

Native densities, distribution, and diurnal activity of Red Sea lionfishes (Scorpaenidae)

Sarah A. McTee¹, Justin R. Grubich^{2,*}

¹Environmental Defense Fund, 123 Mission St. 28th Flr., San Francisco, CA 94105, USA

²Department of Biology, American University in Cairo, Field Museum of Natural History, 1400 S. Lakeshore Drive, Chicago, IL 60605, USA

ABSTRACT: As invasive lionfish populations continue to expand in the Western Atlantic and Caribbean, understanding the ecology and foraging behavior of lionfish in their native habitats will help identify biotic constraints that may improve management of invaded reefs. The most comprehensive survey of lionfish, concluded to date, of native Red Sea lionfish was undertaken to identify potential differences in vertical distribution, density and diurnal cycles of foraging behavior. The overall, combined density of lionfish was estimated at 47.9 fish ha⁻¹, the highest yet recorded throughout their native range. The most commonly encountered lionfish species were *Pterois miles* (26.4 fish ha⁻¹) and *P. radiata* (20.8 fish ha⁻¹). The density of *P. miles* was significantly greater at the northernmost site surveyed and also significantly greater at depths less than 15 m, with individuals often observed in aggregations. In contrast, *P. radiata* were often solitary and evenly distributed along the reef profile. Despite ecological differences between these 2 species, the majority of foraging activities for both *P. miles* and *P. radiata* occurred around or after sunset. These results validate that the shallow coral reef habitats of the Red Sea host the highest densities of lionfish in their native range and highlight areas of ecological variability among native lionfish species.

KEY WORDS: Coral reef fishes · Foraging behavior · Species diversity · Invasive species

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The invasion of the Western Atlantic and Caribbean by lionfish (e.g. *Pterois volitans* and *P. miles*, 2 ecologically synonymous species) was identified by Sutherland et al. (2010) as one of the top 15 global challenges in marine conservation. Invasive species not only affect native biodiversity, but are often associated with significant economic and ecological costs. Establishment of non-native species in both terrestrial and aquatic habitats has become increasingly common with increasing globalization (Kolar & Lodge 2002, Kellner & Hastings 2009, Liao et al. 2010); however, few cases can match the speed and magnitude of the human-mediated geographical range expansion of lionfish in the Western Atlantic and Caribbean over the last decade (Whitfield et al. 2002, Freshwater

et al. 2009, Morris and Akins 2009, Schofield 2009, 2010). The extraordinary predatory abilities of lionfish in combination with their defensive venomous spines, lack of natural predators (Albins & Hixon 2013) and life history strategy that includes early age at maturity and high fecundity (Morris 2009) have likely facilitated their expansive invasion.

In their native habitats, lionfishes are commonly found on reef slopes (Fishelson 1975, Harmelin-Vivien & Bouchon 1976) within the coral matrix, on reef walls, or underneath overhangs (Grubich et al. 2009). *P. volitans/miles* also frequent soft-bottom areas (Fishelson 1975) and other marine habitats (Kulbicki et al. 2012). Observed native densities differ by species, but generally range from 0.27 to 26.3 fish ha⁻¹ (Kulbicki et al. 2012). Lionfishes are known to primarily forage during crepuscular and

*Corresponding author: justinrg@gmail.com

nocturnal hours in native habitats of the Gulf of Aqaba, East Africa, and Indo-Pacific (Fishelson 1975, Harmelin-Vivien & Bouchon 1976, Darling et al. 2011, Cure et al. 2012). While few trophic data exist from native habitats, the diet of *P. volitans/miles* from the Indian Ocean was found to consist primarily of small crustaceans and coral reef fishes (Harmelin-Vivien & Bouchon 1976).

Due to the potential repercussions of the establishment of *P. volitans/miles* throughout the Caribbean and western Atlantic, the scientific community has made substantial efforts to study invasive lionfish populations during the last 10 years (Côté et al. 2013). Recently, comparative studies have begun to establish significant differences between native and invasive populations, with invasive populations trending towards a more diverse prey assemblage, greater daily consumption rates, and larger body size (Darling et al. 2011, Cure et al. 2012). Lionfish in the Atlantic and Caribbean are not restricted to coral reefs, but are also utilizing habitats in and around mangroves (Barbour et al. 2010), seagrass meadows (Biggs & Olden 2011), and coastal estuaries (Jud & Layman 2012), consistent with their occurrence and distribution within native habitats (Kulbicki et al. 2012). Given that *P. volitans* can occupy a variety of habitats and has the ability to reduce the abundance and recruitment of fish species in invaded habitats (Albins & Hixon 2008, Green et al. 2013), invasive lionfish have the potential to affect native biodiversity and trophic structure in several marine ecosystems throughout the western Atlantic and Caribbean.

As the body of knowledge regarding the invasive populations continues to grow, research into the ecology and behavior of lionfish species within their native habitats is, and will, continue to be useful. Assessments of lionfish behavior and habitat utilization within their native ranges provide fundamental comparative data necessary to ascertain whether invasive populations are exhibiting atypical traits, which may indicate a release from abiotic or biotic constraints present in their native habitat. Additionally, such comparisons speak to the effects lionfish may have on local ecosystems, highlight ways in which *P. volitans/miles* may be adapting to the newly invaded habitats, and give a measure to the extent of their successful invasion in the Atlantic and Caribbean.

Thus far, the Red Sea region has the highest recorded densities of *Pterois miles* in their native range (Fishelson 1997, Kulbicki et al. 2012). These estimates, however, are based on surveys that were limited in both scope and geographic range. To expand our understanding of Red Sea lionfishes, the

coral reefs of the northern Red Sea and Gulf of Aqaba were surveyed to investigate 3 basic questions: (1) do densities of lionfishes vary geographically within the Red Sea, (2) do lionfish species exhibit depth preferences along the coral reef profile, and (3) does foraging activity and hunting behavior vary among lionfish species?

