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Fouling of a boat hull by the invasive zooxanthellate coral *Oculina patagonica* - could shipping be enhancing its unique large-scale spread?

Eduard SERRANO[1], Marta RIBES[2], Manel BOLIVAR[1] and Rafel COMA[1]

[1] Centre d'Estudis Avançats de Blanes-Consejo Superior de Investigaciones Científicas (CEAB-CSIC),
Accés Cala Sant Francesc 14, 17300 Blanes, Spain
[2] Institut de Ciències del Mar-Consejo Superior de Investigaciones Científicas (ICM-CSIC),
Passeig Marítim Barceloneta 137-149, 08003 Barcelona, Spain

Corresponding author: Eduard SERRANO; eserrano@ceab.csic.es

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Abstract

The zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae) is an invasive species that was first recorded in the Mediterranean Sea in 1966 and currently has expanded its distribution across both the western and eastern Atlantic. Here, we reviewed data from multiple databases to compile historical distribution records of *O. patagonica* and analyze its spread. The chronological review highlights the unique spread of this zooxanthellate coral during the last two decades, expanding its distribution in multiple directions and establishing populations in disjunct regions separated by ~12,000 km, including most biogeographic regions within the temperate Mediterranean, the subtropical eastern Atlantic and the tropical Gulf of Mexico. The biogeographic distribution discontinuities documented in *O. patagonica* are difficult to explain by larval dispersion alone; therefore, other mechanisms may contribute to its large-scale spread pattern. This study provides the first observation of several *O. patagonica* colonies fouling the hull and metal crevices of a recreational boat in the western Mediterranean (37°N, 1°W). The presence of several mature *O. patagonica* colonies on a single ship, rather than a single coral colony rafting on natural or artificial floating substrates, could greatly increase its potential for spread, coupled with its ecological and biological traits adapted to rafting. We hypothesized that the travel of coral populations by shipping may act as a dispersal vector contributing to explaining the long-distance dispersal events and secondary introductions experienced by this invasive species. The broad spread of *O. patagonica*, which is able to drive phase shifts from macroalgae dominance to coral dominance, is consistent with the ongoing process of coral-mediated tropicalization of high-latitude shallow rocky reefs under current global change.

Keywords: invasive species; tropicalization; invasion pathway; scleractinian coral; fouling; recreational boats.

Introduction

Biological invasions are a major component of global change, facilitating the redistribution of species at global scales and often impacting native biodiversity, ecosystem functioning, and human well-being (Molnar *et al.*, 2008; Simberloff *et al.*, 2013). The rapid globalization and increasing trends of trade and travel in recent decades have accelerated the transport of species beyond their native range limits of distribution, with marine ecosystems ranking among the most affected (Blakeslee *et al.*, 2011; Burrows *et al.*, 2011). The main vectors of human-mediated transport of marine organisms include ballast water and fouling on the hulls of commercial ships, recreational yachting boats, artificial canals, aquaculture and the aquarium trade, and mobile floating platforms (Katsanevakis *et al.*, 2013; Galil *et al.*, 2014). Knowledge about the vectors of transport used by alien species is essential to prevent their introduction and spread to nonnative ecosystems (Lockwood *et al.*, 2005; Blakeslee *et al.*, 2011). Shipping (i.e., the movement of vessels and transport of floating barges, platforms and floating docks) is considered among the most relevant pathways for the introduction of marine alien species (IMO, 2011; Iacarella *et al.*, 2020). Maritime traffic has increased during recent decades, coupled with further construction of harbors and marinas (Hulme, 2009). Artificial reefs, such as breakwaters and docks, provide suitable habitats for the colonization of alien benthic species, which are usually more successful than native species (Bulleri & Chapman, 2010). Therefore, artificial reefs and maritime traffic likely facilitate the 'hitch-hiking' opportunities and the stepping-stone introduction process known for invasive species, a process predicted to increase in future global change scenarios (Burrows *et al.*, 2011; Anderson *et al.*, 2015; Iacarella *et al.*, 2020).

Studies of boat movements and the abundance of nonindigenous species fouling boat hulls indicated that yachting could act as a key dispersal vector for alien species (Ulman *et al.*, 2019; Iacarella *et al.*, 2020). The long distances (>1,000 km) that recreational boats can travel and their relatively low speeds (compared to commercial ships) make them idyllic transportation pathways for fouling species (Anderson *et al.*, 2015; Ferrario *et al.*, 2016). Oil and gas platforms spend a great deal of time stationary developing rich fouling communities and, therefore, can also be an important dispersal vector for invasive species (Sammarco *et al.*, 2012; López *et al.*, 2019). Despite shipping being one of the most important vectors for species invasion, biofouling on boat hulls remains a largely unregulated vector, and vessels continue to carry fouling species, especially in niche areas such as sea chests, gratings and water intake pipes (Clarke Murray *et al.*, 2011; Ulman *et al.*, 2019). Unfortunately, biofouling guidelines, established by the International Maritime Organization in 2011, remain the recommended practices despite a high risk of invasion by shipping being documented in several regions worldwide (Molnar *et al.*, 2008; IMO, 2011; IMO Glofouling Partnership Project, https://www.glofouling.imo.org). Attention given to hull cleaning is generally voluntary, aiming to improve boat hydrodynamics and fuel consumption (Clarke Murray *et al.*, 2011; Fernandes *et al.*, 2016).

Well-known fouling organisms include algae and marine invertebrates such as barnacles, mollusks, bryozoans, ascidians and sponges, whereas zooxanthellate scleractinian corals are extremely rare (but see Bertelsen & Ussing, 1936). However, some corals are transported on oil and gas platforms and raft on flotsam (i.e., metal gas tanks and plastic debris; Hoeksema *et al.*, 2012, 2018; Creed *et al.*, 2017). For instance, some azooxanthellate coral *Tubastraea* spp., native to the Indo-Pacific, have invaded the western and eastern Atlantic after transport was likely facilitated by mobile floating platforms (Creed *et al.*, 2017; López *et al.*, 2019).

The temperate Mediterranean Sea is a hotspot of biological invasions (Costello *et al.*, 2021). It probably hosts the greatest variety of introduction vectors in the oceans, including heavy commercial and recreational maritime traffic, aquaculture, and its connection through the Suez Canal to the Red Sea (Galil *et al.*, 2014). In an era of global change, several zooxanthellate scleractinians are gradually shifting their distribution range poleward, tracking the migration of suitable seawater temperatures or increasing abundances in native areas, which threatens the general dominance of macroalgae at high-latitude shallow rocky reefs (Burrows *et al.*, 2011; Vergés *et al.*, 2014). However, none of these range-expanding zooxanthellate corals has experienced invasive behavior (Blackburn *et al.*, 2011) similar to that of *Oculina patagonica* (Scleractinia, Oculinidae). The first record of the coral *O. patagonica* was a single large colony (i.e., 135 cm in mean diameter) discovered in 1966 in the Mediterranean Sea (Zibrowius, 1974). This previously unknown species in the Mediterranean Sea was identified based on an ~10,000-year-old fossil species from the southwestern Atlantic: '*Oculina patagonica* de Angelis, 1908', and its invasion pathway into the Mediterranean Sea was tentatively attributed to its transoceanic transport as a fouling organism on a ship hull (Zibrowius, 1974). In fact, the conspicuous coral *O. patagonica* (i.e., large colonies thriving in shallow-water rocky reefs) was previously unknown in museum collections and fossil records from the Mediterranean basin, even though rare, cryptic and small coral fauna were well represented. Unfortunately, living specimens have never been recorded in the southwestern Atlantic, and the biogeographic origin and taxonomic identification of *O. patagonica* in the Mediterranean remain uncertain (Leydet & Hellberg, 2015). Therefore, the species maintains a cryptogenic status (i.e., it cannot be reliably assigned to be either native or alien) within the European Alien Species Information Network database (Zenetos *et al.*, 2017).

