

## REVIEW ARTICLE

WILEY

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

Guillaume Marchessaux<sup>1,2</sup>  | Vojsava Gjoni<sup>1,2,3</sup>  | Mario Francesco Tantillo<sup>1,2</sup> |  
Théo Bejean<sup>1</sup> | Gianluca Sarà<sup>1,2</sup> 

<sup>1</sup>Laboratory of Ecology, Department of Earth and Marine Science (DiSTeM), University of Palermo, Palermo, Italy

<sup>2</sup>National Biodiversity Future Center (NBFC), Palermo, Italy

<sup>3</sup>Department of Biology, University of South Dakota, Vermillion, South Dakota, USA

## Correspondence

Guillaume Marchessaux, Laboratory of Ecology, Department of Earth and Marine Science (DiSTeM), Viale delle Scienze Building 16, University of Palermo, Palermo 90128, Italy.

Email: [guillaume.marchessaux@gmail.com](mailto:guillaume.marchessaux@gmail.com)

## 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 nocturnal 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 (Yılmaz & 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.

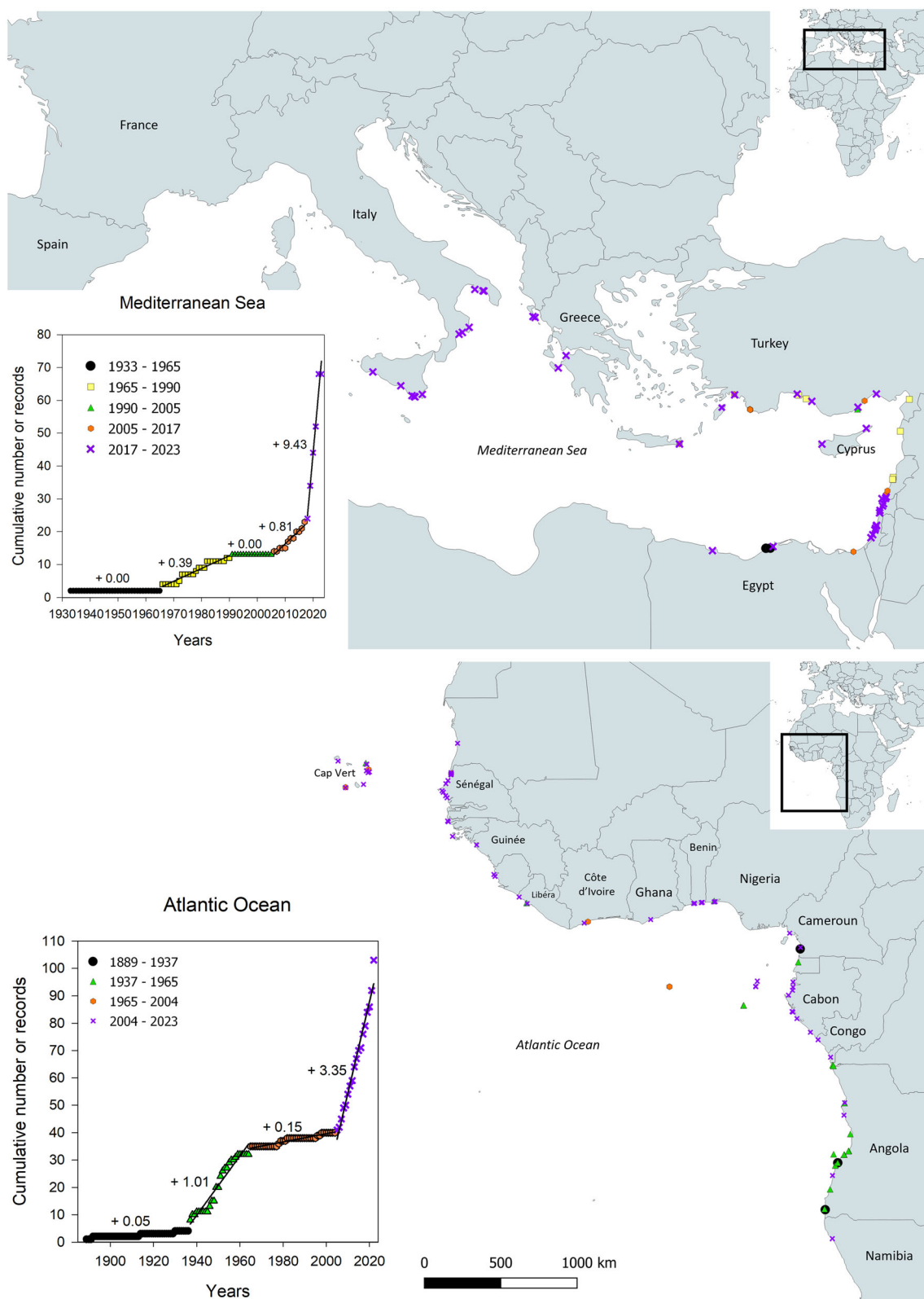
## 2 | MATERIALS AND METHODS

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 wordcloud plots.

