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# Targeted census of lionfishes (Scorpaenidae) reveals high densities in their native range

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## Abstract

Indo-Pacific lionfishes generally exhibit cryptic behaviours and so can be missed when conducting non-targeted surveys. Here, the authors report the results from targeted surveys of lionfish at Moorea, French Polynesia. Lionfish from three species (*Pterois antennata*, *Pterois radiata*, *Dendrochirus biocellatus*) were observed at a mean density of 267 individuals ha$^{-1}$. This is substantially higher than previous estimates from the same area (Moorea) and represents the highest reported density of lionfishes from their Pacific range. Overall, this study highlights the importance of targeted survey techniques for detecting cryptic species on coral reefs.

**KEYWORDS**
coral reefs, *Dendrochirus*, French Polynesia, lionfish, Moorea, *Pterois*

Lionfishes occur naturally on coral reefs across the Indo-Pacific region, where they are considered cryptic, crepuscular, habitat-generalist fishes that spend much of the day under ledges or in crevices (McTee & Grubich, 2014). The majority of reported estimates of lionfish density within their native ranges have been calculated from data collected using non-targeted methodologies, *i.e*., recording lionfish as a component of more general fish surveys; however, these types of surveys are likely to underestimate the number of lionfish present (Green *et al*., 2013; Kulbicki *et al*., 2012). For example, estimates from non-targeted surveys suggest that *Pterois* lionfishes occur

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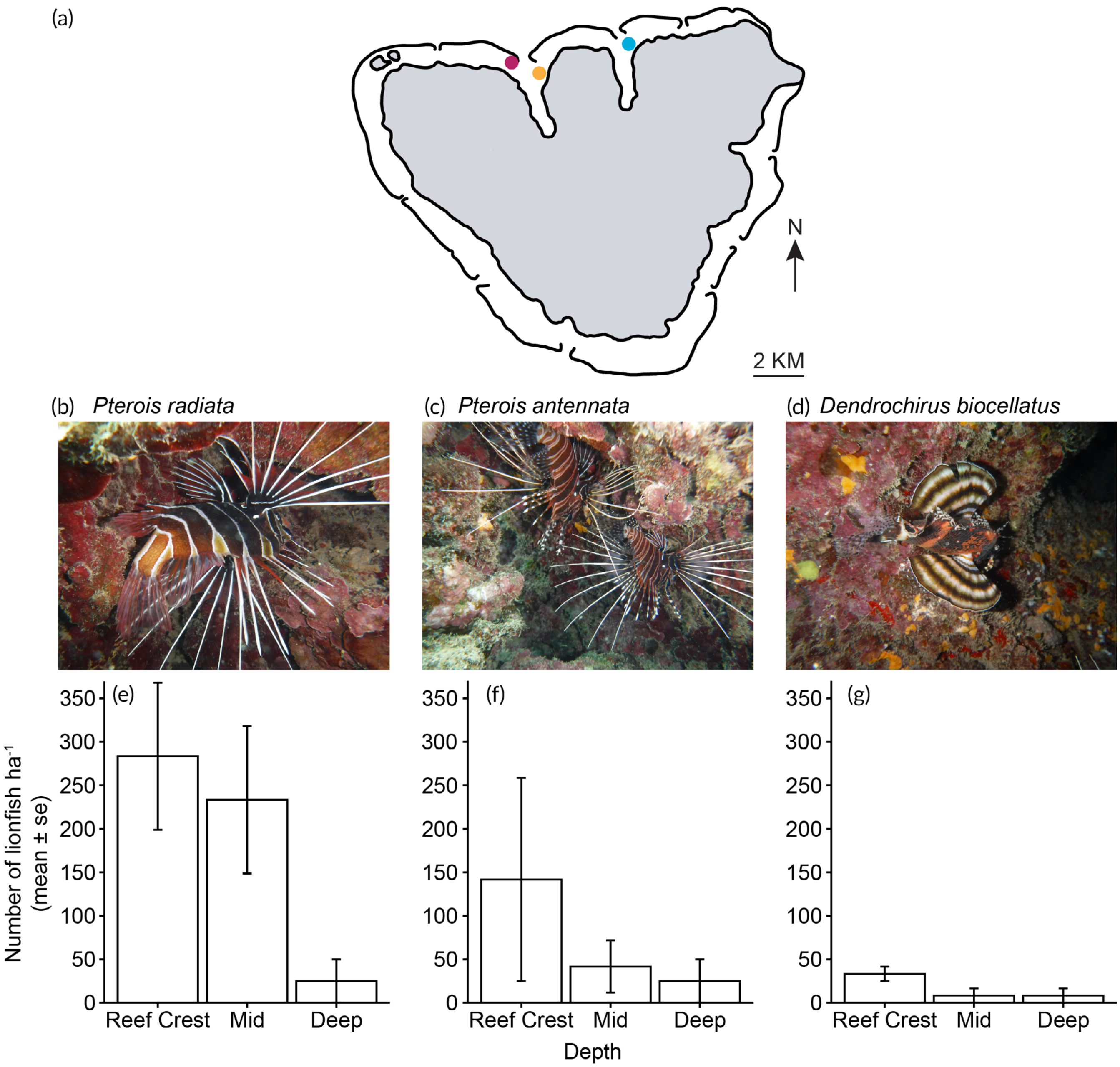