Invasive alien species are species whose introduction outside their natural past or present distribution threatens biological diversity (i.e., must successfully spread through its new environment, outcompete native organisms, increase in population density and harm ecosystems in its introduced range; e.g., Blackburn *et al.*, 2011; Valéry *et al.*, 2013; Essl *et al.*, 2019). During recent decades, the distribution of *O. patagonica* has shifted its range in multiple directions within the Mediterranean Sea (Fine *et al.*, 2001; Salomidi *et al.*, 2013; Serrano *et al.*, 2013, 2018). Additionally, it has recently been found alive in the western Atlantic (in 2015 in the Gulf of Mexico, contrasted with genetic analyses; García *et al.*, 2018) and the eastern Atlantic (in 2016 in the Canary Islands; Brito *et al.*, 2017). Therefore, the current geographic distribution of the species is expanding outside the Mediterranean Sea, and according to biogeographic criteria, it should be considered an alien species in at least one of these regions. Regarding the impact criteria, *O. patagonica* has been able to diminish structural complexity and species richness, and challenge the ecosystem structure and function via regime shifting from macroalgal dominance to coral dominance in the temperate Mediterranean Sea (Zabala & Ballesteros, 1989; Serrano *et al.*, 2012; Tsirintanis *et al.*, 2022). Therefore, the coral *O. patagonica* should be considered an invasive alien species because it meets the biogeographic and impact criteria in some regions of its distribution. The broad spread of *O. patagonica* and its invasive behavior are consistent with the ongoing process of zooxanthellate coral-mediated tropicalization of shallow-water rocky ecosystems documented in other subtropical and temperate areas under current global change (Vergés *et al.*, 2014; Serrano *et al.*, 2018).

The larval stage of zooxanthellate coral species is generally short (Harrison, 2011). The maximum settlement competency period for autotrophic coral larvae, such as those of *O. patagonica*, is 1-3 months (Fine *et al.*, 2001; Brooke & Young, 2005; Harrison, 2011), and the combination of molecular research and oceanographic models has described significant gene flow and connectivity among coral populations over maximum distances of hundreds of kilometers (Jones *et al.*, 2009; Nunes *et al.*, 2011). However, although gradual expansion over a vast area has been documented for *O. patagonica* (Serrano *et al.*, 2013, 2018), there are important biogeographic discontinuities in the distribution of the species (i.e., establishing populations in disjunct regions separated by thousands of kilometers and crossing oceans) that cannot be explained by stepping-stone expansion. Therefore, mechanisms other than the natural dispersion of coral larvae by marine currents may contribute to the documented large-scale dispersal events documented in *O. patagonica.* In this sense, the large-scale dispersal of gonochoric coral species, such as *O. patagonica* (Fine *et al.*, 2001), requires the traveling of a relevant number of reproductively mature colonies on a mobile floating structure (rafting) that, to date, has not been observed. Here, we provide a chronological review of the geographical spread of the zooxanthellate coral *O. patagonica* and report the first observation of a coral population fouling a boat hull, which constitutes a plausible mechanism explaining the long-distance dispersal events and secondary introductions documented in this currently range-expanding species.

Materials and Methods

To examine the geographic distribution of the coral *O. patagonica*, we retrieved peer-reviewed scientific literature until August 2022 from multiple databases related to cross-disciplinary research, such as Web of Science (http://www.webofknowledge.com/), Science Direct (https://www.sciencedirect.com) and Google Scholar (https://scholar.google.com), typing "*Oculina patagonica*" as a keyword. To reconstruct the chronological spatial expansion of *O. patagonica*, we also retrieved the year of the first species record for each biogeographic region and mapped data on the species' records.

In June 2015, we discovered several *O. patagonica* colonies fouling an 8-m length recreational boat landed at Mazarrón Harbor, south-Balearic Sea, western Mediterranean (37.564°N, 1.256°W). We measured all *O. patagonica* colonies encrusted on the fiberglass hull and the niche areas, such as the metal parts near the motor engine. The surface areas of the colonies were estimated using in situ measurements of the longest axis of the skeleton of the colony (length, L) and its longest perpendicular axis (width, W) to the nearest half-centimeter. The surface area of the colony (S, cm^2) was calculated using the formula $S = \pi[(L + W)/4]^2$ according to Fine *et al.* (2001).

Results

Geographic distribution of *O. patagonica*

The global dataset compilation on reported locations with the presence of *O. patagonica* showed that the current species' distribution includes most biogeographic regions across the temperate Mediterranean Sea (from 4.569°W to 34.498°E in longitude and 36.491°N to 31.671°N in latitude), the Canary Islands (subtropical eastern Atlantic, 28.478°N, 16.237°W) and the tropical Gulf of Mexico (19.172°N, 96.113°W; Fig. 1 and references therein). Since the first record of *O. patagonica* in the Mediterranean in 1966, the presence of the species has been recorded from most Mediterranean biogeographic regions in locations separated in space up to ~3,800 km in linear distance. Within the Mediterranean, the coral *O. patagonica* was first recorded in the Ligurian Sea in 1966, in the Balearic Sea during the 1970s, in the Levant Sea during the 1980s, in the Alboran Sea and adjacent eastern Atlantic coast, Algerian and Tunisian waters, and the Aegean Sea during the 2000s, and in the Adriatic Sea, Gulf of Lyons and the Ionian Sea during the 2010s (Fig. 1). Beyond the Mediterranean, the species was first recorded in the Gulf of Mexico in 2015 and the Canary Islands in 2016, ~8,600 and ~1,400 km of linear distance from the previously known distribution range, respectively. In most cases, the first record of *O. patagonica* in each biogeographic region was based on several coral colonies or abundant populations, with the Adriatic Sea being the only region with only one recorded colony (Fig. 1 and references therein). Therefore, the distribution of *O. patagonica* has expanded in multiple directions, and abundant coral populations have been documented in disjunct regions crossing oceans and separated in space by ~12,000 km.

Examination of the existing scientific literature (peer-reviewed manuscripts, gray literature and authors' unpublished data) showed a total of 426 locations on which *O. patagonica* was recorded (updated in August 2022). The coral *O. patagonica* has been recorded in 3 locations in the Canary Islands and in 8 locations in the Gulf of Mexico (Fig. 1a). Within the Mediterranean, the current geographic distribution pattern of *O. patagonica* is continuous (i.e., >1 location with the species per 10 km coastal length) in the southwestern and eastern Mediterranean regions, with the Balearic Sea being the most invaded region by the species (n = 234 reported locations), followed by the Alboran Sea (n = 53 locations) and the Aegean Sea (n = 52 locations). In contrast, the species' distribution pattern is fragmented (i.e., <1 location with the species per 10 km coastal length) in the northwestern and central regions (Fig. 1b).

