and spatial distribution of sampling sectors along the lagoon coastline. Coastal sectors are classified according to naturality (natural vs urbanised areas) and hydrodynamic confinement, defined by water renewal time: Confinement 1 (<300 days), Confinement 2 (300 – 350 days) and Confinement 3 (>350 days). Sampling sectors are indicated by stars. The three inlets connecting the lagoon to the Mediterranean Sea (*Encañizadas*, *Estacio* and *Marchamalo*) are depicted with bidirectional arrows, whereas the sampling sectors directly exposed to their influence are highlighted with a dotted circle.

2.3. Statistical analysis

The presence of the blue crab was recorded for each sampling replicate as a binary response (presence/absence), while abundance was measured as the number of individuals captured per replicate. These metrics were used in the statistical analyses since both represent complementary dimensions of the establishment process. For descriptive and graphical presentation, presence was expressed as "Frequency of occurrence" (FO), while abundance was standardised as "Catches Per Unit of Effort" (CPUEs), expressed as the number of individuals captured per 100 m^2 of sampled area.

Long-term colonisation trajectories were analysed using Generalised Additive Models (GAMs) implemented in the mgcv package (Wood, 2017). A hierarchical GAMs modelling framework was implemented to elucidate the long-term effects on the response variables through a sequential model-building approach. First, an intercept-only null model was compared with models including season, sampling sector, or both as parametric factors, to identify the most suitable baseline model accounting for seasonal variability and spatial differences among sectors. Second, a smooth term representing the long-term temporal trend (based on quarterly replicates throughout the study period) was added to the selected baseline model to assess whether occurrence and abundance showed directional changes over time beyond seasonal and site-related variation. Third, to test whether temporal dynamics differed among hydrodynamic contexts, factor-smooth interactions were fitted between the long-term temporal trend and hydrodynamic confinement categories, allowing the shape of the temporal trajectories to vary among confinement levels. An analogous modelling framework was applied to evaluate differences associated with type of coastline. Additionally, to assess the potential role of lagoon-sea connectivity in shaping colonisation dynamics, separate hierarchical GAMs were fitted considering only the sampling sectors associated with each of the three lagoon inlets (*Encañizadas*, *Estacio* and *Marchamalo*). Following the same procedure, an intercept-only model was first compared with models including season, inlet, or both as parametric factors. A common long-term temporal smooth was then added to the selected baseline model, followed by inlet-specific temporal smooths to assess whether temporal trajectories differed among inlets.

All long-term temporal trends were fitted using penalised cubic regression splines with a restricted basis dimension (k = 4). Given the quarterly sampling design over seven years, this restriction was intended to capture broad long-term trends rather than short-term fluctuations, while seasonal variability was explicitly accounted for whenever season was retained in the corresponding models. A binomial model family was used for occurrence models, while negative binomial was used for abundance. Model selection was based on Akaike's Information Criterion corrected for small samples (AICc), following an information-theoretic approach in which increasingly complex models were retained only when they improved model fit by more than two AICc units relative to simpler formulations (Burnham and Anderson, 2002). The suitability of the final GAM models was verified using diagnostics for basis dimension and concurvity (Table S1), the agreement between observed and model-predicted zero frequencies (Table S2) and the dispersion of Pearson residuals (Table S3). Temporal dependence was assessed separately for each sector or inlet using autocorrelation functions of seasonally averaged Pearson residuals and Ljung-Box tests (Table S4).

Following the characterisation of long-term colonisation trajectories, permutational multivariate analyses of variance (PERMANOVA) were conducted to assess whether temporal changes in blue crab occurrence and abundance were associated with the ecological periods defined by severe eutrophication and mass-mortality events (i.e., MMEs periods) (Zamora-López et al., 2025). PERMANOVAs were performed to assess whether response variables varied among MMEs periods according to hydrodynamic confinement and type of coastline. Season was included as an additional factor to account for recurrent seasonal variability, whereas year was nested within MMEs periods and sampling sector was nested within the corresponding spatial factors to control the hierarchical spatiotemporal structure of the monitoring design. This approach allowed us to determine whether blue crab metrics differed among environmental contexts and whether these relationships changed throughout successive eutrophication episodes. Secondly, to further explore spatial patterns related to lagoon–sea connectivity, additional PERMANOVAs were restricted to sectors associated with lagoon inlets. In these analyses, MMEs periods were crossed with inlet identity to assess whether temporal changes in occurrence and abundance differed among the three main exchange areas. Season was retained to account for seasonal variability, whereas year was nested within MMEs periods to control for interannual variation within each disturbance phase. All PERMANOVA analyses were performed using the 'adonis2' function from the vegan package (Oksanen et al., 2026), with statistical significance assessed using 999 permutations.

We used chlorophyll-a concentration as a complementary environmental proxy for eutrophication in the lagoon. Chlorophyll data were obtained from the Mar Menor seasonal monitoring programme of the regional environmental agency (CARM, 2024). To ensure seasonal representativeness across surveys, seasonal values were averaged using a three-month temporal window preceding each sampling season of blue crab. Chlorophyll concentrations were logarithmically transformed prior to analysis, and biological data were aggregated by year and season, with each year–season combination treated as one observation. Relationship between chlorophyll-a and both occurrence and abundance were analysed using GAMs, fitted with penalised cubic regression splines and restricted basis dimension ($k = 4$). The relationship with the abundance was modelled using a negative binomial distribution, whereas the relationship with occurrence was modelled using a quasi-binomial distribution. The same diagnostic criteria described above was applied to both models.

Size structure was analysed by examining seasonal and interannual variations in carapace width (CW) using ridgeline density plots. Density distributions were generated for each season–year combination across the entire study period and were further stratified by hydrodynamic confinement level to explore potential spatial differences. Ridgeline plots were produced using the *ggridges* extension of *ggplot2* package (Wilke, 2022).

The spatio-temporal variation in sex-ratio (males:females) was also analysed using Pearson's chi-squared test to evaluate potential changes from a 1:1 ratio in the relative contribution of males and females. All statistical analyses were conducted in the R software (R Core Team, 2025).

3. Results

The blue crab was detected in 158 of the 1494 samples taken between 2018 and 2024, both inclusive. In total, 389 individuals were recorded, with a peak of abundance in 2023, accounting for 37.79% of the total catches. Relatively high numbers were also recorded in 2019 and 2024, with 86 and 89 individuals, respectively. From 2021 onwards, 39.58% and 39.58% of the recorded total corresponded to recruits and juveniles, respectively.

3.1. Spatio-temporal dynamics of population establishment

Both frequency of occurrence (FO) and abundance (CPUEs) displayed a marked pattern during the study period, showing clear seasonal and interannual variations (Fig. 2). During the pre-MMEs period (2018-2019), the species showed low occurrence and abundance, with few detections mainly concentrated during summer and an initial CPUEs peak in 2019 (Fig. 2). After the first severe eutrophic event (autumn 2019), both crab occurrence and abundance severely depleted, remaining at low levels until a slight recovery observed during 2021. Nevertheless, both metrics decreased again after the second eutrophic event recorded in summer 2021 (Fig. 2). From 2022 onwards, occurrence and abundance progressively increased, particularly during spring and summer, with the highest CPUEs values recorded in 2023, while intermediate levels were generally observed in autumn and minimal values during winter. A similar seasonal pattern persisted in 2024, although CPUEs values were slightly lower than those recorded in the previous year (Fig. 2).

GAM analyses identified seasonality and interannual variation as significant factors shaping both occurrence and abundance patterns of *C. sapidus*. The inclusion of the temporal smooth substantially improved model performance for both occurrence and abundance, revealing an overall increase in both response variables throughout the study period (Fig. S0; Table 2). Model comparisons further indicated that hydrodynamic confinement significantly influenced abundance dynamics, with temporal trends differing among the three confinement levels, whereas no equivalent effect was detected for occurrence (Table 2; Fig. 3). In contrast, coastline naturality did not improve model performance on either metric and was therefore not included in the best-supported models (Table 2).

Temporal trend revealed distinct colonisation trajectories along the confinement gradient. In the least confined areas (Confinement 1), blue crab abundance increased steadily throughout the study period, consistent with a continuous expansion process in these areas. A similar, although more gradual, temporal increase was observed under intermediate confinement conditions. In contrast, the most confined areas (Confinement 3) showed a markedly non-linear trajectory for abundance, characterised by an initial increase, a sharp decline during the disturbance phase associated with the MMEs, and a subsequent recovery during the post-MMEs period (Fig. 3).

