Received: 15 November 2023 | Revised: 26 January 2024 | Accepted: 7 February 2024

DOI: 10.1002/aqc.4119

REVIEW ARTICLE

WILEY

The expansion of the Atlantic–Mediterranean ghost crab *Ocypode cursor* (Linnaeus, 1758): Distribution, environmental niches and future perspectives

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Funding information
National Biodiversity Future Center (NBFC)

Abstract

The tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) found in the Mediterranean Sea and the Atlantic Ocean is currently a great example that elucidates concerns within scientific and conservation communities. This species, native to the subtropical Atlantic Ocean and the warmest southeastern Mediterranean Sea (Egypt), has been extending its distribution in both regions since the 1980s, likely due to the warming sea temperatures. These small nocturn crabs are typically found inhabiting sandy beaches and dune environments. This species is an opportunistic predator eating terrestrial and marine prey, especially on sea turtle eggs. Despite its status as a threatened species by two European conventions, there is a lack of knowledge of its ecology and biology. Sometimes considered as an indicator of good ecological status of beaches where it lives, this ghost crab could nevertheless benefit from climate change to extend its distribution range. This review aims to create a baseline on the current knowledge and gaps in the published scientific literature on the ghost crab. Additionally, through an analysis of the existing literature, we also offer insights into the potential risk of beach erosion associated with the expansion of this species.

KEYWORDS

Atlantic Ocean, climate change, ghost crab, Mediterranean Sea, species expansion, tufted ghost crab

1 | INTRODUCTION

The environmental challenges facing the Mediterranean Sea are well documented in literature where overfishing, pollution, habitat destruction and the introduction of non-native species are considered among the major threats to the Mediterranean Sea's biodiversity (Coll et al., 2010). Furthermore, climate change is causing rising sea temperatures and acidification (Findlay & Turley, 2021), which in turn affects the distribution and abundance of marine species (Hastings et al., 2020; Worm & Lotze, 2021). As global temperatures continue to rise, the Mediterranean is experiencing a trend towards warmer waters (Pastor & Khodayar, 2023), with average temperatures increasing by up to 1.5°C over the past century (Pastor et al., 2019). This increase in temperature is leading to changes in the distribution and abundance of marine species, with some species shifting towards cooler waters or deeper depths, while others are experiencing declines in population sizes (Free et al., 2020; Garzke et al., 2015; Poloczanska et al., 2016; Stuart-Smith, 2021).

Climate change is changing the distribution of many species generating with direct consequences on the whole community. Exploiting climate change, certain species are expanding their ranges into areas that were previously too cold, such as northern latitudes and higher elevations (Freeman et al., 2018), and adjusting their breeding and migration patterns to synchronize with changing seasonal cycles (Langan et al., 2021; Poloczanska et al., 2016). Furthermore, certain species are adapting to changes in food availability by altering their diets or shifting to different prey species (Robinson et al., 2009). The expansion of the distribution of these species in some cases can pose a threat to species already present in the new areas, belonging to local biodiversity, going to alter and modify the niches and balances of ecosystems. While it is important to recognize that many species are facing significant challenges due to climate change, understanding the adaptive strategies of species can provide valuable insights for conservation strategies and management efforts (Brakes et al., 2021). Nonetheless, it is crucial to acknowledge that these adaptations may not be sustainable in the long term and that the overall impacts of climate change on some species (e.g. stenotherms and specialists) are overwhelmingly negative.

The case of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) found in the Mediterranean Sea and the Atlantic Ocean can be a pivotal example that elucidates concerns within scientific and conservation communities. This species, native to the Atlantic Ocean and the southeastern Mediterranean Sea, has been extending its distribution in both regions since the 1980s, likely due to the warming sea temperatures (Pisano et al., 2020). These small nocturne crabs are typically found inhabiting sandy beaches and dune environments (Lucrezi et al., 2009). It boasts a distinctive appearance, characterized by a square-shaped body (3–4 cm in width) and two large stalked eyes atop its head. Coloration spans from sandy yellow to grey, which provides effective camouflage against the sand. Known for its remarkable agility, this crab can swiftly and efficiently move in any direction, because of its specialized legs adapted for running on sand. Despite their small size, ghost crabs are ecologically important for the coastal ecosystem. This species plays a vital role in maintaining the equilibrium of its habitat, as they function both as predators and scavengers (Schuchman & Warburg, 1978; Tiralongo et al., 2020). Ghost crabs feed on a variety of small invertebrates, including mollusks, crustaceans and insects and are also known to scavenge on carrion (Sakai & Türkay, 2013). Additionally, ghost crabs are also an important source of food for other animals, such as birds and fish at higher trophic levels (Rae et al., 2019; Schlacher & Lucrezi, 2014). In various regions, species of the *Ocypode* genus are known as ecological engineers in sandy habitats. They construct either permanent or semi-permanent burrows, which serve as shelter for all life stages of these crabs, from juvenile to adult (Yilmaz & Barlas, 2020). These deep, complex burrows in beaches and dunes offer them a refuge from predators and maintain a constant temperature, particularly during summer. Although *O. cursor* is sometimes considered as an indicator of favourable ecological status by scientists (Aheto et al., 2011), a pertinent question emerges: Is *O. cursor* benefitting from climate change to the extent that its distribution is expanding in new regions? And does this extension terrestrial and marine biodiversity while contributing to beach erosion in areas where the species were absent previously?

In this review, we aim to collate data and information to stimulate reflection concerning *O. cursor* and its ability to broaden its distribution in response to climate change. This study aims to create a baseline for the gaps in the scientific literature on the ghost crab. Additionally, through an analysis of the existing literature, we also offer insights into the potential risk of sandy beach erosion associated with the expansion of this species.

