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Severe, rapid and widespread impacts of an Atlantic blue crab invasion

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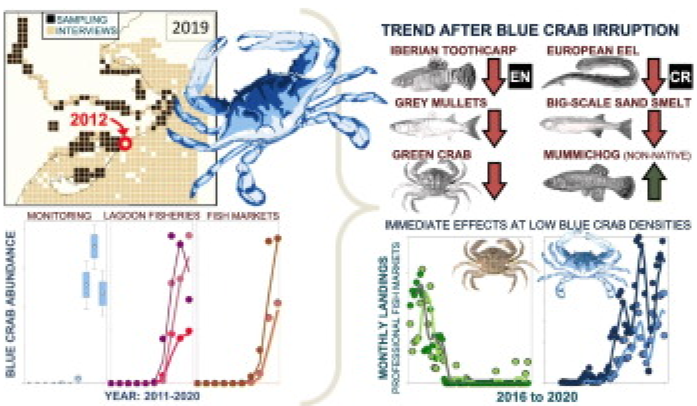
Highlights

- Blue crab occupied all the Ebro Delta and became abundant in roughly two years.
- Five year time-lag between first detection and exponential abundance increase.
- Blue crab drives several species declines, including severely threatened taxa.
- Previously abundant native green crab has virtually disappeared in the Ebro Delta.
- Blue crab is a new keystone species in invaded Mediterranean coastal areas.

Abstract

The Atlantic blue crab (*Callinectes sapidus*) has rapidly invaded coastal environments in the western Mediterranean, but there is no consistent assessment of its impacts yet. We use interviews and long-term data series in the Ebro Delta (NE Spain) to: i) characterise the evolution of the blue crab invasion; and ii) identify its impacts. The blue crab was first recorded in 2012, but its expansion started around 2016, with an exponential increase in abundance between 2017 and 2018. Aquatic communities have tended to be dominated by the blue crab, coinciding with the steep and consistent declines of several species, including threatened and commercially exploited ones. Blue crab impacts seem to be exerted even at low abundances, arguably hindering the recovery of declining species. The blue crab is becoming a keystone species in invaded systems and efforts should be made to understand its many-folds impacts in order to prevent or mitigate them.

Graphical abstract



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Keywords

Biological invasions; *Callinectes sapidus*; Coastal ecosystems; Ebro Delta; Keystone species

1. Introduction

Invasive alien species are widely recognized as important drivers of environmental change, modifying the composition and structure of biological communities, the functioning of ecosystems and the services they provide to humans (Simberloff et al., 2013). In spite of this, some invasions seem to have no environmental impact (e.g. Thomas and Palmer, 2015) and a growing number of studies report weak effects of invasive species (Crystal-Ornelas and Lockwood, 2020). The absence of evidence of impacts may be mistakenly assumed to be evidence of absence of impact for different reasons, including lack of pre-invasion information, the temporal decoupling between the incidence of impacts and their assessment (i.e. invasion debt; Essl et al., 2011) or the difficulty in disentangling the effects of invasions and of other drivers of environmental change (Simberloff et al., 2013). These issues probably generate the scarcity of invasion biology studies that explicitly deal with impacts, which in the case of marine taxa constitute less than 10% of the total number of works focussed on non-natives (Watkins et al., 2021). As the assessment of impacts is critical to set priorities for the management of invasive species, research should carefully assess those cases of successful invaders for which reports on environmental impacts are scarce, unclear, or lacking. We herein argue that the Atlantic blue crab (*Callinectes sapidus*) in European waters represents one of those cases.

Callinectes sapidus (henceforth, the blue crab) has a broad native area along the American eastern coasts, extending from the Gulf of Maine (Canada) to Rio de la Plata (Argentina) (Mancinelli et al., 2021). This species is able to occupy a wide range of coastal aquatic systems and often acts as a keystone species in them (Boudreau and Worm, 2012; Glaspie et al., 2020). Across its native range it is subjected to commercial exploitation (e.g. Seitz, 2020), which is also incipient in some non-native areas (Glamuzina et al., 2021). The blue crab was recorded for the first time in Europe in the early 20th century and records of the species slowly increased thereafter, although the rate of expansion has accelerated recently (roughly, since 2010) (Mancinelli et al., 2021). Several population outbreaks have been recently recorded across the Mediterranean (e.g. Fuentes et al., 2019; Culurgioni et al., 2020). Noticeably, population outbreaks of a large invasive crustacean with broad habitat and trophic niches are expected to produce important impacts in the recipient communities. However, to date there are no robust descriptions of the environmental impacts of the blue crab across its large, and still growing, non-native range (Mancinelli et al., 2017b). This knowledge gap precludes the adoption of informed management decisions dealing with the management of this recent invasion.

Here, we describe the rapid invasion of coastal wetlands in the Ebro Delta (Spain, NE Mediterranean) by the blue crab and the concurrent steep decline in abundance of several species, with the ultimate scope of providing a first thorough assessment of the impacts of this species in the Mediterranean. To this end, we compiled a wide body of information available on the distribution and abundance of the blue crab and several other taxa from monitoring programmes, fisheries statistics, and interviews with local stakeholders. We related recent changes in species abundances to the spread and increase in abundance of the blue crab, in order to identify those species being more susceptible to the invasion. A further effort was made to generalize our results to highlight the risk associated with the recent and rapid spread of the blue crab in Mediterranean coastal waters and adjacent marine and coastal systems.

2. Methods

2.1. Study area

The Ebro Delta (40°43′N 00°43′E) is a large (~320 km^2) coastal wetland formed by the deposition of sediments as the Ebro River enters the Mediterranean Sea (Fig. 1). The Delta has two sand spits, which form two semi-closed shallow bays. Land uses in the Delta are mainly linked to rice-based agriculture, which occupy ~66% of the surface. Rice irrigation relies on two main inflow channels that ramify into a complex network of smaller channels when entering the Delta (Fig. 1; Clavero et al., 2015). From rice fields the water is channelled either back to the river or to the sea through an equally complex outflow network. Remaining semi-natural systems (lagoons and marshes) are currently protected by the Ebro Delta Natural Park. Rice is irrigated with low-conductivity water, and the outflows have important impacts on composition of the biological communities of these semi-natural systems (Clavero et al., 2016). Here, we use fisheries data (see below) from three coastal lagoons: i) Encanyissada (477 ha surface, a 379 ha vegetation fringe, 115 cm maximum depth, and an average conductivity of 29 $mS \times cm^{-1}$); ii) Tancada (180 ha surface, a 75 ha vegetation fringe, 55 cm maximum depth, average conductivity 39 $mS \times cm^{-1}$); and ii) Canal Vell (239 ha surface, a 34 ha vegetation fringe, 80 cm maximum depth, average conductivity 18 $mS \times cm^{-1}$).

