



OPEN Upstream migration of the invasive blue crab in the Po River, Italy, highlights the vulnerability of freshwater ecosystems

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The Atlantic blue crab (*Callinectes sapidus*) is one of the most rapidly expanding invaders in the Mediterranean Sea, where it has established populations across all coastal and estuarine habitats. While its impacts in these environments are well documented, little is known about its occurrence and ecological role in inland waters. This study provides the first evidence of significant upstream migration of blue crabs along the Po River and nearby branches (Northern Italy), beyond typical coastal habitat distributions. Blue crab occurrences were based on 50 validated geo-referenced records collected between 2022 and 2025 through fishermen reports. Environmental variables and blue crab upstream distance were analyzed to explore possible drivers of this migration. The potential trophic interactions between blue crab and riverine fish species were also examined through a systematic literature review. The findings revealed that upstream dispersal reached distances of more than 160 km from the sea, primarily driven by adult males. No clear correlation was found between upstream distance reached by blue crab and water temperature, conductivity, dissolved oxygen, or river discharge, suggesting that ecological dynamics, rather than abiotic filtering, likely drive inland expansion. The literature review highlighted only a few documented trophic interactions in European freshwaters, although potential predation by invasive fish species and competition with native fauna may occur. These results underscore the urgent need for targeted monitoring and research to evaluate the ecological consequences of blue crab invasion in freshwater systems, particularly regarding its potential impacts on biodiversity, food web dynamics, and ecosystem functioning.

Keywords Biological invasion, Atlantic blue crab, Freshwater, Non-native species, Mediterranean basin, *Callinectes sapidus*

The Atlantic blue crab (*Callinectes sapidus*) has become a species of growing concern in the Mediterranean Sea, representing a major threat to both biodiversity and human activities in recent years¹. Native to the Atlantic coast of North America, the species was first recorded in the Mediterranean in the early 1940s, likely introduced via ballast waters². The Mediterranean population began to spread rapidly around 2017, with timing depending on the area^{3,4}, establishing *C. sapidus* as one of the most impactful invasive alien species in the basin¹.

The species' invasion success is likely driven by its broad environmental tolerance, adaptability and dietary plasticity⁵. These traits are recognized as key determinants of invasive potential, allowing for establishment and persistence under variable environmental conditions. Reproductive dynamics also play a crucial role, as *C. sapidus* is euryhaline and its reproductive success strongly depends on estuarine salinity regimes. In its native range, mating typically occurs in oligohaline to mesohaline portions of estuaries, after which inseminated females migrate toward higher-salinity coastal waters to spawn⁶. This migration is essential for successful egg development and larval survival, which require specific salinity ranges: hatching fails below 9 ppt or above 33 ppt⁷. Following hatching, larvae (zoeae) enter polyhaline to euhaline coastal waters, remaining planktonic for several weeks before metamorphosing into the megalopa stage. Megalopae are subsequently transported back into estuaries by wind-driven circulation, tides and currents, where they settle and transform into juveniles. During ontogenetic development, juveniles tolerate a broad range of estuarine salinities, whereas adults show

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distinct sex-related spatial patterns: males typically remain in lower-salinity habitats, while mature females migrate to higher-salinity waters to spawn, completing the reproductive cycle^{6,8,9}.

In its native range, experimental and field studies have shown that male blue crabs migrate into freshwater and low-salinity river habitats to molt, achieving greater size increments compared to individuals remaining in estuarine waters (e.g.¹⁰). During this upstream migration, some individuals can travel considerable distances, reaching up to 100 km from the estuary (e.g.¹¹).

In the Mediterranean, invasive blue crabs have been reported throughout the basin¹², including area near or at the mouths of rivers in North Africa (e.g.¹³), Spain (e.g.³), France (e.g.¹⁴), Italy (e.g.^{4,15,16}) and Croatia (e.g.¹⁷). Due to their generalist and opportunistic feeding habits, blue crabs exert strong predatory and competitive pressures in these coastal ecosystems. This often leads to native species decline, alterations of food webs and overall biodiversity loss^{3,18–20}.

While the impacts of blue crabs in Mediterranean coastal waters have been extensively documented (e.g.^{21,22}), their occurrences and ecological consequences in freshwater systems remain largely uninvestigated, with only a few exceptions (e.g.^{23,24}). As in their native range, blue crabs show high tolerance to a wide range of salinities also in invaded areas, enabling some individuals to migrate far upstream. The most extreme case of upstream migration in the Mediterranean region was reported in the Guadalquivir River (Iberian Peninsula), where specimens were found up to 108 km from the sea²⁴.

This expansion into freshwater habitats highlights a critical gap in understanding the full invasive impact of blue crabs across Mediterranean saltwater, brackish, and freshwater ecosystems. This study aims to investigate the invasion of blue crabs from the delta to the lower and middle reaches of the Po River, the longest river in Italy and the third largest source of freshwater input in the Mediterranean Sea²⁴. We document their upstream expansion using validated data from fishermen records from 2022 to 2025. This timeframe encompasses the period immediately before, during and after the peak of the invasion in the area in 2023, which attracted considerable attention due to its dramatic socio-economic impacts in coastal lagoons^{21,22,25}. Additionally, we explore the potential relationship between blue crab upstream invasion and environmental variables, as well as the potential ecological effects on local fisheries through a systematic literature review. While our data cannot provide quantitative estimates of blue crab abundance or density in the Po River, these findings provide insights into invasion dynamics in this brackish-freshwater ecosystem and can inform future monitoring and management programs.

