Critical analysis of data representing negative impacts of lionfish (*Pterois volitans*) invasion on native communities:
Is it really that bad?

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Abstract

Marine predatory species that are introduced into a new environment can pose a serious threat to native communities through competition with native predators and predation on reef fishes. Such an example is the Indo-Pacific lionfish (*Pterois volitans*), introduced in 1985 off the coast of Florida where it spread across the Western subtropical Atlantic and Caribbean and has reached high densities in some areas. High densities combined with the invader characteristics (such as the ability to efficiently consume native prey) may limit resources for other native predators. As a result, researchers and conservationists are concerned about these potential impacts on native communities. Therefore the question arises how bad it actually is. This study reviewed a substantial amount of the available literature on lionfish invasions, based on observational (n=16) or experimental (n=12) designs, to determine whether these concerns can be approved from any concrete data.

Two approaches have been used: 1) all information available is interpreted in the light of the invasion theory, based on opportunistic observations and 2) conclusions were only based on factual data. As a result, some studies only focussed on particular areas where invaded lionfish occurred in relative higher densities than from its native range, neglecting areas of lower lionfish densities. Moreover, specific lionfish characteristics determining the extent of the invasion impact, such as the ability to outcompete native species, were made from inconclusive data. Only part of the actual data was investigated, like information on lionfish diet but not on specific diet overlap with other native species through stable isotope analysis. On the contrary, there was even some evidence of lionfish not fitting the profile of a successful invader. Natural predation on the lionfish did occur. Also here, there was lack of specific

knowledge, like natural mortality rates of lionfish caused by predation of predators such as large grouper species, which might control lionfish population growths.

In order to find the best possible answer in questioning the actual impacts of lionfish on native communities, conclusive data on lionfish diet, consumption rates and from natural predation is needed. In conclusion, researchers should focus more on what has truly been investigated rather than assume that lionfish certain characteristics of successfully invade new communities will answer this question itself.

Introduction

Marine invasive species are getting much more attention lately, due to increasing numbers of introductions in marine and coastal areas and through negative effects they may have on native marine life (Bax et al. 2003, Molnar et al. 2008). The question hereby is why a particular species was able to infiltrate in native communities. This may be explained by the characteristics of the invader itself (Parker et al. 2001, Shea and Chesson 2002). For instance, being an efficient predator and superior in outcompeting other native predators for resources (Morris Jr and Akins 2009, Green et al. 2011, Green et al. 2012) and/or the possession of a high reproductive rate. Another factor is that recipient communities were not able to resist the invasion. These communities may have no or only few natural predators that will eat the invasive species and therefore not able to control the invaders' population growth. However, marine communities consists of complex structures with all kinds of species interactions (Morris Jr et al. 2009), making it difficult to assess the particular role of invader in its new environment.

A good example of a recently developed marine invasive species is the Indo-Pacific lionfish (*Pterois volitans*), which was introduced in 1985 off the coast of Florida US (Schofield 2009) and just recently observed to continuing to disperse into non-native areas (Schofield 2010, USGS-NAS 2014), from subtropical western Atlantic to southern Caribbean waters (Fig 1). In some of those areas, the lionfish were found in higher densities compared to its native range (Kulbicki et al. 2011). In addition, the potential ability of lionfish to consume native prey in a highly efficient manner (Green et al. 2012), made researchers and policy makers concerned about the potential consequences of this invasion. Some researchers even hypothesized that the invaded lionfish may alter entire marine communities through predation on reef fishes and deplete these resources for other native predators (Baltz 1991). As a consequence, eradication programs were established to control this invader in the Atlantic and Caribbean waters (de León et al. 2013).

