



Review

Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean



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ABSTRACT

The invasion of western Atlantic marine habitats by two predatory Indo-Pacific lionfish, *Pterois volitans* and *P. miles*, has recently unfolded at an unprecedented rate, with ecological consequences anticipated to be largely negative. We take stock of recently accumulated knowledge about lionfish ecology and behaviour and examine how this information is contributing to our general understanding of the patterns and processes underpinning marine predator invasions, and to the specific issue of lionfish management. Lionfish were first reported off Florida in 1985. Since their establishment in The Bahamas in 2004, they have colonised 7.3 million km² of the western Atlantic and Caribbean region, and populations have grown exponentially at many locations. These dramatic increases potentially result from a combination of life-history characteristics of lionfish, including early maturation, early reproduction, anti-predatory defenses, unique predatory behaviour, and ecological versatility, as well as features of the recipient communities, including prey naïveté, weak competitors, and native predators that are overfished and naïve to lionfish. Lionfish have reduced the abundance of small native reef fishes by up to 95% at some invaded sites. Population models predict that culling can reduce lionfish abundance substantially, but removal rates must be high. Robust empirical estimates of the cost-effectiveness and effects of removal strategies are urgently needed because lionfish management will require a long-term, labour-intensive effort that may be possible only at local scales. The ultimate causes of the invasion were inadequate trade legislation and poor public awareness of the effects of exotic species on marine ecosystems. The lionfish invasion highlights the need for prevention, early detection, and rapid response to marine invaders.

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1. Introduction

Species invasions are occurring worldwide at an unprecedented rate and represent a major threat to the world's flora and fauna (Vié et al., 2009; Vitousek et al., 1997). More than half a century ago, Elton (1958) drew attention to the ecological damage caused by non-native species. Since then, two goals have dominated the invasion ecology research agenda: identifying the traits of introduced species that make them likely to become invasive, and the characteristics of ecological communities that make them susceptible or resistant to invasions. General answers to these questions have proven elusive. Different species traits correlate with success at different stages of the invasion process, and these vary broadly among taxa (Cadotte et al., 2006; Kolar and Lodge, 2001). Similarly, attempts to identify the characteristics of native communities that determine invasibility have generated much theory about the role of species diversity (Levine, 2000), fluctuating resources (Davis et al., 2000), habitat heterogeneity (Melbourne et al., 2007) and propagule pressure (Williamson, 1996), as well as a multitude of empirical tests of these hypotheses. The importance of any or all of these mechanisms may shift with the spatial scale of analysis and over time as invasions unfold (Strayer et al., 2006).

Our understanding of invasion patterns, and particularly processes, in the marine realm has lagged far behind the terrestrial world, even though invaders occur in virtually all marine ecoregions (Molnar et al., 2008). Like their terrestrial counterparts, most marine invaders tend to occupy low trophic levels (Fig. 1; see also Byrnes et al., 2007). Accordingly, evidence for some of the above mechanisms of community invasibility exists for invasions of sea-grass, algal and sessile invertebrate assemblages, which essentially function like terrestrial plant communities and are strongly influenced by competitive interactions (Callaway and Walker, 1997). Marine invaders, in particular vertebrates, occupying higher trophic levels are much rarer (Fig. 1) but they present interesting cases to test current hypotheses because of their potential to be involved in predatory interactions which, in the sea, are affected strongly by the relative body sizes of predators and prey (Kerr and Dickie, 2001) and are an important force structuring marine communities (Hixon, 1991; Jennings et al., 2001).

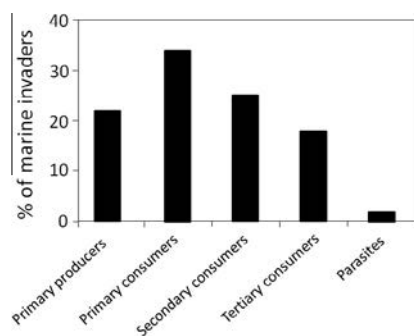


Fig. 1. Percentage of marine invading species in relation to trophic group. Data were derived from the Global Marine Invasive Species Assessment database (<http://conserveonline.org/workspaces/global.invasive.assessment>), which contained 334 species at the time of the review. We assigned each species to the highest trophic group given for that species.

One such invasion by predatory fishes has recently unfolded in the western Atlantic at a rate and magnitude never before documented in any marine system. It involves two species of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*; Fig. 2). In their native ranges, *P. miles* occurs in the Indian Ocean from South Africa to the Red Sea and east to Sumatra, while *P. volitans* is distributed throughout the western Pacific from southern Japan to Western Australia and east to the Pitcairn Group in the South Pacific (Kulbicki et al., 2012; Schultz, 1986). Although genetically distinct (Kochzius et al., 2003), these sister species are difficult to tell apart visually (Freshwater et al., 2009). First documented off Florida in the 1980s, lionfish are now established as invasive species along the eastern coast of the USA, the Gulf of Mexico and the Caribbean Sea (Schofield, 2009), and rapid increases in abundance on many reefs have followed their swift range expansion (Green et al., 2012; Green and Côté, 2009). Lionfish consume a wide range of native fish and invertebrate species (Côté et al., 2013; Morris and Akins, 2009; Muñoz et al., 2011), and are well defended from predation by venomous fin spines (Halstead et al., 1955). The potentially extreme ecological impacts of this invasion (Albins and Hixon, 2011) provide an urgent impetus to understand patterns and underpinning processes associated with invasive marine predators.

As a result of this pressing need for information, the original trickle of research on lionfish, which for many years focussed mainly on venomology (e.g., Halstead et al., 1955; Saunders and Taylor, 1959) and mechanics of suction feeding (e.g., Muller and Osse, 1984), has been transformed into a torrent of new data on ecology, behaviour, and genetics, particularly from populations in the invaded range (Fig. 3). It therefore seems timely to take stock of this newly accumulated knowledge to examine how this information is contributing to the management of the lionfish invasion and to general understanding of invasions by predatory fishes. With this in mind, we conducted a review of the literature on lionfish in April 2013. We searched the Web of Knowledge™ with the keywords *Pterois* AND (*miles* or *volitans*), as well as Google Scholar with the keywords *Pterois* and “lionfish invasion”, to retrieve all



Fig. 2. Invasive Indo-Pacific lionfish in the Atlantic. The photograph was taken off New Providence Island, Bahamas, in July 2010 (photo credit: I.M. Côté).

