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Abstract

Invasive species often severely impact ecosystems and human activities in the areas that they invade. Lionfishes (*Pterois miles* and *P. volitans*) are regarded as the most successful invasive fishes in marine ecosystems. In the last 40 years, these Indo-Pacific predators have colonised the tropical western Atlantic Ocean, with well-documented detrimental effects on the local fish communities. Around 10 years ago, a second invasion began in the Mediterranean Sea. Given the invasive potential of lionfish and the fact that the ecology and biodiversity of the temperate/sub-tropical Mediterranean offer a different setting from the tropical western Atlantic, specific knowledge on this second invasion is needed. Here, we (i) provide a citizen science-based update on the location of the invasion front in the Mediterranean, (ii) review the scientific knowledge available on the ecology of invasive lionfish, (iii) discuss such knowledge in the context of invasion ecology and (iv) suggest future research avenues on the lionfish invasion in the Mediterranean. While the history and development of the Mediterranean invasion are resolved and some mitigation plans have been implemented locally, the study of the interactions of lionfish with Mediterranean species and their impact on the local biodiversity is in its infancy. Closing this gap will lead to important fundamental insights in invasion ecology and will result in predictions on the impact of lionfish on the ecology and ecosystem services of the Mediterranean. Such information will

have practical implications for policy makers aiming to devise sound and efficient mitigation plans.

Introduction

Invasive species are species that establish and spread in a new range at a high colonisation rate (Ricciardi 2013), often with detrimental effects on the local ecosystems. Invasive species can cause environmental degradation (Anderson and Rosemond 2007, Ehrenfeld 2010, Villamagna and Murphy 2010), carry and spread parasites (Gozlan et al. 2005, Iglesias et al. 2015) and compete for resources with native species (Bergstrom and Mensinger 2009, Polo-Cavia et al. 2010). Among the most severe ecological problems associated with biological invasions is biodiversity loss through local extinction of native species. This is particularly relevant when there is a direct trophic interaction between invader and local species. For example, invasive mammalian predators caused the extinction of more than 100 prey species worldwide (Doherty et al. 2016) and the invasion of Lake Victoria by the Nile perch (*Lates niloticus*) drove almost 200 endemic cichlids to extinction (Witte et al. 1992). Because of their dramatic ecological impacts, invasive species are regarded as one of the most serious environmental problems of our time (Ricciardi 2013).

The lionfishes *Pterois miles* and *P. volitans* (hereafter, lionfish) are the most invasive fishes in the marine realm (Côté and Smith 2018). Native to the Indo-Pacific Ocean and Red Sea, both species reached the western Atlantic Ocean through intentional or accidental releases by aquarists (Kulbicki et al. 2012, Côté and Smith 2018). Lionfish were first spotted in Atlantic waters in 1985 and became a common sight at certain locations in the late 1990s (Whitfield et al. 2002, Schofield 2009). Despite considerable control efforts at the local scale (de León et al. 2013, Dahl et al. 2016, Harris et al. 2019, 2020, Goodbody-Gringley et al. 2023), lionfish have colonised the entire tropical western Atlantic and continue to expand their invasive range along the Brazilian coast (Côté and Smith 2018, Soares et al. 2022, 2023). Lionfish are generalist predators (Green et al. 2011, 2014, Green and Côté 2014, D’Agostino et al. 2020) and are having a severe impact on the ecosystems of the western Atlantic by predating extensively on various local benthic and demersal fishes, including endemics of high conservation value (Albins and Hixon 2008, Green et al. 2012, 2014, Benkwitt 2015, Rocha et al. 2015, Ingeman 2016). Lionfish predation can reduce recruitment of juveniles and the biomass of local species by up to 65% (Albins and Hixon 2008, Green et al. 2012). Such marked effects on the local biodiversity have been associated with impacts on the stability of coral reef ecosystems and their degradation (Lesser and Slattery, 2011). More recently, a second lionfish invasion has begun in the Mediterranean Sea, which is being colonised by *P. miles* (Kletou et al. 2016, Bariche et al. 2017, Phillips and Kotrschal 2021). This second invasion raises concerns on possible impacts on the biodiversity and ecosystem services of the Mediterranean (Kletou et al. 2016, Savva et al. 2020).

The Mediterranean is a unique ecosystem: it is the largest enclosed sea on earth and a highly biodiverse basin home to more than 11000 animal species, some of which are found nowhere else in the world (Coll et al. 2010, Psomadakis et al. 2012). For example, of the approximately 540 native species of Mediterranean fishes, around 9% are endemic (Psomadakis et al. 2012). In addition, the sea provides economically valuable services to approximately 150 million people in the numerous countries on its coasts (Coll et al. 2010). At the same time, the Mediterranean biodiversity is suffering from many anthropogenic stressors (Bianchi and Morri 2000, Coll et al. 2010) and it is the most invaded sea in the world, largely due to the Suez Canal. The Suez Canal was dug in 1869 to connect the Mediterranean with the Red Sea for commercial purposes (Costello et al. 2021). Initially, there was little scope for invasions due to the small size of the canal and the presence of bitter lakes creating a hypersaline barrier between the two seas. However, the Suez Canal has been widened multiple times in recent years, increasing its capacity to carry propagules and reducing the salinity of the bitter lakes (Galil et al. 2017, Castellanos-Galindo et al. 2020). New species enter the Mediterranean every year and the Suez Canal is now the source of two thirds of the exotic species present in the basin (Galil et al. 2014, 2015, 2017, Fortič et al. 2023).

