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The costs of an invasion: How the blue crab impaired ecosystem services in the most productive lagoon of northwestern Adriatic

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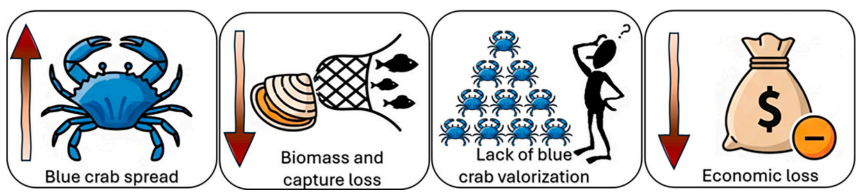
HIGHLIGHTS

- Blue crab invasion reshapes ecosystem service flows in coastal lagoons.
- Statistical evidence links blue crab to Manila clam aquaculture collapse.
- Manila clam farming biomass dropped by 71.5 % after invasion.
- Small-scale fisheries reduced, with losses in native fish and crustaceans.
- Blue crab supply chain revenues fail to offset socio-economic damages.

GRAPHICAL ABSTRACT



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ABSTRACT

The introduction of non-native species can disrupt ecological processes and impair ecosystem services, particularly in intensively exploited systems such as coastal lagoons. The Atlantic blue crab (*Callinectes sapidus*) has recently expanded rapidly in the northern Adriatic, raising ecological and economic concerns. This study documents and evaluates its impact on provisioning services in the Sacca di Goro lagoon (Po Delta, Northern Italy), the most productive site for Manila clam in Europe. Net revenues from the emerging blue crab supply chain were also assessed by accounting for sales and disposal costs.

Crab abundance showed no association with environmental variables. By contrast, a statistically significant negative relationship was detected with Manila clam production, which declined by 71.8 %, corresponding to annual losses of about €65 million. Small-scale fisheries also recorded reduced catches of native and commercially valuable species, with estimated losses of €0.18 million yr^{-1}. Revenues from the blue crab supply chain were positive in 2023 (+€0.41 million yr^{-1}) but turned negative in 2024 (−€0.71 million yr^{-1}) due to disposal costs and falling market prices. Thus, to date, not only are the revenues from blue crab sales negligible, but they are also outweighed by the high costs of disposal.

This case shows how invasive species can simultaneously erode biodiversity and ecosystem services while failing to provide viable alternatives. It provides quantitative evidence of aquatic invasion costs and highlights the importance of integrating such assessments into ecosystem-based management and policy.

1. Introduction

Biological invasions represent one of the most pervasive drivers of global environmental change, exerting substantial pressure on biodiversity, ecosystem functioning and human well-being (IPBES, 2019; Simberloff et al., 2013; Turbelin et al., 2023). Although their impacts

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have traditionally been framed in terms of species extinction, alteration of native communities and biotic homogenization, a growing body of literature now recognizes that biological invasions also alter the quantity, quality and resilience of ecosystem services (Gallardo et al., 2024; Vilà et al., 2010). The introduction of non-native species has been demonstrated to exert an influence on ecosystem services through a range of direct and indirect mechanisms, including predation on native species, competition for resources, changes in nutrient cycling, habitat alteration and trophic cascades (Moi et al., 2025; Ricciardi et al., 2017; Walsh et al., 2016). Such disruptions have the capacity to affect both the supply side (i.e. ecological production of services) and the demand side (i.e. human access and use), leading to economic losses, social conflicts and management costs (Carneiro et al., 2024). Among the most affected are those related to the provisioning of goods, such as fisheries and aquaculture, which have an intricate relationship with biodiversity and exhibit heightened sensitivity to alterations in species composition and trophic interactions (Katsanevakis et al., 2014).

These dynamics are particularly evident in coastal and estuarine ecosystems, which are highly vulnerable to biological invasions (De Giorgi et al., 2024). As dynamic and productive systems located at the interface between land and sea, they host intense interactions between natural and anthropogenic processes. Their high ecological turnover, nutrient enrichment and exposure to global trade routes make them hotspots for both species introductions and ecosystem service delivery (Tsirintanis et al., 2023). In the Mediterranean region, more than 1000 non-native marine and brackish species have been recorded, with this figure exhibiting a consistent upward trend due to climate change, global shipping, aquaculture trade and the opening of artificial corridors such as the Suez Canal (Katsanevakis et al., 2013).

In recent years, growing attention has been given to the spread of the Atlantic blue crab (*Callinectes sapidus*), a large, predatory brachyuran crab native to the western Atlantic (Mancinelli et al., 2021). The species has successfully invaded several regions worldwide, including the eastern Mediterranean, often forming abundant populations with high ecological plasticity (De Giorgi et al., 2024). In 2023, the blue crab rapidly spread along the northern Adriatic coast of Italy, raising concern due to its potential to prey on commercially valuable species and damage fishing gears (Chiesa et al., 2025; Marchessaux et al., 2023). Following its initial detection in 2007 and more consistent records since 2010 (Manfrin et al., 2015), the Sacca di Goro lagoon in the Po River Delta (northern Italy) has recently become one of the most severely invaded sites by blue crab in the Mediterranean and has emerged as an emblematic case study (Gavioli et al., 2025). This coastal lagoon is characterized by high ecological productivity and is among the leading European sites for Manila clam (*Ruditapes philippinarum*) aquaculture, in addition to supporting small-scale artisanal fisheries (Gaglio et al., 2019; Gavioli et al., 2025). Since 2023, the dramatic increase of blue crab abundance has raised serious concerns over its impacts on key provisioning ecosystem services that sustain the local economy and communities (Sabelli, 2023).