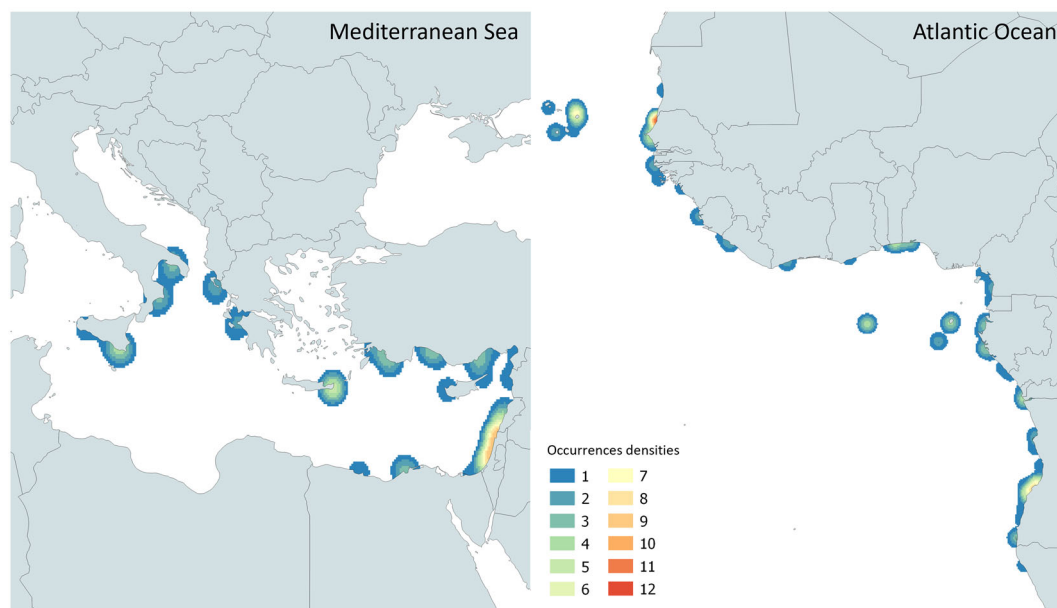
To assess the current world distribution of *O. cursor*, occurrences data were extracted from free access databases such as GBIF (Global Biodiversity Information Facility, <https://www.gbif.org/>) and OBIS (Ocean Biodiversity Information System, <https://obis.org/>). The GPS points, the year and the 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 (Castrì 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





**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.

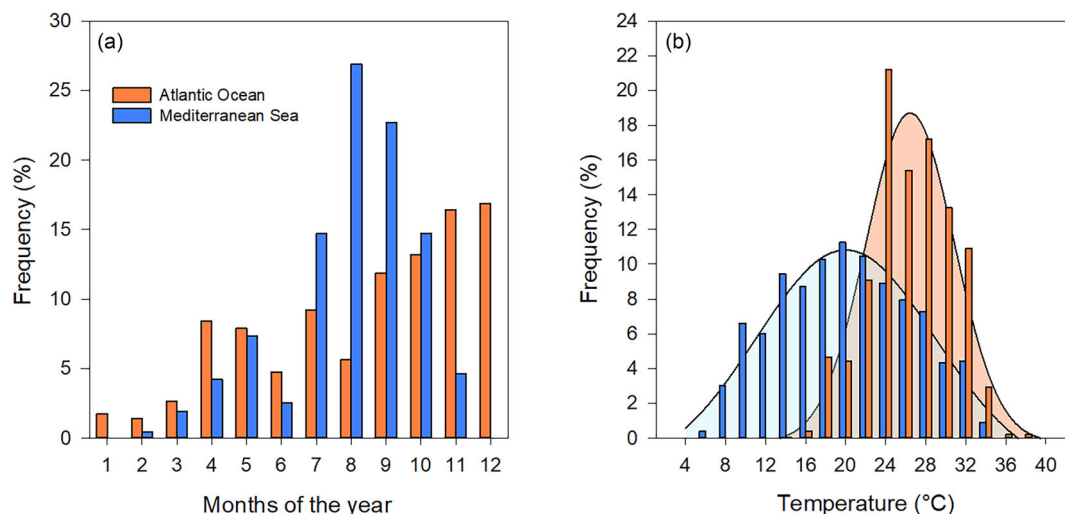
The continuous increase in sea temperatures may be the primary factor, or one of the primary factors, facilitating the species' distribution (Pastor et al., 2019). Thus, the warming of the sea could lead to secondary contact between subpopulations from the Atlantic and Mediterranean. However, the habitat 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-Obobo, 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 (Barakali 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; Türeli 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; Isoni 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; Yilmaz & 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; Yilmaz & 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.

