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Research Article

Population dynamics, habitat use and trapping efficiency of the invasive crab *Callinectes sapidus* in a Mediterranean hypersaline coastal lagoon

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Abstract

The blue crab (*Callinectes sapidus*) has rapidly invaded several coastal lagoons along the Western Mediterranean. However, there are still no comprehensive assessments of its population biology, habitat use and trapping efficiency in critical habitats. A two-year study (November 2021 – September 2023) was conducted in a natural corridor zone placed between the hypersaline Mar Menor coastal lagoon and the Mediterranean Sea. Our main goal was to assess the population structure, habitat use and trapping efficiency (four types of traps) of the blue crab. The blue crab shows a population dynamic and structure that reflects its full settlement and reproductive movements across the study area. Most captures corresponded to adults and subadults, peaking in summer, and largest crabs were recorded in November. A significant relationship was found between crab size, habitat type (*Cymodocea nodosa* meadows, *Caulerpa prolifera* meadows and bare substrates) and trap effectiveness. Trapping efficiency varied with both habitat characteristics and crab size, showing a positive relationship of juveniles and adults with muddy substrates, while water depth had a negative influence on juveniles and subadults. However, results supported great plasticity at the microhabitat scale. Fyke nets were identified as the most effective trapping method. Trap type significantly affected the number of captures as a function of crab size and sex, with subadults and females being predominantly captured in fyke nets. These findings provide novel insights into the species' population biology in invaded regions and cost-efficient control methods, enabling the design of priority management strategies in shallow waters to minimize impacts from crab invasions and to ensure ecological integrity.

Key words: *Callinectes sapidus*, control, management, population, Spain, transitional waters

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Introduction

Biological invasions are increasingly recognised as a driver of global environmental change, contributing to biodiversity loss and ecosystem alterations (Roy et al. 2023). Invasive non-native species disrupt native ecosystems (Pyšek et al. 2020), generate substantial economic costs (Zenni et al. 2021) and can even facilitate the spread of human diseases (Guang Li et al. 2019). This issue is further exacerbated in aquatic environments, which face multiple anthropogenic pressures (Borgwardt et al. 2019; Poikane et al. 2020). Moreover, the inherent challenges of detecting and monitoring aquatic invasions and their impacts further exacerbate the

vulnerability of these ecosystems (Gallardo et al. 2015; Guareschi et al. 2021). In the Mediterranean basin, this problem is pronounced, with numerous invasive species establishing populations in marine, transitional, and freshwater habitats (Muñoz-Mas and García-Berthou 2020; Zamora-Marín et al. 2023a, 2023b).

The successful establishment of invasive species, particularly within the order Decapoda, is often linked to their auto-ecology and life history traits, including high reproductive output, wide ecological tolerance, and aggressive behaviour (Brockerhoff and McLay 2011; Rato et al. 2021). Among decapods, the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896, (henceforth, the blue crab), which is considered one of the 100 worst invasive species in the Mediterranean Sea (Streftaris and Zenetos 2006), has become a prominent invader across Mediterranean estuarine and coastal ecosystems (Mancinelli et al. 2021). Native to the Atlantic coast of the Americas, from Canada to Argentina (Millikin and Williams 1984; Nehring 2011; Scalici et al. 2022), this species thrives in diverse aquatic environments ranging from marine waters to estuaries and river deltas. The invasion process of blue crab along European waters, including the Mediterranean basin, the Black Sea, and parts of the Atlantic, highlights its capacity to adapt and expand rapidly in non-native regions (Aydin 2017; González-Ortegón et al. 2022; Castriota et al. 2024).

The high ecological plasticity of the blue crab, its broad diet range, and low level of direct competition with native crustaceans have facilitated its rapid spread along the Spanish coast (González-Ortegón et al. 2022; Clavero et al. 2022). The complex life cycle of this species involves differential macrohabitat use, with estuaries and offshore waters acting as key nursery and reproductive grounds, respectively (Ogburn and Habegger 2015). This marked plasticity in habitat selection combines with a generalist feeding strategy that includes predation on both invertebrates and vertebrates, as well as detritus and carrion consumption (Mancinelli et al. 2016; Prado et al. 2022; Ortega-Jiménez et al. 2024; Vivas et al. 2025). Both traits have promoted a significant predation pressure on both commercially important and threatened species in the Spanish coast, such as the European eel *Anguilla anguilla* (Linnaeus, 1758) (Clavero et al. 2022). As a result of its significant ecological and economic impacts, the blue crab has recently been identified as one of the most problematic aquatic invasive species in the Iberian Peninsula (Oficialdegui et al. 2023).

Despite the increasing number of records documenting the ongoing expansion of blue crab in the Mediterranean basin (Mancinelli et al. 2021; Gil-Fernández et al. 2024), there are still significant knowledge gaps on its demographic and ecological characteristics in recently invaded environments (Mancinelli et al. 2017b). So far, few studies provide quantitative data on the abundance and structure of established populations (e.g. Clavero et al. 2022; Marchessaux et al. 2023a, Mancinelli et al. 2024). Furthermore, field studies assessing effectiveness of different fishing methods and mesh size have been rarely conducted (Özdemir et al. 2015; Glamuzina et al. 2021). This lack of methodological assessments hampers efforts to effectively control blue crab populations and mitigate ecological and economic impacts associated with its invasion.

In 2004 the blue crab was first documented in the Mar Menor coastal lagoon (Giménez-Casalduero et al. 2016), which is one of the largest hypersaline lagoons in the Mediterranean region. The Mar Menor supports a diverse fishery and provides critical habitats for both commercially valuable and conservation-priority species (Pérez-Ruzafa et al. 2020). Despite its legal protection under multiple international and national frameworks (e.g. Ramsar Convention and Natura 2000 network), the Mar Menor has continued to experience significant anthropogenic pressures. Recently,

it became the first European ecosystem to be recognized as a legal entity, granting its explicit rights (Gobierno de España 2022). However, these conservation efforts have not been sufficient to mitigate human-induced impacts, which have escalated in recent years, leading to severe ecological consequences (Álvarez-Rogel et al. 2020). In this context, the blue crab colonization and rapid expansion have exacerbated both ecological degradation and economic losses (Vivas et al. 2025). However, a comprehensive understanding of its population dynamics, habitat preferences, and the suitability of different control measures within this unique hypersaline lagoon remains lacking. This study aims to address these knowledge gaps by assessing key population traits and trapping effectiveness of the blue crab in hypersaline and ecologically sensitive habitats of the Mar Menor coastal lagoon. More specifically, our objectives were: (1) to evaluate spatiotemporal variation in crab abundance and population structure; (2) to determine habitat use and potential effects mediated by season, size and sex of individuals; and (3) to assess the effectiveness of four different trapping methods that could potentially be used for population control. Our findings provide critical insights for managing this invasive species and mitigating its impacts on native biota and local fisheries.

Methods

Study area

The study was conducted in a natural inlet (named "Encañizadas"; Province of Murcia, southeastern Spain) that is a functional and unique natural connection between the Mar Menor coastal lagoon and the Mediterranean Sea. The Mar Menor is one of the largest (136.5 km^2) and most iconic coastal lagoons within the Mediterranean basin (Pérez-Ruzafa et al. 2020). Its salinity and water temperature currently range around 41–45 g/l and 13–28 °C, respectively (Pérez-Ruzafa et al. 2019). The Encañizadas area is placed at the northern end of a 21-km long sand bar and is included within the Salinas y Arenales de San Pedro del Pinatar Natural Park. This area also gains protection under international agreements, such as the Convention on Wetlands of International (it is a Ramsar site), Special Protected Areas of Mediterranean Importance and Natura 2000 Network (Robledano et al. 2018). Thus, the Encañizadas area concentrates several estuarine habitats of conservation-concern and endangered species listed in European Directives and international normative (e.g. *Sterna hirundo* Linnaeus, 1758, *Sternula albifrons* (Pallas, 1764), *Apricaphanius iberus* (Valenciennes, 1846) and *Anguilla anguilla* (Linnaeus, 1758)). A traditional fishing system is still practised in the area, which has contributed to preserving the ecological uniqueness of the Encañizadas as well as enhancing its cultural and ethnographic value (Belando et al. 2014; Robledano et al. 2018).