There are important differences between the Mediterranean and the tropical western Atlantic. The Mediterranean is a temperate/sub-tropical sea dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011, La Mesa et al. 2011, Kleitou et al. 2021). By contrast, the tropical western Atlantic is dominated by coral reefs, similarly to the native range of lionfish (Kulbicki et al. 2012, Côté and Smith 2018). The species composition and biodiversity of the Mediterranean are also profoundly different from those found in tropical seas (Kallianiotis et al. 2000, Brokovich et al. 2006, Albins and Hixon 2008, La Mesa et al. 2011). Given the invasive potential of lionfish and the fact that the ecology and biodiversity of the temperate/sub-tropical Mediterranean offer a different setting from the tropical western Atlantic, specific knowledge on this second invasion is needed. This information will be essential to understand and predict the impact of lionfish on the Mediterranean and to design rational and effective mitigation strategies. Here, we offer an update on the spread of lionfish in the Mediterranean and we review the available information on the ecology of this species. We discuss the current knowledge on lionfish ecology and their spread in the context of invasion ecology and highlight major knowledge gaps on the Mediterranean invasion that require future investigation.

Lionfish in the Mediterranean Sea

The origin and history of the invasion

The first lionfish ever reported in the Mediterranean was caught by a trawler off the coast of Israel in 1991 (Golani and Sonin 1992). From that moment, no more lionfish were reported until 2012, when two specimens were captured in Lebanon (Bariche et al. 2013). Soon after, lionfish were reported in Turkey, Cyprus, Greece and Italy (Turan et al. 2014, Crocetta et al. 2015, Iglésias and Frotté 2015, Oray et al. 2015, Turan and Öztürk 2015, Azzurro et al. 2017). Lionfish were first considered invasive in the Mediterranean in 2016, when they were reported in large groups and numbers in Cyprus (Kletou et al. 2016). Lionfish continue to expand their range westwards (Azzurro et al. 2017, Phillips and Kotrschal 2021) and have now established and successfully colonised large part of the eastern Mediterranean (Gökoğlu et al. 2017, Turan et al. 2017, Dimitriadis et al. 2020, Ulman et al. 2020, Vavasis et al. 2020). Genetic studies revealed that the lionfish found in the Mediterranean originate from the Red Sea and that they most likely entered their new range during multiple invasion events through the Suez Canal (Bariche et al. 2017). This origin of Mediterranean lionfish is corroborated by the absence of established populations of *P. volitans* in the basin; while both *P. miles* and *P. volitans* are found in the aquarium trade and, consequently, in the invaded western Atlantic, only *P. miles* is present in the Red Sea (Hamner et al. 2007, Kulbicki et al. 2012, Wilcox et al. 2018). Thus, the lionfish population of the Mediterranean is considered the result of *P. miles* entering through the Suez Canal and the reports of *P. volitans* in this sea (e.g., Gürlek et al. 2016, Gökoğlu et al. 2017; Ayas et al. 2018) are most likely the result of misidentifications or descriptions of individuals that came from isolated aquarium releases.

Today, invasive lionfish populations are confined to the eastern part of the Mediterranean (Dimitriadis et al. 2020, Phillips and Kotrschal 2021), with only sporadic sightings elsewhere.

The northernmost report of lionfish is that of an individual found near the island of Vis, in Croatia (Dragičević et al. 2021) while the westernmost lionfish was sighted in the Alboran Sea, Spain (Fortič et al. 2023). Since no established populations are present at these locations, the individuals in Croatia and Spain may be the result of isolated aquarium releases. The northernmost part of the Aegean Sea has also remained free from lionfish, probably due to the colder waters (Dimitriadis et al. 2020, Phillips and Kotrschal 2021).

Tracking an ongoing invasion

Lionfish entered the Mediterranean from one of its easternmost locations and continue to expand westwards and northwards (Bariche et al. 2017, Phillips and Kotrschal 2021), calling for continuous updates to pinpoint the location of their current invasion front. Citizen science is an effective tool to track the expansion of invasive species (López-Gómez et al. 2014, Larson et al. 2020, Hermoso et al. 2021). This is especially true for species such as lionfish; they are appreciated by divers for their attractive morphology and colouration, increasing the chances of citizens spotting and recognising them. Lionfish are also difficult to misidentify, especially in the Mediterranean, where closely related species (i.e., native scorpionfishes) have a markedly different appearance. Finally, the awareness among lay people and stakeholder on the invasiveness of lionfish is high (Kleitou et al. 2021), making divers attentive and willing to collaborate with scientists. Citizen science is therefore particularly suited to monitor the invasive range of lionfish in the Mediterranean, a sea where the diving industry is well established and dive centres are numerous (Phillips and Kotrschal 2021).