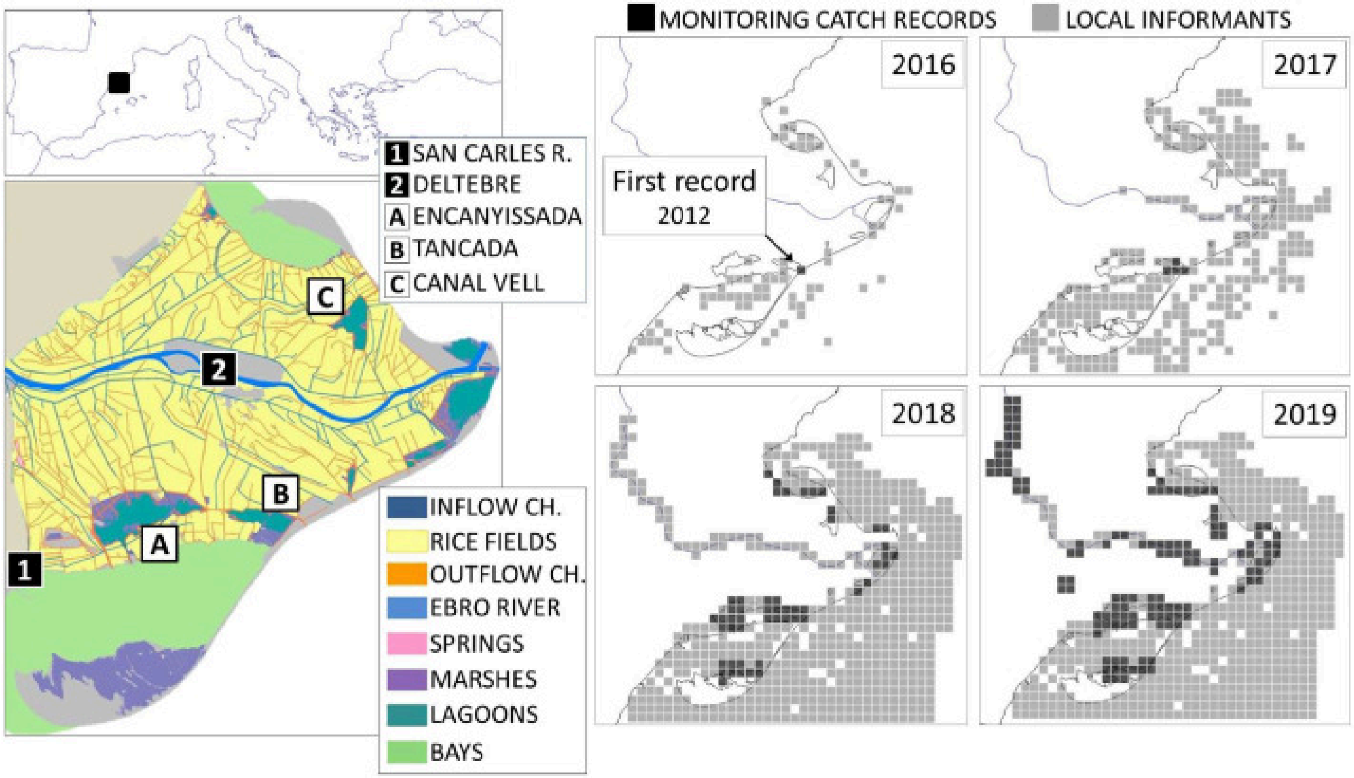

Fig. 1. Left maps: location of the Ebro Delta within the Mediterranean Basin (above) and main aquatic habitats in the Ebro Delta (bellow), with indication of the lagoons hosting relevant fisheries (white squares) and the main professional fish markets (black squares). Right maps: temporal evolution of the distribution blue crab records in the Ebro Delta, indicating if the record was obtained through interviews or through monitoring activities developed by the Ebro Delta Natural Park. Interviews were developed in 2018 (see methods) and thus interview-derived data are the same in the 2018 and 2019 maps. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Blue crab expansion

The blue crab was first detected in the Ebro Delta in 2012 in La Tancada lagoon (Fig. 1; Castejón and Guerao, 2013). We compiled subsequent blue crab records in the Delta, the lower Ebro River, and surrounding coastal waters from a variety of sources. These sources include the results of 1880 sampling events carried out by the Ebro Delta Natural Park between 2011 and 2020, employing a variety of sampling schemes and techniques (mainly fyke nets, but also gill-nets and electrofishing), a collection of blue crab occasional observations, and 73 interviews with local stakeholders (e.g. fishermen, managers, naturalists) who identified the areas of blue crab presence and its temporal variation, undertaken in 2018. We assigned all records to a year and to a specific square within a 1×1 km grid to plot them in maps.

2.3. Blue crab impacts: data and analyses

We assessed the impacts of the blue crab on aquatic communities of the Ebro Delta based on long-term datasets (i.e., at least a decade) on the relative abundances of fish and crab species in the area. These data derived from three sources: i) direct species catches during standardised fish monitoring; ii) harvest reports from lagoon fisheries guilds; and iii) official landings at professional fish markets in the Ebro Delta. Harvest data from the lagoon fisheries are not included in the figures obtained from fish markets, thus ensuring the independence of the two data sources.