PERMANOVA results supported a significant relationship between abundance and the interaction of confinement level and periods associated with the MMEs (pseudo-$F = 3.18$, $Df = 4$, $p = 0.016$) (Table S5), indicating that population dynamics in the most confined areas were significantly affected by the eutrophication-driven dystrophic events (Fig. S1; Fig. S2). Despite these differences in abundance dynamics, occurrence followed a comparatively similar temporal pattern across the three levels of confinement (Fig. 3).

In the least confined areas, crab abundance was generally higher during the post-MMEs period, particularly in spring and summer. In contrast, in the most confined areas, the highest crab abundance was recorded in the pre-MMEs period, particularly in summer (Fig. S1). Overall, these patterns reflect that crab abundance was more strongly influenced by confinement, compared to occurrence. No consistent differences in occurrence or abundance patterns were detected between natural and urbanised shorelines, although a very sharp decline was observed during the summer in natural areas, coinciding with the MMEs period (Fig. S2). Finally, complementary GAMs showed a significant negative relationship between chlorophyll-a concentration and blue crab occurrence, whereas abundance showed a similar but non-significant negative tendency (Fig. S4; Table S6). Thus, higher chlorophyll-a concentrations were consistently associated with reduced occurrence.

Overall, these results indicate that the colonisation dynamics of *C. sapidus* in shallow habitats were primarily structured by temporal progression and seasonal variability, while hydrodynamic confinement

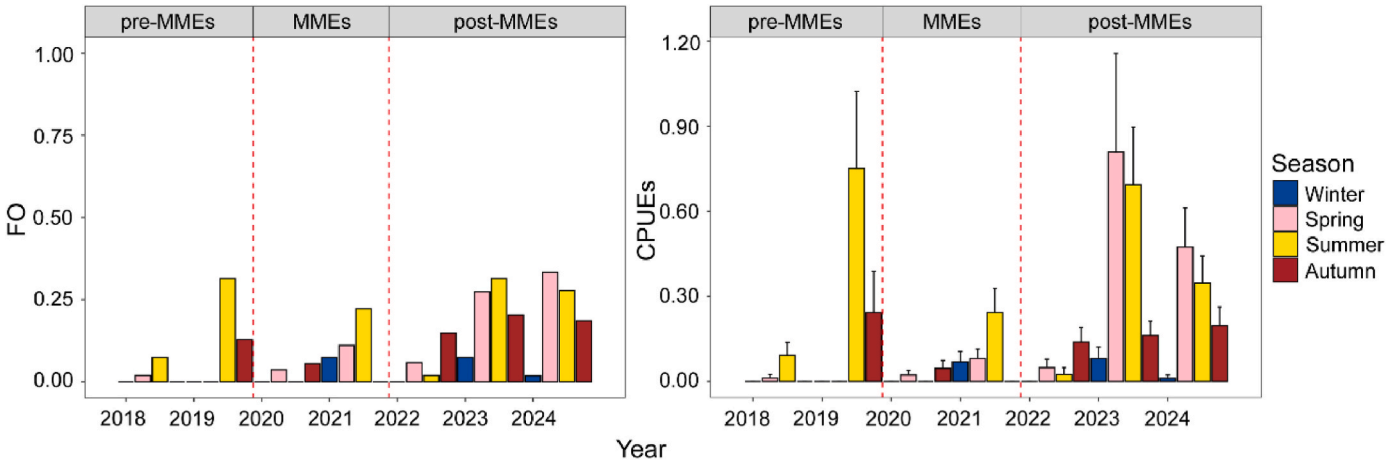


Fig. 2. Seasonal and interannual variation in Frequency of Occurrence (FO) and Catches Per Unit of Effort (CPUEs) of the Atlantic blue crab (*C. sapidus*) in Mar Menor shallow waters from 2018 to 2024. Bars represent seasonal mean values (± Standard error). The vertical dotted lines indicate the periods defined by episodes of severe eutrophication (MMEs): pre-MMEs, from 2018 to 2019 (both inclusive); MMEs, from 2020 to 2021 (both inclusive); and post-MMEs, from 2022 to 2024 (both inclusive).

Table 2
Model comparison of the Generalised Additive Models (GAMs) evaluated for alternative spatio-temporal influence hypotheses on occurrence and abundance of *C. sapidus*. Models ranged from intercept-only (Model structure = 1), season-only, sector-only and season-plus-sector formulations to models incorporating a temporal effect such as a smoothing of the time scale, either globally or varying according to the degree of hydrodynamic confinement or the type of coastline (natural versus urbanised). Timescale was structured as a three-month progression. Akaike Information Criterion (AICc) and the deviance explained are provided for each model.

Model type	Label	Model structure	Hypothesis	AICc	Deviance explained
Occurrence ~ Spatio-temporal influence	O_ M0.1	1	Null model	1010.602	0
	O_ M0.2	Season	Occurrence depends on seasonality	962.4196	5.37
	O_ M0.3	Sector	Occurrence depends on sector	926.5896	11.7
	O_ M0	Season + Sampling sector	Occurrence depends on seasonality and sector	874.0731	17.6%
	O_M1	Season + Sampling sector + s(Time scale)	Occurrence depends on seasonality, sector and time scale.	815.4232	23.6%
	O_M2_Conf	Season + Sampling sector + s(Time scale, by = Confinement)	Occurrence depends on seasonality, sector and time scale dynamics, differing among confinement levels.	816.1839	24%
	O_M3_Nat	Season + Sampling sector + s(Time scale, by = Naturality)	Occurrence depends on seasonality, sector and time scale dynamics, differing between natural and artificial coastlines	816.3835	23.9%
Abundance ~ Spatio-Temporal influence	A _M0.1	1	Null model	1513.684	3.5e-10
	A _M0.2	Season	Abundance depends on seasonality	1462.586	12.5
	A _M0.3	Sector	Abundance depends on sector	1429.575	24
	A _M0	Season + Sampling sector	Abundance depends on seasonality and sector.	1363.738	35.5%
	A _M1	Season + Sampling sector + s(Time scale)	Abundance depends on seasonality, sector and time scale.	1329.265	41%
	A _M2	Season + Sampling sector + s(Time scale, by = Confinement)	Abundance depends on seasonality, sector and time scale dynamics, differing among confinement levels.	1326.97	42.3%
	A _M3_Nat	Season + Sampling sector + s(Time scale, by = Naturality)	Abundance depends on seasonality, sector and time scale dynamics, differing between natural and artificial coastlines	1332.246	41%

emerged as the main spatial factor modulating abundance trajectories across the lagoon.

3.2. Colonisation trajectories among inlet-associated sectors

GAMs revealed significant inlet-specific effects on blue crab occurrence, showing different interannual dynamics (Fig. 4; Table 3). The sector associated with *Encañizadas* showed a moderately progressive but non-linear increasing trajectory for occurrence throughout the study period, characterised by a pronounced increase after 2021 and a stabilisation during 2023-2024. *Marchamalo* displayed a more gradual and sustained increasing trend through the study period. In contrast, a significant temporal pattern was not detected in *Estacio* inlet. Similar patterns were found for abundance, though a slightly more linear pattern was observed at *Encañizadas* (Fig. 4).

PERMANOVA analyses corroborated the spatio-temporal structure associated with inlets and found a significant relationship with the MMEs periods. The interaction between inlet and MMEs was significant for both occurrence (pseudo-F = 6.63, Df = 4, p = 0.001) and abundance (pseudo-F = 2.82, Df = 4, p = 0.023), showing that the effect of the major eutrophic disturbances differed among the inlets (Table S7). Differences among inlets became evident in summer and were particularly pronounced in the recovery period following MMEs (Fig. S3). In the *Encañizadas*-associated sector, values of occurrence and abundance increased markedly during the post-MMEs and remained consistent from spring to autumn. In contrast, a strong seasonal influence was detected under the influence of *Marchamalo* inlet, with highest values of both metrics in summer during the post-MMEs period. Meanwhile, very low values were recorded in *Estacio* inlet, limiting any inferences about its role.

