Assessing the viability of complete lionfish eradication in the western Atlantic and Caribbean – Insights from past successes and failures within the marine environment

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Abstract

Over the past three decades, two species of lionfish (*Pterois volitans* & *P. miles*) have been introduced and become widespread in the western-Atlantic and Caribbean, resulting in one of the most devastating marine invasions to date. With a distinct advantage over competitors due to prey naïveté and few known predators, lionfish numbers have exploded at the cost of many native fish species. To prevent a collapse of the native system, scientists and involved parties have been searching for methods to control and preferably eradicate this exotic invader. In this study, a series of examples from past eradication attempts within the marine environment is used to gain useful insights on key elements leading towards success, as well as lessons learned from complete failures. These insights revealed two crucial factors to be providing a hindrance to success of lionfish eradication, being insufficient knowledge on species biology and biotic controls in their native range, together with a lack of tools and strategies for large-scale lionfish removals with minimal collateral damage. Until these constraints are dealt with, complete eradication cannot realistically be pursued and efforts should focus on protecting endangered species and mitigating effects within protected areas instead.

Finally, two potential future scenarios are discussed. Lionfish are either likely to stabilize in numbers and live in conjunction with native species through evolutionary adaptation of the latter, or provide a self-induced biotic control by exceeding the carrying capacity of the system. This study concludes by providing a link to a recent article about cannibalism amongst lionfish, indicating that the latter 'doom' scenario has possibly already been initiated.

CONTENT PAGE

1. Introduction

The ongoing invasion by two species of lionfish (*Pterois volitans* and *P. miles*) in the Northwestern Atlantic and Caribbean marks one of the most dramatic marine invasions in history. Popular mainly in the aquarium trade, the two species have made their way from their native range in the Indo-Pacific towards these vulnerable coastal waters, likely by means of release by dissatisfied aquarium owners (Whitfield et al. 2002; Semmens et al., 2004) and/or by hurricane Andrew destroying private aquaria in southeastern Florida in 1992 (Courtenay, 1995). Apart from sporadic observations by divers in 1994 (Hare & Whitfield, 2003), the first official report dates back from 2002 when the red lionfish (*P. volitans*) was reported to be established along the coast of North-Carolina (Whitfield et al., 2002). Interestingly, the similar-looking common lionfish (*P. miles*) had already been reported to be a Lessepsian migrator and invaded the Mediterranean Sea through the Suez Canal (Golani & Sonin, 1992). While the population of *P. miles* has remained somewhat stable in the Mediterranean (Galil, 2007), numbers of *P. volitans* in the Northwestern Atlantic have been growing exponentially over the past decade (Whitfield et al., 2007; Claydon et al., 2009) leading to increasing concern among scientists, coastal managers and fishing companies. Recent mitochondrial DNA analyses showed that, whereas both these species are confirmed to have invaded the U.S. East Coast, *P. volitans* comprises about 93% of the invaded population and a strong founder effect resulted in relatively low genetic diversity for both species, compared to their native range (Hamner, 2005; Hamner et al., 2007).

Lionfish, in general, are ornate, aposematic carnivores equipped with venomous dorsal spines serving as a defense mechanism. These crypto-benthic species are largely piscivorous, but have also been observed feeding on benthic invertebrates (Morris, 2009). A correlation was found between diet and body length, with the level of piscivory increasing with total body size (Morris & Akins, 2009). Lionfish are skilled hunters and use an array of strategies to attain a high predator efficiency, ranging from stalking and herding prey with their fanlike pectoral fins (Randall, 2005), to sit and wait ambushing or even blowing jets of water to confuse their prey (Albins & Lyons, 2012). They are also observed to perform communicative group hunting activities, during which they share resources and alert group members to the presence of prey by flared fin display (Lönstedd et al., 2014). These characteristics and feeding strategies have highly contributed to the invasion success of the lionfish in the Northwest Atlantic and Caribbean. With a low level of competition and few natural predators, lionfish experience very little biotic resistance and have undergone ecological release to the point of becoming one of the most harmful invasive species within the marine environment to date. In addition, native species show a high level of naïveté towards this recently introduced marine predator. Several studies (e.g. Albins & Hixon, 2008; Green et al. 2011) showed that native prey exhibit a weak or non-existing response towards lionfish, mainly since there is a lack of native predators that resemble lionfish characteristics. Beaugregory damselfishes, which were found to be among the few prey that do show responsive behavior (Black et al., 2014), were observed to fail in adapting their courtship ritual in the presence of lionfish, and as such still face substantial predation. Differences in hunting behavior and prey size were also observed, with lionfish in their native range relying three times more on jet blowing to confuse native wary prey which were mostly smaller in size (Cure et al., 2012). The relatively larger naïve prey in their invasive range can be obtained with remarkably less effort to greatly increase nutritional input at the same time. As such, prey naïveté remains an important factor contributing to the lionfish's success at this stage of the invasion, and will likely continue to be so until native prey will learn to implement appropriate responsive behavior through evolutionary adaptation.