MATERIALS AND METHODS

Study sites

Survey efforts were focused on 6 sites collectively referred to as the 'northern Red Sea': Dahab, in the Gulf of Aqaba; Sharm El Sheik, at the mouth of the Straits of Turin; Hurghada, just south of the Gulf of Suez; Marsa Shagra and Marsa Nakari, along the southeastern coast of Egypt near Marsa Alam; and Jeddah, Saudi Arabia in the eastern Red Sea (Fig. 1). The Red Sea is unique in that it is characterized by high salinities (40–45 ppt) with little to no freshwater input, small tidal cycles, and a narrow thermal range (e.g. 20–30°C). The Gulf of Aqaba, being a narrow (6–25 km wide) northern extension of the Red Sea, experiences reduced hydrological exchange and similarly high salinities. In general, coral reefs of the northern Red Sea are comprised of fringing reefs beginning only a few meters from the high tide line with short reef slopes that quickly descend to 20–25 m depth, followed by sand-dominated slope habitats extending hundreds of meters deep. The reefs surveyed varied in habitat type, coral cover and vertical relief. In contrast to the Gulf of Aqaba, the Straits of Turin, and Marsa Alam, the continental shelves of Jeddah and Hurghada are larger, extending over 10 km in some places. These extended shelves are covered by a series of inner patch reefs that experience various levels of sedimentation from coastal development and windblown sand, while clearer fringing reefs are found at their most seaward margins.

Red Sea lionfishes

There are potentially up to 6 species of lionfishes that inhabit the coral reefs of the Red Sea and Arabian Basin (Randall 1983, Debelius 2001, Lieske & Myers 2004). The devil firefish *Pterois miles* and the clearfin lionfish *P. radiata* are the most commonly encountered species. Population genetic studies on invasive populations within the Western Atlantic and Caribbean estimate that approximately 7% of the

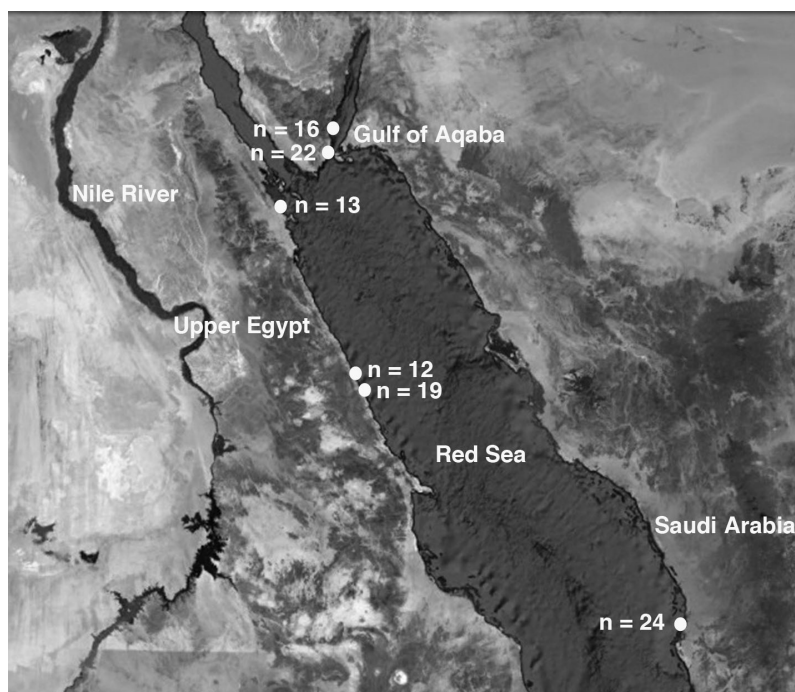


Fig. 1. Location of 6 reef sites (white circles) surveyed for lionfish species distribution, abundance and patterns of foraging behavior in the northern Red Sea region. From north to south: Dahab (Gulf of Aqaba) Sharm El Sheik (Straits of Turin); Hurghada, Marsa Shagra & Marsa Nakari (Egypt, north-western Red Sea); Jeddah (Saudi Arabia, east-central Red Sea). n = total number of transects completed at each study site. Image modified from Google earth v.6.2 (2012)

invasive populations originate from the *P. miles* lineage (Hamner et al. 2007, Betancur-R et al. 2011) whose native range spans from the Red Sea south along the east coast of Africa and throughout the Indian Ocean (Eschmeyer 1986, Kulbicki et al. 2012). Although *P. miles* are considered a genetically distinct species from the Indo-Pacific *P. volitans*, they are ecomorphologically synonymous (Kochzius et al. 2003). *P. radiata* is easily discerned from *P. miles* by its color pattern and white threadlike pectoral fin rays. *P. radiata* is also ecomorphologically distinct from *P. miles* in that it grows to a smaller body size, has a smaller oral gape with thick, fleshy lips, and feeds almost exclusively on crustaceans found in the dense reef matrix, while *P. miles* (and *P. volitans* consequently) feed mainly on reef fishes (Harmelin-Vivien & Bouchon, 1976, pers. obs).

SCUBA surveys

Visual surveys of lionfish species were conducted from January 2010 through June 2011. Using SCUBA, 2 divers performed a total of 106 belt transects ($50 \times$

5 m). Transects were conducted parallel to dominant reef topography along pre-determined depth contours: 5, 10, 15 and 20 m. Surveys beyond 20 m were not possible at many sites due to the structure and topography of the reef, as well as restrictive Egyptian dive regulations. All Scorpaenid species encountered during surveys were identified, including stonefishes (*Synanceia verrucosa*), scorpionfishes (*Scorpaenopsis* spp.), and lionfish species including a shortfin dwarf lionfish (*Dendrochirus brachypterus*). Survey effort, however, was focused on recording the presence of the 2 most commonly encountered species in the region, *P. miles* and *P. radiata*.

