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# Impacts of the invasive blue crab *Callinectes sapidus* on small-scale fisheries in a Mediterranean lagoon using fishery landing data

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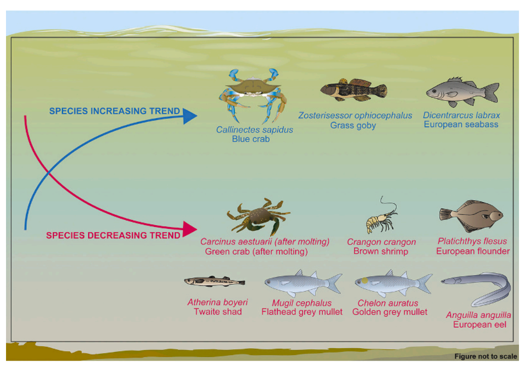
## HIGHLIGHTS

- Atlantic blue crab impacts on Mediterranean biodiversity and fisheries
- Study examines the impact of blue crab on small-scale fisheries in Mediterranean Sea
- Blue crab spread overlaps with decline of several commercial species
- Environmental factors not primary cause of changes in fishery trends
- Integrated management strategies needed to control blue crab abundance

## GRAPHICAL ABSTRACT

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## ABSTRACT

Human activities have introduced numerous non-native species beyond their natural habitats, leading to their establishment in new regions. Among them, the Atlantic blue crab (*Callinectes sapidus*) has significantly impacted biodiversity and fisheries in the Mediterranean Sea. This study investigates the recent population increase of *C. sapidus* associated changes of small-scale fisheries in one Mediterranean lagoon, the Sacca di Goro lagoon within the Po River Delta. We analysed the influence of environmental factors and *C. sapidus* biomass on trends in landings of commercially important species, using multivariate analysis, including principal component analysis (PCA) and redundancy analysis (RDA), as well as variance partitioning, linear regression and change point analysis on fishery landings data. Our results suggest that the spread of *C. sapidus* coincides with a decline in several commercial species, such as the European flounder (*Platichthys flesus*), the big-scale sand smelt (*Atherina boyeri*), the European eel (*Anguilla anguilla*) and the Mediterranean green crab (*Carcinus aestuarii*), suggesting a

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strong ecological and economic impacts of the blue crab invasion. The main mechanisms by which *C. sapidus* could drive this trend likely involve predation and competition, although further investigation is needed for confirmation.

Annually averaged environmental variables (i.e., water temperature, salinity, nitrate and chlorophyll-*a* concentrations) were not significant predictors of commercial species trends, suggesting that the changes in landings cannot be primarily attributed to environmental factors. This study is the first to provide a comprehensive analysis of the potential effects of *C. sapidus* on the relative abundance of key fisheries species in Mediterranean Sea, suggesting a potential link between the rapid increase in its abundance and observed fish landing trends. The results highlight the need for integrated management strategies, including promoting market opportunities for *C. sapidus* and consideration of ecosystem-based management to control its abundance such as the protection of native local predators.

## 1. Introduction

A considerable number of non-native species have been introduced by humans beyond their natural range. Among these, approximately 3500 species have become invasive, posing a significant threat to global biodiversity and ecosystem functioning, as well as causing economic losses (Lovell et al., 2006; Roy et al., 2024). The Mediterranean region, globally recognized as one of the 25 biodiversity hotspots with a high number of endemic species (Myers et al., 2000), is also a hotspot for biological invasions (Roy et al., 2024) with 1000 introduced species in the Mediterranean Sea (Zenetos and Galanidi, 2020).

Non-native species can impact native biodiversity through direct biotic interactions, such as competition and predation and indirectly through alteration of habitat functions and community structure (Tsirintanis et al., 2022). These impacts can ultimately influence human activities and ecosystem services. Non-native species can affect abundance and biomass of living marine resources, sea food quality, fishery landings, jobs in fisheries and aquaculture degradation of habitats and disruption of their functions, predation and competition with species of commercial or conservation interest, diseases transmission, entanglement in nets, and fouling of shellfish gear (Liquete et al., 2013; Katsanevakis et al., 2014). For example, the decline in commercial stocks of the Mediterranean mussel (*Mitilus galloprovincialis*) and the *Pacific oyster* (*Magallana gigas*) in the Black Sea has been related to predation by the invasive, predatory snail *Rapana venosa* (Katsanevakis et al., 2014 and references therein). Similarly, the non-native fish silverstripe blaasop (*Lagocephalus sceleratus*), the Atlantic blue crab (*Callinectes sapidus*) and the African blue swimming crab (*Portunus segnis*) have been reported to interfere with local fisheries by preying on fish catches and damaging fishing nets (Tsirintanis et al., 2022 and references therein). In general, invasive species have detrimental effects; however, in some cases they may provide benefits to humans and native species. For example, the non-native Manila clam (*Ruditapes philippinarum*) is an important species in shellfish aquaculture worldwide and particularly in northern Italy (Tamburini et al., 2022). Some non-native species can serve as a food source for native organisms, as in the case of the red swamp crayfish *Procambarus clarkii* in freshwater ecosystems of the Po River basin (Gavioli et al., 2018).

While the debate on the benefits of non-native species is still open (e.g., Kleitou et al., 2022), the spread of non-native species in the Mediterranean Sea is ongoing. Recently, much attention has been paid to the *C. sapidus*), an invasive species that has spread rapidly across the Mediterranean, so that it has been included among the 100 'worst' invasive species in the Mediterranean (Bonanno and Orlando-Bonaca, 2019; Zenetos and Galanidi, 2020; Gavioli et al., 2024). *Callinectes sapidus* is a crustacean native to the western Atlantic Ocean, which has been reported in the Mediterranean Sea since 1949, probably introduced through ballast water (Nehring, 2011), and which colonized almost all Mediterranean coasts (Mancinelli et al., 2021). Although the causes of the recent spread of *C. sapidus* in the Mediterranean Sea are not yet fully clarified, some hypotheses on its expansion due to thermal and salinity drivers and dispersal mechanism mediated by shipping in the first stage of its invasion (e.g., Marchessaux et al., 2023) were suggested. Nevertheless, its exceptional adaptability to different habitats and food availability has favoured its colonization of different areas throughout the Mediterranean. *Callinectes sapidus* adapt to a wide range of salinity conditions with adult male crabs typically occupying lower salinity waters, while females can be found in higher salinity waters. Specifically, mating occurs in the mesohaline zones of estuaries and other transitional habitats, after which females migrate to marine spawning grounds, characterized by high salinity, where they release their larvae. Larval stages develop in the ocean for approximately 30 days after which they molt into a megalopal stage that disperses into the estuary and settles in structurally complex habitats such as seagrass and shallow detritus (Etherington and Eggleston, 2000, Hines, 2007). All these habitat conditions, essential for the successful reproduction of *C. sapidus,* are common to many coastal sectors of the Mediterranean Sea, and additionally, *C. sapidus* is known to consume a wide range of food resources, and its opportunistic omnivory has been indicated both in the native and introduced ranges of the species. In the Mediterranean region, *C. sapidus*'s diet includes plants, detritus, polychaetes, molluscs, crustaceans, and fish (Carrozzo et al., 2014; Mancinelli et al., 2017; Prado et al., 2022; Encarnação et al., 2025). Among these, bivalves appear to be a favourite prey item for both *C. sapidus* juveniles and adults (Prado et al., 2024b). The large dietary spectrum includes species targeted by commercial and recreational fisheries (Clavero et al., 2022). These life history and habitat requirements likely explain the successful establishment of *C. sapidus* in the Mediterranean and Adriatic Seas. The impact on artisanal fisheries is initially severe, as blue crabs reduce both the quantity and quality of catches, resulting in lower incomes for local fishermen and increases in managing and mitigating costs (e.g., Nardelli et al., 2024).