The diet of lionfish in their invasive range consists mainly of small- to medium-sized reef fishes, with stomach contents revealing a variety of 40 species of at least 20 different families of fish (Morris & Akins, 2009). Long-term effects on reef populations are still unclear, but experiments on translocated reef patches in the Bahamas already showed a decrease in native fish recruitment of 79% in less than 5 weeks (Albins & Hixon, 2008). In one case, a single lionfish was even observed to consume 20 small wrasses (*Halichoeres bivittatus*) in just half an hour, showing their voracious appetite (Ibid.). Similarly, Green et al. (2012) found that a rapid increase in lionfish total biomass of 40% in the Bahamas coincided with a decline of 65% in biomass of 42 prey species in just under two years. Prey consumption has been shown to be highest during crepuscular periods for both their native and invaded range (Fishelson, 1997; Green et al. 2011). However, a report on daytime consumption rates on Bahamian reefs showed results far exceeding the rates for their native range (Côte & Maljkovic, 2010), where lionfish are mostly showing cryptic behavior during the day (Grubich et al., 2009).

Apart from the threat of reducing species richness and abundances, the success of the lionfish may bring along other unwanted side effects. By consistently preying on small herbivorous grazers which are of vital importance to sustain reef resilience (Lewis, 1986; Mumby, 2006), lionfish caused a rapid shift towards an algal dominated community at mesophotic depths in the Bahamas in less than three years (Lesser & Slattery, 2011). As a comparison, the effect of overfishing of important herbivorous fish in Jamaica at similar depths was noticeable only on decadal timescale (Hughes et al., 2010). Reef communities at mesophotic depths play the vital role of being refugia zones for many native species and this observed transition can reduce the resilience of these systems, as well as their contribution to the recovery of shallow-water taxa (Lesser & Slattery, 2011). Some final examples of negative side effects of the invasion include: consumption of important cleaner wrasses to increase parasitism and decrease the overall health level of reef communities (Albins, 2013), and an increase in encounters with fishermen, divers and recreational swimmers which brings along the risk of incidents and envenomation (Hare & Whitfield, 2003).

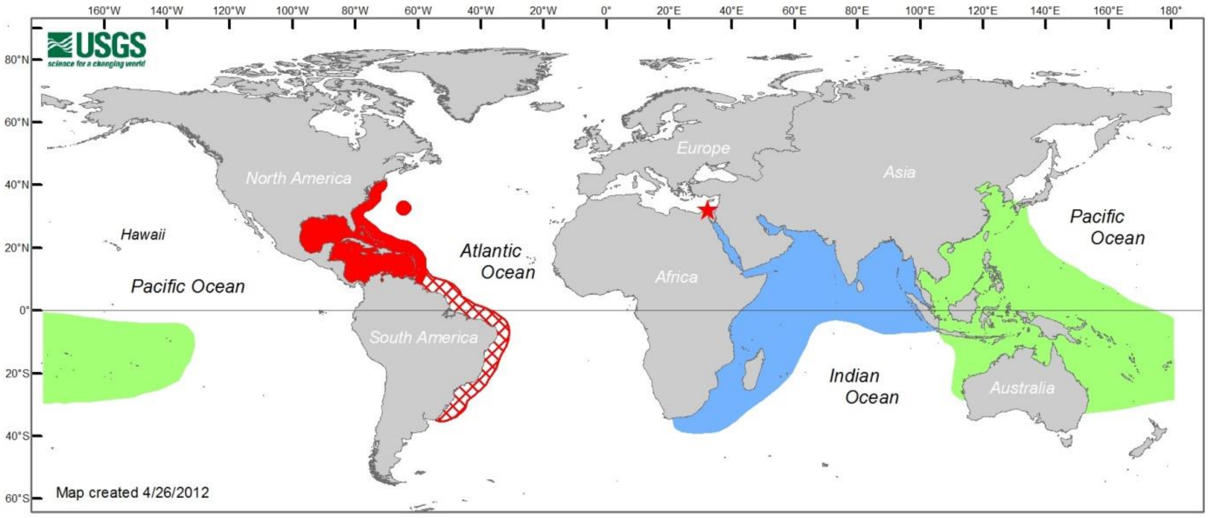

Fig. 1 – Map of native range of *P. volitans* (Green), *P. miles* (Blue) and the invaded range of both species (Red). The red star indicates the occurrence of *P. miles* as a Lessepsian migrator in the Mediterranean, and the red hatched area shows the potential future range of both species according to their lethal thermal minimum (Morris & Whitfield, 2009). Courtesy of the U.S. Geological Survey (USGS).

Pterois species can be found in a large variety of habitats, both in its native and invasive range, including coral reefs, sand bottoms, hard bottoms, submerged artificial structures, seagrass beds and mangroves (Kulbicki et al., 2011; Smith, 2010; Schofield et al., 2014), and a recent study even demonstrated their broad salinity tolerance, likely facilitating the colonization of estuarine environments (Jud et al., 2015). Distribution of the lionfish in its invaded range will likely be limited by its thermal tolerance (Kimball et al., 2004) and the potential 'worst-case' future range of the species was mapped according to its lethal thermal minimum of 10 °C by Morris & Whitfield (2009), likely gradually expanding as a result of global warming (Fig. 1).

