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A potential bottom-up cascade on the abundance of invasive Atlantic blue crab *Callinectes sapidus* in northwestern Adriatic lagoons

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ABSTRACT

The introduction of the Atlantic blue crab (*Callinectes sapidus*) in the Mediterranean Sea dates back to the 1900s; however, the species has recently spread in the region resulting in negative impacts on the structure and functions of invaded ecosystems and local fisheries. This study investigated the covariation between spatio-temporal dynamics of the Atlantic blue crab fishery landings (catch-per-unit-area; CPUE) and environmental explanatory variables (i.e., salinity, water temperature, nitrate and chlorophyll-a used as a proxy of primary productivity) over a four-year period (2020–2023) in four key lagoonal ecosystems of the North Adriatic Sea. Our results showed that the marked increase in Atlantic blue crab CPUE in all studied lagoons since 2020 was strongly related with local primary productivity which likely supports a greater abundance of food resources for the suspension feeding Manila clam (*Ruditapes philippinarum*), a key prey for blue crabs and one of the most important fisheries in the region. Conversely, salinity and water temperature, two key parameters regulating blue crab biology, i.e., mating and subsequent larval spawning, did not significantly influence CPUE in the studied lagoons.

These results suggest that primary production in the lagoons, which directly influences food availability (e.g., Manila clams) for the Atlantic blue crab, is the primary factor driving its apparent invasion success in the study area. Our results provide new insights into understanding the environmental factors that promote its invasion and spread, allowing for targeted control measures such as managed fisheries and water quality.

1. Introduction

The introduction of non-indigenous species (NIS hereafter) through human activities has become a major global ecological challenge, resulting in their establishment in a variety of ecosystems. Aquatic ecosystems are particularly susceptible to NIS introductions compared to terrestrial ones (e.g., Vörösmarty et al., 2010), largely due to human activities such as shipping, aquaculture, and the fish trade, which create multiple, hard-to-control pathways for non-native species (Bernery et al., 2024). Additionally, aquatic ecosystems often exhibit lower resistance to the establishment of NIS, due to the greater availability of underexploited ecological niches, thereby reducing biotic resistance to the invasion (e.g., Tarkan et al., 2021). The successful establishment of NIS can lead to a cascade of negative consequences which correspond to

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the overall loss of aquatic biodiversity, including a decrease of native species abundance, the disruption of food webs, the alteration of habitat structure and, ultimately, the reduction in ecosystem services (e.g., Galil et al., 2018; Katsanevakis et al., 2014).

The Mediterranean Sea is experiencing an increase in the introduction rate of NIS which currently exceeds that of any other region in the world (Zenetos and Galanidi, 2020). Major introduction pathways in the region include shipping and ballast water, Lessepsian migration through the Suez Canal, aquaculture and aquarium releases (Azzurro et al., 2022).

NIS, once established, can affect native biodiversity through direct interactions such as competition and predation, as well as indirectly by altering habitats and food webs (Tsirintanis et al., 2022) ultimately becoming invasive (Blackburn et al., 2011). These impacts can have cascading effects on human activities and the services provided by ecosystems. For instance, non-native species can influence the abundance and biomass of marine resources, impacting seafood quality, catch rates, and employment in fisheries and aquaculture (Katsanevakis et al., 2014; Liquete et al., 2013).

However, despite their overall negative impacts, some NIS may offer benefits to humans and native ecosystems such as food supply and climate change mitigation (Sax et al., 2022). For example, in Cyprus, in the eastern Mediterranean, six non-native taxa accounted for more than 25 % of the total value of fisheries landings and representing a remarkable portion of total landings (Kleitou et al., 2022). Another example is represented by the Manila clam (*Ruditapes philippinarum*), which was voluntarily introduced to the Goro Lagoon in Italy in 1986. It rapidly became established and, over the past decades, has represented a key contributor to the region's economy, generating revenue of €60–70 million per year (Tamburini et al., 2022).

One of the most recent dramatic invasions in the Mediterranean Sea is the Atlantic blue crab (*Callinectes sapidus*). This species is included among the 100 most problematic invasive species in the Mediterranean due to its rapid expansion and population growth in the region (Bonanno and Orlando-Bonaca, 2019; Zenetos and Galanidi, 2020). The Atlantic blue crab is native to the western Atlantic Ocean and has been present in the Mediterranean since early 1900s (Mancinelli et al., 2021), likely introduced via ballast water (Nehring, 2011). In its native area, male crabs typically inhabit lower salinity environments, while females prefer higher salinity areas. Mating occurs in mesohaline estuarine zones, after which females migrate to marine spawning grounds characterized by high salinity to release their larvae. The larvae, known as zoeae, develop in the sea before transitioning to megalopae, which return to estuarine waters for maturation (Hines, 2007).

The suitability of these conditions in many areas along the Mediterranean coasts and the adaptability of the Atlantic blue crab to various environmental conditions and food types and availability have facilitated its proliferation throughout the Mediterranean (Clavero et al., 2022; González-Ortegón et al., 2022; Gavioli, et al., 2025a, 2025b). In its native as well as invaded Mediterranean waters, the Atlantic blue crab is recognized as an active and opportunistic predator, including in its diet bivalves as preferred prey together with a wide range of food items such as plants, detritus, polychaetes, gastropods, crustaceans (including conspecifics) and fish (Virnstein, 1977; Eggleston et al., 1992; Mancinelli et al., 2016; Prado et al., 2020, 2024; Cabiddu et al., 2025). Reported impacts in invaded ecosystems highlight dramatic reductions in Manila clam stock in the Po River Delta area (Chiesa et al., 2025) as well as potential community-scale effects such as the corresponding decline in native potential prey species, including those of commercial interest, as blue crab abundance increased (Nardelli et al., 2024) as reported for example in the Ebro Delta of Spain (Clavero et al., 2022) and Po River Delta in Italy (Gavioli et al., 2025b). Several studies have investigated the trophic ecology, dynamic expansion and social perception related to this NIS in the Mediterranean and along the European Atlantic coast (Carrozzo et al., 2014; Mancinelli et al., 2016; Glamuzina et al., 2021; Ortega-Jiménez et al., 2024, 2025; Gavioli et al., 2025b). Several hypotheses have been proposed regarding the drivers of invasion and recent population establishment success by blue crabs in the Mediterranean and Adriatic Sea, such as its physiological adaptability to varying temperature and salinity (e.g., Herrera et al., 2024). Nevertheless, the key drivers underpinning the recent rapid spread and establishment of the Atlantic blue crab in these regions remain to be fully clarified.