While many studies have focused on the impact of *C. sapidus* on single species, especially bivalves (e.g., Longmire et al., 2022), information on its wider effects at the community level remains in Mediterranean region is sparse.

This study focuses on the Sacca di Goro lagoon, the most productive lagoon in the Po River Delta (northeastern Adriatic Sea), where we investigated, for the first time in Italy, the impact of the invasive *C. sapidus* on the local fishery, which includes the cultivation of the *R. philippinarum*. Although *C. sapidus* has been reported in the northern Adriatic Sea since 1949, its population exploded in recent years, posing a significant threat to the fisheries sector, especially in the Po River Delta where the most important Italian shellfish farms are located. Specifically, by analysing the landings data of the small-scale fisheries from the Goro fish market, the main objectives were to explore: (1) the key factors (i.e., *C. sapidus* landed biomass, water temperature, salinity, nitrate, and chlorophyll *a*) influencing trends in landings of commercially important species that serve as potential prey of blue crabs; and (2) changes in temporal trends in species landed. To our knowledge, this study represents the first analysis of the potential impact of *C. sapidus* on fisheries in Italy.

## 2. Materials and methods

### 2.1. Study area

The Sacca di Goro is a shallow lagoon with a surface area of 20 km$^2$ and an average depth of about 1.2 m, located in north-eastern of Italy (Fig. 1). The lagoon is connected to the Adriatic Sea by a 1.5 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 (Fig. 1). 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).

Despite its relatively small size, the Sacca di Goro lagoon plays a crucial role in the local economy, providing the main income for the local population through fishing, shellfish farming and related activities. At present, local shellfish farming is divided between clams (*R. philippinarum*), mussels (*M. galloprovincialis*) and, to a lesser extent, oysters (*M. gigas*), which together account for almost half of Italy's total farmed shellfish production (Summa et al., 2023; Tamburini et al., 2022).

### 2.2. Fishery and environmental data

Annual landings data from the Goro wholesale fish market were used to assess changes in fishery relative abundance from 2009 to 2023. Landings data included, by definition, only information about species caught and brought to shore by commercial fishers. The dataset was kindly provided by the Veneto Agricoltura, an agency for fisheries innovation in the primary sector of the Veneto Region, as well as the Goro fishermen's consortium (CO.PE.GO) which is the largest cooperative of Manila clam farmers and operates the only wholesale fish market in the entire lagoon north-western Adriatic District. The dataset includes the annual landings of the Goro fishing fleet (in kg). During last years (2017–2023), the fishing effort due to number of boats fishing in the Goro fleet and their equipment did not change significantly, as evidenced by the sales records of the fish market, however to better account for fishing effort the annual landings data have been expressed and analysed as catch per unit of effort (CPUE) dividing the landed quantity at the market (kg wet mass) by the number of fishing boats operating in the area for each year for all species caught in the lagoon (i.e., kg wet mass by taxa per boat-year). The production of *R. philippinarum* has not been expressed as CPUE because it is independent of the fishing effort, since the species is cultivated within the licensed areas according to the strategies of cooperatives and is not caught in the wild (Tamburini et al., 2022). Finally, to verify species trends, we conducted interviews with both randomly selected and trusted fishermen. In all cases, the testimonies confirmed the trends derived from market sales for the most commonly caught species.

Only data related to the Sacca di Goro lagoon fishery, as identifiable from the market bill records, were extracted and included in the analyses. Specifically, we extracted data on annual landings of *C sapidus*, Mugillidae (the Thicklip grey mullet *Chelon labrosus,* the Thinlip mullet *Chelon ramada,* the Golden grey mullet *Chelon auratus,* the Leaping mullet *Chelon saliens* and the Flathead grey mullet *Mugil cephalus*), Gobiidae (the Sand goby *Pomatoschistus minutus* and the Grass goby *Zosterisessor ophiocephalus*), Decapoda (the Green crab *Carcinus aestuarii*, the Brown shrimp *Crangon crangon* and the Baltic prawn *Palaemon adspersus*), predatory fish (the European eel *Anguilla anguilla*, the European seabass *Dicentrarchus labrax* and the Gilt-head bream *Sparus aurata*), lagoon residents (the Twaite shad *Atherina boyeri* and the European flounder *Platichthys flesus*) and Veneridae (*R. philippinarum*). According to fishery market data, *C. aestuarii* was divided into two landing categories: mature female of *C. aestuarii* (called "granzela" in Goro) and *C. aestuarii* after molting (called "moeca" in Goro) (Table 1).

Environmental data, including water temperature, salinity, nitrate and chlorophyll *a* (used as proxy of primary production in the lagoon), were collected from the institutional monitoring program of the project Life AGREE- coAstal laGoon long teRm managEmEnt (LIFE13 NAT/IT/000115) and from the institutional monitoring program of Emilia-Romagna Region Environmental Protection Agency (ARPA Emilia Romagna). These monitoring programs spanned from 2009 to 2023 using common and standardized sampling procedures. The annual average of water temperature, salinity, nitrate and chlorophyll *a* were included in the analysis to investigate their effect on the annual landing data of selected species (Supplementary Table 1).

### 2.3. Data analysis

Variables were mean-centered and standardized prior to the analysis. Principal components analysis (PCA) was used to characterise variation in CPUE data of selected species (Table 1) from 2009 through 2023. Redundancy analysis (RDA) was performed to identify which explanatory variables (i.e., water temperature, salinity, nitrate, chlorophyll *a* and *C. sapidus*) best explain the variation of landed species (response variables). Collinear variables were checked with Variance Inflation Factor (VIF) to exclude variables with VIF $>$ 7 (Lepš and Šmilauer,

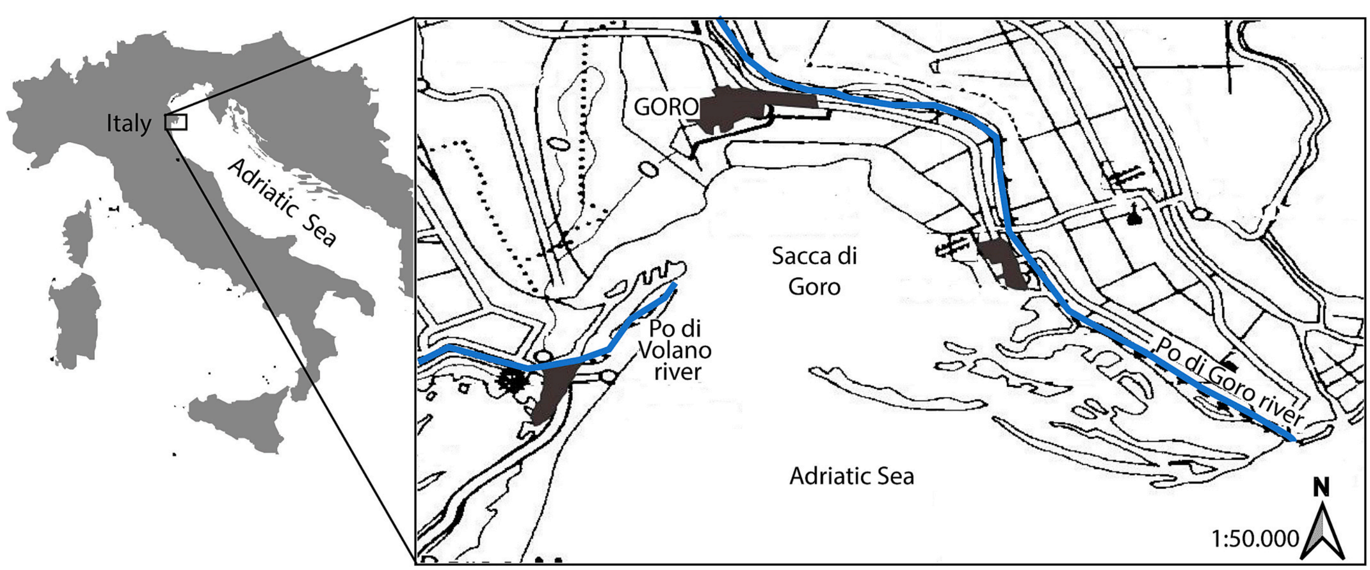


**Fig. 1.** Map of the study area of Sacca di Goro lagoon. Main freshwater inputs are shown in blue, urbanized areas in black.