Standardised sampling was framed in the monitoring of Iberian toothcarp (*Aphanius iberus*) populations (see Clavero et al., 2016), developed by personnel of the Ebro Delta Natural Park. Between 2011 and 2020, 527 sampling events took place in 82 different sites (on average 53 sites sampled each year, range 30–66) using fyke nets (two funnels, 3.5 mm mesh-size and ~100 cm in length) set during 24 h once a year, always between September and October. We counted and identified all captured fish and large decapods (crayfish and crabs), focussing the analyses on species captured in at least 25 sampling events (i.e. 5% of the total effort): blue crab, Iberian toothcarp, large-scale sandsmelt (*Atherina boyeri*), European eel (*Anguilla anguilla*), common goby (*Pomatoschistus microps*), eastern mosquitofish (*Gambusia holbrooki*), grey mullets (Family Mugillidae), mummichog (*Fundulus heteroclitus*), and Mediterranean green crab (*Carcinus aestuarii*).

The fish and crustacean fauna of the Ebro Delta lagoons are exploited by members of the Sant Carles de la Ràpita fishermen guild between October and February, using three passive fishing gears: fyke nets, trammel nets, and a large fixed trap (locally named *pantena*). The fishing guild kindly provided total harvest data per fishing season for the three main lagoons fisheries (Encanyissada, Tancada and Canal Vell) encompassing the last 20 years (2001 to 2020; using the starting year for each fishing season, e.g. 2020 for the 2020–2021 season). We collected data on 10 species or groups of species: blue crab, European eel, large-scale sandsmelt, grey mullets, common carp (*Cyprinus carpio*), sea bream (*Sparus aurata*), sea bass *(Dicentrarchus labrax*), leerfish (*Lichia amia*, including occasional *Trachinotus ovatus* catches), flatfish (Order Pleuronectiformes), and green crab.

Monthly landings of the blue crab and green crab at Deltebre and Sant Carles de La Ràpita professional fish markets were obtained from the Catalan Regional Government. We focussed on crab catches because the fish species traded at professional fish markets differed from those involved in the toothcarp monitoring and lagoon fisheries. We presented landing data on two ways: i) pooled in a yearly basis for the period 2011–2020; and ii) in a monthly basis for the period 2016–2020. This latter monthly approach was used to have a temporally finer view of the synchrony of the abundance patterns of the two crab species.

As for the analyses, we constructed two relative abundance matrices, one with data from toothcarp monitoring and the other with data from lagoon fisheries, in which rows represented sampling events (i.e. unique combinations of site and year) and columns were species or groups of species. We used these matrices as input of two independent principal components analyses (PCAs) to summarize the main gradients of variation in the composition of species assemblages. PCA outputs provide new variables (principal components, PCs) that reflect patterns in the spatio-temporal variability of species abundances. PCs are interpreted through species loadings, which indicate the linear trend of species abundances along PCs (i.e. as correlation coefficients). Sampling events located next one to each other in the space defined by PCs would thus have similar abundances for the set of species analysed. We were specifically interested in the loadings of the blue crab and potentially impacted species along PCs, as well as in the possible temporal influence in PCs. To this latter aim, we regressed the position of sampling events (PCs' scores) against the year of the data. The scores of the PCA on toothcarp monitoring data were also regressed against conductivity data (in $mS \times cm^{-1}$), recorded simultaneously to fish sampling, to evaluate the possible role of this relevant parameter (e.g. Clavero et al., 2021) on the generation of patterns in community structure.

3. Results

3.1. Blue crab expansion

The almost ubiquitous colonization of the Ebro Delta by the blue crab took place rapidly, roughly between 2016 and 2019 (Fig. 1). By 2016, four years after the first detection, local fishermen reported the blue crab from several marine sites, within the two bays and in different lagoons. However, in that year records from sampling activities were still limited to La Tancada lagoon. Fishermen reported a rapid spread of the blue crab between 2016 and 2018, when the species was already perceived as ubiquitous across the Delta and along the Ebro River's main channel. Widespread detection of the blue crab based from sampling activities occurred between 2017 and 2018, having a time-lag of around one year when compared with the fishermen reports (Fig. 1). In 2018 the species was recorded in all lagoons and in saline wetlands within the Delta, as well as in the bays, while in 2019 it was also found along the Ebro River up to the Xerta Dam (the first insurmountable barrier, some 30 km upstream from the Delta plain) and in several low-conductivity aquatic environments.

The timing of the blue crab spatial expansion in the Delta is mirrored in the abundance patterns of the species emerging from data from the toothcarp monitoring program, the commercial lagoon fisheries and fish market landings (Fig. 2). In all cases, blue crab abundance exponentially increased since 2017, while data on catches were only occasional before that date. This increase in abundance seems however to have slowed down (e.g. fish market landings, La Tancada lagoon catches) or even reversed (monitoring data, L'Encanyissada catches) between 2019 and 2020.