The exponential expansion of the Atlantic blue crab within the Mediterranean Sea over the last 5 years (Clavero et al., 2022; Castriota et al., 2024) has highlighted the lack of long-term *in situ* monitoring data for this species, as well as important life history information. This lack of direct ecological observations hinders our understanding of the species' establishment, impacts, and potential future trends (Katsanevakis et al., 2014). Fisheries landing data can help to provide information on species abundance and can also be linked to specific drivers such as climate variables, anthropogenic pressures, or biodiversity indicators to explore the potential drivers of blue crab invasion success in the Mediterranean and Adriatic Seas (Brooks et al., 2016; Coll et al., 2016; Abdelhady et al., 2023; Gavioli et al., 2025b).

This study investigated the relationship between the abundance of Atlantic blue crab and key water quality parameters (i.e., water temperature, salinity, nitrate and chlorophyll-a, as a proxy of primary productivity; Kemp et al., 2005), using fisheries landing data from four lagoon ecosystems in the North Adriatic Sea. We hypothesized that increased water temperature and salinity positively influence blue crab abundance promoting favourable conditions for their reproduction and phenology (e.g., Schneider et al., 2023), ultimately assuming local biotic factors as, key, direct drivers of the species invasion success. Alternatively, we hypothesized that the blue crab abundance might have been regulated by local resource availability through a bottom-up cascade (sensu Hunter and Price, 1992), where the biomass of phytoplanktonic primary producers influences the abundance of filter-feeder bivalve prey, which, in turn, could enhance growth and survival of the local blue crab population.

2. Materials and methods

2.1. Study area

The study area included four hydrogeomorphically and ecologically diverse Italian lagoonal ecosystems located in the Northeastern Adriatic Sea. From north to south: the Grado-Marano lagoon, the Venice Lagoon, a complex of five lagoons in the northern and central part of the Po River delta (i.e, Caleri-Marinetta-Vallona, Barbamarco, Basson, Canarin and Scardovari lagoons), and, finally, the Goro Lagoon, located in the most southern sector of the Po River Delta area (Fig. 1). Specifically, the Grado-Marano lagoon covers an area of approximately 160 $km^2$and is situated between the mouths of the Tagliamento and Isonzo rivers. Its mean depth is approximately 1.2 m, with the deepest areas located in canals and inlets. The lagoon is connected to the sea by five inlets (Acquavita et al., 2015). The lagoon is generally characterised by an abundance of fine-grained sediments, such as mud, silt and clay (Marocco and Princivalle, 1997). The Venice Lagoon is a shallow lagoon with a surface area of 550 km^2 and mean depth around 1 m. The lagoon is connected to the sea by three relatively wide inlets and traversed by shipping canals of different widths and depths (Zucchetta et al., 2016). Sediments are generally a mixture of siliciclastic materials (sand, silt, and clay) and carbonates (Lucchini et al., 2001).The Northern Po Delta lagoonal system consists of a complex of interconnected lagoons and wetlands covering 140 km^2. Major lagoons of this area are the Caleri-Marinetta-Vallona complex, Barbamarco, Basson, Canarin, and Scardovari. Water depths within these environments range from a few centimetres to 5 m, with the substrate primarily composed of mud, silt, and sand.

The Goro Lagoon, located in the southernmost portion of the Po River delta, is a shallow lagoon with a surface area of 26 km^2 and an average depth of about 1.2 m. Its bottom includes areas dominated by