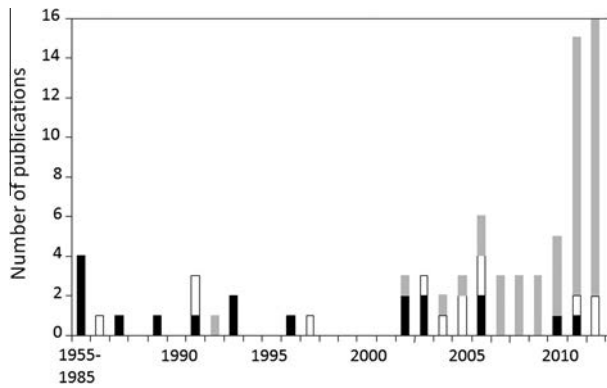


Fig. 3. Annual numbers of scholarly publications on lionfish since 1955. The year 1985 includes all studies published between 1955 and 1985. The year 2012 includes publications for the first 3 months of 2013. Studies of venemology are shown in black bars; ecological, genetic or physiological studies of lionfish conducted in the native range are shown in white and those from the introduced range, in grey.

available scholarly papers (which yielded the statistics in Fig. 3) and unpublished reports. We also conducted the searches using synonyms of *P. volitans* and *P. miles*. We retrieved all papers and synthesised their contribution to our ecological understanding of these species, of the invasion and of ways to manage it.

Our specific goals were to outline the factors that may have contributed to the rapid geographic spread of lionfish and their subsequent population increases after colonisation, and summarise the documented and predicted impacts of this invasion. We then evaluate how this information is contributing to our understanding of invasions by marine predators and of how to manage shallow-water ecosystems affected by this invasion.

2. Brief history of the lionfish invasion

The lionfish invasion is probably the best documented marine invasion to date. Sightings of lionfish by concerned citizens, including marine scientists, recreational divers, and fishers, have



Fig. 4. Distribution of Indo-Pacific lionfish *Pterois volitans* and *P. miles* in the northwestern Atlantic as of July 2012. Data courtesy of Dr. Pamela J. Schofield, USGS Nonindigenous Aquatic Species Database.

accumulated quickly in well-publicised and publically available databases, such as the US Geological Survey Nonindigenous Aquatic Species (USGS-NAS) database (Schofield et al., 2012), and the Reef Environmental Education Foundation (REEF) Volunteer Survey Project database. These observations have allowed the lionfish invasion to be tracked in nearly real time (Fig. 4; see the animated version of this map at <http://nas.er.usgs.gov/queries/FactSheets/LionfishAnimation.aspx>).

Lionfish sightings databases reveal the following chronology of events. Lionfish were first documented off the coast of Florida in 1985 (Schofield, 2009). There were sporadic sightings in southeast Florida until 2000, when reports of juvenile lionfish emerged from as far north along the US east coast as Long Island, New York, and east to Bermuda (Ruiz-Carus et al., 2006; Whitfield et al., 2002). Sightings in 2000 and 2001 were concentrated off the coast of North Carolina (Whitfield et al., 2002), where lionfish became as abundant as the commonest native grouper species by 2004 (Whitfield et al., 2007). The same year, lionfish were first seen on Bahamian coral reefs (Schofield, 2009), at which point the invasion front rapidly proceeded eastward and then southward. By 2012, lionfish had become established around every island and along most of the Central and South American coasts of the Caribbean Sea, as well as in the eastern portion of the Gulf of Mexico (Schofield et al., 2012). Confirmed sightings of newly established populations in the western Gulf of Mexico suggest that lionfish will soon complete their invasion of this basin. Thus, in just 8 years since their establishment in The Bahamas, lionfish have colonised an area of some 7.3 million km² of the western Atlantic, Caribbean Sea and Gulf of Mexico.

The most likely vector of introduction into Florida waters, the location of first sightings, is the release of lionfish from aquaria (Semmens et al., 2004; Whitfield et al., 2002). Lionfish are popular aquarium fishes (Wood, 2001). Moreover, off the southeast coast of the US, the non-native marine fish species sighted by recreational divers are disproportionately among the species most frequently imported by the local aquarium trade (Semmens et al., 2004). Genetic analyses have confirmed the presence of both *P. volitans* and *P. miles* on the US Atlantic coast, in Bermuda and The Bahamas, but only *P. volitans* has been identified so far elsewhere in the introduced range (Betancur-R et al., 2011; Hamner et al., 2007; Morris and Green, 2012).

The progression of the invasion reconstructed from sightings data confirms insights obtained from genetic analyses and dispersal models. All lines of evidence suggest that the invasion proceeded by current-driven dispersal of pelagic larvae from successively invaded locales in a stepping-stone fashion, with the original founding population located off southeast Florida (Betancur-R et al., 2011; Freshwater et al., 2009). Lionfish populations of the US Atlantic coast have low genetic diversity compared to native populations (Betancur-R et al., 2011; Hamner et al., 2007). This finding is consistent with a strong founder effect, arising from the release of one small group or multiple releases of individual lionfish with a small number of haplotypes. If multiple releases occurred, then they have probably been confined geographically, i.e., most likely to south Florida (Johnston and Purkis, 2011). The genetic similarity between lionfish from The Bahamas and those from North Carolina (Freshwater et al., 2009) supports the idea that the source of Bahamian lionfish is egg and/or larval dispersal from one or more populations that were already established on the east coast of the United States (Betancur-R et al., 2011; Hamner et al., 2007). The time lag between the colonisation of the US east coast and that of The Bahamas is explained by biophysical models of connectivity and genetic analyses, which suggest limited exchange between these two regions owing to the northward flowing Gulf Stream current (Carlin et al., 2003; Cowen et al., 2006; Roberts, 1997). The lower genetic diversity observed in lionfish

from the Caribbean than from the northwest Atlantic (i.e., US, The Bahamas, Bermuda) suggests a secondary founder effect (Betancur-R et al., 2011). This genetic discontinuity matches another time lag in lionfish spread – the first Caribbean sightings were reported 3 years after the initial colonisation of The Bahamas (Schofield, 2009) – as well as the presence of a putative barrier to dispersal between The Bahamas and Caribbean islands to the south (Cowen et al., 2006). The nature of this barrier is currently unclear; it may be a temperature or salinity discontinuity or an ocean circulation constraint (Cowen et al., 2006).

Ocean currents are the likely transport mechanism of lionfish eggs and larvae (Hare and Whitfield, 2003). Indeed, simulations using a simple cellular automata algorithm suggest that consideration of current speed and direction alone can fairly accurately recreate the spatial sequence of invasion revealed by the USGS-NAS sightings database (Johnston and Purkis, 2011). These simulations, carried out in early 2010, led to predictions of increases in lionfish population densities at the initial sites of introduction in south Florida, from larvae originating from the newly colonised upstream locations in the Florida Keys and Caribbean, as well as imminent establishment throughout the Gulf of Mexico (Johnston and Purkis, 2011). These predictions came to pass later that year (Schofield, 2010).