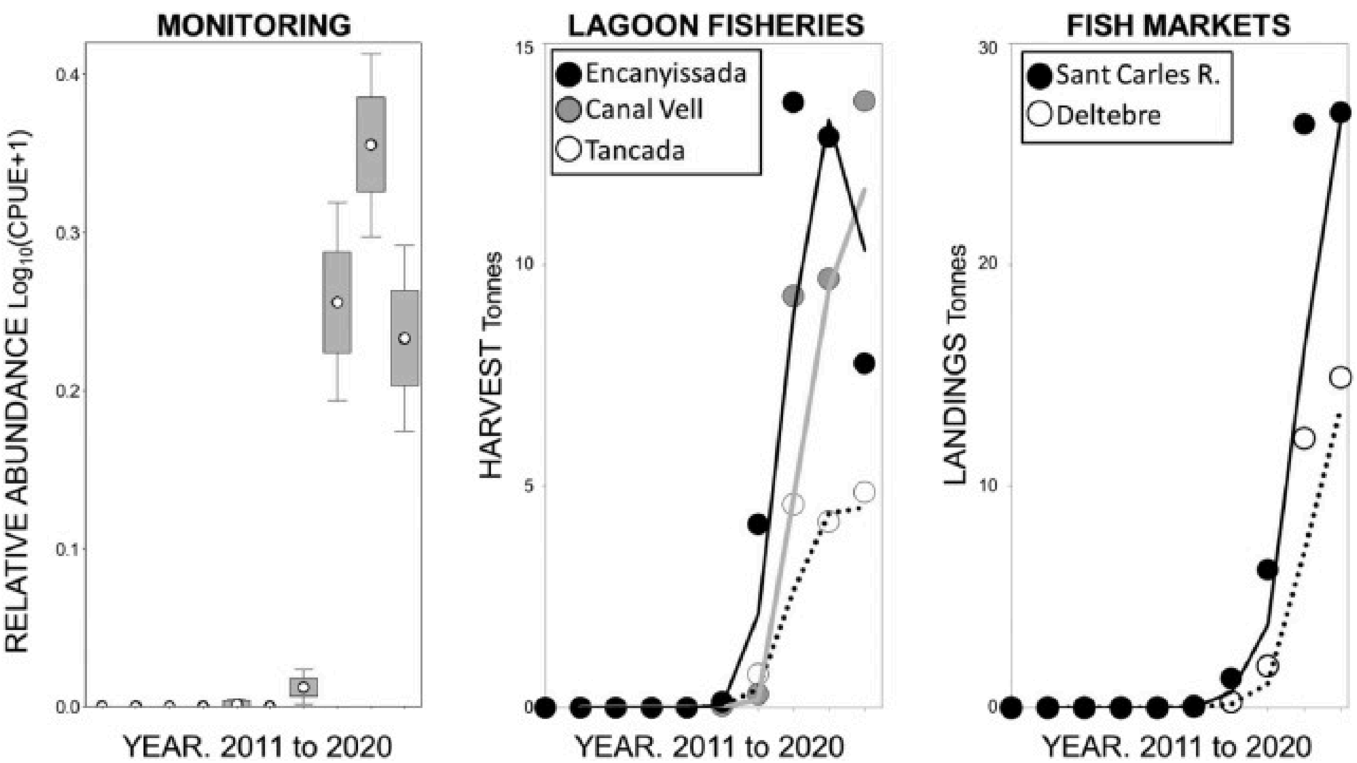

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Fig. 2. Yearly variation (2011–2020) of the relative abundance of blue crab recorded in Spanish toothcarp (*Aphanius iberus*) monitoring (left panel), by lagoon fisheries (central panel, showing data for each individual lagoon) and in professional fish markets (right panel, with data for each of the two main markets). In the monitoring panel, dots indicate average values, boxes are standard errors and whiskers are 95% confidence intervals. In the lagoon fisheries and professional fish markets panels dots are absolute values and lines are

weighted average lines with a 2-year period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Blue crab impacts

For both monitoring and lagoon fisheries data, the main gradients of variation in community composition (PC1s) opposed the relative abundance of the blue crab and that of the European eel, the green crab and grey mullets (Fig. 3). Also in both cases, PC1s showed a clear temporal variation, with more recent surveys being characterised by higher abundances of blue crab. The PC1s also showed different opposite abundance patterns between the blue crab and either the common goby (from monitoring data) or the sea bass, the sea bream, the common carp, and the large-scale sandsmelt (for fisheries data). The PC2 from monitoring data was also influenced by the blue crab, discriminating sampling events with high relative abundance of this species from those from abundant toothcarp or mummichog catches (Fig. 3). This gradient was not related to time (year-score regression; R^2<0.01), but to conductivity (conductivity-score regression; R^2=0.31), suggesting that the blue crab might have a limited capacity to invade the most saline habitats within the Ebro Delta. These habitats mainly comprise hypersaline shallow wetlands, with conductivities often surpassing 40 mS×cm^{-1}, occasionally reaching 100 mS×cm^{-1}, some of them traditionally exploited for salt production although only one of such exploitations remain active. PC2 emerging from the fisheries data was characterised to its positive extreme by freshwater species (common carp and, to a lesser extent, sandsmelt) and by marine-related species (sea bream, flatfish) to its negative end. The harvest in all three lagoons has converged in recent times (i.e. towards the positive end of PC1, see Fig. 3) to a dominance of blue crab, blurring the variability of its freshwater vs marine biological character among lagoons and among years within lagoons.