However, there is still a high uncertainty about the actual impacts of the lionfish invasion. There is, for instance, surprisingly little information available about historical data on lionfish biology and ecology from its home range, the Indo-Pacific, as well as actual data provided from experimental studies (Albins and Hixon 2008, Albins 2013) demonstrating the ecological role of lionfish in the invaded area. Most of this information were provided from observational studies (Whitfield et al. 2007, Green et al. 2011, Cure et al. 2012) and reviews (Whitfield et al. 2002, Hare and Whitfield 2003, Morris Jr et al. 2011). This study aimed to evaluate the gaps of data needed to actually determine the impact of the lionfish invasion. For this, I reviewed a substantial amount (circa 50 peer-reviewed publications) of the available primary literature on lionfish invasions from Web of Science. At first, a general review was made on what is known about lionfish biology and ecology that may contributes to its role as successful invader. And secondly, the actual impacts of the lionfish invasion was investigated by applying the following criteria: 1) separate observational studies from experimental studies; 2) critically evaluate the evidence available for negative effects on invaded communities; 3) identify gaps in data needed to assess the severity and likely outcome; and finally make recommendations for future research.

General review

Invasion of the lionfish

Two species of *Pterois,* the red lionfish (*P. volitans*) and the common lionfish (*P. miles*), have been observed outside their home range (Schofield 2010). This study was only focussed on the red lionfish (hereafter referred to as lionfish) that originated from the Philippines (Fig 1), as they were far more abundant (about 93%) than the other *Pterois* species found in the non-native area, the Atlantic region (Hamner et al. 2007).
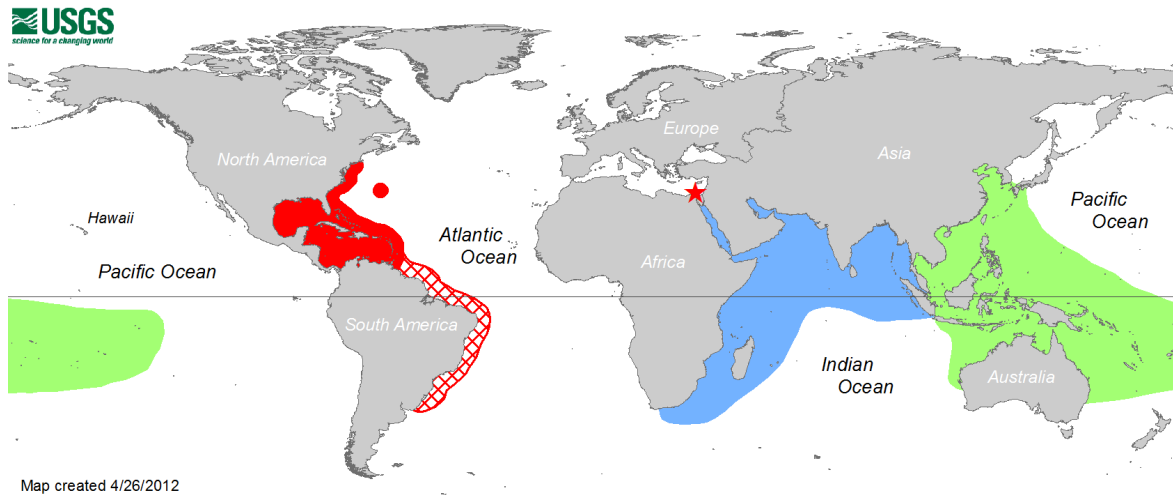

Map created 4/26/2012

Figure 1. Distribution range from two species of lionfish in their native range, *Pterois volitans* (green) and *P. miles* (blue, red star indicates their migration via the Suez Canal), and non-native area (Drake et al.), the Atlantic (Kulbicki et al. 2011), whereas lionfish future distribution predicted by Morris and Whitfield (2009) is shown in red hatching.

The first invasive lionfish was detected in 1985 (Fig 2), off the coast of Dania beach, south Florida (Morris Jr et al. 2009), and resembled those of the Philippines. This fish is popular in the aquarium trade which is most likely the cause of its release in a new area. The story goes that a lionfish was discarded from a dissatisfied aquarium enthusiast and later on, in 2000 (Fig 2), from multiple releases. The lionfish continued to disperse more north to North Carolina and Bermuda. Over the years, they extended their distribution range southwards, where USGS (USGS-NAS 2014) documented multiple sightings across the Caribbean Sea. Recently in 2013, the lionfish were discovered in the Gulf of Mexico and it has been predicted (Morris and Whitfield 2012) that further dispersal will continue along the coast of South America (Fig 1).