2 | MATERIALS AND METHODS

An in-depth literature review was performed across Web of Science (WoS) and Google Scholar databases searching for records of all information on the ghost crab *O. cursor* using terms (singly or in combination) 'Ocypode' or '*Ocypode cursor*' or 'Tufted ghost crab'. Papers were ordered into a database including the authors' names, the paper's title, abstract, keywords and journal name (Supplementary Table S1). Because of the small number of papers available on this species, we choose to not divide them into different topics/groups. All articles collected on the ghost crab *O. cursor* were read, and information about its distribution, ecology and behaviour was extracted and presented in the discussion to highlight the current knowledge and lack of knowledge on this species.

To highlight the scientific interest in the tufted ghost crab *O. cursor*, we have plotted the cumulative number of published articles across the time (years) using the software Sigmaplot 12.5. In parallel, to highlight the scientific interest in *O. cursor*, we deployed a quantitative lexical analysis methodology using the IRaMuTeq textual analysis software, an interface based on R software and Python language, to extract information from all abstracts using descriptive statistics (Ratinaud & Déjean, 2009). The results based on the frequency of words were presented as worldcloud plots.

To assess the current world distribution of *O. cursor*, occurrences data were extracted from free access databases such as GBIF (Global Biodiversity Information Facility, https://www.gbif.org/) and OBIS (Ocean Biodiversity Information System, https://obis.org/). The GPS points, the year and the month of observations were extracted and compiled into a global database divided into two main areas: the Mediterranean Sea and the Atlantic Ocean. To define the expansion spatial and temporal dynamics, the cumulative number of records was calculated and the temporal pattern through the population's increasing rate over time based on evident slope changes of the cumulative curve of all occurrences was determined for both areas. Distribution maps were produced using the software QGIS (3.10.7-A Coruña) considering only the year of the first record and not the number of specimens, to reduce the effect of possible preferential sampling (Castriota et al., 2022). The cumulative curve of *O. cursor* occurrences was calculated and divided into arbitrary intervals based on the most evident slope changes, corresponding to the phases of expansion (Olenin et al., 2017; Perzia et al., 2022), for each time interval identified, the equation of the regression line was calculated in order to obtain the different rate of occurrences increase over time. On the maps, the time periods were presented as a function of the slope changes for both distribution areas. Kernel densities of occurrences were calculated using the spatial statistics toolbox on

QGIS in order to investigate the population's hotspot areas (Perzia et al., 2022).

Further, temperatures (minimum, maximum and average) were extracted from World Clim (http://www.worldclim.org) and overlapped to the ghost crab distribution as extrapolated according to the above methods to define the species' thermal niche in the Mediterranean Sea and the Atlantic Ocean. Values of temperatures were extracted for each occurrence point using the 'Point sampling tool' on QGIS, and the frequency of records as a function of temperature was calculated and plotted using Sigmaplot 12.5 and compared with the frequency (%) of ghost crab observations as a function of the months of the year calculated from the occurrences data information collected before.

3 | RESULTS AND DISCUSSIONS

The literature review performed revealed a total of 41 published articles on the ghost crab *O. cursor* (Figure 1a; Supplementary Table S1). Despite the low number of articles, there has been an exponential growth in the quantity of articles published over the years (e.g. from 2 articles in 1978 to 41 articles in 2022). Additionally, an analysis of the word's frequency used in the publications' abstract showed a predominance of articles published on the species in general, with terms like 'Ghost' and 'crab' being the most recurrent words. Moreover, there is a significant emphasis on the topics related to burrows and beach habitats as shown in Figure 1b.

3.1 | Distribution

The distribution of the ghost crab *O. cursor* encompasses two distinct and geographically widely separated subzones: the central-eastern Mediterranean basin and the tropical and subtropical Atlantic coasts of Africa (Figure 2). In the Mediterranean, *O. cursor* was historically observed in Egypt (1933–1965), and since 1966, its distribution range has expanded eastward, with an increase of 0.4 occurrences year^{-1} between 1965 and 1990 and a maximum of 9.43 occurrences year^{-1}. In the Atlantic, the species was historically recorded in Angola and Cameroon (1889–1937). The species expanded northward for Angola populations and westward for Cameroon between 1937 and 1965, with a rate of +1.01 occurrences year^{-1}. Since then, the species has expanded to all African Atlantic coasts with an increase of 3.35 occurrences year^{-1} between 2004 and 2023, which is three times less than in the Mediterranean over the last 7 years.

Kernel densities (K) in both the Mediterranean and Atlantic show several hotspots where ghost crab populations are concentrated (Figure 3). In the Mediterranean, the main hot spot is along the eastern coasts (from Egypt to Lebanon), but other hot spots can be observed in Turkey, Greece and southern Italy. In Africa, several hot spots (K > 7) are observable in Nambia, Angola, Benin and especially in Senegal and Cape Verde.

