Regional Studies in Marine Science 98 (2026) 105058

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

# Environmental drivers of juvenile Atlantic blue crabs (*Callinectes sapidus*) abundance in Northern Adriatic

Anna Gavioli [a], Giorgio Mancinelli [b,c,d], Mattia Lanzoni [a,*], Piero Franzoi [e], Fernanda Moroni [f], Davide Cardi [a], David B. Eggleston [g], Robert R. Christian [h], Giuseppe Castaldelli [a]

[a] Department of Environmental and Prevention Sciences, University of Ferrara, Ferrara, Italy
[b] Department of Biological and Environmental Sciences and Technologies, University of Salento, Lecce 73100, Italy
[c] National Biodiversity Future Center (NBFC), Palermo 90133, Italy
[d] Consorzio Nazionale Interuniversitario per le Scienze del Mare, Roma 00196, Italy
[e] Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, via Torino 155, Venezia 30172, Italy
[f] Po River Basin District Authority, Parma 43121, Italy
[g] Department of Marine, Earth and Atmospheric Sciences, NC State University, Raleigh, NC, USA
[h] Department of Biology, East Carolina University, Greenville, NC, USA

ARTICLE INFO

*Keywords:*
Invasive species
Coastal lagoons
Nursery habitat
Salinity
Refuge availability

ABSTRACT

The Atlantic blue crab (*Callinectes sapidus)* is a highly invasive species posing significant ecological and economic threats to coastal lagoons in the Mediterranean Sea. Due to its recent spread in the Mediterranean, management is hindered by a critical knowledge gap concerning spatiotemporal variation in abundance of juvenile stages that use lagoons as nursery habitat. This study addresses this gap by providing the first field surveys of juvenile blue crab abundance and its environmental drivers in the northwestern Adriatic Sea. Four coastal lagoons in Northern Italy (Goro, Fattibello, Comacchio, Pialassa Baiona) were sampled in spring and autumn 2024 using a beach seine net designed to capture small crabs, with a total of 343 crabs (5–145 mm CW) collected. Carapace width-weight relationships indicated negative allometric growth. Zero-inflated Poisson models and Random Forest analysis identified refuge availability, salinity, and lagoon-sea connectivity as the key predictors of juvenile abundance. Abundance was highest in areas with refuges (e.g., *Phragmites* sp. marsh grass areas, artificial substrates) and in lower salinity waters, consistent with the characteristics of nursery habitats identified in blue crab's native habitats. The Goro lagoon, featuring high connectivity with the sea and refuge availability, was identified as a primary spring recruitment site, evidenced by a peak in small juveniles (<14 mm CW). These results highlight environmental factors that may create "invasion hotspots" providing crucial information for targeted management and control strategies in invaded Mediterranean ecosystems.

## 1. Introduction

Coastal lagoons host high levels of biodiversity due to their dynamic and varied ecosystems which also provide high productivity and ecosystem services (Pérez-ruzafa et al., 2019, Geppi et al., 2023, Rodrigues-Filho et al., 2023). Despite the ecological and economic importance of lagoons, human activities are severely impacting these ecosystems through overexploitation of fish stocks, physical modifications of the environment, the introduction of non-indigenous species (NIS), pollution, and eutrophication, making them one of the most threatened habitats worldwide (Cataudella et al., 2015, Newton et al., 2018, Milardi et al., 2020, Lewin et al., 2023).

Within the Mediterranean basin, a growing concern among NIS is the Atlantic blue crab (*Callinectes sapidus*). This species is native to the Atlantic coast of North America and first appeared in the Mediterranean Sea in the mid-20th century. Its population has grown exponentially in the last decade, with negative consequences for native aquatic communities, ecosystems and human activities, particularly the fishing industry. Following the recent and rapid increase in blue crab abundance, there was a corresponding decrease in native species in different areas of the Mediterranean Sea including the Ebro Delta in Spain (Clavero et al., 2022) and the Po River Delta in Italy (Gavioli et al., 2025, Gavioli et al., 2025b), posing a significant threat to local fishing industries (Nardelli et al., 2024, Chiesa et al., 2025, Tiralongo et al., 2025, Gaglio et al.,

* Corresponding author.
*E-mail address:* lnzmtt@unife.it (M. Lanzoni).

https://doi.org/10.1016/j.rsma.2026.105058
Received 17 November 2025; Received in revised form 4 March 2026; Accepted 10 May 2026
Available online 12 May 2026

2025).

While the causes behind the spread of the blue crab in the Mediterranean are still being investigated, prevailing hypotheses point to factors such as commercial shipping and oceanic currents facilitating its subsequent dispersal throughout the region (Mancinelli et al., 2017, Fuentes et al., 2019).

Furthermore, the successful establishment and population growth of the blue crab are thought to be driven by its great adaptability to a broad range of environmental conditions and its opportunistic diet (Hines, 2007, Lipcius et al., 2007 and references therein).

The blue crab thrives in different salinities throughout its life cycle, as salinity is a key factor involved in its migratory process and reproduction. In its native habitat, mating occurs in the brackish waters of estuaries, where males commonly live. After mating, females migrate to higher salinity areas to incubate eggs and then release planktonic zoeal larvae. These larvae develop at sea before metamorphosing into a postlarval, megalopal stage. The megalopae then migrate back into estuaries to mature, utilizing a strategy known as flood-tide transport or storm-driven transport (Forward et al., 2003, Eggleston et al., 2010). For flood tide transport, megalopae ascend into the water column primarily during flood tides, often at night, and remain near the bottom during ebb tides. This strategy allows them to effectively ingress into and move up estuaries, until they reach suitable nursery habitats in lower salinity areas (Ogburn et al., 2012, Forward and Welch, 2016). For storm-driven megalopal influx to estuaries, large water volumes containing megalopae may be pushed into estuaries via strong winds. For example, in Pamlico Sound, North Carolina, the second largest estuary in the United States, of the annual megalopal settlement peaks at a given site during 1996–2005, a total of 65–85% were associated with named tropical storms or hurricanes (Eggleston et al., 2010).

Once in the estuary, megalopae develop into juvenile crabs, preferring productive and vegetated shallow waters for growth (Lipcius et al., 2007, Ciotti et al., 2025). Habitats such as seagrass beds, salt marshes, and oyster reefs offer critical refuge from predation and cannibalism, and both megalopae and early juvenile crabs actively seek out these areas (Dittel et al., 1995; Lipcius et al., 2005). The growth and seasonal movements of the species are also strongly regulated by water temperature. Optimal temperatures for the species, typically ranging from around 19–29°C, are crucial for the development of eggs and larvae, with spawning activities peaking in warmer months. The blue crab's metabolism and its growth rate are favoured by warmer waters, which accelerate molting frequency (Rodríguez-Ruiz et al., 2025). Conversely, colder temperatures, particularly below approximately 10–12°C, lead to a significant slowdown in metabolic activity, growth cessation, and the onset of a quiescent period where crabs burrow into the mud (Brylawski and Miller, 2006, Glandon et al., 2019).

The species also demonstrates a high tolerance for low oxygen, although this adaptability varies by life stage, with larval stages being more sensitive than adults (Bell et al., 2003).

The recent and rapid invasion of the blue crab across the Mediterranean Sea presents a significant ecological and economic threat which requires population dynamic models to predict its impact at varying scales in space and time. However, parameterization of these models is hindered by a significant knowledge gap concerning juveniles of small size (carapace width $< 15$ mm), which represent a crucial recruitment phase (Voigt and Eggleston, 2023, Voigt et al., 2025). This gap is due primarily to methodological challenges in sampling. Most studies of the blue crab in the Mediterranean Sea rely on crab traps (pots) or fyke nets (e.g., Bardelli et al., 2023, Kevrekidis et al., 2023, Mancinelli et al., 2024). However, these passive gears are well-known to be size-selective and biased toward larger, more mobile individuals (Guillory and Prejean, 1997, Özdemir et al., 2015). Consequently, small juvenile crabs, which are less mobile and hide in the shallow habitats, are typically underrepresented by these capture methods (Herrero-Reyes et al., 2025). Moreover, any juveniles entering fyke nets alongside adults are likely to be subject to cannibalism, as demonstrated in field experiments in the Chesapeake Bay (Bromilow and Lipcius, 2017), further biasing abundance estimates. In its native habitat, robust estimates of juvenile blue crab abundance rely on active sampling gears, such as trawl or seine net surveys (e.g., Taylor and Fehon, 2021). This knowledge gap has resulted in limited information on the population growth, distribution and environmental factors influencing the blue crab's invasion success. There is a clear need for studies in the Mediterranean that use sampling methods, such as seine nets, to overcome this bias and target juveniles effectively in their nursery habitats.

This study aims to fill this methodological and knowledge gap by providing the first investigation of relative juvenile blue crab abundance in estuarine lagoons in the northeastern Adriatic Sea, the northeasternmost arm of the Mediterranean Sea. Specifically, this study aims to (1) establish quantitative relationships between body size (e.g., carapace width) and weight, which provide crucial information for stock assessment models (Hüseyin Atar and Seçer, 2003, Katselis et al., 2013). While robust allometric relationships require sampling the entire population spectrum, this study provides crucial, currently lacking data on these underrepresented juvenile stages of blue crab in its invaded area. Furthermore, these parameters are not merely descriptive but are essential for developing robust, stage-structured population models and for assessing changes in body condition in response to environmental stressors (Muchlisin et al., 2010). This study also aims to (2) disentangle the key environmental drivers that explain variation in juvenile blue crab abundance, from physicochemical factors (water temperature, salinity, dissolved oxygen) to habitat features (refuge availability and lagoon connectivity).