Overall, these patterns not only highlight the importance of inlets in the blue crab colonisation dynamics of the Mar Menor but also suggest that colonisation dynamics were spatially heterogeneous across inlets, with the northern sector showing the most consistent expansion trajectory through the study period.

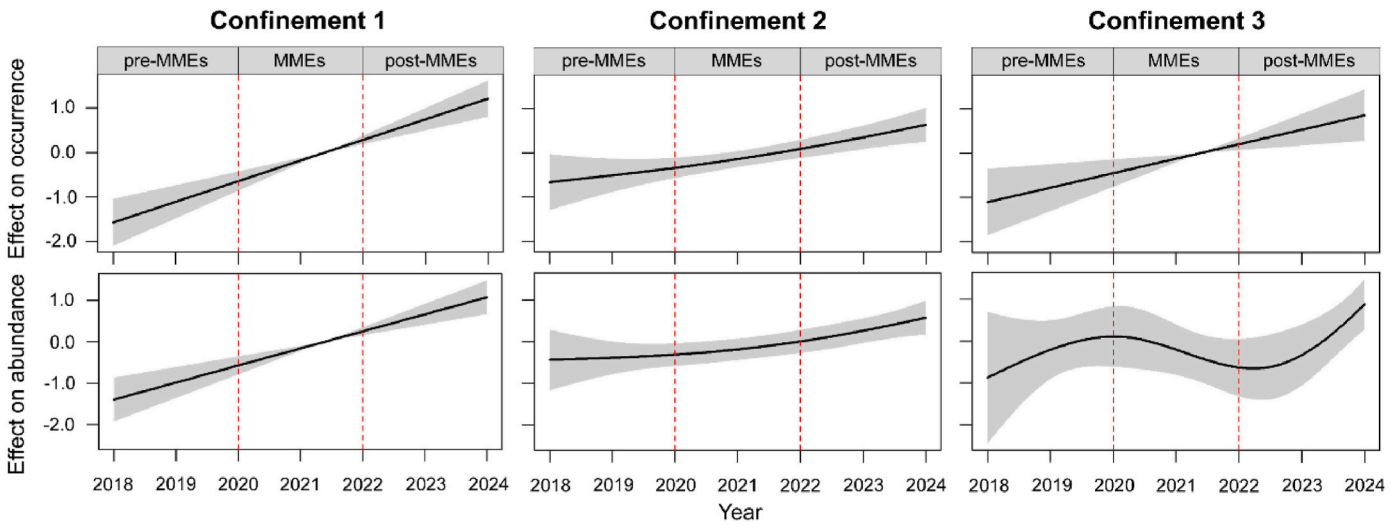


Fig. 3. Confinement-specific temporal effects on occurrence and abundance of *Callinectes sapidus*, derived from generalised additive models (GAMs). Smooth terms are represented as solid lines and shaded areas indicate 95% confidence intervals. The vertical dotted lines indicate the periods defined by episodes of severe eutrophication (MMEs): pre-MMEs, from 2018 to 2019 (both inclusive); MMEs, from 2020 to 2021 (both inclusive), and post-MMEs, from 2022 to 2024 (both inclusive).

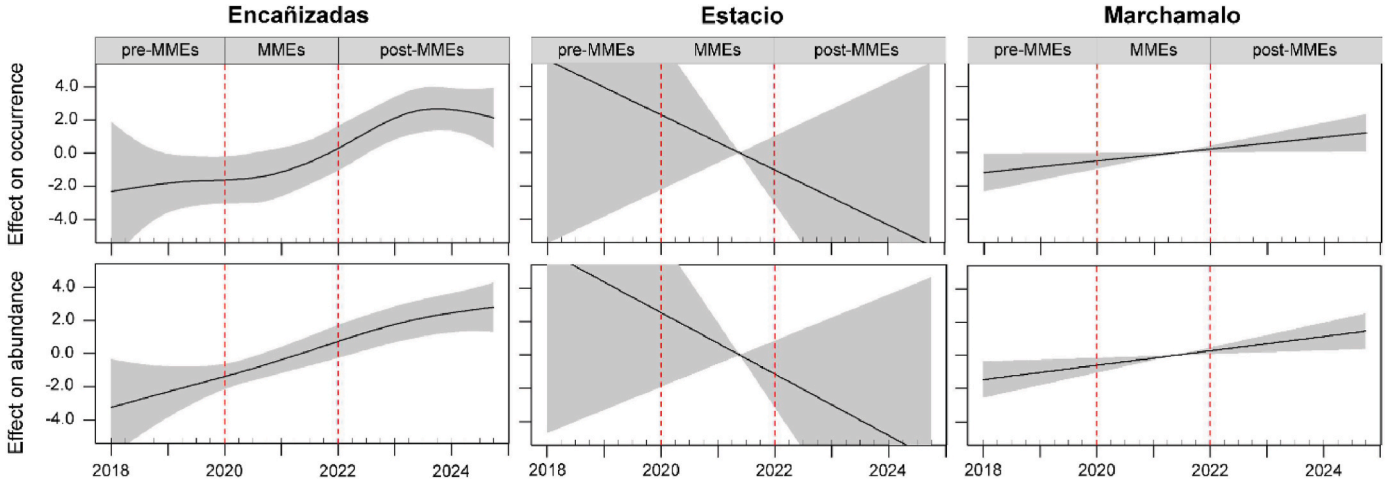


Fig. 4. Temporal effects on occurrence and abundance of *C. sapidus* in inlet-associated sectors of the Mar Menor lagoon, derived from Generalised Additive Models (GAMs). Panels represent the temporal trajectories estimated for the sampling sectors associated with the three lagoon inlets: *Encañizadas*, *Estacio* and *Marchamalo*. Smooth terms are represented as solid lines and shaded areas indicate 95% confidence intervals. The vertical dotted lines indicate the periods defined by episodes of severe eutrophication (MMEs): pre-MMEs, from 2018 to 2019 (both inclusive); MMEs, from 2020 to 2021 (both inclusive); and post-MMEs, from 2022 to 2024 (both inclusive).

3.3. Temporal variation in population structure

Size frequency distributions exhibited a marked spatio-temporal structuring across confinement levels, with pronounced seasonal shifts in carapace width (CW) and changes in the dominant size classes through the study period (Fig. 5). By assigning measured crabs to pre-established size classes, we identified clear seasonal recruitment pulses as well as interannual variability in population structure and cohort composition. This was particularly evident from 2023 onwards. Size-class structure was dominated by pre-adult individuals, with a recruit: juvenile:adult ratio of 2.66:2.55:1 (Table S8). Interannual variation was observed, with 2023 showing the highest proportion of small-size classes (3.88:4.31:1). In 2024 the size class distribution was more balanced, although it remained skewed toward non-adult individuals (1.77:1.27:1).

Seasonal differences were also evident. Winter was exclusively composed of recruits, while summer was dominated by juveniles (1.73:5.45:1). In contrast, autumn was characterised by a particular reduced contribution of juveniles (1.14:0.07:1) (Table S8).

Recruitment was mostly observed in winter in the least confined areas (Fig. 5), although an intense recruitment pulse was also recorded in 2023 under intermediate confinement conditions. In contrast, the most confined sectors were largely dominated by juveniles and adults throughout the study period, with no evident recruitment pulses.

A clearer seasonal progression in size structure became apparent in the least confined areas (Fig. 5). Winter and spring were mainly dominated by recruits and early juveniles (88.70%), whereas summer showed a predominance of juveniles and adults (78.89%) with a very limited representation of recruits. During autumn, the population structure shifted towards larger adult individuals (45.16%) together with the occurrence of a new cohort of recruits (51.61%). Less consistent demographic patterns were found during the first years of the study, although winter was already dominated by recruits.

Analyses of the sex ratio revealed a male-biased population structure

Table 3
Model comparison of the Generalised Additive Models (GAMs) evaluated for alternative inlet-specific effects hypothesis on occurrence and abundance of *C. sapidus*. Models ranged from intercept-only (Model structure = 1), season-only, inlet-only and season-plus-inlet formulations to models incorporating a temporal effect as a smooth of the time scale, either globally or varying according to inlet identity. The time scale was structured as a three-month progression. Akaike Information Criterion (AICc) and the deviance explained are shown for each model.