The current disjointed distribution of the species appears to be the result of fragmentation of a single large population during the Würm glaciation of the Pleistocene (Thiede, 1978), with the disappearance of the species from the temperate Atlantic Ocean and the western Mediterranean basin (Vecchioni et al., 2019). This disjuncture is thus in line with ancient isolation between the Mediterranean and Atlantic populations of the species, which could indeed constitute two well-characterized independent evolutionary lineages or even two cryptic species; recent genetic studies have shown that Mediterranean and Atlantic populations belong to a single lineage (Vecchioni et al., 2019). As demonstrated by our analysis of the current distribution of *O. cursor* in the Mediterranean and the Atlantic, the expansion of this species continues northward in both areas, along the recently colonized Ionian coast and the western zone

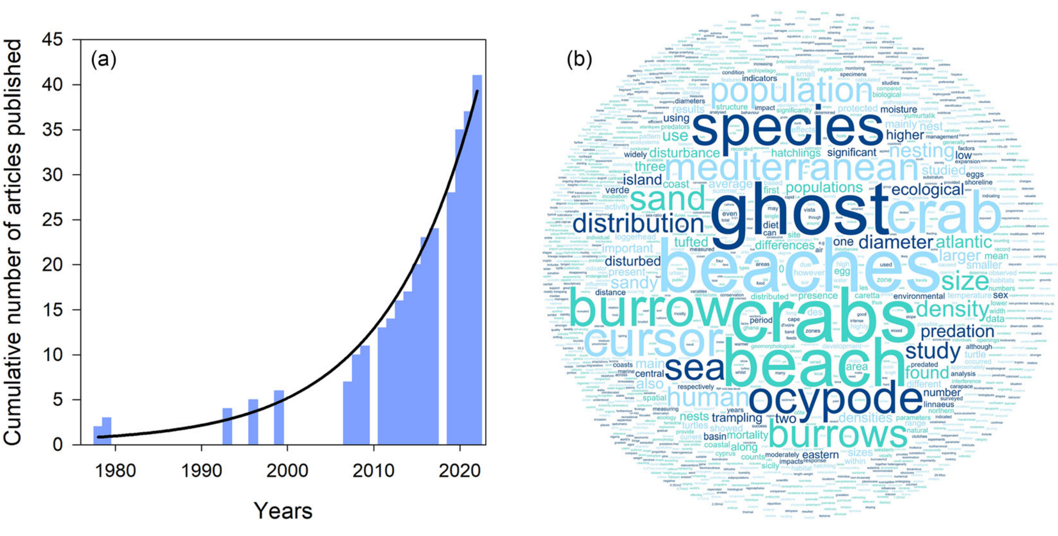

FIGURE 1 (a) Temporal evolution of the number of scientific articles published on *Ocypode cursor* and (b) wordcloud based on the words' frequency on the abstracts ($n = 41$).

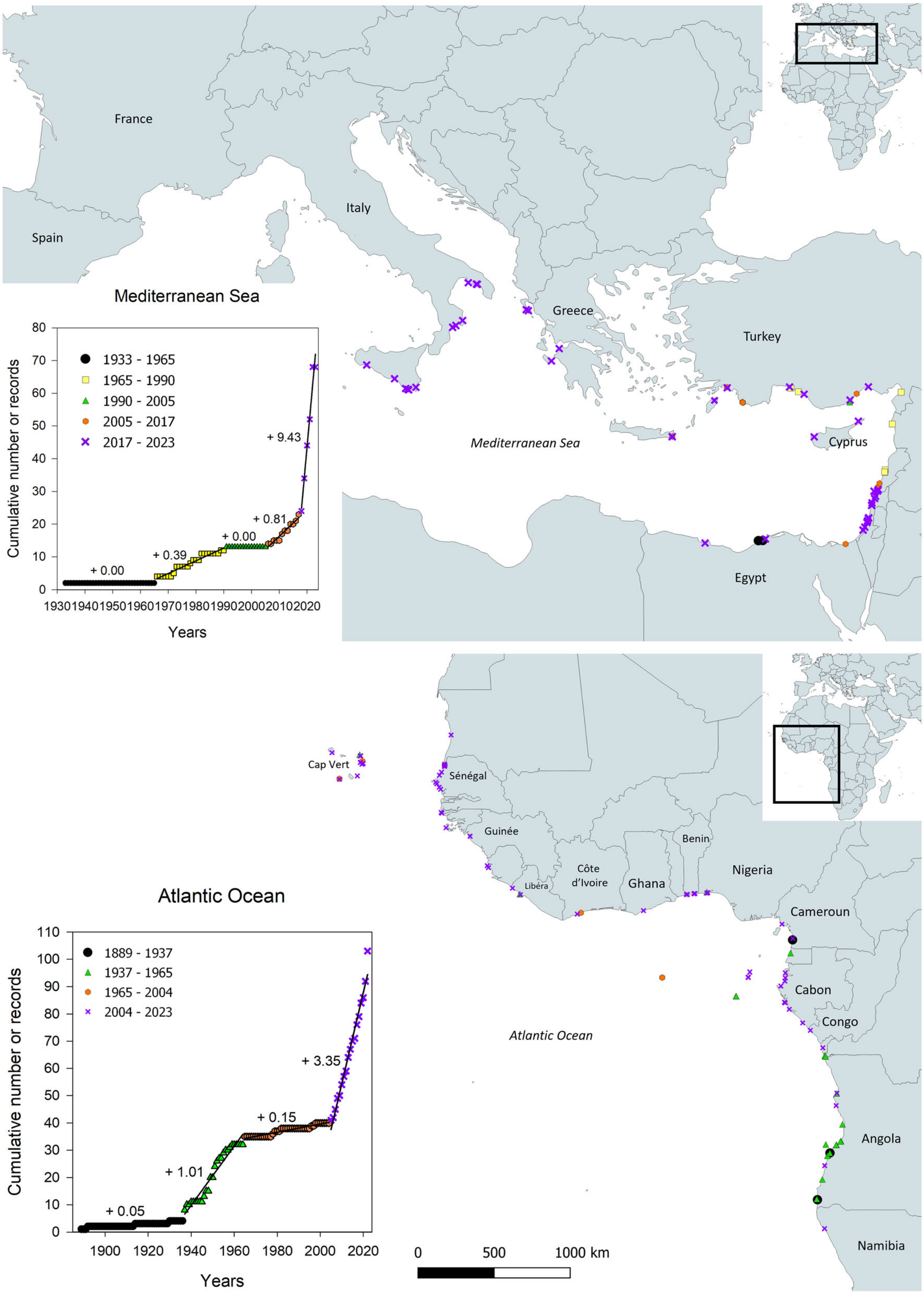

FIGURE 2 Spatial and temporal evolution of *Ocypode cursor* distribution by time periods. The plots represent the temporal evolution of the cumulative number of records in the Atlantic Ocean and Mediterranean Sea and linear regression curves showing the species' expansion dynamics.