## 2. Materials and methods

### 2.1. Study area

The study was conducted in four coastal lagoons in north-eastern Italy, located in the south of the Po River Delta, the largest delta system in the country (685 $km^2$). The study area includes the Goro, Fattibello, Comacchio and Pialassa Baiona lagoons (Fig. 1). The region has a Mediterranean climate, with summer temperatures exceeding 30 °C and winter temperatures reaching below 0 °C. The typical annual rainfall is around 600–700 mm, with a peak during autumn.

All selected lagoons are designated as protected areas within the Natura 2000 network, underscoring their high value for biodiversity conservation.

A total of 11 sites were sampled across the lagoons. Four sampling sites were in the Goro Lagoon, a shallow lagoon with a surface area of 20 $km^2$ and an average depth of about 1.2 m. The lagoon is connected to the Adriatic Sea via a 3.3 km wide channel and receives freshwater inputs from the Po di Volano River, in its western part, and from the Po di Goro River in the eastern part. The substrate of the lagoon is variable and includes areas dominated by mud, silt, or sand, as well as harder substrates (Bezzi et al., 2019).

The Goro Lagoon holds socio-economic importance for the study area since, historically, its shellfish farming industry targeting clams, mussels, and oysters accounted for nearly half of Italy's total farmed shellfish production (Tamburini et al., 2022, Summa et al., 2023). However, this economic activity has recently suffered a severe collapse following the widespread invasion of the Atlantic blue crab (Gavioli et al., 2025).

Sampling was conducted at a single site within Fattibello Lagoon, a small (7 $km^2$) and shallow (~1 m average depth) basin connected to the sea via the Navigabile and Logonovo channels (total width 104 m). The substrate in the lagoon is variable, including areas dominated by mud, silt, sand, or hard substrates, and aquatic vegetation is largely absent. The selection of a single site was a methodological constraint as the prevalence of inconsistent and untrawlable substrates limited the effective use of a seine net to a few, small, contiguous areas that shared similar environmental features. Consequently, these areas were treated

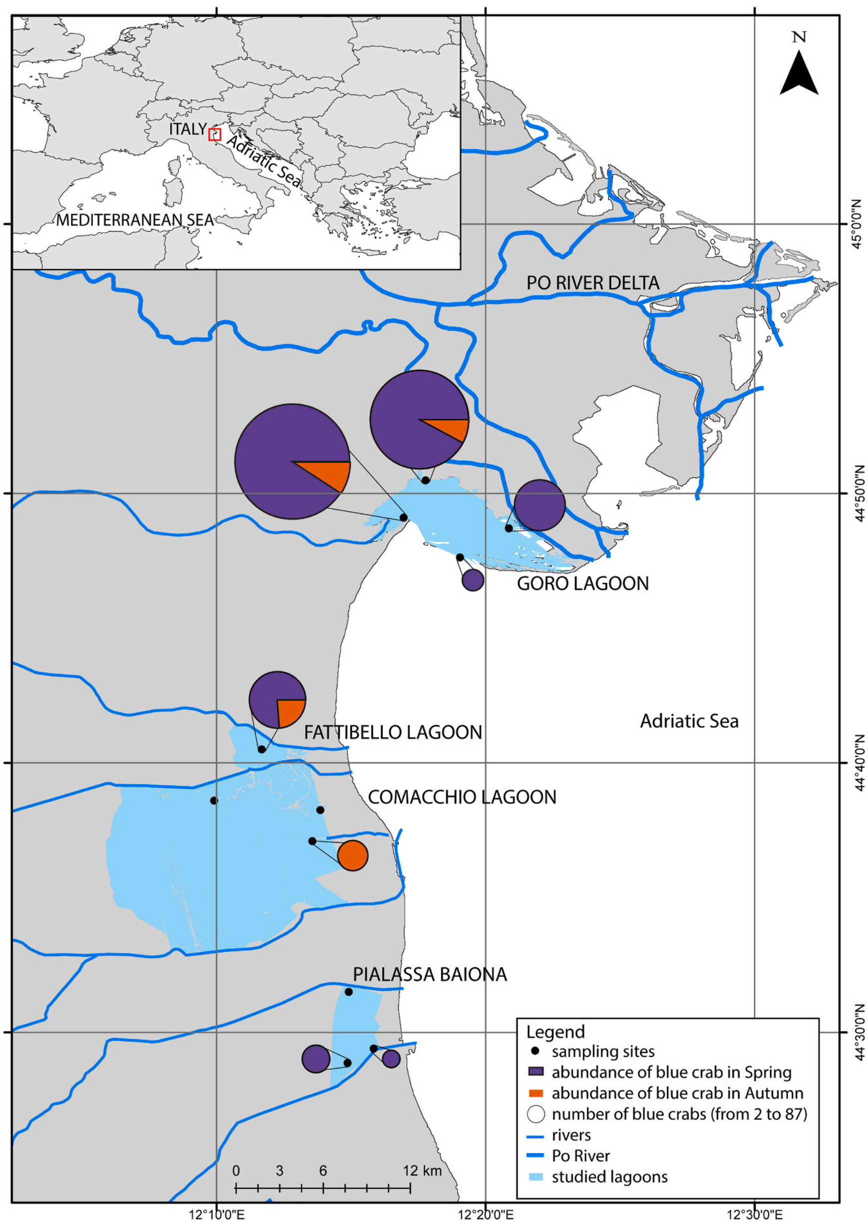


**Fig. 1.** Map of the study area showing the sampling sites (black dots) within the Goro, Fattibello, Comacchio and Pialassa Baiona lagoons. Pie charts illustrate the relative abundance of the blue crab (*Callinectes sapidus*) during spring (purple) and autumn (orange) periods for each sampling sites. The size of each pie chart is proportional to the total number of blue crabs captured at that site (ranging from 2 to 87 individuals per 280 $m^2$).

as one representative sampling site.

Three sampling sites were in the Comacchio Lagoon that covers an area of ~100 $km^2$. Depth varies from a minimum of a few centimetres on the shallowest sandbanks to a maximum of 3 m in the deepest channels with average depth of 1 m. The lagoon is connected to the Adriatic Sea by two canals (Gobbino and Foce canals), both of which are hydraulically regulated by gateways.

Finally, three sampling sites were located inside the Pialassa Baiona lagoon. The Pialassa Baiona is a eutrophic, micro-tidal lagoon with a surface area of 10 $km^2$ with an average depth of 1 m, and with the deepest zones located in channels which can reach 8 m depth. It connects to the Adriatic Sea via a 100 m wide canal, which also provides access to the Port of Ravenna, a major commercial harbour in north-eastern Italy (Matteucci et al., 2005).

The lagoons are generally characterised by a historical loss of seagrass beds, and the dominant vegetation is now primarily common reed (*Phragmites spp*.), which is particularly prevalent in Goro (Viaroli et al., 2018, Sfriso et al., 2019, 2025).

### 2.2. Field sampling

Sampling of juvenile crabs was conducted in 2024 within shallow waters using a manually operated beach seine net (10.0 length, 1.9 m height, 2 mm mesh). To ensure a consistent methodology, sampling stations were randomly established in areas suitable for seine net sampling. This method has an operational constraint of a maximum water depth of 1 m to ensure efficient deployment of the gear and the safe movement of field operators.

To ensure comprehensive collection of both benthic and water-column specimens, the net was equipped with a weighted lead line along its bottom edge, maintaining continuous contact with the substratum during the sampling. At each sampling site, two replicate samples were collected to assess within-site variability. For each replicate, two operators manually towed the net along a pre-measured 20-meter linear transect, maintaining a constant mouth width of 7 m.

At each sampling station, the presence of potential refuges for juvenile crabs was visually recorded. Refuges were defined as natural features, such as aquatic vegetated areas (e.g., reed beds), or artificial structures, including gravel substrates, woody debris, bank stabilization materials, and mussel farm infrastructure.

A 200 m radius buffer was created around each sampling station, and the presence or absence of refuge areas including macrophyte beds, oyster reefs, or artificial substrates (e.g., wooden piles, breakwaters) was recorded using satellite imagery in QGIS software (QGIS.org, 2024). Refuge availability generated by satellite imagery was ground-truthed during field sampling.

In each sampling site, during the crab sampling, a multi-parameter probe (YSI ODO/CT) was used to measure water temperature (°C), salinity (PSU) and oxygen expressed as degree of saturation (%). In 2024, sampling sites were surveyed in late spring (May–June) to detect the recruitment and growth period and early autumn (October–November). Sampling was not performed during the full summer to minimize the confounding influence of unusual environmental stressors (extreme high-water temperature), which can alter activity levels and not reflect baseline conditions.

### 2.3. Laboratory activity

All captured crab specimens were transported to the laboratory for processing. This included identification to species level, counting and determining sex based on abdominal morphology. For each blue crab, the carapace width (CW; to the nearest mm) was measured as the distance between the two anterolateral spines of the cephalothorax. The wet weight (W; to nearest 0.01 g) was also recorded.