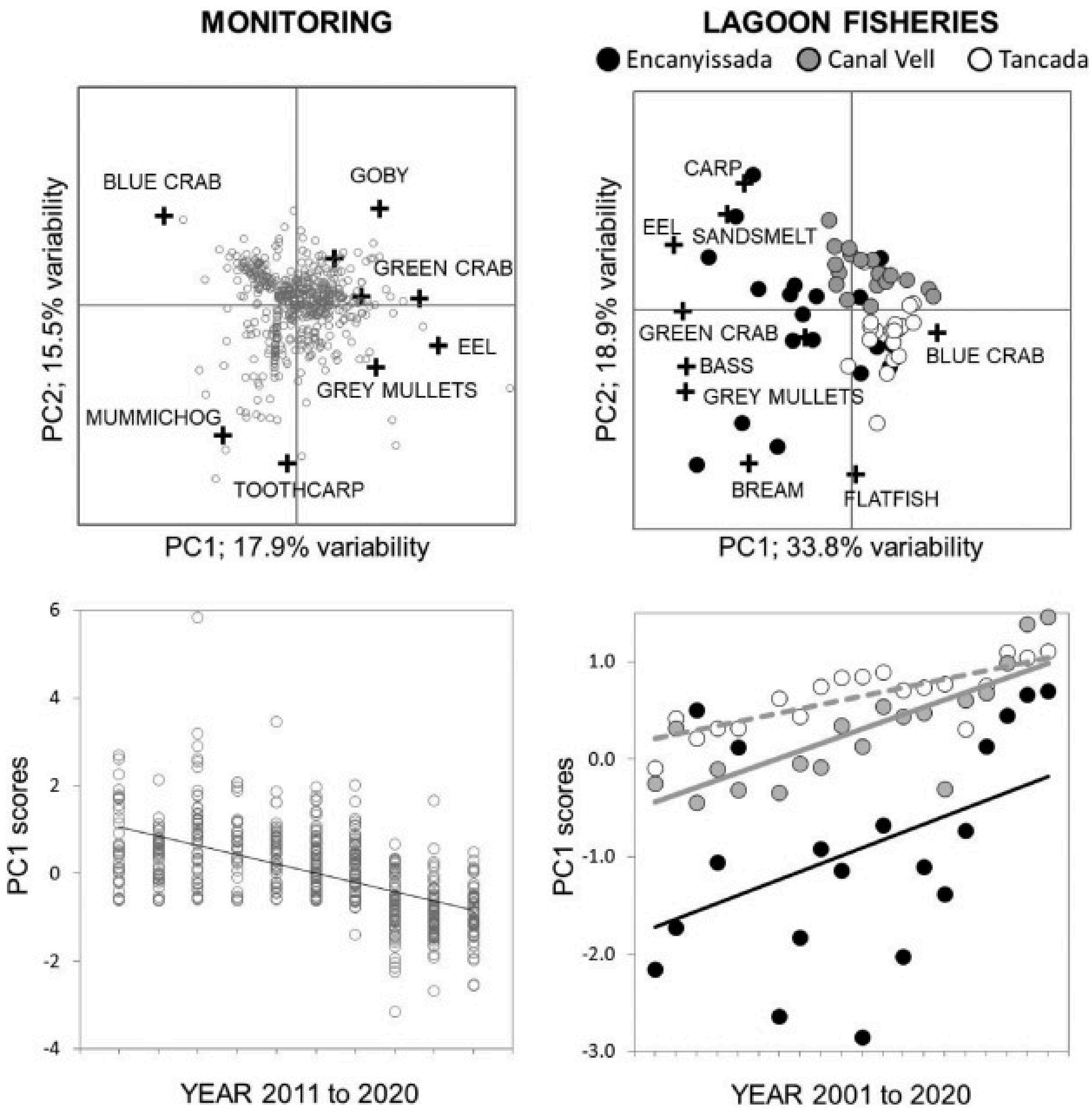

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Fig. 3. Results emerging from the principal component analyses (PCAs) applied to: i) data obtained through the monitoring of toothcarp populations (left panels); and ii) harvest data from lagoon fisheries (right panels). Upper panels show simultaneously species loadings (crosses; used to interpret principal components or PCs) and the scores (i.e. position along PCs) of sample units, either sampling events (for monitoring data) or yearly harvest data for each lagoon (for lagoon fisheries, with different colours coding the three lagoons studied). Note that for this simultaneous representation score axes have a mean of zero, to fit with the range of species loadings (−1 to +1). Mentioned species or group of species: BLUE CRAB (*Callinectes sapidus*), GOBY (*Pomatoschistus microps*), GREEN CRAB (*Carcinus aestuari*). EEL

(*Anguilla anguilla*), GREY MULLETS (Fam. Mugillidae), MUMMICHOG (*Fundulus heteroclitus*), TOOTHCARP (*Aphanius iberus*), CARP (*Cyprinus carpio*), SANDSMELT (*Atherina boyeri*), BASS (*Dicentrarchus labrax*), BREAM (*Sparus aurata*), FLATFISH (Order Pleuronectiformes). Lower panels show the temporal evolution of sample unit scores along PC1, for monitoring data (left, 2011–2020; R^2=0.34) and lagoon fisheries (right, 2001–2020, R^2=0.19, 0.63 and 0.63 for Encanyissada, Canal Vell and Tancada lagoons, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The monitoring dataset showed that the relative abundances of several species varied over the study period, but revealed a steep and continuous decline of the green crab, the eel, the sandsmelt, the toothcarp, and the grey mullets from 2017, when the abundance of the blue crab increased exponentially (Fig. 4). The green crab has practically disappeared from the monitored areas since 2018, although the decline seems to have started around 2016. Between 2018 and 2020 the relative abundance of the eel has attained minimum values in the monitoring series and seems to be in an ongoing decline process. Minimum abundance values in 2020 along the whole series and continuous recent declines are also observed for sandsmelt, toothcarp and grey mullets. The common goby and the mosquitofish do not show evident signs of abundance declines, while the mummichog is the only species with increasing abundances among those analysed (Fig. 4).