Nowadays, lionfish are observed in a wide area in the Atlantic, found over a range of different habitats (Biggs and Olden 2011), from shallow reefs to depths of 300 meters (Albins 2013). This makes it difficult to identify their relative occurrence across the entire invaded area. As a consequence, little data is available on lionfish relative densities, whereas lionfish sightings are well documented (Fig 1,2).
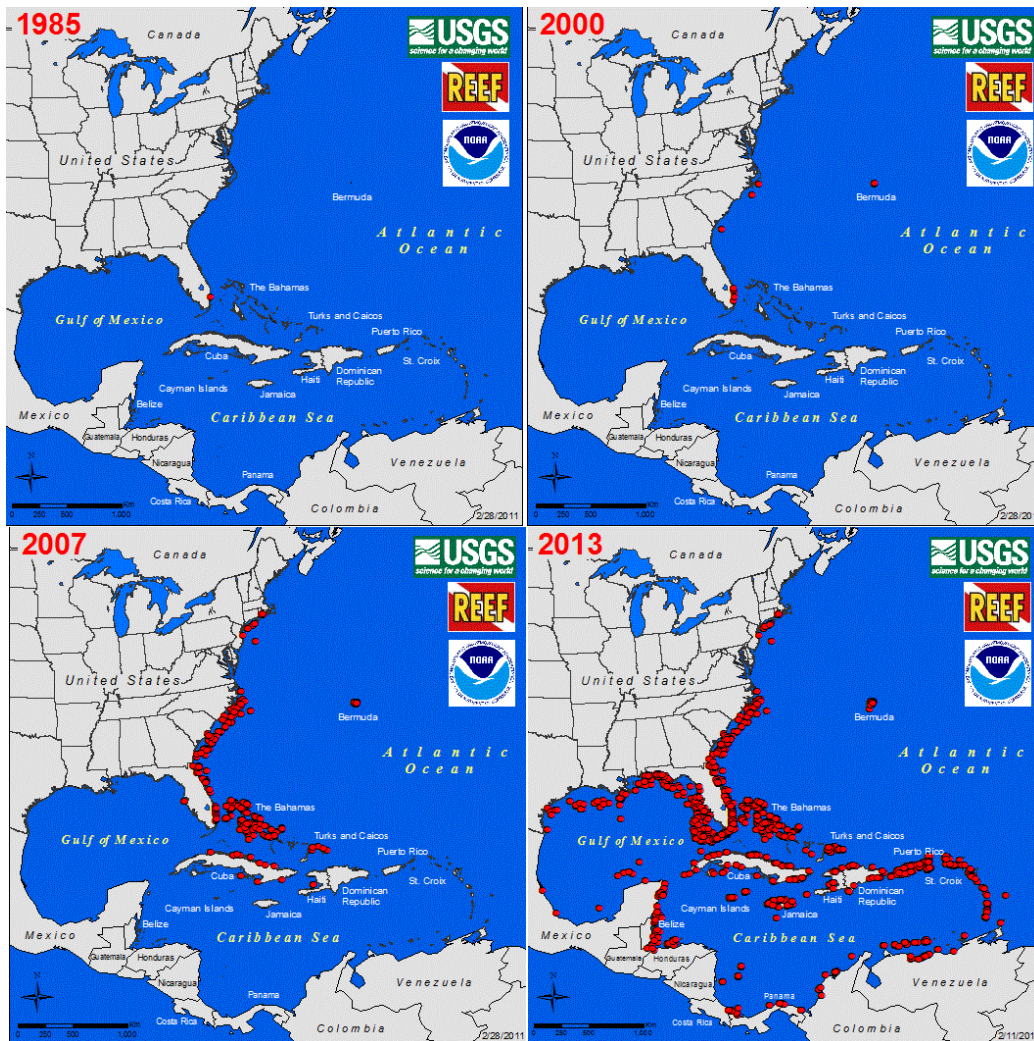
Figure 2. Lionfish spatial and temporal distribution in the non-native range, from the first introduction off the coast of Dania Beach, Florida in 1985 to migrate further north (in 2000) and south; across the Caribbean Sea (2007) and into the Gulf of Mexico and further along the coast of South America (2013).