Given the cryptic nature of lionfish in their native habitat, each transect was surveyed twice. Following the initial survey by the first diver, a second diver would search crevices, overhangs and other reef structures, ensuring all lionfish in the transect area were accounted for. This survey method is similar to the lionfish-focused surveys (LFS) subsequently described by Green et al. (2013), differing slightly in the search pattern and thereby

duration. In this study, instead of swimming in the S-shaped pattern characteristic of a LFS, the second diver would zigzag across the transect according to the presence of habitat features and substrate where lionfish may be sheltering and that required additional inspection. As a result, the duration of the surveys was dictated by habitat rugosity and benthic features encountered. The majority of transects ($n = 65$) were conducted between 9:00 and 14:00 h; however, survey effort was distributed throughout the day, starting an hour after sunrise (7:00 h; $n = 8$), through the late afternoon (14:20–17:00 h; $n = 25$) and during or after sunset, which occurred at approximately 18:00 h ($n = 8$). For dives conducted after sunset, dive lights were covered with red filters to minimize diver influence and disruption to lionfish foraging behavior.

To better elucidate the normal foraging behavior and activity patterns of native lionfish species, notes on movement and/or activity were recorded for all lionfish encountered. Lionfish that were sheltering, or exposed but stationary on substrate, were considered 'inactive'. Lionfish actively swimming, suc-

cessfully feeding, or engaged in attempted foraging behavior were noted as 'active'. Free-swimming surveys for lionfish were also conducted at each site, allowing for more detailed observations, as well as photo and video documentation of lionfish foraging behavior.

Statistical analysis

One-way ANOVAs using standard least squares regression were used to evaluate differences in density among sites as well as depth distributions for *P. miles* and *P. radiata*. To account for unequal variances in our data (due to the large number of transects with zero lionfish counts) we adjusted the degrees of freedom using the Welch modification (Welch 1947). All comparisons were run on JMP statistical software v.5.01.

RESULTS

Lionfish density

Combining observations of *Pterois miles* and *P. radiata* for all surveys, the overall mean density of Red Sea lionfishes was 47.9 fish ha⁻¹. Significant variation

in the density of *P. miles* was detected among the 6 sites (Welch ANOVA: $F_{5,36.5} = 3.26$, $p = 0.016$); Pair-wise comparisons identified Dahab as having significantly greater densities of *P. miles* (mean \pm SD: 87.3 ± 117.5 fish ha⁻¹) compared to the other 5 sites (Tukey-Kramer HSD = 2.18, $\alpha = 0.05$; Table 1). In contrast, *P. radiata* densities were not statistically different between the 6 sites (Welch ANOVA $F_{5,42.5} = 1.59$, $p = 0.185$; Table 1). A strong latitudinal gradient in lionfish densities was observed across the study sites, which spanned more than 6 degrees latitude (i.e. 22.2 to 28.5° N) (Fig. 1). Lionfish densities in the northern-most site of Dahab were 31.5 times greater than in southern reefs off Saudi Arabia (87.3 ± 117.5 vs. 1.7 ± 8.2 fish ha⁻¹) (Table 1). The reefs of Hurghada and Marsa Alam, which are centrally located, yielded intermediate densities ranging from 13.3 ± 46.2 to 18.9 ± 46.9 fish ha⁻¹.

Depth distribution

Red Sea lionfishes were found vertically distributed throughout the reef matrix, among fringing reef crests, walls and reef slopes, sand flats with patch reef outcroppings, and especially among larger coral bommies and pinnacles. Densities of *P. miles* were significantly greater at shallower depths (i.e. ≤ 14 m),

Table 1. Density of the lionfish *Pterois miles* and *P. radiata* reported from their native habitats. Regional variation in lionfish density was observed in this study, with significantly greater densities of *P. miles* in Dahab compared to other sites. When available, the number of sites, transects (n) surveyed, and mean density \pm 1 SD are provided

Ocean basin	Region	Site	— Density (ind. ha ⁻¹) —		Source
			<i>P. miles</i>	<i>P. radiata</i>	
Red Sea	Gulf of Aqaba	Dahab (n = 22)	87.3 ± 117.5^a	36.4 ± 47.7	This study
		Straits of Turin	7.5 ± 16.1	25.0 ± 28.8	
	NW Red Sea	Hurghada (n = 13)	15.4 ± 34.8	15.4 ± 35.1	
		Marsa Shagra (n = 12)	13.3 ± 46.2	10.0 ± 18.1	
		Marsa Nakari (n = 19)	18.9 ± 46.9	21.1 ± 40.8	
	Eastern Red Sea	Jeddah (n = 24)	1.7 ± 8.2	11.7 ± 22.0	
	NW Red Sea	Safaga (2 sites; n = 6)	20.8	12.5	
Safaga (2 sites; n = 6)		8.25	20.75	Alter & von Mach (2010)	
Indian		Kenya (6 sites)	8 ^b	9	Kulbicki et al. (2012)
		Kenya (7 sites; n = 23)	25.1 ± 45.7	8.6 ± 22.7	Darling et al. (2011)
		Reunion	6.2	na	Letourneur et al. (2008)
		Mauritius	3	na	Graham et al. (2007)
Indo-Pacific		Pohnpei (10 sites)	0.81 ^b	0.27	Kulbicki et al. (2012)
		Guam (14 sites)	0.39 ^b	2.51	
		Cebu (6 sites)	1.8 ^b	0	
		Palau (28 sites)	na	~13.1	Grubich et al. (2009)
		Moorea	na	0.9	Lecchini et al. (2006)