Materials and methods

Study area: the Po river and its delta

The Po River (Fig. 1) is the longest river in Italy (~ 652 km) and 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^{26,27}. Key environmental variables such as water temperature, salinity, dissolved oxygen, and river discharge exhibit strong spatial and temporal variability across the delta and its branches, shaping species distributions and ecological interactions. The delta is characterized by pronounced saltwater intrusion, with the saline wedge extending several kilometers upstream during periods of low river discharge²⁸. This intrusion influences water chemistry and habitat suitability for aquatic species, including invasive organisms. Water regulation through dams and artificial channels further affects freshwater distribution and the upstream penetration of the saline wedge, with the Isola Serafini dam representing the first unpassable barrier, at more than 180 km from the delta, for aquatic species along the river.

Notably, the Po Delta experienced a dramatic peak in blue crab abundance in 2023, particularly in the nearby Sacca di Goro lagoon^{4,16,29}, which led to the rapid upstream expansion of this invasive species and its potential ecological and socio-economic impacts on aquaculture and fisheries.

Historically, the Po River and its delta were characterized by high productivity and consistent presence of professional fishermen along the river course³⁰. Nowadays, traditional professional fishing is mostly located in the Po Delta and near coastal areas, whereas in the upstream reaches it has been replaced by recreational fishing. While most professional fishermen operate in lagoons and coastal waters, only around 5% of vessels operate in the Po delta branches. This is due to the disappearance of historically important fishing techniques, such as sturgeon fishing³⁰, and the near extinction of eel fishing³¹. Those who are still operating in the freshwater section of the delta earn their income from selling freshwater fish such as common carp (*Cyprinus carpio*), mullet (*Chelon labrosus*), wels catfish (*Silurus glanis*) and pikeperch (*Sander lucioperca*), as well as seabass (*Dicentrarchus labrax*) and eels in the sections facing the sea mouths. In the river section upstream of the delta, fewer than five professional fishermen remain, while most fishing activities are amateur and involve releasing the catch, such as carp and catfish fishing.

Upstream records along the river Po course

To assess the upstream dispersal of the blue crab within the freshwater reaches of the Po River and three of its delta branches, we collected and validated occurrence records using a face-to-face interview-based approach with local fishermen. Although with this approach it is not possible to provide quantitative estimates of the abundance and density of blue crabs in the Po River, it is increasingly recognized as effective for studying invasion dynamics^{32–34}. Interviews were conducted annually in early autumn (September–October) from 2022 to 2025 at selected fishing spots, evenly distributed along the right bank of the Po River, from the delta to the Isola Serafini dam, covering a stretch of approximately 250 km (Fig. 1). These sites were characterized by fixed fishing infrastructure such as piers and jetties housing traditional huts and lift nets. To ensure methodological consistency, the same locations and interview protocols were maintained each year.

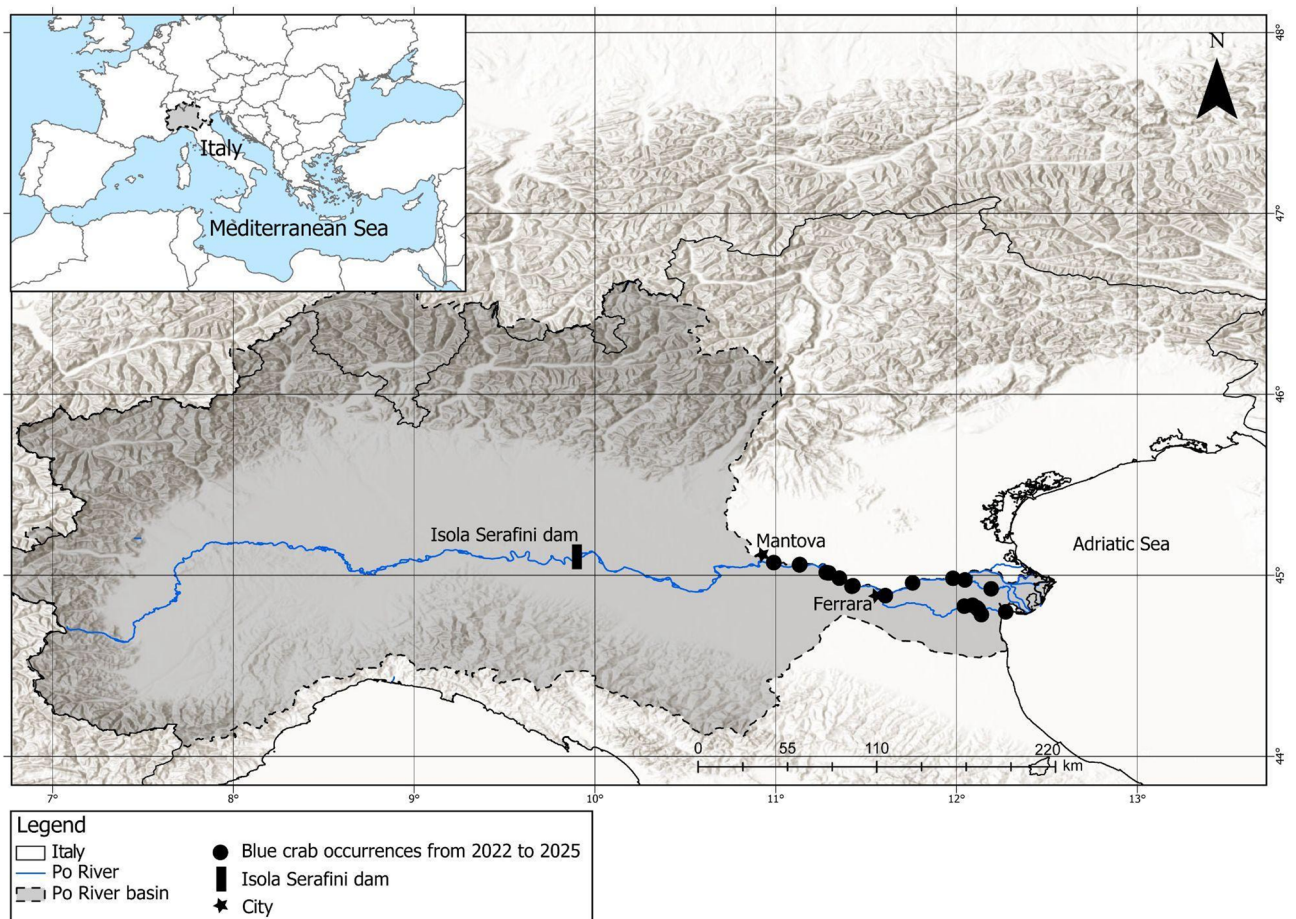


Fig. 1. Study area and upstream occurrence of blue crabs reported along the Po River from 2022 to 2025.