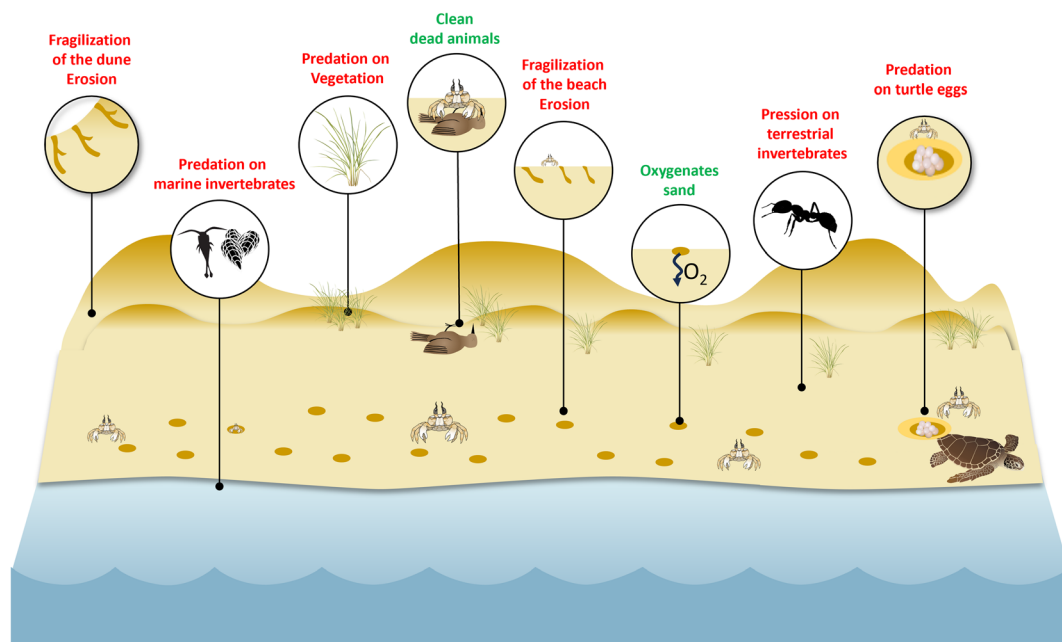
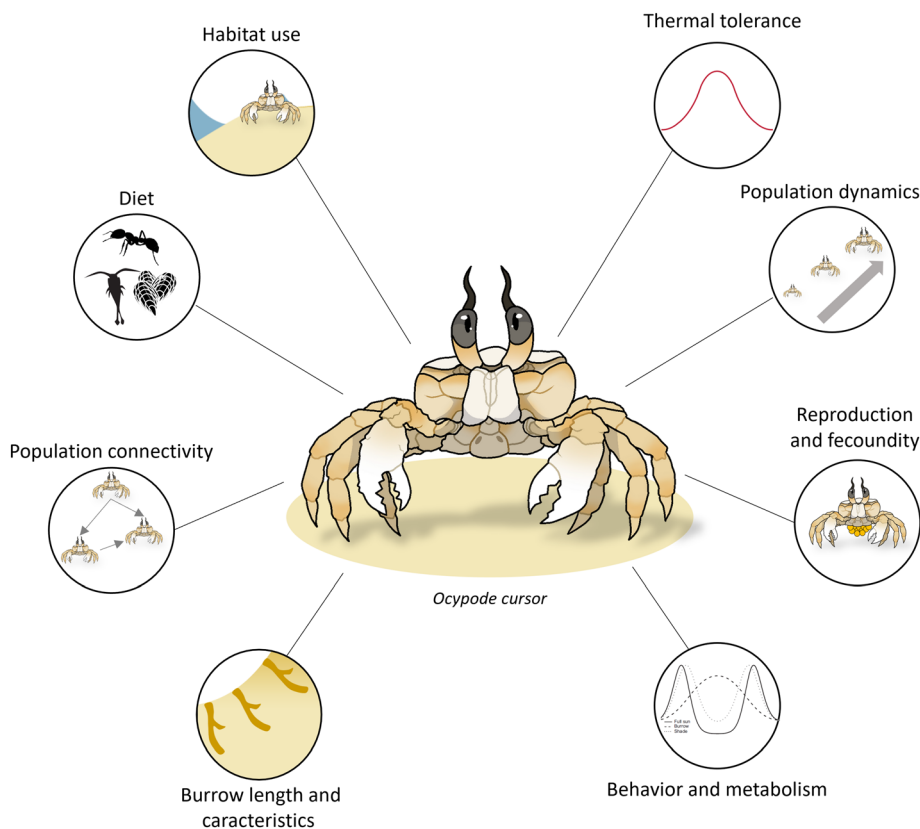
### 3.6 | Evaluating the ecological significance of the ghost crab distribution: main concerns and future perspectives

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; Blankensteijn, 2006; Chan et al., 2006; Ewa-Obobo, 1993; Turra et al., 2005; Valero-Pacheco et al., 2007), there are limited studies specifically focused on the *O. cursor* (Ewa-Obobo, 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 preyed 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.

## ORCID

Guillaume Marchessaux  <https://orcid.org/0000-0001-5557-2274>

Vojsava Gjoni  <https://orcid.org/0000-0003-1740-6093>

Gianluca Sarà  <https://orcid.org/0000-0002-7658-5274>

## REFERENCES

- Agostini, S., Harvey, B.P., Milazzo, M., Wada, S., Kon, K., Floc'h, N. et al. (2021). Simplification, not “tropicalization”, of temperate marine ecosystems under ocean warming and acidification. *Global Change Biology*, 27(19), 4771–4784. <https://doi.org/10.1111/gcb.15749>
- Aheto, D.W., Asare, C., Mensah, E. & Aggrey-Fynn, J. (2011). Rapid assessment of anthropogenic impacts of exposed sandy beaches in Ghana using ghost crabs (*Ocypode* spp.) as ecological indicators. *Momona Ethiopian Journal of Science*, 3(2).
- Alberto, R. & Fontoura, N. (1999). Age structure and spatial distribution of *Ocypode quadrata* (Fabricius, 1787) on a sandy beach from the south coast of Brazil (Crustacea, Decapoda, Ocypodidae). *Revista Brasileira de Biologia*, 59(1), 95–108. <https://doi.org/10.1590/S0034-71081999000100013>
- Amaral-Zettler, L.A., Zettler, E.R. & Mincer, T.J. (2020). Ecology of the platisphere. *Nature Reviews Microbiology*, 18(3), 139–151. <https://doi.org/10.1038/s41579-019-0308-0>
- Bal, M., Çağrı Yapan, B. & Özkan, K. (2021). The response of tufted ghost crab, *Ocypode cursor*, populations to recreational activities in an urbanized coast with small-scale protected zones. *Zoology in the Middle East*, 67(1), 32–41. <https://doi.org/10.1080/09397140.2021.1877383>

