



# Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion

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**ABSTRACT:** Lionfish (*Pterois volitans* and *P. miles*) have become a major concern in the western Atlantic and Caribbean since their introduction in the 1980s. Invasive lionfish can reach very high population densities on coral reefs in their invaded range, yet there are few data from their native range in the Indo-Pacific for comparison. We compiled data on the geographical distribution and density of Indo-Pacific lionfishes in their native ranges from published and unpublished underwater visual censuses and field collections. We found that lionfish in their native Indo-Pacific range are unevenly distributed, with higher densities in the Indian Ocean than in the Pacific. Lionfish densities increase significantly with increasing latitude, and are significantly higher in continental areas than around islands. In the Indo-Pacific, lionfishes are found not only on reefs but also on soft bottoms and in nearshore habitats such as seagrass beds and mangroves, and near estuaries. Native lionfish can be found at depths greater than 75 m. Because lionfish can be cryptic and secretive, we estimate that only ~1/8 of Indo-Pacific lionfishes are detected during general underwater visual censuses. In the Pacific Ocean, the relative abundance of lionfish in the catch of reef-fish larvae is of the same order of magnitude as the relative abundance of adult lionfish within reef fish assemblages. Overall the observed densities of lionfishes in the Indo-Pacific are much lower (max. 26.3 fish ha<sup>-1</sup>) than the densities reported in their invaded Atlantic range (max. 400 fish ha<sup>-1</sup>). We found no effects of fishing or pollution on the densities of lionfishes.

**KEY WORDS:** *Pterois* · Indo-Pacific · Ecology · Visual census · Larvae · Invasive species

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## INTRODUCTION

Invasive species are widely considered to be a major threat to native ecosystems from the perspectives of ecology (Molnar et al. 2008, Lambertini et al. 2011), evolution (Mooney & Cleland 2001), and economics (Pimentel et al. 2005). Addressing invasions requires knowledge of the ecology of invasive species in their native range.

Over the past decade, 2 species of lionfish (*Pterois volitans* and *P. miles*) native to the Indo-Pacific (Fig. 1) have become invasive species in the western Atlantic and Caribbean (Hare & Whitfield 2003, Morris & Whitfield 2009). Collectively, these 2 species rapidly expanded their initial ranges off Florida (Whitfield et al. 2002, Freshwater et al. 2009), and now inhabit most of the region between Cape Hatteras (North Carolina) to the north and Venezuela to

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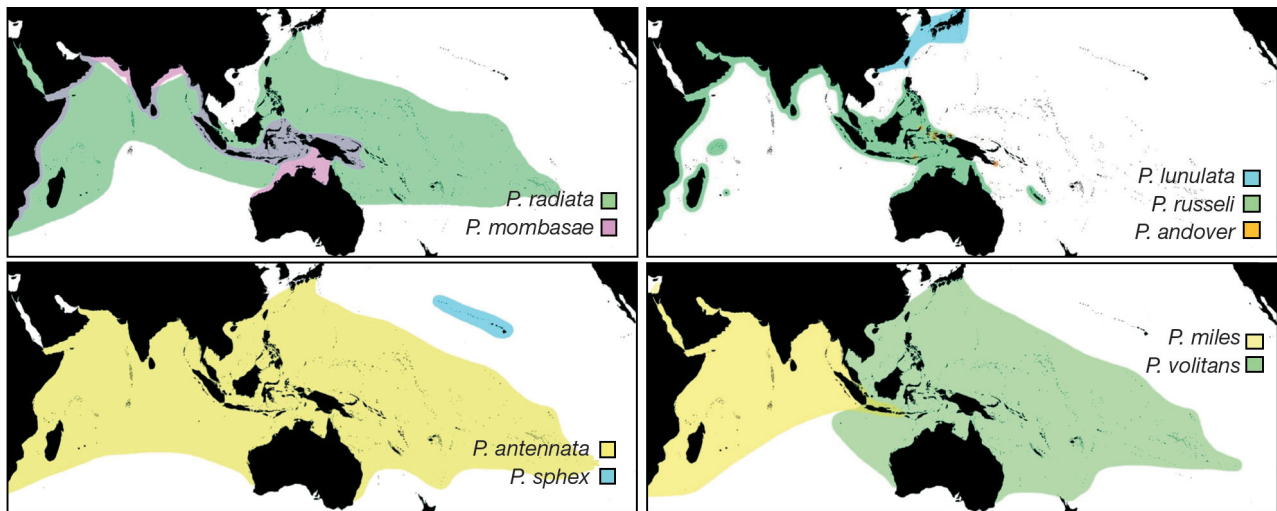


Fig. 1. *Pterois* spp. Geographical distribution of the 9 native lionfish species in the Indo-Pacific region

the south (Schofield 2009), with recent expansions into the Gulf of Mexico and the Lesser Antilles. (Juveniles are found as far north as Rhode Island, but do not survive over winter.) It is expected that lionfish will soon be found in all coastal waters with temperatures above their lethal limit of 10°C in the western Atlantic, extending as far south as the Brazil–Uruguay border (Kimball et al. 2004). Invasive lionfish have broad diets of small crustaceans and especially fishes (Morris & Akins 2009, Muñoz et al. 2011), and exhibit high kill rates (Côté & Maljković 2010). An individual invasive *P. volitans* is capable of reducing the recruitment of native fishes on small patch reefs by about 80% in 5 wk (Albins & Hixon 2008), so there is justifiable concern that this may become one of the worst marine invasions in history (Albins & Hixon 2011).

Although the invasion is rapidly expanding, information on the biology and ecology of lionfishes in their Indo-Pacific range is still largely anecdotal (Morris et al. 2009, Morris & Whitfield 2009). By contrast, information on lionfishes in the invaded regions is rapidly expanding, with studies focused on invasive lionfish distribution and abundance (Whitfield et al. 2002, 2007, Schofield 2009, 2010, Darling et al. 2011), reproduction (Ruiz-Carus et al. 2006, Morris et al. 2011), larval duration (Ahrenholz & Morris 2010), population genetics (Hamner et al. 2007, Freshwater et al. 2009), food habits (Albins & Hixon 2008, Morris & Akins 2009, Côté & Maljković 2010, Muñoz et al. 2011), and ecological impacts (Albins & Hixon 2008, 2011).

As is true of many invasive species, lionfishes can reach very high densities, even to >400 fish ha<sup>-1</sup> in

some areas of the SE United States (Morris & Whitfield 2009) and the Bahamas (Green & Côté 2009), which is considerably higher than any densities so far described from their native range (seldom >10 fish ha<sup>-1</sup>; Green & Côté 2009, Grubich et al. 2009).

Our objective was to facilitate a better understanding of the lionfish invasion and its potential threats to Atlantic coral reefs by compiling and analyzing data from multiple sources in order to document the distribution and abundance of the fish in their native range. Our approach was original in several ways. First, we addressed factors such as predation, competition, biogeography and dispersal that may limit these species in their native range, and we discussed how these factors might influence their Atlantic invasion. Second, we compared the relationships between lionfish and their regional trophic structure (e.g. predators, competitors) in the native and invaded ranges. Third, we examined habitat use by lionfishes in both their native and invaded ranges to assess the capacity of these species to colonize new regions. Overall, we went beyond the simple compilation of data of invasive lionfish in their native range. We took a macroecological approach to species invasions in order to evaluate the potential effects of large-scale factors on the dynamics of the lionfish invasion.

## MATERIALS AND METHODS

### Geographical ranges

The geographical ranges of the 9 described *Pterois* species were extracted from 2 unpublished data-

bases, one compiled by R. Myers (Coral Graphics) and the other by the Institute for Research and Development, Nouméa Center. These 2 databases are constructed upon data from 110 sampling sites across the Indo-Pacific. The proportions (relative to the total number of species) of Scorpaenidae (the family of lionfish) and other piscivore species were extracted from the same databases for the Indo-Pacific, and from a similar database for the Atlantic (Halpern & Floeter 2008).

### Underwater population estimates

Population-density data came from a literature search and from previously unpublished observations. The literature search, which was based on the keyword 'Pterois', considered both indexed literature (as available through [http://thomsonreuters.com/products\\_services/science/science\\_products/a-z/web\\_of\\_science/](http://thomsonreuters.com/products_services/science/science_products/a-z/web_of_science/)) and non-indexed literature (available through search engines such as Google-Scholar, Google or Yahoo), the search being limited to the Indo-Pacific region. Data from the literature were gathered from both the Pacific and Indian Oceans (Table 1).