About lionfish biology and ecology

The lionfish is mainly famous for its poisonous character, which is located in its venomous spines, used to protect itself from predators (Fishelson 1997). This protection is further promoted by its appearance that has conspicuous colours consisting of contrasting stripes and the shape with wide fans of spines making them look less vulnerable to predators (Hare and Whitfield 2003, Côté et al. 2013). Lionfish are also very efficient predators, making use of behavioural traits, such as slow movement and specific piscivorous behaviour of 'blowing' jets of water towards prey in order to confuse them (Albins 2013). Finally, lionfish can spawn throughout the year and even several times per month, with an estimated annual fecundity of over two-million eggs per female (Morris and Whitfield 2009). These biological and ecological traits contribute to their success as an invasive species.

Invasion theory: what leads to a successful invasion?

There are many reasons why a particular species is able to successfully infiltrate in a new environment. If these reasons are known the effects of this invaded species on native communities will also become clearer. First, the invader needs specific characteristics to be able to establish itself in new ecological and biological circumstances (Kolar and Lodge 2001). Second, invasive species are more successive in areas that can be characterised as disturbed systems or where the invaded community structure is relatively simple (Shea and Chesson 2002). And finally, it is likely that a combination of these factors results of the succession of the species invading a new community (Lodge 1993).

Invaders' characteristics

The level of success of an invader is determined by various characteristics; being a good competitor for food and space (Shea and Chesson 2002), its morphology; avoiding natural predation (Parker et al. 2001) and reproductive behaviour (Drake et al. 1989). For example when the invader is a predator that is better in obtaining prey than their native competitor, this may have a direct effect on prey abundances and therefore indirectly on native predatory species that are depending on these resources (Shea and Chesson 2002). Even more, with the introduction of a new predatory species the pressure exerted on native prey might become too high, which may eventually disturb the entire structure of the food web (Zavaleta et al. 2001).

Another factor that determines the success of an invasive species is the lack of biotic control. This is so called ecological release where the species' native biotic control, such as predation, competition, diseases and parasites, is not or in less extent occurring in the invaded area (Parker et al. 2001). Lack of natural predation on the invader may due to; (1) the invaders' morphology traits, or (2) native predators not recognizing the invader as a potential prey species. The invaders' morphology traits can be translated into certain defence mechanisms with which natural predators are not familiar and therefore not able to deal with (Lönnstedt and McCormick 2013).

Degraded recipient systems

It is furthermore possible that invaded communities themselves provide opportunities for introduced species to become invasive. Low invasion resistance of resident communities can be characterised of systems already been disturbed, due to loss of biodiversity from other stressors, such as fisheries (Bax et al. 2003) or climate change (Occhipinti-Ambrogi 2007). These degraded recipient systems are more easily invaded than complex 'healthy' systems. The reason for this is that natural predators on the invader may already be lost or simply not occur in disturbed or simpler communities. If there is not such a control of natural predation on the invader, the invader might able to avoid this natural predation enable it to reach high densities (Kolar and Lodge 2001, Lönnstedt and McCormick 2013).

Cumulative effects

Finally, a combination of invader characteristics and the status in which the recipient community are dealing with the invader explain more about the outcome of the invasion. For instance, species competitive ability is greater in a higher diverse community where more species had to compete for similar resources. If the invader is used to heavily compete for resources in their native area and invades a simpler community wherein native species not experienced such strong predator-prey competition, then the invader would be a better competitor than these native species. Another cumulative effect, where the invader is able to increase their population size, appears when invaders reproduction rate is higher than the rate of consumption from natural predation on the invader.

Types of data currently addressed in the literature

Different kinds of data were provided by the literature to explain how lionfish fit the role of a problematic invader. Here, the aim was to separate those data in order to evaluate the relevance of the information that was given. I discriminate between data supported from observations that were focussed on natural predictions of the invasion theory and the data obtained from experimental studies specifically aimed to determine key aspects on lionfish invasions.