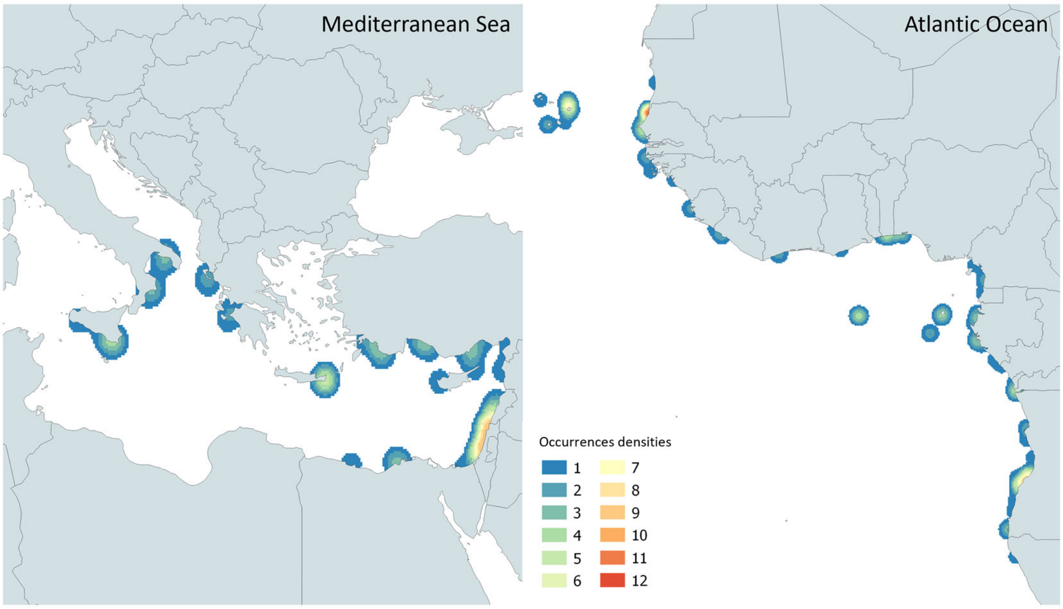

FIGURE 3 Kernel densities of occurrences of the ghost crab *Ocypode cursor* in the Mediterranean Sea and in the Atlantic Ocean. Colors represent low densities (cold spots; blue = 1) and high densities (hotspots; red = 12).

of Sicily. Our study highlights the swift distribution of the species in the Mediterranean Sea (Deidun et al., 2017; Di Martino & Stancanelli, 2020; Karaa et al., 2019; Mancinelli et al., 2019; Mytilineou et al., 2016) and in the Atlantic.

The continuous increase in sea temperatures may be the primary factor, or one of the primary factors, facilitating the species' distribution (Pastor et al., 2019). Thus, the warming of the sea could lead to secondary contact between subpopulations from the Atlantic and Mediterranean. However, the habitat discontinuity represented by long stretches of rocky coast in northern Sicily could serve as a barrier to the species' dispersion to other areas in Italy, even though ocean currents are expected to play a significant role in overcoming these obstacles and, consequently, in the secondary colonization of other beaches, for example, through transport on floating objects (e.g. detached macroalgae, seagrass and wood) or through larval dispersal (Peña-Toribio et al., 2017).

3.2 | Temperature and behaviour

Temperature is one of the most important factors affecting the abundance and activity of *Ocypode* spp. Ghost crabs (Dubey et al., 2013; Haque & Choudhury, 2014; Lucrezi et al., 2009; Martins et al., 2022). Our results on the analysis of the frequency of crabs' observations as a function of the months showed different patterns between the Atlantic Ocean and the Mediterranean Sea (Figure 4a). In the Atlantic Ocean, *O. cursor* was observed all the year-around with a frequency spike across the late autumn–early winter (November–December). On the contrary, ghost crab was observed during the summer period in the Mediterranean Sea with a maximum in August and September (Figure 4a). The analysis of frequencies of occurrences with temperature (Figure 4b) showed that both Atlantic and Mediterranean populations appeared to have different thermal frequency ranges: A maximum frequency was recorded around 20°C in the Mediterranean, which was lower than in the Atlantic where the maximum frequency was recorded around 27°C. Such a difference highlights a great capacity of thermal adaptation due to local conditions suggesting a remarkable population effect (Fusi et al., 2015; Verberk et al., 2016).