- Barakali, D., Snaddon, J.L. & Snape, R.T. (2020). Revisiting the population of the ghost crab, *Ocypode cursor*, on the sandy beaches of northern Cyprus after two decades: are there causes for concern? *Zoology in the Middle East*, 66(2), 132–139. <https://doi.org/10.1080/09397140.2020.1729556>
- Barcelona Convention. (2018). *Document—annex II: endangered or threatened species that the parties shall manage with the aim of maintaining them in a favourable state of conservation. They shall ensure their maximum possible protection and recovery*. Available at: <https://eunis.eea.europa.eu/references/1818/species> [Accessed 9th October 2023].
- Barros, F. (2001). Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. *Biological Conservation*, 97(3), 399–404. [https://doi.org/10.1016/S0006-3207\(00\)00116-6](https://doi.org/10.1016/S0006-3207(00)00116-6)
- Beheshti, K., Endris, C., Goodwin, P., Pavlak, A. & Wasson, K. (2022). Burrowing crabs and physical factors hasten marsh recovery at panne edges. *PLoS ONE*, 17(1), e0249330. <https://doi.org/10.1371/journal.pone.0249330>
- Bern Convention. (1982). *Document—annex II: strictly protected fauna species*. Available at: <https://eunis.eea.europa.eu/references/1566/species> [Accessed 9th October 2023].
- Bezerra, L.E.A. & Matthews-Cascon, H. (2006). *Population structure of the fiddler crab Uca leptodactyla Rathbun 1898*. Brachyura: Ocypodidae. in a tropical mangrove of northeast Brazil.
- Blankensteyn, A. (2006). Use of the ghost crab *Ocypode quadrata* (Fabricius) (Crustacea, Ocypodidae) as an indicator of human impact on the sandy beaches of the island of Santa Catarina, Santa Catarina, Brazil. *Revista Brasileira de Zoologia*, 23(3), 870–876.
- Brakes, P., Carroll, E.L., Dall, S.R.X., Keith, S.A., McGregor, P.K., Mesnick, S.L. et al. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B: Biological Sciences*, 288(1949) rsob.2020.2718, 20202718. <https://doi.org/10.1098/rspb.2020.2718>
- Branco, J.O., Hillesheim, J.C., Fracasso, H.A., Christoffersen, M.L. & Evangelista, C.L. (2010). Bioecology of the ghost crab *Ocypode quadrata* (Fabricius, 1787) (Crustacea: Brachyura) compared with other intertidal crabs in the southwestern Atlantic. *Journal of Shellfish Research*, 29(2), 503–512. <https://doi.org/10.2983/035.029.0229>
- Castriota, L., Falautano, M., Maggio, T. & Perzia, P. (2022). The blue swimming crab *Portunus segnis* in the Mediterranean Sea: invasion paths, impacts and management measures. *Biology*, 11(10), 1473. <https://doi.org/10.3390/biology11101473>
- Cau, A., Gorule, P.A., Bellodi, A., Carreras-Colom, E., Moccia, D., Pittura, L. et al. (2023). Comparative microplastic load in two decapod crustaceans *Palinurus elephas* (Fabricius, 1787) and *Nephrops norvegicus* (Linnaeus, 1758). *Marine Pollution Bulletin*, 191, 114912. <https://doi.org/10.1016/j.marpolbul.2023.114912>
- Chan, B.K.K., Chan, K.K.Y. & Leung, P.C.M. (2006). Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia*, 560, 43–49. <https://doi.org/10.1007/s10750-005-1088-2>
- Chartosia, N., Kitsos, M.-S., Tzomos, T.H., Mavromati, E. & Koukouras, A. (2010). Diet composition of five species of crabs (Decapoda, Brachyura) that show a gradual transition from marine to terrestrial life. *Crustaceana*, 83(10), 1181–1197. <https://www.jstor.org/stable/41038629>
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J. et al. (2010). The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8), e11842. <https://doi.org/10.1371/journal.pone.0011842>
- Corrêa, M.O.D.A., Andrade, L.S., Costa, R.C., Castilho, A.L., Bertini, G. & Fransozo, A. (2014). Vertical distribution by demographic groups of ghost crab *Ocypode quadrata* (Crustacea: Brachyura). *Biologia*, 69(7), 905–915. <https://doi.org/10.2478/s11756-014-0385-5>