Observational data on lionfish invasion

Lionfish were observed in higher densities in some non-native areas than in its native range (Kulbicki et al. 2011). This can be ascribed to lower predation on the lionfish, where natural predators of lionfish, such as grouper species, were less abundant in invaded areas (Morris Jr et al. 2009). Food availability for the lionfish might also be greater in the invaded area and/or lionfish might have better access to more prey items without much competition from other predators. This theory was supported by observations of invaded lionfish feeding more on different prey items. Lionfish diet in their native area consisted mainly of small fish and invertebrates (Green et al. 2011, Layman and Allgeier 2011) where the invaded lionfish also predated on parrotfish and juveniles of important commercially species (Albins 2013). As mentioned earlier, if invaded lionfish is truly capable of outcompeting other predators, depleting its prey, then this may lead to a simplification of the food web. Eventually, one would predict that only the lionfish itself will cause its own decline due to scarcity of food. If this is really true, what are the costs to the invaded community and is there any actual data supporting this hypothesis?

Table 1. An overview of studies that revealed certain aspects on the lionfish invasion referring to; the theory on invasive species, detailed descriptions, area and whether this has been observed (O), reviewed (R) or experimented (E).

Theoretical aspects on invasive species	Details	Area	O, R or E	References
Invaders' characteristics				
Feeding ecology	*Diet:* -Damselfish, cardinal fish and gobies -Less divers and no parrotfish vs. Atlantic	Indo-Pacific Red Sea Phillipines and Guam	E E	(Fishelson 1997) (Cure et al. 2012)
	-Damselfish, wrasses, basslets and juveniles of parrotfish, grunts. -±90% small fish, 10% crustacean -Higher diversity of prey vs. Indo-Pacific	Atlantic Bahamas Bahamas Bahamas Bahamas Bahamas and Cayman Islands	E E E E E R	(Morris Jr and Akins 2009), (Layman and Allgeier 2011), (Albins and Hixon 2008) (Green et al. 2012), (Morris Jr and Akins 2009) (Cure et al. 2012) (Albins 2013), (Morris Jr et al. 2009), (Morris and Whitfield 2012)
	Consumption rates: -8.5 g day^{-1} -Equal kill rates vs. Atlantic -79% decline of small fish -65% decline of small fish -1.44 kills h^{-1} -Equal kill rates vs. Indo-Pacific	Indo-Pacific Red Sea Phillipines Atlantic Bahamas Bahamas Bahamas Bahamas	E O E E O O R	(Fishelson 1997) (Cure et al. 2012) (Albins and Hixon 2008) (Green et al. 2012) (Côté and Maljkovic 2010) (Cure et al. 2012) (Ruttenberg et al. 2012),(Morris Jr et al. 2011a)
	Food competition: -Diet overlap with grey and schoolmaster snapper -Lionfish 2.5 > Coney in reducing small fish	Atlantic Bahamas Bahamas	E E R	(Layman and Allgeier 2011) (Albins 2013) (Hare and Whitfield 2003), (Beets 1997)
Morphology traits	-Defensive venomous spines -Cryptic form, behavior	Indo-Pacific Red Sea	E O R	(Halstead et al. 1955) (Lönnstedt and McCormick 2013), (Fishelson 1997) (Côté et al. 2013)
Reproductive behavior	-High reproductive rates	Atlantic North Carolina, USA and Bahamas	O R	(Morris Jr et al. 2011b) (Morris Jr et al. 2009), (Albins 2013)

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Lack of natural predation	Identifying predators:	Indo-Pacific		
	-Cornetfish	Red Sea	O	(Bernadsky and Goulet 1991)
		Atlantic		
	-Tiger grouper	Bahamas	O	(Maljković et al. 2008)
	-Nassau grouper	Bahama	O	(Maljković et al. 2008)
	Lionfish control:	Atlantic		
	-Related with Grouper abundance	Bahamas	O	(Mumby et al. 2011)
	-Not related with higher Grouper abundance	Bahamas, Cuba, Mexico	O	(Valdivia et al. 2014)
			R	(Cure et al. 2012), (Morris and Whitfield 2012)

What evidence is present from experimental data?