The number of burrows appears in the literature as a crucial variable to assess the erosion role exerted by burrowing species. Accordingly, the literature review showed that the greatest number of burrows is typically observed during the summer season (Schuchman & Warburg, 1978; Tiralongo et al., 2020) and that the density of large specimens was mainly concentrated in the upper part of the beaches (closer to the dunes), where they are able to get the best protection from the waves generated by storms (Schuchman & Warburg, 1978; Tiralongo et al., 2020). In these high zones, only a few individuals remain active almost all year around and we can derive that they breed in these areas (Tiralongo et al., 2020), particularly during the cold winter months. It would appear that temperatures below 15°C reduce the activity of crabs, which could enter hibernation, which coincides with the low burrow abundances observed by Tiralongo et al. (2020). Although temperature plays a key role in crab activity, other factors, such as for instance windy conditions, can prompt crabs to close the entrance to their burrows, as demonstrated for another species of the genus *Ocypode* (Alberto & Fontoura, 1999). The daily temperature fluctuation is a significant factor influencing ghost crab activity (Strachan et al., 1999). In both July and September, the number of crabs emerging from the burrows showed hourly variation over 24 h. The study showed that, during both observed time periods, crabs began to emerge at sunset (around 18:00). Their number increased reaching a pick at 00:00, before gradually decreasing until

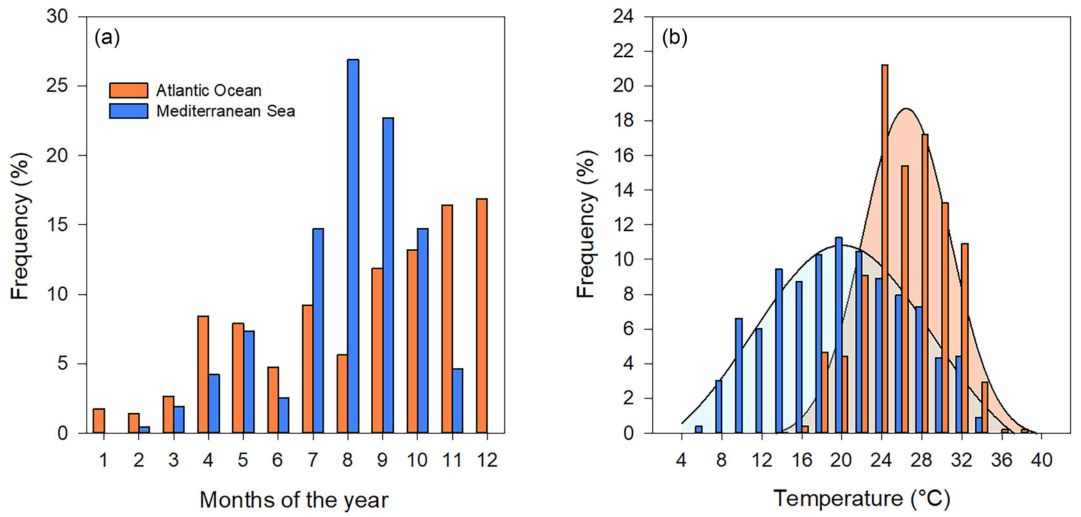

FIGURE 4 (a) Frequency (%) of the number of ghost crab's occurrences as a function of the month of the year and (b) frequency (%) of the number of ghost crab occurrences as a function of temperature (°C), in the Mediterranean Sea and the Atlantic Ocean.

sunrise (around 06:00). On the other hand, between July and September, the number of emerging organisms fell by half, showing the effect of daily temperature on the emergence of individuals. For the rest of the time, ghost crabs remained in their burrows. The diurnal activity is a key factor to explore to define the behaviour and the ecology of ghost crabs. As observed by Sinclair et al. (2016) in the nocturnal porcelain crab *Petrolisthes violaceus*, the metabolism of the species varied at different times of the day, with active metabolism (e.g. maximum metabolism during activity) occurring at sunset and sunrise. This corresponds to the emergence of organisms from their burrows for feeding. A similar study should be undertaken for *O. cursor* to understand how sunlight and temperature may influence the behaviour of these species over a 24-h cycle.

3.3 | Burrowing

Similarly to other genus *Ocypode*, *O. cursor* has a typical burrowing behaviour, that is it digs cavities in the sand, which may extend to depths of up to 1 m deep (Schuchman & Warburg, 1978; Shiber & Izzidin, 1978; Strachan et al., 1999; Tiralongo et al., 2020). These burrows represent a refuge for ghost crabs, which are protected from the sun and very high summer temperatures (e.g. up to 50°C in Greece, Strachan et al., 1999). Due to their depth in the sand, burrows offer constant lower temperatures and humidity to allow crabs to breathe (Chan et al., 2006). Burrows are generally long (a sort of tunnel-shape), with an adjoining chamber where the crab can protect itself from outside intrusion (Schuchman & Warburg, 1978; Shiber & Izzidin, 1978). Substrate plays a key role in ghost crab abundance and distribution (Ewa-Oboho, 1993; Gül, 2022; Jonah et al., 2015; Schuchman & Warburg, 1978). The density of shallow burrows also seems to vary with the seasons, with a maximum recorded density of small and medium-sized organisms a few centimeters from the shore in summer (Barakalı et al., 2020; Schuchman & Warburg, 1978; Tiralongo et al., 2020; Türeli et al., 2014), suggesting that crabs in this zone find suitable conditions to avoid desiccation due to high temperatures. Conversely, in autumn and winter, burrows were concentrated in the high zone of beaches near the dunes, certainly linked to the high humidity of these areas, enabling large numbers of small and medium-sized crabs to survive during the cold periods when they hibernate, as observed in other species of the genus *Ocypode* (Branco et al., 2010; Corrêa et al., 2014; Haley, 1969). Indeed, small specimens of the genus *Ocypode* are less resistant to desiccation and less efficient at digging burrows than adults (Corrêa et al., 2014; Fisher & Tevesz, 1979). On the other hand, larger crabs dig deeper and more complex burrows far from shore, reflecting the increasing depth of the water table (Rodrigues et al., 2016; Tureli et al., 2009). Nonetheless, the availability of food (e.g. bather food scraps and stranded organic matter) can also affect the abundance and distribution of crabs along the beach shoreline (Jonah et al., 2015; Lucrezi et al., 2009; Lucrezi et al., 2009). This is due to the fact that on beaches, where a substantial portion of food scraps from bathers is prevalent, crabs can discover more abundant food sources and meet their energy needs more effortlessly compared to beaches with limited or no food scraps.