^aWelch ANOVA: *P. miles*: $F_{5,36.5} = 3.26$, $p = 0.016$
^bDensities reported for *P. volitans/miles* complex

(Welch ANOVA: $F_{3,54} = 3.11$, $p = 0.034$). A similar, yet non-significant trend was observed in *P. radiata* (Welch ANOVA: $F_{3,47} = 2.62$, $p = 0.061$) which reflects the moderate densities of *P. radiata* at the deepest (20 m) depth category (Fig. 2). Although overall densities for both species were lower at transects conducted at 15 and 20 m; lionfish were observed at depths of up to 37 m during free swimming surveys. In areas where lionfish densities were high, *P. miles* tend to be found aggregated in groups of 2 or more, often associated with large coral pinnacles or bommie outcroppings located near sandy habitats along the reef slope. *P. radiata* were generally solitary.

Activity and behavior

Similar to observations from other native habitats, *P. miles* and *P. radiata* were both primarily active at night and during crepuscular periods (Fig. 3). Although one-third of the survey effort (36 of 106 transects) and over 25% of lionfish observations (38 of 138 lionfish) occurred between 11:00 to 14:00 h, no active lionfish were observed during this time period. Activity levels of both *P. miles* and *P. radiata* increased throughout the afternoon (from 0 to 25%, $n = 48$) as sunset (18:00 h) approached. In surveys con-

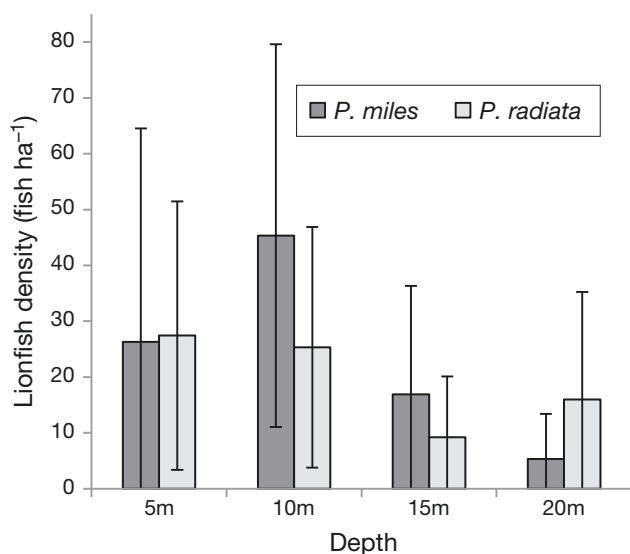


Fig. 2. Distribution of Red Sea lionfish *Pterois miles* and *P. radiata* by depth. Density of *P. miles* was significantly different among the 4 depth categories, with higher densities observed at shallower depths of 5 and 10 m (Welch ANOVA $F_{3,54} = 3.11$; $p = 0.034$). A similar trend was observed for *P. radiata*; however, no significant difference was detected (Welch ANOVA $F_{3,48} = 2.62$; $p = 0.061$). Sample sizes (n) shown indicate the number of transects completed at each depth. Data are mean density \pm SD

ducted from 17:00 h onwards, 94% of lionfish encountered ($n = 18$) were active (Fig. 3).

While some of the *P. miles* observed were solitary, they often exhibited a type of group hunting behavior where multiple individuals with pectoral fins flared would slowly swim together to herd and corner prey. These hunting packs were often encountered at night over sandy bottoms, in close proximity to their daytime coral shelters, where they were observed successfully feeding on nocturnal cardinal fishes (e.g. *Apogon* spp.). During crepuscular hours, *P. miles* were also observed actively pursuing schools of reef-dwelling fairy basslets *Pseudanthias squamipinnis*, silversides *Atherinomorus lacunosus* and sand-burrowing fishes such as shrimp gobies (e.g. *Amblyeleotris* spp.). Actively hunting fish exhibited several behaviors including chasing baitfish at the surface, hovering inverted mid-water, and slowly cruising near the bottom with pectoral fins flared (Fig. 4). Nocturnal observations of *P. radiata* hunting behavior indicated a strong preference for areas with dense coral cover to pursue cryptic invertebrate prey (authors' pers. obs.).

DISCUSSION

Red Sea densities

This study provides the first comprehensive regional assessment of native lionfishes in the Red Sea. In total, we observed 127 lionfish (*Pterois miles* = 70; *P. radiata* = 57) across 106 transects throughout the

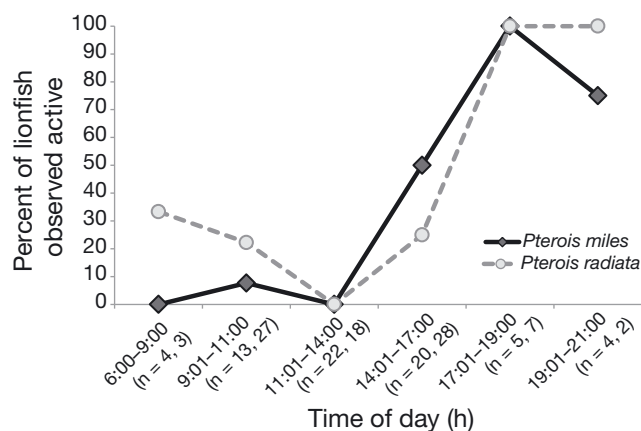


Fig. 3. Activity patterns for 138 lionfish observed in the northern Red Sea. Data points represent percent of lionfish observed that were 'active'. n = total number of each species of lionfish (*P. miles* and *P. radiata* respectively) observed during that time period. Sunrise occurred at approximately 6:00 and sunset at 18:00 h