As a follow-up to Phillips and Kotrschal (2021), we contacted dive centres on the Mediterranean coast to ask whether they see lionfish during their dives and if they remember the first year that they saw them. We used a list of dive centres on the Mediterranean coast compiled in 2021 (Phillips and Kotrschal, 2021). From this list, we contacted all the dive centres that were still open and reachable via email in April 2023. In most countries, we sent emails in two languages: the first language spoken in the country and English. Translations into local languages were provided by native speakers. We sent emails in two languages to make our survey accessible to those who do not speak English fluently and to foreigners running dive centres in countries of which they do not speak the local language. Dive centres in Egypt, Albania, Montenegro, Malta and Israel were contacted only in English. We sent a reminder to every dive centre that did not respond within a week, and we recorded responses for four weeks after the reminder. We used the GPS coordinates of the location of dive centres as an estimation of the point where lionfish are seen as most dives are done in the waters close to a dive centre. Any response that we received in a language different from English were translated through Google translate. When a dive centre reported a range of years as an answer to the date of the first sighting (e.g., 2020-2021) we considered the most recent year in the range as year of first sighting. Data were analysed in RStudio (version 3.6.2, R Core Team, 2019). Maps were produced with the package ‘leaflet’ (version 2.0.4.1, Cheng et al., 2021).

Contacting 996 dive centres yielded 326 responses (Fig. 1A). Of these, 82 reported lionfish sightings, mostly in the eastern Mediterranean (Fig. 1B). Lionfish were seen by almost every dive centre that responded from Israel, Cyprus, Turkey, Greece, and Albania. The lionfish reported at the furthest locations from the Suez Canal were reported in Croatia (42.6513°N, 18.0608°E), Malta (35.9500°N, 14.4063°E) and the Italian islands of Sicily (36.7330°N, 15.1205°E) and Sardinia (40.5699°N, 8.2430°E). When compared with the results by Phillips and Kotrschal (2021) (Fig. 1C), our data show that, in just two years, lionfish have expanded their invasive range in the Mediterranean at two fronts: the northern Aegean Sea and the southern Adriatic Sea. While most of the dive centres reported no lionfish in 2021 in the northern part of the Aegean, they almost all did in 2023; the only two dive centres reporting no lionfish in the northern Aegean were also the ones with the northernmost coordinates. A limited expansion can be seen also in the southern Adriatic, where two dive centres reported lionfish sightings in 2023 while none did in 2021.