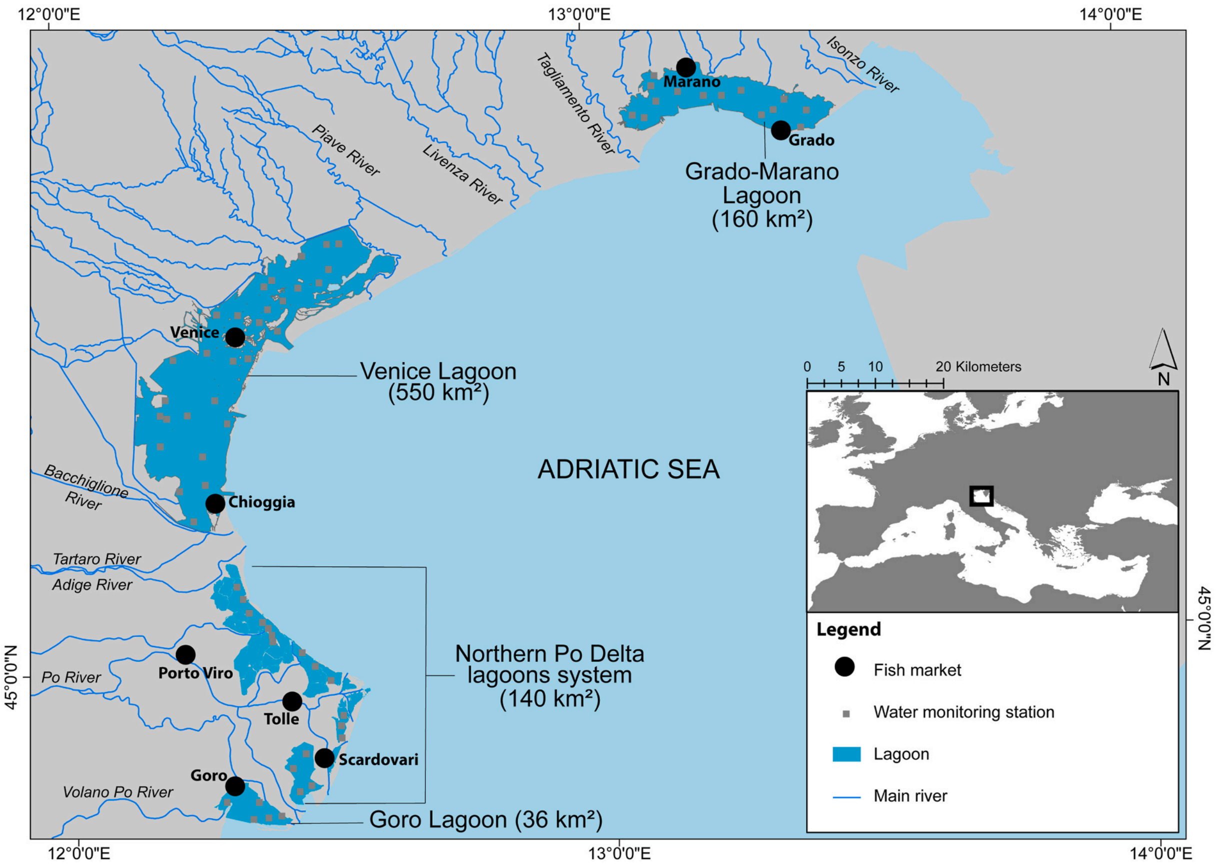

Fig. 1. Map of the study area in North Adriatic Sea showing the four investigated lagoon ecosystems (blue), major Italian rivers (blue lines), the fish market locations (black dots) and the water monitoring station (grey squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mud, silt, sand, as well as artificial substrates such as reefs and navigation markers (Tamburini et al., 2022).

All these lagoonal ecosystems are designated within the European Natura 2000 network of protected areas due to their substantial biodiversity. They support a rich diversity of species and habitats, including salt marshes, seagrass meadows, subtidal and intertidal sand and mud flats, and meandering creeks. In addition, they provide several ecosystem services and serve as a significant source of economic benefit through fisheries and aquaculture. For example, they support the local economy through the farming of Manila clams *R. philippinarum,* with Goro Lagoon alone accounting for a significant portion of the national production (Tamburini et al., 2022).

2.2. Data collection

To assess changes in blue crab abundance, annual landings data of blue crab (kg wet mass per year) were obtained from the fish markets of Grado and Marano (within Grado-Marano Lagoon), Venice and Chioggia (within the Venice Lagoon), Porto Tolle, Porto Viro and Scardovari (within the Northern Po Delta) and Goro (within Goro Lagoon) (Fig. 1). This dataset was kindly provided by the Veneto Agricoltura (https://www.venetoagricoltura.org/home), the public agency dedicated to supporting and developing the primary sector of agriculture, agri-food, forestry, and fisheries. The data spanned in the period between 2020 and 2023, which was chosen because it represents the first consistent period during which the blue crab was present in the official market registers. Prior to 2020, records of blue crab were sporadic or entirely absent, reflecting the negligible densities of the species prior to the step increase in the area (Chiesa et al., 2025; Gaglio et al., 2025; Gavioli et al., 2025b; Tiralongo et al., 2025). The dataset reflected consistent fishing methodology, as for the considered period, landing of blue crab mainly derived from traditional small-scale artisanal fisheries using fyke nets, locally known as "cogolli”. The fyke net was the dominant gear involved in traditional fishing to target finfish species such as European eel *Anguilla anguilla*, the Sand smelt *Atherina boyeri* and shrimps *Palaemon* spp. (e.g., Franzoi et al., 2021). Starting in the second half of 2023, an emergency containment campaign, involving the use of baited metal traps similar to those employed by crab fishermen in the blue crab’s native area (Tonolli, 2024), was performed in the Goro and Scardovari lagoons. This was an attempt to limit the disastrous impact on Manila clam farming areas. Financed by regional authorities, these containment campaigns are ongoing and remain limited to the Scardovari and Goro lagoons.

Most of the blue crabs captured during these control activities were dumped or sold directly at the dock without passing through fish markets (Gaglio et al., 2025). Therefore, to ensure consistency of the data within the landing dataset from the various lagoons throughout the study period, the catches from the blue crab control activities in Goro and Scardovari in the second half of 2023 were excluded from this study.

The studied lagoons in northwestern Adriatic Sea have peculiar features with shallow water and large intertidal areas which imposed shared operational limits on fishing effort such as similar boat and fishing gear among lagoons. Landed biomass of blue crab in the considered period are mostly the result of small artisanal fishery which typically deploy a standardized array of fyke nets (average of 5 fyke nets per boat) due to boat capacity and a standardized soak times (average of 36 h) across the region. The variation in effort per boat is low, making the number of boats fishing in each lagoon a robust proxy for fishing capacity at the large scale (Johnson et al., 2017; Samy-Kamal and Mehanna, 2023).

As result, to account for the different fishing efforts in each lagoon, the annual landings data of Atlantic blue crab obtained from the fish markets (in kg of wet mass) were divided by the number of fishing boats operating in each lagoon annually to calculate the Catch-Per-Unit-Effort (CPUE; in kg of wet mass per boat per year). Data on boat numbers were provided by local fishing cooperatives.

These CPUE values were then used to analyse of the relationship between blue crab CPUE and environmental explanatory variables (see below).

To ensure the geographic attribution of Atlantic blue crab CPUE, we verified with the presidents of fishing cooperatives that the Atlantic blue crabs landed at a specific market were harvested by fishermen operating within a particular lagoon. This is possible because, in these traditional lagoonal fisheries, the distribution of fyke nets in each area and the access of fisherman to each area is mainly based on unwritten laws and customs passed down through many generations (Raicevich et al., 2018). The fishing effort data for blue crabs was then verified by the market directors, who also confirmed the absence of significant Atlantic blue crab deliveries by other fishermen, such as trawlers operating in open waters.

Manila clam biomass data for each lagoon system were obtained from local fishermen's consortia, and was used to generate total biomass (kg of wet mass) rather than CPUE (see e.g., Turolla, 2008), as the clams are cultivated within licensed areas within each single lagoon, according to cooperative strategies, and not harvested from wild populations (Tamburini et al., 2022).