Lionfish competitive ability

To actually determine whether lionfish are capable of outcompeting native predators, data has to be collected on which species have a dietary overlap with the lionfish. The use of stable isotopes analysis provides an efficient method to gather information about the species signature in what they have been eating over a longer period of time. So far, only one study could be found that conducted this analysis and showed that invaded lionfish, native grey snapper (*Lutjanus griseus*) and schoolmaster snapper (*Lutjanus apodus*) shared similar resources, which were mainly small fish and crustacean (Layman and Allgeier 2011). When a certain dietary overlap is found, species diets can be investigated into more detail through the use of stomach content analysis. The results showed that lionfish were more exclusively feeding on small fish while native snappers fed more on crustacean (Layman and Allgeier 2011). The more specialized feeding pattern of the lionfish was associated with a higher site-fidelity by the lionfish. However, lionfish can also be characterised as a generalist feeders, as they occur over a wide range of habitats that coexists with different kind of food availability (Green et al. 2011). Thus, lionfish can be a specialist or a generalist depending on the locality and opportunities. Therefore, this approach cannot be compared with studies in other invaded areas and is therefore of limited value in further studies.

Furthermore, when a certain dietary overlap exists, more research is needed on whether lionfish are actually limiting those resources for other predators. The more efficient predator may exert higher pressure on prey abundances and had therefore higher predation rates. A study comparing invaded lionfish with a native similarly sized predator, the coney grouper (*Cephalopholis fulva*) showed that lionfish predation rates on small native coral-reef fishes was 2.5 ± 0.5 times (mean ± SEM) greater than that from the native grouper species (Albins 2013). Unfortunately, analysis of whether these two species were directly competing for food was not investigated. Therefore, this experiment is inconclusive and had first to examine those specific species that shared dietary sources with the invaded lionfish.

Finally, density measures of invaded lionfish in relation to prey abundances and predatory species competing for similar resources provide more conclusive data on how lionfish affect their invaded community. A study that came close to determining these changes in fish biomass, starting to investigate lionfish specific diet through stomach content analysis (Green et al. 2012), showed a 65% decline of

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lionfish prey abundances and a rapid increase of lionfish populations, comprising nearly 40% of the total predatory biomass. However, this relationship of lionfish increases on behavior of other predatory species through competing for food, were made from indirect dietary studies and/or these species were categorized into the same trophic level only based on similar body sizes (Green et al. 2012). Therefore, these data do not represent the lionfish presence directly influencing native predatory species.

Observational evidence suggests that lionfish were more successive in non-native areas, reaching higher densities than in its native range (Table 1). Comparative studies between those areas could tell us more about why lionfish can be more successful as an invader than in its natural habitat. Are, for instance, predation rates higher as lionfish experienced less competition from predators of the invaded community? One study tested this hypothesis and found partial support by finding differences in feeding patterns, where invasive lionfish had a broader diet and Atlantic prey of lionfish was twice as large as Pacific prey (Green et al. 2011, Cure et al. 2012). Therefore, lionfish obtained, on average, higher prey biomass in the invaded area. However, predation rates of native and invasive lionfish showed no difference (Cure et al. 2012). As there is no clear correlation found between growth of lionfish population and higher food availability, it might also be that other factors were the main cause of their increase.

The lack of natural predation

Until recently it was believed that lionfish had no predators in invaded regions and were therefore able to avoid this biocontrol. However, there is some evidence that predation on lionfish does occur in invaded areas. Native groupers were found to prey upon the invaded lionfish (Maljković et al. 2008). However, the frequency of this lionfish consumption is unknown. More data on each of those potential predators would provide more information on this part. The first study showing that different grouper species were preying on the invaded lionfish was just recently published (Maljković et al. 2008). A tiger grouper (*Mycteroperca tigris),* in the Bahamas were found with a single lionfish inside its stomach. Moreover, 5 randomly samples were taken from the native Nassau grouper, *Epinephelus striatus,* and respectively 2 of them showed a digested lionfish. This result demonstrated that the potential frequency of lionfish consumption can be considerably high. Experimental data of grouper predation rates can support this observation. Two related studies provided this type of information with controversial outcomes (Mumby et al. 2011, Valdivia et al. 2014). One of the studies was conducted inside a marine park on one of the Bahamian reefs (Mumby et al. 2011) that is known of supporting the highest grouper biomass in the Caribbean (Kramer 2003). Here, a significant correlation was found between higher mean biomass of groupers (800g 100m^{-2}) and the reduction (50%) of lionfish biomass. In contrast, the other study surveying a wider range across the same area showed no correlation between grouper and lionfish biomass (Valdivia et al. 2014). In both cases, there was no actual direct evidence provided on the cause of the lionfish reduction, either by grouper predation or other factors. Nevertheless, inside the marine park with significantly higher grouper biomass (Mumby et al. 2011) than the average of the entire Caribbean (178g 100m^{-2}), of which overfishing of large-bodied groupers is likely the cause (Sadovy 2005), there happened to be 7- fold reduction in lionfish biomass.