In response to its growing abundance, the valorization of blue crab biomass through commercial exploitation and marketing has been proposed as an alternative economic resource, with the aim of mitigating losses from traditional fisheries and aquaculture (Mancinelli et al., 2017). Despite these efforts, a critical assessment of the economic viability of blue crab exploitation is still lacking, especially in contexts where the species causes significant damage to native stocks and infrastructure. Without clear cost-benefit analyses, there is a risk of overestimating the commercial value of the invader while underestimating the ecological and financial burdens it imposes. For this reason, empirical data on blue crab impacts on ecosystem services, including quantification of both benefits and damages, are essential to inform balanced and adaptive management strategies. Despite the growing urgency of the issue, precise quantitative data on ecological impacts and economic consequences of the blue crab invasion in transitional environments are limited. There is a need to fill this gap with empirical research that can inform adaptive management and policy responses at both local and regional scales. In this context, this study aims to contribute to this effort by:

(i) Evaluating its impact on provisioning services, particularly Manila clam (*R. philippinarum*) aquaculture and small-scale fisheries in the Sacca di Goro lagoon, through a comparative analysis of pre- and post-invasion data;
(ii) Estimating the net economic balance of the emerging blue crab supply chain, including the revenue from crab harvesting institutionally financed for the control of the species and the costs of biomass disposal.

2. Materials and methods

2.1. Study area: the Sacca di Goro lagoon and the Po river

The Po River, the longest river in Italy (652 km), flows eastward across the northern part of the country and discharges into the Adriatic Sea through a complex delta system. This delta forms a highly dynamic landscape composed of freshwater channels, wetlands and coastal lagoons, which are key habitats for biodiversity and ecosystem services (Gaglio et al., 2023,).

One of the most prominent coastal systems within the delta is the Sacca di Goro lagoon, a shallow brackish environment of approximately 2000 ha, with an average depth of 1.5 m (Fig. 1). Despite its relatively small size (26 km^2), the lagoon is highly productive and hosts extensive Manila clam aquaculture. Due to the consistency of its production over time, it was the most important site in Europe until 2023. Manila clam aquaculture and artisanal fisheries play a crucial socioeconomic role in the southern part of the Po River delta (Gaglio et al., 2024; Gavioli et al., 2025). Specifically, clam aquaculture is carried out in geographically defined licensed areas located in the central part of the lagoon and accounts for nearly half of the national production. Small-scale fisheries target a variety of species, contributing to local livelihoods and sold by the local wholesale fish market. These practices are not only economically significant but also deeply rooted in local cultural traditions, reflecting a long-standing relationship between communities and the natural resources of the Po Delta (Gaglio et al., 2023). This historical socio-ecological balance has contributed to the designation of the Po Delta as a UNESCO Man and the Biosphere (MAB) Reserve, recognizing its value as a model for sustainable development. Moreover, due to its high productivity and ecological value, the Sacca di Goro lagoon is recognized and protected at multiple governance levels: it lies within the Po Delta Regional Park, is part of the Natura 2000 network and has been designated as a Ramsar wetland of international importance (Gaglio

Fig. 1. The Sacca di Goro lagoon and its location in northern Italy.

et al., 2019). Nonetheless, this culturally embedded use of natural resources has been significantly compromised since 2023, when the biological invasion of the blue crab rapidly intensified.

2.2. Manila clam, blue crab and environmental data collection and analysis

The Manila clam production data from 2010 to 2024 were obtained from the Goro fishers consortium (CO.PE.GO.). For the same period, landing data for blue crabs were obtained from the Goro fish market. However, from late 2023 through 2024, the captured blue crabs expanded beyond the official market, underestimating the total harvest. Therefore, to provide a more accurate total catch estimate for this period, the fish market data of blue crabs were supplemented with quantities directly sold at dockside and quantities discarded obtained from Goro fishers consortium (CO.PE.GO.) and Emilia-Romagna region, and then considered to account for the total catch.

Annual average of key environmental parameters in the Goro Lagoon from 2010 to 2024, i.e., water temperature, salinity, nitrate and chlorophyll-a (a proxy for primary production), were acquired from the LIFE AGREE project (LIFE13 NAT/IT/000115) and the Emilia-Romagna Region Environmental Protection Agency (ARPAE). Both sources used standardized sampling protocols.

Linear regression models in the *MASS* R package (Venables and Ripley, 2002) were used to analyze the relationships between environmental factors, Manila clam production and blue crab abundance. Specifically, the influence of environmental variables (annual averages of water temperature, salinity, nitrate and chlorophyll-a concentrations) on crab abundance and the combined effect of both environmental variables and blue crab abundance on Manila clam production were assessed in separate models. For all models, predictor variables were scaled (centered and divided by their standard deviation) and response variables were square-root transformed to better meet the assumptions of linear regression. Model validity was confirmed through visual inspection of residual plots.

Finally, the relative importance of each environmental predictor was quantified using the *relaimpo* R package (Grömping, 2006), which partitions the total R^2 among predictors by averaging over all possible orderings of the predictors in the model. All these analyses were performed in RStudio (R Core Team, 2024).