A total of 52 fishermen participated in the interviews on a voluntary and anonymous basis. Each interview lasted ~20 min and followed a structured protocol to collect data on: (i) the specific location of blue crab captures during the year; (ii) estimated catch quantity (number of individuals or biomass) per fishing session; (iii) biometric details (sex, size or size range of captured crabs); and (iv) fishing effort (gear type and hours fished). All information was validated by the authors through direct visual inspection of specimens and/or analysis of photographs. Fishermen received scientific training from the authors to distinguish *C. sapidus* from other taxa, although misidentification risk was minimal due to the absence of other native or non-native freshwater crabs in the Po River.

Due to the turnover among fishermen at specific sites throughout the study period, repeated interviews with the same fishermen were not always possible. To address this, interviewees were asked to report historical observations from previous years. Unlike the verified catch data obtained during the interviews, these retrospective reports could not be validated by authors and are therefore presented as qualitative information in Table S1.

To ensure spatial accuracy, the recorded blue crab were georeferenced using handheld GPS units during site visits. Where direct access was not feasible, locations were determined from high-resolution satellite imagery (Google Earth). All occurrence records were summarized in a georeferenced dataset (Table S1), providing a basis for further analysis of dispersal mechanisms and colonization pathways in freshwater systems. Additionally, to quantify the progression of blue crab invasion along the river, the upstream distance from the river mouth was also calculated for each occurrence location in ArcGIS Pro³⁵.

All interviews were conducted in accordance with relevant guidelines and regulations. The interview protocol was approved by the Emilia-Romagna Region as part of a long-lasting collaboration between fishermen, management authorities and research institutions. Participants remained anonymous and no personal data (such as name, age, or gender) were recorded. Verbal consent to participate in the interview was obtained from all respondents; written informed consent was not required.

Environmental variables

To account for environmental conditions during blue crab detections, we included data on water temperature (°C), electrical conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) and dissolved oxygen (%) for the Po River and its delta branches. These parameters were obtained from institutional monitoring programs operated by the Regional Environmental

Protection Agencies of Veneto Region (ARPAV), Emilia-Romagna Region (ARPAE) and Lombardia (ARPA Lombardia). Samplings were performed bi-monthly at fixed monitoring stations along the Po watercourse, from 2022 to 2024. Mean values of water temperature, electrical conductivity and dissolved oxygen were calculated for the warm season (April–October) of each year with confirmed blue crab occurrences (2022–2024) and subsequently spatially interpolated across the Po River using Ordinary Kriging with a linear semivariogram model in ArcGIS Pro³⁵. Water monitoring for 2025 is ongoing; therefore, data for that year were not included in this analysis. Monthly mean discharge data ($\text{m}^3 \cdot \text{s}^{-1}$) for the Po River were obtained from the permanent monitoring station at Pontelagoscuro (Lat 44.888296; Long 11.608072) for the period 2000–2025. These 25-year values were used to calculate a long-term average discharge ($1412.2 \text{ m}^3 \cdot \text{s}^{-1}$), which served as a historical baseline, enabling the identification of hydrological anomalies such as drought and flood periods during the recent expansion of the blue crab in the Po River Delta (2017–2025⁴). Spearman's non-parametric correlation analysis was conducted in Rstudio³⁶ to assess the association between environmental variables and the maximum annual upstream migration distance reached by blue crabs. For this analysis, spatially averaged warm-season values of water temperature, electrical conductivity, and dissolved oxygen were included, along with the annual mean discharge.

Literature review: potential trophic interactions between blue crab and Po river fish species

To investigate potential trophic interactions between the invasive blue crab and local fish species, including both positive (e.g., blue crab consumed by fish) and negative (e.g., predation by or competition with fish) interactions, we adopted a two-step literature-based approach. First, we compiled a list of fish species documented in the Po River section from Isola Serafini to the delta over the past decade, based on field surveys (see e.g.^{37–39}). Second, we conducted a systematic literature search in Scopus (last accessed September 26, 2025) following the PRISMA protocol⁴⁰. This procedure entailed systematic article selection, screening and extraction of relevant data. Eligibility was restricted to articles published in English, with research queries limited to article titles, keywords and abstracts. Laboratory studies or articles not directly addressing the research topic were excluded. Search queries combined the scientific and common names of each Po River fish species with the terms “blue crab” and “*Callinectes sapidus*”. All retrieved papers were subjected to screening based on the full text, with studies not reporting interactions between blue crabs and the specified fish species were discarded. From each selected article, we extracted information on the study region, the type of interaction (i.e., crab as predator or crab as prey) and the type of observation (i.e., direct or indirect) (Table S2).

Additionally, a broader literature search was performed using a general query to capture other potential ecological interactions in inland waters. The full query was: (“*Callinectes sapidus*” OR “blue crab”) AND (“freshwater” OR “river” OR “stream” OR “Po River” OR “Italian river” OR “inland water”) AND (“fish” OR “ichthyofauna” OR “freshwater species”) AND (“predation” OR “competition” OR “diet” OR “feeding” OR “interaction” OR “trophic”) (Figure S1).