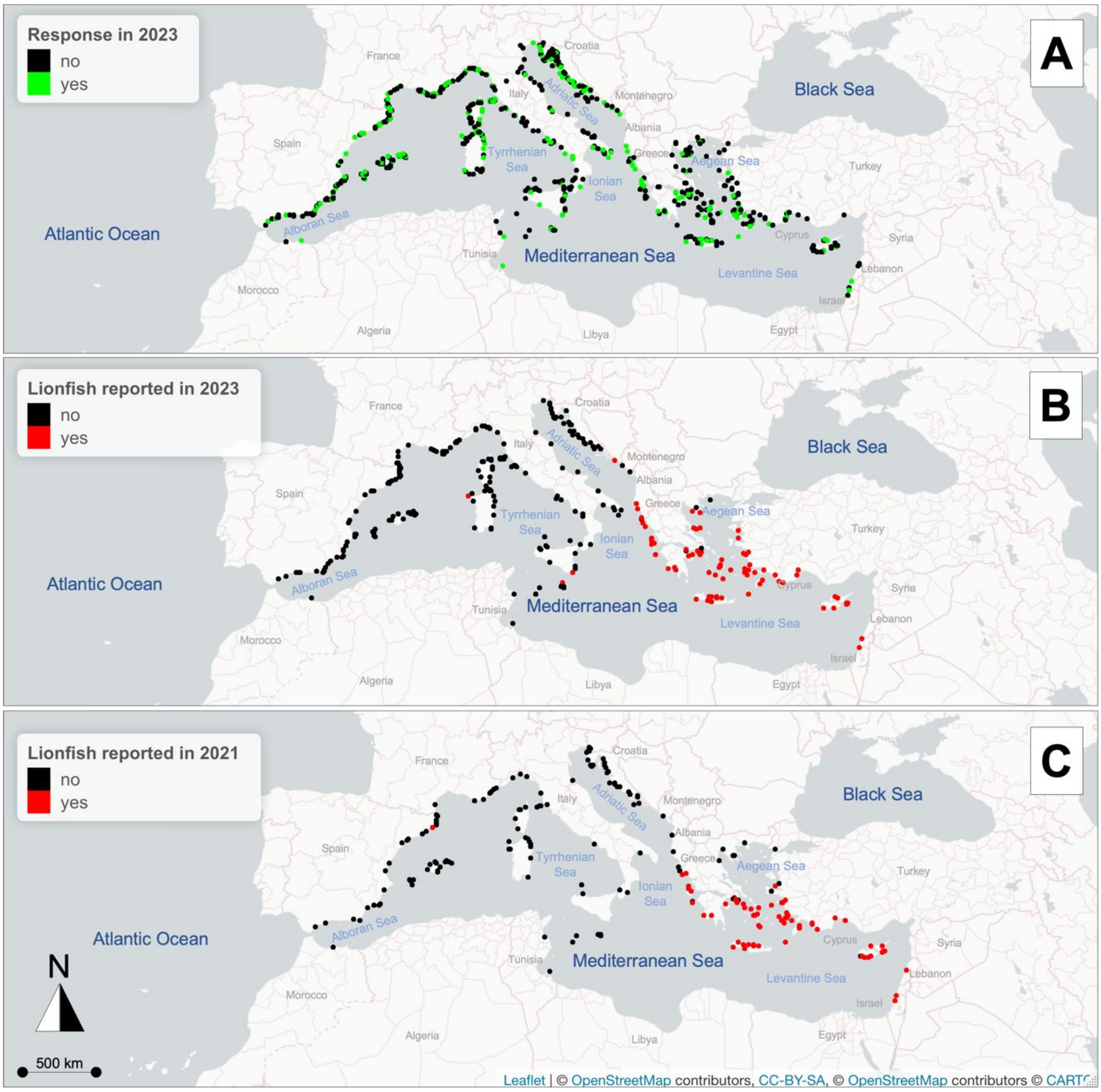

Figure 1. Maps of respondents and lionfish sighting. **A** map of respondents to our survey in 2023. Each dot represents a dive centre that we contacted, with green dots representing dive centres that responded and black dots representing dive centres that did not. **B** map of responses to our survey in 2023. Each dot represents a dive centre that responded to our survey in 2023 with red dots representing dive centres that reported lionfish sightings and black dots representing dive centres that reported no sightings. **C** map of responses to the survey in 2021 (Phillips and Kotrschal 2021). Each dot represents a dive centre that responded to the survey in 2021 with red dots representing dive centres that reported lionfish sightings and black dots representing dive centres that reported no sightings.

The years and locations where lionfish were first seen (Fig. 2) corroborate an expansion of the lionfish invasive range in the Mediterranean. Lionfish were first seen in the northern Aegean, Ionian Sea and southern Adriatic between 2020 and 2022. Individuals in Sicily, Sardinia, Croatia and Malta were also seen only in the most recent year range. This suggests that lionfish found at these locations are probably not just the results of aquarium releases; if that was the case, we could have also expected reports in the past. More likely, these individuals have been transported by strong currents from the eastern Mediterranean, either as larvae or eggs. It is important to note that none of the dive centres reporting lionfish in Malta, Italy and Croatia provided pictures and, therefore, misidentification is still a possibility for these sightings. The dive centres reporting sightings at these locations confirmed that there are no established lionfish populations there.

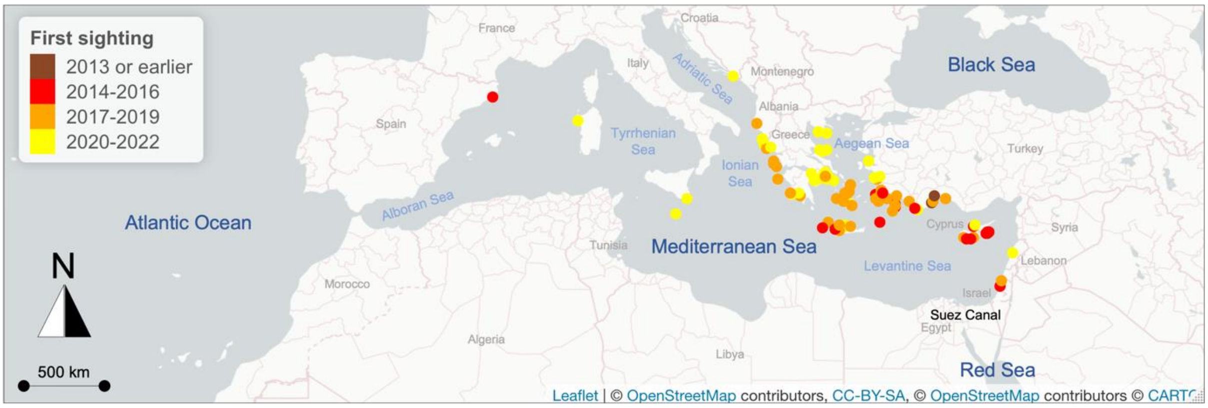

Figure 2. Map of years of first sighting. Map of years of first sighting. Each dot represents a dive centre that reported lionfish sightings, either in 2021 or 2023, and included in their response the year when lionfish were first sighted. The colour of a dot shows the year range when lionfish were first sighted.

Our results show that the invasive range of lionfish continues to expand rapidly in the Mediterranean. Similarly to most coral reef fishes, lionfish eggs hatch into pelagic larvae (Ahrenholz and Morris 2010, Vásquez-Yeomans et al. 2011). Larvae are the life stage with the highest dispersal potential in coral reef fishes (Shanks 2009) and are arguably the main contributor to the dispersal of lionfish, which are highly site-attached as adults (McCallister et al. 2018, Gavriel et al. 2021, Phillips et al. in review). Remarkably, several lionfish sightings were reported in areas that were considered to have minimum winter temperatures that are too cold for this species (northern Aegean and southern Adriatic) (Johnston and Purkis 2014, Dimitriadis et al. 2020), although it is too early to conclude that lionfish will establish at these locations.