**Table 1**
Annual CPUE (kg wet mass by taxa per boat-year) average, minimum and maximum of landed species in the Sacca di Goro fish market in the period 2009–2023.

| Family | Scientific name | Common name | Average (CPUE) | Minimum (CPUE) | Maximum (CPUE) |
|---|---|---|---|---|---|
| Anguillidae | *Anguilla anguilla* | European eel | 92 | 8 | 228 |
| Atherinidae | *Atherina boyeri* | Twaite shad | 330 | 27 | 875 |
| Moronidae | *Dicentrarchus labrax* | European seabass | 92 | 53 | 157 |
| Sparidae | *Sparus aurata* | Gilt-head bream | 91 | 26 | 195 |
| Gobiidae | *Pomatoschistus minutus* | Sand goby | 20 | 0 | 245 |
| Gobiidae | *Zosterisessor ophiocephalus* | Grass goby | 42 | 14 | 167 |
| Mugilidae | *Chelon auratus* | Golden grey mullet | 455 | 118 | 740 |
| Mugilidae | *Chelon labrosus* | Thicklip grey mullet | 29 | 3 | 69 |
| Mugilidae | *Chelon ramada* | Thinlip mullet | 5708 | 2935 | 8004 |
| Mugilidae | *Chelon saliens* | Leaping mullet | 75 | 23 | 161 |
| Mugilidae | *Mugil cephalus* | Flathead grey mullet | 114 | 18 | 314 |
| Pleuronectidae | *Platichthys flesus* | European flounder | 69 | 2 | 257 |
| Portunidae | *Callinectes sapidus* | Atlantic blue crab | 1086 | 0 | 9124 |
| Carcinidae | *Carcinus aestuarii* (after molting) | Green crab (after molting) | 612 | 39 | 2346 |
| Carcinidae | *Carcinus aestuarii* (mature female) | Green crab (mature female) | 5384 | 118 | 936 |
| Crangonidae | *Crangon crangon* | Brown shrimp | 45 | 0 | 127 |
| Palaemonidae | *Palaemon* spp. | Baltic prawn | 970 | 530 | 1431 |

2003). Variance partitioning was also run to identify the marginal and the conditional effects of each descriptor variable. The marginal effect of a descriptor variable estimates its independent contribution to explaining the amount of variability in the response data. The conditional effect estimates the effect of each explanatory variable in addition to all variables (Lepš and Šmilauer, 2003). To identify when *C. sapidus* landings data showed a break or change point from 2009 to 2023, a Lanzante's procedure for single change point detection with Wilcoxon-Mann-Whitney test was applied (Pohlert, 2020). Simple linear regression was used to investigate temporal trends in CPUEs after the year of change point in *C. sapidus* CPUE data. The angular coefficients of standardized CPUEs were analysed to determine both the direction and the magnitude of *C. sapidus* on the landed species. Multiple linear regression was used to test the relationship between *C. sapidus* CPUE and

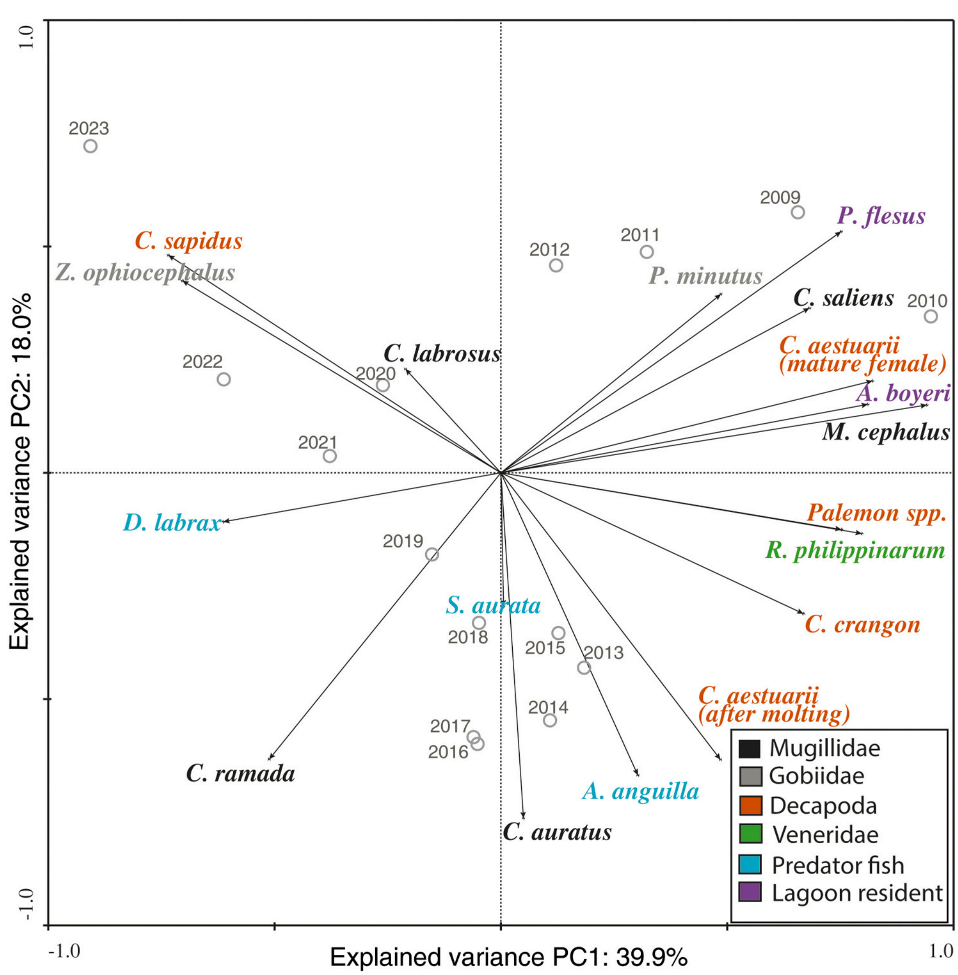


**Fig. 2.** Biplot of principal component analyses (PCA) showing landed species in the fish market of the Sacca di Goro lagoon from 2009 to 2023 (grey circles). Species colours referred to Mugillidae (black), Gobiidae (grey), Decapoda (red), Veneridae (green), predator fish (light blue) and lagoon resident (purple). The extended scientific names and the common names of the species are provided in Table 1.

environmental variables. Multivariate analyses (i.e., PCA and RDA) were performed in CANOCO 4.5 (Lepš and Šmilauer, 2003). The linear regression and the change point analysis (Pohlert, 2020) were performed in RStudio software (R Studio Team, 2024).