Water quality parameters data were obtained from an institutional monitoring program by the Regional Environmental Protection Agencies of Friuli Venezia-Giulia (ARPAFVG), Veneto Region (ARPAV) and Emilia-Romagna Region (ARPAE), performed seasonally, with data collected every 4 months at fixed sampling stations. To mitigate local heterogeneity, environmental variables were spatially averaged across all monitoring stations within each lagoon (Fig. 1). This approach provides a description of the lagoon at a broad spatial scale, suitable for large scale comparison. Water temperature (in °C), salinity (PSU), nitrate concentration ($mg \cdot l^{-1}$), and chlorophyll-a ($\mu g \cdot l^{-1}$), as proxy of primary productivity, were sampled from 2020 to 2023 and used in this study as annual averages in each lagoon. Furthermore, the annual amplitude of both temperature and salinity was calculated as the difference between their respective annual maximum and minimum values within a specific lagoon, in order to account for the extent of the fluctuation in each lagoon.

2.3. Statistical analysis

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

Prior to analysis, Atlantic blue crab CPUE and environmental variables were log transformed and mean-centered and scaled to unit variance (Bates et al., 2015).

The linear mixed effects (LME) models were used to investigate the relationship between Atlantic blue crab CPUE and the annual average of environmental variables (i.e., water temperature, water temperature amplitude, salinity, salinity amplitude, nitrate concentration, and chlorophyll-a concentration) from 2020 to 2023. LME models are robust even with small sample size (Wiley and Rapp, 2019) and were performed in *lme4* R package (Bates et al., 2015). The year of data collection and the lagoon system were tested as a random effect to account for the temporal and spatial variability, respectively.

To avoid correlation among explanatory variables, a Spearman correlation coefficient of 0.7 was used as an upper threshold to remove variables from the analysis (Dormann et al., 2013).

Primary production in the studied lagoon is driven predominantly by phytoplankton, which is also the primary food source for the Manila clam. Aquatic macrophytes are present in localized areas of the Grado-Marano and Venice lagoons, but are completely absent from all other considered lagoons (e.g., Sfriso et al., 2001; Viaroli et al., 2008; Falace and Sfriso, 2009). We used chlorophyll-a concentration as a proxy for phytoplanktonic primary productivity. This relationship was further confirmed by a significant correlation between chlorophyll-a levels and the abundance of Manila clams ($r_s = 0.9$; $p < 0.05$).

Multicollinearity among the explanatory variables was further assessed using the Variance Inflation Factor (VIF), with a threshold of VIF <4 indicating acceptable levels (Zuur et al., 2009).

A set of candidate models, built using the remaining environmental variables as fixed effects, was then compared. The best model was selected based on the Akaike Information Criterion (AIC; Akaike, 1974) corrected for small sample sizes (AICc; Hurvich and Tsai, 1993) using MuMIn R package (Bartòn, 2025). The selection of the best model was based on Akaike weights (models with large Akaike weights have strong support) and low AICc values (Snipes and Taylor, 2014).

The final model was validated by visually checking residual patterns (Zuur and Ieno, 2016). The marginal R^2 (i.e., the proportion of the total variance explained by the fixed effect) and the conditional R^2 (i.e., the proportion of the variance explained by both fixed and random effects) were also calculated for the best LME model (Nakagawa et al., 2017) through *sjPlot* R package (Lüdecke, 2024).

To assess the trophic coupling between primary producers and benthic consumers, a nonlinear regression analysis fitted to a hyperbolic equation was used to examine the relationship between chlorophyll-a concentration (proxy for phytoplankton primary production) and Manila clam production (proxy for dominant benthic fauna in terms of biomass). The analysis covered the period from 2017 to 2023, including both the years before Atlantic blue crabs were consistently reported in local markets, as well as the years after their presence was documented.

3. Results

During the study period, water quality parameters varied among lagoons, often with trends separating northern from southern lagoons. The annual mean water temperature (±SD) was higher in Northern Po Delta lagoons (20.9 ± 0.6 °C) and Goro Lagoon (18.8 ± 1.5 °C) than in the Venice Lagoon and Grado-Marano Lagoon (17.5 ± 1.5 °C and 16.4 ± 0.8 °C, respectively; Fig. 2a). The annual water temperature amplitude was comparable across all lagoons (Fig. 2b). The annual mean salinity (±SD) was the highest in the Venice (31.8 ± 1.6 PSU) and Grado-Marano lagoons (29.1 ± 1.5 PSU), while the lower values recorded in Northern Po Delta lagoons (27.6 ± 3.0 PSU) and Goro Lagoon (20.9 ± 2.8 PSU) (Fig. 2c). The annual salinity amplitude showed a high variability in Northern Po Delta lagoons (21.8 ± 3.1 PSU) and Goro Lagoon (25.1 ± 4.1 PSU) while a relatively lower variation was observed in Venice (25.6 ± 4.0 PSU) and Grado-Marano lagoons (22.6 ± 3.4 PSU) (Fig. 2d). Annual mean nitrate and chlorophyll-a concentrations were highest in the Goro Lagoon (5.7 ± 0.1 $\mu g\ l^{-1}$ and 0.8 ± 0.03 $mg\ l^{-1}$, respectively) (Fig. 2e and f). No significant correlations ($P > 0.05$) resulted among environmental variables and year of sampling (Supplementary Fig. 1).

The Grado-Marano lagoon had the lowest blue crab CPUEs, remaining close to zero until 2022, with a slight increase in 2023 (724 CPUE). The Venice Lagoon showed blue crab CPUE below 500 until 2023, when it reached a maximum of 1062 CPUE. Similarly, the Northern Po Delta Lagoon system maintained blue crab CPUE below 500 until a steep increase was observed from 1872 CPUE in 2022 to 7560 CPUE in 2023. The Goro Lagoon showed the highest blue crab CPUE throughout the study period, peaking at 9124 CPUE in 2023 (Fig. 3a–d).

Annual mean salinity was excluded from the linear mixed model analysis due to its strong correlation with annual mean nitrate ($r_s = -0.93$, $P < 0.05$) and annual salinity amplitude ($r_s = -0.70$, $P < 0.05$; Supplementary Fig. 1). Furthermore, annual temperature amplitude and annual mean nitrate were also excluded from the mixed model analysis due to high collinearity (VIF>4).