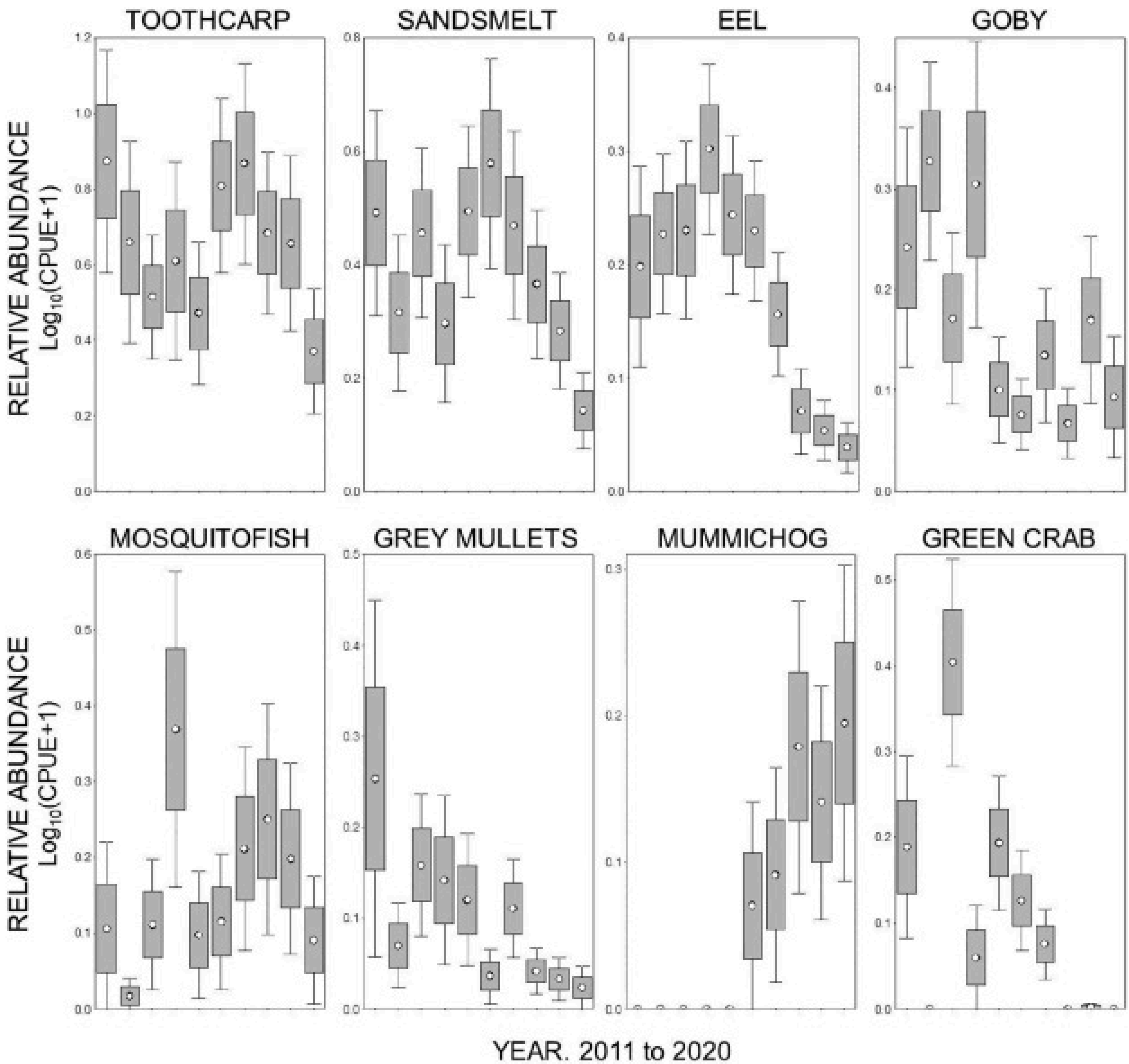

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Fig. 4. Yearly variation of the relative abundance of the most common species captured during Iberian toothcarp monitoring during the three phases described for the blue crab invasion in the Ebro Delta (see Fig. 3). Dots indicate average values, boxes are standard errors and whiskers are 95% confidence intervals. Species codes as in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Data from lagoon fisheries and professional market landings support the drastic, recent declines of different species coinciding with the surge of the blue crab. The green crab has disappeared from commercial harvest in the three lagoons, where the eel and the sandsmelt have also steeply declined since 2016 (Fig. 5). Overall fish catch has also followed a constant recent decline, which might not be fully attributable to blue crab invasion, since it apparently started before the species arrival to the Delta. However, all recent declines were steep and consistent across lagoons and species, coinciding with the recent spread of the blue crab. Landings of green crab at fish markets quickly collapsed coinciding with the first commercial catches of the blue crab, practically disappearing since 2018 (Fig. 6). Noticeably, this collapse preceded the exponential increase in blue crab abundance, suggesting that severe impacts may occur at relatively low blue crab densities.

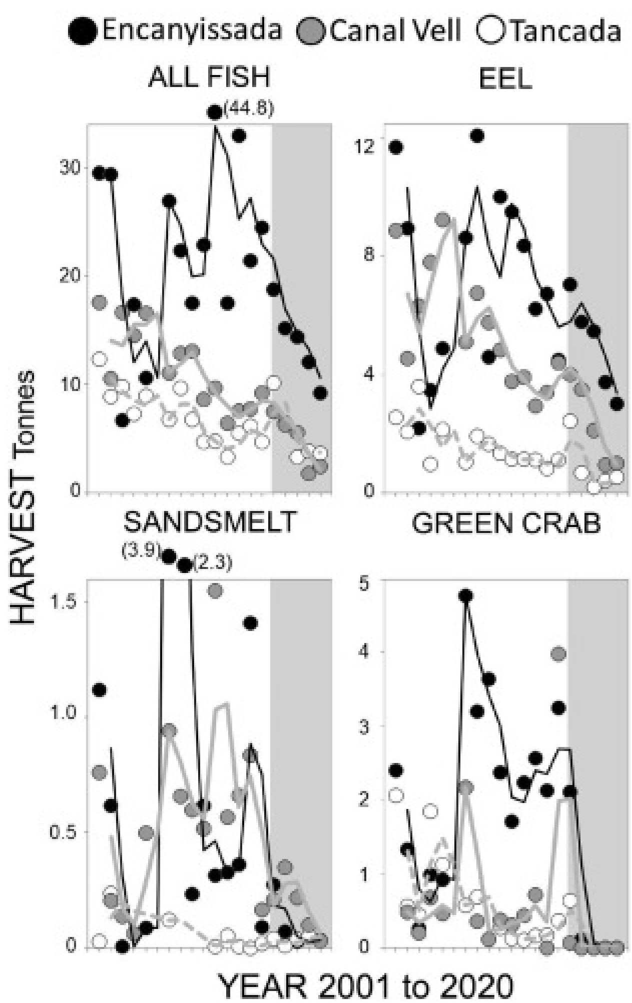

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Fig. 5. Yearly evolution of the harvest of lagoon fisheries in the Ebro Delta for the period 2001–2020, with shaded background areas marking the period 2016–2020. Values are shown for the whole fish catch and for that of the eel, the sandsmelt and the green crab, in all cases separately for the three analysed lagoons. Weighted average lines with a 2-year period are presented to illustrate temporal trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