Results

Upstream dispersal and environmental variables

Interviews with fishermen revealed that blue crabs expanded upstream along freshwater reaches and branches of the Po River, extending from the delta to the Isola Serafini dam, between June 2022 and July 2025. This distribution reflects substantial upstream dispersal from the brackish environments of the delta (Fig. 1). A total of 50 geo-referenced occurrences were validated (Fig. 1; Table S1), with the maximum upstream migration exceeding 160 km inland, reaching the area near the city of Mantova in 2023 (Fig. 1). Notably, no blue crabs were reported by fishermen in the river stretch between Mantova and Isola Serafini dam.

Despite the heterogeneous and not standardizable fishing effort, blue crab abundance generally decreased with increasing distance from the delta for each year considered (Fig. 2a, b; Table S1). Most captured individuals were adult males, with females recorded only sporadically. Measured carapace widths ranged from 7 to 20 cm, showing no apparent size gradient along the upstream trajectory (Table S1). Notably, in the Po di Volano and Po di Goro branches, adult crabs were collected in substantial biomass in 2023 and 2024 (up to 150 kg per sampling event), highlighting the high biomass near the Po delta (Fig. 2b; Table S1).

Among environmental variables, water temperature peaked in 2022 and retained stable levels through 2023–2024 with no clear spatial pattern (Fig. 3a, d, g). Electrical conductivity also peaked in 2022, showing a clear spatial pattern along the Po River reflecting saltwater intrusion (Fig. 3b, e, h). In contrast, dissolved oxygen levels were homogeneously distributed along the river course with no temporal trend (Fig. 3c, f, i).

The 2022 peaks of water temperature and electrical conductivity coincided with the lowest mean annual discharge of the study period ($535.9 \text{ m}^3 \cdot \text{s}^{-1}$), the same year in which the blue crabs were first detected in freshwaters of Po River, 146 km upstream (Fig. 4). In 2023, discharge remained low (mean annual discharge = $970.1 \text{ m}^3 \cdot \text{s}^{-1}$), and blue crabs reached the maximum upstream distance reported (160 km). Conversely, in 2024, discharge was highest, with annual mean value of $2158.6 \text{ m}^3 \cdot \text{s}^{-1}$, and blue crabs were reported at maximum 127 km upstream (Fig. 4). In 2025, discharge maintained relatively high (mean annual values = $1486.9 \text{ m}^3 \cdot \text{s}^{-1}$), with blue crabs reported at a maximum of 146 km upstream (Fig. 4). Spearman correlation analysis indicated no significant associations between the maximum annual migration distance reached by blue crabs and warm-season values of water temperature, electrical conductivity, dissolved oxygen and the annual mean discharge ($P > 0.05$).

Trophic interactions with fish species

Of the 27 fish species reported in the lower stretch of the Po River (Table S2), only 3 species exhibited documented interactions with blue crab (Fig. 5; Table S2). In North America, largemouth black bass (*Micropterus salmoides*) and blue catfish (*Ictalurus furcatus*) are known predators of blue crabs^{41–44}. Conversely, among the species present in the freshwaters of Po River, the only one reported to respond negatively to blue crab was the European

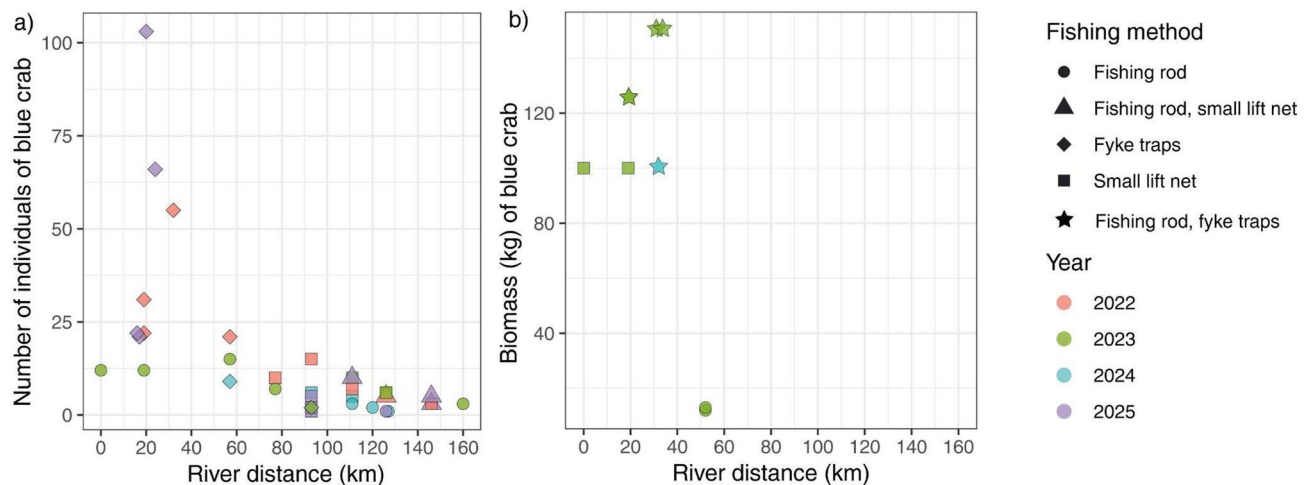


Fig. 2. Number (a) or biomass (b) of blue crabs reported per capture event categorized by fishing methods (circle= fishing rod; triangle=fishing rod and small lift net; diamond=fyke net and square=small lift net) from 2022 to 2023.

eel³ (Fig. 5; Table S2). The broader research query reported 44 scientific papers of which only two met the criteria for relevance, after excluding duplicates and references that did not specifically address trophic relationships between blue crab and fish species (Figure S1). One retained study reported blue crab predation on the winter flounder, *Pseudopleuronectes americanus*, a marine species that migrate into upstream tidal reaches in New England⁴⁵. The other study, conducted in Morocco's Moulouya River, hypothesized negative ecological effects of the blue crab on both European eel (*Anguilla anguilla*) and Yahyaoui barbel (*Luciobarbus yahyaoui*)⁴⁶.