Two types of previously unpublished observations were compiled. These were (1) general censuses not specifically aimed at lionfishes, and (2) censuses specifically targeting lionfishes. General-census data were gathered from a large number of field surveys conducted from East Africa eastward to the Marquesas Islands and Rapa. Only surveys counting 'all species' of reef fishes were included. Densities were converted into fish ha<sup>-1</sup> when the sampled area was available. We examined more than 10 000 transects covering >268 ha. Our area spanned 57 islands or nations in the Pacific and 8 nations in the Indian

Oceans (Table 1).

Table 1. *Pterois* spp. Number of lionfish observed and their densities in the Indo-Pacific based on published visual censuses. Only data based on 'total counts' (i.e. counts recording all or most observed species) are reported

| Region                                    | Species             | No. lionfish observed     | Density (ind. ha <sup>-1</sup> ) | Reference                  |
|---|---------------------|---------------------------|----------------------------------|----------------------------|
| <b>Pacific Ocean</b>                      |                     |                           |                                  |                            |
| Middleton & Elizabeth Reef (SE Australia) | <i>P. volitans</i>  | 2                         | 2.4                              | Oxley et al. (2004)        |
| Millenium atoll (Kiribati East)           | <i>Pterois</i> spp. | 0                         | 0                                | Barott et al. (2010)       |
| Guam                                      | <i>Pterois</i> spp. | 0                         | 0                                | Amesbury et al. (1999)     |
| Midway                                    | <i>P. sphex</i>     | <5                        |                                  | Schroeder & Parrish (2006) |
| Hawaii                                    | <i>P. sphex</i>     | 0                         | 0                                | Beets et al. (2010)        |
| Lord Howe (SW Pacific)                    | <i>P. volitans</i>  | 9                         | 2.7                              | Valentine et al. (2008)    |
| Kermadec (SW Pacific)                     | <i>P. volitans</i>  | 2                         | prob. ~7.4                       | Cole et al. (1992)         |
| Brunei                                    | <i>Pterois</i> sp.  | 1                         | 1.1                              | Chou et al. (1992)         |
| Taiwan                                    | <i>P. volitans</i>  | 1                         | 2.2                              | Chen et al. (2004)         |
| Seribu (Indonesia)                        | <i>P. volitans</i>  | 8                         | 2.4                              | Suharsono et al. (1996)    |
| Moorea (Polynesia)                        | <i>P. radiata</i>   | 2                         | 0.9                              | Lecchini et al. (2006)     |
| Rongelap (Marshall Is.)                   | <i>Pterois</i> spp. | 0                         | 0                                | Pinca et al. (2002)        |
| Ryukyu                                    | <i>P. antennata</i> | 3                         | 8.9                              | Nakamura & Sano (2004)     |
| Peninsular Malaysia                       | <i>Pterois</i> spp. | 0                         | 0                                | Harborne et al. (2000)     |
| Kiritimati (Line Is.)                     | <i>Pterois</i> spp. | 0                         | 0                                | Sandin et al. (2008)       |
| Yap (W Micronesia)                        | <i>Pterois</i> spp. | 0                         | 0                                | Smith & Dalzell (1991)     |
| <b>Indian Ocean</b>                       |                     |                           |                                  |                            |
| Reunion (SW Indian)                       | <i>P. antennata</i> | 18                        | 3.6                              | Letourneur (1996b)         |
|   | <i>P. miles</i>     | 31 (out of 43 200 fishes) | 6.2                              | Letourneur et al. (2008)   |
|   | <i>P. antennata</i> | 21 (out of 20 324 fishes) | 16.7                             | Letourneur (1998)          |
| Mauritius (SW Indian)                     | <i>P. miles</i>     | 5 (out of 44 000 fishes)  | 3                                | Adjeroud et al. (1998)     |
|   |                     |                           |                                  | Graham et al. (2007)       |
| Mauritius                                 | <i>P. miles</i>     | 3                         | 2.5                              | Chinae et al. (2001)       |
| Mayotte (SW Indian)                       | <i>P. antennata</i> | 1 (out of 4340 fishes)    | 2.8                              | Letourneur (1996a)         |
| Natal                                     | <i>Pterois</i> spp. |                           | 0.3 to 6                         | Berry et al. (1982)        |
| Red Sea (Egypt)                           | <i>P. miles</i>     | 5                         | 20.8                             | Alter et al. (2008)        |
|   | <i>P. radiata</i>   | 3                         | 12.5                             |                            |
| Red Sea                                   | <i>P. miles</i>     | 80                        | prob. >20                        | Fishelson (1997)           |

Ocean. A variety of underwater visual census (UVC) methods was used (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m446p189\\_supp.pdf](http://www.int-res.com/articles/suppl/m446p189_supp.pdf)). Transects were 25 or 50 m long and fish were counted within 2 to 5 m wide belts along these transects. These surveys were not specifically designed to census lionfish, but were intended to count as many species as possible. The observers did not conduct intensive searches in holes, crevices or under ledges, where lionfish tend to hide during daytime in the Indo-Pacific. The second kind of surveys, lionfish-specific censuses, were characterized by, first, their focused target (only *Pterois* spp. were recorded), and second, their methods: observers searched all holes, crevices and ledges within 5 m to each side of the transect line. The length of transects was different for each team, ranging from 50 to 500 m (see Table 3). Some of these lionfish-specific censuses, called Type 1 transects, were performed in habitats chosen at random within the reefs of a region, whereas the others, Type 2 transects, were performed in habitats specifically selected for their reported abundance of *Pterois* spp. Type 1 transects therefore provided an indication of the overall density of *Pterois* spp., whereas Type 2 transects were expected to yield an upper estimate, or maximum density, of *Pterois* spp.

### Fish catches

We employed a variety of methods at New Caledonia and Chesterfield Islands (Table S2 in the Supplement) to capture lionfish, including trawls (shrimp and fish trawl), rotenone, gill nets, and fyke nets. Shrimp trawl nets had a 14 m long head-rope and a 2 cm cod-end mesh. Trawling speed was 2.3 knot, and tow duration was 33 min (1.2 ha tow<sup>-1</sup>). Fish trawl nets had an 18 m long head-rope, a 2 cm cod-end mesh; trawling speed was 3 knot, and tow duration was 20 min (1.4 ha tow<sup>-1</sup>). Tow depth was between 4 and 83 m. Trawls were run over soft bottoms where large sponges (e.g. *Ircinia* spp.), small coral heads, and at times branched *Acropora* coral fields were present, areas potentially inhabited by lionfish. Rotenone was applied at stations established mainly on coral reefs and sometimes on algae beds, both from 0 to 15 m depth. Gill nets and fyke nets were set along the shoreline, usually near mangroves or estuaries. On each station 3 gill nets were set in a row, with, sequentially, a mesh size of 30, 50 and 75 mm. Each net was 75 m long and 4 m high. Fyke nets had a 50 m leading net and a 3-way chamber

with a cod-end mesh of 10 mm. Soak time was 2 h for the gill nets and 12 h for the fyke nets. Both gill nets and fyke nets were set perpendicular to the shoreline; gill nets were set at high tide. The catchability of lionfish by trawls or rotenone is unknown (but see Kulbicki & Wantiez 1990), yet is assumed to be very high, as these fish swim fast only in short bursts and tend to stay motionless when confronted, relying on cryptic behavior and their venomous spines for defense (Morris & Whitfield 2009).

### Detectability

Given that lionfish can be highly secretive within the reef framework, a major question arises regarding detectability during visual surveys. We addressed this issue by means of 3 methods. First, the densities observed during UVCs were compared to the densities obtained from rotenone stations in the same habitats and regions (rotenone stations being <100 m from UVC stations) because rotenone captures most fish in an area (Ackerman & Bellwood 2002). Second, the detection curves derived from 'distance sampling' (Buckland et al. 2001) were compared for all species combined, for lionfishes alone, and for another cave dwelling genus, *Myripristis* spp. In this method, the observer estimates the perpendicular distance between any observed fish or group of fish and the transect line (Labrosse et al. 2001). These distance distributions are used to estimate densities and to yield information on how objects are detected as the distance of observation increases (Buckland et al. 2001). This is a common method for evaluating reef-fish detectability (Kulbicki 1998, Kulbicki & Sarramégnia 1999, Kulbicki et al. 2010, Bozec et al. 2011). Distance sampling was performed on 7209 transects in the South Pacific (Table S1 in the Supplement). Third, within the same study location, the densities obtained from all-species transects were compared to densities from Type 1 UVC transects that specifically targeted *Pterois* spp.