### 2.4. Data analysis

All statistical analyses were performed using RStudio (R Studio Team, 2024).

The CW-W relationships were estimated using the function of $W = a{\cdot}CW^b$, where $a$ is the initial growth coefficient and $b$ describes the relative growth rate (Froese, 2006). Furthermore, the CW-W relationships were also investigated by sex and combined sexes by comparing slopes using analysis of covariance (ANCOVA).

The frequency distribution of CW was determined by categorizing specimens into size classes adapted from Mancinelli et al., (2024), focusing on a southern Adriatic lagoon: CW < 14 mm, CW 15–25 mm, CW 26–96 mm and CW > 97 mm.

To account for the connectivity between the lagoon and the sea, the width of the lagoon mouth was measured using satellite imagery in QGIS software (QGIS.org, 2024).

To investigate the influence of physicochemical factors (water temperature, salinity, dissolved oxygen) to habitat features (refuge availability and lagoon-sea connectivity) on blue crab abundance, the zero-inflated Poisson model in the *pscl* R package (Jackman, 2024) was applied.

Zero-inflated model analysis was chosen to account for the high frequency of zero counts in the count data (Zeileis et al., 2008). Blue crab abundance was used as the response variable. It was expressed as the number of individuals per 280 $m^2$, representing the total area sampled at each site.

A set of candidate models, encompassing all possible combinations of predictor variables and their interactions, was generated using the *dredge* function within the *MuMIn* R package (Bartòn, 2025). The best-fit model was then selected based on Akaike Information Criterion corrected for small sample sizes (AICc; Akaike, 1974), models with $\Delta$AICc < 2 were retained as equally probable (Grueber et al., 2011). Multicollinearity of best-fit models was checked using the Variance Inflation Factor (VIF) threshold of 7. Model validation was performed by inspecting residual plots of the zero-inflated models (Zeileis et al., 2008). The importance of the variables in each model was calculated through a Random Forest in *randomForestSRC* R package (Ishwaran and Kogalur, 2023). Plots were obtained using *ggplot2* R package (Wickham, 2016).

## 3. Results

Spring water temperatures were relatively constant across the sampling sites, ranging between 23.77 °C and 26.8 °C (Table 1). In contrast, autumn temperatures were more variable ranging between 11.4 °C (Pialassa Baiona) and 19.28 °C (Goro Lagoon). Both dissolved oxygen and salinity exhibited high spatial and seasonal variability, with oxygen saturation ranging from 53.45% to 126.17% and salinity fluctuating widely from near-freshwater (1.33 ppt) to marine levels (32.99 ppt). Refuge availability showed no seasonal variation and was detected exclusively in Goro and Fattibello lagoons, while being absent in Comacchio and Pialassa Baiona lagoons. Lagoon-sea connectivity was maximal in Goro lagoon, followed by Fattibello lagoon (Table 1).

A total of 343 blue crab specimens were collected in the study area, with a marked decline observed in the southernmost lagoons (Fig. 1).

The CW of blue crab ranged from 5 to 145 mm, with a mean value of 41.24 mm, and W ranged from 0.01 to 200.44 g (Table 2).

Females (N = 118) showed slightly lower CW (mean 38.00 mm) than males (N = 225; mean 43 mm). Blue crabs exhibited negative allometric growth, where their body weight increased at a slower rate than their carapace width ($b<3$; $P < 0.001$; Table 2). This growth pattern differs among sexes, as shown by the significant interaction term of the ANCOVA (df = 1, F-test = 55.65, $P < 0.001$), indicating a difference in allometric slope between males and females.

The Goro lagoon showed a wide range of CW for both sexes, with a bimodal distribution for females suggesting two potential cohorts and a wider distribution for males (Fig. 2), suggesting the presence of two distinct cohorts likely resulting from different recruitment phases. Furthermore, the lagoon also recorded the highest number of small-sized blue crabs (<14 mm) in spring (Fig. 3), suggesting evidence of a recruitment event of a new cohort close to the spring sampling period.

In both the Goro and Fattibello lagoons, males reached larger maximum sizes than females. Notably, the largest male specimen (CW = 145 mm) was caught in the Fattibello lagoon in autumn (Figs. 2, 3).

The Comacchio and Pialassa Baiona lagoons presented a narrower CW distribution, with relatively few large females collected (Fig. 2). Comacchio and Goro were the only lagoons to record the presence of juvenile crabs (CW<14 mm; Fig. 3). The Pialassa Baiona lagoon consistently showed low blue crab numbers, with only a few individuals observed in the middle CW length class during spring (Figs. 2, 3).

The selection of top models suggested that the number of blue crabs was explained mainly by season, refuge availability and salinity (Model 1, Table 3). Model 2, which also included the variables from Model 1, further highlighted the importance of lagoon connectivity, showing a positive relationship with crab abundance (Model 2, Table 3). Random Forest analysis identified salinity and refuge availability as strong predictors in both models, with lagoon connectivity also important for Model 2. Season, however, showed less predictive power across both models (Fig. 4).

## 4. Discussion

Information on the juvenile blue crab distribution and abundance patterns in the Mediterranean and Adriatic Seas is scarce, likely due to the recent and rapid increase in blue crab abundance, and lack of sampling programs targeting these small size classes.

This study directly addressed this knowledge gap by using a seine net, a sampling method that is suitable for capturing small specimens (Taylor and Fehon, 2021). To the best of our knowledge, this approach enables the first comprehensive investigation of juvenile blue crab distribution and abundance patterns in the eastern Mediterranean Sea.

**Table 1**
Mean and standard deviation (SD) of the environmental variables measured across lagoons (Goro, Fattibello, Comacchio and Pialassa Baiona lagoons) during the sampling campaign in 2024.

| Variables | Season | Goro Lagoon | Fattibello Lagoon | Comacchio Lagoon | Pialassa Baiona |
|---|---|---|---|---|---|
| | | (Mean±SD) | (Mean±SD) | (Mean±SD) | (Mean±SD) |
| Water temperature (°C) | Spring | 26.23 ± 1.55 | 26.8 | 23.77 ± 0.90 | 26.43 ± 1.53 |
| | Autumn | 19.28 ± 3.46 | 18.9 | 16.13 ± 1.97 | 11.4 ± 0.2 |
| Dissolved oxygen | Spring | 53.45 ± 5.93 | 98.5 | 57.53 ± 2.81 | 126.17 ± 5.51 |
| (% saturation) | Autumn | 124.2 ± 9.13 | 95.3 | 92.8 ± 8.2 | 95.1 ± 5.1 |
| Salinity (ppt) | Spring | 15.45 ± 6.62 | 25.5 | 23.92 ± 11.67 | 32.99 ± 0.93 |
| | Autumn | 11.06 ± 7.37 | 1.33 | 32.3 ± 0.2 | 31.45 ± 0.05 |
| Refuge availability | Spring | Yes | Yes | No | No |
| | Autumn | Yes | Yes | No | No |
| Lagoon-sea connectivity (m) | | 3376 | 104 | 36 | 44 |

**Table 2**
Carapace width–weight (CW-W) relationships of blue crab *Callinectes sapidus* with both sexes pooled (Total) and separate for female and male (N = number of individuals; *a* and = regression coefficients; $R^2$= square correlation coefficient).

| | | CW (mm) | | | W (g) | | | CW-W coefficients | | |
|---|---|---|---|---|---|---|---|---|---|---|
| N | Sex | Min | Max | Mean | Min | Max | Mean | *a* | *b* | $R^2$ |
| 343 | Total | 5 | 145 | 41 | 0.01 | 200.44 | 19.63 | 0.0004 | 2.62 | 0.96 |
| 118 | Female | 6 | 135 | 38 | 0.02 | 127.99 | 15.38 | 0.0006 | 2.516 | 0.99 |
| 225 | Male | 5 | 145 | 43 | 0.01 | 200.44 | 21.86 | 0.0006 | 2.55 | 0.98 |