The study area comprises 181 hectares dominated by large flooding surfaces, which are crossed by small sand islets and a network of hypersaline shallow channels with pseudo-tidal influence (Robledano et al. 2018). We divided the study area into two different sampling sectors (Fig. 1). The Mar Menor sector (MM) was in the inland section and was strongly influenced by the littoral dynamics of the lagoon itself, whereas the Mediterranean sector (MED) was mostly influenced by the Mediterranean dynamics. Sampling locations in both sectors were carefully established to ensure a balanced representation of bottom types (i.e. habitat types) characterising shallow waters across the study area. We evenly distributed trapping sites across three different habitat types: (1) vegetated bottoms dominated by *Cymodocea nodosa* (Ucria) Ascherson, 1870

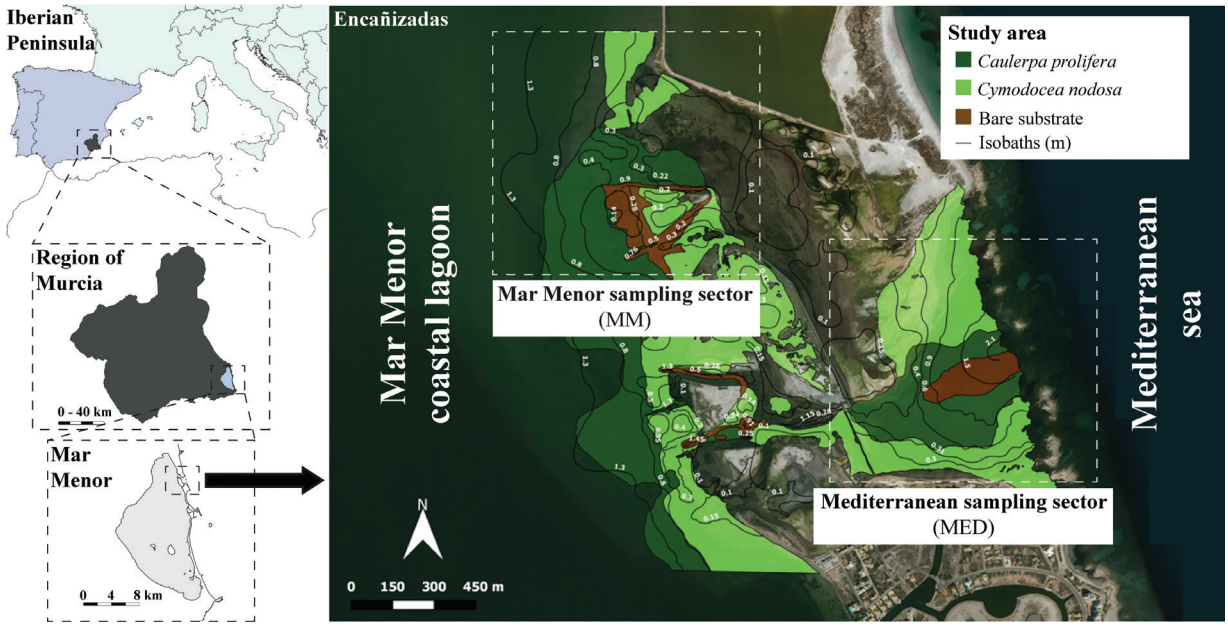


Figure 1. Geographical location of the study area in the Mar Menor coastal lagoon (southeastern Spain). Sampling sectors are framed in dashed-line squares: Mar Menor (MM) and Mediterranean (MED). Distribution of habitat types (*Caulerpa prolifera*, *Cymodocea nodosa* and bare substrate) across shallow areas and variation of water depth levels (isobaths) is also depicted. Modified from Belando et al. (2014).

meadows, (2) vegetated bottoms dominated by *Caulerpa prolifera* (Forsskål) J.V.Lamouroux, 1809 meadows, and (3) sandy muddy bottoms dominated by areas without vegetation (bare bottoms) (Fig. 1). Bottom habitat classification was defined based on the cartographic information of the submerged biocenosis in the study area (Belando et al. 2014), which was revised and updated prior to the start of the sampling.

Blue crab in the Mar Menor

The blue crab was first recorded in the Mediterranean in the 1950s, but its occurrence along the Spanish Mediterranean coast is more recent, with the species being documented in the Mar Menor for the first time in 2004 (Giménez-Casalduero et al. 2016). Following its detection in the Ebro Delta in 2012 (Castejón and Guerao 2013), the blue crab rapidly spread across various transitional coastal ecosystems along the Spanish Mediterranean coast (González-Wangüemert and Pujol 2016; Clavero et al. 2022), eventually crossing the Strait of Gibraltar (González-Ortegón et al. 2022). In southeastern Spain, the blue crab has shown a remarkable adaptability, inhabiting a wide range of salinity levels, from nearly freshwater systems to hypersaline environments (Bedmar et al. 2024), such as the Mar Menor coastal lagoon.

As mentioned above, the first recorded capture of the blue crab in the Mar Menor dates to 2004, when three specimens were collected in the Encañizadas site. However, the first evidence of a self-maintaining population in the lagoon dates from 2016 (Vivas et al. 2025), when fisheries data confirmed its establishment. Commercial landings increased up to 900 kg in 2018 (Guijarro-García et al. 2019). Given the absence of recorded individuals during the intervening years, it seems reasonable to suggest that the recent demographic explosion of the species in the Mar Menor may be attributed to multiple arrival events. Therefore, the blue crab has had a constant presence in the lagoon for over a decade, with its growing population potentially influenced by habitat changes linked to eutrophication (Guerrero-Gómez et al. 2024).

Data collection

Sampling visits were conducted every two months from November 2021 to September 2023, thus totalling 12 sampling visits and encompassing two complete annual cycles of monitoring (sampling periods). Both sectors were sampled consecutively (Fig. 1) and traps were deployed for 24 hours on average. We evaluated the crab trapping effectiveness of 4 types of traps (Fig. 2): (1) collapsible cylindrical traps (CCT), consisting of a cylindrical net with two openings placed on rigid folding rings; (2) fyke nets (FN), cone-shaped traps assembled on rigid rings (Glamuzina et al. 2021), which incorporate a 200 cm cloth wall at the entrance to guide fishes into inside; (3) flat 'bee-hive' type traps (BHT), a cylindrical plastic-net container with a single entrance on the top; (4) minnow traps (MT), small cylindrical and rigid structures with two entrances at both sides (Harrison et al. 1986). At each habitat type, we deployed three units of each type of trap with the aim of assessing trapping effectiveness in each of the sectors. Accordingly, we deployed a total of 36 traps per sampling sector during each sampling visit: 3 traps x 4 trap types x 3 habitat types. Traps were always baited with fresh chicken to promote crab attraction and to allow for an increased trapping effectiveness. During trap retrieval, we recorded the number of blue crabs captured per trap and their sex based on their apron shape (Jivoff and Hines 1998). Carapace width (hereafter CW) was measured between the two most external lateral spines by using a vernier calliper (± 1 mm). Additionally, we also recorded species-level abundance and richness data of other non-target animal taxa unintentionally captured by traps.