Over the past decade, a collaboration of scientists, fishing companies and coastal managers have been looking for appropriate methods to take control on the lionfish invasion and preferably eradicate the species altogether, to prevent further harm to the ecosystem. Such efforts can be particularly risky, since it involves removing every single individual capable of reproducing which is often not feasible and can lead to substantial amounts of collateral damage (Simberloff, 2003).

In this literature study, some useful examples of eradication attempts from the past within the marine environment will be discussed. Important factors leading to a successful eradication of the invasive species will be analyzed and, where possible, compared to their current status for the lionfish invasion. In case of a failed attempt, the risks involved in undergoing such measures will become clear, together with the possible impact of the eradication failure to the ecosystem. Examples of full eradication of a marine invader are scarce, since the wide geographic and broad depth range of the ocean makes monitoring of species and performing targeted removals extremely difficult. Yet, there are examples in which human intervention prevented marine invaders to become dominant and harmful within their invaded range, and factors leading up to these successes likely yield valuable implications for the lionfish invasion. On the other hand, aiming for full eradication can be risky and without the proper management and communication, can lead to extremely high costs without ever reaching the desired goal.

The aim of this study is to come to a consensus as to whether full eradication is feasible at this stage of the lionfish invasion. Insights from past cases will be used to assess both the potential of current efforts and the risks involved. In the final section, a perspective of potential future scenarios will be discussed regarding the lionfish populations of the western Atlantic and the Caribbean.

2. Examples of eradication attempts of marine invaders

In the following section, a couple of examples of eradication attempts within the marine environment will be discussed. The first two examples involve cases in which the attempts turned out to be successful in eradicating the invading species. The specific methods used are evidently species-specific, yet the level of strategic planning and execution of the appropriate response often applies to marine invasions in general, and will undoubtedly yield important implications for the lionfish invasion. The third and fourth example represent eradication failures, but with two very different implications. As is true for a success, a failure can also provide future cases with useful insights, e.g. on what elements to improve, or on the potential risks of aiming at complete species eradication. All these important factors will contribute to the discussion about the efficacy of human efforts to take control in the ongoing lionfish invasion, which will be dealt with in section 3.

2.1 *Perna perna* – Detection and successful eradication of a brown mussel in New-Zealand

The first example involves the dredge-based eradication of *P. perna* at a 44m deep soft bottom in Central New-Zealand. This species of brown mussel, native to Africa and South America, was discovered on a semi-submergible drilling rig in late 2007 prior to departure for Australia (Hopkins & Forrest, 2010). Subsequent defouling measures that took place in Central New-Zealand had unwillingly transferred the risk towards the sea bed around the defouling site, where this non-indigenous species now became established (Hopkins et al., 2011). Multiple eradication strategies were proposed, of which dredging, i.e. removal of the sediment and debris from the bottom, was considered to be the most viable option (Ibid.). The goal of the eradication efforts was not to aim for a zero density goal, as is often the strategy of pest control efforts (e.g. Bax et al., 2002; or species able to reproduce asexually), but rather to remove the target below the density required for successful reproduction.

Previous knowledge on the reproductive biology of the invasive species proved imperative here, as *P. perna* is a dioecious species, i.e. colonies containing either male or female individuals, which were found to require close proximity for successful fertilization (Hopkins et al., 2011). Sufficiently lowering the species density beyond the threshold thus proved successful in preventing further reproduction. In general, several elements were recognized to have contributed to the success, being: 1) early detection and quick decision making, 2) sufficient resources to complete the program, 3) appropriate and effective control procedures for the specific target, 4) knowledge of the species biology, 5) the ability to detect and remove all invasive organisms, or reduce their density towards levels in which they are unable to sustain themselves, and finally 6) prevention of reinvasion (Ibid.). Although all these necessary requirements were met in this particular example, they were already previously recognized by Coutts & Forrest (2007), as their inability to meet several of these requirements lead to the eventual failure of their removal efforts and resulted in substantial costs (discussed in more detail in section 2.4).

2.2 *Terebrasabella heterouncinata* – Apparent eradication of a polychaete sp. in California

Another small-scale example of a successful eradication in a marine habitat took place in 1996 in California. The previously unknown species of sabellid polychaete, now described as *T. heterouncinata*, was introduced through commercial aquaculture as a contaminant on South-African abalone (Culver & Kuris, 2000). These boring organisms proved particularly harmful to the abalone by deforming the shell structure (Fig. 2), leading to reduced growth and increased mortality rates (Ruck et al., 1998; Oakes & Fields, 1996).