An *O. patagonica* population fouling a boat hull

A total of 19 colonies of the coral *O. patagonica* were found encrusted on an 8-m length recreational boat landed at Mazarrón Harbor, south-Balearic Sea, western Mediterranean (Fig. 1b). Coral colonies grew on the fiberglass hull and in the niche areas of the boat, such as the metal parts near the motor engine (Fig. 2). The coral colonies were encrusting (i.e., <5 mm in height) and located from ~10 cm depth from the waterline to 65 cm depth at the keel of the boat. The maximum diameter of the coral colonies ranged from 1 to 16 cm, with an area of 1–154 cm^2

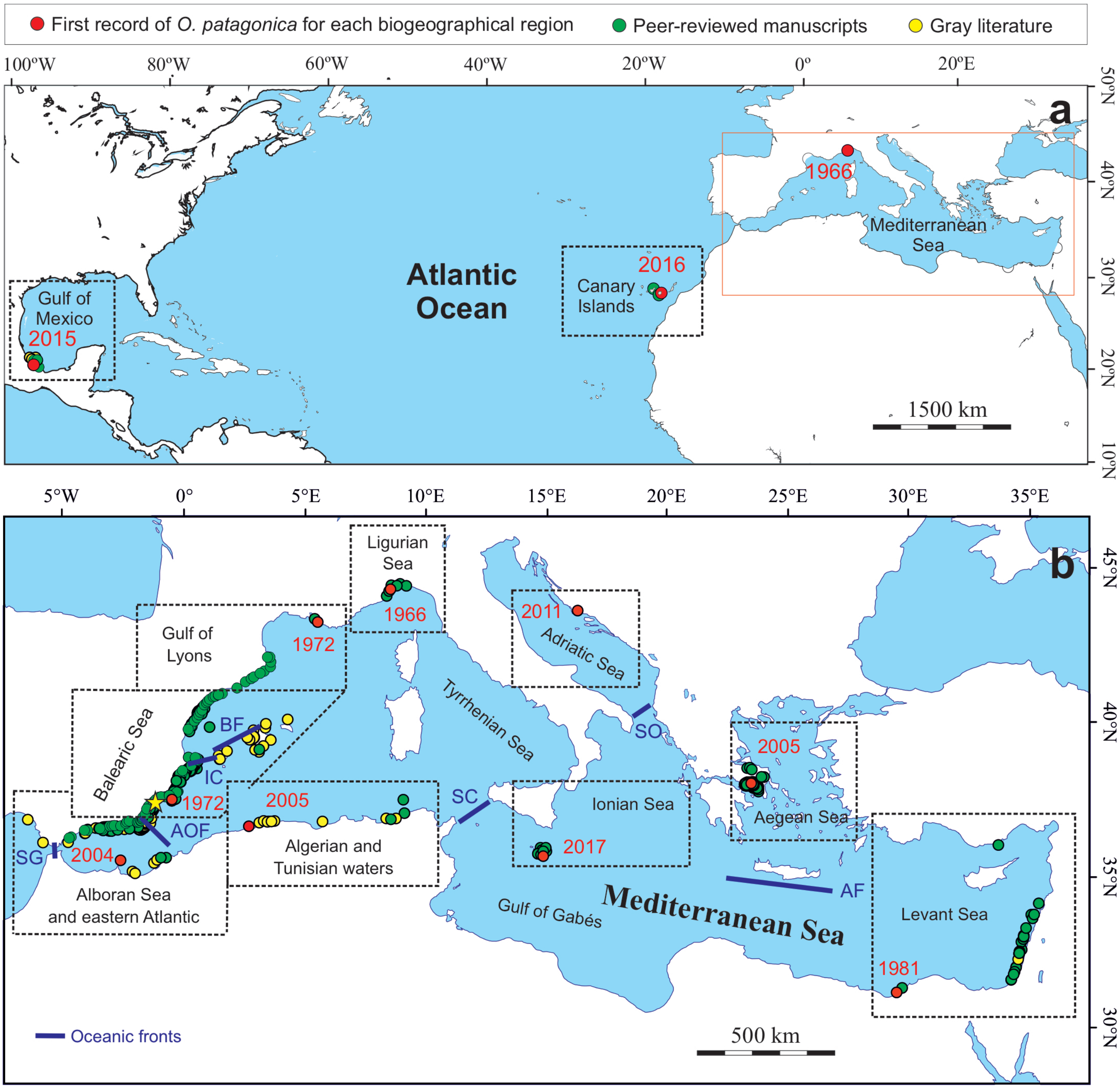

Fig. 1: Map of the historical distributional records of *Oculina patagonica*. Distribution of *O. patagonica* in (a) the Mediterranean Sea, the Canary Islands and the Gulf of Mexico, and (b) for each biogeographic region within the Mediterranean Sea. The location and year of the first record of *O. patagonica* are indicated for each biogeographic region (*red circles*). The positions of the 426 locations in which the species has been recorded are indicated, distinguishing between records from peer-reviewed manuscripts (*green circles*) and gray literature and authors' unpublished data (*yellow circles*; updated in August 2022). The location of the coral population fouling a recreational boat at Mazarrón Harbor (southeastern Balearic Sea) is indicated by a *yellow star*. The positions of the oceanographic fronts (*SG*: Strait of Gibraltar, *AOF*: Almeria-Oran Front, *IC*: Ibiza Channel, *BF*: Balearic Front, *SC*: Sicily Channel, *SO*: Strait of Otranto, *AF*: Aegean Front) are indicated (adapted from Millot, 2005). Information sourced from Armoza-Zvuloni *et al*., 2011, 2012; Bachetarzi *et al*., 2016; Ballesteros, 1998; Bitar & Zibrowius, 1997; Brito *et al*., 2017; Chartosia *et al*., 2018; Coma *et al*., 2011; Cutajar *et al*., 2020; Cvitković *et al*., 2013; Çinar *et al*., 2006; Dailianis *et al*., 2016; Fine *et al*., 2001; García *et al*., 2018; González-Gándara *et al*., 2015; Grimes *et al*., 2018; Israely *et al*., 2001; Lamouti & Bachari, 2011; Lamouti *et al*., 2011; Leydet & Hellberg, 2015; López *et al*., 2019; Moreno, 2010; Rebzani-Zahaf *et al*., 2013; Rubio-Portillo *et al*., 2014; Salomidi *et al*., 2013; Sartoretto *et al*., 2008; Serrano *et al*., 2012, 2013, 2018; Templado *et al*., 2006; Terrón-Sigler *et al*., 2015, 2016; Zibrowius, 1974; Zibrowius & Ramos, 1983; authors' unpublished data.