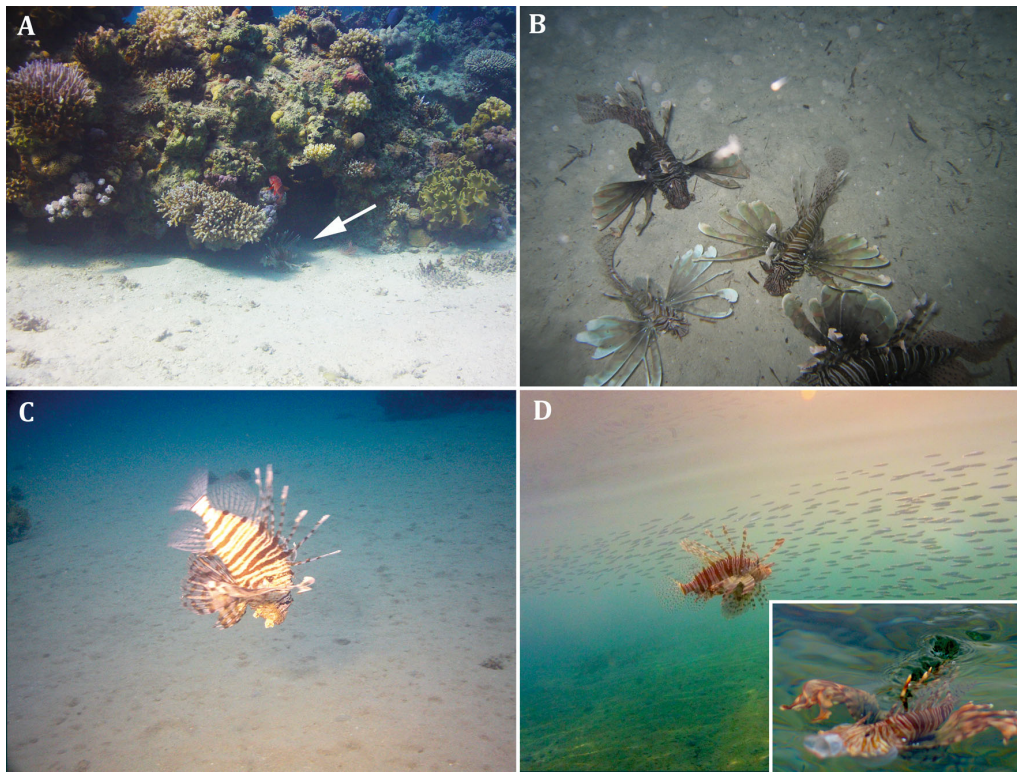


Fig. 4. Activity and foraging behaviors of the Red Sea lionfish *Pterois miles*: (A) mid-day diurnal resting underneath coral overhang (arrow), (B) nocturnal group hunting over open sand, (C) crepuscular mid-water stalking in head-down vertical orientation, (D) late afternoon active pursuit of reef silver side *Atherinomorus lacunosus* with suction strike breaking the surface (inset; photo K. Stoutenburg)

northern Red Sea (Fig. 1). For comparison at an ocean-basin scale, Kulbicki et al. (2012) compiled data from over 10 000 transects from the Pacific and Indian oceans, which recoded only 64 and 61 lionfish from each area respectively. The overall lionfish density we found in the Red Sea ($47.9 \text{ fish ha}^{-1}$) is 13 times greater than the lionfish surveys compiled by Kulbicki et al. (2012) from the Indian Ocean (3.6 fish ha^{-1}), and is 177 times greater than Pacific Ocean density estimates ($0.27 \text{ fish ha}^{-1}$) (Table 1). Our results confirm that the Red Sea basin harbors some of the highest densities of lionfishes for any portion of their native geographic range.

While our results confirm the Red Sea has the highest native densities, it is apparent that densities of some invasive populations in the Atlantic and Caribbean are unusually high (Table 2). Many of the studies published from the Bahamas and Caribbean indicate lionfish density commonly exceeds 100 fish ha^{-1} , with many sites in the Bahamas exhibiting densities exceeding 400 fish ha^{-1} . Although it is not uncommon for invasive species to start off with high population densities that decrease over time (Sakai et al. 2001), the magnitude of the difference in abundance sug-

gests some invasive populations are experiencing a release from abiotic forces or interspecific interactions that constrain lionfish densities within their native range.

Within the Western Atlantic and Caribbean, it has been suggested that native groupers may act as biotic controls of lionfish density, commonly referred to as the 'biotic resistance' hypothesis. Several studies have shown support for this hypothesis. Among protected marine reserves where fishing is banned, high grouper abundance and species richness has been associated with low lionfish densities in invaded and native habitats (Grubich et al. 2009, Mumby et al. 2011). However, several recent investigations have brought into question the validity of biotic resistance in controlling invasive lionfish populations. Hackerott et al. (2013) and Valdivia et al. (2014) did not find any evidence to support biotic resistance when comparing densities of invasive lionfish to large and small native grouper species that might prey upon or compete for resources with lionfish. Likewise, Kulbicki et al. (2012) found no correlation between *Pterois* spp. densities and the density or diversity of piscivores between protected and unpro-

Table 2. Density (mean \pm SD or range) of invasive lionfish *Pterois volitans* from studies in the Western Atlantic and Caribbean. In instances where authors reported density in fish m^{-2} or fish $100 m^{-2}$, density was extrapolated to fish ha^{-1} . Location, number of sites and total number of transects are also reported