For each sampling event, water temperature (°C), conductivity (µS/cm), salinity (g/l), dissolved oxygen (mg/l), and oxygen saturation (%) were measured three times

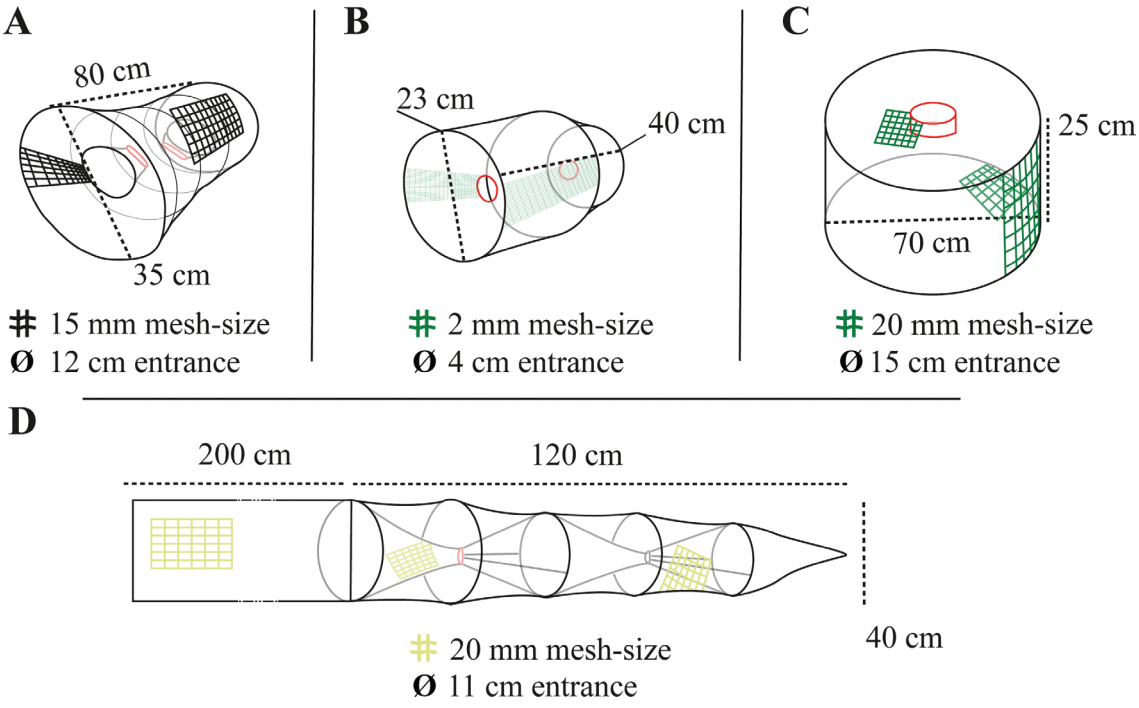


Figure 2. Illustration of the different trap types used for blue crab sampling across shallow waters of the Mar Menor coastal lagoon (SE Spain). **A.** Collapsible cylindrical trap (CCT); **B.** Minnow trap (MT); **C.** Flat 'bee-hive' type trap (BHT); **D.** Fyke net (FN). Length, height, mesh size and entrance diameter (Ø) of each trap type is indicated. Trap entrances are marked in red.

at each habitat type per sampling sector by using a multiparameter WTW® Multi340i or HACH® HQ30d. Submerged habitat variables were recorded at trap level. Using the trap position as the centre of a square of 10 m^2 surface area, six variables related to microhabitat structure and presence of refuge for fauna were considered: submerged vegetation cover per m^2 (%), water depth (cm), percentage of substrate size categories, according to Bain and Stevenson (1999): mud, sand, gravel, pebble and boulder. Submerged vegetation variables were visually assessed always by the same observers. Water depth was manually recorded by using a 1-cm marked portable stick.

Data analysis

The relative abundance of the blue crab was computed as capture per unit effort (hereafter CPUE), which was calculated as the number of individuals captured per trap per 24 hours. The maturity stage of crabs was classified in age classes (i.e. juveniles, subadults and adults) based on CW size, since this measurement has been successfully proven as a proxy of crab maturity (Fisher 1999). Following Ju et al. (2003), size-based age classes were established into three main categories: juveniles (CW < 80 mm), subadults (80 mm ≤ CW < 120 mm) and adults (CW ≥ 120 mm).

A model calibration was performed to determine whether habitat (i.e. habitat type) and trapping effectiveness are both or separately linked with the size (i.e. size classes), or with the sex of the blue crabs. Furthermore, sex was modelled according to its potential relationship with sampling sector and trapping effectiveness. Four hypotheses were tested for every model to assess the influence of size or sex with these factors (Suppl. material 1: table S1). Log-Gaussian Generalized Additive Models (GAMs) were performed using the "mgvc" package (Wood 2011) for modelling effects from habitat and trapping effectiveness, using sampling period, month, type of trap, habitat type, dissolved oxygen, water temperature, salinity, water depth, mud cover and the cover of the meadow as predictive variables. For the sampling sector and trapping effectiveness, we considered as predictor variables the "sampling period" (e.g. 2021/22), "month", "trap type", "sampling sector" and "habitat type". Hence, response variables were CPUE based on the age classes and sex. Model ranking and selection were based on the estimate of the standard correction to Akaike's Information Criterion (AICc), to reduce biases caused by small sample size (Miller et al. 2023). When model comparisons yielded an inadequate support for the identification of the best model (AICc difference lower than 2), then the most parsimonious formulation (i.e. the model retaining less interactions) was selected (Cavanaugh and Neath 2019). Additionally, the deviance explained was calculated as a measure of model fitting. A stratified pairwise sampling (Tukey adjustment) from package "emmeans" (Lenth 2020) was also carried out to assess the relationship between the factors. All statistical analyses were conducted through the R free software (R Core Team 2023).

Results

Environmental variables

Our environmental assessment reflected the hypersaline nature of the study area (Table 1), with an average salinity of 42.3 g/l in the sector with greater lagoon influence (MM), which was slightly higher than the recorded in the more

Table 1. Summary table of the environmental characteristics and the microhabitat structure metrics. Data for the two sampling periods and the whole study period are presented in different columns, providing mean values ± standard error separately for the two sampling sectors: Mar Menor (MM) and Mediterranean (MED).

Environmental variables	Nov 2021 – Sept 2022		Nov2022 – Sept 2023		Nov 2021 – Sept 2023	
	MM	MED	MM	MED	MM	MED
Water temperature (°C)	21.2 ± 0.7	20.2 ± 1.1	21.6 ± 0.7	22.7 ± 0.6	21.4 ± 0.5	22.7 ± 0.5
Conductivity (µS/cm)	63.0 ± 0.2	51.2 ± 2.2	63.1 ± 0.2	57.5 ± 0.3	63.0 ± 0.1	57.6 ± 0.2
Salinity (g/l)	42.2 ± 0.2	34.1 ± 1.4	42.4 ± 0.3	38.2 ± 0.1	42.3 ± 0.1	38.3 ± 0.1
Dissolved oxygen (mg/l)	10.4 ± 0.5	10.4 ± 1.6	9.3 ± 0.3	9.2 ± 0.3	9.9 ± 0.3	10.4 ± 0.8
Oxygen saturation (%)	115.4 ± 5.6	102.2 ± 5.4	106.0 ± 4.0	104.8 ± 3.8	111.2 ± 3.6	109.6 ± 2.7
Water depth (cm)	44 ± 0	54.4 ± 1.7	43.6 ± 1.0	64.3 ± 1.5	42.3 ± 0.7	59.5 ± 1.2
Mud substrate (%)	37.9 ± 1.5	17.9 ± 1.0	26.9 ± 1.5	11.8 ± 0.7	32.3 ± 1.1	14.9 ± 0.7
Sand substrate (%)	59.0 ± 1.3	76.6 ± 1.7	68.8 ± 1.4	88.0 ± 0.7	64.0 ± 1.0	82.4 ± 1.0
Gravel substrate (%)	3.1 ± 0.4	0.7 ± 0.2	3.8 ± 0.4	0.1 ± 0.1	3.4 ± 0.3	0.4 ± 0.1
Pebble and boulder (%)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Submerged vegetation cover (%) (*C. prolifera*)	95 ± 1.2	97.1 ± 0.7	97.3 ± 0.8	72.8 ± 3.0	96.1 ± 0.7	86.1 ± 1.8
Submerged vegetation cover (%) (*C. nodosa*)	74.6 ± 3.1	78.7 ± 2.2	79.7 ± 2.3	99.2 ± 0.3	77.2 ± 1.9	89.6 ± 1.4
Submerged vegetation cover (%) (Bare)	2.6 ± 0.6	1.5 ± 0.4	1.1 ± 0.2	0.3 ± 0.2	1.9 ± 0.3	0.9 ± 0.2

Mediterranean-influenced sector (MED). Water temperature remained homogeneous across both sectors, showing similar mean values and a temporal range between a minimum of 12.5 ± 0.1 °C (MM, January 2022) and a maximum of 35.2 °C ± 0.1 °C (MM, July 2022). The shallow nature and dominance of fine-grained substrate of the study area are also reflected in habitat structure parameters, with mean depths not exceeding 64.3 ± 1.5 cm and substrates predominantly composed of muds and sands (Table 1).