- Costa, L.L., Arueira, V.F., Ocaña, F.A., Soares-Gomes, A. & Zalmon, I.R. (2022). Are ghost crabs (*Ocypode* spp.) smaller on human-disturbed sandy beaches? A global analysis. *Hydrobiologia*, 849(15), 3287–3298. <https://doi.org/10.1007/s10750-022-04900-1>
- de Carvalho-Souza, G.F., Cuesta, J.A., Arana, D., Lobato, C. & González-Ortegón, E. (2023). Westward range expansion of the blue swimmer crab *Portunus segnis* (Forskål, 1775) (crustacea, Decapoda, Portunidae) into Atlantic European waters. *BiolInvasions Records*, 12(4). <https://doi.org/10.3391/bir.2023.12.4.16>
- Deidun, A., Crocetta, F., Sciberras, A., Sciberras, J., Insacco, G. & Zava, B. (2017). The protected taxon *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Decapoda: Ocypodidae)—documenting its well-established presence in the central Mediterranean. *The European Zoological Journal*, 84(1), 96–103. <https://doi.org/10.1080/11250003.2017.1281355>
- Di Martino, V. & Stancanelli, B. (2020). First record of *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Decapoda: Ocypodidae) from the Algerian coast, western Mediterranean Sea. *Journal of the Black Sea/Mediterranean Environment*, 26(3).
- Dubey, S.K., Chakraborty, D.C., Chakraborty, S. & Choudhury, A. (2013). Burrow architecture of red ghost crab *Ocypode macrocera* (H. Milne-Edwards, 1852): a case study in Indian Sundarbans. *Exploratory Animal and Medical Research*, 3(2), 136–144.
- Eiroa Suárez, A., Aguilera i Rodà, M., Varo-Cruz, N., López, Ó. & López-Jurado, L.F. (2008). Rate predation on the nesting of *Caretta caretta* because of *Ocypode cursor* in Calheta de Pau beach. Boa Vista Island (Cape Verde Rep.).
- Ewa-Obobo, I.O. (1993). Substratum preference of the tropical estuarine crabs, *Uca tangeri* Eydoux (Ocypodidae) and *Ocypode cursor* Linne (Ocypodidae). *Hydrobiologia*, 271, 119–127. <https://doi.org/10.1007/BF00007548>
- Findlay, H.S. & Turley, C. (2021). Ocean acidification and climate change. In: *Climate change*. Elsevier, pp. 251–279. <https://doi.org/10.1016/B978-0-12-821575-3.00013-X>
- Fisher, J.B. & Tevesz, M.J. (1979). Within-habitat spatial patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). *Crustaceana*. Supplement (5), 31–36. <https://www.jstor.org/stable/25027480>
- Free, C.M., Mangin, T., Molinos, J.G., Ojea, E., Burden, M., Costello, C. et al. (2020). Realistic fisheries management reforms could mitigate the impacts of climate change in most countries. *PLoS ONE*, 15(3), e0224347. <https://doi.org/10.1371/journal.pone.0224347>
- Freeman, B.G., Lee-Yaw, J.A., Sunday, J.M. & Hargreaves, A.L. (2018). Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, 27(11), 1268–1276. <https://doi.org/10.1111/geb.12774>
- Fusi, M., Giomi, F., Babbini, S., Daffonchio, D., McQuaid, C.D., Porri, F. et al. (2015). Thermal specialization across large geographical scales predicts the resilience of mangrove crab populations to global warming. *Oikos*, 124(6), 784–795. <https://doi.org/10.1111/oik.01757>
- Garzke, J., Ismar, S.M.H. & Sommer, U. (2015). Climate change affects low trophic level marine consumers: warming decreases copepod size and abundance. *Oecologia*, 177(3), 849–860. <https://doi.org/10.1007/s00442-014-3130-4>
- Giraldes, B.W., Coelho, P.A., Coelho Filho, P.A., Macedo, T.P. & Freire, A.S. (2021). The ghost of the past anthropogenic impact: reef-decapods as bioindicators of threatened marine ecosystems. *Ecological Indicators*, 133, 108465. <https://doi.org/10.1016/j.ecolind.2021.108465>
- Gül, M.R. (2022). Combined influence of human disturbance and beach geomorphology on ghost crab, *Ocypode cursor*, burrow density and size in the eastern Mediterranean. *Zoology in the Middle East*, 68(3), 225–236. <https://doi.org/10.1080/09397140.2022.2116170>
- Hagger, J.A., Galloway, T.S., Langston, W.J. & Jones, M.B. (2009). Application of biomarkers to assess the condition of European marine