(36 ± 10 cm^2, mean ± SE). The size of the coral colonies on the parts of the boat hull made of fiberglass (starboard, port and stern sides; 1-44 cm^2, n = 13) was smaller than that of those growing on the metal crevices near the motor mount (3-154 cm^2, n = 6). The boat owner told us that the boat was recently landed (i.e., seven days prior to the photographs) and that it was moored at Mazarrón Harbor and occasionally sailing at a local scale, although the hull was unmaintained for ~4 years. The coral colonies appeared brown–yellowish in color, indicating that

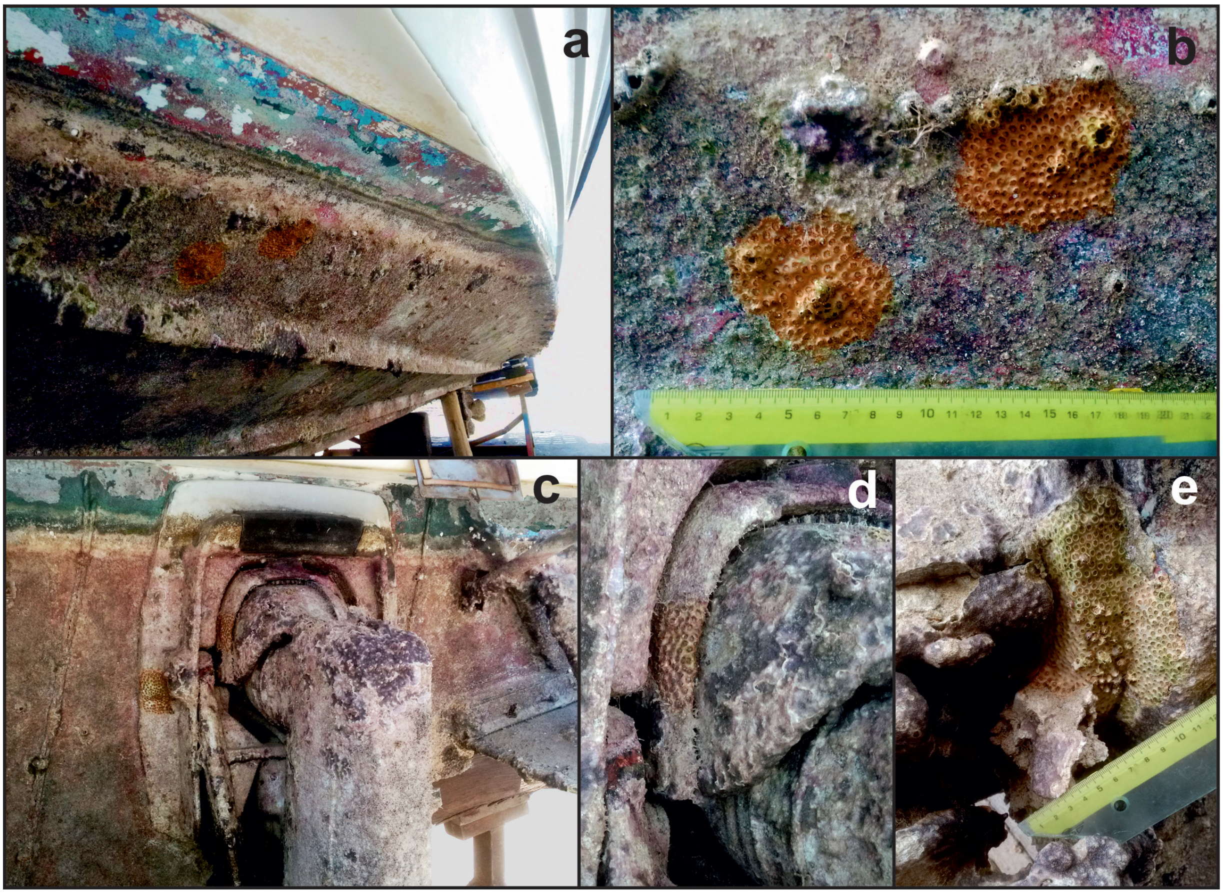

Fig. 2: Photographs of the invasive zooxanthellate coral *Oculina patagonica* fouling a recreational boat in the southeastern Balearic Sea (western Mediterranean). (a) General view of coral colonies fouling an 8-m length recreational boat. (b) Close-up of the fiberglass hull and (c-e) metal crevices near the motor engine.

they were alive prior to landing (Fig. 2). In addition to *O. patagonica* colonies, fouling on the boat hull included a thin layer of filamentous and encrusting calcareous algae, barnacles, bryozoans and polychaetes (Fig. 2).

Discussion

Disjunct geographic distribution of O. patagonica

The literature review revealed the historical geographic distribution and spread of the zooxanthellate coral *O. patagonica*, showing that during recent decades, this invasive species has expanded in multiple regions across oceans, separated by ~12,000 km in linear distance (Fig. 1 and references therein). *O. patagonica* experienced a rapid northward expansion along ~400 km of the Catalan coast (western Mediterranean) at 22 km year^{-1} over 1992-2010, which has been related to the interplay of local and medium-distance dispersal (up to 180 km) that created new invasion foci (Serrano *et al.*, 2013). Currents contribute to the regional dispersal of sexually produced planulae larvae (i.e., autotrophic coral larvae, such as those of *O. patagonica*, can survive up to 1-3 months in the water column before settlement; Fine *et al.*, 2001; Harrison, 2011). Larvae of similar species, such as *Oculina varicosa*, actively swam in a laboratory setting for 1-2 weeks before beginning to exhibit benthic-probing behavior, and settlement on the sides of the culture containers was observed after 3-4 weeks, although some larvae continued swimming for up to 42 days, after which time the experiment was terminated (Brooke & Young, 2005). The combination of molecular research and oceanographic models has described significant gene flow and connectivity among coral populations over maximum distances of hundreds of kilometers (Jones *et al.*, 2009; Nunes *et al.*, 2011). Therefore, larval dispersal by marine currents could explain the secondary introductions experienced by *O. patagoniga* within a biogeographical region, or between nearby regions. However, large-scale dispersal events between disjunct regions of the Mediterranean and crossing oceans, such as those experienced by *O. patagonica* (e.g., ~1,400 km from the Mediterranean to the Canary Islands and ~8,600 km to the Gulf of Mexico; Fig. 1), are difficult to explain only by coral larvae dispersal. In this study, we report the first observation of a population of *O. patagonica* fouling the hull of a recreational boat, and we hypothesized that the capacity of *O. patagonica* to foul mobile floating structures may add maritime transport as a plausible dispersal vector contributing to explaining the broad geographical spread and the long-distance dispersal events experienced by this invasive species.