Although the sequence of invasion was accurately duplicated by a current-only model, it is less clear how well the model predicted the timing of invasion of various parts of the lionfish's new Atlantic and Caribbean range. Freshwater et al. (2009) suggested that lionfish spread has in fact occurred faster than predicted by another circulation model (Cowen et al., 2006). Côté and Green (2012) estimated the rate of advance of the invasion's southward front through the Caribbean at approximately 250–300 km yr⁻¹ between 2004 and 2009. The speed of the northward front from the Caribbean into the Gulf of Mexico appears to have been even faster (~400 km yr⁻¹; Schofield, 2010). By comparison, when reviewing the rates of spread of introduced marine organisms ranging from macroalgae to fishes, Kinlan and Hastings (2005) found an average yearly movement of invasion fronts of 52 km (±10.6 km, SE; n = 38 species). Nearly 80% (30 of 38 species) of marine invaders expanded their ranges by less than 100 km yr⁻¹. The most mobile

invaders were a polychaete worm (*Marenzelleria viridis*, 246.7 km yr⁻¹) and a mussel (*Perna perna*, 235 km yr⁻¹), clearly owing to larval rather than adult dispersal. Notwithstanding the potential effects of local oceanographic conditions, if these numbers are representative of the spreading capacity of marine species in novel environments, then lionfish appear to be particularly good dispersers.

3. Mechanisms facilitating spread

Invasiveness in fishes is associated with a number of life-history and behavioural characteristics (García-Berthou, 2007; see also Morris and Whitfield, 2009, for an application to lionfish). Here, we examine potential correlates of two aspects of lionfish invasiveness: rate of geographic spread in a new environment (this section) and rate of population increase after establishment (Section 4). Reproductive output, larval behaviour and dispersal and post-settlement movement may contribute to the spread of marine invasive species, while the lack of physical, physiological or biotic barriers may ensure that far-dispersing larvae, juveniles and adults encounter suitable habitat. Dispersal barriers in particular have implications for the future spread of lionfish.

3.1. Larval dispersal

In the marine environment, having a long pelagic larval phase might seem like a key trait needed to disperse widely across large expanses of unsuitable habitat. In this respect, lionfish are unremarkable. Relative to other reef fishes (Lester and Ruttenberg, 2005), lionfish have an average pelagic larval duration (mean ± SD: 26 ± 3.5 days; Ahrenholz and Morris, 2010). However, pelagic larval duration is a poor correlate of geographic range size in marine fishes, particularly in the Atlantic (Lester and Ruttenberg, 2005; Luiz et al., 2012). Moreover, the rate of spread of marine invasive species correlates best with the propensity for occasional long-distance dispersal (Kinlan and Hastings, 2005). Two characteristics – high reproductive output and well-protected eggs or larvae – might increase the lionfish's likelihood of long-distance dispersal.

Table 1

Fecundity and minimum age at sexual maturity of Indo-Pacific lionfish and of ecologically similar native Caribbean reef-fish mesopredators. A fuller list of mesopredator species, which are deemed ecologically similar to lionfish in the Bahamas, is given in Green et al. (2012), but we included here only those species for which either fecundity or growth information is available. 'Method' refers to the method used to estimate fecundity: 1 = Vitellogenic oocyte count (total ovary count); 2 = Vitellogenic oocyte count (extrapolation from ovary subsample); 3 = Count of eggs spawned in captivity. Fecundity is presented either as per spawning event (PE) or as annual fecundity (A). PE/A denotes cases where per event fecundity is also annual fecundity; PE/A? indicates uncertainty about the similarity of these values. When available, the range of fish sizes (cm) corresponding to fecundity estimates and sampling locations are given. Within each species, fecundity and ages at maturity were not usually obtained from the same populations. Sources: 1: Morris (2009); 2: Thompson and Munro (1978); 3: Sadovy and Eklund (1999); 4: Sadovy et al. (1994); 5: Fishbase.org (accessed 18 January 2013); 6: Ault et al. (1998); 7: Sadovy et al. (1992); 8: Watanabe (2001); 9: Barbour et al., 2011; 10: Whiteman et al., 2005.

Species	Common name	Method	Fecundity	Minimum age at maturity	Growth rate <i>k</i> (cm per year)
<i>Pterois volitans</i> (introduced range)	Red lionfish	3	PE: 10,790–41,392 ¹ A: 2,000,000 ¹ (25.0–35.0 TL)	<1 year ¹	0.47 ⁹
<i>Lutjanus analis</i>	Mutton snapper	?	PE/A: 373,000–1,370,000 ⁸ (46–55 cm TL; Bahamas)	2 years ⁶	0.13–0.25 ⁵
<i>Lutjanus apodus</i>	Schoolmaster	–	–	–	0.35 ⁵
<i>Lutjanus griseus</i>	Grey snapper	–	–	–	0.10–0.24 ⁵
<i>Lutjanus jocu</i>	Dog snapper	–	–	–	0.10 ⁵
<i>Lutjanus mahogoni</i>	Mahogany snapper	–	–	–	0.10 ⁵
<i>Cephalopholis fulva</i>	Coney grouper	1	PE/A?: 67,883–282,389 ² (23.2–24.3 TL; Jamaica)	1.1 year ⁶	0.14–0.63 ⁵
<i>Epinephelus adscensionis</i>	Rock hind	–	–	–	0.11–0.17 ⁵
<i>Epinephelus guttatus</i>	Red hind	1	PE/A: 96,000–526,000 ² (26.0–41.0 TL; Jamaica)	2 years ⁷	0.12–0.24 ⁵
		2	PE/A: 978,620 (mean) ¹⁰ (mean: 36.7 TL; US Virgin Islands)		
<i>Epinephelus striatus</i>	Nassau grouper	1	PE/A: 350,000–6,500,000 ³ (30.0–70.0 SL; Belize)	4 years ³	0.06–0.22 ⁵
		1	PE/A: 11,724 – 4,327,440 ³ (47.5–68.6 SL; Bahamas)		
<i>Mycteroperca tigris</i>	Tiger grouper	1	PE/A: 308,060–1,972,434 ⁴ (25.5–37.5 SL; Puerto Rico)	2 years ⁴	0.11 ⁵

Larval behaviour could be important too. Reef fish larvae show a range of behaviours, such as sustained directional swimming and judicious choice of depth that result in faster movement (e.g., Leis et al., 2007), which can influence dispersal. Nothing is currently known of lionfish larval behaviour.

3.2. Continuous reproduction and high fecundity

Lionfish spawn in pairs and females produce ~10,000–40,000 eggs per spawning event (Morris, 2009), which is lower than the per-event fecundity of many native Caribbean mesopredators (Table 1) that have been classified as ecologically similar to lionfish on the basis of similarity of diet at comparable body sizes on reefs in The Bahamas (Albins, 2013; Green et al., 2012). However, egg maturation in lionfish is asynchronous (Morris et al., 2011a), hence females can release eggs nearly continuously when conditions are favourable. In North Carolina and The Bahamas, female lionfish are likely to spawn approximately every 4 days during the summer months, with less frequent spawning during the colder months (Morris, 2009). Spawning is likely to occur more frequently in the southern parts of the introduced range. The annual fecundity of an average female lionfish may exceed 2 million eggs (Morris, 2009), which would place lionfish near the top end of the annual fecundity ranges in Table 1, since the per-event fecundity for most of these native species also represents annual fecundity.