**FIGURE 1** Lionfishes observed during targeted surveys at three sites at Moorea, French Polynesia. A total of 90 transects (total area surveyed = 3600 $m^2$) were conducted across three depths ["Reef Crest" (*c.* 1–3 m depth); "Mid" (3 m below the reef crest, *c.* 4–6 m depth); and "Deep" (6 m below the reef crest, *c.* 7–9 m depth)] at the three locations (a). Three species of lionfish were observed: clearfin lionfish *Pterois radiata* (b, e); spotfin lionfish *Pterois antennata* (c, f); and twinspot lionfish *Dendrochirus biocellatus* (d, g). Density is averaged (mean ± se) across the three locations. ● Site 1, ● Site 2, ● Site 3

at an average density of 0.17 individuals $ha^{-1}$ and 3.6 individuals $ha^{-1}$ for the entire Pacific and Indian Ocean regions, respectively (Kulbicki *et al.*, 2012), which contrasts with substantially higher densities, for example, 44.99 ± 9.91 individuals $ha^{-1}$ (mean ± S.E.; *Pterois volitans, Pterois antennata, Dendrochirus zebra, Dendrochirus brachypterus*) reported from targeted surveys in the Philippines (Cure *et al.*, 2014) and 95 individuals $ha^{-1}$ (*Pterois miles*) reported from mark-release-recapture studies in the Red Sea (Bos *et al.*, 2018). In addition, Green *et al.* (2013) compared the results of two commonly used, non-targeted underwater visual survey methods (belt transect surveys and stationary visual census) with targeted searches and found that the non-targeted methods detected fewer than 30% of the lionfish present in an area, and failed to detect any lionfish at all in more than 50% of cases where one or more individuals had been detected by the targeted surveys.

There are five lionfish species found in French Polynesia: spotfin lionfish *Pterois antennata*; clearfin lionfish *Pterois radiata*; red lionfish *Pterois volitans*; twinspot lionfish *Dendrochirus biocellatus* (Siu *et al.*, 2017); and Tuamotu's dwarf lionfish *Dendrochirus* *tuamotuensis* (reported only from the Tuamotu Archipelago) (Matsunuma *et al*., 2017). To date, two studies (Kulbicki *et al*., 2012; Lecchini *et al*., 2006) have provided estimates of lionfish densities from visual censuses in French Polynesia. Both of these studies were indiscriminate in their approach (*i.e*., general fish censuses, which were not specifically aimed at recording lionfishes), and provided an overview of fish densities in the area using a standardized survey methodology. Lecchini *et al*. (2006) detected two species of lionfish (*D. biocellatus* and *P. radiata*) at Moorea, with both being reported at densities of 1 lionfish ha$^{-1}$ on the barrier reef and outer slope sites (zero recorded from fringing reef sites); whereas Kulbicki *et al*. (2012) reported only on *Pterois* spp. (recorded at the genus level), which were observed in densities ranging from 0.25 (Tuamotu)—7.1 (Rapa) individuals ha$^{-1}$. Further, an earlier study, which employed chemical (rotenone) poisoning across two fringing reef (250 m$^2$) and two barrier reef sites (175 m$^2$) at Moorea, reported one *P. antennata* from one of the barrier reef sites, suggesting a much higher density (mean = 50 lionfish ha$^{-1}$ for the barrier reef) (Galzin, 1979). Despite these studies being non-targeted in their approach, and primarily recording lionfish species that are not invasive throughout the western Atlantic and Mediterranean, they have been used as evidence for the purported natural low density of lionfishes within their native range compared to their invaded western Atlantic range (*e.g*., Bos *et al*., 2018; Kulbicki *et al*., 2012). In this study, the authors conducted targeted surveys on the fringing reefs surrounding Moorea, French Polynesia, to provide an updated density estimate for all lionfish species at this location and investigate whether lionfish density changed with survey depth.