Discussion

Upstream migration uncoupled from environmental variables

While our data cannot provide quantitative estimates of the abundance and density of the blue crabs in the Po River, our study provides the first evidence in Italy that blue crabs can disperse considerable distances upstream within large river systems. Individuals were recorded over 160 km from the mouth of the Po River, an unprecedented distance in non-native ranges. In fact, while the species can migrate up to 195 km inland in its native area⁴⁷, such extensive upstream penetration in invaded systems is less frequently reported²³. Confirmed European records, including the Guadalquivir River in Spain²⁴ and the Weser River in Germany⁴⁸, generally extend up to ~ 100 km from the coast.

However, the upstream migration of blue crabs along freshwater reaches is not unexpected, as it aligns with their euryhaline physiology and life history strategy. The species exhibits a high degree of adaptability to diverse salinity conditions throughout its life cycle, with a distinct sexual spatial preference driven by different physiological and reproductive requirements. Specifically, adult males and juveniles predominantly occupy lower salinity habitats for molting, mating and nursery purposes^{49,50}. In contrast, adult females predominantly select meso- and polyhaline waters for reproduction, as high salinity is needed for successful egg development and larval hatching^{49,50}. Consistent with this pattern, most blue crabs observed in the upper Po River (i.e., freshwater habitat) were males, while females were predominantly found in brackish and salt habitats near the coast. This observation aligns with species' biology in which reproductive activity is primarily restricted to the transition zones between brackish and freshwater environments⁶.

In addition to biological traits, environmental conditions can further shape habitat use and dispersal capacity in this species. Key environmental variables, including water temperature, salinity, dissolved oxygen and river discharge, are known to influence blue crab growth, molting, survival, migration and reproduction in coastal systems^{6,50}. While larval and early juvenile stages are generally restricted to high-salinity, warm waters, adults and late juvenile stages display wider thermal tolerance and superior osmoregulatory capabilities, allowing them to exploit a broad range of conditions⁵⁰. Furthermore, the interaction between these factors can make it difficult to disentangle their single effect. For example, river discharge can regulate salinity gradients in estuaries and in turn it can affect movement patterns, such as larval drift⁵¹.

Nevertheless, Spearman's correlation analysis revealed no significant association between the environmental variables and the maximum annual upstream migration distance of blue crabs, suggesting that the measured physico-chemical parameters alone do not directly determine the maximum upstream distance reached. The ecological plasticity of the blue crab likely allows it to overcome abiotic filtering, while propagule pressure from nearby coastal and transitional habitats could facilitate its inland expansion.

Instead, upstream expansion may be influenced by density-dependent processes, with individuals moving inland to escape intraspecific competition in coastal lagoons and nearshore habitats. Fine-scale environmental gradients, such as localized salinity fluctuations or small-scale dissolved oxygen dynamics, may also play a role. However, these patterns were not resolved in the present dataset and the large spatial scale of the analysis may have masked their effects. In the fully riverine section, the Po River is channeled and characterized by a steep