Ocean basin		Location	Density of <i>P. volitans</i> (ind. ha^{-1})	Source
Caribbean	Bahamas	New Providence Island (3 sites; n = 12)	393.3 \pm 144.4	Green & Côté (2009)
	Bahamas	Lee Stocking Island (1 site; n = 15–30)	2009: ~530 2010: ~640	Lesser & Slattery (2011) ^a
	Honduras	Roatan (21 sites; n = 21)	~17.1	Biggs & Olden (2011) ^b
	Bahamas	New Providence Island (13 sites; n = 75)	101.7 \pm 103	Darling et al. (2011)
	Bahamas	Exuma Cays Land & Sea Park (12 sites; n = 96)	~3–30	Mumby et al. (2011)
	Bahamas	Cape Eleuthera (33 sites; n = 60)	300 \pm 600	Green et al. (2013a)
	Bahamas, Cuba, Belize & Mexico	(71 sites; n ~ 6–8 site ⁻¹)	440	Hackerott et al. (2013)
Western Atlantic	USA	North Carolina (17 sites; n = 17)	21.2 \pm 5.1	Whitfield et al. (2007)
Florida Straits	USA	Florida Keys (see Smith et al. 2011)	2009: 0 2010: 1.6 \pm 0.4 2011: 6 \pm 0.9	Ruttenberg et al. (2012)

^aDensity extrapolated from reported densities of 0.053 and 0.064 fish m^{-2}
^bNumber of sites and density of lionfish not specifically reported. Density based on 531 reported observations from 21 (50 m^2) transects

tected areas of the western Indian Ocean. The pooling of all *Pterois* spp., however, neglects to account for pronounced ecological differences in diet and body size between lionfishes, which influence their trophic roles in native reef fish communities (Fishelson 1975, Harmelin-Viven & Bouchon 1976). Additionally, protected areas status may not be a good indicator of local fishing pressure on food fishes (i.e. groupers and snappers), especially along the coastal margins of east Africa where enforcement capacity is limited.

In the Gulf of Aqaba, controlled removal of small and medium-sized groupers (*Cephalopholis* spp.) from coral reefs resulted in numerical increases of lionfishes and other coral reef predators, as well as low subsequent recruitment of these groupers species, providing some experimental support for biotic resistance in the form of resource competition (Shpigel & Fishelson 1991). In the present study, the Gulf of Aqaba (Dahab), along with the Straits of Turin, exhibited the highest densities of lionfish of the sites surveyed. In light of the biotic resistance debate, it is worth noting that these sites have the greatest annual influx of coral-reef related tourism, which is centered around the popular Sinai Peninsula resort destinations of Sharm El Sheik and Dahab. From 1989 to 2006, SCUBA-diving related

activities in these 2 destinations increased by 1421% and 8395%, respectively (Hilmi et al. 2012). Such dramatic increases in tourism can increase demand for and fishing of local coral-reef fishes such as groupers (Serranidae) and snappers (Lutjanidae) (Sheppard et al. 2009). Additionally, coastal development, pollution, and overfishing have been reported as major threats to this area, affecting up to 55% of local reef habitats in the Gulf of Aqaba (Khalaf & Kochzius 2002, Kotb et al. 2008, Burke et al. 2011). In contrast, vast areas of coastline along Saudi Arabia, where the lowest densities of lionfish were observed, are isolated from human impacts, and the coral reef habitats have experienced little degradation due to tourism-related coastal development or overfishing. In fact, Saudi Arabian reefs have among the highest estimates of grouper densities in the Red Sea (i.e. 30% greater compared to Egyptian reefs; Kotb et al. 2008).

Our results indicate a strong latitudinal signal for lionfish densities at a regional scale within the northern Red Sea, which reflects a similar trend identified at an ocean-basin scale by Kulbicki et al. (2012). Whether the underlying causal mechanism is linked to abundances and diversity of groupers (*Cephalopholis* spp.) via competitive exclusion or some other combination of abiotic factors remains to be estab-

lished. Many coral-reef grouper species are territorial and have overlapping trophic niches with lionfish species, such as *P. volitans* and *P. miles* (Harmelin-Vivien & Bouchon 1976, Shpigel & Fishelson 1989a,b, Morris & Akins 2009); however, it is important to recognize that Indo-Pacific, Indian Ocean, and Red Sea groupers are highly diverse, have co-evolved with lionfishes over millions of years, and are not uniform in either their trophic roles, diet ontogeny, territoriality, or body sizes (Shpigel & Fishelson 1989a,b, St. John 1999).

Behavior and habitat use

Reef fishes are known to exhibit pronounced behavioral changes related to diurnal cycles, with crepuscular periods often associated with a pulse of predatory activity (Helfman 1986) as well as migrations between foraging, spawning and sheltering habitats (Domeier & Colin 1997). Twilight periods offer a unique temporal feeding opportunity for piscivorous species, as the ability of both diurnal and nocturnal species to detect predators is visually comprised at this time (Hixon 1991). In addition to visual advantages, the abundance of preferred lionfish prey species may also increase during these periods (Fishelson 1975), resulting in optimum foraging conditions.

The absence of reef substrate or shelter at depths greater than 15 m was reflected in total lionfish abundance, as both *P. miles* and *P. radiata* tend to be concentrated at shallower depths. In areas where lionfish densities were high, *P. miles* were often found aggregated in groups of 2 or more. In addition, our observations in the Red Sea revealed that *P. miles* incorporate a suite of different hunting strategies during foraging (Fig 4). In contrast, *P. radiata* is a more specialized predator that was primarily observed individually hunting among the complex coral reef matrix. The observed affinity of *P. miles* for other conspecifics at high population densities may facilitate a competitive advantage in prey resource acquisition compared to other reef predators. Lionfish are slow-swimming predators that must get within a body length of the prey in order to use their extraordinary suction feeding ability. Thus, hunting in groups over open sandy habitat may counteract their slow swimming speeds by increasing the effectiveness of herding prey within strike range. At the same time, the long venomous spines of multiple lionfishes may provide an effective deterrent to other piscivorous competitors.