### Larvae and new-settler samples

Fish larvae were collected during several programs in the Indo-Pacific, and by 2 methods: light-traps and crest-nets. Light-traps (Doherty 1987) were set near reefs, at from 2 to 4 m below the surface, at night. Soaking time was usually from 2 to 6 h. Crest nets (Dufour et al. 1996) were set on the reef crest, just behind the surf zone. They were usually set for sev-

eral days, larvae being retrieved from the cod end twice a day. In some of these programs lionfish larvae were counted, thus yielding information on the relative abundance of these species. Similarly, by means of various recruitment surveys, reef fish were sampled near the time of settlement, generating some information on the relative abundance of settlement-stage lionfish.

### Statistical analyses

We used a generalized linear model (GLMz: backward and stepwise; error distribution: normal; link function: power) to test the potential influence of several large-scale factors on *Pterois* densities. These densities were log-transformed to normalize their distributions and reduce variance. The factors tested were (1) distance to the biodiversity center, taken as Indonesia at 107°E on the equator (Bellwood & Meyer 2009) and log-transformed; (2) latitude, absolute value; (3) hemisphere (north or south); (4) sea surface temperature (SST; annual mean at the regional level; Locarnini et al. 2006); (5) ocean and coast type (island or continent) and (6) the first-degree interactions of all categorical factors. A GLM tested whether the density of *Pterois* was a function of regional diversity in terms of (1) total species richness, taken as the total number of species known in each region; (2) piscivore regional richness, taken as the number of reef-fish species known to feed on fish within each region; (3) medium-size-piscivore (from 10 to 40 cm, the same size-class as lionfish) regional richness; (4) Scorpaenidae regional richness, taken as the number of reef-dwelling scorpaenid species within each region; and (5) *Pterois* regional richness. No interaction was tested, as all these factors were considered to be continuous variables.

## RESULTS AND DISCUSSION

### Geographical distribution

Most *Pterois* have a wide geographical distribution (Fig. 1), although 2 species, *P. sphex* and *P. andover*, have restricted ranges (Fig. 1). *P. volitans*, the primary species invading western Atlantic and Caribbean coral reefs, is restricted to the Pacific Ocean, unlike *P. antennata* and *P. radiata*, which occur throughout the entire Indo-Pacific. *P. miles* (see Schultz 1986, Kochzius et al. 2003 for the status of this species), the second invasive species, presently

restricted to the east coast of the USA (Freshwater et al. 2009), has a native range restricted to the Indian Ocean. The ranges of *P. volitans* and *P. miles* overlap in the Indonesian region (Fig. 1), but the precise boundaries of this overlap are at present not well defined. *P. volitans* has the most southern range limit, being reported at 34°S, near northern New Zealand. *P. lunulata* and *P. volitans* have the northernmost range, being found off South Korea (35°N). Both regions have a mean SST of 19°C and a minimal average winter temperature of 14°C (Locarnini et al. 2006). The number of *Pterois* species per region varies from 2 in the south Pacific and around Hawaii to 8 in the western Pacific (Table 2). The proportion of Scorpaenidae and of piscivore species to the regional reef fish assemblage (from 1.8 to 3.4% and from 14 to 21.6% respectively) does not vary substantially across the Indo-Pacific (Table 2).

### Densities on reefs

Despite a large sampling effort (>3.6 million fish counted on >10 000 transects), only 64 lionfish were detected during the general visual censuses in the Pacific Ocean. *Pterois volitans* was the most commonly observed species among lionfishes (Tables 1 & 3). We observed an average density of 0.17 *Pterois* ind. ha<sup>-1</sup> for the entire Pacific, yet densities varied considerably among regions, and, in many regions, no lionfish were detected. The highest densities were detected on the limits of the geographical range of these species, with 5.0 fish ha<sup>-1</sup> in the Marquesas (8°S) and 7.2 fish ha<sup>-1</sup> at Rapa (27°S). The relative density (*Pterois* ind. per million fish) ranged from 0 in many locations to 120 at Rapa, with an average value of 17 for the entire Pacific (Table 3).

Censuses specifically targeting lionfish in the Pacific always detected *Pterois* spp. at from 2.7 to 9 fish ha<sup>-1</sup> based on Type 1 transects, and from 6.4 to 32.9 fish ha<sup>-1</sup> for Type 2 transects (Table 3). All these focused transects were performed in Micronesia and the Philippines.

The number of lionfish detected by all-species transects in the Indian Ocean was of the same order of magnitude (61 fish) as in the Pacific, but the sampling effort was far lower (<220 000 fish over 389 transects). Lionfish were observed in every study, except at the Glorieuses Islands (Mozambique Channel), and there was little variation among locations (Tables 1 & 3). The highest densities were observed in the northern Red Sea (Egypt and Israel), with estimates of >20 *Pterois* ind. ha<sup>-1</sup>. On average, the density of *Pterois* in

Table 2. *Pterois* spp. Species richness of reef fishes by region throughout the Indo-Pacific and the Atlantic. Medium piscivores: 10–40 cm total length. *Pterois* density values corrected for detectability (see 'Materials and methods: Detectability'). See Fig. 3 for Indo-Pacific regional boundaries. –: no data; I: invader

| Region                     | Total species | <i>Pterois</i> spp. |                    | Scorpaenidae |     | All piscivores |      | Medium piscivores |     |
|----------------------------|---------------|---------------------|--------------------|--------------|-----|----------------|------|-------------------|-----|
|                            |               | n                   | n ha <sup>-1</sup> | n            | %   | n              | %    | n                 | %   |
| <b>Indo-Pacific</b>        |               |                     |                    |              |     |                |      |                   |     |
| West Indian (WI)           | 1395          | 5                   | 29.6               | 34           | 2.4 | 265            | 19   | 89                | 6.4 |
| NW-Indian (NWI)            | 1869          | 6                   | 177                | 42           | 2.2 | 335            | 17.9 | 123               | 6.6 |
| SW-Indian (SWI)            | 1496          | 5                   | 28                 | 39           | 2.6 | 284            | 19   | 87                | 5.8 |
| Mascareignes (MAS)         | 1310          | 4                   | 64                 | 38           | 2.9 | 244            | 18.6 | 91                | 6.9 |
| Central Indian (CI)        | 2001          | 5                   | 16.8               | 41           | 2   | 339            | 16.9 | 132               | 6.6 |
| East Indian (EI)           | 2581          | 7                   | –                  | 46           | 1.8 | 406            | 15.7 | 165               | 6.4 |
| China Sea–Philippines (CP) | 3361          | 5                   | 6.2                | 90           | 2.7 | 506            | 15.1 | 228               | 6.8 |
| Hawaii                     | 649           | 2                   | 4                  | 26           | 4   | 140            | 21.6 | 53                | 8.2 |
| Indonesia-Malaysia (IND)   | 3459          | 7                   | 10.8               | 72           | 2.1 | 491            | 14.2 | 223               | 6.4 |
| Melanesia (MEL)            | 2054          | 3                   | 0.2                | 47           | 2.3 | 305            | 14.8 | 124               | 6   |
| Micronesia (MIC)           | 1792          | 3                   | 0.6                | 39           | 2.2 | 253            | 14.1 | 99                | 5.5 |
| North Polynesia (NPOL)     | 705           | 3                   | 0                  | 16           | 2.3 | 129            | 18.3 | 47                | 6.7 |
| NW Pacific (NWP)           | 2794          | 4                   | 44.4               | 79           | 2.8 | 459            | 16.4 | 202               | 7.2 |
| South Polynesia (SPOL)     | 1079          | 3                   | 13.5               | 32           | 3   | 190            | 17.6 | 80                | 7.4 |
| South Pacific (SP)         | 1024          | 2                   | 39.4               | 31           | 3   | 170            | 16.6 | 64                | 6.3 |
| SW Pacific (SWP)           | 2262          | 7                   | 2.2                | 78           | 3.4 | 353            | 15.6 | 142               | 6.3 |
| West Pacific (WP)          | 3146          | 8                   | 0                  | 79           | 2.5 | 439            | 14   | 194               | 6.2 |
| <b>Atlantic Ocean</b>      |               |                     |                    |              |     |                |      |                   |     |
| Carolinian                 | 441           | I                   | I                  | 14           | 3.2 | 40             | 9.1  | 17                | 3.9 |
| West Caribbean–Florida     | 750           | I                   | I                  | 20           | 2.7 | 48             | 6.4  | 18                | 2.4 |
| East Caribbean             | 734           | I                   | I                  | 20           | 2.7 | 48             | 6.5  | 18                | 2.5 |
| NE Brazil                  | 388           | –                   | –                  | 14           | 3.6 | 37             | 9.5  | 15                | 3.9 |
| SE Brazil                  | 379           | –                   | –                  | 11           | 2.9 | 39             | 10.3 | 14                | 3.7 |

the Indian Ocean was 3.6 ind. ha<sup>-1</sup>, which is 13 times higher than in the Pacific. Similarly the relative density of *Pterois* was 343 ind. per million fish, which is 20 times greater than in the Pacific.