## 3. Results

The aquacultural production of *R. philippinarum* ranged from $10.2 \times 10^7$ kg to $1.88 \times 10^7$ kg with a mean value of $1.41 \times 10^7$ kg and catches outside the licensed areas for farming are zero. From fishing activities, the maximum annual CPUE were reported for *C. sapidus*, ranging from 0 CPUE in 2009 to 9124 CPUE in 2023, followed by *C. ramada* ranging from 2935 to 8004 CPUE. The lowest average CPUE values was reported for *C. labrosus* which ranged from 3 to 69 CPUE, *P. minutus* which ranged from 0 kg to 245 CPUE, *Z. ophiocephalus* which ranged from 14 to 167 CPUE and *C. crangon* which ranged from 0 to 127 CPUE (Table 1; Supplementary Fig. 1).

Among environmental parameters, annually averaged water temperature and salinity were relatively constant over the study with values ranging from 15.9 to 21.6 °C and 16.8 to 24.6 PSU, respectively, and overall means of 18 ± 2 SD °C and 20 ± 2 SD PSU, respectively. Annually averaged nitrate and chlorophyll values showed larger variability: nitrate ranged from 0.42 to 1.36 mg $L^{-1}$ with an average value of 0.87 mg $L^{-1}$, whereas chlorophyll ranged from 1 to 16 μg $L^{-1}$ with average value of 8 μg $L^{-1}$.

The first axis of the PCA explained 39.9 % of the variability in species CPUE data, whereas the second axis explained the 18.0 % of the variability (Fig. 2). The first PCA axis illustrates how *C. sapidus* CPUE is opposite most of the other species, such as crustaceans (*C. crangon*, *P. adspersus* and *C. aestuarii* after molting) and fish lagoon residents (*P. flesus* and *A. boyeri*). Along the same axis, recent years (2020–2023) were characterized by higher abundances of *C. sapidus* (Fig. 2).

All explanatory variables showed VIF < 7 and were included in the RDA, which explained 49.3 % of the species variance. The first axis of RDA explained most of the variance (26.3 %) and was mainly described by *C. sapidus* which was opposite many landed species such as *R. philippinarum*, *C. aestuarii* (mature female), *C. crangon, A. boyeri, A. anguilla and M. cephalus* (Fig. 3a). The second axis of RDA was mainly described by salinity (11.5 % of explained variance). Among the explanatory variables of CPUE species, *C. sapidus* showed the highest marginal and conditional effects on the landed species, while the other environmental variables showed lower values with nitrate and salinity showing the lower effects (Fig. 3b).

The multiple linear regression with water temperature, salinity, nitrate, and chlorophyll as descriptors of *C sapidus* CPUE was not statistically significant ($R^2_{adj} = 0.27$, $F = 2.13$, $P$-value>0.05).

The annual CPUE of *C. sapidus* remained consistently low, below 1.5, until 2017. The change point analysis revealed a significant shift in CPUE trends in 2017 ($p < 0.001$), the year when the exponential growth began (Fig. 4).

Overall, the landings data showed declines in most landed fishery species starting in 2017, overlapping with the exponential increase in *C. sapidus*. Unexpectedly, some species have increased since 2017, while others didn't show a significant trend (Fig. 5; Supplementary Fig. 1). In particular, the grass goby *Z. ophiocephalus* showed increasing landings after the increase of *C. sapidus* (Fig. 5a), while the much smaller sand goby *P. minutus* decreased progressively (Fig. 5b). Among the predatory fish, *A. anguilla* showed a decreasing trend, while *D. labrax* and *S. auratus* increased (Fig. 5c). Lagoon dwellers (*A. boyeri* and *P. flesus*) and Mugilidae showed a steady decline (Fig. 5d,e,f). Mugilidae (except *C. labrosus*) reached minimum landings in 2023, corresponding to the maximum landings of *C. sapidus* (Fig. 5e,f). Decapods such as *C. crangon*, *C. aestuarii* in molt and *C. aestuarii*, females with eggs, *Palaeomon* spp. (Fig. 5g), and *T. philippinarum* (Fig. 5h) all declined relative to 2017, although not monotonically relative to *C. sapidus*.

Plotting the angular coefficient of linear regression models of CPUE

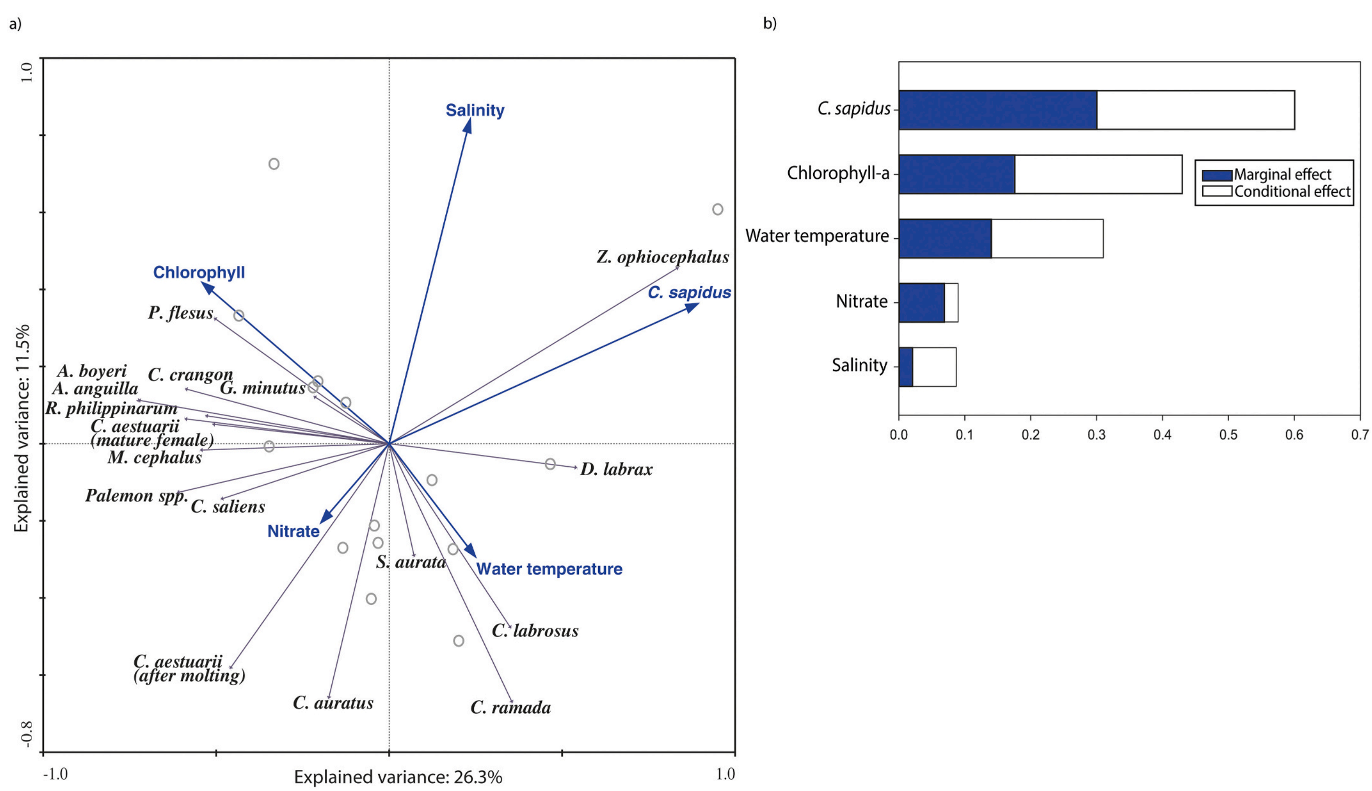


**Fig. 3.** a) Triplot of redundancy analysis (RDA) of landed species in the fish market of the Sacca di Goro lagoon (black arrow) and explanatory variables (blue arrow) from 2009 to 2023 (grey circles). (b) Marginal and conditional effects of each explanatory variable potentially affecting the landed species. The extended scientific names and the common names of the species are provided in Table 1.