3.3. High survival of eggs and larvae?

During each spawning event, female lionfish produce two buoyant masses of eggs embedded in a gelatinous matrix, which are fertilised externally by the male (Fishelson, 1975; Morris et al., 2011a). This reproductive strategy offers numerous potential advantages. The gelatinous matrix may entrap the sperm, potentially enhancing fertilisation by preventing sperm dilution (Morris et al., 2011a). This matrix is also thought to contain a chemical deterrent to predation (Moyer and Zaiser, 1981). In addition, buoyant egg masses and larvae may facilitate broad and rapid dispersal by temporarily keeping the eggs near the surface where wind-driven currents are stronger than they are at depth (Betancur-R et al., 2011; Freshwater et al., 2009).

3.4. Post-settlement dispersal

Although movement at the egg and larval stages undoubtedly contribute the most to the overall geographic spread of marine invasive species, movement by post-settlement individuals can also increase distribution range (Kinlan and Hastings, 2005). There is so far limited information on the movements of lionfish, although this is an active area of current research. The only study published to date suggests that relatively small lionfish occupy small home ranges and are highly sedentary: three-quarters of the small (≤ 25 cm TL) lionfish tagged along the shore of an estuarine river in Florida had moved less than 10 m from their tagging locations after ~30 days at liberty (Jud and Layman, 2012). Fewer than 5% of tagged fish had moved more than 100 m, and the longest movement recorded was 420 m in 67 days by a 126 mm (standard length) lionfish (Jud and Layman, 2012).

However, this high degree of site fidelity is perhaps not characteristic of larger lionfish, and of lionfish living in less linear habitats. Ongoing studies in The Bahamas suggest that adult lionfish associated with coral reef patches regularly roam considerable distances (>200 m) over sand between reefs, with occasional very long-distance (2 km) travels (authors' unpublished data). It remains to be seen whether extensive movement after settlement occurring at the patch scale can explain some of the discrepancy between the expected rate of lionfish spread based on current-dri-

ven larval dispersal and the observed distribution at the regional scale (Freshwater et al., 2009).

3.5. Ability to cross environmental barriers

Invading species that are ecological generalists, in terms of either food or habitat, are often more successful at establishing new populations, and thereby expanding their range (Moyle and Marchetti, 2006; Romanuk et al., 2009). Within the Caribbean region, the spread of lionfish has undoubtedly been helped by the fact that lionfish appear to be habitat generalists. Juvenile and adult lionfish have been found in a wide variety of natural habitats, including temperate hard-bottom reefs (Whitfield et al., 2002, 2007), shallow and mesophotic coral reefs (Albins and Hixon, 2011; Biggs and Olden, 2011; Lesser and Slattery, 2011), seagrass beds (Claydon et al., 2012), mangroves (Barbour et al., 2010), and estuarine rivers up to 6.5 km from the ocean, in nearly fresh water (Jud et al., 2011; Z. Jud, personal communication). In fact, they may be found wherever some three-dimensional structure is available. Suitable structure includes human-made habitats such as wrecks, discarded fishing gear and other debris (Smith, 2010), in otherwise featureless surroundings (Fig. 2). It is not known whether newly settled lionfish exhibit the same habitat versatility as older lionfish. The extent to which individuals move among habitat types is also unclear.

Beyond the Caribbean basin, the distribution of lionfish, as well as that of other tropical marine fishes, is potentially limited by three major dispersal barriers: a thermal barrier to the north, a salinity barrier to the south, and a deep-water barrier to the east. The thermal barrier to the north is determined by the tolerance of fish species to cold water. Physiological experiments show that, in the laboratory, the critical thermal minimum (CT_{min}) for lionfish is 10 °C (Kimball et al., 2004). This threshold is several degrees lower than the CT_{min} measured for other Indo-Pacific reef fishes introduced via the aquarium trade to the US east coast (~15 °C for eight damselfish species, Eme and Bennett, 2008). As a result, while introduced damselfish are expected to survive only south of Cape Canaveral, Florida (Eme and Bennett, 2008), the range limit of lionfish along the east coast of North America should be Cape Hatteras, North Carolina, some 900 km to the north – a region reached by lionfish in 2000 (Whitfield et al., 2002). Sightings from more northern locations probably represent temporary summertime range expansions by juveniles, but winter water temperatures are currently too cold to permit overwintering by lionfish.

The other two barriers to dispersal by Caribbean invaders are the salinity barrier to the south presented by the Amazon-Orinoco Plume (AOP), and the deep-water barrier to the east in the form of the mid-Atlantic Barrier (MAB) – a continuous stretch of more than 3000 km of open water with depths of more than 7000 m. These barriers are permeable, as evidenced by genetic analyses of populations established on both sides of the barriers (e.g., Robertson et al., 2006; Rocha et al., 2005). In fact, many fish species native to the western Atlantic have crossed them: 40% of western Atlantic fishes are found on both sides of the AOP, while 11% have distributions that span the MAB (Luiz et al., 2012). Lionfish possess the key characteristics associated with the ability to cross the AOP. Such species are typically relatively large and able to use multiple habitat types, which may allow them to traverse stretches of adverse conditions through a stepping-stone effect (Luiz et al., 2012). In contrast, the propensity to raft (i.e., to aggregate under drifting flotsam) appears to be an important determinant of the ability to cross the MAB (Luiz et al., 2012). To our knowledge, lionfish have not yet been reported in rafting assemblages. Their demersal habit may make this behaviour unlikely.

4. Mechanisms facilitating population increases

Like many introduced species both on land and in the sea, lionfish have undergone dramatic population increases once established in their non-native range (Fig. 5). For example, in the Florida Keys, USA, where lionfish were first reported in 2009, lionfish abundance increased 3–6-fold between 2010 and 2011 alone (Ruttenberg et al., 2012). Note that real abundances may be much higher than those reported so far that derive from standard underwater survey methods because these methods substantially underestimate lionfish numbers (Green et al., 2013; Kulbicki et al., 2012). Lionfish population densities in some Atlantic locations far surpass those observed in the native range (Darling et al., 2011; Green and Côté, 2009; Kulbicki et al., 2012; Whitfield et al., 2007). They might continue to increase, at least in some locations, given that field experiments in The Bahamas indicate that lionfish populations have not yet reached levels where density dependence indicative of within-species competition is evident (Benkwitt, in press).

Population explosions by invasive species can occur in part owing to intrinsic characteristics of the invader (e.g., fast life history, competitive ability), but they can also be facilitated by characteristics of the recipient community (e.g., the scarcity of effective native competitors, predators and parasites, resource availability, etc.). Both sets of factors may be conferring to lionfish great potential for population growth.