Abundance and population structure

A total of 1981 specimens from 31 different taxa of macrofauna were caught over the study period (November 2021 – September 2023). From the total captures, 538 individuals corresponded to *C. sapidus* being the second dominant species behind the native shrimp *Palaemon elegans* (819 captures) (Suppl. material 1: table S2). Our results revealed the highest abundance of *Callinectes sapidus* during the warmer months in both sampling sectors (Suppl. material 1: table S4), with July and September totalling 25.6% and 39.3% of total catches (juveniles included), respectively. This temporal pattern was particularly pronounced in the MED sector, which exhibited a significantly lower number of captures as compared to the MM sector (75.9% of total captures in MM) (Figs 3, 4). Moreover, although the sex-ratio was dominated by males in most of the sampling events (Fig. 3), the MED sector recorded higher female catches within the study area, particularly in warmer months. However, this sector showed either negligible or no captures during the remaining sampling months (November, January, March, and May). Furthermore, ovigerous females (n = 4) were only captured in the MED sampling sector.

Out of the total captures, 400 individuals were males and 135 were females, with 3 undetermined specimens, resulting in a sex ratio of 2.96:1 (males:females). However, markedly evident differences were observed between sampling sectors (Fig. 4), with sex ratios of 4.41:1 in MM and 1.15:1 in MED. The target population was dominated by subadults (49.8% of total catches) and adults (37.6%) specimens, whereas juveniles comprised a lower portion of the population (12.6%). Months

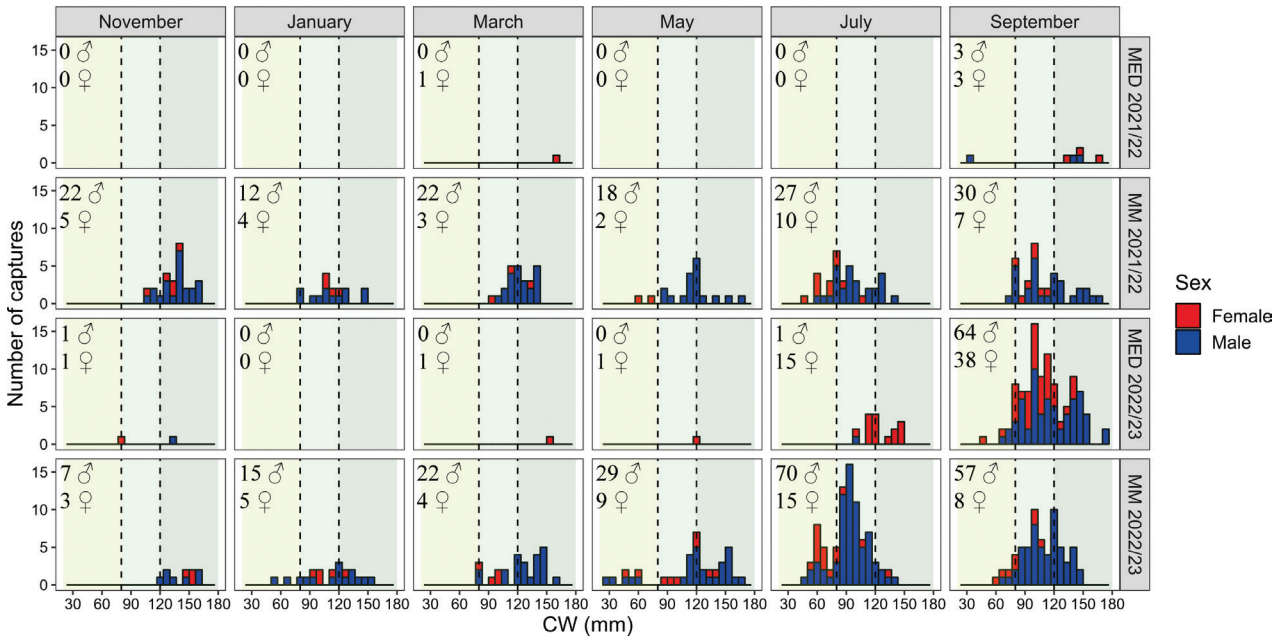


Figure 3. Spatiotemporal variation in the number of captures of blue crabs in Encañizadas according to sex. Crab sampling was conducted throughout two complete sampling periods (2021/22 and 2022/23). Columns correspond to months whereby crab samplings were carried out, whereas rows represent captures for each sampling period in each of the two sampling sectors: Mar Menor (MM) and Mediterranean (MED). The dashed line distinguishes the three size classes (juveniles, subadults and adults).

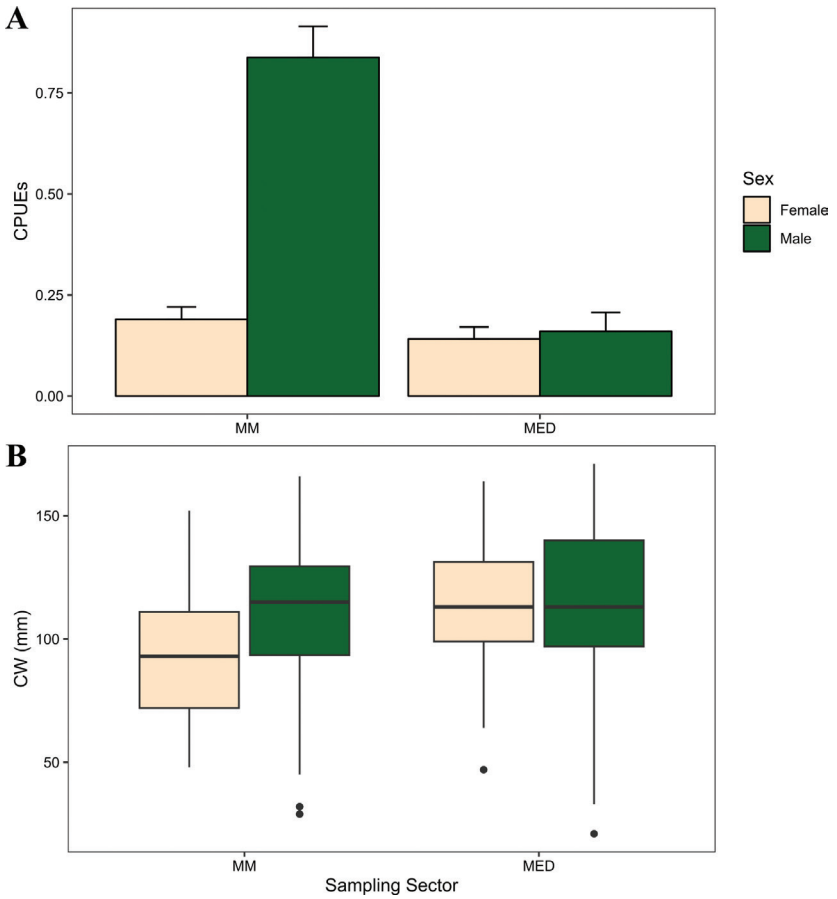


Figure 4. Spatial differences between study sectors in CPUEs (**A**) and CW (**B**) values of blue crabs according to sex in the Mar Menor coastal lagoon. Values of captures per unit effort (CPUEs) and carapace width (CW) are shown as mean ± standard error. Both spatial approaches address the two study sectors separately: Mediterranean (MED) and Mar Menor (MM).

with highest activity for *C. sapidus* (May to September) showed the greatest CW size range in the studied population, particularly in the MM sector. In the MED sector, only the sampling conducted at the end of the warm periods displayed a wide size range (Fig. 3; mean CW: 111.6 ± 2.6 mm), with a high abundance of adults and subadults. During the colder months, the size distribution was dominated by larger individuals, with the highest CW recorded in November in the MM sector (mean CW: 136.3 ± 2.7 mm). The largest individuals recorded corresponded to two males (CW: 171 mm; both captured in MED during September 2023), while the smallest individual was also a male (CW: 21 mm) recorded in MED during September 2023.