- sites. *Environmental Pollution*, 157(7), 2003–2010. <https://doi.org/10.1016/j.envpol.2009.02.038>
- Haley, S.R. (1969). Relative growth and sexual maturity of the Texas ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). *Crustaceana*, 17(3), 285–297. <https://www.jstor.org/stable/20101641>
- Haque, H. & Choudhury, A. (2014). Ecology and behavior of the ghost crab, *Ocypode macrocera* Edwards, 1834 occurring in the sandy beaches of Sagar Island, Sundarbans. *International Journal of Engineering Science Invention*, 3(4), 38–43.
- Hastings, R.A., Rutterford, L.A., Freer, J.J., Collins, R.A., Simpson, S.D. & Genner, M.J. (2020). Climate change drives poleward increases and equatorward declines in marine species. *Current Biology*, 30(8), 1572–1577. <https://doi.org/10.1016/j.cub.2020.02.043>
- Heithaus, M.R. (2013). 10 predators, prey, and the ecological roles of sea turtles. *The Biology of Sea Turtles, Volume III*, 3, 249.
- Isoni, W., Maulida, N., Muhajir, M.I., Lesmana, P.S. & Ismail, D.A. (2022). Characteristics of turtle laying habitat on vemara beach, Banyuwangi Regency, East Java. In: *IOP conference series: earth and environmental science*. IOP Publishing, 012087.
- Jonah, F., Agbo, N., Agbeti, W., Adjei-Boateng, D. & Shimba, M. (2015). The ecological effects of beach sand mining in Ghana using ghost crabs (*Ocypode* species) as biological indicators. *Ocean and Coastal Management*, 112, 18–24. <https://doi.org/10.1016/j.ocecoaman.2015.05.001>
- Kampouris, T.E., Syranidou, E., Seridou, P., Gagoulis, K., Batjakas, I.E. & Kalogerakis, N. (2023). MPs and NPs intake and heavy metals accumulation in tissues of *Palinurus elephas* (JC Fabricius, 1787), from NW Aegean Sea, Greece. *Environmental Pollution*, 316, 120725. <https://doi.org/10.1016/j.envpol.2022.120725>
- Karaa, S., Rjijer, J., Bradai, M.N. & Jribi, I. (2019). New record of *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Decapoda: Ocypodidae) from the Tunisian coasts, the central Mediterranean Sea. *Journal of the Black Sea/Mediterranean Environment*, 25(1), 101–107.
- Kim, D.-I., Jang, S.-J. & Kim, T. (2023). The first record of *Ocypode sinensis* (Decapoda: Ocypodidae) from the Korean peninsula: how the complete mitochondrial genome elucidates the divergence history of ghost crabs. *Journal of Marine Science and Engineering*, 11(12), 2348. <https://doi.org/10.3390/jmse11122348>
- Langan, J.A., Puggioni, G., Oviatt, C.A., Henderson, M.E. & Collie, J.S. (2021). Climate alters the migration phenology of coastal marine species. *Marine Ecology Progress Series*, 660, 1–18. <https://doi.org/10.3354/meps13612>
- Lucrezi, S., Schlacher, T.A. & Robinson, W. (2009). Human disturbance as a cause of bias in ecological indicators for sandy beaches: experimental evidence for the effects of human trampling on ghost crabs (*Ocypode* spp.). *Ecological Indicators*, 9(5), 913–921. <https://doi.org/10.1016/j.ecolind.2008.10.013>
- Lucrezi, S., Schlacher, T.A. & Walker, S. (2009). Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach. *Environmental Monitoring and Assessment*, 152, 413–424. <https://doi.org/10.1007/s10661-008-0326-2>
- Mancinelli, G., Manna, M. & Carlino, P. (2019). The tufted ghost crab *Ocypode cursor* in the Salento Peninsula (SE Italy): new records from Caretta caretta nesting sites. *Thalassia Salentina*, 41, 133–136. <https://doi.org/10.1285/i15910725v41p133>
- Marchessaux, G., Gjoni, V. & Sarà, G. (2023). Environmental drivers of size-based population structure, sexual maturity and fecundity: a study of the invasive blue crab *Callinectes sapidus* (Rathbun, 1896) in the Mediterranean Sea. *PLoS ONE*, 18(8), e0289611. <https://doi.org/10.1371/journal.pone.0289611>
- Marco, A., Abella Pérez, E., Monzón Argüello, C., Martins, S., Araujo, S. & López-Jurado, L.F. (2011). The international importance of the archipelago of Cape Verde for marine turtles, in particular the loggerhead turtle. *Caretta caretta*: Zoologia Caboverdiana. <http://hdl.handle.net/10553/18267>