2.3. Assessment of provisioning services and blue crab supply chain

To quantify the impact of blue crab on local provisioning services, we conducted an integrated analysis of both the traditional economic outputs of the Sacca di Goro lagoon, namely clam aquaculture and small-scale fisheries, and the emerging but unstable blue crab supply chain. The objective was to assess changes in productivity, market value and net revenues associated with the blue crab invasion during 2023–2024, in comparison with the pre-invasion period. Monetary values were normalized using deflation coefficients provided by the Italian National Institute of Statistics (ISTAT) and expressed in constant 2024€ yr^{-1} (source: http://rivaluta.istat.it/). Data on Manila clam production, local wholesale fish market, blue crab sales, both through formal market channels and direct dockside sales, and disposal quantities were obtained from CO.PE.GO. and from the Emilia-Romagna Region.

2.3.1. Clam aquaculture

Annual data on Manila clam production figures from 2010 to 2023 were compiled to establish a long-term baseline and assess production losses following the 2023 invasion of blue crab. It is important to note that no significant production decline was observed in 2023, as licensed aquaculture farmers preemptively harvested and sold all available biomass while the blue crab population reached peak abundance. As a result, 2023 production figures do not reflect the ecological pressure exerted by the invasive species.

Production losses for 2024 were calculated as the percentage deviation from the 14-year average (2010–2023), a period selected due to the relative stability of clam production and revenues over this time span. Monetary losses were estimated using annual average gross sale prices for clams (€ kg^{-1}), as reported by the Italian Chamber of Commerce pricing authority (BMTI – https://www.bmti.it/).

2.3.2. Small-scale fisheries

Information on catch composition and associated market losses was assessed by comparing annual species-specific biomass and corresponding unit prices (€ kg^{-1}) between the baseline period (2016–2022) and the 2023–2024 average, based on wholesale fish market records. The year 2016 was selected as the baseline starting point because, prior to this year, fish landings at the Goro market exhibited higher interannual variability and/or reduced catches due to fluctuations in fishing effort, changes in target species and variability in market dynamics. The 2016–2022 period, by contrast, represents a phase of relative stability in small-scale fishery composition and volumes, thus providing a more reliable benchmark for assessing the ecological and economic impacts of the invasion.

The net impact of the blue crab invasion on fisheries was estimated by comparing two contrasting trends:

(i) Increased revenues from species whose catches increased after the growth of blue crabs probably due to increased food availability from blue crab juveniles and/or reduced overall fishing pressure, as operating trammel and gill nets had become impossible due to the excessive presence of adult blue crabs (Gavioli et al., 2025).
(ii) Decreased revenues from species that were probably negatively affected by direct predation and/or trophic or spatial competition from blue crabs, as well as changes in fishing techniques prompted by the need to adapt fishing gear to avoid damage to the gear from adult crabs that were caught accidentally (Gavioli et al., 2025).

2.3.3. Blue crab harvest and disposal

To assess the potential of blue crab as an exploitable resource, the annual net monetary value was calculated based on selling prices and the costs associated with disposal and management covered by institutions. Specifically, data on harvested and discarded quantities, along with corresponding unit costs and prices, were used to compute economic balances.

Revenues from blue crab sales were estimated using two sources:

(i) formal market transactions recorded between 2010 and 2024; and
(ii) direct dockside sales reported by fishers in 2023 and 2024, when crab densities increased dramatically.

Annual incomes were calculated based on average unit prices observed in each year. Disposal costs were estimated using a reference value of 1.50 € kg^{-1}, corresponding to the reimbursement provided by the Emilia-Romagna Region to cover the costs of collection, transport, disposal and administrative handling of excess or unsellable biomass. Although representing a partial economic offset for fishing and aquaculture operators, the reimbursement was treated as a cost for the system, representing the resources spent by authorities to manage the invasion.

3. Results

3.1. Relationships between Manila clam production, blue crab abundance and environmental drivers

The relationships between Manila clam production, blue crab abundance and environmental drivers, over the 2010–2024 period were investigated to explore potential ecological interactions. Water temperature, salinity, nitrate and chlorophyll-a did not have a significant effect on the abundance of the blue crab (overall model: $F = 0.68$, $p = 0.62$; Fig. 2a, Table S1a), evidencing that at local scale the recent spread of the species is not related to a temporal changes in water quality or primary productivity. These factors are relatively homogeneous within this small lagoon, where the species can move from one side to the other in a short amount of time.

Conversely, the model for Manila clam production was statistically significant ($F = 4.62$, $p < 0.05$) and revealed a strong influence of biotic interactions. Among all predictors, the abundance of the blue crab emerged as the only significant variable, with a clear and strong negative association with clam yields. Variance partitioning showed that blue crab abundance alone explained 67 % of the model's R^2, suggesting a dominant role of predation pressure and/or interference mechanisms over other environmental factors in driving clam production dynamics (Fig. 2b; Table S1b).

3.2. Changes in provisioning services

The invasion of blue crab in the Sacca di Goro lagoon has led to substantial alterations in local provisioning services.

In 2024, the clam biomass harvested in the licensed areas exhibited a 71.8 % decrease compared to the 2010–2023 average, marking a substantial decline from an average of 14,030 t yr^{-1} to 3963 t yr^{-1}. This decline has been estimated to result in a significant monetary loss of 65.2 million € (in 2024-adjusted values) and represents the most severe collapse since the beginning of aquaculture activity in the lagoon (Fig. 3j), as evidenced by the long-term trend in clam production shown in Fig. S1. Despite the sharp biophysical decline, the economic impact was partially buffered by a concurrent rise in unit market prices, which increased due to reduced supply.