Reef censuses targeting Indian Ocean lionfish irrespective of habitat (Type 1 transects) showed densities of 36 *Pterois* ind. ha<sup>-1</sup>, which is 4 to 13 times higher than the results of censuses conducted by similar methods in the Pacific (Table 3). Census targeting Indian Ocean habitats known to harbor lionfish (Type 2 transects) showed very high densities of 200 *Pterois* ind. ha<sup>-1</sup>, which is 6 to 31 times higher than what was shown in the Pacific using similar methods.

Unfortunately, many of the unpublished observations for the Indian Ocean recorded *Pterois* at the genus level, which does not permit an evaluation of which species are most abundant. However, from the literature (Table 1), from the unpublished work of P. Chabanet, and from surveys by Darling et al. (2011), a tentative pattern emerges for the Indian Ocean (Tables 1 & 3): *P. miles* and *P. antennata* exhibit the highest densities, with *P. radiata* displaying lower densities. Other species (*P. mombasae*, *P. russeli*) that occur in the Indian Ocean (Fig. 1) were not detected in these UVCs.

### Densities in other habitats

A total of 641 000 fish were captured in the compiled fishery catches. As in UVCs, very few *Pterois* (51 ind.; 73 ind. per million fish) were caught by fishing methods (Table 4). Shrimp trawls that sampled waters at depths mainly between 10 and 30 m caught the largest numbers (Table S2 in the Supplement). The highest densities were deduced from trawl catches on seafloors 10 to 20 m deep (0.68 ind. ha<sup>-1</sup>), followed by areas <10 m deep (0.37 ind. ha<sup>-1</sup>). The deepest recorded catch was at 75 m (and the deepest trawl was 83 m). These densities are of the same magnitude as those recorded from UVCs (Tables 1 & 3) in the same regions. *Pterois* spp. has also been reported in trawl surveys from several other locations in the Pacific, reaching at times fairly high frequencies. In the Arafura Sea, *P. russeli* was reported in 13 out of 206 trawls and *P. volitans* once in 206 trawls (Ramm 1997). *P. volitans* occurred in 0.02% of the trawls in the Kimberley region of NW Australia (Newman et al. 2008), and *Pterois* spp. accounted for 0.015% of experimental trawl catches in Sarawak, Malaysia (Rumpet et al. 1999). Similar findings have been reported in the Indian Ocean, including the presence of *Pterois*

Table 3. *Pterois* spp. Densities of lionfish and related data based on previously unpublished underwater visual censuses. For targeted counts, Type 1: censuses targeting *Pterois* spp. but with no *a priori* selection of habitat; Type 2: censuses targeting both *Pterois* spp. and habitats known to harbor *Pterois* spp. Team 1: M. Hixon & J. Beets; Team 2: E. Darling & J. K. O'Leary; Team 3: K. Cure & J. McIlwain. NA: not available

| Region               | No. islands/<br>nations | No. of<br>transects  | Area<br>covered (ha)                        | No. of all fish<br>observed | <i>Pterois</i> ind.                       |                    |  |       |  |       |
|----------------------|-------------------------|----------------------|---|-----------------------------|---|--------------------|--|-------|--|-------|
|                      |                         |                      |   |                             | n   | n ha <sup>-1</sup> | n million <sup>-1</sup>                          |       |  |       |
| <b>Pacific Ocean</b> |                         |                      |   |                             |   |                    |  |       |  |       |
| Fiji                 | 3                       | 528                  | 13.2  | 192 732                     | 1   | 0.08               | 5.2  |       |  |       |
| Society              | 2                       | 600                  | 4.1   | 142 383                     | 2   | 0.48               | 14   |       |  |       |
| Tuamotu              | 13                      | 844                  | 16.0  | 253 591                     | 4   | 0.25               | 16   |       |  |       |
| Indonesia            | 1                       | 185                  | 9.3   | NA                          | 0   | 0                  | 0  |       |  |       |
| Rapa                 | 1                       | 28                   | 0.28  | 16 679                      | 2   | 7.1                | 120  |       |  |       |
| Marquesas            | 4                       | 157                  | 0.8   | 35 736                      | 4   | 5.0                | 112  |       |  |       |
| New Caledonia        | 5                       | 6034                 | 150.8                                       | 2 463 872                   | 47  | 0.31               | 19   |       |  |       |
| New Caledonia        | 3                       | 306                  | 15.4  | 186 096                     | 4   | 0.26               | 22   |       |  |       |
| Palau                | 1                       | 78                   | 0.98  | 10 725                      | 0   | 0                  | 0  |       |  |       |
| Samoa                | 8                       | 365                  | 6.5   | 71 614                      | 0   | 0                  | 0  |       |  |       |
| Solomon Islands      | 13                      | 330                  | 4.1   | 162 048                     | 0   | 0                  | 0  |       |  |       |
| Tonga                | 3                       | 619                  | 15.5  | 159 479                     | 0   | 0                  | 0  |       |  |       |
| Wallis & Futuna      | 2                       | 130                  | 4.1   | NA                          | 0   | 0                  | 0  |       |  |       |
| Total Pacific        | 57                      | 10 204               | 241.1                                       | ~3 695 000                  | 64  | 0.27               | 17   |       |  |       |
| <b>Indian Ocean</b>  |                         |                      |   |                             |   |                    |  |       |  |       |
| Glorieuses Is.       | 1                       | 39                   | 0.98  | 29 750                      | 0   | 0                  | 0  |       |  |       |
| Geysers Bank         | 1                       | 48                   | 0.78  | 26 980                      | 4   | 5.2                | 148  |       |  |       |
| Kenya                | 1                       | 132                  | 6.6   | 43 120                      | 25  | 3.8                | 580  |       |  |       |
| Madagascar           | 1                       | 59                   | 2.95  | 22 200                      | 5   | 1.7                | 225  |       |  |       |
| Maldives             | 1                       | 21                   | 1.2   | 27 030                      | 3   | 2.5                | 111  |       |  |       |
|                      |                         | 24                   | 1.2   | 14 050                      | 2   | 1.7                | 142  |       |  |       |
| Mayotte              | 1                       | 15                   | 0.75  | 16 040                      | 6   | 8.0                | 374  |       |  |       |
| Mozambique           | 1                       | 25                   | 1.25  | 17 135                      | 6   | 4.8                | 350  |       |  |       |
| Tanzania             | 1                       | 26                   | 1.3   | 22 500                      | 6   | 3.6                | 267  |       |  |       |
| Total Indian         | 8                       | 389                  | 17.0  | ~218 800                    | 61  | 3.59               | 343  |       |  |       |
| <hr/>                |                         |                      |   |                             |   |                    |  |       |  |       |
| Targeted counts      | No. of<br>sites         | Area covered<br>(ha) | <i>P. antennata</i><br>n n ha <sup>-1</sup> |                             | <i>P. radiata</i><br>n n ha <sup>-1</sup> |                    | <i>P. volitans/miles</i><br>n n ha <sup>-1</sup> |       | All <i>Pterois</i><br>n n ha <sup>-1</sup> |       |
| <b>Type 1</b>        |                         |                      |   |                             |   |                    |  |       |  |       |
| Pohnpei (Team 1)     | 10                      | 3.68                 | 6   | 1.63                        | 1   | 0.27               | 3  | 0.81  | 10   | 2.71  |
| Guam (Team 1)        | 14                      | 7.54                 | 32  | 4.24                        | 19  | 2.51               | 3  | 0.39  | 54   | 7.16  |
| Cebu (Team 1)        | 3                       | 6.1                  | 44  | 7.21                        | 0   | 0                  | 11   | 1.8   | 55   | 9.01  |
| Kenya (Team 2)       | 6                       | 1.0                  | 19  | 19.0                        | 9   | 9.0                | 8  | 8.0   | 36   | 36.0  |
| Total Type 1         | 33                      | 18.32                | 90  | 4.91                        | 29  | 1.58               | 36   | 1.96  | 155  | 8.46  |
| <b>Type 2</b>        |                         |                      |   |                             |   |                    |  |       |  |       |
| Guam (Team 3)        | 23                      | 20.95                | 76  | 3.62                        | 7   | 0.33               | 51   | 2.43  | 134  | 6.39  |
| Negros (Team 3)      | 16                      | 6.35                 | 89  | 14.01                       | 0   | 0                  | 112  | 17.63 | 201  | 31.65 |
| Bohol (Team 3)       | 9                       | 3.86                 | 57  | 14.76                       | 0   | 0                  | 70   | 18.13 | 127  | 32.9  |
| Kenya (Team 2)       | 1                       | 0.11                 | 8   | 67.6                        | 0   | 0                  | 14   | 110.5 | 22   | 178.1 |
| Total Type 2         | 49                      | 31.27                | 230   | 7.35                        | 7   | 0.22               | 247  | 7.89  | 484  | 15.47 |

in experimental trawls in the northern Red Sea (El-Ganainy et al. 2005) or among the discarded fish in the Sri Lanka trawl fishery (Fernando 1972).