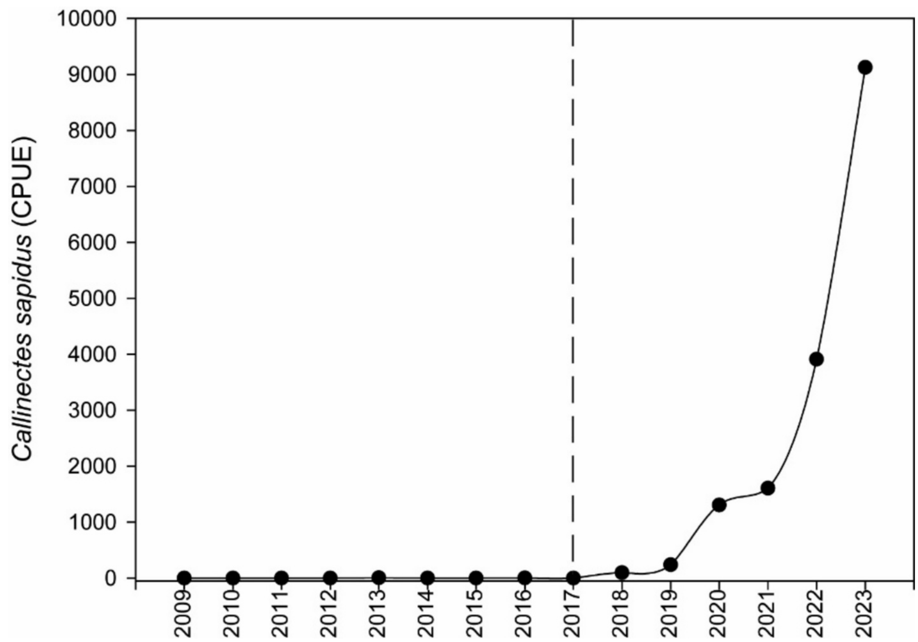


**Fig. 4.** Annual CPUE (kg wet mass by taxa per boat-year) data of the Atlantic blue crab *Callinectes sapidus* from 2009 to 2023. The year when the exponential growth of *C. sapidus* began, i.e., the point of change ($p < 0.001$) is 2017, as shown by the vertical dashed line.

for each target species showed the greatest decrease for *C. aestuarii*, *C. aurata*, *A. boyeri*, *A. anguilla*, followed by *C. crangon*, *M. cephalus*, and *P. flesus* (Fig. 6, Supplementary Fig. 1). Although a declining trend was also evident for other species such as *Palemon* spp. and *R. philippinarum*, the linear regression models did not detect these changes as significant (Fig. 6, Supplementary Fig. 1). Conversely, the grass goby *Z. ophiocephalus* and the sea bass *D. labrax* showed a significant and positive increasing trend, overlapping with that of *C. sapidus* (Fig. 6, Supplementary Fig. 1).

## 4. Discussion

The annual fisheries landings data (expressed as CPUE) from the Sacca di Goro lagoon highlight the recent, exponential increase in blue crab abundance, coinciding with a decline in numerous commercial and non-commercial species. In the RDA, among the explanatory variables, *C. sapidus* had the greatest effect on determining the CPUE of landed species, while environmental variables (i.e., chlorophyll, water temperature, nitrate, and salinity) showed smaller effects. Furthermore, the annual CPUE of *C. sapidus* was not affected by these environmental variables. *Carcinus aestuarii* in molt and a number of fish species such as *C. aurata*, *A. boyeri and A. anguilla* experienced the highest negative impact in response to the increase of *C. sapidus*, conversely *Z. ophiocephalus* and *D. labrax* showed significant increases in their abundance.

Before addressing these results, some methodological considerations are necessary.

In the present study, a non-experimental approach based on the analysis of landing data was adopted to investigate the effects determined by the invasion of *C. sapidus* on the fish assemblage of the Goro Lagoon. Observational data obtained from surveys and fishery landings have long been used for causal inference on large-scale ecological questions in marine systems where experimental manipulation cannot be easily performed (e.g., Estes et al., 1998; Aebischer et al., 1990). Noticeably, the fundamental challenge of non-experimental settings lies in the often-cited “correlation does not imply causation”: any conclusive inference on the effect of a factor of interest remains open to the possibility that hidden, not explicated drivers might have influenced the observed outcomes in a non-random manner. Although overall fishing effort remained relatively constant during the study period, we standardized landed species data by effort to account for potential variations. We also examined water temperature changes among climatic variables, which revealed negligible effects. Consequently, we are confident that neither fishing effort nor water temperature significantly biased our fishery data. However, the Goro Lagoon is exposed to multiple anthropic pressures (e.g., Tamburini et al., 2022). For example, effects related to changes in freshwater inputs and discharge of contaminants influencing the lagoon trophic condition and ultimately exerting a bottom-up control cannot be excluded (see Clavero et al., 2022 for similar considerations on the blue crab invasion in the Ebro Delta, Spain). The Regional Environmental Protection Agency has not reported any exceptional events related to water quality, and the basic water quality parameters did not show any deterioration during this period (Supplementary Table 1). Therefore, the likelihood of a bottom-up effect of water features on the observed phenomena is very unlikely.

Further evidence based on additional, independent observational data (e.g., monitoring surveys for conservational purposes, as in Clavero et al., 2022), or on laboratory trials or field manipulations are necessary to corroborate our conclusions (Larsen et al., 2019). Future long-term non-experimental studies allowing the implementation of advanced causal inference methods (e.g., structural causal modelling) will also lead to a more accurate assessment of the community-wide effects of the blue crab in the lagoon (Arif and MacNeil, 2023).

### 4.1. Temporal dynamics of the invasion by Callinectes sapidus of the study area

*Callinectes sapidus* was first reported in the Sacca di Goro in 2007 as a single adult specimen, with more frequent observations since 2010 (Manfrin et al., 2015) when adults began to be delivered to the fish market in low quantities (<10 kg until 2012; Fig. 4). Although no real demographic study has been carried out in Sacca di Goro, the population has gradually increased, with a significant shift in 2017, followed by a dramatic abundance shift, paralleled by an accumulation of evidence of the ecological impact of the species on the recipient community. *Callinectes sapidus* landings reached a total of 200 tons of adult specimens sold in the Goro fish market in 2023 (Fig. 4). Unlike what was reported for the Ebro Delta, Spain (Clavero et al., 2022), no reversing trend in