3.4 | Feeding habits

Similar to numerous species within the *Ocypode* genus, the ghost crab *O. cursor* is an opportunistic predator preying on a variety of marine and terrestrial aquatic organisms. There are very few published studies on the diet of *O. cursor*. This ghost crab is known to be a scavenger, feeding not only on animal carcasses but also on human food (e.g. picnic remains on the beach) and plant organic matter (Strachan et al., 1999). *O. cursor* also feeds on marine invertebrates, as it is often observed at night close to the water's edge (Strachan et al., 1999). Like many species of the genus *Ocypode*, *O. cursor* co-occurred and built their burrows close to nests of sea turtle *Caretta caretta* (Mancinelli et al., 2019), and taking advantage of proximity, they can rely their feeding on eggs and young hatchling turtles (Chartosia et al., 2010; Isroni et al., 2022; Strachan et al., 1999). A study of stomach contents revealed 84 prey items found in the stomach of *O. cursor*, belonging to five prey categories (Chartosia et al., 2010). Insects such as the ant *Cataglyphis* sp. were the dominant prey of *O. cursor*, followed by macroalgae and crustaceans (e.g. Copepoda, Mysidacea and Decapoda). These two studies highlighted the lack of knowledge about the diet of ghost crabs, also because the species is often observed in the first 10 cm of water where it may feed on marine invertebrates. Indeed, during the ongoing monitoring of a ghost crab population in Menfi (Sicily, Italy), we observed ghost crabs feeding on the mollusk *Arcopagia crassa* (pers. obs.). The limited information available in the literature on the feeding habits of *O. cursor* highlights the ability of this species to adapt its diet to the different areas where it occurs. However, these aspects need to be explored in greater detail, in particular to determine the effect of human tourism on the diet of *O. cursor* (Bal et al., 2021), the effect of temperature on ingestion rates and the importance of determining the diet in relation to the different stages of the species' life cycle (e.g. juveniles, immature/mature organisms).

3.5 | Population structure and life cycle

Studies focusing on the population structure of the *O. cursor* crab are scant as also on reproduction and life cycle in general (Schuchman & Warburg, 1978; Tiralongo et al., 2020; Yilmaz & Barlas, 2020; Yılmaz & Barlas, 2020). A study published in 2020 (Tiralongo et al., 2020) compared the structure of two populations in the Mediterranean (Italy) and Africa (Côte d'Ivoire). The size and sex distribution of individuals showed similarities, but the number of cohorts differed between the two areas studied. There are virtually no specific studies on the reproductive biology of tufted ghost crabs. Other studies carried out on species of the genus *Ocypode* showed that the size at first maturity of females varied considerably, ranging from 36 to 38.57 mm CW (carapace width) for *O. rotundata* (Naderi et al., 2018; Naderi & Pishehvarzad, 2019; Najafi, 2014) and from 19.2 to 26 mm CW for *O. quadrata* (Haley, 1969; Pombo et al., 2017). Females appear to be larger than males (Tiralongo et al., 2020; Yılmaz & Barlas, 2020). In terms of carapace width–weight relationships, there is positive allometric growth ($b > 3$), indicating that growth in wet weight (WW) is more important than growth in size (CW) (Schuchman & Warburg, 1978; Tiralongo et al., 2020). This difference may be due to greater food availability and less intra-species competition. It has been shown that the presence of large numbers of tourists on beaches favours the presence of ghost crabs, thanks to the food scraps used by the crabs as an additional food source. Other factors, such as different morphological characteristics, temperature, salinity, sex and stage of maturity can affect the values of slope (b) of the CW–WW relationship in ghost crab species (Schuchman & Warburg, 1978; Tiralongo et al., 2020). No data are available on the reproductive period of ghost crabs or on female fecundity (e.g. number of eggs per unit of total mass). Ovigerous females remain in deep burrows in the sand during egg incubation, leaving them only when the eggs are ready to hatch. This behaviour seems to be supported by other studies on other species of the *Ocypode* family, where only very low numbers of ovigerous females have been observed (Bezerra & Matthews-Cascon, 2006). Also, a recent study showed the impact of human disturbances (e.g. tourism) on the ghost crabs' well-being where the crab size was smaller in disturbed areas (Costa et al., 2022), but more studies are needed to explore these aspects.

3.6 | Evaluating the ecological significance of the ghost crab distribution: main concerns and future perspectives

The potential positive or negative impacts of ghost crab *O. cursor* distribution remain largely uncharted, and its influence on coastal ecosystems remains entirely unexplored (Figures 5 and 6). Despite its rapid expansion in the Mediterranean Sea and Atlantic Ocean along with its colonization of new areas, the legal status of *O. cursor* as a protected species distinct consideration and effective management. Indeed, the species is included in the list of Annex II 'Strictly protected fauna species' of the Bern Convention on the conservation of European wildlife and nature habitats (Bern Convention, 1982) and in Annex II 'Endangered or threatened species that the Parties shall manage with the aim of maintaining them in a favorable state of conservation. They shall ensure their maximum possible protection and recovery' of the Barcelona Convention Protocol concerning Specifically Protected Areas and Biological Diversity in the Mediterranean (Barcelona Convention, 2018).