4.1. Fast life-history

Early maturation is one of the most important life-history characteristics contributing to high intrinsic rates of population increases in marine fishes (Denney et al., 2002). Lionfish appear to grow more quickly than some native western Atlantic mesopredators (Table 1). They also grow much more rapidly in the invaded Atlantic than in their native Pacific range (Pusack et al., unpublished data). They can become sexually mature within their first year of life (Morris, 2009), which appears to be earlier than for comparable mesopredators on Atlantic coral reefs (Table 1). Early age at maturity, combined with frequent, year-round reproduction

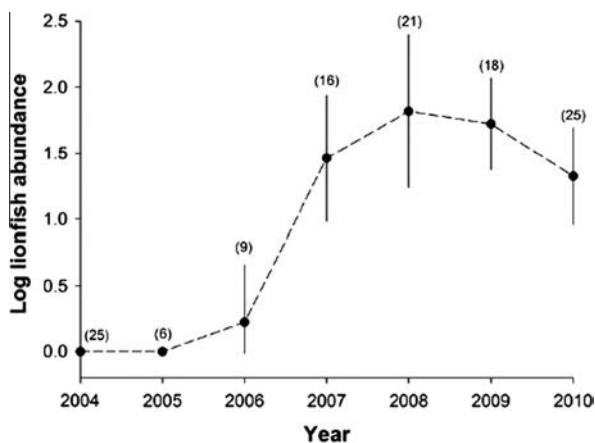


Fig. 5. Typical trajectory of population growth for Indo-Pacific lionfish introduced to the Atlantic. The data were derived from the Reef Environmental Education Foundation (www.reef.org) database for coral reefs off southwest New Providence, Bahamas. Abundance is the number of lionfish sighted per survey, recorded in \log_{10} scale. Points represent log-scale means with 95% confidence intervals. The number of surveys is given in parentheses for each year. From Green et al. (2012; doi:<http://dx.doi.org/10.1371/journal.pone.0032596.g001>).

(see Section 3.2), would result in chronic lionfish propagule pressure on habitats near and far.

4.2. Competitive ability

Some studies have suggested that invaders may have superior competitive ability compared to species native to the recipient habitat (e.g., Keane and Crawley, 2002; Vilà and Weiner, 2004). It is not clear whether this is the case for lionfish. Analyses of stable isotopes, which reveal both the source of dietary carbon and trophic level at which consumers are feeding, show extensive overlap between lionfish and some native Caribbean mesopredators (e.g., schoolmaster *Lutjanus apodus* and grey snappers *L. griseus*, Layman and Allgeier, 2012). However, field experiments suggest that even with such dietary overlap, the presence of lionfish does not affect the growth rate of a similar-sized Atlantic fish predator, the coney grouper *Cephalopholis fulva*, where they co-occur, nor do coney affect lionfish growth (Albins, 2013). Nevertheless, lionfish are capable of achieving significantly faster growth and prey consumption rates than coney (Albins, 2013; see also Table 1). In fact, Albins (2013) suggested that, by virtue of their faster growth rate, lionfish might quickly become predators of their contemporary cohort of native groupers. At the moment, there is no evidence to suggest that lionfish compete overtly with native mesopredators, but their hunting mode, trophic versatility and the naïveté of their prey, may make lionfish effective exploitation competitors in the long term (see also Section 5.1). More field experiments are needed to test this possibility.

Lionfish are gape-limited stalking predators. While their predation rates and tactics are similar between their native and invaded range (Cure et al., 2012), the slow, hovering hunting style employed by lionfish (Côté and Maljković, 2010; Green et al., 2011) and one of their prey capture techniques, which consists of blowing jets of water at prey (Albins and Lyons, 2012), are unique among Atlantic fishes. As a result, lionfish likely benefit from the naïveté of native prey in the invaded range (Cure et al., 2012), because their behaviour and appearance (i.e., bold striping and broad pectoral fins) are not perceived as a predation threat. Interestingly, native gobies in captivity spent more time under cover when in visual contact with a lionfish than with a native piscivore (Nassau grouper) or a native invertivore (French grunt, *Haemulon flavolineatum*), although only the native predator depressed other aspects of goby behaviour (e.g., feeding, moving, bobbing) (Marsh-Hunkin et al., 2013).

At the population level, lionfish are trophic generalists. In the Atlantic, they exploit a wide range of native fishes and crustaceans (Albins and Hixon, 2008; Côté et al., 2013; Layman and Allgeier, 2012; Morris and Akins, 2009; Muñoz et al., 2011; Valdez-Moreno et al., 2012). In The Bahamas alone, they consume at least 57 species of reef fishes from 25 families (Côté et al., 2013). Their diet is broader and their prey larger in the invaded than in the native range (Cure et al., 2012). In the western Atlantic, their diet appears to be more species-rich, on average, than that of ecologically similar mesopredators. The classic study by Randall (1967) provides some information on the food habits of nine fish species deemed to be ecologically similar to lionfish (Green et al., 2012) and for which the sizes of the specimens examined overlapped with the size range of lionfish in the Atlantic. At equivalent sampling effort, derived from a species accumulation curve of lionfish prey (Côté et al., 2013), there are more prey fish species in the stomachs of lionfish and of these native predators (mean difference [lionfish – native] $\pm 1SE = 3.9 \pm 1.5$ prey species; one-sample *t*-test, $t_8 = 2.58$, $p = 0.03$; Fig. 6). The sample size is small, hence these results could change with more data. Nevertheless, the generalist diet of lionfish may allow them to thrive in a range of habitat types

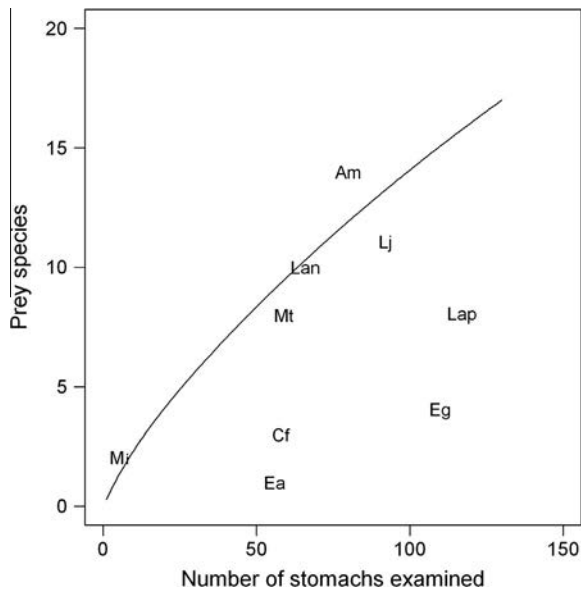


Fig. 6. Comparison of prey fish species richness in the diets of invasive Indo-Pacific lionfish and native Caribbean mesopredators. The line shows the accumulation curve of prey species identified visually for a sample of 130 lionfish captured in The Bahamas. Labels show the number of prey species recorded through visual identification, and the number of specimens examined, for nine ecologically similar native reef fishes (data derived from Randall (1967)). Am: *Aulostomus maculatus*; Lan: *Lutjanus analis*; Lap: *L. apodus*; Lj: *L. jacu*; Cf: *Cephalopholis fulva*; Ea: *Epinephelus adscensionis*; Eg: *E. guttatus*; Mi: *M. interstitialis*; Mt: *M. tigris*.

and also facilitate prey switching when particular prey types are depleted over time (e.g., Green et al., 2012).