Furthermore it is helpful to know what the natural predators of lionfish are in their native area (Bernadsky and Goulet 1991). However, it is known that in the Indo-Pacific community structures are more diverse with relative higher number of piscivore species than in the Atlantic (Kulbicki et al. 2011). Therefore, the probability of predatory species feeding on the lionfish is higher in their native area than in the invaded area, but this has yet to be investigated into more detail. Another source of predation on lionfish may derive from smaller predators feeding on the larval stage of the lionfish. No information could be found on which species are reducing lionfish populations by predating on their early life stages. From these gaps in knowledge, it is not sure if lionfish is completely capable of avoiding this biotic control.

Lionfish succession in non-native areas: are densities really that high?

From literature, it was mainly reviews (Whitfield et al. 2007, Kulbicki et al. 2011, Ruttenberg et al. 2012) and reported sightings (Darling et al. 2011) (Green and Côté 2009) that issued lionfish reaching higher densities in the invaded area than in their home range (Table 1). Surprisingly little information is available from comparative studies recording densities between lionfish in invaded and native areas. In contrast to what many studies referred to, a study by Darling et al. (2011) recorded no clear difference between total average lionfish density (± 71 ind ha^{-1}), concluding from 5 different lionfish species (*Pterois sp.*) in the native area and the lionfish species (± 100 ind ha^{-1}), *Pterois volitans,* in the non-native area. However, a review study by Kulbicky et al. (2012) showed the opposite with significantly higher lionfish densities (max 400 ind ha^{-1}) in the Atlantic than the Indo-Pacific (max 26.3 ind ha^{-1}). This was mainly referred to by studies restricted to one particular invaded area; the Bahamas (Table 1). In contrast, lionfish have also been recorded to have relative lower densities in the Bahamas, whereas on 8 of the 13 sites surveyed were less than 65 individuals of lionfish recorded (Darling et al. 2011) which is lower than the maximum (± 71 ind ha^{-1}) of lionfish densities recorded in the native area (Table 1).

Table 2. Lionfish densities recorded in native versus non-native areas. Data were obtained from different type of studies; Experimental (E), Observational (O) or Reviews (R).

Lionfish densities	Native vs. non-native areas	Type of data	References
	Indo-Pacific		
± 25 ind ha^{-1}	Kenya (*P.miles*)	E	(Darling et al. 2011)
± 71 ind ha^{-1}	Kenya (5 *sp*. Pterois)	E	(Darling et al. 2011)
max 26.3 ind ha^{-1}	Total range	R	(Kulbicki et al. 2011)
	Atlantic		
Randomly sighted (1-5 ind.)	North Carolina - Florida	O	(Whitfield et al. 2002)
±15 ind ha^{-1}	North Carolina - Florida	O	(Whitfield et al. 2007)
Randomly sighted (1-5 ind.)	Florida - Dry Tortugas	R	(Ruttenberg et al. 2012)
Randomly sighted (1-5 ind.)	Bahamas	O	(Freshwater et al. 2009)
± 340 ind ha^{-1}	Bahamas	E	(Green and Côté 2009)
± 100 ind ha^{-1}	Bahamas	E	(Darling et al. 2011)
Randomly sighted (1-5 ind.)	Total range	O	(REEF 2014, USGS-NAS 2014)
Randomly sighted (1-5 ind.)	Total range	R	(Schofield 2009, 2010)
max 400 ind ha^{-1}	Total range	R	(Kulbicki et al. 2011) 11

Conclusion: How bad is it?