Model type	Label	Model structure	Hypothesis	AICc	Deviance explained (%)
Occurrence ~ Inlet influence	O_Inlet_M0.1	1	Null model	184.4474	−1.87e-13
	O_Inlet_M0.2	Season	Occurrence differs among seasonality	172.6635	9.83
	O_Inlet_M0.3	Inlet	Occurrence differs among inlets	170.3184	9.98
	O_Inlet_M0.4	Season + Inlet	Occurrence differs among seasonality and inlets	158.486	19.9
	O_Inlet_M0	Season + s(Time scale)	Occurrence differs among seasonality annuality	155.8231	20.2
	O_Inlet_M1	Season + Inlet + s(Time scale)	Occurrence differs among seasonality and the different inlets and the year	138.4567	32.0
	O_Inlet_M2	Season + Inlet + s(Time scale, by = Inlet)	Occurrence differs among seasonality and the different inlets, those last with annual differences	131.1484	38.3
Abundance ~ Inlet influence	A_Inlet_M0.1	1	Null model	293.8105	4.85e-10
	A_Inlet_M0.2	Season	Abundance differs among seasonality	278.9894	23.2
	A_Inlet_M0.3	Inlet	Abundance differs among inlets	282.6327	17.5
	A_Inlet_M0.4	Season + Inlet	Abundance differs among seasonality and inlets	264.0837	39.4
	A _Inlet_M0	Season + s(Time scale)	Abundance differs among seasonality annuality	260.5396	40.5
	A_Inlet_M1	Season + Inlet + s(Time scale)	Abundance differs among seasonality and the different inlets and the year	249.5045	52.9
	A_Inlet_M2	Season + Inlet + s(Time scale, by = Inlet)	Abundance differs among seasonality and the different inlets, those last with annual differences	237.6935	60.3

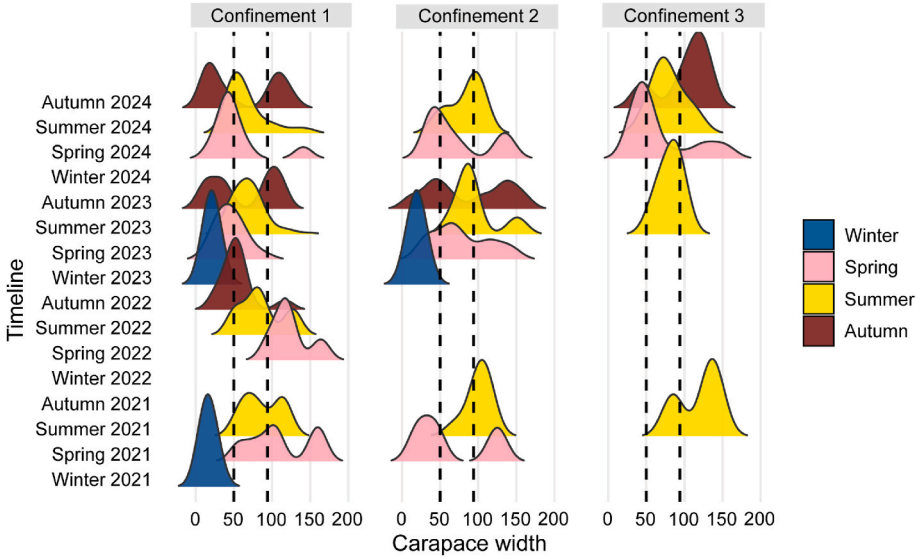


Fig. 5. Ridgeline density plots showing the seasonal variation between 2021 and 2024 in carapace width (CW, mm) of *C. sapidus* across three levels of water confinement. Colours indicate seasons (winter, spring, summer, autumn). Dashed vertical lines indicate reference size thresholds used to establish size classes: Recruits (CW < 50 mm), Juveniles (50 ≤ CW < 94 mm) and Adults (94 mm ≤ CW). Density curves represent kernel-smoothed size-frequency distributions.

(Table S8). This deviation from the theoretical equilibrium was particularly pronounced and significant during 2023 ($\chi^2 = 11.6$; Df = 1; $p < 0.001$), whereas in 2024 the bias was weaker and not consistently different from the 1:1 ratio ($\chi^2 = 0.59$; Df = 1; $p = 0.442$). Seasonal differences were also evident, with males significantly more dominant during spring ($\chi^2 = 5.84$; Df = 1; $p = 0.016$), while winter and autumn showed sex ratios closer to the equilibrium. Spatially, the least confined sectors exhibited a clear imbalance in favour of males ($\chi^2 = 9.53$; Df = 1; $p = 0.002$), whereas the most confined level displayed sex ratios close to 1:1. No significant deviation from a 1:1 sex ratio was detected among inlet-associated sectors. Overall, these results indicate that hydrodynamic confinement influenced not only cohort composition and size structure, but also the spatial organisation of both sexes within the lagoon.

4. Discussion

4.1. Colonisation dynamics in a eutrophication-disturbed coastal lagoon

We have documented the progressive expansion in the coastal lagoon and characterised the demographic structuring process under a scenario of severe environmental instability. Previous studies have investigated the population ecology of the blue crab in coastal environments across its non-native range, mostly focusing on trophic interactions, impacts on fisheries and environmental drivers of crab abundance (Gavioli et al., 2025, 2026a; Cicala et al., 2025; Mancinelli et al., 2024). However, the processes governing the spatial and temporal dynamics of colonisation within coastal lagoons remain poorly understood. In this context, our study provides a first long-term assessment of the establishment patterns of *C. sapidus* in a Mediterranean coastal lagoon.

Our results indicate that the colonisation of blue crab in Mar Menor followed a progressive but markedly non-linear trajectory. Population

dynamics in shallow habitats were strongly structured by seasonality and hydrodynamic confinement, while eutrophication-driven dystrophic events acted as major disturbance pulses altering the temporal trajectory of the invasion process. Shallow habitats emerged as key environments supporting recurrent recruitment pulses, population persistence and post-disturbance recovery of the blue crab, reinforcing their role as sensitive proxies for tracking establishment patterns in highly disturbed coastal lagoons.

The progressive increase in occurrence and abundance recorded after 2022 strongly supports that blue crab is currently undergoing an active establishment phase within the lagoon.

4.2. Hydrodynamic confinement as a colonisation filter

Hydrodynamic confinement emerged as an important spatial factor modulating the colonisation dynamics of *C. sapidus* within the lagoon. While occurrence was relatively widespread across the system, abundance and population structure varied markedly along the confinement gradient, indicating that not all sectors provide similarly suitable conditions for population growth and recruitment.

In coastal lagoons, water renewal and lagoon-sea connectivity strongly influence ecosystem functioning and environmental stability (Pérez-Ruzafa et al., 2019b). Highly confined sectors are commonly associated with greater environmental variability, lower oxygen availability and greater accumulation of organic matter and pollutants (Huang et al., 2024). Such conditions may reduce habitat quality for early life stages, which are particularly sensitive to environmental stressors such as hypoxia (Tankersley and Wieber, 2000). Our results align with these statements. Recruitment pulses were mainly concentrated in the least confined sectors, which also showed the strongest increase in abundance throughout the study period and the highest representation of recruits and juveniles. These areas are characterised by greater hydrodynamic exchange and proximity to lagoon-sea connections, both of which may favour larval supply, megalopal settlement and early juvenile survival (Etherington and Eggleston, 2000; Lipcius et al., 2007).

The strong dominance of small-size classes in the least confined sectors suggests that these habitats act as primary recruitment and retention zones within the lagoon. In contrast, highly confined sectors were largely dominated by juveniles and adults, with little evidence of recurrent recruitment pulses, suggesting either lower survival of recruits, perhaps caused by intra- and inter-specific competition, or a rapid redistribution of individuals after settlement in those sectors.

The observed differences among inlet-associated sectors are consistent with an important role of lagoon connectivity as an ecological filter shaping the colonisation process. Sampling sectors associated with *Encañizadas* exhibited the clearest positive temporal trajectory and were strongly dominated by pre-adults individuals, suggesting that this sector may represent an important entry and retention area for early life stages within the lagoon. In contrast, *Marchamalo* showed weaker temporal trends and size structures dominated by larger individuals, suggesting a secondary role in the recruitment dynamics within the lagoon. Temporal trends at Estacio were statistically indeterminate, as the low number of individuals recorded at this inlet limited the ability to identify a consistent temporal trajectory.