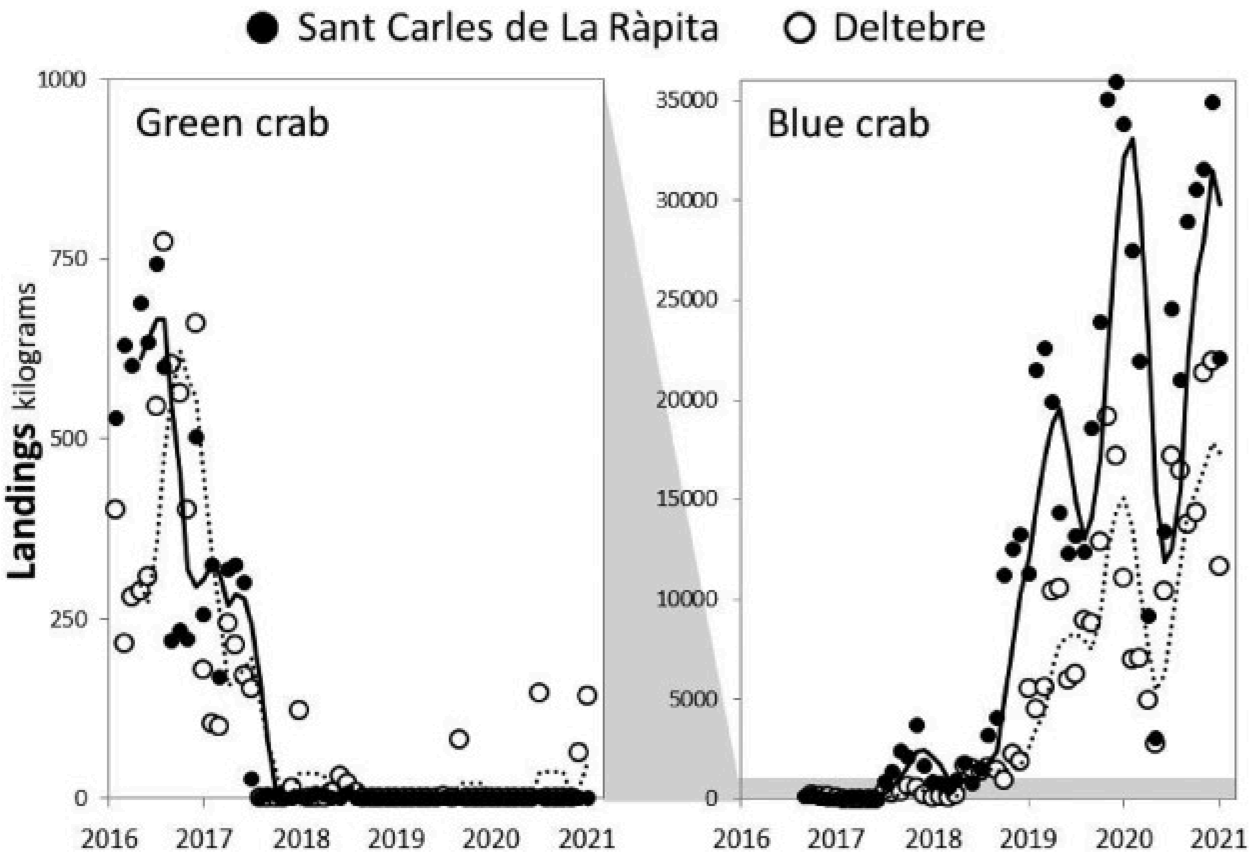

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Fig. 6. Monthly evolution of the landings of the green and blue crabs in the two main commercial slices of the Ebro Delta, for the period 2016–2020. Weighted average lines with a 4-month period are presented to illustrate temporal trends. The shaded area in the right panel indicates the area occupied by values in the left panel, to highlight the differences in the Y-axis scales between the two panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Blue crab expansion

The blue crab currently occurs in all main aquatic habitats in the Ebro Delta, including all reachable reaches of the Ebro River. The existence of biodiversity monitoring schemes in the Ebro Delta allowed a fine-scale temporal and spatial description of the distribution and abundance patterns of the blue crab. However, it must be noted that distribution patterns obtained through personal interviews to local informants anticipated by at least one year and in a spatially coherent way those obtained through monitoring sampling. This result highlights the potential of citizen science approaches to describe coastal invasions in general (Lehtiniemi et al., 2020) and that of the blue crab in particular (Cerri et al., 2020; Encarnação et al., 2021).

The spread of the blue crab across the Ebro Delta lagged for at least four or five years since its first detection in the area. This time-lag could be related to the life history of the species, taking place in both marine and brackish or freshwater habitats and involving important reproductive migrations (van Engel, 1958). Mating tends to occur in the upper estuaries, sometimes more than 100 km away from spawning sites (Turner et al., 2003). Ovigerous females migrate to marine waters to release the larvae, which are then transported offshore (Carr et al., 2004). Blue crabs settle in coastal areas in a megalopa stage, preferently in vegetated nursery areas (Forward et al., 2004). The adjustment of this reproduction strategy to new areas could explain delays in the booming of its invasion, in the Ebro Delta and elsewhere. The surge of the invasion, both in terms of spatial occupation and abundance, may have occurred only when a significant number of blue crabs in the Ebro Delta started reproducing. The large fertility of the blue crabs (Seitz, 2020) and the spatial configuration of the Ebro Delta (with two semi-closed bays favouring juvenile settlement near spawning areas; see Fig. 1) would have promoted the blooming of the blue crab population in recent years. Future studies should analyse reproductive behaviour of the blue crab in the Ebro Delta (e.g. females migration routes, location of mating areas, juvenile settlement) to identify the areas or life stages in which the blue crab would be more vulnerable, potentially opening windows of opportunity for the control of the species.

In recent times, the increase in the abundance of the blue crab seems to have slowed down or even reversed (Fig. 2). Although these could be stochastic or environmentally-driven changes in population densities, it is possible that the blue crab population had reached peak abundance values after only three years of exponential growth, as suggested by Prado et al. (2021). Should this have happened, it is probable that blue crab abundance in the Ebro Delta would decrease and stabilize at lower levels than those observed between 2018 and 2020, following a boom-and-bust process (Strayer et al., 2017). Predation could be involved in the limitation of blue crab abundance, attending at the wide array of aquatic and terrestrial organisms that can consume blue crabs (e.g. Guillory and Elliot, 2001), although there is not yet information on this from invaded areas. Also, the high fishing pressure in recent years (see Fig. 6) could also have had a role in limiting blue crab populations (Lipcius and Stockhausen, 2002). It is important to maintain the monitoring and data gathering effort to characterise the evolution of the blue crab invasion and identify its main drivers.

4.2. Blue crab as driver of declines

The declines of several species, reported by diverse data sources, and coinciding with the surge of the blue crab, solidly suggest a causal role of this invasive species. These impacts are arguably driven by predation, because the blue crab efficiently consumes a wide variety of invertebrate and vertebrate prey (e.g. Mancinelli et al., 2017a) and has been previously shown to influence the structure of prey communities (e.g. Kneib, 1982). Noticeably, Prado et al. (2021) estimated that animals constituted on average one third of blue crab diet in the Ebro Delta. This percentage is lower than those reported in other areas, both within native (e.g. Laughlin, 1982) and invaded (e.g. Mancinelli et al., 2016) ranges. Prado et al. (2021) obtained their samples in 2019 and suggested that relatively low proportion of animals in blue crab diet could be related to prey depletion. Our results indirectly support this view, since by 2019 all reported declines were already evident. Belgrad and Griffen (2016) found that high animal consumption increased blue crab fitness and suggested that an increasing role of plant material in its diet would negatively affect population growth, by reducing fertility and increasing mortality and intraspecific aggressions. Prey depletion would also promote cannibalism, involving a reduction in the survival of juvenile individuals that can affect population growth (Moksnes et al., 1997). Thus, the decline of several species due to blue crab predation could impose ecological limits to the growth of the population of this invasive species, potentially generating the boom-and-bust process mentioned above. Importantly, our results suggest that several species declines started with relatively low blue crab abundance, so a hypothetical low-density blue crab population in the post-bust period (sensu Strayer et al., 2017) would still have a large potential for impact and would arguably constitute a barrier for the recovery of declining taxa.