The capture of different size classes was influenced by habitat type and trapping effectiveness, a pattern reflected from the dependence observed in the best fitted model (Suppl. material 1: table S3). Most of the blue crabs were caught in the MM sector, with only 130 individuals from the MED sector. In addition, there were no catches in the MED sector in five sampling months. Both results showed the strong influence of the study sector (lagoon or marine) on both crab presence and abundance. In fact, GAM model fitting analyses indicated that the best explanatory model for catches considers a significant relationship between the sampling sector and the sex of captured individuals (Suppl. material 1: table S3).

The pairwise test showed that there were not significant differences in the abundance of males and females in the MED sector, while the abundance of males in MM sector was significantly higher than females. The test also demonstrated that blue crab females showed a significant preference for the MED sector, whereas males demonstrated a clear selection for the MM sector (Suppl. material 1: fig. S1). According to the coefficients of the best model (Suppl. material 1: table S3), major differences in sex-ratio were found between study sectors.

Habitat use

Based on the low number of captures obtained from the MED sector, analyses of habitat use and trapping effectiveness were conducted exclusively considering captures from the MM sector, which provides a reliable representation of the blue crab population in the study area.

The habitat type was found to exert an influence on the catches of blue crabs (Fig. 5), particularly significant in the case of subadults and adults. The habitat type with the highest crab abundance was found to be bare substrate, showing this one as the most suitable for trapping the species. In contrast, vegetated habitat dominated by *C. prolifera* showed the lowest abundance (Fig. 5). The best fitted GAM model revealed that selection of habitat type by blue crabs relied on size (Figs 5, 6, Suppl. material 1: table S3). The influence of bare substrate was more significant for the subadult size class, but weaker for adults, which also showed a higher selection for vegetated habitats dominated by *C. nodosa*. Juveniles showed a significant preference for bare substrate, but just with respect to *C. prolifera* meadows (Suppl. material 1: fig. S2).

In addition, the results showed a significant influence of the microhabitat structure on the abundance of the different size classes. According to the model smoothers (Fig. 6), an effect of prevailing substrate was found, with a significant effect of muds, mainly on juvenile and adult abundance. Water depth also showed a significant effect on size class abundance, with lower juvenile and subadult abundance in deeper waters, this relationship being particularly more marked for juveniles (Fig. 6).

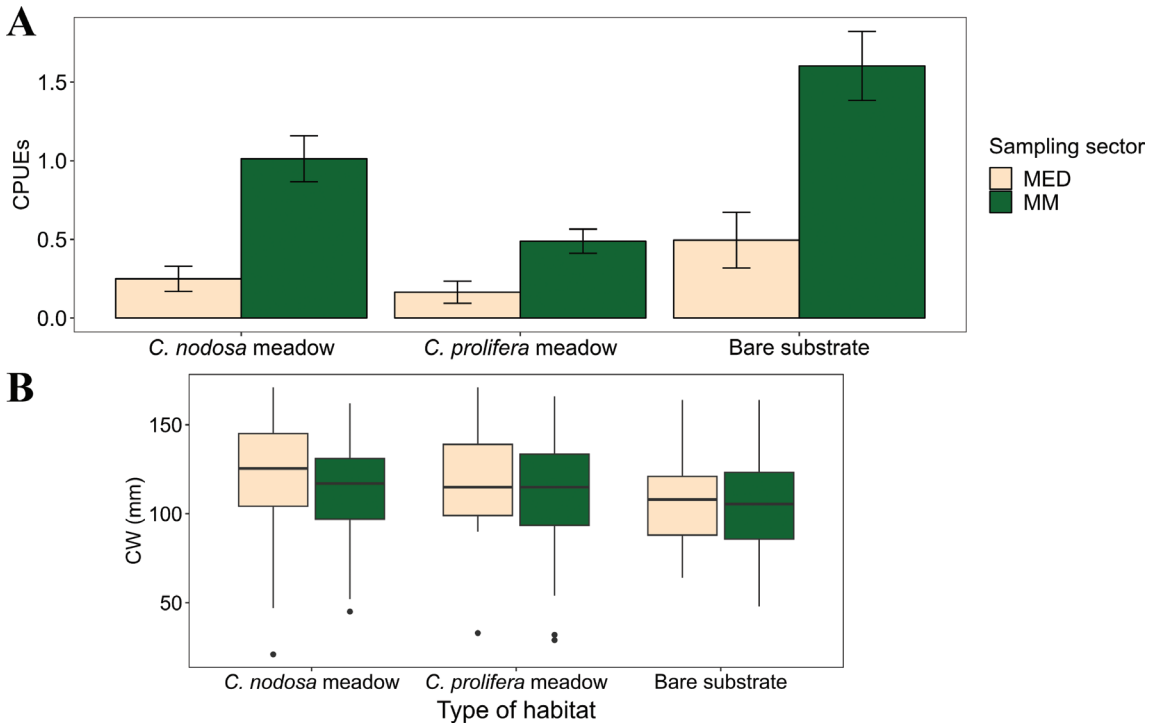


Figure 5. Spatial differences in CPUEs (**A**) and CW (**B**) values of blue crabs according to habitat. Values of capture per unit effort (CPUEs) and carapace width (CW) are shown as the mean ± SE. Both spatial approaches address the two study sectors separately: Mediterranean (MED) and Mar Menor (MM). The three types of bottom habitat are shown: *Cymodocea nodosa* meadows, *Caulerpa prolifera* meadows and bare substrate.

A pairwise test was carried out between habitat type and crab size. Adults did not show differences between *C. nodosa* meadows and bare substrate, but both habitat types were prevailing on *C. prolifera* meadows (Suppl. material 1: fig. S2). Both subadults and juveniles showed clear habitat preferences for bare substrate bottoms as when compared to vegetated ones, although in the case of juveniles, only with respect to *C. prolifera* (Suppl. material 1: fig. S2).

Trapping effectiveness

During the study period, we set a total of 216 traps of each type, including FN, BHT, MT and CCT. Trapping effectiveness of these four trap types was assessed by comparing CPUEs and size of individuals (CW) caught by each method (Table 2, Fig. 7). Regarding to relative abundance, FN and CCT were significantly more effective than BHT and MT. However, there were significant size-mediated differences, with FN traps being more effective for a broader size range (Table 2, Fig. 7). The MT exclusively captured juveniles, although their effectiveness in terms of CPUEs was very low.

Table 2. Summary table showing number of captures, CPUEs and CW (mm) by trap and size class. Captures per unit effort (CPUEs) and carapace width (CW) are shown as mean ± standard error. Minimum and maximum values of CW according to trap type are also shown. Total captures of juveniles, subadults and adults are included in brackets.