These contrasting patterns likely reflect differences in inlet typology and its habitat complexity. Unlike the artificial and structurally simplified channels of *Estacio* and *Marchamalo* (Table 1), *Encañizadas* constitutes a shallow semi-natural inlet characterised by extensive shallow habitats and greater structural heterogeneity (Erena et al., 2020). Such conditions are known to favour settlement success and juvenile survival in blue crab populations through increased refuge availability and feeding opportunities (Perkins-Visser et al., 1996; Moksnes and Heck Jr, 2006). Furthermore, the importance of this transitional area as part of the home range of the blue crab resident population has been recently highlighted (Herrero-Reyes et al., 2025), as well as its role as transient area or spawning corridor.

4.3. Eutrophication as a key modulator of colonisation dynamics

The MMEs recorded during the study period coincided with marked changes in the temporal trajectory of the invasion, particularly in the most confined sectors of the lagoon. Both events were accompanied by abrupt declines in blue crab abundance, consistent with negative short-term effects of severe hypoxic disturbances. Although adult blue crabs can actively avoid hypoxic areas through spatial displacement (Bell and Eggleston, 2005; Eggleston et al., 2005), the magnitude and rapid onset of the dystrophic crises in the Mar Menor may have exceeded the species' behavioural capacity to escape these disturbances. This interpretation is supported by the absence of increases in crab abundance across shallow areas during disturbance periods, suggesting that population declines may have been associated with mortality, rather than with large-scale redistribution processes. Furthermore, critical tolerance thresholds may be reduced under certain conditions of physiological stress, such as infections caused by pathogens or increased metabolic demand associated with high temperatures (Brill et al., 2015). The latter scenario is particularly relevant in the shallow waters of the lagoon's most hydrodynamically confined areas, where thermal stress may be more pronounced.

However, our results suggest that the relationship between eutrophication and invasion dynamics may not be strictly negative. Following both disturbance events, *C. sapidus* populations showed signs of gradual recovery and subsequent enhanced expansion. This pattern suggests that eutrophication may act as a non-linear factor, producing short-term negative effects through hypoxia, while potentially facilitating invasion processes over longer timescales through habitat degradation and community restructuring. Disturbed ecosystems are often more susceptible to invasions because habitat degradation reduces biotic resistance and increases ecological opportunities for generalist species (Marvier et al., 2004). In the Mar Menor, eutrophication episodes profoundly altered benthic communities and faunal organisation (Guerrero-Gomez et al., 2024; Sala-Mirete et al., 2025; Zamora-López et al., 2025), potentially increasing resource availability for opportunistic predators such as *C. sapidus*. Previous studies conducted in the lagoon have shown that blue crab trophic ecology is strongly associated with crustacean prey inhabiting shallow habitats (Vivas et al., 2025), many of which may benefit from increased organic matter and primary production under eutrophic conditions. This interpretation is partially consistent with that found by Gavioli et al. (2026a), who linked increased blue crab abundances in Adriatic coastal lagoons with enhanced primary productivity and prey availability.

The negative relationship between chlorophyll-a concentration and occurrence indicates that higher chlorophyll-a levels were consistently associated with reduced occurrence. However, given the recovery following the disturbances and the previous studies, we hypothesise that under moderate enrichment conditions, increased primary production may enhance food availability, as recently reported in (Sala-Mirete et al., 2025) and indirectly favour blue crab populations. In contrast, under severe eutrophication scenarios, ecosystem degradation —particularly hypoxia and dystrophic disturbances— likely overrides these trophic benefits and negatively affects survival and recruitment. Consequently, the effect of eutrophication on *C. sapidus* populations appears to be non-linear, potentially facilitating invasion processes under conditions of moderate nutrient enrichment, while becoming clearly detrimental under severe eutrophication.

4.4. Population structure and evidence of establishment

The observed population structure is consistent with an ongoing establishment and consolidation phase of *C. sapidus* within the lagoon. The clear predominance of recruits and juveniles over adults, together with recurrent recruitment pulses and progressive cohort transitions,

indicates sustained local recruitment and successful demographic renewal.

Seasonal patterns revealed a well-defined annual demographic cycle. Winter was dominated by recruits, indicating recent settlement events. Spring and summer were characterised by strong juvenile dominance, reflecting rapid growth of newly recruited cohorts, consistent with growth rates for early life stages under favourable environmental conditions (Cunningham and Darnell, 2015). By autumn, the population structure shifted towards larger adult individuals together with the emergence of the new cohort of recruits, suggesting overlapping generations and recurrent recruitment dynamics. These patterns are broadly consistent with recruitment and growth dynamics described for this species in other invaded coastal systems (Marchessaux et al., 2023b). Although it is possible that some large, mobile adults – those inhabiting deeper waters or actively avoiding the net – may have been under-represented, seine nets have been shown to be a suitable method for representing population structure, as they capture a wide range of sizes of swimming crabs, including individuals larger than the size at sexual maturity (Bellchambers and de Lestang, 2005).

Sex-ratio patterns also reflected spatial structuring associated with confinement. Less confined sectors showed stronger male dominance, whereas highly confined areas displayed more balanced sex ratios. Such differences may be related to sex-specific habitat use, differential mobility or reproductive behaviour, although additional studies would be necessary to clarify the mechanisms underlying these spatial patterns. Overall, the combination of recurrent recruitment and the increasing complexity in the population structure through time reinforce that *C. sapidus* is currently undergoing active population establishment and spatial consolidation across the Mar Menor coastal lagoon.

Despite the statistical support for the selected models and the significant effects identified, a considerable proportion of the variability, particularly regarding occurrence, remained unexplained. This suggests that other environmental and ecological factors not considered in the current models, such as prey availability, predation pressure, or small-scale habitat conditions, may also contribute to the observed patterns. Further research incorporating these processes could elucidate their relative influence on the settlement patterns of the blue crab in disturbed environments. Therefore, hydrodynamic confinement, connectivity between the lagoon and the sea, and eutrophication should be interpreted as important, though not exclusive, factors explaining the colonisation patterns of *Callinectes sapidus*.

5. Conclusions

The colonisation dynamics of the Atlantic blue crab in the Mar Menor coastal lagoon were strongly influenced by spatial heterogeneity, particularly by hydrodynamic confinement and lagoon-sea connectivity. Shallow, well-connected, and structurally complex sectors consistently emerge as the main recruitment and retention areas for early life stages, highlighting their importance in regulating establishment success within the lagoon. Eutrophication-driven dystrophic events could act as major non-linear modulators of the invasion process. While severe hypoxic disturbances may have caused short-term population declines, long-term habitat degradation and community-associated changes may have indirectly facilitated subsequent recolonisation and demographic expansion of the species. Our results further demonstrate that shallow habitats act as highly sensitive indicators of invasion dynamics, capturing recruitment pulses, demographic transitions and post-disturbance recovery. These critical areas provide information on blue crab population dynamics data with a more accurate ecological resolution than fishery-dependent datasets, which are typically biased towards adult and commercially targeted fractions of the population. Therefore, shallow waters represent key environments for long-term biomonitoring, allowing us to unravel establishment processes of invasive coastal species. According to our findings, an effective management of blue crab invasions in coastal lagoons requires an integrated framework that explicitly accounts for hydrodynamic confinement, lagoon-sea connectivity, habitat structure, and disturbance regimes. Specifically, monitoring and control measures should prioritise shallow areas with lower hydrodynamic confinement, as well as the connections between the lagoons and the open sea. Rapid response monitoring following major eutrophication episodes would also facilitate the early detection during the ecosystem's recovery. Although these patterns were derived from *C. sapidus*, they could also apply to other invasive crabs. Therefore, early warning and rapid-response measures focused on these variables might help to detect incipient colonisation before new populations become established. These spatially and seasonally targeted measures may be more effective than uniform control measures applied across the entire lagoon.

CRediT authorship contribution statement

Antonio A. Herrero-Reyes: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Adrián Guerrero-Gómez:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Antonio Zamora-López:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Mar Torralva:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **José M. Zamora-Marín:** Writing – review & editing, Supervision, Investigation. **Francisco J. Oliva-Paterna:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108521.