The key life-history traits for a species to successfully invade by shipping

The life-history strategy of a successful rafter must facilitate settlement and survival on floating substrates during large-scale travel on mobile structures under a wide range of environmental conditions and the capacity to grow and reproduce in the new area to colonize. In this sense, the broad geographical spread of *O. patagonica* could be related to its life-history strategies, characteristic of an opportunistic colonizer (Harrison, 2011; Darling *et al.*, 2012; Cardeccia *et al.*, 2016). First, in addition to the natural rocky substrates, *O. patagonica* has been documented to settle in a wide range of substrates, such as nonfloating and stationary concrete boulders and walls of artificial reefs (e.g., harbor dikes and breakwaters) and submerged metal objects and trash (e.g., plastic bags, metal cans, lost nylon fishing lines; Fine *et al.*, 2001; Coma *et al.*, 2011; Salomidi *et al.*, 2013; Serrano *et al.*, 2018). Additionally, an abundant *O. patagonica* population was found on a mobile floating dock that had been stationary for ~5 years, located in a recreational marina at the commercial Cartagena Bay, south-Balearic Sea, western Mediterranean (37.588°N, 0.987°W; authors' unpublished data). The floating dock was made of concrete, and the coral colonies were located from near the water surface to the deepest part of the dock (i.e., 1 m in depth). Therefore, the finding of *O. patagonica* colonies fouling the fiberglass hull and the metal parts of a boat, and the concrete floating dock, add mobile floating structures to the broad types of substrates in which *O. patagonica* can thrive. Second, *O. patagonica* has been documented to survive and grow under a wide range of environmental conditions (e.g., in tide pools at temperatures of 10-40°C and salinities of 28-50‰, polluted areas, and in areas affected by severe sand scouring) owing to its broad trophic capacities (i.e., it is a facultative zooxanthellate coral; Fine *et al.*, 2001; Serrano *et al.*, 2012; Zaquin *et al.*, 2019; Martinez *et al.*, 2021). In comparison to the nearby natural rocky reefs, artificial reefs foster the abundance of *O. patagonica* and likely act as a focus for successful coral reproduction and dispersal (Salomidi *et al.*, 2013; Serrano *et al.*, 2013, 2018). The finding of *O. patagonica* growing in the shaded niche areas of the boat (i.e., metal parts near the motor engine) and inside polluted harbors agrees with the broad tolerance to environmental conditions documented for the species. In addition, *O. patagonica* under stress has been documented to show a polyp dissociation from their connective coenosarc (i.e., loss of coloniality, Dalmatian mortality pattern) and rapid tissue regeneration afterward, which appears to be a decisive biological characteristic that enables the species to withstand unfavorable environmental conditions (Serrano *et al.*, 2017). Therefore, the survival of *O. patagonica* under stress conditions such as those expected during rafting on mobile floating structures seems plausible.

Finally, the dispersal and population growth of *O. patagonica* is based on sexual and asexual propagules, which provide alternatives for its spread once it arrives to a new area. Regarding sexual reproduction, it is a gonochoric broadcast spawner that reproduces annually overlapping the full moon of September, with small gametes and high gonadal production, and has an early age of first reproduction of 1-2 years (i.e., colony surface area of >4 cm^2; Fine *et al.*, 2001; Brooke & Young, 2005). Therefore, most of the coral colonies fouling the hull of the recreational boat were likely to be fertile (i.e., their mean size was 36 cm^2). In addition, the sex ratio has been described as 1:1 in most of the studied coral populations, and normal gametogenesis has been observed under a wide range of environmental conditions in most Mediterranean regions (i.e., Ligurian Sea, Gulf of Lyons, Balearic Sea and Levant Sea), including both pristine and highly polluted locations, and in bleached colonies during stress or that thrive in dark habitats (Fine *et al.*, 2001; Armoza-Zvuloni *et al.*, 2011, 2012). Additionally, the sexual reproduction of *O. patagonica* colonies can acclimatize to chronic disturbances, such as recurrent bleaching episodes and persistent metal pollution (i.e., although the first year of disturbance can significantly affect reproduction success, the species is capable of acclimating and successfully reproducing the second year of repeated disturbance; Armoza-Zvuloni *et al.*, 2011, 2012). Therefore, the finding of likely fertile populations of *O. patagonica* fouling mobile structures, in contrast to that of a single colony, may enhance the success of colonization by sexual reproduction when traveling to new areas. The coral *O. patagonica* can also reproduce asexually via polyp expulsion, in which individual polyps, including their calices, lift on elongated calcareous stalks before detaching and settling elsewhere near the 'mother' colony and form a new colony through budding (Kramarsky-Winter *et al.*, 1997). The onset of asexual reproduction in *O. patagonica* has been related to adverse conditions such as extreme temperatures and sand abrasion. Therefore, the onset of polyp expulsion under stress conditions during rafting may contribute to local colonization upon arrival to new areas. In conclusion, the life-history traits of *O. patagonica*, such as ecological generalization, broad tolerance to environmental conditions and high reproductive and dispersal capabilities, are considered among the most efficient and successful strategies within zooxanthellate corals and likely may have contributed to its large-scale spread.

The successful invasion of the zooxanthellate scleractinian *O. patagonica* resembles only that of the invasive azooxanthellate scleractinian *Tubastraea coccinea* (Scleractinia, Dendrophylliidae), which has also experienced invasive behavior during recent decades (Blackburn *et al.*, 2011) in the tropical and subtropical western Atlantic Ocean, both in the northern (Caribbean Sea and the Gulf of Mexico) and southern hemispheres (Brazil; reviewed in Creed *et al.*, 2017). As a native of the tropical Indo-Pacific, its occurrence in the western Atlantic was first recorded from some Caribbean islands, where it may have been introduced in the 1930s as a fouling organism on an oil platform or a ship hull. The capacity of *T. coccinea* to reproduce both sexually and asexually (Glynn *et al.*, 2008; Capel *et al.*, 2014) and to settle and grow readily on artificial substrates (oil and gas platforms, buoys and drilling ships) may have assisted its wide geographic dispersal (Creed *et al.*, 2017), and these life-history traits are similar to those documented for *O. patagonica*. Both species have a broad tolerance to varying environmental parameters, are generalists in terms of substratum utilization and opportunistic colonizers of high fecundity (e.g., can successfully outcompete the surrounding native benthic organisms for space occupancy), and benefit from human-related impacts (e.g., their population growth is enhanced in artificial habitats, which likely act as corridors for successful dispersal; Fine *et al.*, 2001; Sammarco *et al.*, 2012; Serrano *et al.*, 2013, 2018; Creed *et al.*, 2017).

Fouling on mobile floating structures and the spread of **O. patagonica**

Several zooxanthellate corals (e.g., *Pocillopora* spp., *Millepora* spp., *Porites* spp., *Astrangia poculata*) have been documented to raft long distances by marine currents on natural (e.g., volcanic pumice and wood) and artificial floating substrates (e.g., plastic float and metal objects; Jokiel, 1984; Hoeksema *et al.*, 2012, 2018; Sammarco *et al.*, 2012;). Although shipping is considered among the most relevant pathways for the introduction of marine alien species (IMO, 2011), to our knowledge, the only report of zooxanthellate corals fouling a ship was in the 20th century, when a ship from the Bermudas (Caribbean Sea) was carried to Denmark (northeastern Atlantic; Bertelsen & Ussing, 1936). Here, we report the first observation of a population of the invasive coral *O. patagonica* fouling a boat hull moored at Mazarrón Harbor (south-Balearic Sea, western Mediterranean) and occasionally sailing at a local scale, although the hull was unmaintained for ~4 years. The size of the coral colonies growing on the metal crevices near the motor mount (i.e., up to 16 cm in maximum diameter) was larger than that of those growing on the parts of the boat hull made of fiberglass (up to 7 cm). Based on published growth rate values for *O. patagonica* (mean of 1-2 cm in diameter yr^{-1}; Fine *et al.*, 2001; Serrano *et al.*, 2017), the coral colonies fouling the boat hull were likely to be at least four years old, which is consistent with the period the boat remained unmaintained. In accordance, the largest colonies were found on the metal crevices near the motor mount, which are the less accessible parts for hull cleaning, compared to the other parts of the boat hull made of fiberglass (starboard, port and stern sides).