Lionfish assemblages were surveyed on reefs surrounding Moorea in French Polynesia (17° 29′ S, 149° 49′ W) in November–December 2019 (Figure 1a). Sampling was conducted at three fringing reef sites (Site 1: 17° 29′ 18″ S 149° 49′ 08″ W, Site 2: 17° 29′ 37″ S 149° 51′ 07″ W, Site 3: 17° 29′ 24″ S 149° 52′ 08″ W; Figure 1a), which were selected as they had a steep and extended reef slope (>250 m in length) with a defined reef crest. The three sites were estimated to be similar in benthic composition, with low coral cover (<5%) and substrate dominated by sediment-laden algal turfs (*c*. 40%) and fine sediment such as silt or sand (*c*. 20%). Ten 20 m transects were conducted at three depths at each location (*n* = 30 per location): along the reef crest (*c*. 1–3 m depth); 3 m below the reef crest (*c*. 4–6 m depth); and 6 m below the reef crest (*c*. 7–9 m depth). Each transect was conducted by two divers on scuba, with the divers recording all lionfish within 1 m either side of the transect tape (total area surveyed per transect = 40 m$^2$). Given the cryptic nature of lionfishes in their native range, survey teams searched all caves, crevices and overhangs (hereafter referred to collectively as "caves") to ensure that all lionfish in the transect area were recorded. For each lionfish, divers recorded the species, an estimate of total length (to the nearest 10 mm), whether it was in a cave or out in the open, and whether it was alone or with other lionfish. Individual lionfishes were also photographed where possible, which enabled the later confirmation of species identification. Surveys were conducted between 11 am and 1 pm, to ensure that there were no differences in density due to increased behaviour which may be observed at certain times of day (*e.g*., McTee & Grubich, 2014).

Statistical analyses were conducted within the statistical programme R, version 4.2.2 (R Core Team, 2022) on RStudio, version 2022.7.2.576 (RStudio Team, 2022). The authors used a generalized linear mixed-effects model (glmer) with a Poisson distribution in the {lme4} package (Bates *et al*., 2015) to investigate whether lionfish density varied across the different lionfish species and at different survey depths. In the full model, the number of lionfish (*i.e*., count data) was the dependent variable, lionfish species and survey depth as well as the interaction between these two variables were included as fixed effects and survey location was included as a random effect. A top-down approach was used to arrive at the most parsimonious model: there was no significant interaction between lionfish species and survey depth, so the final model included the two fixed factors (species and survey depth) without the interaction term. Model assumptions were examined using the {DHARMa} package (Hartig, 2020). *Post hoc* tests were conducted using the {emmeans} package (Lenth, 2022). Figures were plotted using the {ggplot2} package (Wickham, 2016).

In total, the authors observed 96 adult lionfish from three of the four species known to occur at Moorea [*P. antennata* (*n* = 25, size range = 50–200 mm), *P. radiata* (*n* = 65, size range = 60–200 mm) and *D. biocellatus* (*n* = 6, size range = 70–100 mm)] across 90 transects (3600 m$^2$) (Figure 1). Lionfish density varied significantly across species ($\chi^2_2$=59.69, $P$ < 0.01), and *post hoc* analyses revealed that *P. radiata* was significantly more abundant than both *P. antennata* ($P$ < 0.01) and *D. biocellatus* ($P$ < 0.01), and *P. antennata* was also significantly more abundant than *D. biocellatus* ($P$ < 0.01) (Figure 1). Interestingly, the larger species of lionfish, *P. volitans*, which is the only species to date to have caused a major invasion, was not recorded during the surveys; although one individual was observed at one of the transect sites, it was not within the boundaries of the transects and thus was not included. The observation that *P. radiata* was the most abundant species recorded during the surveys, followed by *P. antennata*, with *D. biocellatus* and *P. volitans* observed the least frequently corresponds with observations from Helen Reef Atoll in the Palau Archipelago (Grubich *et al*., 2009), but contrasts with reports from elsewhere in the Indo-Pacific region where *P. radiata* is considered comparatively rare (Hayes, 2020; Kulbicki *et al*., 2012). In addition, 54% of *P. radiata* observed on the transects were observed with other lionfish, which contrasts with other Pacific locations where *P. radiata* was always observed singly (Donaldson *et al*., 2011).

In the Indo-Pacific region, lionfishes primarily forage during crepuscular and nocturnal hours (*e.g*., Cure *et al*., 2012; Darling *et al*., 2011; Fishelson, 1975; Harmelin-Vivien & Bouchon, 1976; McTee & Grubich, 2014), and thus it was unsurprising that lionfishes were most frequently observed in caves or under overhangs (95%), *vs*. in the open (5%), during the presented daytime surveys – a behaviour which is likely to contribute to low detection of lionfishes during non-targeted surveys. All three observed species were found at each depth surveyed; nonetheless, the authors observed a significant effect of depth on lionfish density ($\chi^2_2$=42.42, $P$ < 0.01). *Post hoc* analyses indicated that there was no significant difference in lionfish density along the reef crest compared to 3 m below the reef crest ($P = 0.07$), but the lionfish densities were significantly greater at both the reef crest ($P < 0.01$) and 3 m below the reef crest ($P < 0.01$) compared to 6 m below the reef crest.