- Marco, A., da Graça, J., García-Cerdá, R., Abella, E. & Freitas, R. (2015). Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. *Journal of Experimental Marine Biology and Ecology*, 468, 74–82. <https://doi.org/10.1016/j.jembe.2015.03.010>
- Martins, R., Marco, A., Patino-Martinez, J., Yeoman, K., Vinagre, C. & Patrício, A.R. (2022). Ghost crab predation of loggerhead turtle eggs across thermal habitats. *Journal of Experimental Marine Biology and Ecology*, 551, 151735. <https://doi.org/10.1016/j.jembe.2022.151735>
- Mytilineou, C., Akel, E.K., Babali, N., Balistreri, P., Bariche, M., Boyaci, Y. et al. (2016). *New Mediterranean biodiversity records* (November, 2016).
- Naderi, M., Hosseini, S.A., Pazooki, J., Hedayati, A., Zare, P. & Lastra, M. (2018). Reproductive biology of the ghost crab, *Ocypode rotundata* Miers, 1882 (Decapoda, Ocypodidae) at Qeshm island, Persian Gulf. *Crustaceana*, 91(9), 1039–1059.
- Naderi, M. & Pishehvarzad, F. (2019). Morphological survey of the burrows of the ghost crab *Ocypode rotundata* (Miers, 1882) in the southwestern Qeshm Island. *Iranian Scientific Fisheries Journal*, 28(4), 163–167. <https://doi.org/10.22092/ISFJ.2019.118884>
- Najafi, A. (2014). *Population and reproductive biology of ghost crab Ocypode rotundata* (Miers, 1882) in Chabahar, Oman Sea, Iran. PhD Thesis, Thesis. Chabahar, Iran: Chabahar Maritime University.
- Olenin, S., Gollasch, S., Lehtiniemi, M., Sapota, M. & Zaiko, A. (2017). Biological invasions. In: Snoeijis-Leijonmalm, P., Schubert, H., & Radziejewska, T. (Eds.) *Biological oceanography of the Baltic Sea*. Dordrecht: Springer Netherlands, pp. 193–232.
- Pastor, F. & Khodayar, S. (2023). Marine heat waves: characterizing a major climate impact in the Mediterranean. *Science of the Total Environment*, 861, 160621. <https://doi.org/10.1016/j.scitotenv.2022.160621>
- Pastor, F., Valiente, J.A. & Palau, J.L. (2019). Sea surface temperature in the Mediterranean: trends and spatial patterns (1982–2016). In: Vilibić, I., Horvath, K., & Palau, J.L. (Eds.) *Meteorology and climatology of the Mediterranean and Black Seas*. Cham: Springer International Publishing, pp. 297–309.
- Peña-Toribio, A., López-López, E., Flores-Martínez, J.J., Sanchez-Cordero, V., Gómez-Lunar, Z. & Ruiz, E.A. (2017). Genetic diversity of the Atlantic ghost crab *Ocypode quadrata* (Decapoda: Ocypodidae) in two beaches with different anthropogenic disturbance in the north coast of Veracruz, Mexico. *Tropical Conservation Science*, 10, 194008291771038. <https://doi.org/10.1177/1940082917710388>
- Perzia, P., Spinelli, A., Interdonato, F. & Castriota, L. (2022). Ecological indicators from spatial statistics to describe the Atlantic fangtooth moray distribution in the Mediterranean Sea. *Transactions in GIS*, 26(7), 2802–2817. <https://doi.org/10.1111/tgis.12981>
- Pisano, A., Marullo, S., Artale, V., Falcini, F., Yang, C., Leonelli, F.E. et al. (2020). New evidence of Mediterranean climate change and variability from sea surface temperature observations. *Remote Sensing*, 12(1), 132. <https://doi.org/10.3390/rs12010132>
- Poloczanska, E.S., Burrows, M.T., Brown, C.J., García Molinos, J., Halpern, B.S., Hoegh-Guldberg, O. et al. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 62. <https://doi.org/10.3389/fmars.2016.00062>
- Pombo, M., de Oliveira, A.L., Xavier, L.Y., Siegle, E. & Turra, A. (2017). Natural drivers of distribution of ghost crabs *Ocypode quadrata* and the implications of estimates from burrows. *Marine Ecology Progress Series*, 565, 131–147. <https://doi.org/10.3354/meps11991>
- Rae, C., Hyndes, G.A. & Schlacher, T.A. (2019). Trophic ecology of ghost crabs with diverse tastes: unwilling vegetarians. *Estuarine, Coastal and Shelf Science*, 224, 272–280. <https://doi.org/10.1016/j.ecss.2019.02.023>
- Ratinaud, P. & Déjean, S. (2009). IRaMuTeQ: implémentation de la méthode ALCESTE d'analyse de texte dans un logiciel libre. *Modélisation appliquée Aux Sciences Humaines et Sociales MASHS*, 8–9.
- Rebello, R., Barbosa, C., Granadeiro, J.P., Indjai, B., Novais, B., Rosa, G.M. et al. (2012). Can leftovers from predators be reliably used to monitor