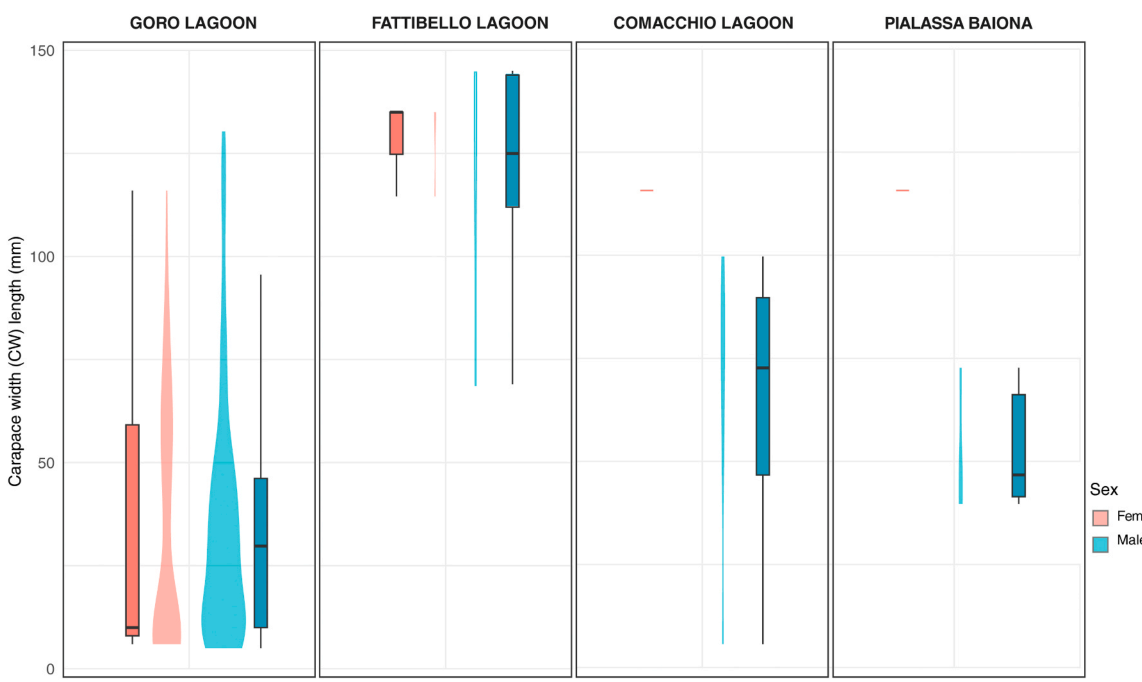


**Fig. 2.** Carapace width (CW) distribution of the Atlantic blue crab (*Callinectes sapidus*) males (in blue) and females (in red) across the Goro, Fattibello, Comacchio, and Pialassa Baiona lagoons. Violin plots show the distribution density of CW, while box plots indicate the median (horizontal line), interquartile range (box), and 1.5 times the interquartile range (whiskers).

Research on preceding life stages leading blue crab populations is also limited. A unique study focusing on the larval stages (zoeae and megalopae) of blue crabs was detected for the Gulf of Valencia, in Western Mediterranean Sea (Gil-Fernández et al., 2024). Building on this finding, our study examines the distribution and abundance of juveniles after the larval stage.

Analysing morphometric relationships such as the ratio of carapace width to weight is important for understanding population dynamics and resource management (e.g., Poot-Lopez et al., 2019; Triay-Portella et al., 2024). Invasive blue crab populations across the Mediterranean show wide plasticity in growth, which is dependent on sex, life history stage and local environmental conditions (Jellyman et al., 2013, Mancinelli et al., 2024). In this study, we found negative allometric growth for both sexes, meaning carapace width increased faster than weight. This pattern is reported in other invaded Mediterranean areas, including northern Tunisia (Fassatoui et al., 2021), Turkey (Hüseyin Atar and Seçer, 2003, Sumer et al., 2013), Greece (Kampouris et al., 2020) and Croatia (Dulčić et al., (2011), Glamuzina et al., (2023)). Conversely, positive allometric growth in blue crabs was documented in Egypt (Abdel Razek et al., 2016) and southern Italy (Marchessaux et al., 2023), highlighting population-specific growth trajectories. We also found that males reached greater body size and exhibited faster growth than

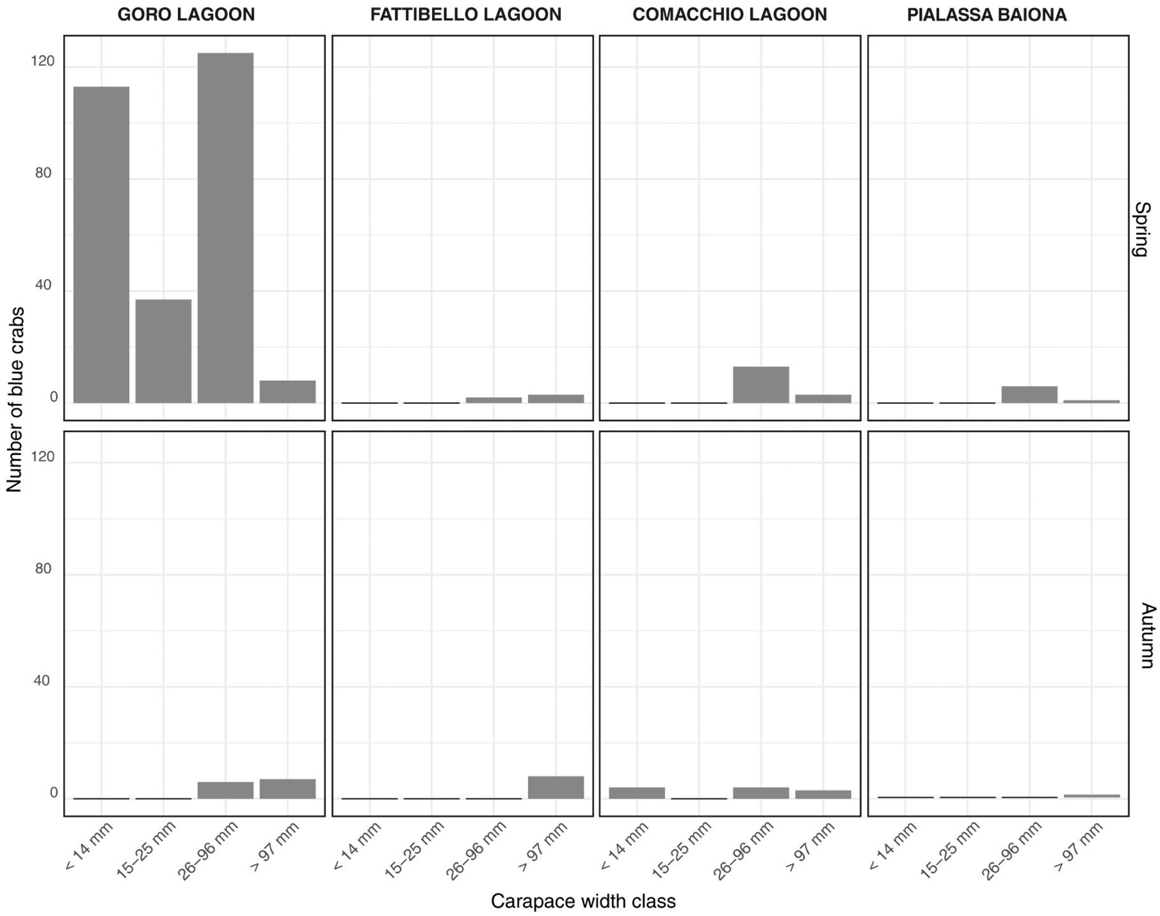


**Fig. 3.** Number of Atlantic blue crab (*Callinectes sapidus*) specimens across carapace width classes in the Goro, Fattibello, Comacchio and Pialassa Baiona lagoons during the spring and autumn.

**Table 3**
Summary of highly plausible zero-inflated regression models selected by ΔAICc < 2. The table presents the estimate of the best-retained variables (i.e., season, refuge availability, salinity, and lagoon connectivity) for each model, along with key model descriptors: degrees of freedom (df), corrected Akaike Information Criterion (AICc), delta corrected AIC (ΔAICc), and Akaike weights (W).

| Model | Intercept | Season | Refuge availability | Salinity | Lagoon connectivity | df | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.41 | + | 1.16 | -0.07 | / | 5 | 148.9 | 0 | 0.65 |
| 2 | 1.12 | + | 1.27 | -0.05 | 0.19 | 6 | 150.1 | 1.27 | 0.35 |

females, a common pattern among crustaceans, which reflects different energy allocation strategies between the sexes (Noori et al., 2015).

The abundance of different life stages of blue crab varies according to environmental and habitat features. Our model identified season, salinity, refuge availability, and lagoon connectivity as the key drivers of blue crab abundance in the study lagoons. A peak in abundance of juvenile crabs (<14 mm) occurred in spring in the Goro lagoon, which hosts the highest refuge availability and largest connection to the sea as discussed above. Conversely, in autumn, juveniles were predominantly collected in the Comacchio lagoon, despite its lower refuge availability and narrow sea connection.

These patterns suggest that whereas Goro can act as first entry point during the spring recruitment, other lagoons could support later cohorts or undergo different seasonal pulses or larval supply due, for example, to different sea currents. The extended temporal window for juvenile collection across both seasons suggests a prolonged recruitment period in the study area, also observed in other Adriatic regions such as southern Italy (Mancinelli et al., 2024). However, further investigation into hydrodynamic features and larval dispersal is needed to better understand larval drift in the Adriatic Sea.

Notably, water temperature was not retained as a significant variable. Although the water temperature decreased between the spring and autumn surveys, it remained above the reported 11°C threshold for inducing winter dormancy in blue crabs (e.g., Bauer and Miller, 2010) and within an optimal activity range. However, it is also important to consider potential lagged effects on environmental conditions not captured during surveys. For example, summer heat waves may induce physiological stress on aquatic species, pushing the blue crab to migrate to cooler or more oxygenated waters (Glandon et al., 2019, Mancinelli et al., 2024), outside the study area. Such effects could explain the relatively low crab abundances observed in the subsequent autumn, even if autumn water temperatures were not limiting in themselves.