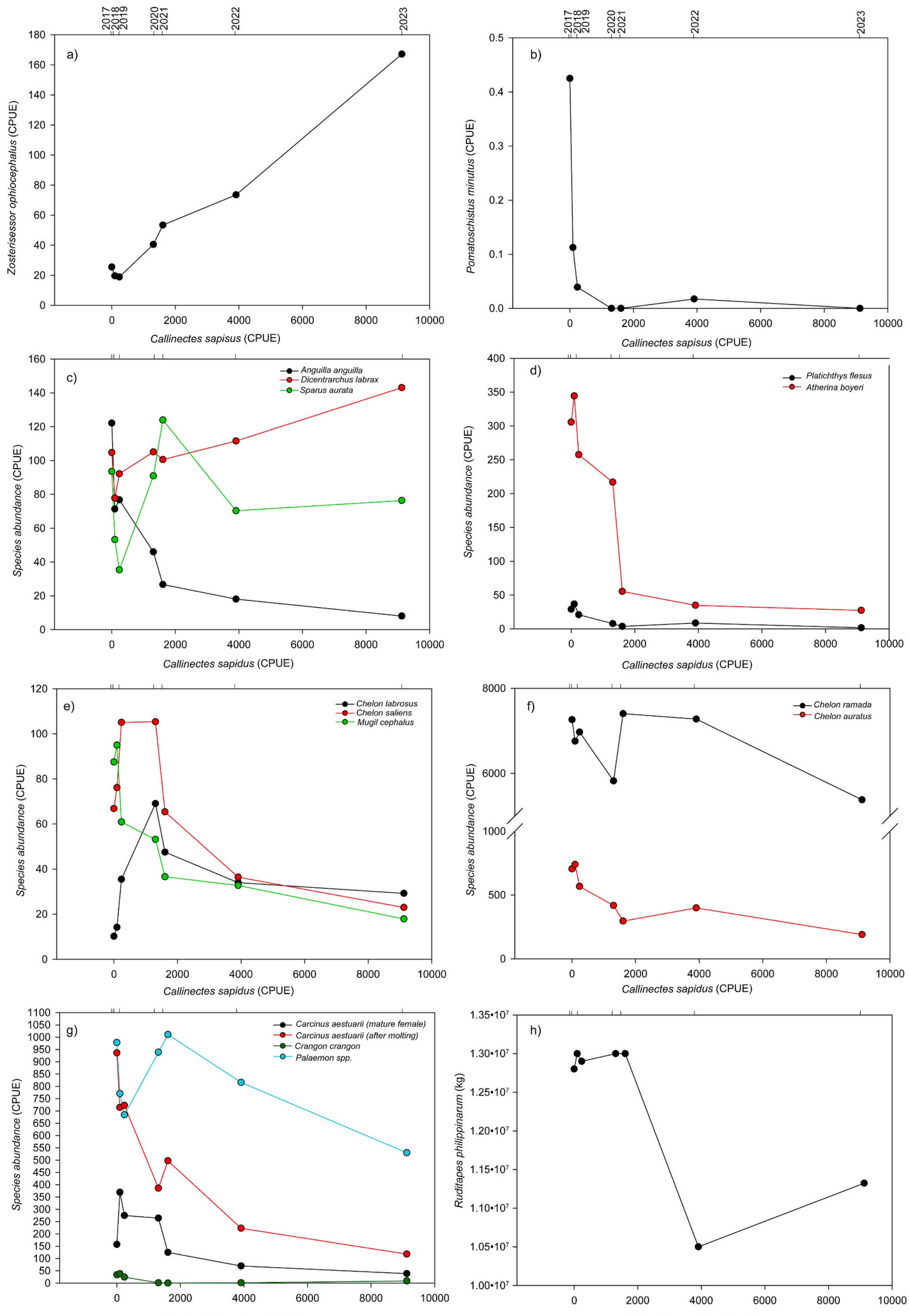


**Fig. 5.** Annual landing CPUE (kg wet mass by taxa per boat-year) data of Gobiidae (a–b), predator fish (c), lagoon resident species (d), Mugillidae (e–f), Decapoda (g) and Veneridae species (h) related with the blue crab *Callinectes sapidus* CPUE. Years (2017–2023) are also shown in the upper part of each graph. The common names of the species are provided in Table 1.

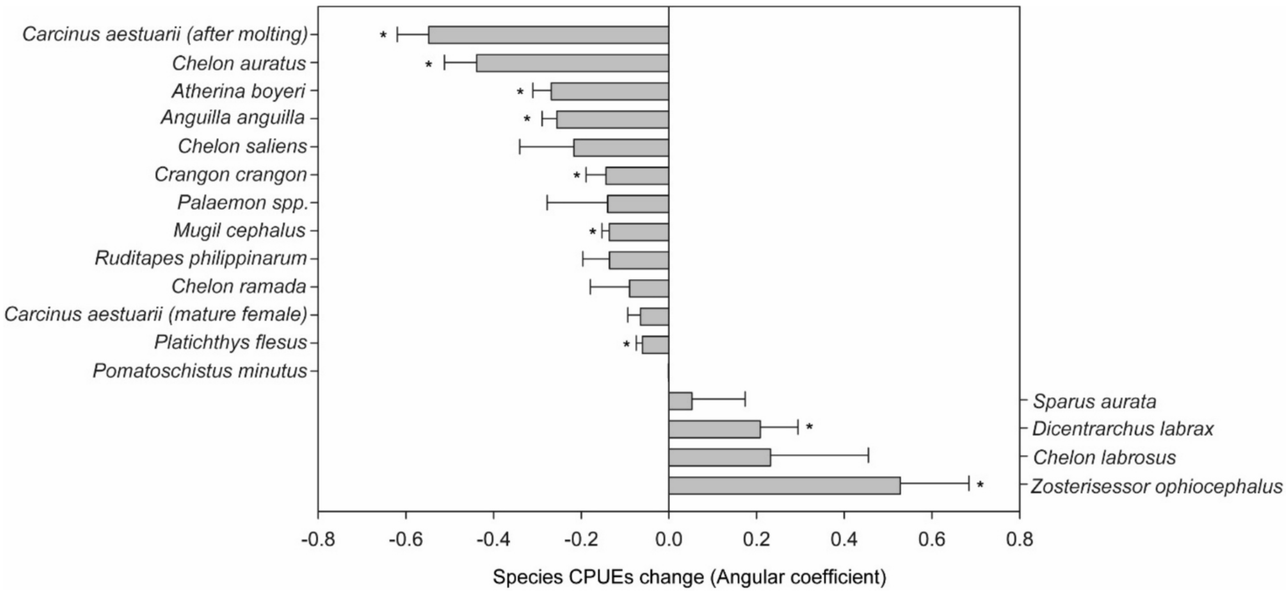


**Fig. 6.** Angular coefficients as magnitude of landed species change with standard errors from linear regression models of each species' over the 2017–2023 period. Values below 0 indicate decreasing CPUE of landed species, values above 0 indicate increasing CPUE of landed species. Significance ($p$-value $<0.05$) of the regression is indicated by an asterisk (*). The common names of the species are provided in Table 1.

*C. sapidus* abundance has been observed in the Goro Lagoon, even after 6 years of exponential growth (i.e., a peak of abundance in its invasion has not yet been reached; Fig. 4). Obviously, the species will not increase indefinitely and density-dependent, boom-bust dynamics in subsequent years could potentially stabilize the population at the abundances observed prior to the explosion (Strayer et al., 2017).

Additional factors that may limit the explosive growth of *C. sapidus* populations in the area might include food limitation and cannibalism among conspecifics, natural predators, and fishing pressure.