With our study, we confirm that citizen science is a fruitful approach to monitor lionfish populations at the large scale in the Mediterranean, where the dive industry is strong and awareness towards lionfish is high. Different approaches are needed to monitor the state of the invasion on the southern coasts of the Mediterranean, where data is lacking, and the number of dive centres is extremely low (Fig. 1A). When we contacted members of a Libyan spearfishing association through social media, they reported seeing lionfish relatively frequently on the (eastern) Libyan coast. Moreover, lionfish were reported at several locations on the southern coast of the Mediterranean in the past, including Tunisia (Dailianis et al. 2016, Al Mabruk and Rizgalla 2019). This suggests that, as expected, the lionfish invasion and its expansion are not limited to the northern coast of the Mediterranean.

The evolutionary ecology of invasive lionfish across ranges

The to two species of invasive lionfish (*P. miles* and *P. volitans*) are virtually undistinguishable and show almost identical morphological and ecological traits (Kulbicki et al. 2012). Lionfish have a total of 18 venomous spines; one on each of the first 13 rays of their dorsal fin, one on each of their pelvic fins and three on their anal fin (Aktaş and Mirasoğlu 2017). They show high site fidelity and often return to the same hiding place over the course of several weeks (McCallister et al. 2018, Gavriel et al. 2021, Phillips et al. in review). Lionfish are often found, either individually or in small groups, hiding in caves and crevices during the day and swim in the open only at dawn and dusk to hunt for prey (Fishelson 1975, Cure et al. 2012, McCallister et al. 2018, D′Agostino et al. 2020, Gavriel et al. 2021). Although they have been reported to feed on invertebrates (Valdez-Moreno et al. 2012), fishes make up most of the lionfish diet (Barbour et al. 2010, Harms-Tuohy et al. 2016, Zannaki et al. 2019). Lionfish are stalking, gape-limited predators: they slowly follow their prey, sometimes for several minutes, with flared pectoral fins before striking and swallowing them whole (Green et al. 2011, Green and Côté 2014). They tend to prefer small, shallow-bodied benthic and demersal fishes in the Caribbean (Green and Côté 2014, Ritger et al. 2020) and show a similar prey preference in the Mediterranean, where they also adopt the same hunting strategy (Zannaki et al. 2019, D’Agostino et al. 2020). In their native range and the invaded Atlantic, lionfish are a widespread component of the community of coral reef predators (Lesser and Slattery 2011, Cure et al. 2012, Kulbicki et al. 2012, Côté and Smith 2018).

The eastern Mediterranean offers a markedly different habitat from the coral reefs of the Indo-Pacific and the tropical Atlantic (Kulbicki et al. 2012, Côté and Smith 2018). The

Mediterranean is a sub-tropical environment dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011, La Mesa et al. 2011, Kleitou et al. 2021). Despite these habitat differences, lionfish have established well in the Mediterranean and have already reached higher population densities than in their native range (Kulbicki et al. 2012, Phillips et al. in review). It is perhaps not surprising that lionfish are thriving in the eastern Mediterranean, as in the western Atlantic they have also been reported in habitats that are novel for this species, including mangrove forests, river estuaries and seagrass beds (Barbour et al. 2010, Jud et al. 2011, Claydon et al. 2012). Analysis of the population structure and dissections of females indicate that the Mediterranean population is reproducing and will remain a stable presence (Savva et al. 2020, Mouchlianitis et al. 2022).