The blue crab is a euryhaline species which can tolerate a wide range of salinities from nearly freshwater to hypersaline conditions, with different salinity optima and preferences for each specific life stages (Epifanio, 2019). The negative relationship observed between crab abundance and salinity in this study area likely reflects the prevalence of juveniles and males, which are often found in lower-salinity waters (Epifanio, 2019). Similar results have been observed in the native region of the blue crab, such as in the estuaries within the east coast of United

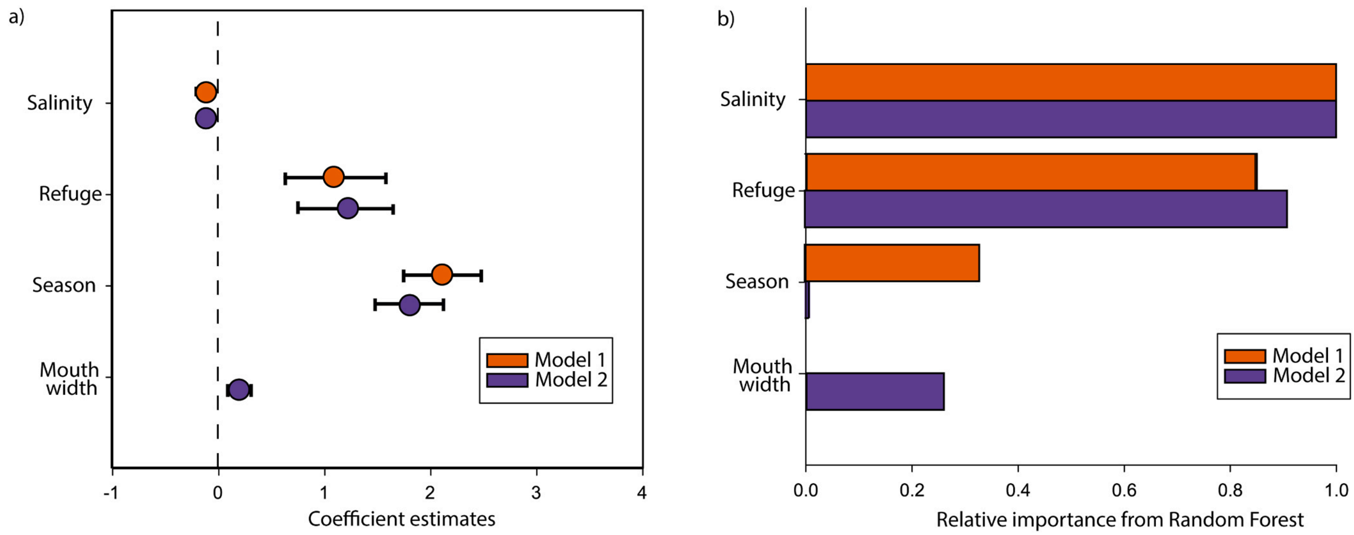


**Fig. 4.** a) Coefficient estimates with 85% confidence intervals (bars) for predictors of the blue crab abundance from top zero-inflated models. Model 1 (in orange) includes Salinity, Refuge availability (presence/absence), and Season (Autumn=1/Spring=2) as predictors. Model 2 (in purple) expands on Model 1 by adding lagoon-sea connectivity (Mouth width). b) Relative importance of estimates for each variable from Random Forest permutation importance analysis.

States (Posey et al., 2005).

The effect of salinity on blue crab abundance could also be indirect and influenced by other factors such as the presence of aquatic vegetation and other types of juvenile habitat (Voigt and Eggleston 2022). In the studied lagoons, historical eutrophication has led to the widespread loss of submerged aquatic vegetation like *Zostera spp*. (Viaroli et al., 2018, Sfriso et al., 2019, 2025). Therefore, the available refuges for juvenile blue crabs are now provided by alternative structures such as common reed (*Phragmites australis*) or artificial substrates such as wooden piles and breakwaters. In Goro lagoon, freshwater inputs from the Po di Volano and Po di Goro mouths create low-salinity areas which, in turn, support dense stands of *Phragmites*. These marsh grasses, along with artificial substrates (e.g., bank-defence stones, oyster aquaculture structures), may provide essential nursery functions (Voigt and Eggleston, 2023, Ciotti et al., 2025). These habitats likely act as both refuges from predation and as feeding grounds for juvenile blue crabs. The importance of refuge areas for blue crab is similar to that observed in the native area of Chesapeake Bay where structured habitats are crucial for juvenile survival (Johnston and Lipcius, 2012).

This study also found a positive relationship between blue crab abundance and lagoon connectivity (i.e., the width of the lagoon mouth or the section of the canal connecting the lagoon to the sea) used as a proxy for larval supply (Epifanio, 1995) suggesting that lagoons with greater connection to the sea and higher rates of water exchange receive great larval input, leading to higher juvenile density. However, we acknowledge that mouth width is a simplified proxy for a more complex network of processes. Hydrodynamic connectivity, which governs water volume exchange and the subsequent influx of larvae, depends on a complex interplay of basin morphology (e.g., channel width and depth) and dynamic forces such as tides, prevailing wind speed and direction, freshwater outflow, and even Coriolis effects (e.g., Eggleston et al., 2015; Etherington and Eggleston, 2000).

This trend is most evident in Goro lagoon, which has a mouth over 3.5 km wide and where the highest densities of juveniles were found, particularly in spring. However, in Goro lagoon, the effects of lagoon-sea connectivity is potentially confounded by other drivers, as freshwater input from the Po River and refuge availability. These co-occurring factors may interact to explain high blue crab densities, making it difficult to isolate the independent effect of connectivity. The wide mouth of Goro lagoon contrasts with the other studied lagoons such as Fattibello lagoon, which are connected to the sea via relatively narrow channels that limit water and larval exchange, resulting in consistently lower juvenile abundance. Conversely, relatively wide connections between lagoon and coastal waters likely amplify the effects of tides, winds and local currents, which are key drivers of recruitment of blue crab larvae and megalopae (Etherington and Eggleston, 2000, Voigt and Eggleston, 2023, Mao and Xia, 2024).

On a regional scale, the proximity of Goro and Comacchio lagoons (<20 km distance) which share similar trophic characteristics, provide a close network of suitable habitats that likely facilitates the establishment and spread of blue crab populations. This regional connectivity may be amplified by larval dispersal. After a pelagic phase of 4–5 weeks, larvae are transported by the prevailing counterclockwise coastal currents in the North Adriatic (Borzelli et al., 1999). These currents could transport larvae released from northern areas in the Adriatic Sea (e.g., Gulf of Trieste) to the Po Delta lagoons within a week, potentially connecting all coastal habitats along the northwestern Adriatic into a large metapopulation, while simultaneously likely prevent larval transport across the Sea from Trieste to Croatia.

Such a high degree of connectivity among estuary populations, if it exists via larval/megalopal connectivity, has also been suggested for blue crab populations along the Brazilian coast (Lacerda et al., 2016). But it contrasts sharply with the wide estuaries of the eastern United States, such as Chesapeake Bay where, for instance, female blue crabs may migrate over 50 km to reach spawning grounds (e.g., Aguilar et al., 2008, Eggleston et al., 2015).

## 5. Implications and limitations

The possible reliance of juvenile blue crabs on refuges like *Phragmites* marsh areas offers a potential for nature-based management. These habitats protect juvenile blue crabs from open-water predators such as the sea bass *Dicentrarchus labrax*, which likely preys on blue crab in the Goro lagoon (Gavioli et al., 2025) as well as adult, cannibalistic blue crabs (Johnson and Eggleston, 2010). However, they may not protect juveniles from predators adapted to foraging in such habitats, such as the European eel (*Anguilla anguilla*). Another eel species, the American eel (*Anguilla rostrata*) is a known blue crab predator in its native range (Hines, 2007), suggesting that restoring the European eel population, which is at a historic low (e.g., Aschonitis et al., 2017), could increase selective predation within nursery habitats.

Finally, although our seine net method was effective for capturing the target juvenile specimens and addressing a key knowledge gap, it was less effective for capturing larger, more mobile adult crabs

(Herrero-Reyes et al., 2025). Therefore, our findings on abundance and distribution patterns are most reflective of the juvenile life stage. Given the rapid spread of the blue crab in the Mediterranean, this study identifies key environmental drivers of juvenile abundance by providing a first baseline; however, future research should employ higher temporal resolution sampling to fully disentangle cohort dynamics.

## 6. Conclusions

This study demonstrated that juvenile blue crab distribution and abundance in the northwestern Adriatic Sea is driven primarily by the interplay of salinity levels, the availability of marsh refuge, and the connectivity between the lagoon and the sea. Complex habitats, such as those containing macrophytes or oyster reefs, provide essential refuges that protect juveniles from predation and enhance survival rates (Eggleston, 1990, Rindone and Eggleston, 2011). Furthermore, high connectivity with marine waters facilitates the recruitment of planktonic larvae, further supporting population establishment.

These insights provide information for developing management strategies for the invasive blue crab. Identifying environmental drivers allows for the creation of predictive maps to pinpoint areas at high risk of invasion (e.g., Siddiolo et al., 2025), as well as model-based estimation techniques that provide density maps for targeted management (e.g., Jones et al., 2025). Management efforts, including early detection and control, should prioritize nursery and feeding grounds as strategic "invasion hotspots" to enhance intervention effectiveness.