Only annual mean water temperature, annual mean salinity

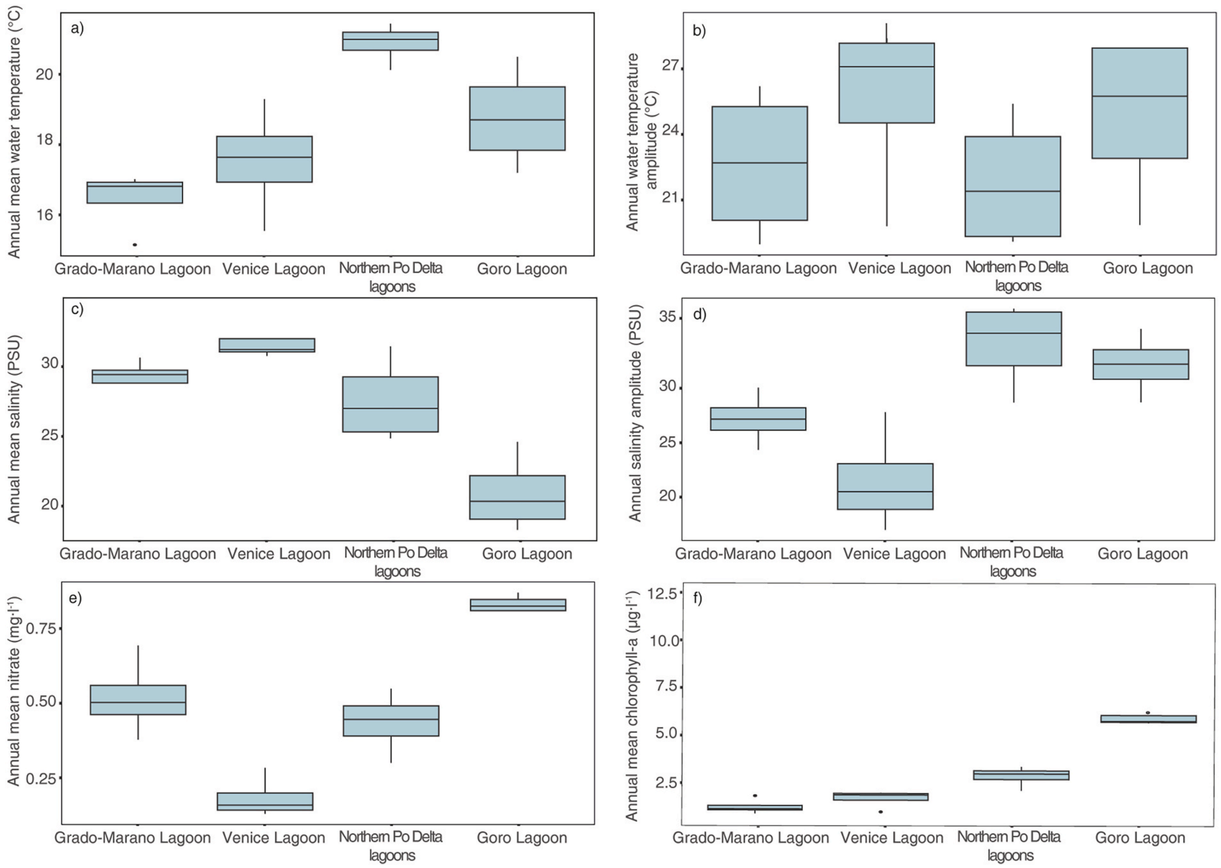

Fig. 2. Boxplots derived from the annual mean values calculated during the study period (2020–2023) of a) annual mean water temperature (°C), b) water temperature amplitude (°C), c) annual mean salinity (PSU), d) salinity amplitude (PSU), e) annual mean nitrate (mg·l^{-1}) and f) annual mean chlorophyll-a (µg·l^{-1}) in the Grado-Marano Lagoon, Venice Lagoon, Northern Po Delta lagoons system and Goro Lagoon.

amplitude and annual mean chlorophyll-a were included in the set of candidate models (Table 1). The best LME model retained from the AIC model selection process included only the annual mean chlorophyll-a as descriptor of blue crab CPUE. Models incorporating annual water temperature and/or salinity consistently ranked lower (Table 1).

Blue crab CPUE was significantly, positively related to annual mean chlorophyll-a (Table 2, Supplementary Fig. 1, Supplementary Figure 2, Fig. 4). The marginal R^2, which accounts for the variance explained only by the fixed effect (i.e., chlorophyll-a concentration), was 0.50, while the conditional R^2, which includes both fixed and random effects (i.e., chlorophyll-a concentration and year of data collection), was 0.81.

From 2017 to 2023, Manila clam production was positively related to annual mean chlorophyll-a concentrations ($R^2_{adj} = 70.98$, $P < 0.05$) in all studied lagoons, with high values of Manila clam production aligning with high annual mean chlorophyll-a concentrations (Supplementary Figure 1, Fig. 4).

4. Discussion

Water quality parameters such as temperature and salinity are widely recognized as important drivers of species distribution patterns within marine ecosystems, frequently used as key predictors in ecological models (Kemp et al., 2005; Pickens et al., 2021). Furthermore, nutrient load and primary productivity play crucial roles in shaping ecosystem properties and processes occurring in coastal lagoons (Viaroli et al., 2008; Cloern et al., 2014). In eutrophic lagoons such those in northwestern Adriatic Sea, increasing nutrient input into coastal lagoons promotes phytoplankton growth (which can be measured by changes in chlorophyll concentrations) and overall primary production (Viaroli et al., 2008).

In our study, neither annual mean water temperature nor annual salinity amplitudes were found to be significant predictors of Atlantic blue crab CPUE; in contrast, in agreement with our alternative scenario, chlorophyll-a concentrations, as a proxy for primary production, promoted greater Atlantic blue crab abundance by influencing the stock of its bivalve prey, suggesting a potential bottom-up cascade in the studied lagoons in the northwestern Adriatic Sea. The following sections investigate and discuss the relations between the abundance of Atlantic blue crabs and environmental variables. We acknowledge that the use of landing data in a non-experimental approach is a matter of debate (Hilborn et al., 2013). Nevertheless, official landing records remain a common tool for answering ecological questions in marine systems where experimental manipulation is challenging (e.g., Aebischer et al., 1990; Estes et al., 1998; Sharma et al., 2025). Regarding our specific dataset, the exclusion of discarded biomass, a practice started in late 2023, means that our trends are conservative estimates.