4.3. Enemy release?

One of the commonest explanations for the establishment and rapid population increase of invasive species is that invaders have left their co-evolved natural enemies behind (the “enemy release hypothesis”, Crawley, 1997; Williamson, 1996). Some invaders are therefore successful because they do not have to contend with the predators, parasites, disease organisms, and competitors that limit their populations at home. The lack of information about lionfish and their interactions with community members in their native range hampers robust testing of the idea of ecological release. Nevertheless, relevant observations from the introduced range are accumulating.

It is likely that lionfish have few predators in their introduced range. The dorsal, anal and pelvic fin spines of lionfish contain a powerful neurotoxin (Halstead et al., 1955; Vetrano et al., 2002), which likely serves as a deterrent to post-settlement predation by naïve native carnivores. Moreover, lionfish do not exhibit the common flight response of most Atlantic fishes to perceived threat, but instead adopt a bold behaviour, with a defensive head-down pose with dorsal spines pointed forward (Green et al., 2011; Whitfield et al., 2007). Captive juvenile lionfish are relatively invulnerable to predation by wild-caught Atlantic predators, even when these predators are starved (Morris, 2009; Raymond et al., unpublished data), although small lionfish have occasionally been found in the stomachs of large Caribbean groupers (Maljković et al., 2008). However, top predators in the region have declined substantially as a result of overexploitation (Baum et al., 2003; Paddock et al., 2009; Stallings, 2009). While there is some evidence that abundant large groupers in a protected area in The Bahamas may be able to inhibit the invasion at an incipient stage (e.g., Mumby et al., 2011), this phenomenon is not observed throughout the region (Hackerott et al., unpublished data), even in areas with high

predator densities. Moreover, it is not clear whether the effect reported by Mumby et al. (2011) is due to actual predation by groupers or to risk of predation, which might change lionfish behaviour and interfere with fitness-related functions such as foraging (i.e., behaviourally mediated indirect interactions, sensu Dill et al., 2003; see also Section 5.1). The physical and behavioural defenses that make lionfish unlikely targets for consumption by Caribbean predators might be expected to be less effective in the native range because of co-evolution. However, there is only one report of predation on lionfish in the native range (Bernadsky and Goulet, 1991), although lionfish have been poorly studied throughout the Indo-Pacific region.

There is currently little information on the diseases and parasites of lionfish, either in the native or in the introduced range. A total of eight species of parasites (three monogenoids, two trematodes, one leech, one copepod and one myxozoan; reviewed by Bullard et al. (2011)) have been recorded from *P. volitans* and *P. miles* in their native range, while one generalist buccal leech (Ruiz-Carus et al., 2006) and one generalist gut fluke (Bullard et al., 2011) have so far been documented in the introduced range. The best evidence so far for enemy release has been the finding that lionfish in the invaded range have lower ectoparasite loads than those in their native range, although one group of generalist parasites (gnathiid isopods) infect lionfish at equally low rates in both ranges (Sikkel et al., unpublished data).

5. Ecological impacts: observed and anticipated

As a mesopredator, lionfish are potentially prey of larger native predators, predators of smaller native fishes and invertebrates, and competitors with native mesopredators. With this central ecological role, invasive lionfish may potentially have both direct and indirect effects on native ecosystems at a variety of levels, the possible mechanisms being both lethal and nonlethal. Given that lionfish consume a broad diversity of native reef fishes (Albins and Hixon, 2008; Morris and Akins, 2009; Muñoz et al., 2011), and feed in the wild at rates that are much higher than in captivity (Côté and Maljković, 2010; Green et al., 2011), the potential for widespread effects on native coral reef communities is substantial. The strength of direct predatory interactions suggests that related indirect effects may also be considerable. Unfortunately, there have been no comparative studies of the ecological effects of lionfish in their native Indo-Pacific range, probably because they are usually uncommon there (Kulbicki et al., 2012).

5.1. Direct effects

Invasive lionfish can cause substantial declines in the abundance of native small reef fishes, including adults of small species (e.g., gobies) and recruits of larger species that would otherwise eventually outgrow lionfish (e.g., parrotfishes). Albins and Hixon (2008) demonstrated experimentally on small patch reefs in The Bahamas that a single lionfish can reduce the abundance of small native fish by nearly 80% in just 5 weeks. In a subsequent experiment on similar reefs, Albins (2013) documented a 94% decline in small fish abundance over 8 weeks, and Albins (unpublished data) showed that such reductions over longer periods eventually lead to local extinctions. Elsewhere in The Bahamas, Green et al. (2012) observed a 65% decline, on average, in prey fish biomass over 2 years following the invasion. These observed declines are consistent with those predicted by ecosystem simulation models (e.g., Arias-González et al., 2011). The severity of predation impacts is unlikely to be uniform across taxa. Green and Côté (unpublished data) found that small, non-cleaning fishes with shallow bodies

and a demersal habit are particularly vulnerable to predation by lionfish on Bahamian reefs.

Beyond reductions in native prey density, a key question is whether predation by lionfish destabilizes or otherwise alters the population dynamics of native prey species. Proximally, the issue is whether mortality caused by lionfish is appreciably greater than that caused by native mesopredators (e.g., small groupers). The answer is yes. In two separate field experiments in The Bahamas, Albins (2013) showed that lionfish caused nearly three times the overall prey mortality caused by native coney grouper, and Pusack et al. (unpublished data) found that lionfish caused nearly twice the mortality of bridled goby (*Coryphopterus glaucofraenum*) compared to the native graysby grouper (*C. cruentata*). Ultimately, the issue is whether invasive lionfish destabilize mechanisms that naturally regulate the local population dynamics of native prey. Field experiments in The Bahamas conducted before the invasion had demonstrated that a variety of future lionfish prey underwent regulating density-dependent per capita mortality caused by native predators. These native prey included blue chromis (*Chromis cyanea*, Hixon and Carr, 1997), gobies (*C. glaucofraenum*: Forrester and Steele, 2000, 2004; Steele and Forrester, 2005; *Gnatholepis thompsoni*: Forrester et al., 2008), bicolor damselfish (*Stegastes partitus*, Anderson et al., 2007; Carr et al., 2002; Johnson, 2008; Hixon et al., 2012), and fairy basslet (*Gramma loreto*, Webster, 2003, 2004). Ingeman and Webster (unpublished data) provided evidence that the strength of density dependence in fairy basslet mortality was not altered by lionfish predation because lionfish simply added density-independent mortality to the underlying density-dependent mortality caused by native predators. (That is, the slope of the density-dependent mortality curve was not altered, but the y-intercept increased significantly.) Nonetheless, the fact that some local populations of fairy basslet were pushed toward 100% mortality in the presence of lionfish is indicative of the danger posed by the additional mortality imposed by the invader. Indeed, on small patch reefs in The Bahamas, a single lionfish can reduce local prey richness by about 5 species of native fish in just 8 weeks (Albins, 2013). Thus, while predation by native mesopredators has been generally reduced in most of the invaded region due to over-exploitation (Paddack et al., 2009; Stallings, 2009), it is becoming clear that lionfish predation does not replace regulating density-dependent mortality in prey fishes formerly provided by native predators. In fact, the high mortality imposed by lionfish, whether density-dependent or not, is pushing prey populations toward extirpation. Given that lionfish are now ubiquitous across coral reefs in the region, mortality caused by lionfish predation may have serious effects on prey population persistence.