Furthermore, our results support an ecosystem-based approach. Restoring populations of native predators, such as the European eel, could strengthen biotic resistance and provide long-term top-down control of blue crab populations (Gavioli et al., 2025). Targeting these key locations and mechanisms offers a more strategic approach to mitigating the impact of blue crabs in the Adriatic Sea and other recently invaded Mediterranean lagoons.

## CRediT authorship contribution statement

**David B. Eggleston:** Writing – original draft, Supervision. **Davide Cardi:** Data curation. **Giuseppe Castaldelli:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Robert R. Christian:** Writing – original draft, Supervision. **Mattia Lanzoni:** Data curation. **Giorgio Mancinelli:** Writing – original draft. **Fernanda Moroni:** Project administration, Data curation. **Piero Franzoi:** Writing – original draft. **Anna Gavioli:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization.

## Funding

This research was supported by Po River Basin District Authority through the project "Study for the assessment of the ecological status of transitional surface water bodies in the Po River hydrographic basin based on the fish fauna biological quality element and through the application of the Habitat Fish Biological Index, with the aim of achieving an overall assessment of the ecological status of these environmental systems" and also by the fish monitoring program of the Emilia-Romagna Region.

## 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.

## Acknowledgements

We would like to thank Luca Bellini, Stefano Bellini, Mattia Corsato and Matteo Melandri for their support with data collection and organization.

## Data availability

Data will be made available on request.

## References

Abdel Razek, F.A., Ismaiel, M., Ameran, M.A.A., 2016. Occurrence of the blue crab *Callinectes sapidus*, Rathbun, 1896, and its fisheries biology in Bardawil Lagoon, Sinai Peninsula, Egypt. Egypt. J. Aquat. Res. 42, 223–229. https://doi.org/10.1016/j.ejar.2016.04.005.

Aguilar, R., Johnson, E.G., Hines, A.H., Kramer, M.A., Goodison, M.R., 2008. Importance of Blue Crab life history for stock enhancement and spatial management of the fishery in Chesapeake Bay. Rev. Fish. Sci. 16, 117–124. https://doi.org/10.1080/10641260701681599.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723.

Aschonitis, V., Castaldelli, G., Lanzoni, M., Rossi, R., Kennedy, C., Fano, E.A., 2017. Long-term records (1781–2013) of European eel (*Anguilla anguilla* L.) production in the Comacchio Lagoon (Italy): evaluation of local and global factors as causes of the population collapse. Aquat. Conserv. Mar. Freshw. Ecosyst. 27, 502–520. https://doi.org/10.1002/aqc.2701.

Bardelli, R., Mancinelli, G., Mazzola, A., Vizzini, S., 2023. The Atlantic blue crab *Callinectes sapidus* spreading in the Tyrrhenian sea: evidence of an established population in the Stagnone di Marsala (Sicily, southern Italy). Nase More 70, 177–183. https://doi.org/10.17818/NM/2023/SI6.

Bartòn K. (2025) Package "MuMIn" Title Multi-Model Inference. Available from: ⟨https://orcid.org/0000-0001-5562-8274⟩.

Bauer, L.J., Miller, T.J., 2010. Temperature-, salinity-, and size-dependent winter mortality of Juvenile Blue Crabs (*Callinectes sapidus*). Estuaries Coasts 33, 668–677. https://doi.org/10.1007/s12237-010-9277-2.

Bell, G.W., Eggleston, D.B., Wolcott, T., 2003. Behavioral responses of free-ranging blue crabs to episodic hypoxia. II. Feeding. Mar. Ecol. Prog. Ser. 227–235.

Bezzi, A., Casagrande, G., Martinucci, D., Pillon, S., Del Grande, C., Fontolan, G., 2019. Modern sedimentary facies in a progradational barrier-spit system: Goro lagoon, Po delta, Italy. Estuar. Coast. Shelf Sci. 227. https://doi.org/10.1016/j.ecss.2019.106323.

Borzelli, G., Manzella, G., Marullo, S., Santoleri, R., 1999. Observations of coastal filaments in the Adriatic Sea. J. Mar. Syst. 20, 187–203. https://doi.org/10.1016/S0924-7963(98)00082-7.

Bromilow, A.M., Lipcius, R.N., 2017. Mechanisms governing ontogenetic habitat shifts: role of trade-offs, predation, and cannibalism for the blue crab. Mar. Ecol. Prog. Ser. 584, 145–159. https://doi.org/10.3354/meps12405.

Brylawski, B.J., Miller, T.J., 2006. Temperature-dependent growth of the blue crab (*Callinectes sapidus*): a molt process approach. Can. J. Fish. Aquat. Sci. 63, 1298–1308. https://doi.org/10.1139/F06-011.

Cataudella S., Crosetti D., Massa F. (2015) Organization Mediterranean coastal lagoons: sustainable management and interactions among aquaculture, capture fisheries and the environment. 293 pp.

Chiesa, S., Petochi, T., Brusà, R.B., Raicevich, S., Cacciatore, F., Franceschini, G., Antonini, C., Vallini, C., Bernarello, V., Oselladore, F., Ciani, M., Di Blasio, L., Campolunghi, M.P., Baldessin, F., Boldrin, L., Marino, G., 2025. Impacts of the blue crab invasion on Manila clam aquaculture in Po Delta coastal lagoons (Northern Adriatic Sea, Italy). Estuar. Coast. Shelf Sci. 312. https://doi.org/10.1016/j.ecss.2024.109037.

Ciotti, B.J., Brown, E.J., Colloca, F., Eggleston, D.B., Hyman, A.C., Le Pape, O., Lipcius, R.N., Maathuis, M.A.M., Poiesz, S.S.H., Rose, K.A., Seitz, R.D., Ventura, D., van de Wolfshaar, K.E., 2025. Measuring juvenile habitat quality for fishes and invertebrates. Biol. Rev. https://doi.org/10.1111/brv.70050.

Clavero, M., Franch, N., Bernardo-Madrid, R., López, V., Abelló, P., Queral, J.M., Mancinelli, G., 2022. Severe, rapid and widespread impacts of an Atlantic blue crab invasion. Mar. Pollut. Bull. 176. https://doi.org/10.1016/j.marpolbul.2022.113479.

Dittel, A.I., Hines, A.H., Ruiz, G.M., Ruffin, K.K., 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. Bull. Mar. Sci. 57, 902–916.

Dulčić, J., Tutman, P., Matić-Skoko, S., Glamuzina, B., 2011. Six years from first record to population establishment: the case of the blue crab, *Callinectes sapidus* Rathbun, 1896 (Brachyura, Portunidae) in the Neretva River Delta (South-Eastern Adriatic Sea, Croatia). Crustaceana 84, 1211–1220. ⟨http://www.jstor.org/stable/23034251⟩ (Available from).

Eggleston, D.B., 1990. Functional responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea virginica* (Gmelin): effects of predator sex and size, and prey size. J. Exp. Mar. Biol. Ecol. 143, 73–90. https://doi.org/10.1016/0022-0981(90)90112-P.

Eggleston, D.B., Millstein, E., Plaia, G., 2015. Timing and route of migration of mature female blue crabs in a tidal estuary. Biol. Lett. 11, 20140936. https://doi.org/10.1098/rsbl.2014.0936.

Eggleston, D.B., Reyns, N.B., Etherington, L.L., Plaia, G.R., Xie, L., 2010. Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement. Fish. Oceanogr. 19, 89–106. https://doi.org/10.1111/j.1365-2419.2009.00530.x.