Type of trap	N Juvenile	N Subadult	N Adult	N Total	CPUEs	CW	CW (min.)	CW (max.)
FN	34	154	102	290	1.41 ± 0.17	109.4 ± 1.5	32	171
BHT	3	16	10	29	0.15 ± 0.03	110.5 ± 4.9	62	166
MT	16	0	0	16	0.08 ± 0.03	54.3 ± 2.6	21	64
CCT	15	98	90	203	1.01 ± 0.14	115.5 ± 1.7	29	162

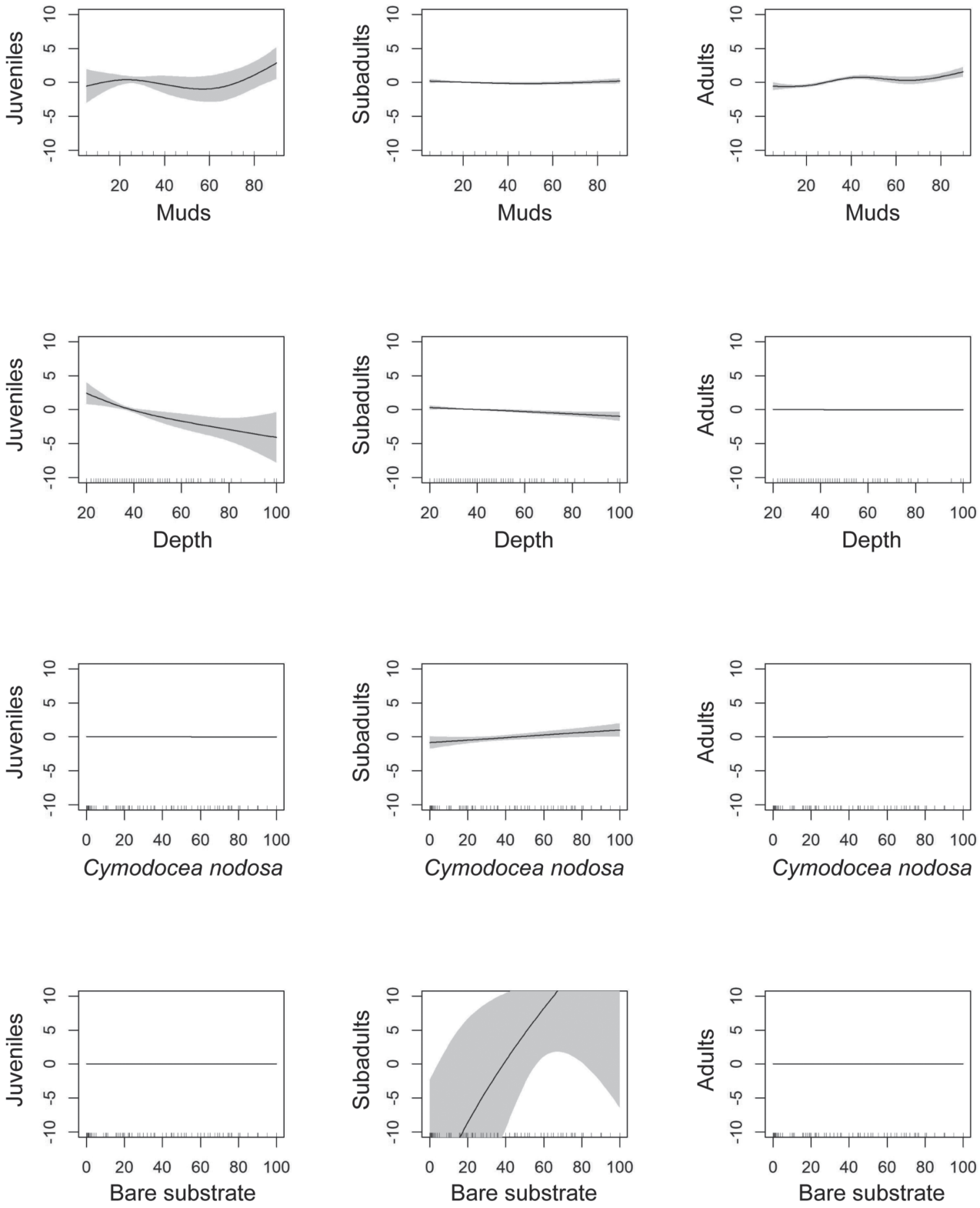


Figure 6. Smoothers of habitat type and microhabitat structure parameters considered in the best fitted GAM model. Vegetation cover is shown as bare substrate and *Cymodocea nodosa* meadow dominance (%), while microhabitat structure is referred to muds (%) and water depth (cm). Fitted smoother values have been adjusted to zero mean and shaded areas reflect 95% confidence intervals.

The fitted GAMs models indicated that the best model to explain the variation in size of blue crab catches was related to the habitat type, but with significant variation in trapping effectiveness by trap type (Suppl. material 1: table S3).

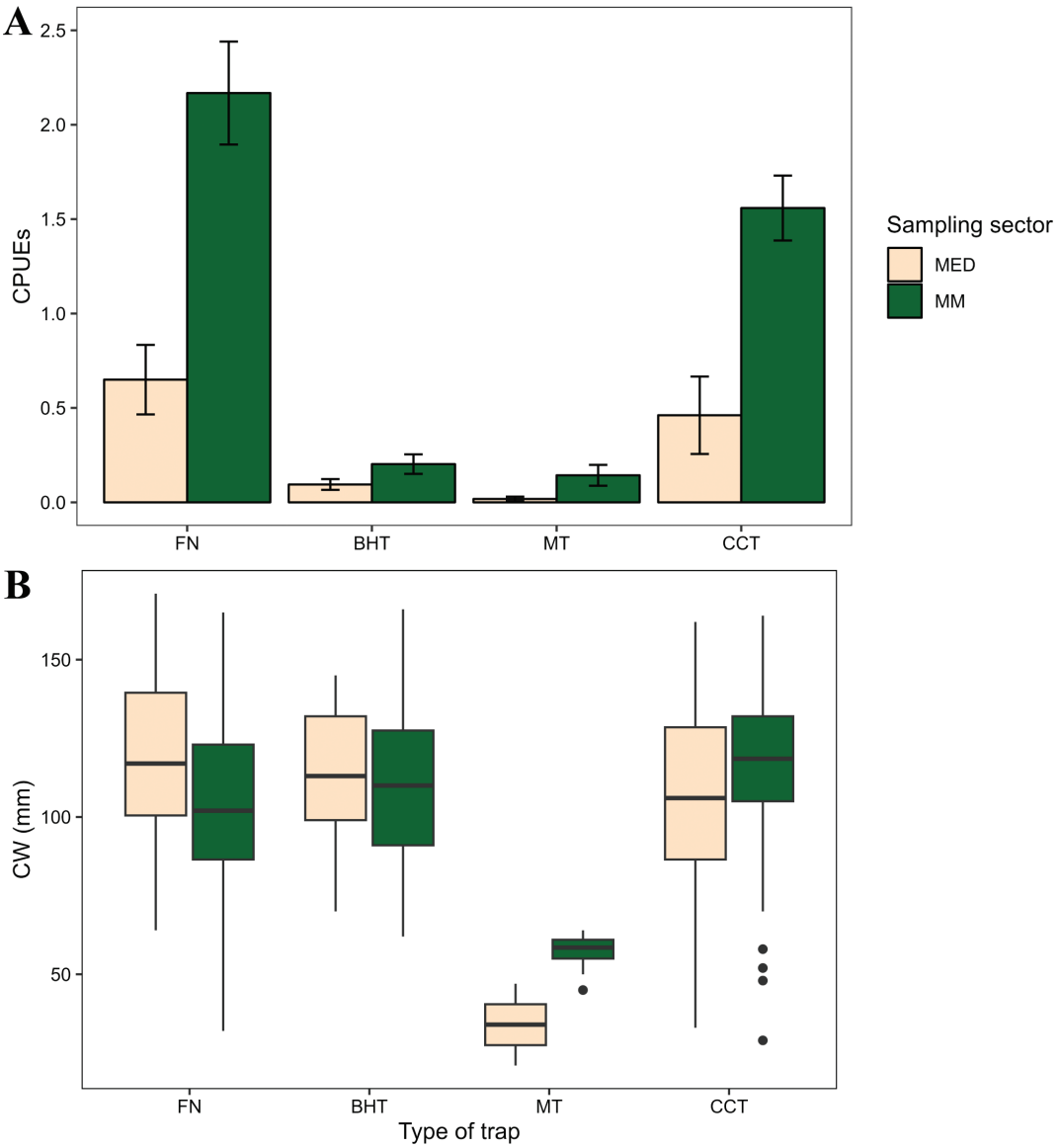


Figure 7. Spatial differences in the CPUEs (**A**) and CW (**B**) of blue crabs according to trap. Values of captures per unit effort (CPUEs) and carapace width (CW) are shown as the mean ± standard error. The four different types of trap are shown: Fyke nets (FN), 'bee-hive' type traps (BHT), minnow traps (MT) and collapsible cylindrical traps (CCT). Both spatial approaches cover the two study sectors separately: Mediterranean (MED) and Mar Menor (MM).