No *Pterois* were caught or observed in or near mangroves in New Caledonia despite the use of sev-

eral collection or observation methods (gill nets, fyke nets, rotenone, UVCs). *Pterois* has been reported from mangroves in Fiji and Vanuatu but with no indication on their abundance (Thollot 1993). Lionfishes have also been reported in nearshore areas of the

Table 4. *Pterois* spp. Depth distribution of catch size and fish mass of lionfish in New Caledonia. n: no. of ind. caught; Wt: average weight per ind. in grams. -: no data

| Depth (m) | Area covered (ha) | <i>P. antennata</i> |    | <i>P. lunulata</i> |     | <i>P. radiata</i> |    | <i>P. volitans</i> |     | <i>Pterois</i> sp. |    | <i>Pterois</i> |                    |                         |
|-----------|-------------------|---------------------|----|--------------------|-----|-------------------|----|--------------------|-----|--------------------|----|----------------|--------------------|-------------------------|
|           |                   | n                   | Wt | n                  | Wt  | n                 | Wt | n                  | Wt  | n                  | Wt | Total n        | n ha <sup>-1</sup> | n million <sup>-1</sup> |
| 0–10      | 158               | –                   | –  | 1                  | 280 | 4                 | 2  | 7                  | 120 | 16                 | 19 | 28             | 0.16               | 87                      |
| 10–20     | 66                | –                   | –  | 3                  | 307 | 1                 | 50 | 1                  | 55  | 8                  | 25 | 13             | 0.20               | 71                      |
| 20–30     | 76                | –                   | –  | –                  | –   | –                 | –  | –                  | –   | –                  | –  | 0              | 0.00               | 0                       |
| 30–40     | 86                | –                   | –  | –                  | –   | –                 | –  | –                  | –   | 1                  | 10 | 1              | 0.01               | 25                      |
| 40–70     | 97                | 1                   | 25 | –                  | –   | –                 | –  | –                  | –   | –                  | –  | 1              | 0.01               | 41                      |
| >70       | 8                 | 1                   | 50 | –                  | –   | –                 | –  | –                  | –   | –                  | –  | 1              | 0.13               | 571                     |
| Total     | 491               | 2                   | 38 | 4                  | 300 | 5                 | 12 | 8                  | 112 | 25                 | 21 | 44             | 0.09               | 68                      |

Philippines (Pinto 1987), Indonesia (Weis & Weis 2005), Thailand (Hajisamae & Yeesin 2010) and northern Australia (Baker & Sheppard 2006), but little information is available on their abundance in these habitats. Similar information is available for mangroves in the Indian Ocean, ranging from Egypt (El-Dawi 1997) to Tanzania and Zanzibar (Lugendo 2007), to Mozambique (Macnae & Kalk 1962, de Boer et al. 2001, Gell & Whittington 2002) and Madagascar (Ory 2008). The relative abundance of *Pterois* in some of the catches in these nearshore areas seems much greater than on reefs or soft bottoms. To compare with the UVC findings (Tables 1 & 3) or catches on soft bottoms (Table 4), we transformed these values as *Pterois* ind. per million fish. In Mozambique, the relative abundances were 2205 ind. per million fish (de Boer et al. 2001); in Madagascar, 314 (Ory, 2008); in seagrass beds in Kenya, 1370 (de Troch et al. 1998); and in Egyptian mangroves, 'frequent' (El-Dawi 1997). These numbers are of the same magnitude as reef-fish densities in the Indian Ocean (Tables 1 & 3), and probably higher. Most of these inshore lionfishes seem to be juveniles, but published data are insufficient for determining the proportion.

### Detectability

Different methods of estimating detectability of lionfish yielded similar results. First, densities obtained from rotenone stations (73 stations over a 1.45 ha area) on shallow reefs were higher (6.2 *Pterois* ind. ha<sup>-1</sup>) than in all-species UVCs, but similar to the densities observed in censuses specifically targeting lionfish in the Pacific (Table 3). The densities calculated from UVCs (204 transects over an area of 10.2 ha,) in the same habitats sampled using rotenone was 0.89 ind. ha<sup>-1</sup>. The ratio of rotenone catch:UVC estimates was 6.96.

Second, the frequency of lionfish sightings related to distance from the transect line (detection curve) decreased faster than for all species pooled (Fig. 2a), suggesting that lionfish are better detected at close range. 78% of the sightings occurring between 0 and 3 m of the transect line. The detection curve for lionfish was similar to that of *Myripristis* spp., a daytime cave-dwelling fish (Fig. 2b). *Myripristis* was abundant and frequent at rotenone stations. Assuming that nearly all *Myripristis* were caught at rotenone stations, this permitted a good estimate of actual density (rotenone) to observed densities (in nearby visual transects). However, because lionfish were uncommon, the ratio between actual density and observed densities are probably less accurate. The ratio of actual:observed was 5.70 for *Myripristis* and 6.96 for lionfish, suggesting that the detectability of these species is comparable.

Third, in Kenya (Table 1), the mean density obtained by all-species censuses was 3.8 *Pterois* ind. ha<sup>-1</sup>, whereas mean density obtained by Type 1 transects was of 36 *Pterois* ind. ha<sup>-1</sup>. This comparison yields a correction factor of 9.47 (36/3.8).

The average of these 3 independent estimates of detectability suggests a correction factor of approximately 8, which means that on all-species transects only 1 *Pterois* would be detected for every 8 actually present.

### Larvae and new settlers

Most of the information available on the relative abundance of lionfish larvae was from the Pacific Ocean, where lionfish larvae were rare in most cases (Table 5), and with the largest proportion being observed at Rangiroa (Lo Yat 2002; 331 ind. per million fish). There may be substantial interannual variation in the proportion of lionfish in the larval pool



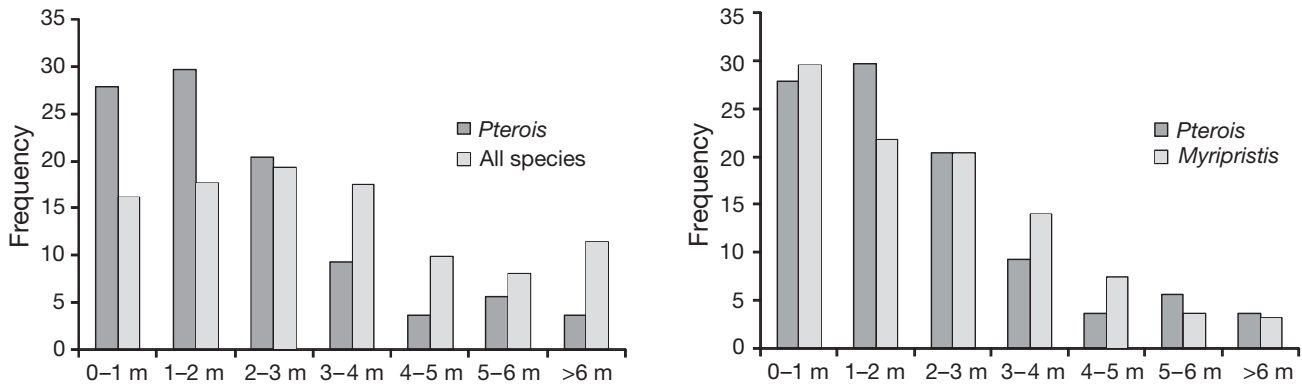


Fig. 2. *Pterois* spp. In the South Pacific, frequency of detection by distance from transect for (A) lionfish versus other species, where *G*-test is significant at  $p < 0.0001$ ; and for (B) lionfish versus *Myripristis*, another cave-dwelling genus, where *G*-test is not significant at  $p = 0.27$ . For lionfish,  $N = 54$  occurrences; for all other species together,  $N = 457\,000$  occurrences; for *Myripristis* alone,  $N = 1409$  occurrences