Nevertheless, taking advantage of the environmental change due to human-caused drivers, first the increasing local temperature and the local food availability augmentation due to additional food supply coming from bathers, ghost crabs are increasing their density at the local level and occurrence frequency and the risk to become a plague for local biodiversity is increasing. To increase our understanding of how, when and where local biodiversity will be more threatened (e.g. sea turtle eggs and hatchlings), we should increase data collection in further research to investigate: (i) the variation in crab abundance across different areas of preferential habitats and (ii) the effect of environmental and climate factors on the population dynamics and primary growth parameters such as length–weight relationships (Barros, 2001; de Carvalho-Souza et al., 2023; Marchessaux et al., 2023) (Figure 5). Such information is necessary to assess the well-being of the populations and to contribute to predicting potential future expansion and establishing a risk-planning action to manage the likelihood of local biodiversity interactions. Also, if the species is expanding its distribution area, several ecological questions arise about the ghost crab's potential impacts in the areas where the species was not previously documented.

The burrowing activity of *O. cursor* could contribute to beach erosion (Figure 6) as reported in the literature for some engineers

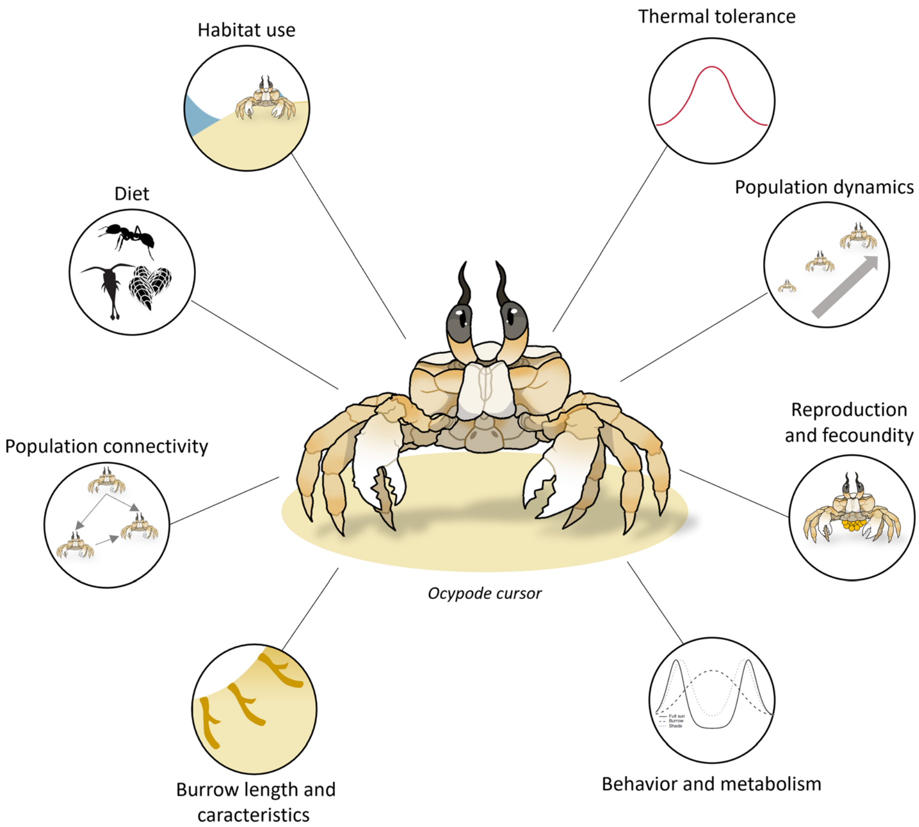

FIGURE 5 Current state of lack of knowledge we need to explore on the ghost crab *Ocypode cursor*.

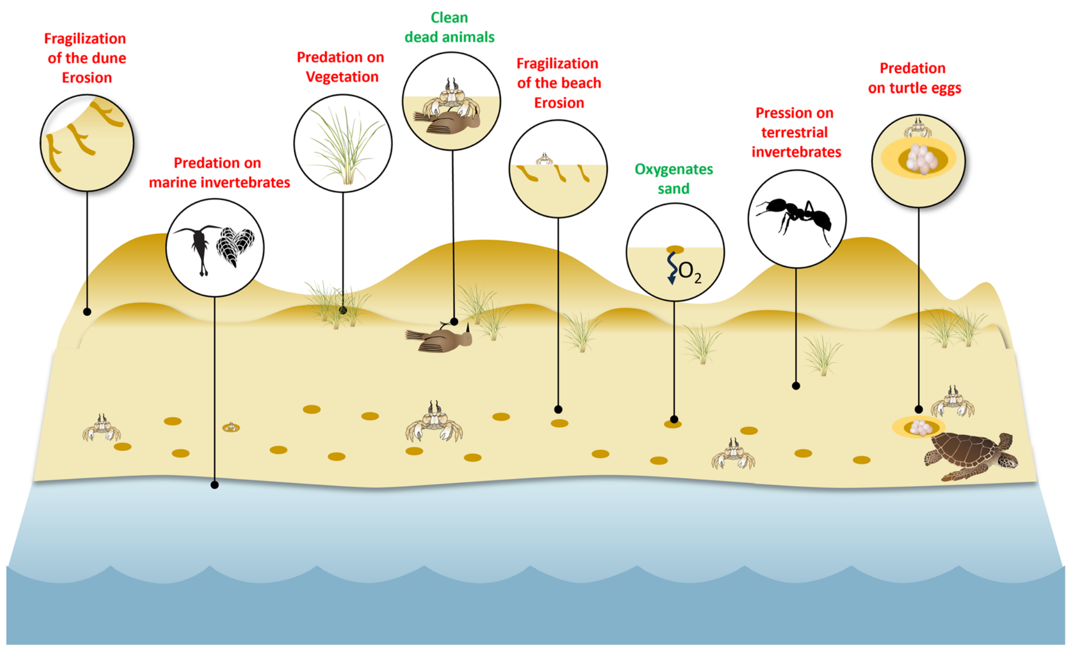

FIGURE 6 Conceptual diagram of the probable impacts of *Ocypode cursor* on beach ecosystems. In red, the potential negative impacts; in green, the possible positive impacts.