Due to the low number of captures obtained with the BHT and MT, trap selectivity was only modelled based on the captures from FN and CCT. The best fitted model (Suppl. material 1: fig. S3) revealed that trap type was one of the most determinant factors influencing the capture of subadult and adult blue crabs. Subadult captures were greater in FN, while CCT appeared to be slightly more efficient in capturing adults (Suppl. material 1: fig. S3). Moreover, the best fitted GAM model on the relationship between sex with habitat type and trap type only showed a dependence on the latter factor. Both FN ($P \leq 0.001$) and CCT ($P = 0.0002$) were significantly more effective in capturing males than females. Additionally, both sexes were captured with greater effectiveness by FN (Suppl. material 1: fig. S4). The coefficients of the best fitted model demonstrated that trap type had a greater effect on female captures, with a positive and significant influence of FN, whereas the effect of CCT exhibited no statistically significant influence (Suppl. material 1: fig. S4).

Discussion

The effective management of invasive species requires a comprehensive understanding of their life cycle and a thorough assessment of the effectiveness of potential control methods. Owing to the considerable ecological plasticity of the blue crab in coping with a wide range of environmental conditions, assessing species life history traits in different environmental settings across the invaded range becomes a pivotal requirement for its effective management. Our study analysed a population of blue crab at a relatively recent invasion stage in a hypersaline coastal lagoon, a type of environment in which the species' population biology has been notably understudied.

Spatiotemporal variation in population dynamics

The spatiotemporal dynamics observed in the abundance and population structure of the blue crab suggest that the Encañizadas area serves as both a part of the home range for the resident population within the lagoon and as a transient or spawning corridor for migratory individuals. In general, population structure of the blue crab in transitional environments (e.g. estuaries and coastal lagoons) exhibits a marked habitat segregation (Mancinelli et al. 2024). Settlement areas are mostly used by resident groups (including males and females), while transit zones act as corridors during the spawning migration of females. These corridors are mostly used by mature and ovigerous females migrating from low-salinity areas (e.g. lower watercourses or littoral wetlands) to high-salinity offshore waters (Carr et al. 2004; Aguilar et al. 2005). The continuous occurrence and higher density of males in the inner lagoon sector (MM) suggest that this area is used as part of the home range for the population established in hypersaline waters of the Mar Menor. This pattern contrasts with reference literature regarding male behaviour in estuarine environments, where males typically inhabit lower salinity areas throughout their whole life cycle (Williams 1954; Hines et al. 1987).

Blue crab abundance was significantly higher during the warmer months of peak activity, particularly in MED. Water temperature, a critical factor influencing the blue crab life cycle (Kevrekidis et al. 2023), likely drives this increase in activity. However, during colder months (November, January, March, and May), crab occurrence in the MED sector was negligible, reinforcing the hypothesis that this area primarily acts as a spawning corridor. Further evidence supporting this assumption includes the more balanced sex ratio observed in the MED sector and the exclusive capture of ovigerous females in this sector. Nevertheless, blue crabs significantly reduce their activity at low water temperatures, often going into winter dormancy by burrowing into the sediment (Millikin and Williams 1984; Kevrekidis et al. 2023; Marchessaux et al. 2023b). Therefore, the absence of individuals during these months in this sector could reflect a physiological response to the decrease in temperature. Similar spatiotemporal patterns have been reported in the native range of the species (Ramach et al. 2009). In estuarine habitats, the migration process typically consists of two phases, from mating areas through outer estuary to marine spawning grounds (Aguilar et al. 2005). Both in native and invaded regions, settlement and spawning areas are often spatially segregated, spanning several kilometres each other and being characterized by differing environmental conditions (Carr et al. 2004; Ortega et al. 2020; Kevrekidis et al. 2023). Our results suggest that the spatial distance between settlement and spawning zones in the Mar Menor may be minimal. The proximity of these zones

and the rapid migration capability of the blue crab, reaching up to 5 km/day (Carr et al. 2004), make it feasible that migration occurs in a single phase, immediately after mating, which would help to explain the scarcity of ovigerous females captured in the Mar Menor during our research, but also in a previous study conducted in the same coastal lagoon (Vivas et al. 2025). Additionally, the hypersaline conditions of the Mar Menor coastal lagoon, exceeding those of the Mediterranean Sea, present an unusual scenario. Reproductive females migrating through the study area move for spawning from hypersaline estuarine waters to lower-salinity offshore waters, conversely to that observed in other native and invaded regions (Carr et al. 2004; Ramach et al. 2009; Marchessaux et al. 2023b). Given that salinity is a key factor in blue crab reproduction (Sandoz and Rogers 1944), the hypersaline conditions showed by the Mar Menor can comprise a physiological constraint for the successful spawning of blue crabs, thus forcing them to migrate towards lower-salinity offshore waters.

The abundance of blue crabs in the MM sector also decreased during the colder months, likely due to its winter dormancy behaviour. Lagoon temperature and other environmental factors, such as elevated salinity, may hinder this behaviour and affect their metabolism, leading some crabs to hibernate in shorter periods or not at all. At the beginning of spring (e.g. March), the rising temperature of the lagoon's inner waters could trigger the activity of larger adults, as supported by our results. Smaller blue crabs seem to emerge later, potentially linked to the establishment of the year's juveniles.

Habitat use and selection

The habitat selection of the blue crab is influenced by physicochemical factors, including salinity, oxygen levels, water depth, substrate structure, and the presence or absence of seagrass meadows (Ramach et al. 2009; Ruas et al. 2014; Ortega et al. 2020; Taylor and Fehon 2021). By focusing on habitat use by this species in shallow waters, our results highlight its high ecological plasticity regarding habitat requirements. Notably, a preference for muddy substrates was found, particularly for juveniles and adults. This habitat preference can be attributed to the physical properties of the substrate, which facilitates the typical burrowing behaviour during hibernation or predator avoidance (Bembe et al. 2017). Moreover, muddy habitats often harbour high densities of benthic invertebrates, such as other small-size crustaceans and filter-feeding molluscs, which are considered among the blue crab's preferred preys (Prado et al. 2022; Vivas et al. 2025). Furthermore, these habitats also offer optimal conditions for crabs to ambush its preys (Kampouris et al. 2019; Johnson 2022).

Water depth emerged as another significant factor influencing the abundance of juveniles and subadults, which match with shallow waters being particularly important for smaller size classes. This selection for shallower habitats may be driven by both intra- and interspecific competition, with cannibalism acting as a major driver. Shallow habitats provide refuge against larger conspecifics and other aquatic predators, which might otherwise prey on juvenile crabs (Ruiz et al. 1993; Dittel et al. 2006).