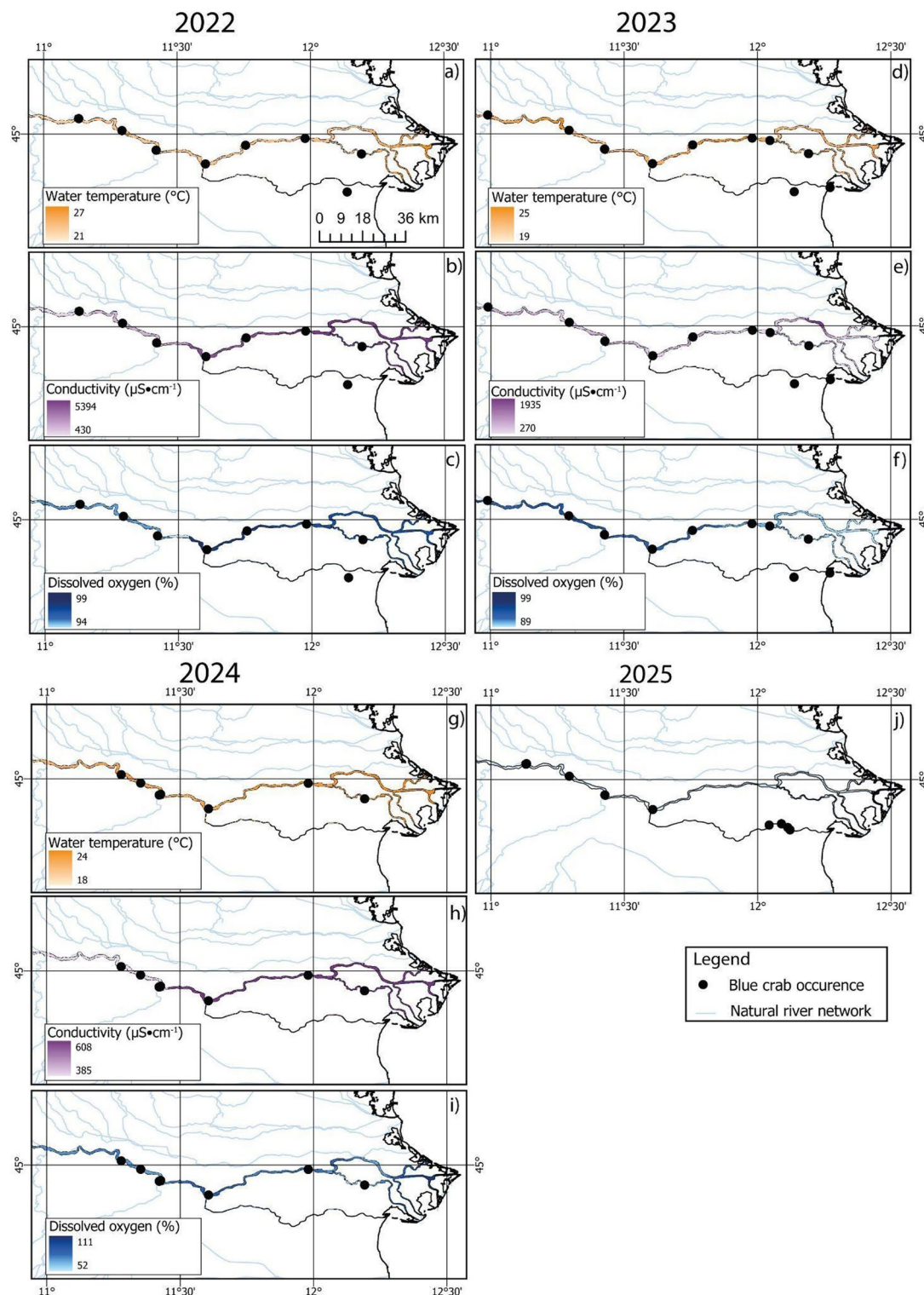


Fig. 3. Mean values of (a) water temperature ($^{\circ}\text{C}$), (b) electrical conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) and (c) dissolved oxygen (%) in the Po River and its main branches in the delta during the warm season (April–October) from 2022 to 2025. Blue crab occurrences are displayed as black circles.

slope and high flow speed, promoting complete water column recirculation and high oxygenation up to the delta, thereby preventing the formation of significant small-scale environmental gradients such as oxygen depletion⁵². Even though there is no clear relation between environmental variables and the maximum upstream distance reached by blue crabs, the potential influence of exceptional hydrological events requires further investigation and cannot be excluded. The 2022 heatwave and drought caused historically high water temperatures, low river

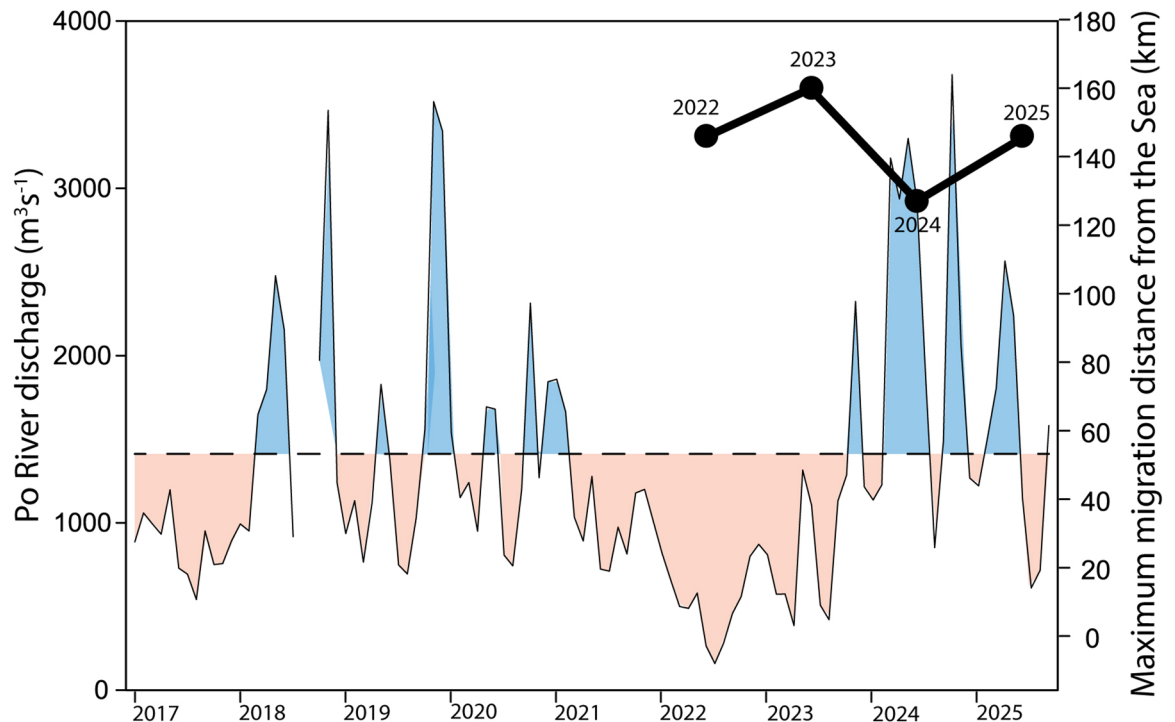


Fig. 4. Monthly mean discharge ($\text{m}^3 \cdot \text{s}^{-1}$) of the Po River at Pontelagoscuro station from January 2017 to September 2025 (plotted on the left axis). The dashed horizontal line represents the mean monthly discharge for the 2000–2025 period ($1412.2 \text{ m}^3 \cdot \text{s}^{-1}$), positive anomalies (periods of flow above the mean) are shown in blue, while negative anomalies (drought periods) are shown in orange. Black points (plotted on the right axis) indicate the annual maximum upstream migration distances from the Sea (km) recorded for the blue crabs; the reference year is reported to each point.

flows, and exceptional saline intrusion on the Po River^{53–55}. These conditions are known to favor blue crab success in Mediterranean systems⁵⁶. Notably, the maximum upstream distance (160 km) was recorded in 2023, following this prolonged period of low flow. Conversely, the subsequent high-discharge event appears to have limited upstream dispersal. However, disentangling these complex drivers would require higher-resolution environmental monitoring paired with standardized blue crab abundance data, which were not available for the present study.