crabs as the striped shore crab *Pachygrapsus crassipes* in California (USA) (Beheshti et al., 2022) or the swamp crab *Sesarma reticulatum* in New Zealand (Vu et al., 2017) contributing to the increase of beach and saltmarshes erosion through their digging activity. The contribution of crabs like *O. cursor* could pose a threat to the stability of dune ecosystems and the biodiversity they sustain, which could be particularly problematic in areas where coastal erosion is already a concern. The destabilization of sand dunes due to erosion could certainly also impact the nesting sites of other species such as shorebirds, which rely on these habitats for breeding and survival

(Von Holle et al., 2019). Given that sand dunes and beaches are important habitats for numerous species, the potential effect of *O. cursor* on these ecosystems can trigger cascading effects on the broader coastal ecosystem (Agostini et al., 2021).

The presence of *O. cursor* can also pose a threat to other species in the area. Many aspects of the ecology of species in the *Ocypode* genus have been extensively studied (Barros, 2001; Blankensteyn, 2006; Chan et al., 2006; Ewa-Oboho, 1993; Turra et al., 2005; Valero-Pacheco et al., 2007), there are limited studies specifically focused on the *O. cursor* (Ewa-Oboho, 1993; Schuchman & Warburg, 1978; Strachan et al., 1999). Ghost crabs are known to feed on the eggs and hatchlings of sea turtles, causing high mortality rate and then impact (Eiroa Suárez et al., 2008; Heithaus, 2013; Marco et al., 2011, 2015; Rebelo et al., 2012; Smith et al., 1996) as observed in Cape Verde where around 50% caused by ghost crabs (Marco et al., 2011, 2015). The burrowing activity of ghost crabs can also impact the nesting sites of other species such as shorebirds, which rely on these habitats for breeding and survival. Hence, it is crucial to monitor the potential impact of *O. cursor* on sand dunes and beaches newly colonized by this species, as well as on the broader coastal ecosystem. Implementing measures to mitigate its negative impacts on native biodiversity and ecosystem stability is imperative (Amaral-Zettler et al., 2020). Also, as observed in the literature, *O. cursor* could influence the terrestrial biodiversity of the areas in which it has newly arrived. This species presents high densities in small areas and could therefore weaken populations of insects or marine invertebrates that were not used to being predated by this ghost crab. *O. cursor* is an opportunistic omnivorous predator that feeds on a wide variety of terrestrial and marine prey (Lucrezi et al., 2009; Marco et al., 2011; Trott, 1999; Türeli et al., 2014; Wolcott, 1978). However, despite the typically assigned role of ghost crabs as scavengers, they also act as predators (Wolcott, 1978). Furthermore, their digging behaviour enhances soil oxygenation and facilitates the decomposition of organic matter and nutrient recycling (Dubey et al., 2013).

On the contrary, in areas where the species is historically present, *O. cursor* is considered an indicator of good ecological status of coastal ecosystems (Costa et al., 2022). Studying crabs is of crucial importance, as these decapods are recognized in the literature as excellent bioindicators (Hagger et al., 2009) responding rapidly to spatial disruptions on a broader scale. Their presence and behaviour offer significant insights into the health of marine ecosystems (Giraldes et al., 2021), marine pollution (Cau et al., 2023; Kampouris et al., 2023) and the effects of climate change (Thirukanthan et al., 2023), consolidating their essential role in environmental monitoring. Especially crabs of the genus *Ocypode* are recognized as biological indicators of natural and anthropogenic stressors (Corrêa et al., 2014). In the case of the ghost crab *O. cursor*, given its recent expansion in the Mediterranean and Atlantic, its presence in areas where it was not initially present could be a matter for discussion in terms of preserving fragile coastal ecosystems. In fact, some crabs of the genus *Ocypode*—such as *Ocypode sinensis* in Korea (Kim et al., 2023) or mangrove crabs in Australia (Sharifian et al., 2021)—are known to expand their distribution due to climate change. The status of *O. cursor* is unclear, and the main question is as follows: "Is *O. cursor* a winner from climate change?" A deeper understanding of the species' ecology can help determine whether climate change is influencing its expansion and better understand how this recent colonizer influences food webs and terrestrial and marine ecosystems (Figures 5 and 6).

In conclusion, our review provides a comprehensive perspective on the biology, ecology and distribution of the ghost crab *O. cursor*. These initial findings serve as an important starting point to stimulate further research on the expanding species' biology and to discuss its protection status within the European scale and possible management measures where the density reaches so high level that these crabs become a threat to local biodiversity. An essential aspect to necessitated clarification is the reproductive biology of the species. Specifically, findings on ovigerous females, the reproduction period and larval growth rates are still unexplored in the literature.

ACKNOWLEDGEMENTS

This study is part of the National Biodiversity Future Center (NBFC, Italy; Piazza Marina 61, 90133 Palermo). Guillaume Marchessaux and Vojsava Gjoni are funded by the NBFC and Mario Francesco Tantillo by a national PhD student fellow. The authors are grateful for comments from reviewers and the editor to improve the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All articles' references collected in this review are available in the supplementary materials.

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SUPPORTING INFORMATION

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How to cite this article: Marchessaux, G., Gjoni, V., Tantillo, M.F., Bejean, T. & Sarà, G. (2024). The expansion of the Atlantic–Mediterranean ghost crab *Ocypode cursor* (Linnaeus, 1758): Distribution, environmental niches and future perspectives. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 34(3), e4119. https://doi.org/10.1002/aqc.4119