Besides consuming native prey, lionfish could conceivably also be prey of native predators, yet to date, there is no evidence that native predators (sharks, large groupers, etc.) consume substantial numbers of lionfish (see Section 4.3 above). High densities of grouper may nonetheless interfere behaviourally with the ability of lionfish to forage effectively. Pusack (unpublished data) demonstrated experimentally in The Bahamas that patch reefs with high densities of large Nassau grouper *Epinephelus striatus*, which do not eat and otherwise ignore new recruits of other species, had significantly greater recruitment of native fishes in the presence of lionfish than did nearby reefs with fewer groupers and the same number of lionfish.

Although invasive lionfish may be behaviourally displaced by large groupers, they may nonetheless compete effectively with smaller native predators. In a cross-factored field experiment in The Bahamas, Albins (2013) demonstrated that, on the same patch reefs starting at the same body size, lionfish grew six times as fast as native coney grouper (see also Section 4.2). Time will tell whether competition between invasive lionfish and native mesopredators substantially alters the abundance of these species.

In addition to competing for food, lionfish can potentially compete for shelter with native species. Henderson and Côté (unpublished data) found that the shelters used by lionfish and by commercially important Caribbean spiny lobster *Panulirus argus* differed in height above the substratum when the two species co-occurred but not when one of the species was absent from a site. Nevertheless, suitable shelters appeared abundant, suggesting that competition is probably weak if it does occur.

5.2. Indirect effects

Indirect effects occur when a strong interactor directly alters the abundance of another species, which in turn alters the abundance of a third species that interacts directly with the second species (but not directly with the strong interactor). As a strong predator and potential competitor, lionfish may indirectly affect native species that directly interact with the species they consume or otherwise displace. Albins and Hixon (2011) described a possible cascade of effects that could manifest if lionfish greatly decrease the density of herbivorous fishes. In response to reduced herbivory, macroalgae could potentially increase and overgrow corals, contributing to the degradation of reefs. Lesser and Slattery (2011) provided circumstantial evidence consistent with this possibility from deep reefs in The Bahamas.

Another possibility is that lionfish could consume or interfere with the activities of native cleaning gobies (*Elacatinus* spp.), thereby indirectly causing an increase in the ectoparasite loads of native reef fishes. Côté and Maljković (2010) observed lionfish approaching and disrupting cleaning stations, including consumption of a facultative cleaner, the bluehead wrasse *Thalassoma bifasciatum*. It is unknown whether such interactions substantially disrupt cleaning mutualism to a level that affects parasite loads.

6. Outlook

From a scientific viewpoint, the human-caused invasion of the tropical and subtropical western Atlantic by lionfish is a large-scale, uncontrolled experiment with profuse spatial replication, which is giving us a rare, though unfortunate, opportunity to test and expand ideas about marine invasions. At the same time, it has given rise to a significant new threat to the persistence of native reef fishes and their habitats in a region where coastal ecosystems in general, and coral reefs in particular, are already degraded by multiple stressors (Alvarez-Filip et al., 2009; Gardner et al., 2003).

6.1. Insights into invasion ecology

Invasions by marine predatory species are rare. Before lionfish, known cases were limited to the peacock grouper *Cephalopholis argus* (Dierking et al., 2009), the black-tailed snapper *Lutjanus fulvus*, and bluelined snapper *L. kasmira* (Friedlander et al., 2002) – all introduced to the Hawaiian Islands from other Pacific islands in the 1950s to enhance fisheries – and the red drum *Sciaenops ocellatus*, brought from the northwestern Atlantic to Taiwan for aquaculture in 1987 (Liao et al., 2010). At least two of these (peacock grouper and blue-lined snapper) now dominate the density and biomass of coral reef fish communities in their introduced range (Dierking et al., 2009; Friedlander et al., 2002). Although genetic studies can reveal something of the population history of these species since their introduction (e.g., Gaither et al., 2012), there has been no documentation of their geographic spread, population increases, and impacts on native biota. The wealth of such real-time information on the lionfish invasion, gathered by both the for-

mal scientific community and citizen science (e.g., Ruttenberg et al., 2012), makes this invasion truly unique.

Why have lionfish populations experienced exponential growth at each new location colonised in their introduced range? These dramatic increases appear to have been driven by a perfect storm of species and ecosystem characteristics, which potentially include intrinsic life-history traits of lionfish, such as early maturation, prolific reproductive output, anti-predatory defenses, and ecological versatility, and features of the recipient Atlantic ecosystems, including naïve prey, weak competitors, and naïve predators that are overexploited. It is not clear why, with life-history traits that appear to promote a high intrinsic rate of population growth, neither *P. volitans* nor *P. miles* is particularly abundant in its native range (Kulbicki et al., 2012). One possibility is that some of the characteristics that make lionfish effective invaders have already diverged, probably phenotypically rather than genetically, and lionfish in the native range in fact exhibit slower life histories and/or narrower resource use. There is evidence that lionfish body size (Darling et al., 2011) and aspects of hunting behaviour (Cure et al., 2012) are different between the native and introduced ranges. Lionfish also grow twice as fast in the Atlantic than in their native Indo-Pacific range (Pusack et al., unpublished data). However, longitudinal studies that can properly test for evolution of increased competitive ability (sensu Blossey and Nötzold, 1995) or predatory ability are needed. Alternatively, it may simply be that invasive lionfish in the Atlantic have escaped natural Indo-Pacific enemies that have yet to be identified.

The lionfish invasion is currently a unique event in the western Atlantic, and it is difficult to predict whether subsequent predatory invasions will occur there in the future. Nonetheless, the lionfish invasion is offering a model to test the importance of species diversity (Levine, 2000), fluctuating resources (Davis et al., 2000), habitat heterogeneity (Melbourne et al., 2007) and propagule pressure (Williamson, 1996) in the invasibility of marine habitats. Formal tests of these mechanisms have yet to be conducted using lionfish, but they should be possible. However, any conclusion may be strengthened by a comparison to the invasion by *P. miles* of the Mediterranean Sea. *P. miles* was first caught in the Mediterranean in 1991 off the central coast of Israel (Golani and Sonin, 1992). The most probable route of introduction was passage through the Suez Canal, which opened in 1869. The distribution of *P. miles* remains inexplicably limited to the eastern end of the Mediterranean (Golani, 1998). *P. miles* and *P. volitans* could, in spite of their morphological similarity (Freshwater et al., 2009), differ in key life-history traits that affect population dynamics. It is also possible that the answer lies in critical ecosystem differences between the Mediterranean and the western Atlantic, which would provide substantial insights into the factors facilitating invasions by marine predators.