Epifanio C.E. (1995) 57 Bulletin of Marine Science Transport of Blue Crab (Callinectes sapidus) Larvae in the Waters off Mid-atlantic States.
Epifanio, C.E., 2019. Early life history of the blue crab *Callinectes sapidus*: a review. J. Shellfish. Res. 38, 1–22. https://doi.org/10.2983/035.038.0101.
Etherington, L.L., Eggleston, D.B., 2000. Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. Mar. Ecol. Prog. Ser. 204, 179–198.
Fassatoui, C., Hatira, S., Romdhane, M.S., 2021. Size-weight relationships and condition factor of the invasive Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 (Decapoda: Brachyura: Portunidae) from northern Tunisia: a preliminary investigation. J. Crustace Biol. 41. https://doi.org/10.1093/jcbiol/ruab039.
Forward, R.B., Tankersley, R.A., Welch, J.M., 2003. Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. Bull. Mar. Sci. 347–365. ⟨https://www.researchgate.net/publication/279907099⟩ (Available from).
Forward, R.B., Welch, J.M., 2016. Selective tidal-stream. Transp. Blue Crab Callinectes Sapidus Overv. ⟨https://www.researchgate.net/publication/279907099⟩ (Available from).
Froese, R., 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. J. Appl. Ichthyol. 22, 241–253. https://doi.org/10.1111/j.1439-0426.2006.00805.x.
Fuentes, M., Torrent, L., Barrera, S., Boix, D., 2019. Rapid invasion of the American blue crab *Callinectes sapidus* Rathbun, 1896 in the North-East of the Iberian Peninsula. BioInv. Rec. 8, 113–118. https://doi.org/10.3391/bir.2019.8.1.12.
Gaglio, M., Gavioli, A., Turolla, E., Lanzoni, M., Castaldelli, G., 2025. The costs of an invasion: How the blue crab impaired ecosystem services in the most productive lagoon of northwestern Adriatic. Sci. Total Environ. 1007, 180952.
Gavioli, A., Mancinelli, G., Eggleston, D.B., Christian, R.R., Turolla, E., Lanzoni, M., Castaldelli, G., 2025b. A potential bottom-up cascade on the abundance of invasive Atlantic blue crab Callinectes sapidus in northwestern Adriatic lagoons. Mar. Environ. Res. 107801.
Gavioli, A., Mancinelli, G., Turolla, E., Lanzoni, M., Paesanti, V., Soana, E., Eggleston, D. B., Christian, R.R., Castaldelli, G., 2025. Impacts of the invasive blue crab *Callinectes sapidus* on small-scale fisheries in a Mediterranean lagoon using fishery landing data. Sci. Total Environ. 974. https://doi.org/10.1016/j.scitotenv.2025.179236.
Geppi, E., Riera, R., Colodro, I., Pérez-Ruzafa, Á., 2023. Small but key to nature conservation: small packed communities in a small lagoon from a biodiversity hotspot. Estuar. Coast. Shelf Sci. 295. https://doi.org/10.1016/j.ecss.2023.108546.
Gil-Fernández, A., Rodilla, M., Prado, P., Falco, S., Eggleston, D.B., 2024. Early life stages of the invasive Atlantic blue crab Callinectes sapidus in the Western Mediterranean Sea. Estuar. Coast. Shelf Sci. 296, 108593. https://doi.org/10.1016/j.ecss.2023.108593.
Glamuzina, L., Pešić, A., Marković, O., Tomanić, J., Pećarević, M., Dobroslavić, T., Šćepanović, M.B., Conides, A., Grđan, S., 2023. Population structure of the invasive Atlantic blue crab, *Callinectes sapidus* on the Eastern Adriatic coast (Croatia, Montenegro). Nase More 70, 153–159. https://doi.org/10.17818/NM/2023/SI3.
Glandon, H.L., Halimeda Kilbourne, K., Miller, T.J., 2019. Winter is (not) coming: warming temperatures will affect the overwinter behavior and survival of blue crab. PLoS ONE 14. https://doi.org/10.1371/journal.pone.0219555.
Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: Challenges and solutions. J. Evolut. Biol. 24, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x.
Guillory V., Prejean P. (1997) Blue Crab, Callinectes sapidus, Trap Selectivity Studies: Mesh Size.
Herrero-Reyes, A.A., Guerrero-Gómez, A., Zamora-López, A., Torralva, M., Zamora-Marín, J.M., Oliva-Paterna, F.J., 2025. Population dynamics, habitat use and trapping efficiency of the invasive crab *Callinectes sapidus* in a Mediterranean hypersaline coastal lagoon. NeoBiota 102, 351–375. https://doi.org/10.3897/neobiota.102.148388.
Hines, A.H., 2007. Chapter 14: ecology of Juvenile and Adult Blue Crabs. In: Kennedy, S. V., Cronin, L.E. (Eds.), The Blue Crab: Callinectes sapidus, pp. 565–654.
Hüseyin Atar H., Seçer S. (2003) 27 Turk J Vet Anim Sci Width/Length-Weight Relationships of the Blue Crab (Callinectes sapidus Rathbun 1896) Population Living in Beymelek Lagoon Lake.
Ishwaran H., Kogalur U.B. (2023) Fast Unified Random Forests for Survival, Regression, and Classification (RF-SRC).
Jackman S. (2024) pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory.
Jellyman, P.G., Booker, D.J., Crow, S.K., Bonnett, M.L., Jellyman, D.J., 2013. Does one size fit all? An evaluation of length-weight relationships for New Zealand's freshwater fish species. N. Z. J. Mar. Freshw. Res. 47, 450–468. https://doi.org/10.1080/00288330.2013.781510.
Johnson, E.G., Eggleston, D.B., 2010. Population density, survival and movement of blue crabs in estuarine salt marsh nurseries. Mar. Ecol. Prog. Ser. 407, 135–147. https://doi.org/10.3354/meps08574.
Johnston, C.A., Lipcius, R.N., 2012. Exotic macroalga *Gracilaria vermiculophylla* provides superior nursery habitat for native blue crab in Chesapeake Bay. Mar. Ecol. Prog. Ser. 467, 137–146. https://doi.org/10.3354/meps09935.
Jones, S.A., Liang, D., Tamburri, M.N., Miller, T.J., 2025. Application of Local Area Estimation Using Kriging to Provide Abundance Estimates of Blue Crab in Chesapeake Bay in Support of Management of Dredged Material. Estuaries Coasts 48 (5), 1–11.
Kampouris, T.E., Kouroupakis, E., Batjakas, I.E., 2020. Morphometric relationships of the global invader *Callinectes sapidus* rathbun, 1896 (Decapoda, brachyura, portunidae) from Papapouli lagoon, NW Aegean Sea, Greece. with notes on its ecological preferences. Fishes 5. https://doi.org/10.3390/fishes5010005.
Katselis, G.N., Moutopoulos, D.K., Dimitriou, E.N., Koutsikopoulos, C., 2013. Long-term changes of fisheries landings in enclosed gulf lagoons (Amvrakikos gulf, W Greece): influences of fishing and other human impacts. Estuar. Coast. Shelf Sci. 131, 31–40. https://doi.org/10.1016/j.ecss.2013.07.004.
Kevrekidis, K., Kevrekidis, T., Mogias, A., Boubonari, T., Kantaridou, F., Kaisari, N., Malea, P., Dounas, C., Thessalou-Legaki, M., 2023. Fisheries biology and basic life-cycle characteristics of the invasive Blue Crab Callinectes sapidus Rathbun in the Estuarine Area of the Evros River (Northeast Aegean Sea, Eastern Mediterranean). J. Mar. Sci. Eng. 11. https://doi.org/10.3390/jmse11030462.
Lacerda, A.L.F., Kersanach, R., Cortinhas, M.C.S., Prata, P.F.S., Dumont, L.F.C., Proietti, M.C., Maggioni, R., D'Incao, F., 2016. High connectivity among blue crab (*Callinectes sapidus*) populations in the Western South Atlantic. PLoS ONE 11. https://doi.org/10.1371/journal.pone.0153124.
Lewin, W.C., Dorow, M., Henseler, C., Oesterwind, D., Weltersbach, M.S., Strehlow, H.V., 2023. Temporal development of fish communities in brackish lagoons of the Baltic Sea considering the invasion of the non-indigenous round goby (*Neogobius melanostomus*). Reg. Stud. Mar. Sci. 62, 102953. https://doi.org/10.1016/j.rsma.2023.102953.
Lipcius, R., Eggleston, D., KJr, Heck, Seitz, R., van Montfrans, J., 2007. Ecology of postlarval and young juvenile crabs. In: Kennedy, V., Cronin, L. (Eds.), The blue crab, Callinectes sapidus. Maryland Sea Grant College, College Park, MD, pp. 535–564.
Lipcius, R.N., Seitz, R.D., Seebo, M.S., Colón-Carrión, D., 2005. Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 69–80. https://doi.org/10.1016/j.jembe.2004.12.034.
Mancinelli, G., Chainho, P., Cilenti, L., Falco, S., Kapiris, K., Katselis, G., Ribeiro, F., 2017. On the Atlantic blue crab (*Callinectes sapidus* Rathbun 1896) in southern European coastal waters: time to turn a threat into a resource? Fish. Res. 194, 1–8. https://doi.org/10.1016/j.fishres.2017.05.002.
Mancinelli, G., Lago, N., Scirocco, T., Lillo, O.A., De Giorgi, R., Doria, L., Mancini, E., Mancini, F., Potenza, L., Cilenti, L., 2024. Abundance, size structure, and growth of the invasive Blue Crab *Callinectes sapidus* in the Lesina Lagoon, Southern Adriatic Sea. Biology 13. https://doi.org/10.3390/biology13121051.
Mao, M., Xia, M., 2024. Modeling Blue Crab (*Callinectes sapidus*) Larval transport and recruitment dynamics in a shallow Lagoon-Inlet-Coastal ocean system. J. Geophys. Res. Oceans 129. https://doi.org/10.1029/2023JC020785.
Marchessaux, G., Gjoni, V., Sarà, G., 2023. Environmental drivers of size-based population structure, sexual maturity and fecundity: a study of the invasive blue crab *Callinectes sapidus* (Rathbun, 1896) in the Mediterranean Sea. PLoS ONE 18. https://doi.org/10.1371/journal.pone.0289611.
Matteucci, G., Rossini, P., Guerzoni, S., Arcangeli, A., Fonti, P., Langone, L., Miserocchi, S., 2005. Recent evolution of sedimentary heavy metals in a coastal lagoon contaminated by industrial wastewaters (Pialassa Baiona, Ravenna, Italy). Hydrobiologia 550, 167–173. https://doi.org/10.1007/s10750-005-4374-0.
Milardi, M., Soana, E., Chapman, D., Fano, E.A., Castaldelli, G., 2020. Could a freshwater fish be at the root of dystrophic crises in a coastal lagoon? Sci. Total Environ. 711, 135093. https://doi.org/10.1016/j.scitotenv.2019.135093.
Muchlisin, Z.A., Musman, M., Siti Azizah, M.N., 2010. Length-weight relationships and condition factors of two threatened fishes, *Rasbora tawarensis* and *Poropuntius tawarensis*, endemic to Lake Laut Tawar, Aceh Province, Indonesia. J. Appl. Ichthyol. 26, 949–953. https://doi.org/10.1111/j.1439-0426.2010.01524.x.
Nardelli, L., Fucilli, V., Pinto, H., Elston, J.N., Carignani, A., Petrontino, A., Bozzo, F., Frem, M., 2024. Socio-economic impacts of the recent bio-invasion of *Callinectus sapidus* on small-scale artisanal fishing in southern Italy and Portugal. Front. Mar. Sci. 11. https://doi.org/10.3389/fmars.2024.1466132.
Newton, A., Brito, A.C., Icely, J.D., Derolez, V., Clara, I., Angus, S., Schernewski, G., Inácio, M., Lillebø, A.I., Sousa, A.I., Béjaoui, B., Solidoro, C., Tosic, M., Cañedo-Argüelles, M., Yamamuro, M., Reizopoulou, S., Tseng, H.C., Canu, D., Roselli, L., Maanan, M., Cristina, S., Ruiz-Fernández, A.C., Lima, R.F. de, Kjerfve, B., Rubio-Cisneros, N., Pérez-Ruzafa, A., Marcos, C., Pastres, R., Pranovi, F., Snoussi, M., Turpie, J., Tuchkovenko, Y., Dyack, B., Brookes, J., Povilanskas, R., Khokhlov, V., 2018. Assessing, quantifying and valuing the ecosystem services of coastal lagoons. J. Nat. Conserv. 44, 50–65. https://doi.org/10.1016/j.jnc.2018.02.009.
Noori, A., Moghaddam, P., Kamrani, E., Akbarzadeh, A., Kalvani Neitali, B., Pinheiro, M. A.A., 2015. Condition factor and carapace width versus wet weight relationship in the blue swimming crab *Portunus segnis*. Anim. Biol. 65, 87–99. https://doi.org/10.1163/15707563-00002463.
Ogburn, M.B., Hall, M., Forward, R.B., 2012. Blue crab (*Callinectes sapidus*) larval settlement in North Carolina: environmental forcing, recruit-stock relationships, and numerical modeling. Fish. Oceanogr. 21, 20–32. https://doi.org/10.1111/j.1365-2419.2011.00606.x.
Özdemir, S., Gökçe, G., Çekiç, M., 2015. Determination of Size Selectivity of Traps for Blue Crab (*Callinectes sapidus* Rathbun, 1896) in the Mediterranean Sea. Tar. ıM. Bilim. Derg. 21, 256. https://doi.org/10.15832/tbd.50094.
Pérez-ruzafa, A., Pérez-ruzafa, I.M., Newton, A., Marcos, C., 2019. Coasts and Estuaries Coastal Lagoons: Environmental Variability, Ecosystem Complexity, and Goods and Services Uniformity. Elsevier Inc, pp. 253–276. https://doi.org/10.1016/B978-0-12-814003-1.00015-0.
Poot-Lopez, G.R., Lopez-Rocha, J.A., Gonzalez-Salas, C., Guillĕn-Hernandez, S., VillegasHernandez, H., 2019. Sex related differences in density, selectivity and vulnerability of the Atlantic blue crab, *Callinectes sapidus* (Rathbun, 1896), in the southern Gulf of Mexico. Reg. Stud. Mar. Sci. 32, 100846. https://doi.org/10.1016/j.rsma.2019.100846.
Posey, M.H., Alphin, T.D., Harwell, H., Allen, B., 2005. Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of