The Mediterranean Sea hosts a great number of large floating objects, such as navigational buoys, components of aquaculture plants, harbor pontoons, oil platforms and marine litter, where rich fouling communities can develop (Simberloff, 2009; Galil *et al.*, 2014; Rech *et al.*, 2018). Given the high abundance of marinas across the Mediterranean Sea and the heavy maritime traffic, several alien species may have been introduced by shipping, either as fouling organisms or in a larval stage in ballast waters (Galil, 2012; Zenetos *et al.*, 2012). In this sense, the high abundance of *O. patagonica* in artificial reefs is likely to enhance the 'hitch-hiking' opportunities and the stepping-stone invasion process (Serrano *et al.*, 2018; Ulman *et al.*, 2019). Although the distances and seasonality in which boats move are variable, the magnitude of boat flux during the Mediterranean tourist season in September, the period of spawning of *O. patagonica*, is still significant (Fine *et al.*, 2001; Ferrario *et al.*, 2016; Ulman *et al.*, 2019). In this sense, the capacity of the invasive coral *O. patagonica* populations to foul mobile floating structures and their high abundance on artificial reefs indicates that rafting on mobile floating structures at regional and transoceanic scales could play a significant role in the dispersal potential of the species. At present, only another alien zooxanthellate coral species has already been recorded in the Mediterranean (i.e., *Oulastraea crispata*), and shipping has been considered a plausible vector for the introduction of this species because although it is native to the Indo-Pacific, its native distribution range does not include the Red Sea (i.e., natural dispersion via the Suez Canal is not a plausible explanation; Mariani *et al.*, 2018).

The coral *O. patagonica*, together with *Tubastraea* spp., was first recorded in the Canary Islands on artificial substrates in the two principal commercial harbors (Gran Canaria and Santa Cruz de Tenerife), and their invasion has been related to the sea transport of large oil platforms (López *et al.*, 2019). Similarly, *O. patagonica* was first recorded in several natural locations near the commercial harbor of Veracruz (Gulf of Mexico), and its introduction could have been caused by accidental transportation as a fouling organism on the hull of ships or as larval stages in ballast water (García *et al.*, 2018). Interestingly, the maintenance activities of oil platforms in Canary Islands harbors began in the early 2010s, a few years before coral invasions, and the platforms come mainly from the western Atlantic and the Mediterranean Sea, areas where both species occur (Pajuelo *et al.*, 2016; López *et al.*, 2019). Despite only *Tubastraea* spp. being found fouling the transported oil platforms to the Canary Islands, the concomitant invasion of *O. patagonica* suggests that both species were introduced throughout fouling on slow-moving vessels and platforms (Creed *et al.*, 2017; López *et al.*, 2019). Usual maritime routes for recreational boats to cross the Atlantic toward the tropical western Atlantic include a stop in the Canary Islands, a shipping route that matches the current geographic distribution of *O. patagonica*. Additionally, the locations in the Canary Islands and the Gulf of Mexico where *O. patagonica* has been recorded are harbors with major cargo-handling facilities characterized by heavy maritime traffic, or natural locations nearby (García *et al.*, 2018; López *et al.*, 2019). Therefore, the transoceanic transport of *O. patagonica* as a fouling organism on the hulls of ships and floating structures appears to be a likely vector of introduction contributing to explaining the large-scale spread and secondary introductions documented in this range-expanding zooxanthellate coral. Further studies assessing the presence of invasive species on the hulls of boats and other floating mobile structures are required to determine the importance of shipping as a dispersal vector and to improve management actions. The capacity of *O. patagonica* to form dense colony aggregations and drive regime shifts from macroalgal- to coral-dominated states at invaded high-latitude shallow rocky reefs is consistent with the ongoing phenomenon of coral-mediated tropicalization of shallow-water rocky ecosystems documented in other subtropical and temperate areas under current global change (Vergés *et al.*, 2014). The fact that the role of biological invasions on global environmental change is becoming unprecedented (e.g., Molnar *et al.*, 2008, Hulme, 2009) and that vessel hull fouling has been documented to be an important vector of dispersal (Anderson *et al.*, 2015) points to the need for the International Maritime Organization Biofouling guidelines (IMO, 2011) to no longer be recommended practices but becoming mandatory.

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Declarations

Conflicts of interest: We declare no conflicts of interest associated with this manuscript. **Availability of data and material:** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. **Code availability:** Not applicable**. Authors' contributions:** All authors contributed to the study conception and design, performance of fieldwork and analysis of data. The first draft of the manuscript was written by Eduard Serrano and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. **Ethics approval:** All applicable international, national and/or institutional guidelines for water sampling were followed and all necessary approvals have been obtained.

References

Anderson, L.G., Rocliffe, S., Haddaway, N.R., Dunn, A.M., 2015. The role of tourism and recreation in the spread of non-native species: a systematic review and meta-analysis. *PloS ONE* 10(10):e0140833.

Armoza-Zvuloni, R., Segal, R., Kramarsky-Winter, E., Loya, Y., 2011. Repeated bleaching events may result in high tolerance and notable gametogenesis in stony corals: *Oculina patagonica* as a model. *Marine Ecology Progress Series*, 42, 149-159.

Armoza-Zvuloni, R., Kramarsky-Winter, E., Rosenfeld, H., Shore, L.S., Segal, R. *et al.*, 2012. Reproductive characteristics and steroid levels in the scleractinian coral *Oculina patagonica* inhabiting contaminated sites along the Israeli Mediterranean coast. *Marine Pollution Bulletin*, 64, 1556-1563.

Bachetarzi, R., Rebzani-Zahaf, C., Benabdi, M., 2016. Biodiversity marine assessment of 'Agueli Island' (Wilaya of Algiers), Algeria. *Rapport Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 41, 446.

Ballesteros, E., 1998. Addicions a la fauna d'invertebrats bentònics marins de l'Arxipèlag de Cabrera (Illes Balears, Mediterrània Occidental). *Bolletí de la Societat d'Història Natural de les Balears*, 41, 41-48.

Bertelsen, E., Ussing, H., 1936. Marine tropical animals carried to the Copenhagen Sydhavn on a ship from the Bermudas. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kobenhavn*, 100, 237-245.

Bitar, G., Zibrowius, H., 1997. Scleractinian corals from Lebanon, Eastern Mediterranean, including a non-lessepsian invading species (Cnidaria: Scleractinia). *Scientia Marina*, 61, 227-231.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P. *et al.*, 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26, 333-339.

Blakeslee, A.M.H., Canning-Clode, J., Lind, E.M., Quilez-Badia, G., 2011. Biological invasions in the 21st century: ecological impacts, predictions, and management across land and sea. *Environmental Research*, 111, 891-892.

Brito, A., López, C., Ocaña, Ó., Herrera, R., Moro, L. *et al.*, 2017. Colonización y expansión en Canarias de dos corales potencialmente invasores introducidos por las plataformas petrolíferas. *Vieraea*, 45, 65-82.

Brooke, S., Young, C.M., 2005. Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. *Marine Biology*, 146, 665-675.

Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology*, 47, 26-35.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S. *et al.*, 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334, 652-655.

Capel, K.C.C., Migotto, A.E., Zilberberg, C., Kitahara, M.V., 2014. Another tool towards invasion? Polyp 'bail-out' in *Tubastraea coccinea*. *Coral Reefs*, 33, 1165.