In contrast, the impacts of blue crab on local fisheries resulted in more heterogeneous outcomes. According to the analyses presented by Gavioli et al. (2025), the invasion produced both gains and losses, depending on the ecological response of individual species. On the one hand, the captures of three fish species, i.e. thinlip grey mullet (*Chelon ramada*), golden grey mullet (*Chelon aurata*) and sand smelt (*Atherina boyeri*), and two crustaceans, i.e. brown shrimps (*Crangon crangon*) and native crab (*Carcinus aestuarii*) suffered a significant decrease. On the other hand, an increase in catches was exhibited by three other species, i.e. grass goby (*Zosterisessor ophiocephalus*), rock goby (*Gobius paganellus*) and european seabass (*Dicentrarchus labrax*).

Overall, the net annual economic impact of the blue crab invasion on small-scale fisheries is estimated at −117,283 € yr^{-1}, resulting from a decrease of landed biomass of 30.99 t yr^{-1} of considered species. Fig. 3 illustrates the species-specific trends in both biomass and monetary terms across time, while Table S2 reports the variations for each impacted species between the two analyzed periods.

The fish species negatively affected were *C. ramada* (−22 % in terms of average harvested biomass), *C. aurata* (−52 %) and *A. boyeri* (−92 %),

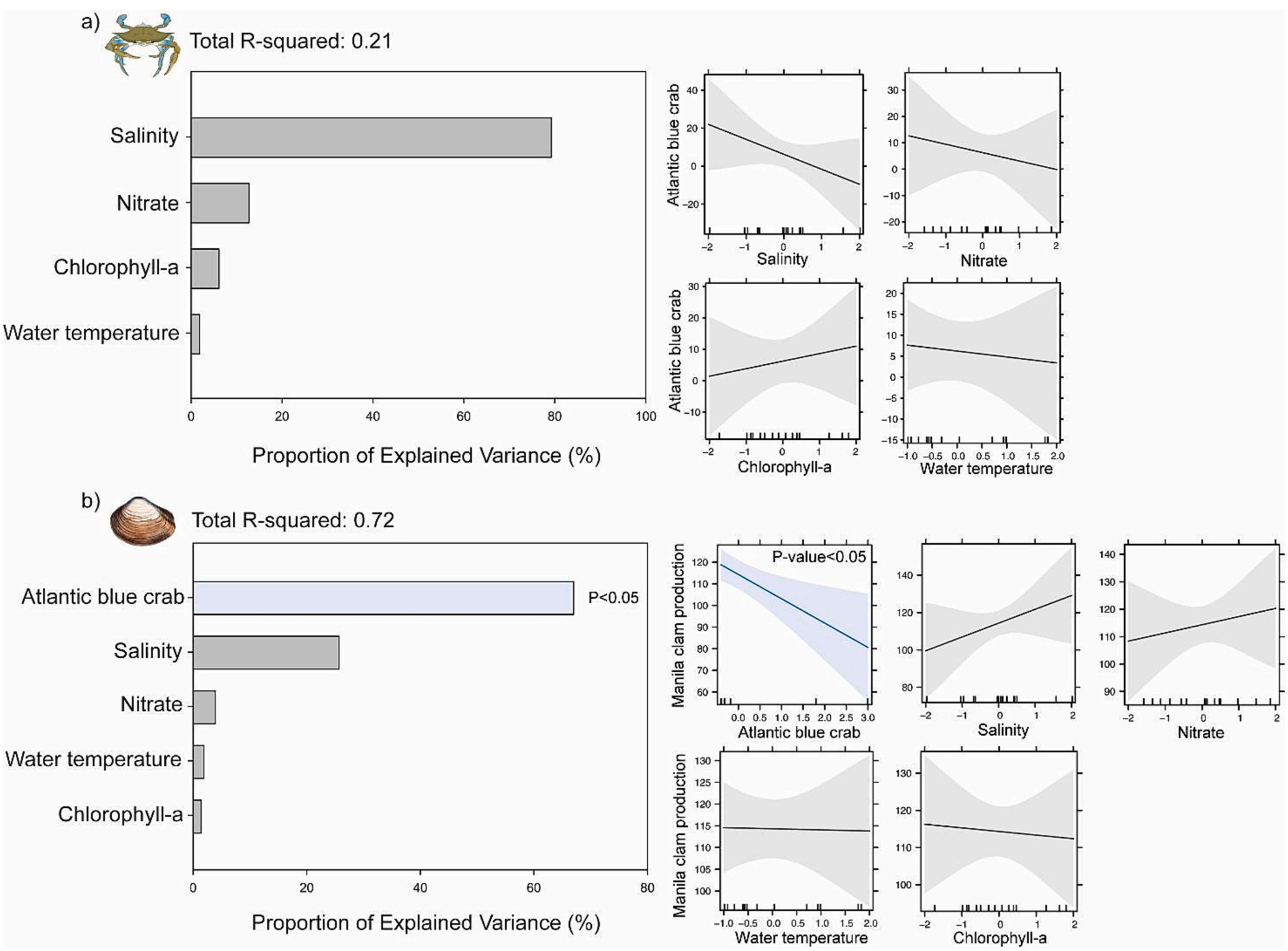

Fig. 2. The combined relative importance of predictors associated with the Atlantic blue crab *Callinectes sapidus* catches (a) and the Manila Clam *Ruditapes philippinarum* production (b) with effect plots on the left. Significant predictors were displayed in blue.