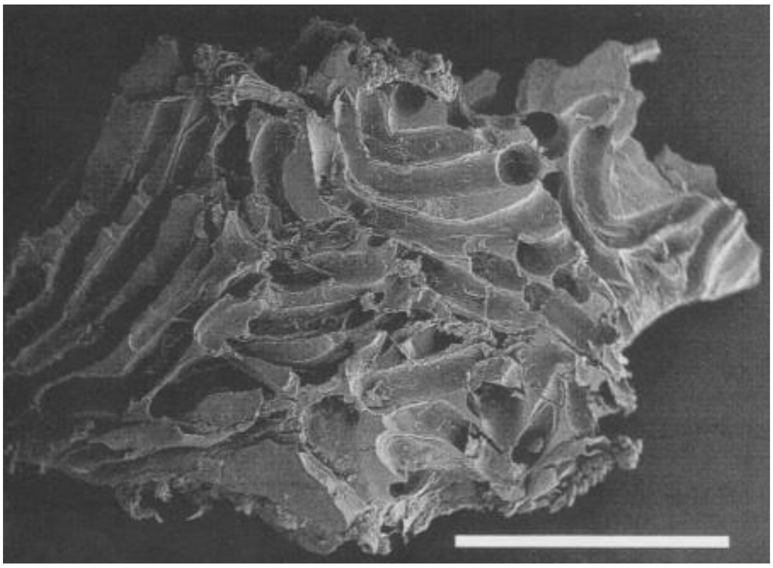

Fig. 2 - Large number of bore holes inside the shell showing the heavy infestation by *T. heterouncinata*. Scale bar length is 2.0mm. From Fitzhugh & Rouge (1999).

Eventual economic costs were substantial for the abaloid industry, increasing the urge for eradication efforts. In addition, the sabellids were discovered outside an Abalone Mariculture Facility (AMF) in well-established populations, raising concern to the potential impacts on native species (Culver & Kuris, 2000). Eradication efforts were started in cooperation with the AMFs and the Californian Department for Fish and Game (CDFG) and involved removal of all animals and shell debris related to the facilities, together with approximately 1.6 million shells of the intertidal black turban snail *T. funebralis* which were the most abundant and susceptible hosts for transmission (Ibid.). These measures on first sight seem remarkable and in many cases it would likely be ecologically undesirable to remove such a large amount of native potential hosts from the system. In this case however, the threshold removal density necessary to prevent further transmission of the sabellids did not prove harmful to the local turban snail, as *T. funebralis* numbers remained large within the area (Ibid.). In combination with the targeted removals of shell debris and escaped mollusks from the facility, this approach proved to be a successful strategy in eradicating this harmful invader. Furthermore, some additional factors contributed to this success. First, detection of the invading species occurred in a relatively early stage before the species could become widely distributed. Also, knowledge on its biological characteristics proved of vital importance in developing the appropriate strategy. Although all ontogeny stages of this polychaete are difficult to detect without microscope (Fitzhugh & Rouge, 1999), the dependency on living gastropods for establishment enabled targeted removals of susceptible hosts and prevention of further dispersal (Culver & Kuris, 2000). Collaboration and clear communication between the different parties involved were shown to be essential to ensure persistent efforts, even past the point of initial success (Ibid.).

The final important element to this successful eradication was the continued monitoring process. An extensive study consisting of nine follow-up surveys conducted between 2001 and 2009, verified the ongoing absence of *T. heterouncinata* in the area, thus confirming the eradication of this host-dependent invasive marine worm (Moore et al., 2013).

2.3 *Sargassum muticum* – Failed eradication attempts of a brown algae in Europe

Native to the waters of Japan, the brown macroalgae *S. muticum* is a well-known marine invasive species that had made its way towards both the Pacific coast of North America in the 1940s (Scagel, 1956), and the Western European coasts in the early 1960s (Critchley et al., 1983). In both cases, species introduction likely took place through the importation of Pacific oysters from Japan (Harries et al., 2007a). While this species was considered a marine pest in North America causing substantial ecological damage (Fletcher & Fletcher, 1975), the negative impact has been less pronounced along the coasts of Western Europe. *S. muticum* is a pseudo-perennial algal species which forms dense colonies in the sublittoral zone during summer (Fig. 3). Once present in large amounts, *S. muticum* effectively competes for space and resources with native algae species and was found to induce differences in the structure and composition of faunal communities (Harries et al., 2007b). In addition, the large algal canopies formed near the surface are thought to create a screen which blocks diffusing light


Fig. 3 – Thick algal patch of *S. muticum* at the surface, showing its ability to compete for both light and space with native algae species.

and thus potentially reduce or even prevent growth of other macro algae (Ibid.). Out of concern of harmful effects to native biota, several eradication efforts were conducted in England and France to remove *S. muticum* from the system, without any positive results (e.g. Critchley et al., 1986). The method of dispersal, i.e. release of zygotes and small-scale jump-dispersal via aqua culturing and floating segments of thalli (Stiger-Pouvreau & Thouzeau, 2015), proved to be main factor precluding a successful eradication of this species.