Cardeccia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B.S., Gollasch, S. *et al.*, 2016. Assessing biological invasions in European Seas: biological traits of the most widespread non-indigenous species. *Estuarine, Coastal and Shelf Science*, 201, 17-28.

Chartosia, N., Anastasiadis, D., Bazairi, H., Crocetta, F., Deidun, A. *et al.*, 2018. New Mediterranean Biodiversity Records (July 2018). *Mediterranean Marine Science*, 19, 398-415.

Clarke Murray, C., Pakhomov, E.A., Therriault, T.W., 2011. Recreational boating: a large unregulated vector transporting marine invasive species. *Diversity and Distributions*, 17, 1161-1172.

Costello, M.J., Dekeyzer, S., Galil, B.S., Hutchings, P., Katsanevakis, S. *et al.*, 2021. Introducing the World Register of Introduced Marine Species (WRiMS). *Management of Biological Invasions*, 12, 792-811.

Coma, R., Serrano, E., Linares, C., Ribes, M., Díaz, D. *et al.*, 2011. Sea urchins predation facilitates coral invasion in a marine reserve. *PloS ONE* 6(7):e22017.

Creed, J.C., Fenner, D., Sammarco, P., Cairns, S., Capel, K. *et al.*, 2017. The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors. *Biological Invasions*, 19, 283-305.

Cutajar, M., Evans, J., Borg, J.A., Abela, H., Schembri, P. J., 2020. Distribution, abundance and colony size of the invasive coral *Oculina patagonica* de Angelis, 1908 (Cnidaria, Scleractinia) in Malta. *BioInvasions Records*, 9, 737-744.

Cvitković, I., Despalatović, M., Nikolić, V., Žuljević, A., 2013. The first record of *Oculina patagonica* (Cnidaria, Scleractinia) in the Adriatic Sea. *Acta Adriatica*, 54, 87-92.

Çinar, M.E., Bilecenoglu, M., Öztürk, B., Can, A., 2006. New records of alien species on the Levantine coast of Turkey. *Aquatic Invasions*, 1, 84-90.

Dailianis, T., Akyol, O., Babali, N., Bariche, M., Crocetta, F. *et al*., 2016. New Mediterranean biodiversity records (July 2016). *Mediterranean Marine Science*, 17, 608-626.

Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., Côté, I.M., 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, 15, 1378-1386.

Essl, F., Dullinger, S., Genovesi, P., Hulme, P.E., Jeschke J.M. *et al.*, 2019. A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience*, 69, 908-919.

Fernandes, J.A., Santos, L., Vance, T., Fileman, T., Smith, D. *et al.*, 2016. Costs and benefits to European shipping of ballast-water and hull-fouling treatment: impacts of native and non-indigenous species. *Marine Policy*, 64, 148-155.

Ferrario, J., Marchini, A., Borrelli, P., Berzolari, F.G., Occhipinti-Ambrogi, A., 2016. A fuzzy 'boater' model to detect fouling and spreading risk of nonindigenous species by recreational boats. *Journal of Environmental Management*, 182, 198-207.

Fine, M., Zibrowius, H., Loya, Y., 2001. *Oculina patagonica*: a non-lessepsian scleractinian coral invading the Mediterranean Sea. *Marine Biology*, 138, 1195-1203.

Galil, B.S., 2012. Truth and consequences: the bioinvasion of the Mediterranean Sea. *Integrative Zoology*, 7, 299-311.

Galil, B.S., Marchini, A., Occhipinti-Ambrogi, A., Minchin, D., Narščius, A. *et al.*, 2014. International arrivals: widespread bioinvasions in European Seas. *Ethology, Ecology & Evolution*, 26, 152-171.

García, N.A.C., Campos, J.E., Tello-Musi, J.L., Pérez-España, H., Chiappa-Carrara, X., 2018. First record of the invasive coral *Oculina patagonica* de Angelis, 1908 (Cnidaria, Scleractinia) in the Gulf of Mexico. *Check List*, 14, 613-617.

Glynn, P.W., Colley, S.B., Maté, J.L., Cortés, J., Guzman, H.M. *et al.*, 2008. Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the Equatorial Eastern Pacific: Part V. Dendrophylliidae. *Marine Biology*, 153, 529-544.

González-Gándara, C., Domínguez-Barradas, C., De la Cruz-Francisco, V., Solís-Marín, F.A., Carricart-Ganivet, J.P., 2015. *Esponjas, corales escleractinios, equinodermos y peces de arrecifes coralinos del norte y sur de Veracruz*. Universidad Veracruzana, Informe final SNIB-CONA BIO, proyecto No. JF124, México D.F., 57 pp.

Grimes, S., Benabdi, M., Babali, N., Refes, W., Boudjellal-Kaidi, N. *et al.*, 2018. Biodiversity changes along the Algerian coast (Southwest Mediterranean basin): from 1834 to 2017: a first assessment of introduced species. *Mediterranean Marine Science*, 19, 156-179.

Harrison, P.L., 2011. Sexual reproduction of scleractinian corals. p. 59-85. In: *Coral reefs: an ecosystem in transition*. Dubinsky, Z. & Stambler, N. (Eds). Springer, Dordrecht.

Hoeksema, B.W., Roos, P.J., Cadée, G.C., 2012. Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam. *Marine Ecology Progress Series*, 445, 209-218.

Hoeksema, B.W., Pedoja, K., Poprawski, Y., 2018. Long-distance transport of a West Atlantic stony coral on a plastic raft. *Ecology*, 99, 2402-2404.

Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46, 10-18 .

Iacarella, J.C., Lyons, D.A., Burke, L., Davidson, I.C., Therriault, T.W. *et al.*, 2020. Climate change and vessel traffic create networks of invasion in marine protected areas. *Journal of Applied Ecology*, 57, 1793-1805.

IMO, 2011. *2011 Guidelines for the control and management of ship's biofouling to minimize the transfer of invasive aquatic species*. International Maritime Organization, MEPC 62/24/Add.1 https://wwwcdn.imo.org/localresources/en/OurWork/Environment/Documents/RESOLUTIONMEPC.207%5B62%5D.pdf

Israely, T., Banin, E., Rosenberg, E., 2001. Growth, differentiation and death of *Vibrio shiloi* in coral tissue as a function of seawater temperature. *Aquatic Microbial Ecology*, 24, 1-8.

Jokiel, P.L., 1984. Long distance dispersal of reef corals by rafting. *Coral Reefs*, 3, 113-116.

Jones, G.P., Almay, G.R., Russ, G.R., Sale, P.F., Steneck, R.S. *et al.*, 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs*, 28, 307-325.

Katsanevakis, S., Zenetos, A., Belchior, C., Cardoso, A.C., 2013. Invading European Seas: assessing pathways of introduction of marine aliens. *Ocean & Coastal Management*, 76, 64-74.

Kramarsky-Winter, E., Fine, M., Loya, Y., 1997. Coral polyp expulsion. *Nature*, 387, 137.

Lamouti, S., Bachari, N.E.I., 2011. Records of alien species along the Algerian coast. In: *7th International Conference on Marine Bioinvasions*, *Barcelona, 23-25 August 2011*. ICMB, Barcelona.