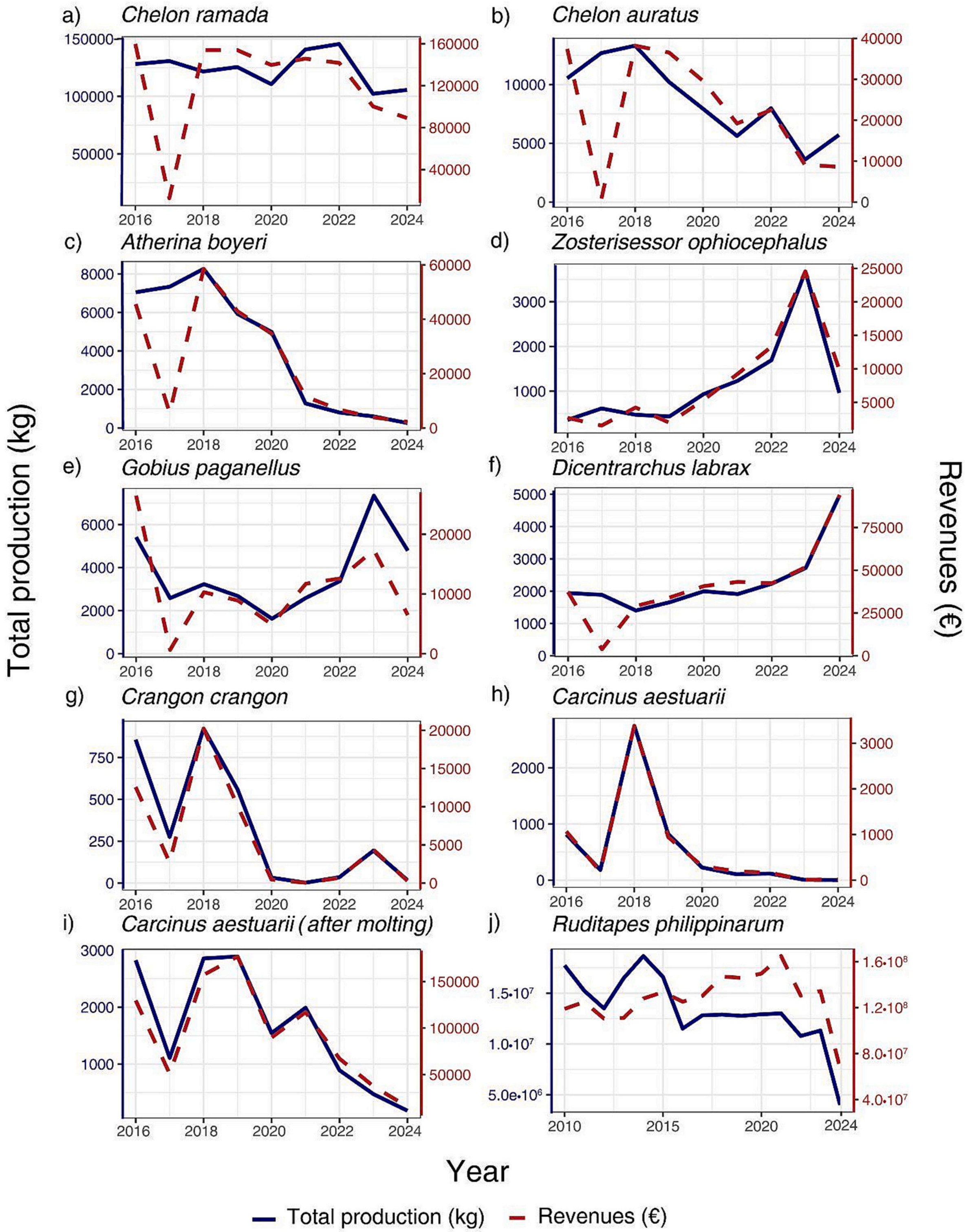

Fig. 3. Trends in total production (kg; blue line) and revenues (2024 €; red dashed line) in the Sacca di Goro lagoon for native fishes (panels a–f) and crustaceans (panels g–i) over the period 2016–2024, and for Manila clam (*Ruditapes philippinarum*) aquaculture (panel j) over the period 2010–2024. *Carcinus aestuarii* is represented both as hard-shell crabs (panel h) and as soft-shell crabs harvested after molting (panel i).

corresponding to monetary losses of approximately 79,000 € yr^{-1}.

Conversely, certain demersal and benthic species, such as gobies and *D. labrax*, showed moderate increases in catch biomass and revenues. Such species approximately doubled in biomass an additional annual income of around 53,000 € yr^{-1}, suggesting a possible indirect benefit from the increased availability of juvenile blue crabs or reduced fishing pressure due to gear damage elsewhere in the lagoon.

Among crustaceans, the effects of the 2023–2024 perturbation appear to be variable and species-specific in magnitude. Brown shrimp (*C. crangon*), one of the main traditional targets of small-scale fisheries in the Sacca di Goro lagoon, showed a decline in harvested biomass compared to the 2016–2022 average (−278 kg yr^{-1}), corresponding to a net monetary loss of approximately 4347 € yr^{-1}. While not dramatic from a monetary point of view, this decrease contributes to the overall erosion of fishery revenues and may be associated with altered benthic conditions, predation or indirect trophic effects.

The most substantial crustacean-related loss was observed for the native soft-shell crab fishery, which exhibited a significant reduction in catch volume (−1688 kg yr^{-1}), translating into a net annual loss of approximately 86,214 € yr^{-1}. This is particularly relevant given the high market value of soft-shell crabs, which are typically harvested during specific seasonal windows and require careful handling and processing.