However, current evidence indicates that effects of this invader on the ecosystem are not necessarily deleterious (Harries et al., 2007a), and although the community structure will likely be altered, no reduction in species abundance and diversity is to be expected. Furthermore, in France, the adaptation of native species over the years has mitigated the effects of *S. muticum* on the ecosystem (Stiger-Pouvreau & Thouzeau, 2015). Here, the previously considered harmful invader was observed to be sharing space with native brown algae in rock pools. In addition, at sites with strong water turbidity which hampers photosynthetic activity of native brown algae, *S. muticum* still proved able to thrive and provided local fauna with shelter and protection (Ibid.). Native species of cuttlefish were observed to drop eggs in the main axis and once settled near the shore the invasive brown algae became a food source for amphipods. Consequently, this species is nowadays regarded as part of the local marine flora. This case provides a perfect example of a marine invader that is initially thought to have a deleterious impact on the community, but given time, turns out to become a stable component of the ecosystem and provide shelter and a food source for many native species.

2.4 *Didemnum vexillum* – Eradication failure of a fouling pest in New-Zealand

The colonial ascidian, *D. vexillum*, is suggested to be native to Japan (Locke & Carman, 2009) and has been expanding its distribution on a worldwide scale since the 1970s. Since its discovery in Shakespeare Bay, New-Zealand in 2001 (Kott, 2002), it has become a significant fouling pest within mussel farms which are vital components to the local aquaculture industry (Coutts & Forrest, 2007). Colonies of *D. vexillum* are characterized by rapid growth and both sexual and asexual reproduction, giving them the advantage of quick settlement on artificial and natural substrates. They are particularly harmful to native biota through their ability to form dense mats on the seafloor, unlike any other ascidian, that can alter habitat complexity and the flux of materials from the water column into the sediment (Mercer et al., 2009). These mats inhibit the growth of local epifauna by limiting the habitat availability for settling and even smothering sessile invertebrates (Fig. 4, Carman & Grunden, 2010). They also contain highly acidic compounds as a chemical defense against natural predators which results in very little biotic resistance (Mercer et al., 2009). As a result, after considering feasibility and performing a cost-benefit analysis, eradication efforts were started late 2002 in Shakespeare Bay (Coutts & Forrest, 2007). Treatments typically included: deposition of uncontaminated dredge spoil on soft sediment beds, wrapping of wharf piles in plastic and a combination of water blasting, air drying and chemical techniques (Ibid.). Unfortunately, the efforts proved fruitless due to several factors. First, their

Fig. 4 - Substrate completely covered in *D. vexillum* mats, altering the complexity and structure of the seabed.

responsive measures were not successful in completely eradicating the species from all invaded substrates, leading to re-infestation of previously cleaned areas. As a direct consequence, stakeholders started to question the efficacy of the removal efforts and decided to withdraw from the program in 2004 (Coutts & Sinner, 2004). An important contributing factor to this early shutdown was the lack of historical invasive data on *D. vexillum*, leading to disagreement among the involved parties about the amount of threat to the ecosystem (Coutts & Forrest, 2007). The costs (approximately $NZ0.65 million) up to that point of the program were substantial but yet relatively modest, and several useful insights were gained regarding similar future projects. First of all, baseline knowledge of the native system is imperative, both to recognize areas susceptible to marine invaders and to be able to detect non-native species before they become settled and start posing a threat. In this specific example, government agencies initially identified *D. vexillum* as an indigenous species, which caused a major delay in deciding upon appropriate responsive measures (Ibid.). Furthermore, continued funding throughout the eradicative process and a long-term commitment of involved parties and stakeholders must be realized. This is directly related to the government agency's awareness of the ongoing threat, and the belief that their involvement will yield beneficial results in the long-run. Providing these parties with the necessary environmental insights and economic implications is a key factor, since in many cases, as with *D. vexillum,* the invading species does not always have a history of harmful behavior and stakeholders might not see the urgent need to fund an early eradication program. Therefore, quick decision-making while sufficiently involving stakeholders through clear communication and statement of the mission, is vital to ensure long-term participation and will substantially increase the efficacy of eradication efforts in marine environments.

3. Comparative discussion on lionfish invasion

While the examples from the previous section have provided useful insights on past eradication efforts, the ongoing lionfish invasion represents a unique case in many ways. The following section deals with the current challenges of the invasion and the corresponding responsive measures proposed and undertaken so far. Applying the insights from the previous section, there will be a build-up towards a critical discussion regarding the potential, efficiency and possible risks of current efforts, together with a perspective on two probable future scenarios.

3.1 Challenges of the ongoing lionfish invasion

Despite the increasing occurrence of invasive marine species in relatively pristine habitats today, they have not received as much attention as their continental counterparts, and many marine taxa, habitats and regions remain poorly studied. An extensive literature study by Thomsen et al. (2014), in which 259 scientific papers on aquatic invasions were reviewed, revealed that there have been certain study biases over the past decades which are limiting our current knowledge on this topic. For example, out of the 101 different species studied among the papers, only one was a marine fish (which happened to be the *Pterois* species), whereas freshwater fish were rather well represented (Ibid.). Similarly, while one-fifth of the studies were conducted in estuarine environments, only 1% came from coral reefs which exactly reflects the scientific illiteracy regarding the current lionfish invasion in the Caribbean. Ever since the first report of the invasion in 2002, there has been an ongoing struggle amongst scientists to find the appropriate response tools to mitigate harmful effects. An overview of the current ideas and measures taken is provided in section 3.2.