In the Atlantic, lionfish can have strike success rates as high as 85%, the highest reported in animals in the wild (Vermeij 1982, Green et al. 2011). Such a high predation effectiveness in their invaded range has been attributed, at least in part, to prey naïveté (Côté and Smith 2018) (but see Cure et al. 2012). The ‘naïve prey hypothesis’ (or ‘prey naïveté hypothesis’) posits that prey that are exposed to an exotic predator are not prepared to recognise or effectively react to it due to a lack of coevolutionary history (Sih et al. 2010). Numerous studies support the relevance of prey naïveté in the lionfish invasion in the Atlantic. For instance, several prey species do not react to lionfish with the same readiness as they do with native predators (Anton et al. 2016, Haines and Côté 2019, McCormick and Allan 2016, but see Marsh-Hunkin et al. 2013). In the eastern Mediterranean, exotic prey species from the Red Sea, which coevolved with lionfish, are abundant and occur together with Mediterranean prey. Exotic prey show a markedly higher flight initiation distance when a lionfish is approaching them compared to Mediterranean species, supporting the hypothesis that prey naïveté is also relevant in the Mediterranean invasion (D′Agostino et al. 2020). Experiments on prey naïveté in the context of lionfish invasions raise the question of whether the selection pressure posed by this new predator will result in adaptations in local prey. It follows from the definition of prey naïveté that it can be counteracted by evolutionary adaptation: after a number of generations of coexistence with a novel predator, prey should evolve innate responses (Anton et al. 2020). But how rapidly can such evolutionary adaptations evolve in prey? This is an unresolved question: some estimates based on data on multiple taxa suggest that hundreds of generations are needed (Anton et al. 2020), while there is evidence showing that 10-30 generations can be enough for predators to drive evolutionary changes in prey (O’Steen et al. 2002, Nunes et al. 2014, Melotto et al. 2020). The great variability in the number of generations needed for local prey to evolve innate antipredator behaviours is probably explained by factors such as the pressure posed by predators and the genetic variability of prey populations (Nunes et al. 2014). The potential for prey to adapt to a new predator such as lionfish is of high scientific relevance but also has practical implications because it will determine the long-term effects on the local prey communities of the Mediterranean and western Atlantic. In an experiment in the western Atlantic (Kindinger 2015) the antipredator response of damselfish (*Stegastes planifrons*) to lionfish was measured and compared to that displayed against a control, native predator. Damselfish were generally naïve to lionfish, including individuals from populations that had coexisted with lionfish for three and seven years (Kindinger 2015). Local adaptation by lionfish prey has never been tested in the Mediterranean. Future studies should tackle whether prey can adapt to invasive lionfish by exploiting the ongoing lionfish invasions and considering populations with a wider range of years of coexistence with lionfish.

Prey naïveté interferes with innate predator recognition in animals (Sih et al. 2010, Anton et al. 2020). However, this is not the only mechanism resulting in prey reacting to a predator. Individual fishes can learn which species can pose a threat to their survival through associative learning (Kelley and Magurran 2003). Predator recognition can be learned either directly, when a fish escapes an attack from a predator, or indirectly when an individual observes predation events or associates the presence of a predator with the presence of danger-related cues (e.g. blood, stress pheromones) from other fishes (Brown 2003). Learned predator recognition is pervasive in fishes (Brown 2003, Kelley and Magurran 2003, Mitchell et al. 2011); prey fishes can learn to associate danger cues with the presence of a predator during a single conditioning event and retain a behavioural response to that predator for extended periods of time (Chivers and Smith 1994, 1995, Mitchell et al. 2011). Could native prey fishes compensate for their lack of innate responses to lionfish through learned predator recognition? This is an open question for both the Mediterranean and the Atlantic invasion. Specific work on how well prey species learn that lionfish pose a predation threat is limited to one study on a species from the native range of lionfish. This study suggests that even prey that coevolved with lionfish seem to have difficulties associating them with danger, while other predatory fishes can be learned more readily (McCormick and Allan 2016). This has led to the hypothesis that lionfish circumvent learned predator recognition mechanisms in prey (Côté and Smith 2018). Whether Mediterranean or western Atlantic prey can learn to recognise lionfish as predators is currently unknown and more research is needed to test for the relevance of circumvention of learned predator avoidance in lionfish prey.

The ‘enemy release hypothesis’ posits that exotic organisms benefit from reduced top-down control due to the paucity of natural enemies (e.g., predators, parasites) in their newly colonised ranges (Colautti et al. 2004). The success of lionfish as invaders has been attributed to the lack of natural predators in the areas that they invade (Côté and Smith 2018). However, the natural enemies and source of mortality of lionfish in their native range remain unknown. It seems unlikely that any predator feeds consistently on the venomous and spinous adult lionfish and events of predation remain sporadic and anecdotal, both in their native and invaded ranges (Côté and Smith 2018). The cornetfish *Fistularia commersonii*, and the groupers *Epinephelus striatus* and *Mycteroperca tigris* have been reported to feed on lionfish (Bernadsky and Goulet 1991, Maljković et al. 2008) and there is indication that large groupers may act as biological control agents in the Caribbean (Mumby et al. 2011). In the Mediterranean, the only convincing example of predation is that of an octopus (*Octopus vulgaris*) filmed while catching a lionfish in Cyprus (Crocetta et al. 2021). The scarce knowledge on lionfish predators limits any conclusions on the importance of relaxed predation as an explanation for the high invasiveness of lionfish.

There are other factors than reduced predation on adults that could explain the large population sizes that lionfish reach in their invaded ranges. First, parasites, rather than predators, could be limiting the fitness of adults in their native range (Tuttle et al. 2017). This is supported by data from studies that found relatively low numbers of parasites on invasive lionfish in the Atlantic compared to lionfish in the native Indo-Pacific (Loerch et al. 2015, Sellers et al. 2015, Tuttle et al. 2017). Such comparisons have not yet been performed in Mediterranean lionfish. Second, a main source of mortality for coral reef fishes is predation at or soon after settlement (Carr and Hixon 1995, Webster 2002, Almany and Webster 2006). Predation on larvae and settlement-stage juveniles could therefore be the main source of mortality for lionfish (Phillips and Kotrschal 2021). Lionfish larvae are pelagic and probably less defended than the adults (Kitchens et al. 2017) and could be prey of plankton feeders before settlement and demersal predators at settlement (Phillips and Kotrschal 2021). Relaxed predation on the larval and settlement stage could explain the lionfish population increase in their invaded ranges if there was a lower abundance of plankton feeders and predators than their native range. However, there are no studies comparing the mortality of settling lionfish between the invasive and native ranges of lionfish and any hypothesis involving lionfish larvae and juveniles is difficult to test due to a paucity of information on the reproductive biology of the species, which has never been observed spawning in the wild (Côté and Smith 2018).