southeastern United States. J. Exp. Mar. Biol. Ecol. 81–100. https://doi.org/10.1016/j.jembe.2004.04.021.

QGIS.org, 2024. QGIS Geographic Information System. QGIS Association. https://doi.org/10.5281/zenodo.6139224.

R Studio Team (2024) RStudio: Integrated Development for R.

Rindone, R.R., Eggleston, D.B., 2011. Predator-prey dynamics between recently established stone crabs (Menippe spp.) and oyster prey (*Crassostrea virginica*). J. Exp. Mar. Biol. Ecol. 407, 216–225. https://doi.org/10.1016/j.jembe.2011.06.018.

Rodrigues-Filho, J.L., Macêdo, R.L., Sarmento, H., Pimenta, V.R.A., Alonso, C., Teixeira, C.R., Pagliosa, P.R., Netto, S.A., Santos, N.C.L., Daura-Jorge, F.G., Rocha, O., Horta, P., Branco, J.O., Sartor, R., Muller, J., Cionek, V.M., 2023. 850 Hydrobiologia From ecological functions to ecosystem services: linking coastal lagoons biodiversity with human well-being. Springer International Publishing, pp. 2611–2653. https://doi.org/10.1007/s10750-023-05171-0.

Rodríguez-Ruiz, Á., de Carvalho-Souza, G.F., Herrera, I., González-Gordillo, I., González-Ortegón, E., 2025. Assessing the upper thermal limit constraining the physiological performance of Callinectes sapidus embryogenesis under climate warming scenarios. NeoBiota 102, 63–79. https://doi.org/10.3897/neobiota.102.148122.

Sfriso, A., Buosi, A., Mistri, M., Munari, C., Franzoi, P., Sfriso, A.A., 2019. Long-term changes of the trophic status in transitional ecosystems of the Northern Adriatic Sea, key parameters and future expectations: the lagoon of Venice as a study case. Nat. Conserv. 34, 193–215. https://doi.org/10.3897/natureconservation.34.30473.

Sfriso, A., Buosi, A., Silan, G., Mistri, M., Munari, C., Sfriso, A.A., 2025. Macrophytes and phytoplankton, two primary antithetical producers in degraded water systems. Water 17. https://doi.org/10.3390/w17030338.

Siddiolo, C., Palummo, V., Milisenda, G., Pipitone, C., Rosso, A., Chemello, R., 2025. Assessing habitat suitability and distribution patterns of the Invasive Brachyuran Crabs *Callinectes sapidus* and *Portunus segnis* in the Mediterranean Basin. Mediterranean Marine Sci. https://doi.org/10.12681/mms.38715.

Sumer, C., Teksam, I., Karatas, H., Beyhan, T., Aydin, C.M., 2013. Growth and reproduction biology of the Blue Crab, Callinectes sapidus Rathbun, 1896, in the Beymelek Lagoon (Southwestern Coast of Turkey). Turk. J. Fish. Aquat. Sci. 13, 675–684. https://doi.org/10.4194/1303-2712-v13_4_13.

Summa, D., Turolla, E., Lanzoni, M., Tamisari, E., Castaldelli, G., Tamburini, E., 2023. Life Cycle Assessment (LCA) of Two Different Oyster (*Crassostrea gigas*) Farming Strategies in the Sacca di Goro, Northern Adriatic Sea, Italy. Resources 12. https://doi.org/10.3390/resources12060062.

Tamburini, E., Turolla, E., Lanzoni, M., Moore, D., Castaldelli, G., 2022. Manila clam and Mediterranean mussel aquaculture is sustainable and a net carbon sink. Sci. Total Environ. 848. https://doi.org/10.1016/j.scitotenv.2022.157508.

Taylor, D.L., Fehon, M.M., 2021. Blue Crab (*Callinectes sapidus*) population structure in Southern New England tidal rivers: patterns of shallow-water, unvegetated habitat use and quality. Estuaries Coasts 44, 1320–1343. https://doi.org/10.1007/s12237-020-00867-1.

Tiralongo F., Mancini E., Gattelli R., Di Pasquale C., Rossetti E., Martellucci R., Felici A., Mancinelli G., Mulder C. (2025) The devasting economic impact of Callinectes sapidus on the clam fishing in the Po Delta (Italy): Striking evidence from novel field data. arXiv. https://doi.org/https://doi.org/10.48550/arXiv.2502.07095.

Triay-Portella, R., Martín, J.A., Pajuelo, J., 2024. Growth patterns of the invasive crab *Cronius ruber* (Brachyura, Portunidae) in the Canary Islands (Central-East Atlantic). Reg. Stud. Mar. Sci.

Viaroli, P., Soana, E., Pecora, S., Laini, A., Naldi, M., Fano, E.A., Nizzoli, D., 2018. Space and time variations of watershed N and P budgets and their relationships with reactive N and P loadings in a heavily impacted river basin (Po river, Northern Italy). Sci. Total Environ. 639, 1574–1587. https://doi.org/10.1016/j.scitotenv.2018.05.233.

Voigt, E.P., Eggleston, D.B., 2023. Spatial variation in nursery habitat use by Juvenile Blue crabs in a shallow, Wind-Driven Estuary. Estuaries Coasts 46, 526–540. https://doi.org/10.1007/s12237-022-01143-0.

Voigt, E., Etherington, L., Eggleston, D., 2025. Long-term trends in Juvenile Blue Crab recruitment patterns in a wind-driven estuary. Fish. Oceanogr. https://doi.org/10.1111/fog.70009.

Wickham H. (2016) ggplot2: Elegant Graphics for Data Analysis. https://doi.org/978-3-319-24277-4.

Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression Models for Count Data in *R*. J. Stat. Softw. 27. https://doi.org/10.18637/jss.v027.i08.