3.3. Blue crab supply chain

The commercial presence of the blue crab at the Goro fish market began in 2010, with negligible quantities (0.001 t) sold at relatively low prices (5 € kg^{-1}). For over a decade, landings remained sporadic and economically irrelevant. A significant shift occurred starting in 2018, when recorded volumes increased from 2.3 t to over 36.9 t by 2021. This trend culminated in 2023 with the landing and commercialization of over 474 t, motivating the establishment of a structured supply chain (Fig. 4).

Notably, 2023 marks the first year in which part of the blue crab catch was sold directly at landing sites, reflecting the rapid expansion of informal sales channels beyond the official market. In that year, 273.5 t were sold via the wholesale market, while an estimated 200.7 t were distributed through direct sale, totaling 474.3 t of marketed product. However, the boom in supply was accompanied by a sharp decrease in market value, with gross prices falling from 5.5 € kg^{-1} in 2021 to 2.21 € kg^{-1} in 2023.

In 2024, although the overall marketed quantity remained comparable (453.2 t), a further decline in the unit price to 1.54 € kg^{-1} significantly reduced revenue. Meanwhile, public subsidies for crab disposal (granted at a fixed rate of 1.50 € kg^{-1}) remained unchanged, narrowing the profit margin. As a result, net revenue turned negative in 2024, highlighting a fragile and unsustainable economic scenario. The gross revenue from blue crab sales was 1,056,973 € in 2023, with a net positive balance of 411,349 € after accounting for disposal costs (645,624 €). In contrast, 2024 saw total revenues of approximately 705,382 €, which were insufficient to cover the increasing disposal costs (1,410,317 €), resulting in a net economic loss of 704,935 €.

These findings show that, despite the sharp increase in landings, the commercialization of blue crabs remains economically insufficient to compensate for the substantial losses in traditional provisioning services of the lagoon. On the contrary, due to the high costs of disposal, the supply chain turned negative in 2024, representing an additional economic burden rather than a compensatory opportunity.

4. Discussion

Evaluating the effects of non-native species on human well-being represents a pressing challenge in the context of global environmental change, requiring the integration of ecological, economic and social dimensions. A particularly illustrative case is the blue crab invasion in the northern Adriatic coastal lagoons, which has resulted in significant and measurable impacts on high-value provisioning services, especially those supporting local aquaculture-based livelihoods. The present analysis provides novel and robust evidence from the main European Manila clam farming lagoon, highlighting two major aspects: the severe losses in Manila clam aquaculture and traditional fisheries led by blue crab spread, and the current inconsistency of the emerging blue crab market as an economic buffer to compensate for those losses.

4.1. Absence of strong environmental control in the coastal environment references

The blue crab success is particularly evident in the Sacca di Goro lagoon, where the species reached high biomass and exerted significant ecological pressure. Interestingly, in this transitional environment, typical environmental drivers such as water temperature, salinity and chlorophyll-a concentration did not show a significant effect on blue crab abundance, despite their correlation with heatwave occurrences, which are known to trigger a positive feedback loop in the phenology of both larval and adult stages of blue crabs (Martellucci et al., 2025). This suggests that other biotic factors such as prey availability (i.e., the Manila clam production, in our model) and the paucity of natural predators may have played a stronger role in its recent spread at local scale. Nonetheless, the results suggest that three benthivorous fish species, i.e. *G. paganellus*, *Z. ophiocephalus* and *D. labrax*, may act as potential predators of the blue crab. Although direct evidence for predation on blue crab is lacking, previous studies have reported that these species exhibit dietary habits that include crustaceans, particularly juvenile crabs, in similar environments (Hajji et al., 2010; Rogdakis et al., 2010;

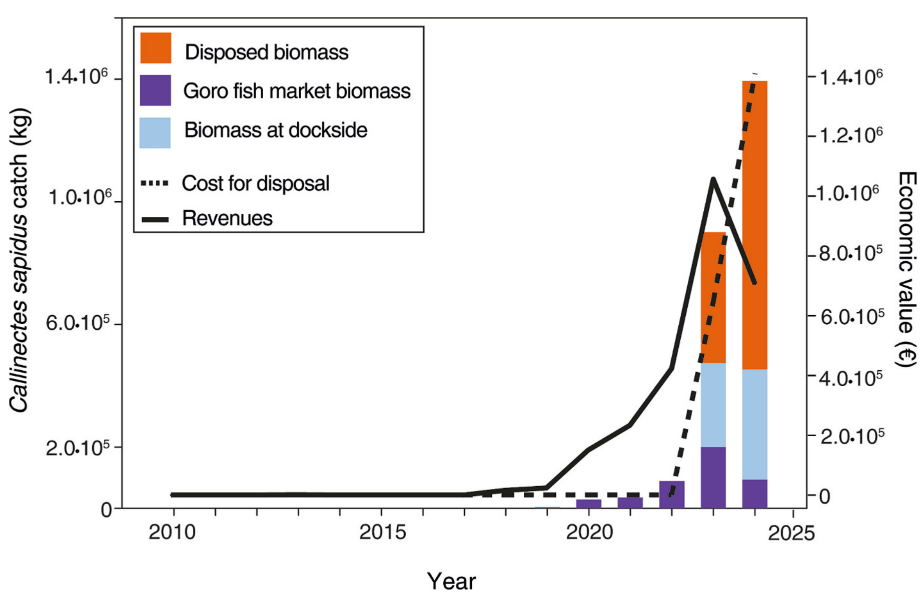

Fig. 4. Trends in blue crab catches (kg), sold at the Goro fish market and dockside or disposed within the containment program, and associated values for revenues (2024 €) and costs (2024 €) over the study period 2010–2024.