There seem to be two different angles from which this question is approached. One is that all information available is interpreted in the light of the invasion theory, based on opportunistic observations. And the other approach where conclusions were only based on actual, quantitative data. If the answer was entirely focussed on particular aspects of the invasion, like observations of higher lionfish densities (Green and Côté 2009, Kulbicki et al. 2011) in some non-native areas compared to their native range (Whitfield et al. 2002, Ruttenberg et al. 2012), it may automatically be assumed that this will have a negative effect on native communities. For instance, these relative high lionfish densities can be predicted to increase to even higher numbers (Darling et al. 2011), since there are only few indications of natural predation on lionfish (Mumby et al. 2011, Valdivia et al. 2014). Then, to make further predictions biased to explain lionfish affecting native marine life, a study showed lionfish had faster prey consumption rate than other native predatory species (Albins and Hixon 2008, Green et al. 2012). According to the invasion theory, the introduction of an extra predatory species in native communities may severely decline prey abundances compared to that of the usual native predator-prey relationships. Furthermore, higher predation pressure of lionfish may eventually results of limiting resources for native predatory species with dietary overlap, such as grey snapper and schoolmaster snapper (Layman and Allgeier 2011). However, when actual data is missing, like the frequency in which natural predators are consuming lionfish, it is not guaranteed that lionfish is a successful invader.

If you look at the actual facts about the lionfish invasion, then a totally different answer is given to the question of how bad it actually is (Mumby et al. 2011). My review indicates that actual data proving that lionfish are outcompeting native species were not conclusive or important aspects to identify these predator-prey relationships were missing. Further data that supported the hypothesis of lionfish were actually preyed upon was provided (Maljković et al. 2008) and a correlation was found between lower lionfish biomass where grouper abundance was high. In the case of higher lionfish reproduction rates compared to the frequency of groupers predating on the lionfish, then the assumption of lionfish being successful in the invaded area might be true. Unfortunately, the mortality rate caused by the predation of groupers on lionfish is unknown, as well as the reproduction rate of lionfish. In order to find the best possible answer in questioning the impacts of lionfish on native communities, much more research has to be done. In conclusion, researchers should focus more on what has truly been investigated rather than assume that lionfish superior qualities of invading new communities will answer the question itself.

Recommendations for future research

First, future research should focus to establish long-term monitoring programs in each particular area where lionfish has first been sighted in the Atlantic (REEF 2014, USGS-NAS 2014). Then, comparisons can be made between those areas where different densities on invaded lionfish were observed. For instance, where lionfish densities were relatively low, it may coincide with higher grouper densities. This direct correlational link between lionfish success and the biotic control through natural predation on the lionfish has still to be proven. More research on whether lionfish were preyed upon can be revealed from analysing stomach contents of potential lionfish predators. So far, this was only being investigated once (Maljković et al. 2008). Furthermore, keeping track on lionfish and grouper densities should tell whether this predator-prey relationship is in balance, or that lionfish may overgrow grouper populations. Simultaneously, research has to be conducted on which smaller-bodied predators are potentially able to feed on the larval stage of lionfish, what is so far never been observed or investigated.

Second, there are more species interactions in the recipient communities promoting invasion resistance. Usually, invaders' exponential growths are followed by an equilibrium state, where densities of the invader may stabilize or even declined through food competition with native species (Parker et al. 2001). In this case, only one study determined native species sharing the same food source with the invaded lionfish (Layman and Allgeier 2011). However, the rate in which these specific species compete for food is rather unknown. Conclusive data comparing lionfish diet, consumption rates and the competitive ability with native species are needed. Then, the potential consequences on native species abundances can be determined by monitoring predator and prey abundances.

If all data has been collected and analysed and still shows an increase of lionfish densities, as well as high predation rates causing an abrupt decline of juveniles of small fish species, then a shift might occur to lionfish eating juveniles of large-bodied fish, such as parrotfish and grunts. This may have cascading impacts through disruption of the food web and reduces the functional role of these herbivores that control coral-algal dynamics. Then, the indirect effects on habitat structure and function can be monitored by the percent cover of benthic organisms in relation to native fish and lionfish densities. If these potential impacts on native communities truly occurred, then active removal on a local scale might help to reduce and maintain lower lionfish densities. To determine whether this would have an effect, areas need to be compared where lionfish are actively managed and where they are not. But so far, there is still a long way to go for researchers in collecting data to cover all the aspects in order to determine the impact of this invasion.

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