Potential ecological interactions with freshwater fish communities and brackish water fisheries

The expansion of the blue crab into freshwater represents a significant concern for the emergence of novel trophic interactions, although data from these environments remain scarce. Detrimental impacts on aquatic diversity in Mediterranean coastal systems are well-documented, including declines in native green crab (*Carcinus maenas*), killifish (*Aphanius fasciatus*) and European eel (*Anguilla anguilla*)³. However, knowledge of blue crab ecology in freshwater systems remains poorly investigated and mainly focused on its native range. Consequently, the progressive upstream invasion of Mediterranean rivers introduces novel trophic interactions that require investigation. In order to provide a preliminary assessment of these potential trophic dynamics, we cross-referenced the known fish assemblage of the Po River with a literature review of documented predator–prey interactions involving blue crab and riverine fish species in both native and invaded ranges. Therefore, the interactions discussed below emerged from published studies and require empirical verification. The European eel currently represents the only documented riverine fish preyed upon by blue crabs in Mediterranean systems, specifically during its early juvenile stages^{3,23}. This suggests a potential localized negative impact, particularly in the delta regions, such as the Po Delta, which serves as corridor for glass eels migrating inland. Furthermore, the generalist and opportunistic diet of blue crabs raises concerns about trophic competition with native benthivorous species. Such competition could have cascading ecological effects, potentially affecting all benthivorous species and in particular the endemic Adriatic sturgeon (*Acipenser naccarii*), a species of high conservation concern.

Conversely, although direct evidence from European rivers is limited, it is plausible that blue crabs could serve as a novel prey resource for fish predators. In their native North American range, blue crabs are consumed by species such as blue catfish (*Ictalurus furcatus*) and largemouth bass (*Micropterus salmoides*)^{41,42}. While the largemouth bass, once invasive in the Po delta, has now largely disappeared, with only very rare specimens found in some marginal backwaters often completely disconnected from the Po river, the blue catfish and the closely related spotted channel catfish (*Ictalurus punctatus*) are now experiencing exponential growth throughout the lower and middle Po river, where well-established populations dominate the total fish biomass. It is therefore

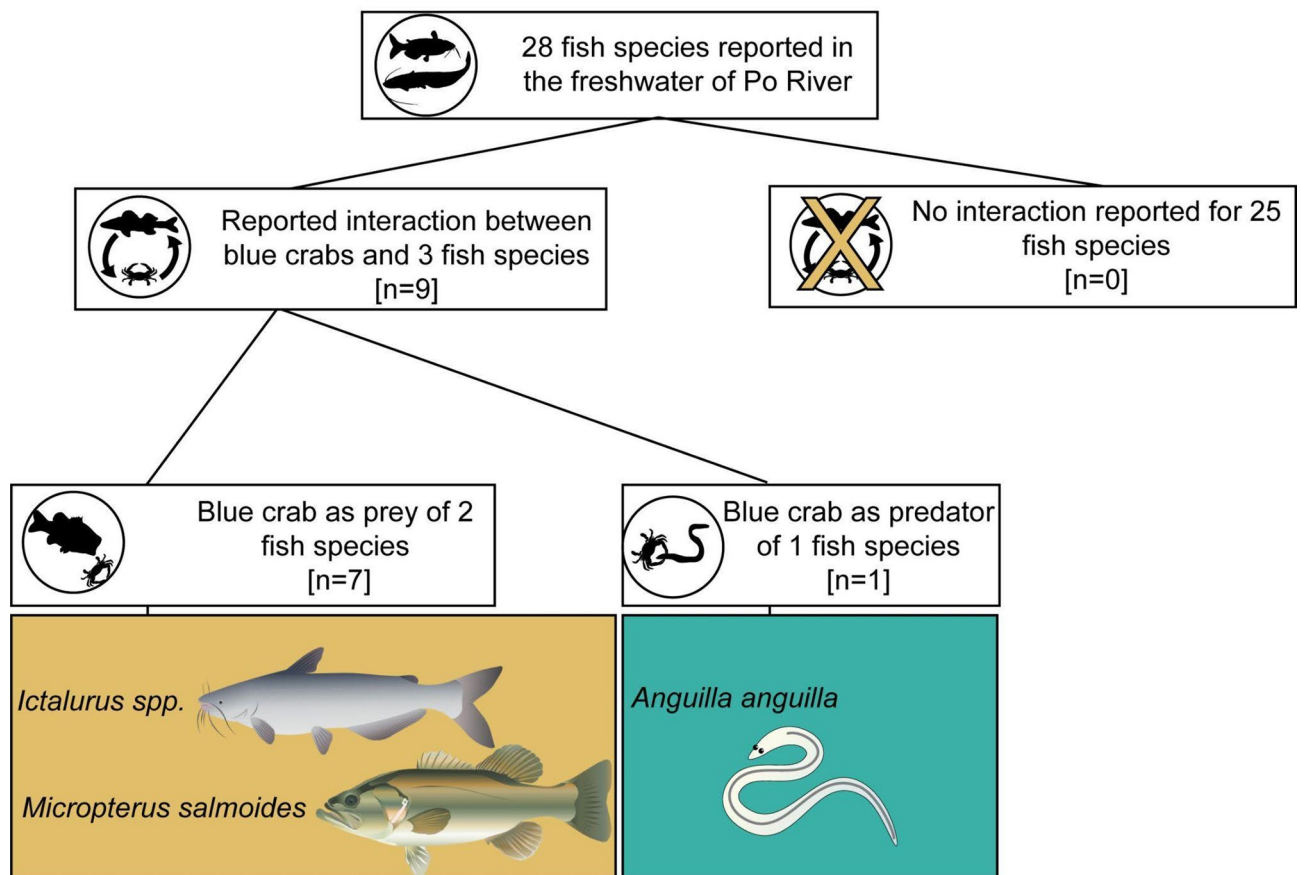


Fig. 5. Flowchart of targeted literature review for the interactions between the blue crab *Callinectes sapidus* and the freshwater fish species present in the Po River. The numbers in square brackets refer to the total number of scientific articles matching the literature review. For more details see Table S2.

biologically plausible that these species may exploit blue crabs in the Po, although this specific interaction should be empirically verified at local scale.