Full eradication efforts, while occasionally successful as discussed in the previous section, have proven particularly difficult for marine environments due to their expansive, inaccessible and at times hostile nature (Hopkins et al., 2011). This, in particular, holds true for the lionfish invasion as populations are interconnected geographically, both via larval dispersal through currents (Morris et al., 2009; Freshwater et al., 2009), and through habitat occupancy from shallow reefs to mesophotic refugia zones (Lesser & Slattery, 2011). With a larval stage duration estimated at 25-40 days (Hare & Whitfield, 2003), lionfish are capable of spreading over large distances and further dispersal into the Lower Caribbean and the Gulf of Mexico seems imminent (Morris et al., 2009). This makes large-scale removals particularly challenging, since local efforts are often undermined by reinfestation from nearby areas. In contrast, for the Mediterranean Sea where the occurrence of *P. miles* was first recognized in 1991 (Golani & Sonin, 1992), oceanographic conditions have been shown to be unfavorable for larval dispersal and the resulting low connectivity between habitats keeps the current population of lionfish stable in the area (Johnston & Perkis, 2014). With estimated fecundity levels of two million eggs yr^{-1} per individual in the Atlantic range (Morris, 2009), successful reproduction further hampers ongoing removals. Since lionfish in their invasive range are thought to reproduce year-round (Ibid.) and there is a lack of evidence on native predators consuming juvenile lionfish, survival rates are exceptionally high and cause major setbacks in local removal efforts.

The broad depth range of *Pterois* species provides another challenge. With a recent extension in depth range to over 112m (Nuttall et al., 2014), there is an increasing need for surveys beyond the regular sampling performed by divers. According to Switzer et al. (2015), there has been a depth-related bias in understanding the lionfish invasion by exclusively considering dive surveys from up to 40m. Whether lionfish first colonize the shallow or deeper parts of reefs also remains debated on, with several articles providing exact opposite statements (e.g. Claydon et al., 2011; Nuttall et al., 2014; Switzer et al., 2015). In any case, the occupancy of deep waters by lionfish implies that a large part of their population remains unexploitable. Although the development of deepwater trap fisheries could provide an alternative to targeted removals by divers (Switzer et al., 2015), high amounts of exploitation and fishing activities will have adverse effects on resilience of these habitats, which serve as refugia zones for many ecologically important species. As such, there is an urgent demand for the development of novel removal strategies with minimal amounts of bycatch, to preserve the pristine conditions of these unique habitats.

3.2 Current state of responsive measures towards the lionfish invasion

Up until now, several efforts have been undertaken in attempt to remove local lionfish populations. In the Bahamas and Bermuda, culling programs were initiated in 2005 and 2006 in which both commercial and recreational fishers were trained and certified in spearing lionfish (Morris et al., 2009). While the short-term results of efforts like these look promising, e.g. over 1.400 individuals were collected in a one-day event and a single team was able to catch 19 lionfish in just 14 minutes (Morris & Whitfield, 2009), there are some negative sides to this method. Most importantly, recent studies have shown that a dedicated, long-term commitment will be necessary for these efforts to have any effect on lionfish populations in the long run (Arias-González et al., 2011; Barbour et al., 2011; Edwards et al., 2014). An age structured population model by Edwards et al. (2014) showed that exploitation rates of 15-35% would have to be realized for recruitment overfishing, but the population would re-establish in 5-20 years if removals were to cease. A similar model used in a study by Barbour et al. (2011) already revealed that, taken into account the published lionfish densities, this would add up to yearly necessary removals of 157-293 individuals per hectare. Locally, these numbers might be feasible for some regions, but to effectively eradicate the species these high exploitation rates need to be applied to all infested areas to prevent re-establishment by dispersal. The realization of such a large-scale removal program seems highly unlikely and will bring along substantial costs, as well as other unwanted side effects. While spearfishing might be the most efficient exploitation method with the least amount of bycatch, the drastic increase in such activities will undoubtedly cause more incidental removals of native species. Especially in Marine Protected Areas (MPAs), these side effects are highly unwanted and will be another potential risk to endangered native species, as well as surrounding coral reefs that are already under much stress. As such, this method could be successful in controlling lionfish numbers on a local scale when implemented for a sustained time period, but becomes impractical on a large scale due to massive costs and deleterious side effects to the native system.