Table 5. *Pterois* spp. Abundance of lionfish among sampled settlement-stage reef-fish larvae and recently settled juvenile reef fish. FP: French Polynesia.

| Region                         | No. of lionfish    | Total no. of larvae | <i>Pterois</i> / Scorpaenidae | Gear or method         | Reference                              |
|--------------------------------|--------------------|---------------------|-------------------------------|------------------------|--|
| Tikehau (FP)                   | 0                  | 19 800              | –                             | Crest net              | R. Galzin (unpubl.)                    |
| Rangiroa (FP)                  | 55                 | 166 124             | 1/200                         | Crest net              | LoYat (2002)                           |
| Moorea (FP)                    | 0                  | 4280                | –                             | UVC                    | COVARE (unpubl.)                       |
|                                | 5                  | 7500                | 5/133                         | Crest net              | Lecchini et al. (2006)                 |
| Wallis                         | 4                  | 62 610              | 4/30                          | Crest net              | Juncker (2005)                         |
| Aitutaki (Cook Is.)            | 2                  | 13 073              | 2/16                          | Crest net & light trap | Malpot et al. (2008)                   |
| Rangiroa (FP)                  | 2                  | 1 158 760           | 2/275                         | Crest net & light trap | Malpot (2005)                          |
| Moorea (FP)                    | (37) <sup>a</sup>  | 31 710              | –                             | Crest net              | Riclet (1995)                          |
| New Caledonia                  | 0                  | 11 560              | –                             | UVC                    | Mellin (2008)                          |
|                                | 0                  | 5420                | –                             | Trap & seine           |  |
| New Caledonia                  | 1                  | 109 340             | 1/75                          | Light trap             | Carassou (2008)                        |
| Great Barrier Reef             | (158) <sup>a</sup> | 56 474              | –                             | Crest net              | Doherty & McIlwain (1996)              |
| Kenya                          | 0                  | 750                 | –                             | Light trap             | Kaunda-Arara et al. (2009)             |
| Reunion                        | (38) <sup>a</sup>  | 15 899              | –                             | Light trap             | Vermond et al. (2009)                  |
|                                | 1                  | 984                 | 1/29                          | Crest net              | Durville et al. (2002)                 |
| Madagascar                     | 1                  | 4049                | –                             | Light trap             | Mahafina et al. (unpubl.) <sup>b</sup> |
| Dampier Archip. (W. Australia) | 0                  | 28 535              | 0/4                           | Light trap             | L. Vigliola (pers. comm.)              |
| Ningaloo Reef (W. Australia)   | (432) <sup>a</sup> | 89 598              | –                             | Crest net              | McIlwain (2003)                        |

<sup>a</sup>Data for all Scorpaenidae  
<sup>b</sup>J. Mahafina, P. Chabanet, G. Lecaillon, J. P. Caminade, C. Ralijaona, J. Ferraris

because, despite a large sampling effort, only 1 lionfish was captured at Rangiroa 3 yr after the original study (Malpot 2005). If one excludes the 2 largest catches of lionfish larvae in these studies (Lo Yat 2002, Riclet 1995), the proportion of lionfish among all larvae (9.3 ind. per million fish) is lower than for adult fish (17.8 ind. per million fish). Nonetheless, the order of magnitude of these estimates is the same. The few studies on larvae in the Indian Ocean do not list *Pterois* specifically, but do indicate the proportion of Scorpaenidae (Table 3). The proportion of *Pterois*

larvae among Scorpaenidae larvae varied from 0.5% (Lo Yat 2002) to 12.5% (Malpot et al. 2008), with an unweighted average of 5.1%.

### Effects of large-scale factors

To compare all the observations in standardized form across different survey methods, a distribution map was constructed using a correction factor of 8 for normal surveys and of 1 for surveys specific to *Pterois*

(Fig. 3). This approach revealed large differences in *Pterois* densities between the Pacific and Indian Oceans (Fig. 3). *Pterois* is generally rare over most of the central Pacific (Micronesia, Melanesia and the western part of Polynesia), with higher densities recorded in the Indian Ocean.

Using a GLMz, we tested the potential influence on *Pterois* densities (log-transformed) of distance to the biodiversity center, latitude, hemisphere, SST, ocean and coast type and the interactions of these variables (see Table S3 in the Supplement for details). This GLM indicated that several large-scale factors affect *Pterois* densities. Latitude was the most significant factor ( $p < 0.0001$ ), with densities of *Pterois* spp. increasing with increasing latitude. Coast type was the second most important factor ( $p < 0.005$ ), with *Pterois* densities being higher in continental areas than around islands. The difference between Indian Ocean and Pacific Ocean densities (Indian Ocean densities being higher) was complex, as 2 interactions involving the factor 'Ocean' were significant: the 'Ocean × Hemisphere' interaction ( $p < 0.05$ ) and the 'Ocean × Coast type' interaction ( $p < 0.001$ ). The first interaction was due to higher relative values in the Southern Hemisphere for the Pacific Ocean than

for the Indian Ocean. The second interaction was due to the greater decrease of *Pterois* densities in the Pacific as compared to the Indian Ocean as one proceeds from continental areas to islands. Distance to the biodiversity center also had a significant effect ( $p < 0.05$ ), *Pterois* densities increasing with this distance. SST was not significant, but this factor was strongly correlated with latitude ( $r = -0.86$ ;  $N = 47$ ) and to a lower extent to hemisphere ( $r = -0.39$ ).

A GLM was used to test (see Tables S4 & S5 in the Supplement for details) whether the density of *Pterois* was a function of regional species richness for the following levels: total richness, piscivore richness (all piscivores), medium-size-piscivore (from 10 to 40 cm) richness, scorpaenid richness, and *Pterois* richness (Table 2). None of these factors proved significant.

### Effects of fishing on lionfishes

Visual-transect data from the Indian Ocean (Kenya, Mozambique, Tanzania, Madagascar and Mayotte) were analyzed according to the status 'protected' (23 *Pterois* ind., 71 700 fish, 242 transects) ver-

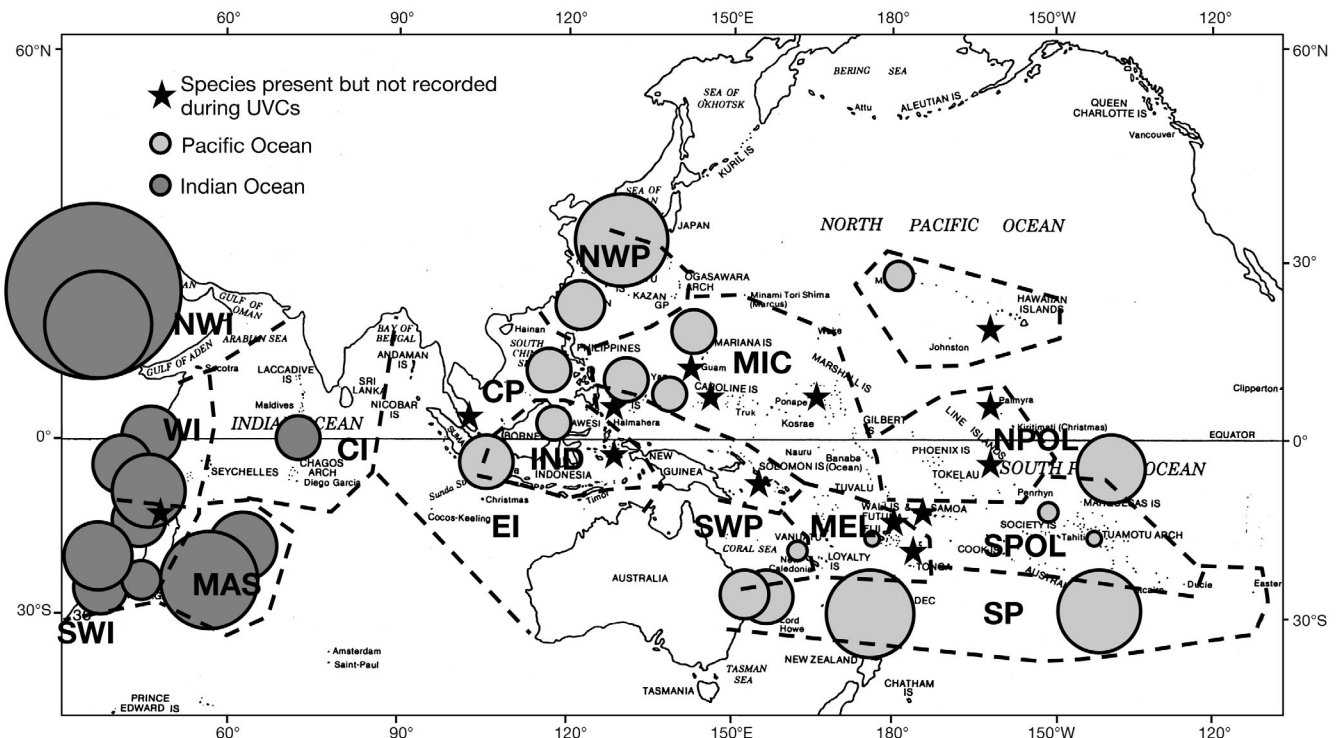


Fig. 3. *Pterois* spp. Geographical distribution of lionfish densities on Indo-Pacific coral reefs. Area of each circle is proportional to observed density. All densities (Tables 1 & 3) corrected for detectability by a factor of 8 for non-specific surveys and by a factor of 1 for lionfish-specific surveys. Stars: underwater visual census (UVC) surveys where no *Pterois* were detected despite presence of these species in species checklists of these areas. See Table 2 for definition of regions