Additionally, apex predators in the Po River, including pikeperch and wels catfish, can reach body sizes potentially sufficient to prey upon adult blue crabs⁵⁷. Similar predatory interactions have been documented for the wels catfish on the invasive red swamp crayfish (*Procambarus clarkii*) in the lower Po basin⁵⁸, supporting the plausibility of comparable predation on blue crab. Moreover, in Po Delta lagoons, native coastal fish such as European seabass have been suggested to prey upon blue crabs⁴, potentially representing a natural biocontrol mechanism.

Among fish predators, the American eel (*Anguilla rostrata*) is also a known predator of blue crabs in its native range⁶, suggesting that adult European eels could fulfill a similar ecological role on blue crab juveniles in the lower stretches of the river. However, the substantial decline of adult European eel populations in the Po River, primarily due to damming and overexploitation³¹, likely reduces this potential predation pressure, which may facilitate the establishment and persistence of blue crab populations.

All the above effects must be considered in relation to the abundance of blue crabs, for which quantitative estimates of abundance and density are currently unavailable in both the Po River and the delta. Nevertheless, catch records from this study suggest higher abundances in the delta compared to the upper reaches, a pattern consistent with the blue crab's biology⁶. Furthermore, studies of quantities caught in the largest Po delta lagoons of Scardovari and Goro^{4,21,22} indicate that a very high number of individuals may move from the lagoons to the adjacent Po branches with ease, even on a daily basis. As previously highlighted⁴, the blue crab invasion has negative effects on catches, at least in the Goro lagoon, of many fish species targeted by professional fishing. Contrarily, for some species, including European seabass, catches have steadily increased following the blue crab expansion. A similar effect is conceivable in the brackish portion of the Po delta branches, although more data are required to investigate this aspect.

Limitations and future research

This study provides valuable insights into the upstream migration of blue crab along the Po River and its delta branches. However, several limitations should be considered. The reliance on interviews with local fishermen for occurrence data was constrained by logistical factors, including the physical inaccessibility of some riverbank reaches and variable participation rates. Consequently, despite our effort, the full upstream extent of the species

may be underestimated. Nonetheless, collaboration with fishermen proved invaluable, as their empirical observations provide information often missing from citizen science datasets⁵⁹.

Another limitation is the qualitative nature of the data, which prevents precise estimates of population density or abundance along the river. Furthermore, while the study effectively identifies the invasion front (maximum annual distance), the sampling design was not intended to resolve the fine-scale movement dynamics or daily behavioral patterns of the species, which would require other approaches such as telemetry or tracking⁶⁰. Similarly, since environmental monitoring was conducted at a broad spatial scale rather than being specifically designed to investigate upstream migration, our ability to resolve fine-scale gradients or to identify the exact abiotic drivers of dispersal is limited.

Furthermore, studies on trophic interactions and community-level impacts of blue crab in freshwater systems remain scarce. The potential effects on native fish species and benthivorous communities are largely unexplored, highlighting a critical knowledge gap.

Future research should focus on the systematic monitoring of blue crab occurrences, combined with high-resolution environmental measurements, local angling and professional fishing catches, and a tracking approach to study movement dynamics. Targeted studies on trophic interactions and community-level impacts should also be conducted. Such efforts are essential to understand the ecological consequences of blue crab invasions in freshwater ecosystems and to support effective management strategies.

Conclusions

This study provides the first evidence of extensive upstream migration of the blue crab in a non-native region, with individuals recorded up to 160 km inland along the Po River from the Adriatic Sea. While the euryhaline nature of the species is well known, large river systems allow blue crabs to penetrate freshwater ecosystems well beyond their typical estuarine range. Such expansion into freshwater habitats represents a notable extension of the species' invasive range and raises concerns about potential ecological impacts. Freshwater reaches of the Po River already host a high proportion of non-native fish species, and the arrival of the blue crab introduces novel interactions that may alter community dynamics.

Direct evidence of predation or competition with local freshwater fish is currently lacking, not only in the Po River but also throughout European freshwater ecosystems. However, the presence of large predatory fish in the Po River, both native and established non-native species, may exert some top-down control over blue crab populations, potentially limiting juvenile or adult abundance. In contrast, in the branches of the Po Delta, where blue crab catches are much higher, a significant positive effect on professional fisheries is expected, as evidenced by a recent study of the Goro lagoon⁴.

The species' high tolerance to varying salinity, temperature and oxygen levels, combined with its opportunistic feeding behavior, suggests a strong capacity for long-term establishment and possible trophic alterations.

Our analyses indicate that key environmental variables may play a limited role in upstream dispersal in the Po River, suggesting that upstream migration may instead be driven by other biological factors like density-dependent processes. However, the contribution of exceptional hydrological events, such as the 2022 heatwave, in influencing blue crab upstream dispersal cannot be excluded. This highlights the potential impact for extreme climatic conditions on invasions, although this aspect requires further research.

Future research should focus on systematic, high-resolution monitoring of blue crab occurrences, coupled with quantitative assessments of population abundance. Experimental studies are needed to evaluate ecological impacts on native fish and benthivorous species, as well as potential trophic interactions. Understanding the drivers of upstream migration and its consequences for freshwater biodiversity is essential for developing effective management strategies and invasion risk assessment⁶¹.

The Po River provides a key example of the blue crab's capacity to colonize freshwater systems far from its native marine and brackish habitats. Observed upstream migration, together with the species' ecological plasticity, underscores the need for proactive monitoring and research to safeguard native freshwater biodiversity and mitigate emerging invasive threats.

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

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Author contributions

GC and ML conceived the study. Data collection and surveys were done by DC, MC, MM, RS and FM. Literature collection, preparation of data and analysis were done by MG and AG. Drafting was done by AG and MG, with revisions from GC. All authors have read and revised the submitted manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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