- marine turtle hatchling sex-ratios? The implications of prey selection by ghost crabs. *Marine Biology*, 159, 613–620. <https://doi.org/10.1007/s00227-011-1839-8>
- Robinson, R.A., Crick, H.Q., Learmonth, J.A., Maclean, I.M., Thomas, C.D., Bairlein, F. et al. (2009). Travelling through a warming world: climate change and migratory species. *Endangered Species Research*, 7(2), 87–99. <https://doi.org/10.3354/esr00095>
- Rodrigues, E., Freitas, R., Delgado, N.D.C. & Soares-Gomes, A. (2016). Distribution patterns of the ghost crab *Ocypode cursor* on sandy beaches of a tropical island in the Cabo Verde archipelago, Eastern Central Atlantic. *African Journal of Marine Science*, 38(2), 181–188. <https://doi.org/10.2989/1814232X.2016.1176602>
- Sakai, K. & Türkay, M. (2013). Revision of the genus *Ocypode* with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura). *Memoirs of the Queensland Museum*, 56(2), 665–793.
- Schlacher, T.A. & Lucrezi, S. (2014). The ecology of ghost crabs. *Oceanography and Marine Biology*, 201–256.
- Schuchman, E. & Warburg, M.R. (1978). Dispersal, population structure and burrow shape of *Ocypode cursor*. *Marine Biology*, 49(3), 255–263. <https://doi.org/10.1007/BF00391138>
- Sharifian, S., Kamrani, E. & Saeedi, H. (2021). Global future distributions of mangrove crabs in response to climate change. *Wetlands*, 41(8), 99. <https://doi.org/10.1007/s13157-021-01503-9>
- Shiber, J.G. & Izzidin, S. (1978). The burrow structure of *Ocypode cursor* (Linnaeus 1758) on three shores south of Beirut, Lebanon. *Cercetari Marine*, 11, 113–127.
- Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S. et al. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? D Vasseur Ed. *Ecology Letters*, 19(11), 1372–1385. <https://doi.org/10.1111/ele.12686>
- Smith, R.C., Godley, B.J. & Broderick, A.C. (1996). *The effect of predation by the ghost crab, Ocypode cursor, on eggs and hatchlings of marine turtles in N. Cyprus. Proceedings of the 16th annual symposium on sea turtle biology and conservation*. South Carolina: Hilton Head Island, pp. 126–127.
- Strachan, P.H., Smith, R.C., Hamilton, D.A.B., Taylor, A.C. & Atkinson, R.J.A. (1999). Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus. *Scientia Marina*, 63(1), 51–60. <https://doi.org/10.3989/scimar.1999.63n151>
- Stuart-Smith, R.D. (2021). Climate change: large-scale abundance shifts in fishes. *Current Biology*, 31(21), R1445–R1447. <https://doi.org/10.1016/j.cub.2021.09.063>
- Thiede, J. (1978). A glacial Mediterranean. *Nature*, 276(5689), 680–683. <https://doi.org/10.1038/276680a0>
- Thirukanthan, C.S., Azra, M.N., Seman, N.J.A., Agos, S.M., Arifin, H., Aouissi, H.A. et al. (2023). A scientometric review of climate change and research on crabs. *Journal of Sea Research*, 193, 102386. <https://doi.org/10.1016/j.seares.2023.102386>
- Tiralongo, F., Arculeo, M., Yeo, M.D., Kakou, B.I. & Adepo-Gourene, A.B. (2020). First data on population structure and growth parameters of *Ocypode cursor* (Linnaeus, 1758) along the Mediterranean and Atlantic coast. *Cahiers de Biologie Marine*, 61(4), 405–413. <https://doi.org/10.21411/CBMA.3AA1FF69>
- Tiralongo, F., Messina, G., Marino, S., Bellomo, S., Vanadia, A., Borzi, L. et al. (2020). Abundance, distribution and ecology of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Ocypodidae) from a recently colonized urban sandy beach, and new records from Sicily (central Mediterranean Sea). *Journal of Sea Research*, 156, 101832. <https://doi.org/10.1016/j.seares.2019.101832>
- Trott, T.J. (1999). Gustatory responses of ghost crab *Ocypode quadrata* to seawater extracts and chemical fractions of natural stimuli. *Journal of Chemical Ecology*, 25, 375–388. <https://doi.org/10.1023/A:1020859115984>
- Tureli, C., Duysak, O., Akamca, E. & Kiyagi, V. (2009). Spatial distribution and activity pattern of the ghost crab, *Ocypode cursor* (L., 1758) in Yumurtalik Bay, North-Eastern Mediterranean–Turkey. *Journal of Animal and Veterinary Advances*, 8(1), 165–171.
- Türeli, C., Yeşilyurt, I.N., Akamca, E. & Erdem, U. (2014). Distribution and population density of the ghost crab, *Ocypode cursor* (Linnaeus, 1758) in Yumurtalik beach, Turkey. *Asian Journal of Agriculture and Biology*, 2(1), 59–66.
- Turra, A., Gonçalves, M. & Denadai, M. (2005). Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches. *Journal of Natural History*, 39(23), 2163–2177. <https://doi.org/10.1080/00222930500060165>
- Valero-Pacheco, E., Alvarez, F., Abarca-Arenas, L.G. & Escobar, M. (2007). Population density and activity pattern of the ghost crab, *Ocypode quadrata*, in Veracruz, Mexico. *Crustaceana*, 80(3), 313–325. <https://www.jstor.org/stable/20107809>
- Vecchioni, L., Marrone, F., Deidun, A., Adepo-Gourene, B., Frogia, C., Sciberras, A. et al. (2019). DNA taxonomy confirms the identity of the widely-disjunct Mediterranean and Atlantic populations of the tufted ghost crab *Ocypode cursor*. (Crustacea: Decapoda: Ocypodidae). *Zoological Science*, 36(4), 322–329. <https://doi.org/10.2108/zs180191>
- Verberk, W.C.E.P., Bartolini, F., Marshall, D.J., Pörtner, H., Terblanche, J.S., White, C.R. et al. (2016). Can respiratory physiology predict thermal niches? *Annals of the New York Academy of Sciences*, 1365(1), 73–88. <https://doi.org/10.1111/nyas.12876>
- Von Holle, B., Irish, J.L., Spivy, A., Weishampel, J.F., Meylan, A., Godfrey, M.H. et al. (2019). Effects of future sea level rise on coastal habitat. *The Journal of Wildlife Management*, 83(3), 694–704. <https://doi.org/10.1002/jwmg.21633>
- Vu, H.D., Wie ski, K. & Pennings, S.C. (2017). Ecosystem engineers drive creek formation in salt marshes. *Ecology*, 98(1), 162–174. <https://doi.org/10.1002/ecy.1628>
- Wolcott, T.G. (1978). Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: scavengers or predators? *Journal of Experimental Marine Biology and Ecology*, 31(1), 67–82. [https://doi.org/10.1016/0022-0981\(78\)90137-5](https://doi.org/10.1016/0022-0981(78)90137-5)
- Worm, B. & Lotze, H.K. (2021). Marine biodiversity and climate change. *Climate Change Elsevier*, 445–464. <https://doi.org/10.1016/B978-0-12-821575-3.00021-9>
- Yilmaz, O. & Barlas, M. (2020). *Studying on relationship between carapace width and habitat properties of tufted ghost crab (Ocypode cursor) living on Iztuzu beach—Turkey*. <https://doi.org/10.22092/ijfs.2019.119311.0>
- Yilmaz, Ö. & Barlas, M. (2020). Testing behavior model for *Ocypode cursor* (Linnaeus, 1758) living on Iztuzu Beach. *Iranian Journal of Fisheries Sciences*, 19(1), 518–524. <https://doi.org/10.22092/ijfs.2019.119311.0>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**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>