sus 'unprotected' (27 *Pterois* ind., 63 400 fish, 320 transects). Protected areas had significantly higher densities of fish (all species pooled; 107 % increase in protected areas; *F*-test:  $p < 0.05$  for Kenya, Tanzania and Mozambique), but no protected-area effect could be detected for *Pterois* (9% increase in protected areas). A similar analysis in New Caledonia, one that compared the densities observed in the harbor of Nouméa (8 *Pterois* ind., 499 000 fish, 807 transects), where pollution and fishing are substantial, with densities from low-perturbation coastal areas (5 *Pterois* ind., 333 000 fish, 374 transects), also indicated no significant differences in the density or relative abundance of *Pterois* ( $\chi^2$ :  $p = 0.59$ ).

## CONCLUSIONS

Our macro-ecological approach examined the distribution of lionfish of the genus *Pterois* in their native Indo-Pacific range to facilitate comparisons with their invaded Atlantic range. We conclude that:

(1) *Pterois* is rare over most of its native range in the Indo-Pacific. Its average densities, even when corrected for detectability, are far less than densities observed in its invaded Atlantic range.

(2) The densities of *Pterois* are higher in the Indian Ocean than in the Pacific Ocean. It is noteworthy that, of the invasive species, *P. volitans* occurs in the Pacific and *P. miles* occurs in the Indian Ocean.

(3) The densities of *Pterois* are higher at the borders of its native range than in central regions, and higher on continental shelves than around islands.

(4) *Pterois* is found over a wide range of habitats in its native range, including coral reefs, soft substrates, algae and seagrass beds, mangroves and estuaries. It has been found in waters up to 75 m deep in its native range.

(5) The abundance ratios between settlement-stage larvae and adults are similar across various locations in the Pacific, indicating broadly similar juvenile survival rates.

(6) There appears to be no correlation at the regional level between *Pterois* species richness or density with the species richness or density of other scorpionfishes or piscivores.

*Pterois* is rare in the Indo-Pacific and thus it is important to discuss problems linked to estimating its presence and abundance in its native range. Our analysis of detectability shows that these fish are not easily detected. In the Indo-Pacific, *Pterois* often hides in holes, crevices or under ledges during daytime and leaves shelters mainly at night, although

*P. volitans* may be found in the open during daytime (Cure 2011). This behavior may reduce *Pterois* detection by observers if a focused sampling protocol is not followed. Our UVC data suggest that, in the Indo-Pacific, only one *Pterois* ind. in 8 is detected by non-specialized survey methods. In the absence of a similar analysis in the Atlantic, it is not possible to say whether a similar detection factor applies there. However, surveys in the Atlantic suggest that invasive *Pterois* are relatively conspicuous and easy to detect as they are frequently out of shelter and active during the day (Côté & Maljković 2010), as confirmed by comparative observations in both native and invaded ranges (Darling et al. 2011, M. Hixon, J. Beets pers. obs.). Changes in behavior are documented for many species that have escaped their natural predators (Mittelbach 1986, Holway & Suarez 1999, Sih et al. 2009). Even if the correction for detectability is applied, the estimated densities of *Pterois* in the Indo-Pacific remain much lower (average of 1.7 ind. ha<sup>-1</sup> in the Pacific, 28.8 ind. ha<sup>-1</sup> in the Indian Ocean) than their densities in the invaded regions (average of 100 ind. ha<sup>-1</sup> in the Bahamas, Darling et al. 2011; to 400 ind. ha<sup>-1</sup>, Green & Côté 2009, Morris & Whitfield 2009). Such high population densities are common for invasive species (Sakai et al. 2001), especially during the early stages of their invasion.

These large differences in density between native and invaded range suggest that *Pterois* has undergone ecological release, escaping natural abiotic or biotic controls operative in its native Indo-Pacific range. These might include predation, disease and parasites, competition and limited dispersal. Examining the sources of ecological release is presently an active area of research. The ratio of settlement-stage to adult abundance at various locations in the Pacific suggests juvenile mortality rates that may not be substantially different from those of other reef fishes (Almany & Webster 2006).

Anecdotal evidence is accumulating that several predatory species, in particular reef sharks and groupers, may occasionally feed on *Pterois* in the Atlantic (Mumby et al. 2011, M. Hixon pers. obs.), but no species in the Atlantic has yet been identified as targeting *Pterois* frequently enough to greatly restrain the invasion.

Does *Pterois* face much less competition in the Atlantic than in its native range? Lack of competition may be an important factor as *Pterois* lionfishes invade a range, since invaders often occupy previously vacant 'niche space' (sensu Cohen & Stephens 1978). *P. miles* and *P. volitans* are mainly piscivorous

(Albins & Hixon 2008, Morris & Akins 2009, Côté & Maljković 2010, Muñoz et al. 2011), although juvenile lionfish also prey on invertebrates. Indirect indicators of interspecific competition used in this study showed no regional or local competitive factors. For example, no correlation was found between lionfish densities and the regional species richness of *Pterois*, other scorpaenids, or piscivore species in general (Table 2). In addition, at the local level, no differences in lionfish densities between fished areas and fisheries closures or between highly disturbed and undisturbed areas were found, suggesting that predation and competition have little or no effect. In the western Atlantic, the proportion of piscivores is nearly half that observed in the Indo-Pacific at the regional level, and the absolute number of piscivore species is also much lower in the Atlantic than in any region of the Indo-Pacific. On the other hand, the proportion of Scorpaenidae in the regional species pool of the Atlantic (3%) is slightly higher than in the Indo-Pacific (2.6%). Lastly, it should be noted that *P. miles* has been reported from the Mediterranean Sea as an invading Lessepsian species (Golani & Sonin 1992), yet this species has so far remained at very low densities in its new range (Galil 2007). Consequently, predation and interspecific competition may not be major limiting factors for *Pterois* in the Indo-Pacific.

Limited dispersal and colonization of new habitats may influence the success of invading species. In their native range, lionfish are found not only on reefs but also in other habitats such as soft bottoms, seagrass beds and even mangroves. Our data show that in New Caledonia *Pterois* spp. are found on soft bottoms at population densities close to those observed on nearby reefs. They have also been observed on soft bottoms in many other Indo-Pacific regions at relatively high densities. Our results also show that *Pterois* has been observed near mangroves and estuaries in several Indo-Pacific regions, often in similar or even larger numbers than what is found on reefs. These results suggest that *Pterois* could become a frequent occupant of non-reef habitats in its invaded Atlantic range. For example, lionfishes have already been observed in seagrass beds and non-estuarine mangroves in the Bahamas (Barbour et al. 2010). Both seagrass beds and mangroves are important nursery habitats for a number of economically and ecologically important species in the Caribbean (Mumby et al. 2004, Verweij et al. 2006). The occupancy of these habitats also suggests that large expanses of non-reef areas may present no obstacle to the spread of lionfish in the Atlantic.

*Pterois* has been reported at 60 m depth and deeper (Froese & Pauly 2010), a finding that is confirmed by trawl surveys (in which *Pterois* was caught at 75 m), indicating the potential capacity of lionfish to disperse via deep waters; however, detailed data on their maximum depth is lacking. This finding is also confirmed in the Atlantic, where lionfish have been caught down to 99 m off the Carolinas (Meister et al. 2005) and observed from a submersible at 300 m in the Bahamas (M. O'Neil pers. comm.). Dispersal through deep water could allow invasive lionfish to pass the Amazon-Orinoco barrier, thereby expanding their southern range, as deep-water pathways have been demonstrated to be important in species distribution in the South Atlantic (e.g. Feitoza et al. 2005). The pelagic larval duration of *Pterois* in the Pacific (41 d for *P. radiata*, Lo Yat 2002; 40 d for *P. volitans*, Ruiz-Carus et al. 2006) is sufficient to ensure its dispersal within archipelagoes such as the Indonesian, Solomon Islands, Vanuatu or New Caledonia, where these fish remain uncommon. Pelagic larval duration of *P. volitans* in the Atlantic ranges from 20 to 35 d (average 26.2 d; Ahrenholz & Morris 2010). Thus the larval duration of this species is sufficient to ensure a wide and rapid establishment in the western Atlantic and Caribbean.