Another approach that has been receiving a growing amount of attention lately, is the advertisement for lionfish meat as a nutritional delicacy. In fact, the species is already considered a healthy food source in their native ranges, and the family of *Scorpaenidae* is also popular in the French cuisine and served in a variety of dishes (Morris et al., 2009). A higher demand for lionfish meat would mean an increased market value and a higher incentive for commercial fisheries to harvest them. While this method would promote the realization of large-scaled removal efforts, the establishment of a lionfish-depending industry seems counterproductive. With the primary goal to reduce lionfish populations to minimal numbers, this would eventually induce commercial fisheries to protect their stock or even reintroduce species in low-density areas to maintain their share of the market value. In addition, the potential risk to the already weak, native system as a result of overexploitation would be even higher than the previously suggested approach of increased spearfishing. Therefore, it would be imperative to develop adequate legislative mandates to prevent the protection of stock, as well as a consideration of long-term economic and ecologic implications for this type of approach to be sustainable.

Finally, scientists have been considering the possibility of a biological control on the lionfish invasion. Lionfish have very few natural predators, in both their native and invaded range, mainly due to their venomous spines which serve as an effective defense mechanism (Morris et al., 2009). However, Bernadsky & Goulet (1991) already reported their potential vulnerability when attacked from behind, as the venom injection would likely be prevented due to the positioning of their spines. Their study included the first report of a possible natural predator of the lionfish in their native range, being the bluespotted cornetfish *Fistularia commersonii*. Analysis of stomach content of this species revealed the presence of a partially digested specimen of *P. miles*, which was consumed tail-first according to its orientation (Ibid.). Further evidence on this particular predation is lacking however, and the likelihood of this species to serve as a biocontrol would be near zero, since this species has a limited distribution in the Pacific coast off Mexico and Panama, and is virtually absent in the Caribbean and western Atlantic. Evidence of predation on lionfish in their invaded range is also limited to a few sporadic observations. Tiger grouper (*Mycteroperca tigris*) and Nassau grouper (*Epinephelus striatus*) have been documented as potential predators (Maljković et al., 2008), as well as nurse sharks (*Ginglymostoma cirratum*) (Diller et al., 2014) and even the green moray eel (*Gymnothorax funebris*) has been observed consuming a wounded lionfish (Jud et al., 2011). While the latter two examples involve single observations, studies on the relation between lionfish and both grouper species have increased over the past years (e.g. Mumby et al., 2011; Valdivia et al., 2014; Raymond et al., 2015). A recent study by Mumby et al. (2011) on a healthy reef system in Exuma Cays, central Bahamas, found a negative correlation between lionfish and the large number of groupers which had been protected within the area over the years. Whereas these results imply a possible top-down control on the lionfish invasion, the majority of the reef systems in the Caribbean have been subjected to substantial amounts of overfishing and the exploited grouper populations would unlikely provide an effective biotic control in these regions. Despite several desperate attempts by scientists to increase biotic resistance by removing naïveté among predators, e.g. conditioning native groupers to consume tethered lionfish (Diller et al., 2014), these efforts cannot realistically be considered to yield any beneficial results on a large spatial scale.

3.3 Feasibility assessment and implications for the future

So far, we have seen that successful marine eradications, although being scarce, are occasionally realized and can restore the state of the ecosystem back to initial pre-invasive conditions. However, accomplishing such an outcome requires a rapid and dedicated approach, as became clear from the examples in section two. To assess the feasibility of current efforts taken regarding the lionfish invasion, a comparison will now be made between crucial factors leading up to previous successes or failures, and their current status for the lionfish invasion.

For any given example of an introduced non-indigenous species that becomes invasive, the cheapest responsive tool is to recognize potential areas of threat and prevent the onset of an invasion altogether. This measure involves a combination of rapid detection and decision making, to minimize dispersal and contain the invasive species whilst still at small numbers. Unfortunately, in the case of the lionfish invasion, it took 15-20 years for the first report to be published on the potential threat of this exotic species. Besides the occasional encounter reports from divers in the 90s (Hare & Whitfield, 2003), the species was not considered a harmful invader until 2002 (Whitfield, 2002). By that time, the dispersal of lionfish larvae by oceanic currents had likely been facilitated for more than a decade and strategic options for taking control inevitably had moved past the initial step of rapid detection and response. The main factor contributing to this delay in risk detection, was the lack of empirical evidence from past studies on the deleterious invasive behavior of *Pterois* species. With no 'history of violence' and little information on the biology of the lionfish in its native range, there seemed to be no urgent need in controlling the lionfish population at the time. On the contrary, for the Mediterranean Sea, the need for raising awareness and implementing constant monitoring efforts on the small and still harmless population of *P. miles*, has already been recognized as a direct result of the knowledge gained from the ongoing invasion in the Caribbean (Bariche et al., 2013).