Data availability

The data that has been used is confidential.

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Supplementary material

Eutrophication and hydrodynamic confinement shape establishment patterns of the invasive Atlantic blue crab in a hypersaline coastal lagoon

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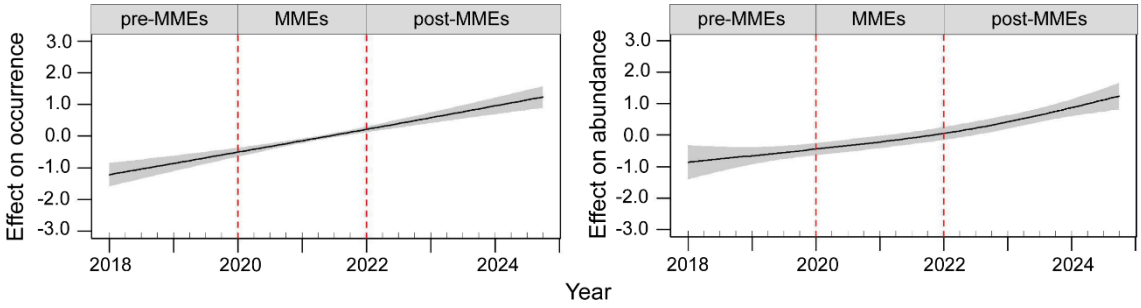


Figure S0. Temporal effects on occurrence and abundance of *C. sapidus*, derived from Generalised Additive Models (GAMs). Smooth terms are represented as solid lines and shaded areas indicate 95% confidence intervals. The vertical dotted lines mark the periods defined by episodes of severe eutrophication (MME): pre-MME, from 2018 to 2019 (both inclusive); MME, from 2020 to 2021 (both inclusive); post-MME, from 2022 to 2024 (both inclusive).

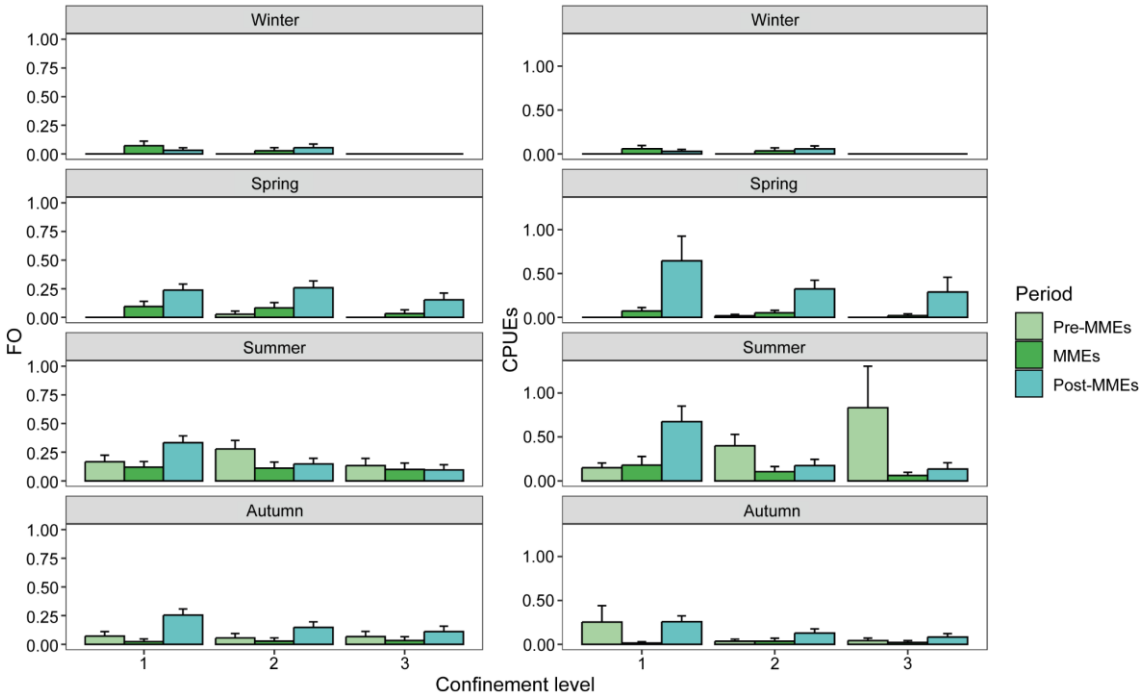


Figure S1. Seasonal variation in Frequency of Occurrence (FO) and Catches Per Unit of Effort (CPUEs) of *C. sapidus* across distinct confinement levels and MMEs periods. Bars represent mean values (± SE) for pre-MMEs period (2018-2019), MMEs period (2020-2021) and post-MMEs period (2022-2023-2024) within each confinement level.

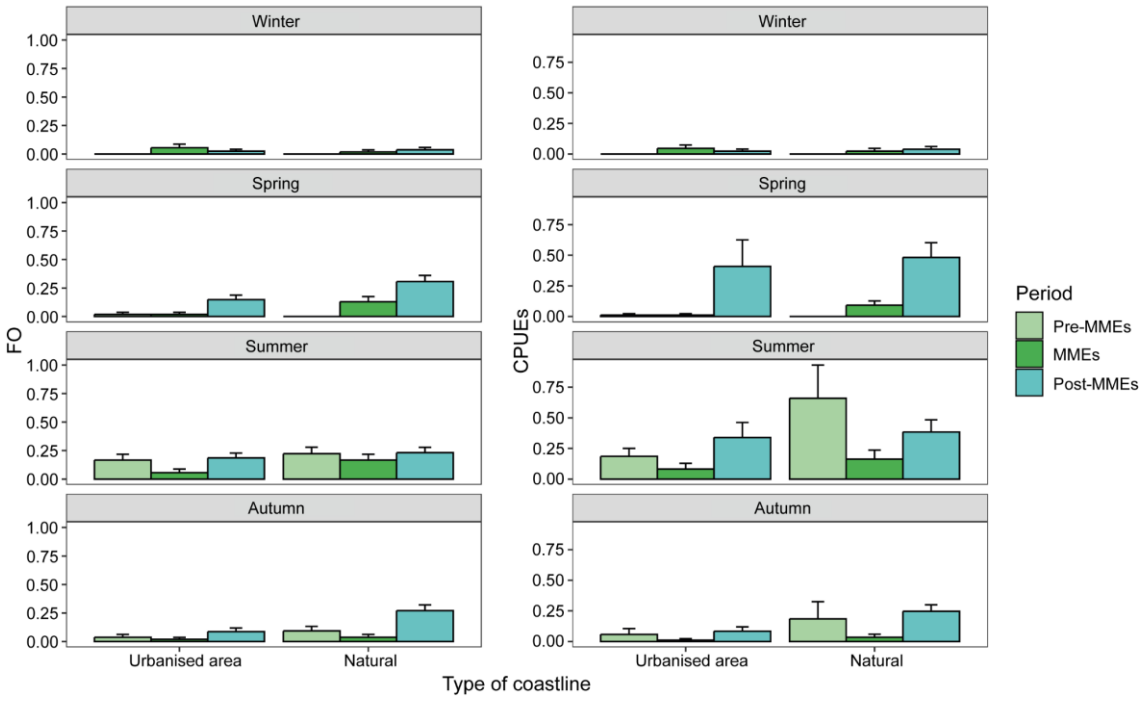


Figure S2. Seasonal variation in Frequency of Occurrence (FO) and Catches Per Unit of Effort (CPUEs) of *C. sapidus* across distinct type of coastline and MMEs periods. Bars represent mean values (± SE) for pre-MMEs period (2018-2019), MMEs period (2020-2021) and post-MMEs period (2022-2023-2024) within each coastline type.