A previous analysis of *Pterois* lionfish density within the native range, using data from non-targeted surveys, estimated 0.17 individuals ha$^{-1}$ for the Pacific Ocean (average relative density = 17 lionfish per million fish) and 3.6 lionfish ha$^{-1}$ for the Indian Ocean (average relative density = 343 lionfish per million fish) (Kulbicki *et al*., 2012). For Moorea specifically, the previously reported estimate of lionfish density, based on non-targeted methods, was 1 individual ha$^{-1}$ for each species observed (*P. radiata* and *D. biocellatus*) across barrier and outer slope reefs (Lecchini *et al*., 2006). Fringing reefs, which were the focus of the present study, were also surveyed by Lecchini *et al*. (2006); however, no lionfish were recorded. In contrast, if observations of *P. antennata*, *P. radiata* and *D. biocellatus* across the three depths within each site are combined, the mean density of lionfishes in Moorea during the targeted surveys was 267 ± 113 individuals ha$^{-1}$ (mean ± S.E.) (range: 150–492 individuals ha$^{-1}$). Interestingly, this is substantially greater than the highest densities previously recorded anywhere within the native range of lionfish, even from targeted surveys [*e.g*., Philippines, 44.99 ± 9.91 individuals ha$^{-1}$ (Cure *et al*., 2014); Red Sea, 47.9 individuals ha$^{-1}$ (McTee & Grubich, 2014); Kenya, 71.7 individuals ha$^{-1}$ (Darling *et al*., 2011)] and mark-release-recapture studies [95 individuals ha$^{-1}$ (Bos *et al*., 2018)], and is comparable with densities recorded from the invaded western Atlantic and Caribbean range [*e.g*., North Carolina, 150 individuals ha$^{-1}$ (Morris Jr. & Whitfield, 2009), Bahamas, 393.3 ± 144.4 individuals ha$^{-1}$ (Green & Côté, 2009), Colombia, 379.03 ± 220 individuals ha$^{-1}$ (González-Corredor *et al*., 2016)]. In addition to detecting very high lionfish densities likely due to the use of targeted surveys, this study's data suggest that the fringing reef around Moorea may be a particularly suitable habitat for lionfishes. Interestingly, the authors' observation of high densities of *P. antennata*, *P. radiata* and *D. biocellatus* and no *P. volitans* at sites dominated by fine sediments contrasts with previous research, which suggests that *P. volitans* utilizes sandy/silty habitats more than other lionfish species and that the lionfishes observed in this study rarely occur in these types of habitats (Cure *et al*., 2014).

Overall, the study results indicate that lionfishes can be far more abundant at locations within their native range than generally considered. Using targeted survey methods, the authors recorded lionfish densities that are substantially higher than those previously reported from French Polynesia. Although the species reported in this study (*P. antennata*, *P. radiata* and *D. biocellatus*) are not those that have invaded the western Atlantic and Mediterranean (*P. volitans* and *P. miles*), they do include those that have previously been used to compare densities of lionfishes in their native *vs*. invaded ranges (*e.g*., Bos *et al*., 2018; Kulbicki *et al*., 2012) and are therefore relevant to this literature. In addition, as these three species comprised *c*. 13% of lionfishes imported into the United States between April 2016 and 2017 (Lyons *et al*., 2019), the possibility of introductions of new species still poses a threat to this region. Importantly, this study's result adds support to a previous study from the Red Sea, which suggests that lionfish densities in their native range have been underestimated (McTee & Grubich, 2014), and highlights the need to use targeted surveys for detecting cryptic species.

## AUTHOR CONTRIBUTIONS

Zara-Louise Cowan, Rohan M. Brooker and William E. Feeney designed the study with input from Camille Gache; Zara-Louise Cowan, Rohan M. Brooker, Julien Gasc, Camille Gache and William E. Feeney collected the data; Zara-Louise Cowan and William E. Feeney implemented the analyses; Zara-Louise Cowan wrote the manuscript; all authors contributed to review and editing.

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## CONFLICT OF INTEREST

On behalf of all authors, the corresponding author states that there is no conflict of interest.

## ETHICS STATEMENT

This study did not involve endangered or protected species and was carried out in accordance with the guidelines of the French Polynesia code for animal ethics and scientific research (https://www.service-public.pf/diren/partager/code/).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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