The omnivorous and opportunistic feeding habits of the blue crab are influenced by ontogenetic development, habitat complexity, and the availability of trophic resources (Florido and Sánchez 2010; Vivas et al. 2025). These could be responsible for the spatial segregation observed in the different size classes, reflecting variations in ecological and trophic behaviour (Seitz et al. 2011; Prado et al. 2022; Taylor et al. 2022). Another factor supporting the preference of juveniles and subadults for shallow waters is their sensitivity to low dissolved oxygen levels (Seitz et al. 2003).

Juvenile blue crabs often respond to hypoxic conditions by moving to shallower areas where oxygen levels are generally higher (Eggleston et al. 2005).

The structural complexity of benthic habitats was represented by the three habitat types studied and their associated microhabitats. While subadults and adults showed a preference for bare substrate, with adults showing a preference for bottoms dominated by *C. nodosa* over *C. prolifera* meadows, juveniles did not show a significant preference for any type of bottom dominated by seagrass meadows. This finding contrasts with the critical role recognized for submerged vegetation as nursery grounds and foraging habitats for the blue crab in both native and invaded ranges (Ruas et al. 2014; Prado et al. 2020; Hyman et al. 2024; Kevrekidis et al. 2023). This lack of habitat preferences in juveniles could be partly due to their low capture rate in our study. Nevertheless, the high salinity of the study area may also influence the use of vegetated bottoms by juvenile blue crabs. For example, in Chesapeake Bay, the higher salinity levels, the lower importance of seagrass habitats for juveniles (Hines 2007).

The preference for bare substrates or *C. nodosa* meadows may reflect the foraging strategies of crabs, since habitat complexity affects the availability of trophic resources by influencing the density and mobility of prey items (Florido and Sánchez 2010). Furthermore, the habitat also influences predator behaviour. Bare substrate allows adults and subadults to move more freely, enabling an improved prey detection and versatile foraging on detritus and benthic invertebrates (Kampouris et al. 2019). In addition, these habitats often provide abundant and accessible prey, such as bivalves, which are a preferred food item for blue crabs (Prado et al. 2022). The absence of interspecific predators in the study area could also explain the greater use of unvegetated habitats, despite the lower refuge availability as compared to seagrass meadows (Aronhime and Brown 2009). On the other hand, *C. nodosa* meadows are known to support high abundance and diversity of invertebrate fauna, which would also explain the selection of this type of habitat by subadults (Sánchez-Jerez et al. 1999; Verdiell-Cubedo et al. 2007). In contrast, *C. prolifera* meadows were associated with low abundances of *C. sapidus* and were avoided by all size classes. *Caulerpa* seagrass species are well-recognized producers of repellent and toxic secondary metabolites, which deter grazers and other benthic organisms (Sánchez-Moyano et al. 2001; Davis et al. 2005). Additionally, *C. prolifera* is considered a markedly harmful invasive species in the Mar Menor coastal lagoon because it alters sediment characteristics by increasing organic matter accumulation, thus leading to anoxic conditions and the production of toxic acid volatile sulfides (Pérez-Ruzafa et al. 2005, 2012). These changes may disrupt food webs (Parreira et al. 2021) and turn these habitats unsuitable for blue crabs, which are highly sensitive to hypoxic conditions (Seitz et al. 2003). Although *C. prolifera* meadows also support invertebrate communities, they are less diverse and abundant than those associated with *C. nodosa* meadows, leading to a reduced availability of food resources for blue crabs, such as fish (Verdiell-Cubedo et al. 2007) and bivalves (Rueda and Salas 2003). Consequently, *C. sapidus* may actively avoid *C. prolifera* meadows due to both ecological and physiological constraints.

Trapping effectiveness

Trap type significantly influenced the effectiveness of capturing blue crabs across different size classes and sexes. Fyke nets (FN) were the most effective traps and captured a wider size range of class sizes. The cloth wall and the multi-chambered

structure of FN likely contributed to a higher biomass of captures and a broader size range, as already reported by Atar et al. (2002) for hoop nets (structurally similar to FN). Our 'bee-hive' type traps (BHT) were ineffective. Despite the excellent swimming ability of blue crabs (Houlihan et al. 1985), the top-entry design of BHT may further reduce their effectiveness in shallow waters. Minnow traps (MT) exclusively captured small juveniles (maximum CW of 64 mm), accounting for 23.5% of the total juvenile captures. This likely reflects the low abundance of juveniles rather than trap performance. Furthermore, MT prevents predation from larger conspecifics once small-sized crabs are inside the trap, making this trap type suitable for prolonged sampling events aimed to identify recruitment areas.

Although cannibalism in blue crabs has been demonstrated (Hines 2007; Bromilow and Lipcius 2017), no evidence of this was observed inside the traps during our study (e.g. carcasses or remains). Juveniles could display avoidance behaviour towards traps containing adult crabs (Moir and Weissburg 2009), which would also explain their low capture rate. The mesh size and cloth wall of FN may reduce juvenile evasion by predators, while their preference for live prey over carrion (Seitz et al. 2011) could also influence the success of capture.

No significant differences were observed between FN and CCT in capturing juveniles or adults. However, FN were slightly more effective for subadult crabs (Suppl. material 1: fig. S3) and in capturing females (Suppl. material 1: fig. S4), likely due to the cloth wall facilitating the entry of mobile individuals, particularly during spawning migrations. This is supported by the fact that 57.2% of adult females were captured using FN.

Management recommendations

In the Mediterranean Sea and associated coastal lagoons, such as the Mar Menor, the blue crab is a highly impactful invasive species with well-documented negative effects on local ecosystems (Mancinelli et al. 2017b; Clavero et al. 2022) and socio-economic activities (Glamuzina et al. 2021). Previous studies have highlighted the urgent need to implement effective management measures aimed to mitigate these impacts. Promoting commercial exploitation of blue crab populations offers a promising approach to control their abundance while offsetting economic losses in invaded areas (Marchessaux et al. 2023c; Mancinelli et al. 2024). However, commercial exploitation should be complemented with targeted management actions aimed to control blue crab populations in ecologically sensitive habitats (Mancinelli et al. 2017a). Minimizing ecological and economic impacts should be a primary goal of post-invasion management strategies. These strategies must be tailored to the species' life history and the environmental conditions of the invaded ecosystem, targeting specific size classes and sexes. For example, identifying spawning corridors is crucial for an effective control, as targeting trapping efforts into these areas could significantly reduce the reproductive output of invasive populations. Our study underscores the complex interplay of ecological, physiological, and behavioural factors driving habitat selection in the blue crab. Sound management implications can be drawn from our results to optimize trapping protocols in shallow spawning corridors. A higher fishing pressure should be applied during warmer months when crab activity peaks, and traps should be deployed in predominantly unvegetated, muddy substrates or mixed habitats with patches of *C. nodosa*. FN and CCT were the most effective traps, with FN performing better for capturing a wider range of

size classes and being particularly effective for the capture of females. Future studies should explore alternative trap materials, mesh sizes, and entrance designs to enhance trapping effectiveness and to boost control strategies.

Our results provide baseline information on blue crab population dynamics, habitat use and trapping efficiency in high salinity waters, which can inform monitoring and management in other invaded regions. By improving trapping protocols and integrating ecological knowledge, control strategies can be tailored to efficiently manage blue crab populations while minimizing impacts on native biodiversity and local fisheries.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Antonio A. Herrero-Reyes: Writing – original draft, review & editing, Investigation, Methodology, Formal analysis, Data curation. Adrián Guerrero-Gómez: Methodology, Formal analysis, Investigation, Writing – review & editing. Antonio Zamora-López: Methodology, Formal analysis,

Investigation, Writing – review & editing. Mar Torralva: Investigation, Writing – review & editing, Funding acquisition, Project administration. José Manuel Zamora-Marín: Investigation, Supervision, Writing – original draft, Writing – review & editing. Francisco José Oliva-Paterna: Investigation, Funding acquisition, Supervision, Writing – review & editing, Validation. All authors have reviewed and contributed to improve the text and figures.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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