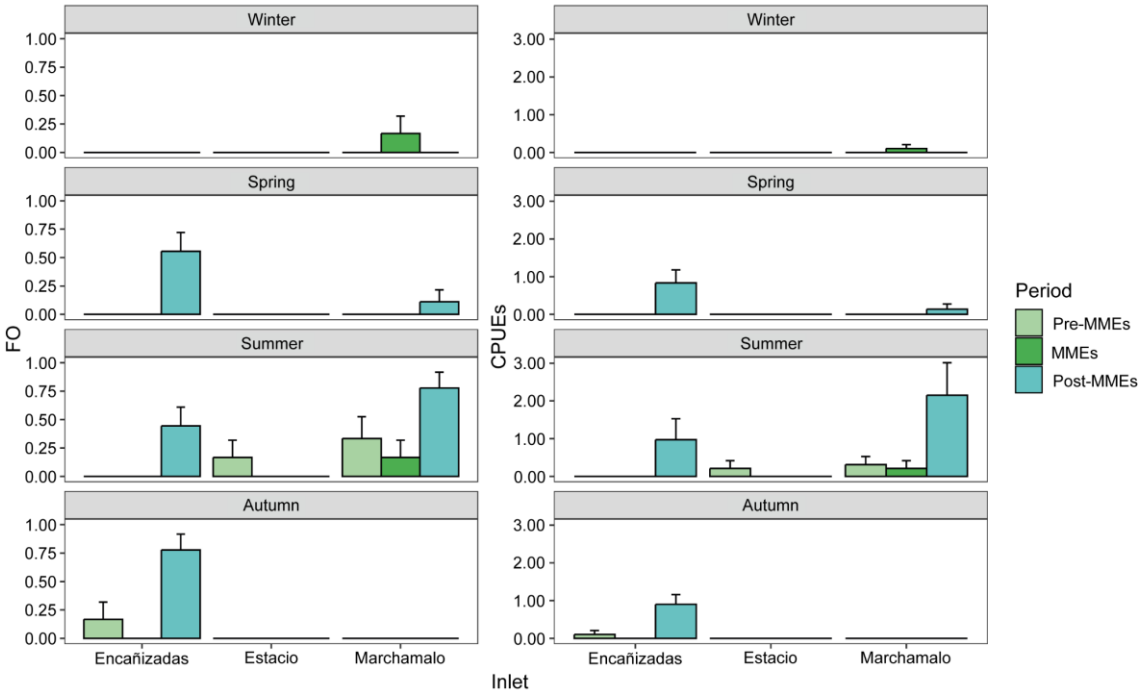


Figure S3. Seasonal variation in Frequency of Occurrence (FO) and Catches Per Unit of Effort (CPUEs) of *C. sapidus* across the different inlets and MMEs periods. Bars represent mean values (± SE) for pre-MMEs period (2018-2019), MMEs period (2020-2021) and post-MMEs period (2022-2023-2024) within each inlet-associated sector.

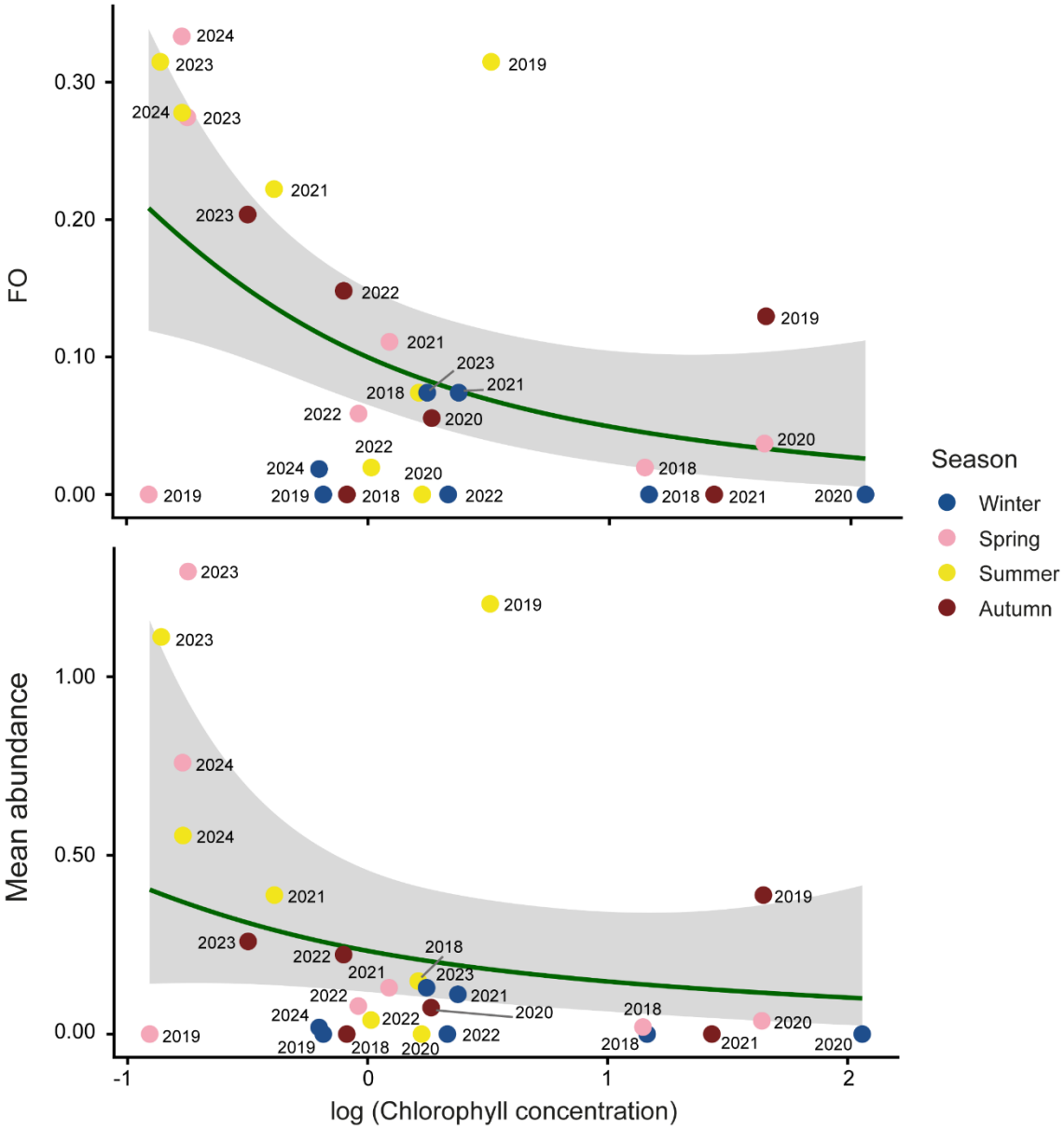


Figure S4. Relationships between log-transformed chlorophyll-a concentration and Frequency of Occurrence (FO) and mean abundance of *C. sapidus*, based on season-year aggregated observations. Solid green lines represent GAM predictions and grey bands indicate 95% confidence intervals. Points represent individual year–season combinations, with colours indicating sampling season.

Table S1. Smooth-term diagnostics for the four selected generalised additive models (GAMs): (1) occurrence throughout the lagoon; (2) abundance throughout the lagoon; (3) occurrence in the inlets; (4) abundance in the inlets. The values shown are the maximum effective basis dimension (k′), the estimated effective degrees of freedom (edf), the k-index and the associated p-value from the basis dimension test, as well as the estimated concurvity. Estimated concurvity ranges from zero to one, with values close to zero indicating limited dependence between model terms and values approaching one indicating potentially problematic concurvity.

Analysis	Smooth term	k′	edf	k-index	p-value	Estimated concurvity
General occurrence	Year	3	1.066	0.729	<0.001	0.008
General abundance	Year × Confinement 1	3	0.968	0.534	<0.001	0.003
	Year × Confinement 2	3	1.433	0.534	<0.001	0.003
	Year × Confinement 3	3	2.546	0.534	<0.001	0.006
Inlet occurrence	Year × Encañizadas	3	0.946	0.864	0.030	0.003
	Year × Estacio	3	0.723	0.864	0.030	0.006
	Year × Marchamalo	3	0.835	0.864	0.024	0.003
Inlet abundance	Year × Encañizadas	3	1.141	0.691	<0.001	0.003
	Year × Estacio	3	0.759	0.691	0.001	0.006
	Year × Marchamalo	3	0.887	0.691	<0.001	0.003

Table S2. Distribution diagnostics for the four selected generalised additive models (GAMs). The values shown are model family, number of observations (N), Pearson's dispersion, observed and expected proportions of zeros according to the model, and the ratio of observed to expected zeros. Pearson's dispersion values close to one indicate that the residual variability is, in general terms, consistent with the fitted distribution. A ratio of observed to expected zeros close to one indicates good agreement between the observed frequencies of zeros and those predicted by the model.