The high effectiveness of lionfish as predators implies that they are a potential threat to the native fish community of the areas that they are invading. Lionfish are indeed having a profound impact on the fish community of the western Atlantic, where they predate heavily on numerous species of very high conservation value (Rocha et al. 2015, Ingeman 2016, Côté and Smith 2018). Invasive lionfish can dramatically reduce the biomass of local species in the Atlantic (Albins and Hixon 2008, Green et al. 2012, 2014), with hypothesised effects on the stability of coral reef ecosystems (Lesser and Slattery 2011). The impact of lionfish on the Mediterranean biodiversity has received little consideration. Preliminary assessments suggest that lionfish are reducing the abundance of certain native species and are therefore altering the community composition of the Mediterranean (Turan and Doğdu 2022). However, manipulative experiments directly linking lionfish density with the density of Mediterranean prey species are currently lacking.

Interactions with humans and control efforts

The high predation rates shown by lionfish raised concerns on their potential effects on economically valuable species and the fishing industry of the Mediterranean (Kleitou et al. 2019a). It is now well-established that lionfish do feed on economically valuable species such as *Spicara spp.* and *Sparisoma cretense* (Zannaki et al. 2019, D'Agostino et al. 2020, Savva et al. 2020). However, specific studies on the impact of lionfish on fisheries are completely lacking, both in the western Atlantic and Mediterranean. Such studies are difficult to conduct as they necessitate large areas and fish stocks are simultaneously subject to many other stressors such as overfishing, climate change and invasive species other than lionfish (Coll et al. 2010). In addition, the possibility of estimating the impacts of lionfish on Mediterranean fisheries is limited by the lack of knowledge on large-scale effects of lionfish on the Mediterranean biodiversity.

Lionfish are venomous and reach large population sizes in their invaded ranges (Kulbicki et al. 2012, Aktaş and Mirasoğlu 2017). Consequently, an additional concern around their invasions is that they could become a danger for bathing tourists, divers or fishermen (Kosker and Ayas 2022). Lionfish cannot actively sting and tend to move away when a swimmer approaches them closely (Côté et al. 2014). This probably explains why only few events of envenomation have been reported in the wild, both in the Mediterranean and western Atlantic. While there is no systematic analysis on lionfish-related accidents, most of the reported incidents in Cyprus involve people (usually fishermen) directly manipulating lionfish out of the water (Jimenez 2021 personal communication).

Lionfish are highly sedentary and easy to identify by divers due to their conspicuous appearance. This resulted in the involvement of local citizens in initiatives aimed at curbing lionfish populations through spearfishing. In so-called ‘culling tournaments’ (or ‘derbies’), citizens are encouraged to hunt for lionfish by means of spearguns (often simpler Hawaiian slings) while free or SCUBA diving (Kleitou et al. 2021). Fishing for lionfish has been incentivised by attempts to create a market for lionfish-derived products such as meat or jewellery (Kleitou et al. 2019b, Simnitt et al. 2020). While jewellery will probably remain a niche product, lionfish meat is appreciated for its taste and increasingly served in local restaurants in the invasive ranges of lionfish (Morris et al. 2011, Simnitt et al. 2020). Culling initiatives were shown to be an effective way of limiting lionfish populations at small scales in the western Atlantic and have the potential to become a management tool with beneficial effects on the conservation of local species (de León et al. 2013, Green et al. 2014, Dahl et al. 2016).

Culling tournaments were organised in the Mediterranean soon after the start of the invasion (Kleitou et al. 2021). Although culling can be effective at the local scale, eradication of lionfish from their invaded ranges is considered impossible for three reasons. First, the effort of having to actively spearfish for lionfish is high and limits the areas that can be covered in culling tournaments (de León et al. 2013, Malpica-Cruz et al. 2016, Kleitou et al. 2021). Second, culling initiatives are restricted to relatively shallow waters (0-40 m), while invasive lionfish can colonise much deeper waters, with large aggregations spotted even beyond 300 m of depth (de León et al. 2013, Nuttall et al. 2014, Gress et al. 2017, Rocha et al. 2018). Third, lionfish adjust to the hunting pressure posed by spearfishers by becoming more wary towards approaching divers, decreasing the effectiveness of repeated culling initiatives in the same areas (Côté et al. 2014). Culling should therefore be seen as a containment measure, rather than a definitive solution and should be focussed on areas of high ecological interest.