Furthermore, while this large scale approach identifies significant ecological patterns, we acknowledge that correlation does not truly indicate causation and suggest these results should be further explored using experimental approaches as feasible.

4.1. *Primary productivity effect on Atlantic blue crab*

Chlorophyll-a is widely recognized as an indicator of phytoplanktonic primary productivity in aquatic ecosystems (Ryther, 1956), especially in eutrophic lagoons (Viaroli et al., 2008). Phytoplankton serves as a direct food source for many zooplankton and benthic filter-feeding organisms, such as clams and mussels (Paerl and Justić, 2011). These filter feeders efficiently transfer energy from primary producers to higher trophic levels, including commercially important crabs and fish

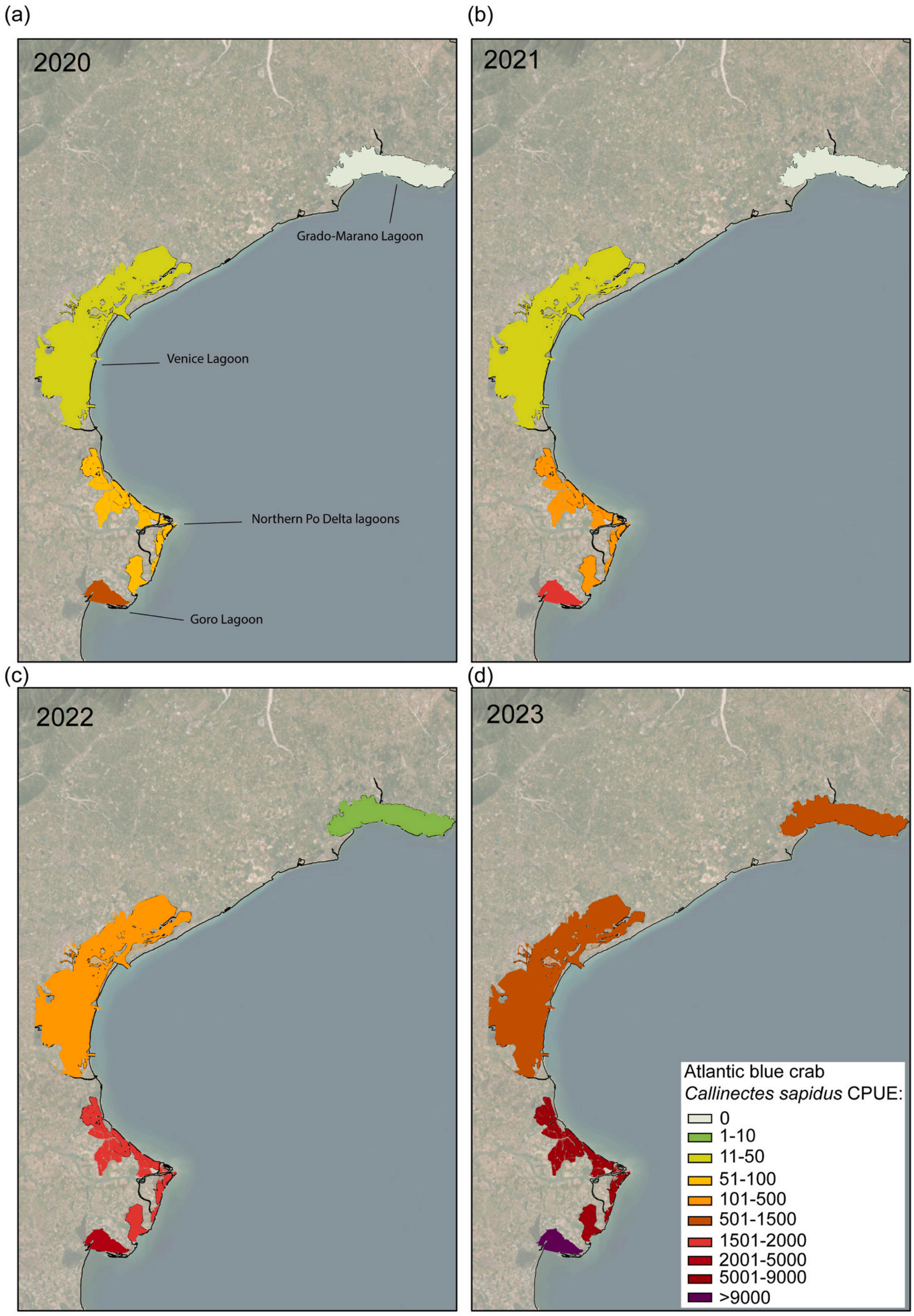

Fig. 3. Atlantic blue crab CPUE (kg of wet mass weight of blue crabs per boat per year) for the 2020 (a), 2021 (b), 2022 (c) and 2023 (d) along the northeastern Adriatic Sea lagoons considered (i.e., Grado-Marano, Venice, Northern Po Delta and Goro lagoons). Colour intensity is proportional to increasing of blue crab CPUE. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(e.g., Kimmerer and Thompson, 2014). In these general terms, elevated chlorophyll-a concentrations indicate greater food resources available, which can significantly influence the recruitment success of juveniles and subsequent growth of various aquatic species, such as the blue swimmer crab, *Portunus armatus*, in Australia (Marks et al., 2020), as well as aid in its stock recovery (Marks et al., 2021).

At the Mediterranean scale, the occurrence of the Atlantic blue crab appears to be linked to nutrient loading (Gavioli et al., 2025a). Higher nutrient inputs are known to stimulate primary production (e.g., Nixon, 1995), and positively correlate with chlorophyll-a concentrations. While chlorophyll-a serves as an indicator of phytoplankton biomass and its associated primary productivity (e.g., Kemp et al., 2005), oligotrophic coastal lagoons can harbour more diverse primary producer communities including macroalgae and aquatic angiosperms compared to eutrophic systems (Sfriso et al., 2022).