Natural predators can selectively affect juveniles, subadults, and adults of *C. sapidus* and, in turn, drive density-driven cycles in their local population sizes (Hines, 2007; Lipcius et al., 2007; Maurer et al., 2017). Predator-prey dynamics and the relative control mechanisms on *C. sapidus* abundance remain largely unexplored in invaded areas of the Mediterranean and Adriatic Seas. In its native range, *C. sapidus* face a variety of predators, including loggerhead sea turtles (*Caretta caretta*), fish, water birds and other crabs (Lipcius et al., 2007; Faria et al., 2016; Molter et al., 2022; Schlicht, 2000), some of which are also present along the Adriatic coast. Consequently, it is possible that such native predators, after an initial lag phase, could begin to limit the spread of *C. sapidus*, as has been reported for another invasive crustacean, the red swamp crayfish *P. clarkii*, which invaded Italian freshwaters at the end of the 1990s (Fasola and Cardarelli, 2015; Gavioli et al., 2018). Our study suggests that two local species, *Z. ophiocephalus* and *D. labrax*, could benefit from the increased availability of juvenile *C. sapidus* as prey, as indicated by their population increases. In fact, adults of *Z. ophiocephalus* can opportunistically feeds on megalopae and juvenile crabs (Hajji et al., 2010; Đođo et al., 2022) as well as *D. labrax* (Rogdakis et al., 2010), as further discussed later.

While the common octopus *Octopus vulgaris* is a potential predator in the Mediterranean (Prado et al., 2024a), its limited presence along the shallow sandy coasts of northeastern Italy suggests a reduced role in this specific area. However, predator-prey dynamics between invasive *C. sapidus* and potential predators in Adriatic coastal environments remains to be explored.

Interannual variations of chlorophyll, water temperature, nitrate, and salinity showed weak effects in explaining the CPUE of landed species, and no significant effect in explaining the blue crab CPUE. This can be attributed to the species' remarkable adaptability and tolerance to varying water quality conditions (Herrera et al., 2024). Warmer waters are known to promote the growth and abundance of *C. sapidus* (Cadman and Weinstein, 1988), however, our analysis did not identify water temperature as a significant factor in the regression analyses, likely due to the yearly range of average temperature in the period, between 16 °C and 22 °C, which is consistent with optimal temperatures for *C. sapidus*. There were no extremely low temperatures during the time series analysed in this study that could have affected *C. sapidus*. Conversely, we cannot rule out the positive effect of a rising temperature trend on blue crab CPUE, as measured in the Po River between 1992 and 2020, particularly noticeable in summer (rising by 0.13 °C per year) and autumn (rising by 0.16 °C per year), along with a 70–80 % increase in the number of warm days (Soana et al., 2024). Therefore, the potential positive effect of rising water temperatures on the spread of *C. sapidus* cannot be excluded.

Similarly, salinity was not retained as a significant factor in *C. sapidus* CPUE from our analysis, although it is known to play a crucial role in its reproduction and life cycle. Adult males use low salinity environments for mating and juveniles use the same environments as nursery habitat, while larvae grow in higher salinities (Hines, 2007). However, our data on landed blue crabs did not permit us to distinguish among blue crab sex or stages. The high abundance of *C. sapidus* in 2023 did coincide with a sharp rise in water temperature and a flooding event in the Po River basin (Arrighi and Domeneghetti, 2024). The spring flood from the Po River introduced fresh waters and relatively high concentrations of nutrients into the nearby coastal areas, including the Sacca di Goro. This nutrient influx subsequently increased the production of the area (Gervasio et al., 2024), potentially enhancing food suitability for *C. sapidus* (Kemp et al., 2005). However, the effects of this episodic event cannot be assessed by our analysis a more detailed seasonal or spatial description of environmental variables, which was not available for this study, could allow a better exploration of the conditions that favour or disfavour the spread of *C. sapidus* in the northern Adriatic. Continuing to monitor this species over the next years will provide valuable insights into the future evolution of the invasion.

### 4.2. Changes in landed species

Multivariate analysis identified *C. sapidus* as the most influential predictor associated with species landings at the fish market. This strong association suggests that *C. sapidus* may directly impact on the population dynamics of different species. Following the increase of *C. sapidus*, several fish species, including *A. boyeri* and *A. anguilla* and various decapod species (e.g., *C. aestuarii*) showed a steep decline. In contrast, *D. labrax*, a predator, and *Z. ophiocephalus*, a Gobidae, experienced an increase. These results suggest that the blue crab may have a significant impact on the lagoon food web at different trophic levels determining a remarkable "re-wiring" of the interactions occurring among native species ultimately reflecting in the fishery (Clavero et al., 2022). The negative impact of *C. sapidus* on landed species is probably linked to direct predation, which may be more severe in introduced areas, as native species fail to recognize and respond appropriately to this novel predation threat due to their lack of experience (Cox and Lima, 2006). *Callinectes sapidus* is known to be a generalist with a wide diet including clams, mussels, oysters, crustaceans, annelids, fish and plants, in both native and introduced areas (Eggleston, 1990; Eggleston et al., 2004; Prado et al., 2024a; Prado et al., 2022; Seitz et al., 2011; Encarnação et al., 2025). Bivalves may be the main food source for *C. sapidus,* and bivalves appear to be a preferred prey item (Prado et al., 2024b).

In the Sacca di Goro, *R. philippinarum* has been the most important fishery economically, involving about 1700 clam farmers by 2021, representing about 60 % of the active workforce in the area (Tamburini et al., 2022). *Ruditapes philippinarum* farming differs significantly from traditional small-scale lagoon fishing, as it is carried out in areas licensed for aquaculture and is based on regulated practices, from sowing clams to harvesting. As a result, the decline in *R. philippinarum* production due to the increase in *C. sapidus* was not yet evident in 2023, as farmers increased harvesting and sales from July onwards, contrary to traditional practices, to prevent losses after blue crab predation. The drastic decision to deplete the stock was taken following evidence that the density of *C. sapidus* reached in the summer of 2023 had exceeded the perceived threshold for coexistence with *R. philippinarum* culture. As a result of this decision, preliminary data for 2024 indicate a reduction in *R. philippinarum* production of >80 % (*Turolla, Paesanti unpublished data*, Supplementary Fig. 2). Predation by *C. sapidus* on clams may be density dependent. Higher clam densities may promote an aggregative response by *C. sapidus* to high-density clam patches, leading to local extinction of clams (Seitz et al., 2003).

While there is evidence that *C. sapidus* is affecting *R. philippinarum* production and causing economic losses in other Po Delta lagoons (Tiralongo et al., 2025), the specific predator-prey dynamics between these species within the Sacca di Goro required specific research.