Populations of invasive species sometimes collapse spontaneously after rapid population growth (Simberloff and Gibbons, 2004). Will this happen with lionfish? It is difficult to tell whether the downturn in lionfish abundance observed recently at some sites in The Bahamas (Fig. 4) marks the start of such a phenomenon. At any rate, various causes, ranging from competition among invasives to interactions with native species, have been proposed to explain specific cases of collapse, but the causes of the majority of invasive population crashes remain unclear (Simberloff and Gibbons, 2004). Repeated collapses of lionfish populations, particularly while other populations remain stable, could offer an unrivalled opportunity to understand the boom-and-bust cycles of invasive species.

6.2. Managing lionfish: Where do we go from here?

Based on the knowledge gained to date on invasive lionfish, in terms of spread, abundance, behaviour and life history, it is

unequivocally clear that lionfish cannot be eradicated from the Atlantic, at least with the tools currently at hand. However, it is equally clear that the lionfish invasion should be managed to mitigate its profound ecological impacts, and the ensuing potential economic consequences which have yet to be estimated. How can this be done?

Various models have been developed to estimate the exploitation rates necessary to lower lionfish abundances. The approaches vary, from food web structure simulations to age-structured and stage-based population models, but the overall conclusions are essentially the same. Substantial reductions in lionfish biomass or abundance can be achieved with frequent removal of lionfish (Arias-González et al., 2011; Barbour et al., 2011; Morris et al., 2010). The exploitation rates necessary to cause these reductions are high (e.g., 27–65% of the population per annum), and cessation of removals leads to quick lionfish recovery (Arias-González et al., 2011; Barbour et al., 2011). Taken together, these studies suggest that the management of the lionfish invasion must be a long-term proposition and, given the intensity of effort required, it is likely to be possible only at small spatial scales.

Robust empirical tests of the effects of lionfish removals are currently lacking. Lionfish culling by concerned individuals and through organised lionfish derbies and tournaments (Akins, 2012) is currently occurring haphazardly throughout the region, but with little monitoring of effects. Frazer et al. (2012) showed that targeted lionfish removals by divers occurring at irregular intervals over 7 months reduced overall numbers as well as the mean size of lionfish on coral reefs in Little Cayman. In a large-scale field experiment, Green et al. (unpublished data) applied a range of lionfish 'exploitation' rates in replicated fashion to Bahamian patch reefs over a period of 2 years. The results suggest that maintaining lionfish abundance at targeted densities is possible with relatively infrequent (i.e., monthly) removals, and that partial culling can halt the erosion of native fish biomass. The latter finding is particularly important because partial culling required substantially fewer resources and less effort to achieve, compared to complete removal of lionfish. More experiments such as this one, in a variety of habitats, urgently need to be carried out to determine the most cost-effective strategies for controlling lionfish, but also whether there are unintended ecological consequences of culling.

Developing a targeted lionfish fishery could increase the geographic scale of lionfish control efforts. However, the prospects are limited for several reasons. Fishing methods such as trawling, seining and hook-and-lining, which could allow rapid population depletion of susceptible species, are largely ineffective with lionfish, which are most easily captured by spearfishing and handnetting (Akins, 2012). A lionfish fishery would therefore be limited to depths accessible to sports divers (<30 m), leaving a potentially large source of deeper lionfish (Lesser and Slattery, 2011) to recolonise shallow areas, unless effective trapping methods can be developed. Efforts at developing a market for lionfish are on-going (e.g., Ferguson and Akins, 2010), but these are hampered by popular misinformation about the toxicity of lionfish flesh. (Only the spines are venomous; the flesh is firm and tasty [Morris et al., 2011b].) Recent reports of ciguatera in large lionfish from areas with high levels of ciguatoxin in other large reef fishes may also dampen enthusiasm for eating lionfish (GCFINET Archives, May 2012, www.listserv.gcfi.org). Moreover, in some nations such as the USA, the creation of a targeted fishery would require management for sustainability (Morris and Whitfield, 2009).

While lionfish are now firmly entrenched within Atlantic marine ecosystems, this invasion should serve as a valuable lesson for preventing similar ecological catastrophes in the future. Ultimately, the root of the lionfish problem was inadequate legislation, which allowed the trade of a potentially invasive species, and poor

Table 2

Urgent research priorities to support management of the lionfish invasion. Priorities were selected, in light of the current review, from a list of research gaps identified by regional managers and scientists (Morris and Green, 2012).

Topic	Importance for management
Egg production and propagule pressure	There is no means to measure propagule pressure, yet it may be one of the most important determinants of lionfish abundance. Estimation could help to prioritise reefs for local removal (e.g., reefs where removals could be effective for longer)
Larval ecology	Currently no information for lionfish <2 cm TL, as lionfish larvae are seldom captured. Identifying habitat requirements of the settlement-stage larvae could suggest avenues for larval trapping
Early post-settlement ecology	Knowledge of early post-settlement mortality could possibly identify and foster population limitation
Extent of adult movement	Knowing how far adults move, why, and whether movement is habitat-dependent could help the spatial design of removal schemes
Optimal removal frequency/intensity	These critical features of removal programs should be set to achieve the best ecological impact per unit time and financial investment

public awareness of the effects of invasive species on marine ecosystems. With the wisdom of hindsight, it is evident that predatory fish species with temperature tolerances that encompass the thermal range of the importing area should not be traded. This legislative deficiency was highlighted in 2005 by Florida's Comprehensive Wildlife Conservation Strategy, which recommended conducting a risk assessment on all marine species available commercially in the Florida pet trade (FWC, 2005). However, legislation requiring risk assessment is still not in effect, at least in Florida (P. Zajicek, personal communication). At least 30 species of non-native reef fishes, which are part of the aquarium trade, have been reported in the coastal waters of this sub-tropical state (Semmens et al., 2004; Schofield et al., 2009), and the recent capture of a large specimen of one of these – the carnivorous humpback grouper *Chromileptes altivelis* – is generating great concern about the possibility of another predatory fish invasion (Wadlow, 2013). The slowness of legal change in Florida may be linked to the fact that the economic benefits of the marine ornamental trade are perceived by a range of stakeholders as far greater than the potential environmental risks of the trade (Zajicek et al., 2009). There have been a number of recent public awareness programs in the USA and throughout the Caribbean region (e.g., by the Reef Environmental Education Foundation, www.reef.org) aimed specifically at the lionfish issue, but there is little information on whether these programs are changing public attitudes towards the release of exotic animals into the wild.

Many questions remain regarding how best to cope with the lionfish invasion. Managers from across the Caribbean region have identified a long list of research areas that are needed to inform on-the-ground action (Morris and Green, 2012). Based on the present review, we highlight in Table 2 what we believe are the most important among these gaps in research needed to support management. Removal programs hold some hope at a local scale. The effectiveness of such programs may be enhanced if combined with strategies to restore populations of potential predators of lionfish (Arias-González et al., 2011). Looking beyond the outcome of management actions for lionfish, this invasion has highlighted the urgent need for effective prevention, early detection, and rapid response to all introductions of exotic species, and particularly those of predators, within our oceans.

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manuscript. Readers can contact the authors for information on unpublished data reported in this review.

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