Beyond helping us to understand the potential mechanisms fostering this invasion, the present data on the distribution of lionfish in their native range may also be useful in predicting the potential evolution of this invasion. Densities of *Pterois* were higher at the boundaries of their native range, near the southern or northern limits of their ranges. In the absence of density data for the entire geographical range of *Pterois* spp. in the Indo-Pacific, this pattern should be interpreted with caution. Such an increase on the border of the geographical range of a species or genus contradicts the prevailing hypothesis that population abundance decreases at the limit of species range (Brown 1984). This pattern may indicate stronger (albeit unknown) limiting factors on lionfish density at the center of their geographical range than at the boundaries.

Our analyses also indicate that, in the Indo-Pacific, *Pterois* is found at higher densities over continental shelves than near islands. Habitat size and diversity is in general greater on continental shelves than on islands; this may favor higher connectivity and consequently higher densities of these habitat generalists over continental shelves. If this pattern emerges in the Atlantic after lionfish densities have stabilized, we would expect higher

densities in the northern and southern parts of their new range and along the continental shelves as compared to islands (mainly Caribbean islands and the Bahamas).

It is difficult to estimate the ultimate impact of lionfish on native reef-fish assemblages in the Caribbean until their numbers have stabilized; it is also difficult to estimate whether the current high densities will stabilize or signify the first stage of an

invasion process. The present densities of piscivorous fishes in the Caribbean are difficult to assess and may be heavily influenced by a long history of fishing. The Atlantic and Gulf Rapid Reef Assessment (AGRRA) database provides a first and probably crude estimate for the Caribbean (Marks 2007), with values ranging from <100 to >881 piscivores  $\text{ha}^{-1}$ , with an average of 458 piscivores  $\text{ha}^{-1}$  (Table 6). Another source of data for the Atlantic (S.

Table 6. *Pterois* spp. Large-piscivore densities for Atlantic and South Pacific reefs. In Marks (2007) only transect data obtained by 'experienced' observers were retained

| Region                     | Area covered (ha) | Piscivores |                    |                | Status   | Source                      |
|----------------------------|-------------------|------------|--------------------|----------------|----------|-----------------------------|
|                            |                   | n          | n $\text{ha}^{-1}$ | No. of species |          |                             |
| <b>Atlantic: Caribbean</b> |                   |            |                    |                |          |                             |
| Bahamas                    | 2.544             | 1574       | 618                | 14             |          | Marks (2007)                |
| Belize                     | 2.754             | 1554       | 564                | 14             |          | Marks (2007)                |
| Bocas del Toro (Panama)    | 0.624             | 410        | 657                | 10             |          | S. Floeter et al. (unpubl.) |
| Cayman Islands             | 2.598             | 1217       | 468                | 13             |          | Marks (2007)                |
| Cuba                       | 9.768             | 7548       | 772                | 15             |          | Marks (2007)                |
| Dominican Republic         | 0.948             | 79         | 83                 | 5              |          | Marks (2007)                |
| Dry Tortugas               | 0.942             | 600        | 636                | 8              |          | Marks (2007)                |
| Jamaica                    | 3.546             | 597        | 168                | 9              |          | Marks (2007)                |
| Mexico                     | 2.256             | 837        | 371                | 12             |          | Marks (2007)                |
| Netherlands Antilles       | 1.764             | 718        | 407                | 9              |          | Marks (2007)                |
| Panama                     | 2.586             | 832        | 321                | 12             |          | Marks (2007)                |
| Puerto Rico                | 1.044             | 251        | 240                | 10             |          | Marks (2007)                |
| St. Vincent                | 0.300             | 8          | 26                 | 2              |          | Marks (2007)                |
| Turks & Caicos             | 1.674             | 929        | 554                | 10             |          | Marks (2007)                |
| USA                        | 2.406             | 2122       | 881                | 15             |          | Marks (2007)                |
| Virgin Islands             | 1.464             | 824        | 562                | 12             |          | Marks (2007)                |
| <b>Atlantic: Brazil</b>    |                   |            |                    |                |          |                             |
| Abrolhos                   | 0.658             | 131        | 199                | 5              |          | S. Floeter et al. (unpubl.) |
| Arraial do Cabo            | 2.405             | 457        | 190                | 11             |          | S. Floeter et al. (unpubl.) |
| St Paul's Rocks            | 0.796             | 492        | 618                | 4              |          | S. Floeter et al. (unpubl.) |
| Guarapari                  | 0.660             | 373        | 565                | 8              |          | S. Floeter et al. (unpubl.) |
| Ilha Grande                | 0.432             | 255        | 590                | 7              |          | S. Floeter et al. (unpubl.) |
| Laje de Santos             | 0.418             | 51         | 122                | 5              |          | S. Floeter et al. (unpubl.) |
| F. Noronha                 | 0.356             | 144        | 404                | 9              |          | S. Floeter et al. (unpubl.) |
| Santa Catarina             | 1.813             | 825        | 455                | 12             |          | S. Floeter et al. (unpubl.) |
| Trindade                   | 1.378             | 226        | 164                | 11             |          | S. Floeter et al. (unpubl.) |
| <b>South Pacific</b>       |                   |            |                    |                |          |                             |
| New Caledonia              | 4.750             | 313        | 66                 | 39             | Fished   | Labrosse et al. (1999)      |
| New Caledonia              | 1.550             | 575        | 371                | 34             | Unfished | Labrosse et al. (1999)      |
| Fiji                       | 0.400             | 203        | 508                | 25             | Fished   | Labrosse et al. (1999)      |
| Fiji                       | 1.000             | 509        | 509                | 29             | Unfished | Labrosse et al. (1999)      |
| Tonga                      | 1.350             | 211        | 157                | 19             | Fished   | Labrosse et al. (1999)      |
| Tonga                      | 1.300             | 501        | 386                | 29             | Unfished | Labrosse et al. (1999)      |
| Polynesia                  | 0.425             | 70         | 167                | 8              | Fished   | Labrosse et al. (1999)      |
| Polynesia                  | 0.700             | 256        | 366                | 27             | Unfished | Labrosse et al. (1999)      |
| <b>Unweighted averages</b> |                   |            |                    |                |          |                             |
| Atlantic-Caribbean         |                   |            | 458                |                |          |                             |
| Atlantic-Brazil            |                   |            | 367                |                |          |                             |
| South Pacific              |                   |            | 316                |                |          |                             |

Floeter et al. unpubl. data) indicates values ranging from 122 to 590 piscivores ha<sup>-1</sup> for Brazil, with an average of 367 piscivores ha<sup>-1</sup> (Table 6). A similar analysis in the South Pacific (where fishing intensity is probably lower than in most of the Caribbean; Stallings 2009) indicates lower densities of piscivores there, with a maximum of 509 piscivores ha<sup>-1</sup> and an average of 316 piscivores ha<sup>-1</sup> (Table 6). In contrast, piscivore diversity is much higher in the South Pacific, with up to 39 species, whereas in the Atlantic the maximum is 15 species (Table 6). These preliminary data suggest a different density-diversity structure of piscivory in these regions. Therefore, the hypothesis that the success of lionfish in the Atlantic is linked to low piscivory levels may not be correct, unless lionfish are filling a functional piscivory niche that was not filled by evolutionary processes or that has been influenced and made vacant by fishing pressure. The densities of *Pterois* in the Atlantic are high for any piscivorous species, with the genus representing probably well over 30% of piscivorous species in some places. The current addition of such a sizeable abundance of piscivores is expected to cause a major imbalance in the reef-fish assemblages of the Atlantic (Albins & Hixon 2011).

In conclusion, the distribution, abundance and ecology of lionfishes in their native Indo-Pacific range may provide some insight into what is causing their success in the Atlantic Ocean. Invasive lionfish almost certainly have escaped the natural controls that limit their density in their native range. This reality justifies reef managers in the invaded Atlantic range in actively limiting the abundance of these invaders by culling programs, provided that such activities do not harm the already stressed coral-reef ecosystems in the region.

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