Tiralongo et al., 2021). Interestingly, the catches of these species have increased concurrently with the massive proliferation of the blue crab in the lagoon. On the other hand, these species may also have benefited from reduced fishing pressure, as fyke nets are now rarely used due to the damage caused by the blue crab itself. However, due to the annual resolution of our environmental data and the inability of our fishery data to distinguish between blue crab sex or life stage, we were unable to conduct a more detailed seasonal or biological analysis.

On the other hand, although the blue crab has been present in the Mediterranean Sea since the early 1900s (Galil, 2011), the drivers of its recent spread are not fully understood either at Mediterranean scale. The success of its invasion is attributed to a combination of biological advantages such as high tolerance to environmental conditions, dietary flexibility and high fecundity (De Giorgi et al., 2024)() and external factors like rising sea temperatures, coastal eutrophication and shipping as vectors for new introductions (Costa et al., 2023; Nehring, 2011). Despite complex temporal dynamics, spatial distribution appears to be primarily linked by food resources, as evidenced by higher blue crab abundances in more productive coastal areas and lagoons in Mediterranean Sea (Gavioli et al., 2024).

4.2. Changes in provisioning services as outcomes of species interactions and limitations of the blue crab supply chain

The impacts of invasion on ecological functions in coastal lagoons are evident through the impairment of key provisioning services. This study provides statistical evidence of a direct relationship between the species' expansion and the observed decline in clam farming productivity, excluding the relevance of other environmental variables.

In the Sacca di Goro lagoon the expansion of blue crab has severely compromised the productivity of the Manila clam, itself a non-native but long-established species that has supported the local economy for almost four decades. This interaction represents an ecological and economic paradox, wherein one non-native species undermines the provisioning services generated by another. Such invasive-on-invasive dynamics complicate traditional paradigms in invasion ecology, where non-native species are often evaluated in isolation from one another (Ricciardi and Simberloff, 2025). However, the negative impacts are not restricted to introduced species. The effects on native species results in altered catch compositions within small-scale fisheries, likely driven by trophic disruption, direct predation and competition. Additionally, fishers have also been forced to modify fishing practices, shifting between gear types. While previously mentioned fish species may prey on juvenile blue crabs, others such as *C. ramada*, *C. aurata* and *A. boyeri* are negatively affected, both through direct predation by the blue crab and through altered fishing practices. The gains from species showing increased abundance are insufficient to offset the overall losses, particularly due to the negative impacts on local crustacean fisheries. Although these shifts in catch composition result in relatively lower economic losses compared to clam aquaculture, they have important implications for the composition and functioning of the fish community, the conservation of vulnerable species and the socio-economic structure of local production systems.

The magnitude of the economic losses is substantial. The decline in clam aquaculture production translates into multi-million-euro annual losses, given that *R. philippinarum* accounts for the majority of the lagoon's revenues. This loss far outweighs the potential gains from blue crab commercialization, as the supply chain remains underdeveloped and unable to absorb large quantities at economically viable prices. Contrarily, the large amounts of biomass destined to disposal represents an additional cost that further exacerbates the local socio-economic context. Similar patterns of high economic damage and low compensatory potential have been documented for other marine and freshwater invasive species, such as the case of invasive bighead and silver carps (Brown et al., 2025).

At the global scale, the economic costs of invasive alien species are substantial and increasing, yet they remain highly uneven across ecosystem types. Recent syntheses indicate that reported costs are disproportionately concentrated in terrestrial environments, whereas aquatic systems remain poorly represented in available invasion cost databases (Cuthbert et al., 2022; Diagne et al., 2021). This bias is likely due not to lower impacts in aquatic systems, but to persistent knowledge gaps and underreporting of economic and non-economic losses in these environments. For example, in Italy, the estimated total cost of biological invasions between 1990 and 2020 amounted to approximately 704.78 million €, with an annual value estimated in the 50.16 million € yr^{-1} in the most recent period, and with only a small fraction attributed to aquatic habitats and their management (Haubrock et al., 2021). Against this background, the yearly loss estimated for the Sacca di Goro, exceeding 65 million € yr^{-1}, stands out as exceptionally high in relation to the lagoon's surface area. This striking figure not only underscores the severe economic vulnerability of small but highly productive coastal ecosystems, but also highlights how outdated and incomplete cost reporting may mask the true magnitude of invasion impacts in transitional waters, reinforcing the urgent need for targeted research and database updates.

Beyond direct monetary estimates, a more comprehensive understanding of such impacts emerges when assessed through the lens of ecosystem accounting frameworks such as the System of Environmental-Economic Accounting – Ecosystem Accounting (United Nations, 2021). For the Sacca di Goro, Gaglio et al. (2024) previously quantified temporal trends in ecosystem extent, condition and services, suggesting that the dramatically raising abundances of blue crabs likely contributed to declines in biotic quality indicators and to the reduced capacity of the lagoon to sustain provisioning services. The present study not only statistically supports these inferences but also provides a direct quantification of the relationship between the species' expansion and the loss of aquaculture and fishery productivity, thus demonstrating the need to better include impacts of non-native species in natural capital accountings.