Our observations confirmed that lionfish in the Red Sea exhibit activity levels typical of crepuscular predatory reef fish, with the majority of hunting occurring around and after dusk (Fig. 3). Multiple investigations of invasive lionfish populations in the Western Atlantic and Caribbean have documented highly variable activity patterns in lionfish foraging, including atypical mid-morning, mid-day, and early afternoon feeding events (Morris & Akins 2009, Côté & Maljkovic 2010), as well as diurnal inactivity and crepuscular feeding (Green et al. 2011, Cure et al. 2012, Jud & Layman 2012). Such variation in observed foraging behavior may be the result of ecological differences in environmental variables among sites. Lionfish activity levels have been found in some regions to be greatly influenced by cloud cover, depth and type of habitat (Cure et al. 2012). Lionfish are versatile predators and can occupy a wide range of habitat types (mangrove, heterogeneous coral reef, sand-dominated reef flats). Given that the type of habitat occupied will likely determine localized environmental variable and prey species encountered, the foraging tactics, and potentially, the time of day feeding activities occur will also likely be influenced by habitat.

Future directions

Recent studies have examined and compared data from multiple lionfish species to investigate differences in density, size, and biomass between native and invasive populations (Darling et al. 2011, Kulbicki et al. 2012). It is important to recognize that, within the diversity of lionfish species, there are potential ecological and behavioral differences that may hold important insights into the role of lionfishes in coral reef communities. While the Western Atlantic and Caribbean invasive species *P. volitans* and *P. miles* are essentially eco-morphologically identical and feed almost exclusively on fishes, not all lionfish species are piscivorous meso-predators, nor do they exhibit the same habitat preferences and behavioral traits (Fishelson 1975, Harmelin-Vivien & Bouchon 1976). Our surveys of Red Sea lionfishes revealed previously unrecognized behavioral and habitat utilization differences between species. With few known ecological drivers that can control lionfish distributions in the Western Atlantic and Caribbean, it will be essential to continue comparative research with native populations to better understand their role in structuring reef fish communities. The Red Sea, with its variable lionfish densities and diverse

coral reef habitats, provides a unique coastal region to examine evolutionary, ecological, as well as anthropogenic factors that affect lionfish distributions in their native range. However, until restrictive policies on experimental marine research and limited access to reef habitats for researchers are eased, scientific progress of this type in the Egyptian Red Sea will unfortunately be limited.

Acknowledgements. We thank Laura Hanna, Mai Yosry, and Nada El Shanawany for their assistance in collecting survey data. Poseidon Divers and Red Sea Dive Expeditions provided logistical support during surveys in the Egyptian Red Sea. Lastly, Michael Berumen and his team at the Red Sea Research Center of the King Abdullah University of Science and Technology were indispensable in providing access, dive support, and laboratory facilities for surveys conducted off the coast of Saudi Arabia. This research was supported by an American University in Cairo Faculty Research Grant to J.R.G.

LITERATURE CITED

- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238
- Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ Biol Fish* 96:1151–1157
- Alter C, von Mach V (2010) Annual Reef Check survey of Kalawy house reef, Safaga, Egypt. Reef Check Germany, Bremen
- Alter C, Milton N, Reiniger M, von Mach V, Molenkamp B (2008) Assessment of the status of Kalawy Bay's fringing reef, Safaga, Egypt. Reef Check Germany, Bremen
- Barbour AB, Montgomery ML, Adamson AA, Diaz-Ferguson E, Silliman BR (2010) Mangrove se by the invasive lionfish *Pterois volitans*. *Mar Ecol Prog Ser* 401:291–294
- Betancur-RR, Hines A, Acero PA, Orti G, Wilbur AE, Freshwater DW (2011) Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *J Biogeogr* 38:1281–1293
- Biggs CR, Olden JD (2011) Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras. *Aquat Invasions* 6:347–353
- Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, DC (USA). http://pdf.wri.org/reefs_at_risk_revisited_hi-res.pdf
- Côté IM, Maljković A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 404: 219–225
- Côté MA, Green SJ, Hixon MA (2013) Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Conserv* 164:50–61
- Cure K, Benkwitt CE, Kindinger TL, Pickering EA, Pusack TJ, McIlwain JL, Hixon MA (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. *Mar Ecol Prog Ser* 467: 181–192
- Darling E, Green S, O'Leary K, Côté I (2011) Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biol Invasions* 13:2045–2051
- Debelius H (2001) Red Sea reef guide. Grupo M&G Difusion, Frankfurt.
- Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. *Bull Mar Sci* 60: 698–726
- Eschmeyer WN (1986) Fishbase. www.fishbase.org/Summary/SpeciesSummary.php?ID=7797&genusname=Pterois&speciesname=miles (accessed Sept 13, 2013)
- Fishelson L (1975) Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier), (Pteroidae, Teleostei). *Pubbl Staz Zool Napoli* 39:635–656
- Fishelson L (1997) Experiment and observation on food consumption, growth and starvation in *Dendrochirus brachypterus* and *Pterois volitans* (Pteroinae, Scorpaenidae). *Environ Biol Fishes* 50:391–403
- Freshwater DW, Hines A, Parham S, Wilbur A and others (2009) Mitochondrial control region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Mar Biol* 156:1213–1221
- Graham NAJ, McClanagan TR, Letourneur Y, Galzin R (2007) Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef. *Environ Biol Fishes* 78:57–69
- Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28:107
- Green SJ, Akins JL, Côté IM (2011) Foraging behavior and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 433:159–167
- Green SJ, Tamburello N, Miller SE, Akins JL, Côté IM (2013) Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs* 32:413–421
- Grubich JR, Westneat MW, McCord CL (2009) Diversity of lionfishes (Pisces: Scorpaenidae) among remote coral reefs of the Palau Archipelago. *Coral Reefs* 28:807
- Hackerott S, Valdivia A, Green SJ, Côté IM and others (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. *PLoS ONE* 8: e68259
- Hamner RM, Freshwater DW, Whitfield PE (2007) Mitochondrial cytochrome *b* analysis reveals 2 invasive lionfish species with strong founder effects in the western Atlantic. *J Fish Biol* 71(Suppl B):214–222
- Harmelin-Vivien ML, Bouchon C (1976) Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Mar Biol* 37:329–340
- Helfman GS (1986) Fish behavior by day, night and twilight. In: Pritchler TJ (ed) *The behavior of teleost fishes*. Chapman & Hall, New York, NY, p 266–287
- Hilmi N, Safa A, Reynaud S, Allemand D (2012) Coral reefs and tourism in Egypt's Red Sea. *Topics Middle Eastern African Econ* 14:416–434 www.luc.edu/orgs/meaa/volume14/meaa14.html
- Hixon MA (1991) Predation as a process structuring reef fish communities. In: Sale P (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, CA, p 475–508
- Jud ZR, Layman CA (2012) Site fidelity and movement patterns of invasive lionfish, *Pterois spp.*, in a Florida estuary. *J Exp Mar Biol Ecol* 414–415:69–74
- Kellner JB, Hastings A (2009) A reserve paradox: introduced