The commercially important species most affected by the rise of *C. sapidus* is the green crab, *C. aestuarii*. This species is sold locally in the marked state when molting or as females with eggs. In its native range along the east coast of North America, *C. sapidus* has been observed to limit the abundance of the European green crab, *Carcinus maenas*, through predation (DeRivera et al., 2005). Therefore, the decline of another European crab, *C. aestuarii*, alongside the increase of *C. sapidus* in Goro lagoon is not surprising and supports similar results found in the Ebro Delta, Spain (Clavero et al., 2022). Another crustacean that showed a steep decline overlapping with the increase of *C. sapidus* was the grey shrimp *C. crangon*. While shrimp of the genus *Crangon* have been reported to prey on blue crab postlarvae (Olmi and Lipcius, 1991), the decline of this species in the Sacca di Goro suggests that blue crab predation on shrimp may be the more significant interaction. Among the fish species, *A. anguilla* and *A. boyeri* showed the most significant and marked declines. *Anguilla anguilla* has historically been an important fishery in the Po Delta area and in the Goro lagoon, representing one of the oldest fishing traditions in the region (Aschonitis et al., 2017). The observed decline in sales on the Goro market, which reflect a broader Mediterranean-scale trend, could be attributed to several cofactors that were already present before the invasion of *C. sapidus*, the most serious of which is a decline in recruitment, probably linked to illegal glass eel fishing in other countries (Aschonitis et al., 2017; Pons-Hernandez, 2024). Predation by *C. sapidus* on glass eels (Bedmar et al., 2024; Scalici et al., 2022) can likely be excluded in the Po Delta and in Sacca di Goro because the glass eels captures in the last six years, monitored by the LIFEEL project (European Commission, 2020), have recorded only few individuals. Abundances were not comparable to those 20 years ago (Lanzoni et al., 2022), reflecting the globally decreasing trend of the species (ICES, 2024). On the contrary, the decreases of immature *A. anguilla* in Sacca di Goro and in the whole Po Delta, likely correspond to a net loss of predation pressure on *C. sapidus*, as eels are known to prey on juveniles of *C. sapidus*, as reported for the American eel *Anguilla rostrata* (Hines, 2007). The loss of *A. anguilla* predators could have even more serious consequences at the scale of the Mediterranean Sea, given the critically endangered status of its population. This could lead to a Europe-wide ban on all fishing activities targeting the eels (ICES, 2024).

The decline of *A. boyeri* could be related to direct predation by *C. sapidus*, especially on juveniles, as the reproductive and oviposition period of *A. boyeri* in Goro lagoon during spring coincides with the period when *C. sapidus* becomes more active (Mancinelli et al., 2017). Another explanation could be related on feeding behaviour of *A. boyeri*, The populations of *A. boyeri* from freshwater and transitional environments are known to feed mainly on zooplankton, yet depending on size, prey availability, and local conditions, an important component of their diet in freshwater and transitional environments may be represented by benthic invertebrates such as amphipods and chironomids (Rosecchi and Crivelli, 1992; Chrisafi et al., 2007; Cicala et al., 2023; Vizzini and Mazzola, 2005). Accordingly, a closer interaction with the bottom sediments increases the probability of predation by the blue crab. Overall, all five species of Mugillidae showed a declining trend with the higher abundances of *C. sapidus*. While the predation of juvenile Mugillidae by *C. sapidus* should be further investigated in this area, Mugillidae species were reported as blue crab prey items in Thermaikos Gulf and Papapouli Lagoon in Greece (Kampouris et al., 2019), suggesting a potential role of *C. sapidus* in these trends. Moreover, *C. sapidus* may interfere with fishing nets used for Mugillidae fishing, potentially reducing their efficiency and resulting in lower catches. This negative impact of *C. sapidus* on nets seems to be common to different areas in the Mediterranean (e.g. Hamiche and Aksissou, 2024).

In the absence of a significant change in fishing effort or in aquaculture inputs on *Z. ophiocephalus* and *D. labrax*, we explain the increase in the populations of the two species, and then in their catchability, as a direct consequence of a much higher food availability represented by *C. sapidus* in its juvenile stages. These positive trends continue into 2024 (*unpublished data*), reinforcing the observed patterns. Crustaceans, including crabs, appear to be an important part of the diet of *D. labrax* and *Z. ophiocephalus*, especially in coastal habitats such as lagoons (Hajji et al., 2010; Rogdakis et al., 2010; Taieb et al., 2013). The provision of new food sources for native predators can be a beneficial outcome of introducing non-native species (Pintor and Byers, 2015) as the cases of *Lepomis* spp., in Wisconsin, which are capable of extensively consuming the introduced rusty crayfish *Orconectes rusticus* (Tetzlaff et al., 2011) or the non-native rabbitfish *Siganus rivulatus* consumed by native predators as the Common dentex *Dentex dentex* in Mediterranean Sea (Giakoumi et al., 2019).

Our study, based on correlational analysis, shows evidence that blue crabs increase concours with decreasing and increasing trends of many commercial species, raising the possibility of a direct impact from this invasive species. We have inferred that many of the changes in species are largely the result of species interactions (i.e., predator-prey interactions). Non-trophic interactions, such as competition for habitat or introduction of parasites by the invasive species, may play unrecognized roles. Further, annually averaged measures of main environmental variables were assessed, but biological responses may be at finer scales in both time and space. To better establish causal links, future research should examine the biological cycles and ecology of the affected species in more details.

## 5. Conclusions

Understanding the impact of invasive species on native species is a key element in managing them, as this knowledge can help prioritise management efforts (Hulme, 2006). This study provides evidence that the increase of *C. sapidus* in an economically important lagoon correlated with the decline of many commercial species inflicting damage on the area's economy and ecosystem. In the Sacca di Goro lagoon, the situation is critical, necessitating measures to limit the spread of the blue crab and mitigate the economic crisis threatening fisheries, particularly *R. philippinarum* production. The decline of fish and bivalve stocks can have severe economic repercussions for the human population and fishery sector of the Goro lagoon, as reported from other lagoons in Mediterranean Sea such as Lesina Lagoon (Cannarozzi et al., 2023) and Mar Menor lagoon (Vivas et al., 2025). At present, in Sacca di Goro, in response to the economic losses caused by the declining trend of *R. philippinarum* production, clam farmers have shifted their focus to targeting blue crabs, as well as a spontaneous attempt to reduce their spread. However, this strategy was not successful in the short term as it primarily targeted adult *C. sapidus*, neglecting juveniles and sub-adults (Lipcius and Stockhausen, 2002). Although eradication of this species is unlikely, more targeted containment measures that consider the biology of the species and operate on a broader scale than the Sacca de Goro may be a more successful strategy (Castriota et al., 2024).

At the local scale, strategies for managing *C. sapidus* should include exploring market opportunities, which are lacking as the species reached a consistent population only in recent years. *Callinectes sapidus* can be consumed and used not only as a food source, but also in biomedical research, in cosmetics and in the textile industries (Marchessaux et al., 2024; Tamburini, 2024).

Although human activities can directly limit the spread of the blue crab, it is also needed to enhance natural mechanisms that can regulate population growth. For instance, encouraging predation by natural predators such as *D. labrax, S. aurata, A. anguilla* and *Z. ophiocephalus*, can potentially contribute to controlling the abundance of blue crab. One effective method to favour the predation by native species on blue crabs is to implement fishing bans for these predator species, whose stocks are severely exploited for some Mediterranean countries (Ahmed, 2011). Successful evidence of this approach was observed, for example, in the invasion of the Percnidae crab, *Percnon gibbesi,* in the north-west Mediterranean Sea (Noè et al., 2018). Additionally, the adaptation to the presence of blue crab and its integration into existing food webs may further contribute to population control. Further research is needed to assess the effectiveness of such measures and to better explore the feeding behaviour of natural predators typical of such coastal area.

We fully agree with the view of Clavero et al. (2022) that a coordinated framework, considering both fisheries and environmental issues, is needed to manage this invasive species at the Mediterranean scale. Continuous monitoring and data collection on the invasion of *C. sapidus* is also crucial to understand its spatial and temporal dynamics and to identify the key factors for its successful establishment and spread.

## CRediT authorship contribution statement

**Anna Gavioli:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Giorgio Mancinelli:** Writing – original draft, Methodology. **Edoardo Turolla:** Data curation. **Mattia Lanzoni:** Data curation. **Vadis Paesanti:** Data curation. **Elisa Soana:** Data curation. **David B. Eggleston:** Writing – original draft, Supervision. **Robert R. Christian:** Writing – original draft, Supervision. **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.scitotenv.2025.179236.

## Data availability

Data will be made available on request.

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