Conclusion and future research avenues

The history and development of the lionfish invasion in the Mediterranean are well-resolved and can be updated promptly through citizen science initiatives involving the aware and collaborative local dive centres (Phillips and Kotrschal 2021). Our update shows that lionfish keep expanding westwards and northwards and are also colonising waters that were considered too cold for them to live in. Future initiatives should keep monitoring the invasion front as lionfish can be expected to continue expanding. Such initiatives should consider approaches that include the southern coast of the Mediterranean. The high awareness of the lay public to the problem of invasive lionfish in the Mediterranean resulted in the organisation of successful control initiatives at an early stage of the invasion process (Kleitou et al. 2021). Fishing for lionfish has been encouraged by promoting the exploitation of lionfish as an economic resource, mainly for consumption of their meat (Morris et al. 2011, Kleitou et al. 2019b, Simnitt et al. 2020). While these initiatives can certainly have beneficial effects at the local scale and contribute to raise awareness towards the major problem of biological invasions, eradication of invasive lionfish is considered impossible.

Studies on the predation ecology of lionfish in the Mediterranean remain scant, especially in comparison with the large body of literature available on the Atlantic invasion (Côté and Smith 2018). Lionfish are thriving in the eastern Mediterranean and are feeding extensively on local fishes of ecological and commercial value (Zannaki et al. 2019, D'Agostino et al. 2020, Savva et al. 2020). However, the community-level impact of lionfish on the local biodiversity remains unknown. This is a major knowledge gap for ecologists and policy makers alike because lionfish feed on both ecologically and economically important species. While assessing the effect of invasive lionfish on the productivity of local fisheries is challenging due to the large scales needed and many confounders, it is possible to experimentally measure community-level effects of predation by lionfish (Albins and Hixon 2008, Green et al. 2012, 2014). Future manipulative experiments will elucidate the effects of invasive lionfish on the Mediterranean fish community.

Prey naïveté is a contributor to the success of lionfish in the Atlantic and Mediterranean, where native prey show virtually no response to this new predator (Anton et al. 2016, D'Agostino et al. 2020). This raises the question of how long it will take local prey to adapt to this new predator through evolutionary change. Invasive lionfish offer an opportunity to test for local adaptations in marine ecosystems, where adaptations to new predators are particularly understudied (Anton et al., 2020). While the high connectivity of marine systems was traditionally thought to limit the possibilities of local adaptations in marine fishes, increasing evidence is suggesting that local adaptation is widespread also in marine systems (Anton et al. 2020). The two ongoing lionfish invasions offer the potential to work with prey populations that have coexisted with lionfish for different lengths of time and can be therefore predicted to show different levels of local adaptation to lionfish.

Individual prey fishes have the potential to learn that lionfish are dangerous through associative learning, even in the absence of coevolutionary history (Brown 2003, Kelley and Magurran 2003). This would give prey an opportunity to rapidly adjust to the presence of new predator. The only study conducted on learned predator response to lionfish suggests that it is more difficult for prey to learn that lionfish are dangerous compared to other predators (McCormick and Allan 2016). Future studies should tackle the same question on prey species from the temperate Mediterranean to test whether the same phenomenon is at play. The alleged ability of lionfish to circumvent learned predator recognition in their prey raises the intriguing question of how they do so. These aspects of lionfish-prey interactions are relevant in the context of predation ecology and can be tested in controlled set-ups in future experiments.

Another major question on the ecology of lionfish, both in their native and invaded ranges, is what their main source of mortality is (Phillips and Kotrschal 2021). This is an important question which could help explain why lionfish reach such high population densities in their invaded ranges. It seems unlikely that any predators feed consistently on adult lionfish because they are well defended by venomous spines and reports of predation events are extremely rare (Côté and Smith 2018). Parasites have been shown to be more abundant on lionfish in their native range compared to the Atlantic, but it is unknown to what extent such parasites exert a control on lionfish population densities (Loerch et al. 2015, Sellers et al. 2015, Tuttle et al. 2017). Studies on lionfish parasites in the Mediterranean are lacking. Finally, lionfish could be preyed upon while in their larval or recruit stage but it is challenging to catch lionfish in high numbers before they are juveniles of a few centimetres in length. This is a critical limitation in the possibilities of directly testing the suitability of lionfish to the diet of plankton feeders (Ahrenholz and Morris 2010, Vásquez-Yeomans et al. 2011).

In conclusion, while the history and development of the lionfish invasion in the Mediterranean are well-resolved and can be easily updated through citizen-science initiatives, the study of the predation ecology of lionfish in the Mediterranean is its infancy, especially at high ecological levels. In addition, the ongoing lionfish invasions offer opportunities to test for major fundamental questions on prey naïveté and learned predator responses. Tackling questions such as the community-level impact of lionfish in the Mediterranean and the evolutionary and learned responses in prey will add to the body of knowledge on the best documented invasion in marine ecosystems. This will result in insights into fundamental questions in invasion and predation ecology, but will also be important for policy-makers to estimate the impact of invasive lionfish on human activities.

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Authors contributions

D.B. and A.K. conceived the study. D.B. collected the data. D.B. analysed the data and wrote the first version of the manuscript. All the authors (D.B., B.A.J.P., R.N., P.A.J., M.N. and A.K.) provided feedback on earlier versions of the manuscript and contributed to its final version.