Lamouti, S., Rebzani-Zahaf, C., Bachari, N.E.I., 2011. Répartition de deux espèces introduites à caractère invasif dans la région centre de la côte algéroise: *Caulerpa racemosa* et *Oculina patagonica*. p. 361-366. In: *2nd Coastal and Maritime Mediterranean Conference*, Tanger, *22-24 November2011*. REVUE PARALIA.

Leydet, K.P., Hellberg, M.E., 2015. The invasive coral *Oculina patagonica* has not been recently introduced to the Mediterranean from the western Atlantic. *BMC Evolutionary Biology*, 15, 79.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, 20, 223-228.

López, C., Clemente, S., Moreno, S., Ocaña, O., Herrera, R. *et al.*, 2019. Invasive *Tubastraea* spp. and *Oculina patagonica* and other introduced scleractinians corals in the Santa Cruz de Tenerife (Canary Islands) harbor: ecology and potential risks. *Regional Studies in Marine Science*, 29, 100713.

Mariani, S., Vicente Ocaña, O., Lopez-Sendino, P., García, M., Ricart, A.M. *et al.*, 2018. The zooxanthellate scleractinian coral *Oulastrea crispata* (Lamarck, 1816), an overlooked newcomer in the Mediterranean Sea? *Mediterranean Marine Science*, 19, 589-597.

Martinez, S., Bellworthy, J., Ferrier-Pagès, C., Mass, T., 2021. Selection of mesophotic habitats by *Oculina patagonica* in the Eastern Mediterranean Sea following global warming. *Scientific Reports*, 11, 1-15.

Millot, C., 2005. Circulation in the Mediterranean Sea: evidences, debates and unanswered questions. *Scientia Marina*, 69, 5-21.

Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6, 485-492.

Moreno, D., 2010. Flora y fauna alóctona del medio marino andaluz. p. 215-229. In: *Especies exóticas invasoras en Andalucía-Talleres provinciales 2004-2006*. Cobos-Aguirre, F.J., Ortega, F. (Eds). Junta de Andalucía, Consejería de Medio Ambiente.

Nunes, F.L.D., Norris, R.D., Knowlton, N., 2011. Long distance dispersal and connectivity in amphi-Atlantic corals at regional and basin scales. *PLoS ONE* 6(7):e22298.

Pajuelo, J.G., González, J.A., Triay-Portella, R., Martín, J.A., Ruiz-Díaz, R. *et al.*, 2016. Introduction of non-native marine fish species to the Canary Islands waters through oil platforms as vectors. *Journal of Marine Systems*, 163, 23-30.

Rech, S., Salmina, S., Borrell-Pichs, Y.J., García-Vazquez, E., 2018. Dispersal of alien invasive species on anthropogenic litter from European mariculture areas. *Marine Pollution Bulletin*, 131, 10-16.

Rebzani-Zahaf, C., Otsmane, A.K., Benali, M., Hellel, R.B., 2013. Scleractinian *Oculina patagonica* de Angelis, 1908: El-Kala Algeria. *Rapport Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 40, 695.

Rubio-Portillo, E., Vázquez-Luis, M., Izquierdo-Muñoz, A., Ramos-Esplá, A.A., 2014. Distribution patterns of alien coral *Oculina patagonica* De Angelis D'Ossat, 1908 in western Mediterranean Sea. *Journal of Sea Research*, 85, 372-378.

Salomidi, M., Katsanevakis, S., Issaris, Y., Tsiamis, K., Katsiaras, N., 2013. Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. *Biological Invasions*, 15, 1961-1971.

Sammarco, P.W., Brazeau, D.A., Sinclair, J., 2012. Genetic connectivity in scleractinian corals across the northern Gulf of Mexico: oil/gas platforms, and relationship to the Flower Garden Banks. *PLoS ONE* 7(4):e30144.

Sartoretto, S., Harmelin, J.G., Bachet, F., Bejaoui, N., Lebrun, O. *et al.*, 2008. The alien coral *Oculina patagonica* De Angelis 1908 (Cnidaria; Scleractinia) in Algeria and Tunisia. *Aquatic Invasions*, 3, 173-180.

Serrano, E., Coma, R., Ribes, M., 2012. A phase shift from macroalgal to coral dominance in the Mediterranean. *Coral Reefs*, 31, 1199.

Serrano, E., Coma, R., Ribes, M., Weitzmann, B., García, M. *et al.*, 2013. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. *PLoS ONE* 8(1):e52739.

Serrano, E., Ribes, M., Coma, R., 2017. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean. *Coral Reefs*, 36, 27-38.

Serrano, E., Ribes, M., Coma, R., 2018. Demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters. *Science of the Total Environment*, 634, 1580-1592.

Simberloff, D., 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution and Systematics*, 40, 81-102.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A. *et al.*, 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28, 58-66.

Templado, J., Calvo, M., Moreno, D., Flores, A., Conde, F., *et al.*, 2006. Comunidades bentónicas. p. 51-152. In: *Flora y fauna de la Reserva Marina y Reserva de Pesca de la Isla de Alborán*. Templado, J., Calvo, M. (Eds). Ministerio de Agricultura, Pesca y Alimentación-Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas, Madrid.

Terrón-Sigler, A., Casado-Amezúa, P., Torre, F.E., 2015. Abundance and distribution of the rapid expansive coral *Oculina patagonica* in the Northern Alborán Sea (Western Mediterranean). *Marine Biodiversity Records*, 8:e45.

Terrón-Sigler, A., Peñalver-Duque, P., León-Muez, D. 2016. *Oculina patagonica*: un coral nativo del Mediterráneo ¿con un comportamiento invasivo? *Chronica Naturae*, 6, 33-38.

Tsirintanis, K., Azzurro, E., Crocetta, F., Dimiza, M., Froglia, C. *et al.*, 2022. Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea. *Aquatic Invasions*, 17, 308-352.

Valéry, L., Fritz, H., Lefeuvre, J.C., 2013. Another call for the end of invasion biology. *Oikos*, 122, 1143-1146.

Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H. *et al.*, 2014. The tropicalization of temperate marine ecosystems:climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281, 201408.

Ulman, A., Ferrario, J., Forcada, A., Seebens, H., Arvanitidis, C. *et al.*, 2019. Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. *Journal of Applied Ecology*, 56, 2620-2629.

Zabala, M., Ballesteros, E., 1989. Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Scientia Marina*, 53, 3-17.

Zaquin, T., Zaslansky, P., Pinkas, I., Mass, T., 2019. Simulating bleaching: long-term adaptation to the dark reveals phenotypic plasticity of the Mediterranean Sea coral *Oculina patagonica*. *Frontiers in Marine Science*, 6, 662.

Zenetos, A., Gofas, S., Morri, C., Rosso, A., Violanti, D. *et al.*, 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, 13, 328-352.

Zenetos, A., Çinar, M.E., Crocetta, F., Golani, D., Rosso, A., 2017. Uncertainties and validation of alien species catalogues: the Mediterranean as an example. *Estuarine, Coastal and Shelf Science*, 191, 171-187.

Zibrowius, H., 1974. *Oculina patagonica*, scléractiniaire hermatypique introduit en Méditerranée. *Helgoländer Wissenshaftliche Meeresuntersuchungen*, 26, 153-173.

Zibrowius, H., Ramos, A., 1983. *Oculina patagonica*, scléractiniaire exotique en Méditerranée- nouvelles observations dans le Sud-Est de l'Espagne. *Rapport Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 28, 297-301.