The impacts of the blue crab are especially relevant in the case of two globally threatened fish species, the Spanish toothcarp and the European eel. The former is an endangered species that has one of its main strongholds in the Ebro Delta. In the area, toothcarp is mainly restricted to high salinity environments, due to the presence of mosquitofish in aquatic habitats influenced by low-conductivity waters used in rice irrigation (Clavero et al., 2016). Toothcarp populations are increasingly threatened by invasive species that occupy saline environments, such as the mummichog (Gisbert and López, 2007) and now the blue crab. The common evolutionary history of these two species (e.g. Kneib, 1982) could favour their coexistence (see Fig. 4), potentially enhancing the negative impacts of both species. The European eel is a critically endangered species, after a population collapse that started in the early 1980s and involved widespread abundance losses surpassing 95% (Kettle et al., 2011). Once widespread across inland water systems the eel continental range is currently limited to a coastal strip, due to the fragmentation effect of dams (Clavero and Hermoso, 2015). In this scenario, the irruption of the blue crab invasion across most of the extant eel continental range can become a relevant new threat for the species. The decline of the eel in the Ebro Delta is consistent with the 56% decrease in eel catch observed in Akgöl Lake (Turkey) following the invasion by the blue crab (Özdilek and Özdilek, 2020). The eel may be susceptible to predation and/or to receiving injuries by the blue crab due to its inactive periods, in which the eel remains in the substrate, either within the circadian cycle (Bašić et al., 2019) or seasonally (Westerberg and Sjöberg, 2015).

Among the several reported declines, the collapse of the green crab was especially intense. The exclusion of this species by the blue crab invasion is in agreement with the observations of Kampouris et al. (2019) in Greece and with the reported interactions between *Carcinus* crabs and the blue crab in the North-Western Atlantic, where the blue crab predation limits the expansion of invasive European green crab, *Carcinus maenas* (de Rivera et al., 2005). The expansion of the blue crab has thus the potential of generating several green crab local extinction episodes and of driving large changes in the decapod assemblages in Mediterranean and North-Eastern Atlantic coastal systems (Farré et al., 2021).

The blue crab invasion in the Ebro Delta could also be driving the decline, and even causing the extinction, of several other exclusive and threatened taxa located in small and singular environments of the Ebro Delta such as the freshwater springs. The blue crab is already present in these springs and its predation activity could drive the local extirpation of the Iberian spined loach (*Cobitis paludica*; Clavero et al., 2021) or the extinction of the freshwater snail *Tarraconia rolani*, known only from this area (Salgado and Soriano, 2014). The Ebro Delta has populations of three freshwater mussels (Salgado and Soriano, 2014), while the Ebro River below the Xerta dam hosted one of the last extant populations of the critically endangered *Pseudunio auricularius* (Altaba, 1990). All these species can be severely impacted by an efficient mussel predator such as the blue crab. Beyond these threatened species, the blue crab can also affect other taxa, including species with commercial value (*Mytillus galloprovincialis*, *Crassostrea gigas*, and *Ruditapes philippinarum*) and invasive species (*Corbicula flumminea* and *Pomacea canaliculata*) (Prado et al., 2020, Prado et al., 2021). The threat that the blue crab may pose on several marine species, including fish, crustaceans and mollusc taxa subjected to commercial fisheries exploitation, remains to be studied.

5. Conclusions

Our study provides solid, though correlative evidence on the impacts of the blue crab in an invaded area. The effects of the blue crab emerged coherently form the analyses of independent long-term data series, and involved drastic declines of several species, some of which are globally threatened. Blue crab invasion has thus the potential of inducing radical changes in the composition and structure of coastal marine and freshwater communities, with direct implications for the conservation of biodiversity and the livelihoods of human populations of coastal areas. It is worth noting that the blue crab may constitute a novel profitable target for fisheries (Glamuzina et al., 2021). In the absence of efficient tools for large-scale control of blue crab populations its exploitation seems reasonable (e.g. Mancinelli et al., 2017b; Oficialdegui et al., 2021), but it must be acknowledged that commercial use does not involve, and often opposes to, population control (e.g. Malpica-Cruz et al., 2021). With the poor set of management options currently at hand, blue crab control actions should prioritise situations in which a local reduction of blue crab densities (e.g. through intense and permanent trapping) would involve positive outcomes for biodiversity and/or socioeconomic activities. These actions would be site-specific, and in the case of the Ebro Delta could concentrate on the most important Iberian toothcarp nuclei or on intensive bivalve farms.

The blue crab seems to have become a keystone species in invaded coastal ecosystems. Our analyses illustrating recent patterns in the Ebro Delta are arguably representative of situations reproducing across the Mediterranean and the NE Atlantic, given the recent spread and abundance increases of the blue crab (Mancinelli et al., 2021). Worryingly, the rapid and severe impacts of other invasive species are also being reported from the same area (Faria et al., 2022). Research into blue crab ecology in invaded areas should thus be a scientific priority, in order to quantify the impacts of this invasion and find tools to prevent or mitigate these impacts through effective control of blue crab populations and their spread.

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CRediT authorship contribution statement

Miguel Clavero: Conceptualization; Formal analysis; Writing - Original Draft **Nati Franch**: Conceptualization; Investigation; Writing - Review & Editing **Rubén Bernardo-Madrid**: Investigation; Writing - Review & Editing **Verónica López**: Investigation; Writing - Review & Editing **Pere Abelló**: Writing - Review & Editing **Josep Maria Queral**: Investigation **Giorgio Mancinelli** Writing - Review & Editing.

Declaration of competing interest

The authors declare that they do not have any conflict of interest related to the data, the results or the implications of this work. All funding sources are indicated, and none of them could influence our work.

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