In this study, the concentration of chlorophyll-a is used as a proxy for overall primary production as phytoplanktonic primary production provides the primary support to the aquatic food webs of these eutrophic lagoons, such as the Goro Lagoon (Christian et al., 1996). In particular, phytoplankton sustains the aquatic food web in the Northern Po Delta and Goro lagoons, where other benthic primary producers like macroalgae and aquatic angiosperms (e.g., *Ruppia cirrhosa*) have progressively disappeared since the 1980s (Viaroli et al., 2010; Gaglio et al., 2017; Sfriso et al., 2025). Consequently, in these lagoons, chlorophyll-a more directly reflects the dominant primary production supporting higher trophic levels. In contrast, the contribution of macroalgae and aquatic

Table 1
Summary of AIC results for LME models selection correlating Atlantic blue crab *Callinectes sapidus* CPUE and explanatory variables (transformed values). Details for each candidate model include the specified fixed and random effects, the underlying hypothesis being tested, the number of estimated parameters for each model (K), the corrected Akaike's information criterion (AICc), the delta corrected AIC (ΔAICc), and the Akaike weights (AICcWt) are shown.

	Fixed effects	Random effects	Hypothesis	K	AICc	ΔAICc	AICcWt
1	Chlorophyll-a	Year	Blue crab CPUE is explained by chlorophyll-a, accounting for variability across years.	4	−0.01	0	0.96
3	Chlorophyll-a * Water temperature	Year	Blue crab CPUE is explained by the effect of chlorophyll-a and water temperature and their interaction, accounting for variability across years.	6	7.55	7.54	0.02
2	Chlorophyll-a + Water temperature + Salinity amplitude	Year	Blue crab CPUE is explained by chlorophyll-a and physical variables, accounting for variability across years.	6	8.95	8.94	0.01
4	Chlorophyll-a + Water temperature + Salinity amplitude		Blue crab CPUE is explained by chlorophyll-a and physical variables.	5	13.87	13.86	0.0
5	Chlorophyll-a + Water temperature + Salinity amplitude	Year + Lagoon	Blue crab CPUE is explained by chlorophyll-a and physical variables, accounting for variability across years and among different lagoons.	7	15.62	15.61	0.0
6	Water temperature + Salinity amplitude	Year	Blue crab CPUE is explained by physical variables, accounting for variability across years.	5	19.12	19.11	0.0

Table 2
Summary of estimates for the best linear mixed effect model correlating Atlantic blue crab *Callinectes sapidus* CPUE and annual mean chlorophyll-a (transformed values). Years were included as random effect.

Predictor	Estimate	Confidence interval	P-value
(Intercept)	−0.41	−0.68–0.15	0.006
Chlorophyll-a	1.09	0.73–1.44	<0.001

angiosperms to primary productivity can be substantially higher than that of phytoplankton in other lagoons like Venice and Grado-Marano (Sfriso et al., 2001; Falace and Sfriso, 2009). Therefore, the observed relationship between the blue crab CPUE and chlorophyll-a suggests a bottom-up trophic effect, where high phytoplanktonic primary production supports high blue crab abundance by providing more food for the benthic secondary producers, such as benthic macrofauna (Christian et al., 1996). In fact, chlorophyll-a concentrations directly sustained filter feeders like the Manila clam (Burkholder and Shumway, 2011; Nizzoli et al., 2011, Fig. 4) which, in turn, are an important dietary component for the Atlantic blue crab (Virnstein, 1977; Eggleston et al., 1992; Mancinelli et al., 2016; Cabiddu et al., 2025; Chiesa et al., 2025), suggesting a potential bottom-up cascade on the abundance of the Atlantic blue crab in the study area.

The Atlantic blue crab is a generalist predator, consuming a wide range of prey including epibenthic invertebrates, fish, other crustaceans, plant matter, and detritus (Hines, 2007; Mancinelli et al., 2016; Gil-Fernández et al., 2024; Ortega-Jiménez et al., 2025). This dietary flexibility makes it unsurprising that higher blue crab CPUEs are found in areas where food resources are abundant.

While aquatic vegetation can serve as nursery ground for the juveniles of Atlantic blue crab (Hines, 2007; Lipcius et al., 2007), further investigation is required on this aspect since crab life history stage and sex information of crabs landed to the market were unavailable. Nevertheless, juvenile crabs were also found in Goro Lagoon, where aquatic vegetation is scarce (*unpublished data*).

Furthermore, a spatial pattern was identified across all four years of data collection, with the blue crab CPUEs showing an increase from the northern lagoons towards the southern ones from 2020 to 2023 (Fig. 3). This pattern, which aligns with chlorophyll-a concentrations, could be explained by the anticlockwise circulation of the Adriatic Sea (Artegiani et al., 1997). This circulation pattern transports nutrient-rich waters discharged by many rivers and canals, which drain the intensively agricultural areas of the Friuli and Veneto regions and, proceeding southwest, to the whole Po River basin. The main rivers contributing to this nutrient load, listed from north to south, include the Isonzo, Tagliamento, Piave, Sile, Brenta, Adige, and Po (Cozzi and Giani, 2011; Sani et al., 2024).Consequently, along the northwestern Adriatic coast, lagoons and coastal environments receive increasingly nutrient-rich and productive waters as they move from north to south, peaking in the southernmost lagoon of the Po Delta, the Goro Lagoon, where the highest abundance of blue crab was recorded throughout the study period. This anti-cyclonic circulation could also help to deliver relatively high concentrations of blue crab megalopae to the southern lagoons compared to the north, however, this hypothesis remains to be tested.

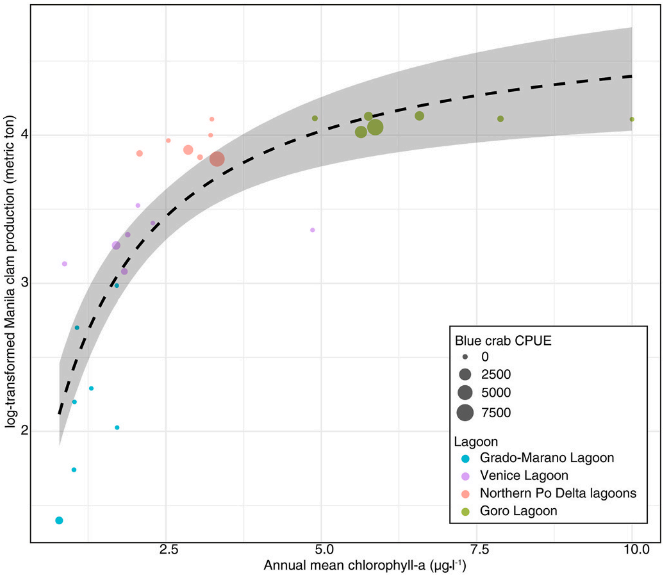

Fig. 4. Relationship between the Manila clam production (metric ton) and the annual mean chlorophyll-a (μg·l^{-1}) in the Northeastern Adriatic Sea lagoons from 2017 to 2023 (N = 24). Data points are coloured by lagoon: Grado-Marano (cyan), Venice (purple), Northern Po Delta (orange), and Goro (green) and scaled by Atlantic blue crab CPUE. The overall non-linear regression curve for Manila clam biomass (black dashed line) and the 95 % confidence interval (grey) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.2. *Water temperature and salinity effects on the Atlantic blue crab*