Analysis	Family	N	Pearson dispersion	Observed zeros	Expected zeros	Zero ratio
General occurrence	binomial	1,494	0.849	0.894	0.894	1.000
General abundance	negative binomial	1,494	1.043	0.894	0.899	0.995
Inlet occurrence	binomial	246	0.886	0.878	0.878	1.000
Inlet abundance	negative binomial	246	0.800	0.878	0.882	0.996

Table S3. Diagnosis of Pearson residuals for the four selected generalised additive models (GAMs). The values shown are the mean and standard deviation (SD) of the Pearson residuals, as well as the number and the percentage of observations with absolute Pearson residuals greater than three. Mean residuals close to zero and standard deviations close to one indicate that the residuals are, generally, centered and appropriately scaled.

Analysis	Mean	SD	Residuals with $\mid r \mid > 3$ (percentage)
General occurrence	−0.006	0.915	27 (1.81%)
General abundance	−0.009	1.013	26 (1.74%)
Inlet occurrence	−0.010	0.927	2 (0.81%)
Inlet abundance	−0.003	0.880	3 (1.22%)

Table S4. Diagnostics of residual temporal autocorrelation for the four selected generalised additive models (GAMs). The table shows the number of evaluable spatial series, the number of these that exceed the approximate 95 per cent limits for autocorrelation at lags 1 and 4 or at any lag between 1 and 8, and the number of significant Ljung-Box tests at lag 4. Autocorrelation values that remain within the approximate 95 per cent limits and non-significant Ljung-Box tests ($p > 0.05$) indicate that there is no detectable residual temporal dependence. Sector AS06 could not be assessed because no blue crabs were detected in this sector, resulting in a residual series that was not informative for the assessment of autocorrelation.

Analysis	Spatial series evaluated	Lag 1 outside limits	Lag 4 outside limits	Any lag 1–8 outside limits	Significant Ljung–Box tests
General occurrence	17 of 18 sectors	0	2	3	1
General abundance	17 of 18 sectors	0	1	1	0
Inlet occurrence	3 of 3 inlets	0	0	0	0
Inlet abundance	3 of 3 inlets	0	0	1	0

Table S5. Results of the PERMANOVA analysis on the occurrence and abundance of *Callinectes sapidus* in shallow habitats of the Mar Menor, assessing the effects of season, hydrodynamic confinement, mass mortality events (MMEs), naturality, sector, and their interactions. The values shown are degrees of freedom (Df), sums of squares (SumOfSqs), explained variance (R^2), pseudo-F statistic (F) and significance level (*p-value*). *** means p ≤ 0.001; ** means p ≤ 0.01; * means p < 0.05; · means not significant.

	Df	SumOfSqs	R^2	F	*p-value*
			Occurrence		
Season	3	4.395	0.03110	18.5828	***
Confinement	2	1.072	0.00759	6.7985	**
MME	2	3.291	0.02330	20.8765	***
Naturality	1	2.419	0.01712	30.6839	***
Sector(Confinement)	14	6.777	0.04796	6.1404	***
Year(MME)	4	4.700	0.03327	14.9071	***
Confinement × MME	4	0.682	0.00483	2.1644	·
MME × Naturality	2	0.959	0.00679	6.0843	**
Confinement × Year(MME)	8	0.718	0.00508	1.1381	·
Sector(Confinement) × MME	28	3.851	0.02726	1.7447	**
Year(MME) × Naturality	4	0.493	0.00349	1.5640	·
Sector(Confinement) × Year(MME)	56	4.330	0.03065	0.9809	·
Residual	1365	107.603	0.76157		
Total	1493	141.290	1.00000		
			Abundance		
Season	3	43.41	0.01813	10.4750	***
Confinement	2	9.41	0.00393	3.4062	*
MME	2	25.00	0.01045	9.0508	**
Naturality	1	15.36	0.00642	11.1181	**
Sector(Confinement)	14	73.90	0.03087	3.8214	***
Year(MME)	4	53.27	0.02225	9.6412	***
Confinement × MME	4	17.59	0.00735	3.1844	*
MME × Naturality	2	2.10	0.00088	0.7586	·
Confinement × Year(MME)	8	38.03	0.01589	3.4413	***
Sector(Confinement) × MME	28	71.37	0.02982	1.8454	**
Year(MME) × Naturality	4	9.85	0.00412	1.7831	·
Sector(Confinement) × Year(MME)	56	148.95	0.06223	1.9256	**
Residual	1365	1885.47	0.78768		
Total	1493	2393.71	1.00000		

Table S6. Results of the GAMs examining the relationships between log-transformed chlorophyll-a concentration and the occurrence and abundance of *C. sapidus*. Model distribution, the effective degrees of freedom (edf), the reference Degrees of Freedom (Ref.df), the statistic and the deviance explained are shown. Asterisks indicate statistical significance: *** means p ≤ 0.001; ** means p ≤ 0.01; * means p < 0.05; · means not significant.

	Distribution	edf	**REF.DF**	Statistic		*p-value*	Deviance explained
Occurrence	Quasibinomial	1.083		F = 2.517		**	26.8%
Abundance	Negative binomial	0.791		χ^2 = 2.229		·	10.2%

Table S7. PERMANOVA results on the occurrence and abundance of *Callinectes sapidus*, evaluating the effects of season, inlet identity, mass mortality events (MMEs), and their interactions, together with interannual variability. The values shown are degrees of freedom (Df), sums of squares (SumOfSqs), explained variance (R^2), pseudo-F statistic (F) and significance level (*p-value*). *** means p ≤ 0.001; ** means p ≤ 0.01; * means p < 0.05; · means not significant.

	Df	SumOfSqs	R^2	F	*p-value*
Occurrence					
Season	3	1.7454	0.06626	7.2412	***
Inlet	2	1.4230	0.05402	8.8554	***
MME	2	2.0038	0.07607	12.4694	***
Year(MME)	4	0.4859	0.01845	1.5118	·
Inlet × MME	4	2.1307	0.08089	6.6297	***
Inlet × Year(MME)	8	0.7155	0.02716	1.1131	·
Residual	222	17.8372	0.67715		
Total	245	26.3415	1.00000		
Abundance					
Season	3	24.79	0.06484	6.6704	***
Inlet	2	9.78	0.02557	3.9463	*
MME	2	22.27	0.05825	8.9888	***
Year(MME)	4	23.24	0.06079	4.6902	**
Inlet × MME	4	13.98	0.03658	2.8222	*
Inlet × Year(MME)	8	13.25	0.03467	1.3375	·
Residual	222	275.01	0.71931		
Total	245	382.33	1.00000		

Table S8. Summary table describing the Number of males (N Male) and females (N Female) captured, sex ratio (M:F), Df for the degrees of freedom, chi-square test (χ^2) for deviation from a 1:1 sex ratio and relative proportion of size classes (Recruits:Juveniles:Adults) of *Callinectes sapidus* at different spatio-temporal scales: year, season, confinement level and inlet. Asterisks indicate statistical significance: *** means p ≤ 0.001; ** means p ≤ 0.01; * means p < 0.05; · means not significant.

	N Male	N Female	Df	Sex ratio M:F	χ^2	Recruits:Juveniles:Adults
General	130	84	1	1.55:1	9.888 **	2.66:2.55:1
Year						
2023	85	46	1	1.85:1	11.600 ***	3.88:4.31:1
2024	45	38	1	1.18:1	0.590 ·	1.77:1.27:1
Season						
Winter	5	3	1	1.67:1	0.500 ·	—
Spring	66	41	1	1.61:1	5.840 *	4.46:2.77:1
Summer	51	31	1	1.65:1	4.880 *	1.73:5.45:1
Autumn	8	9	1	0.89:1	0.059 ·	1.14:0.07:1
Confinement						
1	86	50	1	1.72:1	9.530 **	5.92:5.25:1
2	30	18	1	1.67:1	3.000 ·	1.06:1.17:1
3	14	16	1	0.88:1	0.133 ·	1.38:1.62:1
Inlet						
Encañizadas	18	13	1	1.38:1	0.806 ·	27:5:1
Estacio	0	0	—	—	—	2.18:2.03:1
Marchamalo	14	13	1	1.08:1	0.037 ·	0.5:6.25:1