- heterogeneity may increase regional invisibility. *Conserv Lett* 2:115–122
- Khalaf MA, Kochzius M (2002) Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 239:287–299
- Kochzius M, Soller R, Khalaf MA, Blohm D (2003) Molecular phylogeny of the lionfish genera *Dendrochirus* and *Pterois* (Scorpaenidae, Pteroinae) based on mitochondrial DNA sequences. *Mol Phylogenet Evol* 28:396–403
- Kolar CS, Lodge DM (2002) Ecological prediction and risk assessment for alien fishes in North America. *Science* 298:1233–1236
- Kotb MMA, Hanafy MH, Rirache H, Matsumara S and others (2008). Status of coral reefs in the Red Sea and Gulf of Aden Region. In: Wilkinson CE (ed) Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, p 67–78
- Kulbicki M, Beets J, Chabanet P, Cure K and others (2012) Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Mar Ecol Prog Ser* 446:189–205
- Lecchini D, Polti S, Nakamura Y, Mosconi P, Tsuchiya M, Remoissonnet G, Planes S (2006) New perspectives on aquarium fish trade. *Fish Sci* 72:40–47
- Lesser MP, Slattery S (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol Invasions* 13:1855–1868
- Letourneur Y, Gaertner JC, Durbec JP, Jessu ME (2008) Effects of geomorphological zones, reefs and seasons on coral reef fish communities of Reunion Island, Mascarene Archipelago, SW Indian Ocean. *Estuar Coast Shelf Sci* 77:697–709
- Liao YC, Chen LS, Shao KT (2010) The predatory Atlantic red drum, *Sciaenops ocellatus* has invaded the western Taiwanese coast in the Indo-West Pacific. *Biol Invasions* 12:1961–1965
- Lieske E, Myers RF (2004) Coral reef guide Red Sea. Harper-Collins, London
- Morris JA Jr (2009) The biology and ecology of the invasive Indo-Pacific lionfish. PhD dissertation, North Carolina State University, Raleigh, NC
- Morris JA Jr, Akins JL (2009) Feeding ecology of the invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389–398
- Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* 6: e21510
- Randall JE (1983) Red Sea fishes. IMMEL, London
- Ruttenberg BI, Schofield PJ, Akins JL, Acosta A and others (2012) Rapid invasion of Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida Keys, USA: evidence from multiple pre-and post-invasion data sets. *Bull Mar Sci* 88:1051–1059
- Sakai AK, Allendorf FW, Holt JS, Lodge DM and others (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332
- Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. mile* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions* 4: 473–479
- Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the Western North Atlantic Ocean, Caribbean and Gulf of Mexico. *Aquatic Invasions* 5(suppl 1):S117–S122
- Sheppard CRC, Davy SK, Graham MP (2009) The biology of coral reefs. Oxford University Press, New York, NY, p 192–222
- Shpigel M, Fishelson L (1989a) Food habits and prey selectivity of three species of groupers from the genus *Cephalopholis* (Serranidae: Teleostei). *Environ Biol Fishes* 24: 67–73
- Shpigel M, Fishelson L (1989b) Habitat partitioning between species of the genus *Cephalopholis* (Pisces, Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea). *Mar Ecol Prog Ser* 58:17–22
- Shpigel M, Fishelson L (1991) Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral habitats of the Gulf of Aqaba (Red Sea). *Environ Biol Fishes* 31:131–138
- Smith SG, Ault JS, Bohnsack JA, Harper DE, Luo J, McClellan DB (2011) Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. *Fish Res* 109: 25–41
- St John J (1999) Ontogenetic changes in the diet of coral reef grouper *Plectropomus leopaardus* (Serranidae): patterns in taxa, size and habitat of prey. *Mar Ecol Prog Ser* 180: 233–246
- Sutherland W, Clout M, Cote I, Daszak P and others (2010) A horizon scan of global conservation issues for 2010. *Trends Ecol Evol* 25:1–7
- Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ (2014) Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* 2:e348
- Welch BL (1947) The generalization of 'Student's' problem when several different population variances are involved. *Biometrika* 34:28–35
- Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay Jr WR, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar Ecol Prog Ser* 235: 289–297
- Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biol Invasions* 9:53–64

Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA

Submitted: November 25, 2013; Accepted: May 5, 2014
Proofs received from author(s): July 11, 2014