The failure to realize this first important step has enabled the two lionfish species to become widespread harmful invaders in less than two decades. Keeping to the often used, stepwise eradication scheme provided in section 2.1, the next step would be to ensure sufficient economic funding to initiate targeted removal efforts. While for the lionfish case, economic funding is likely to be realized considering the large amount of ongoing damage to the fishing industry and the entire marine ecosystem, the lack of effective and large-scaled removal methods is holding back the development of adequate control strategies. Before committing large amounts of resources, a combination of pilot studies, background information and risk assessment will need to determine strategic effectiveness and prevent a potential fiasco. As such, step 3 and 4 from section 2.1 should be established prior to the search for economic funding, since management strategies cannot be regarded as realistic without the appropriate control method and necessary information on species biology. This is where the real challenge of the lionfish invasion becomes clear. With very little information on what controls lionfish in their native range, and rapid larval dispersal facilitated by currents in the invaded range, the process of finding either biotic or abiotic controls on the population has proven extremely difficult. Without such control methods, it will be challenging to create confidence and establish a long-term commitment among stakeholder which, as became clear from section 2.4, is essential to fully complete an eradication process. As a result, the only actively-ongoing removal effort involves culling by spearfishing and hand netting, and is carried out by volunteer divers (Ali et al., 2013). These kinds of efforts are thought to be highly effective in reducing lionfish numbers (Frazer, 2012; Côté et al., 2014) and even affect their 'open-roaming' behavior locally (Côté et al., 2014). Unfortunately, as discussed in previous parts of this section, such local efforts cannot realistically lead to a complete eradication. Until we find either the proper tools and techniques for large-scale removals, or make a breakthrough on what provides their control in native ranges, we are far away from a complete eradication. In the meantime, the focus should be on protecting endangered species and mitigating effects on MPAs without any collateral damage. Development of novel techniques with a low amount of bycatch, e.g. using specific kinds of bait or possibly even pheromones (Sorensen, 2014), should be encouraged by financial incentives. Furthermore, in order to minimize collateral damage to MPAs and other areas of high ecological importance, the education and training of special diving teams should be supported to operate around these fragile areas.

The final step in the eradication process, as discussed in section 2.1, involved the prevention of re-invasion of the species. Although as mentioned above, full eradication is highly unlikely in the near future, it is still important to consider this final stage. With aquarium releases being the initial source of introduction in the mid-1980s, there is an urgent need to reconsider import limitations of ornamental species through the aquarium trade. A recent expansion of the Non-Native Wildlife Invasions Prevention Act ensures a thorough screening process of species imported into the US, based on invasiveness and likelihood of establishment (Morris & Whitfield, 2009). With an increase in data on biology and life characteristics of the successful lionfish becoming available, the trade on species sharing similar traits should be closely monitored and restricted when release by owners and potential establishment seem imminent. In the unlikely event of complete eradication, a restriction on the import of lionfish through small aquarium trade should be highly considered to prevent a potential re-invasion.

With the improbability of full eradication in mind, a few potential future scenarios can be discussed. One likely scenario is that lionfish will eventually become a stable component of the western Atlantic and Caribbean marine community. As is often the case in the process of biological invasions, the onset and early stages can be particularly drastic and harmful to the native system, but the effects seem to diminish over time; a process known as 'boom and bust' development (Sih et al., 2010; Lockwood et al., 2007). A lack of evolutionary history between the invader and native species often gives invading species a distinct advantage over competition due to both predator and prey naïveté. Given time, native species may adapt to the presence of the invader, with predators becoming aware of a new potential food source and prey starting to display antipredator responses (Sih et al., 2010). While the subsequent 'bust' part is highly unlikely to lead to the extinction of the invader (Williamson & Fitter, 1996), the harmful effects found at early stages will become less severe. Instead, the invasive species is often found to become a stable component within the system and take over the role of native species, causing a rearrangement of the community structure (Bøhn et al., 2008) as was the case in the example under section 2.3.

The opposite extreme scenario of the boom and bust cycle would imply that lionfish continue in their current fashion of consuming large amounts of native fish, up until the critical point of resource depletion. Taking in mind a previous mention of cannibalism among *P. volitans* species (Allen & Eschmeyer, 1973), they could eventually provide their own biotic control by surpassing the carrying capacity of the system. At the time of writing, an article published by National Geographic (Pyzyck, 2015) mentions current observations of lionfish regurgitating other lionfish, as an indication that the potential scenario of resource depletion might be closer than we think.

4. Conclusion

In this literature study, key factors from past eradication attempts were examined and compared to the current state of the lionfish invasion in the western Atlantic and Caribbean. The considerable delay in recognition of the threat early on, hampered the process of quick detection and rapid decision-making, a strategy commonly used and proven highly effective. As such, this enabled the two lionfish species to become established and widespread within their invaded range. Main factors causing the ongoing struggle of eradicating the species include; insufficient knowledge on the biology of lionfish and the biotic factors that serve as a control in their native range, in combination with the lack of appropriate tools and methods for sustainable large-scaled lionfish removals with minimal bycatch. These two elements have proven essential in past successful eradications and as such need to be the main priority in future efforts and research. Not until these requirements are met, can there be a realistic pursue of eradication with sufficient funding through long-term commitment by stakeholders. Without any further human interference, lionfish are either likely to become a stable component through evolutionary adaptation of the native system, or in the worst case, deplete most of their resources and possibly resort to cannibalism to put a control on their own numbers. In any case, whether the native system will be able to sufficiently recover from the continued effects of the most devastating marine invasion to date, unfortunately remains to be seen.

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