Water temperature and salinity play a crucial role in the invasion dynamics in aquatic ecosystems. For example, invasive species often thrive in environments with fluctuating salinity levels, or salinities within a narrow range (Occhipinti-Ambrogi and Savini, 2003; Christianson and Eggleston, 2021). These two key parameters are informative environmental variables influencing the distribution of the Atlantic blue crab in its native and non-native range (Rome et al., 2005; Marchessaux et al., 2023). For example, water temperature can influence the Atlantic blue crab's feeding activities, larval survival, and development (Rome et al., 2005). Specifically, water temperature determines the growth rate and dormancy of the Atlantic blue crab, with a critical threshold of 9 °C, below which metabolic rates decrease, and dormancy is induced (Brylawski and Miller, 2006). In addition, shorter winters associated with relatively warm water temperatures are predicted to increase overwintering survival, extend seasonal growth, and subsequently increase population size in the native area of the Chesapeake Bay (Glandon et al., 2019).

Furthermore, sub-adult and adult male crabs inhabit lower salinity waters, while females prefer higher salinity waters (Hines, 2007). Prior to their final molt to maturity, female crabs mate with males in the mesohaline zones of estuaries, followed by female migration down-estuary to the spawning grounds in high salinity areas where they release larvae (Hines, 2007). In the Mediterranean Sea, mesohaline and polyhaline lagoons (from 5 to 30 PSU) were found to be the most favourable environments to support Atlantic blue crab populations (Marchessaux et al., 2024).

Unexpectedly, contrary to our hypothesis, mean annual water temperatures and salinity amplitude were not retained as significant predictors of the Atlantic blue crab abundance in this study. The lack of strong relationship with temperature is likely due to the relatively stable conditions observed, as annual mean water temperatures varied within a narrow range of 15 °C–21 °C. This limited thermal variation may have been insufficient to cause detectable spatiotemporal changes in the blue crab population. Similarly, although the study area is influences by both freshwater inputs and marine saltwater, the resulting salinity amplitudes was relatively narrow (21.8 PSU to 25.1 PSU), likely due to stable conditions across the small spatial scale. This wide range of suitable habitats likely masks the effects of localized salinity variations. Furthermore, the lack of correlation is also likely consistent with the physiological tolerance of the blue crab. As an eurythermal and euryhaline species, it can tolerate a wide range of temperature and salinity (Mancinelli et al., 2021; Marchessaux et al., 2024). Consequently, at this broad spatial scale, abiotic variables did not act as limiting factors; instead, the biomass of blue crab appears to be driven by metabolic demand for food resources. In fact, the effects of salinity and temperature on blue crab population could operate at different spatial and temporal scales, consequently their effects may be clearer when analysing seasonal patterns of temperature, long-term temperature dynamics, or specific life stages of the Atlantic blue crab (Rome et al., 2005). For instance, in their native habitat, juvenile blue crabs typically reach higher densities in salt marshes characterized by relatively high salinity, after which they spread to relatively low salinity regions as they grow into sub-adults (Johnson and Eggleston, 2010; Voigt and Eggleston, 2022). Unfortunately, our fisheries landing data, which primarily reflects market-sized crabs, lacks the necessary detail for such analyses of juvenile distribution and abundance patterns. Therefore, we cannot assess the potential effects on processes such as larval development or juvenile recruitment, which are often more sensitive to environmental fluctuations.

5. Conclusions

Our results provide the first large-scale investigation into the potential drivers of the invasion success of the Atlantic blue crab in the economically important northwestern Adriatic Sea region.

Our results reveal a large increase in landed biomass between 2020 and 2023 in all studied lagoons, identifying chlorophyll-a, as a proxy of primary productivity, as the main predictor of this pattern. This result suggest that high abundance of blue crab in this region was mainly driven by trophic availability rather than physiological constraints. Consequently, coastal areas characterized by lower primary productivity may be less vulnerable to severe invasion, as the limited availability of food resources could make it difficult for the Atlantic blue crab to spread. This insight is crucial not only for understanding the ecological requirements of the species but also for predicting its potential spread in the Mediterranean Sea.

Furthermore, in a climate change scenario involving enhanced primary productivity (Barrera-Alba et al., 2009) and given the difficulty of controlling nutrient inputs in the northwestern Adriatic (Viaroli et al., 2018), our finding that primary productivity drives Atlantic blue crab abundance underscores the risk of this invasive species spreading further. To better predict its expansion, future research should prioritize fine-scale investigations into the combined effects of temperature and productivity across different life stages of the Atlantic blue crab. Finally, this work also highlights the importance of integrate local ecological knowledge from fishermen into scientific research, as fishermen act as sentinel for early detection and environmental assessment (Azzurro et al., 2019).

CRediT authorship contribution statement

Anna Gavioli: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Giorgio Mancinelli:** Writing – review & editing, Writing – original draft, Methodology. **David B. Eggleston:** Writing – review & editing, Writing – original draft, Supervision. **Robert R. Christian:** Writing – review & editing, Writing – original draft, Supervision. **Edoardo Turolla:** Data curation. **Mattia Lanzoni:** Data curation. **Elisa Soana:** Data curation. **Emanuele Rossetti:** Data curation. **Antonio Gottardo:** Data curation. **Luigi Vidal:** Data curation. **Aurelio Zentilin:** Data curation. **Giuseppe Castaldelli:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107801.

Data availability

Data will be made available on request.

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