The environmental drivers that had no effect on blue crab abundance also had no significant impact on Manila clam production, which resulted to be strongly negatively affected by blue crab, suggesting a direct predatory relationship. This effect peaked in a loss of 71.5 % of the total clam biomass harvested in the licensed areas in 2024. These findings are consistent with observations in other comparable habitats of the Po River Delta, such as Canarin and Scardovari lagoons. Tiralongo et al. (2025) reported a significant negative correlation between crab populations and clam yields in these lagoons, with clam yields almost completely lost in 2024. On the other hand, the blue crab is a generalist predator known for its varied and opportunistic diet. Its feeding habits include clams, mussels, oysters, crustaceans, annelids, fish and plants in both native and introduced habitats (Eggleston et al., 2004; Eggleston, 1990; Prado et al., 2022). Despite the wide food range items, bivalves appear to be a preferred prey and the main food source for the species (e.g. Encarnação et al., 2025; Prado et al., 2024).

4.3. Management implications: short-term actions and long-term strategies

The rapid expansion of this species in the northern Adriatic lagoons urgently calls for measures and strategies to safeguard local economies and mitigate ecological impacts. This requires the integration of different approaches rather than a single solution, ranging from short-term protective measures to longer-term systemic strategies.

As an immediate response to the invasion, local stakeholders have developed innovative anti-predator systems to protect clam cultures in the Po River Delta (Bonanomi et al., 2025). These systems, designed to physically exclude blue crabs from aquaculture plots, represent adaptive measures that may reduce immediate losses. Nonetheless, their effectiveness seems limited and depends on continuous maintenance, thus raising their costs for large-scale adoption. On the other hand, natural control mechanisms through the enhancement of native predator populations is often envisaged as action to contain invasive species (Gavioli et al., 2025). In this context, the European seabass (*D. labrax*) may exert predatory pressure on juvenile blue crabs, as suggested by the increased catches observed in the lagoon during the expansion phase (Fig. 4f). Although evidence of long-term efficacy is still limited and requires targeted experimentation, measures such as habitat restoration, restocking, or modified fisheries management aimed at reducing fishing pressure on seabass populations could strengthen top-down controls.

Beyond technical countermeasures, long-term strategies are required to adapt the socio-economic systems to the biological invasions. These include revising productive aspects and shifting from production-oriented to multifunctional management.

It has been demonstrated that the diversification of production systems (i.e. provisioning services) may reduce the socio-economic vulnerability of coastal communities to environmental changes (Lazzari et al., 2021). In this sense, complementary market species less vulnerable to blue crab predation have been proposed in the lagoon. In particular, oyster (*Crassostrea gigas*) and mussel (*Mytilus galloprovincialis*) has been envisaged as resources with both a potentially growing market and positive environmental performances in the Sacca di Goro lagoon and adjacent coastal areas (Tamburini et al., 2022). Such diversification acquires increasing value in the light of the currently limited market performances of the blue crab supply-chain demonstrated in this study. Although improvements in supply chain organization may enhance the valorization of blue crab as a fishery resource, to date its exploitation represents more a cost than a reliable opportunity, and its long-term sustainability is uncertain.

In addition to a reconsideration of the role of commercial shellfish species, a transition towards multifunctional lagoon management, incorporating a broader range of ecosystem services and conservation values while revising the use of natural resources, appears strategic in the context of a rapidly changing environment. A recent assessment under the framework of ecosystem accounting showed that restoration efforts aimed at restoring aquatic vegetation and hydraulic balances in the Sacca di Goro are likely to enhance environmental quality and the delivery of multiple non-market services (Gaglio et al., 2024). Such shifts, from production-oriented to ecosystem-based management, align with broader ecological restoration principles and may enhance the resilience of lagoon socio-ecological systems in the long term. Nevertheless, further efforts are needed to identify and quantify ecosystem services other than provisioning that may be impaired by the blue crab invasion, in order to integrate them into decision-making frameworks.

5. Conclusions

This study provides the first quantitative evidence linking the rapid expansion of the blue crab to the decline of aquaculture productivity in a highly productive lagoon, disentangling its role from other environmental drivers. By combining ecological and socio-economic perspectives, the analysis highlights how biological invasions can directly erode key provisioning services, undermining both native and long-established non-native resources.

Beyond its local relevance, this case contributes to the international scientific debate on invasive species by offering statistically supported evidence of their socio-ecological impacts in transitional ecosystems. Such results reinforce the need to move beyond qualitative assessments and towards integrated approaches that connect ecological processes with economic and social outcomes, thereby advancing invasion science within the broader context of sustainability research.

In terms of management, the experience of the Sacca di Goro illustrates that no single solution is sufficient. Protective measures, the enhancement of natural controls, production diversification, and multifunctional management each offer partial responses, but together can reduce vulnerabilities and strengthen resilience.

Overall, management responses to invasive species should balance ecological feasibility, economic sustainability and social acceptability. A portfolio of complementary strategies, combining top-down control, technical protection, production diversification and multifunctionality, offers the most promising path forward to reduce the vulnerability of socio-economic systems and to adaptively manage the pervasive impacts of biological invasions.

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CRediT authorship contribution statement

M. Gaglio: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **A. Gavioli:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **E. Turolla:** Investigation, Data curation. **M. Lanzoni:** Investigation, Data curation, Conceptualization. **G. Castaldelli:** Supervision, 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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Data availability

Data will be made available on request.

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