ORIGINAL PAPER

Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations

**Emily S. Darling · Stephanie J. Green ·
Jennifer K. O'Leary · Isabelle M. Côté**

Abstract The invasion by Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) of the western Atlantic, Caribbean and Gulf of Mexico is emerging as a major threat to coral reef communities across the region. Comparing native and introduced populations of invasive species can reveal shifts in ecology and behaviour that can accompany successful invasions. Using standardized field surveys replicated at multiple sites in Kenya and the Bahamas, we present the first direct comparisons of lionfish density, body size, biomass and behaviour between native and invaded coral reefs. We found that lionfish occur at higher densities with larger body sizes and total biomass on invaded Bahamian coral reefs than the ecologically equivalent species (*P. miles*) does on native Kenyan reefs. However, the combined average density of the five lionfish species (*Pterois miles*, *P. antennata*, *P. radiata*, *Dendrochirus brachypterus* and *D. zebra*) on Kenyan reefs was similar to the density of invasive lionfish in the Bahamas. Understanding the ecological processes that drive these differences can help inform the management and control of invasive lionfish.

Introduction

An invasion is currently unfolding across shallow-water habitats of the northwest Atlantic and Caribbean region. Two species of lionfish, *Pterois miles* and *P. volitans*—generalist carnivores native to the Indo-Pacific region—were introduced to Florida waters, probably through the aquarium trade, in the 1980s and 1990s (Morris and Whitfield 2009). Over the following decade, the range of lionfish expanded northward along the American Atlantic coast, and in 2004, they were first recorded on coral reefs in the Bahamas (Schofield 2009). They have since become established around the Caribbean basin (Schofield 2009, 2010), inhabiting a range of habitats including coral reefs, seagrass meadows and mangroves (Barbour et al. 2010). Their diet in the introduced range is broad (Morris and Akins 2009), and grave concerns have been raised about their impact on native fish fauna [Albins and Hixon 2008; Green et al. (in review)].

E. S. Darling (✉) · S. J. Green · I. M. Côté
Earth to Ocean Research Group, Department
of Biological Sciences, Simon Fraser University,
8888 University Drive, Burnaby, BC V5A 1S6, Canada
e-mail: edarling@sfu.ca

J. K. O'Leary
National Centre for Ecological Analysis
and Synthesis, 735 State Street, Suite 300,
Santa Barbara, CA 93101, USA

Invasions by predatory vertebrates are exceedingly rare in the marine realm (Byrnes et al. 2007). Beyond lionfish, examples to date include the peacock grouper *Cephalopholis argus* (Dierking et al. 2009), the black-tailed snapper *Lutjanus fulvus* and the blue-lined snapper *L. kasmira* (Friedlander et al. 2002)— all introduced to the Hawaiian Islands from other Pacific islands in the 1950s to enhance fisheries—and the red drum *Sciaenops ocellatus,* brought from the northwestern Atlantic to Taiwan for aquaculture in 1987 (Liao et al. 2010). At least two of these (peacock grouper and blue-lined snapper) are now abundant in their introduced range, dominating the density and biomass of coral reef fish communities (Dierking et al. 2009; Friedlander et al. 2002). However, there is little information on the ecology, behaviour or life history of any introduced marine predators in their native range to place their responses to their new environment in context.

Comparisons of invasive species in their native and introduced ranges can reveal potential shifts in ecology and behaviour and ultimately shed light on the factors contributing to invasion success and point to potential control methods. Such comparisons have seldom been made for marine invaders. Our goals in this study were therefore two-fold. First, we first sought to empirically test the widely held notion that lionfish on invaded Caribbean reefs have reached greater abundance than they normally do on reefs in their native range (Green and Côté 2009; Grubich et al. 2009). We also examined differences in lionfish body size and activity levels between the native and introduced ranges as additional gauges of potential ecological differences between the two areas.

Methods

Lionfish surveys

We conducted underwater visual surveys of lionfish on coral reefs in both their native (Kenya) and introduced (Bahamas) ranges. In Kenya, we surveyed seven reef sites (depths: 2–18 m) within the Mombasa Marine National Park and Reserve between March and May 2010. Sites were located on shallow patch reefs in a matrix of sand and seagrass and along a continuous coral reef wall. In the Bahamas, we surveyed 13 reef sites (depths: 5–20 m) along a continuous coral reef wall off the southwest coast of New Providence Island between May and July 2008. Some of the Bahamian sites had wrecks but transects were not conducted near them. Lionfish were first observed on New Providence reefs in 2004 (Schofield 2009; REEF 2010).

The survey method was identical across both locations. At each site, we conducted three to nine belt transects (10 m wide × 50 m long = 0.05 ha) laid parallel to the reef crest. We conducted 98 transects in total (23 in Kenya, 75 in the Bahamas). On each transect, we recorded the abundance, size (total length, TL, to the nearest cm) and species of all lionfish encountered. We spatially stratified transects by reef zone and depth to reduce the possibility of recounting individual lionfish. During each survey, observers (ESD, JKO and SJG) thoroughly searched the transect area for hidden and cryptic lionfish, including looking under overhangs and inside large crevices and spaces within the reef framework. Survey time per transect was ∼30 min.

We also recorded lionfish behaviour during our transect surveys in Kenya and the Bahamas. We classified the behaviour of all lionfish encountered in Kenya (N = 70) and a subset of the lionfish encountered on transects in the Bahamas (208 of 239 lionfish; observations occurred at all sites). The behaviour of each individual lionfish was classified as active (i.e., either hunting, swimming, hovering in the water column or moving over the substratum) or inactive (i.e., resting motionless on the substratum). Hunting lionfish are distinguished by a typical, almost immobile hunting posture where the pectoral fins are fanned out from the body, the dorsal spines erect, the tail undulating and the head is often facing downwards (Côté and Maljković 2010). All surveys were conducted between 09:00 and 16:00.

Analyses

To estimate lionfish body mass, we converted individual lionfish lengths (TL in cm) to weight using the allometric relationship:

$$W = aL^b \tag{1}$$

where a and b were species-specific scaling constants relating body mass, W (wet weight, g), to total length, L (cm). We used scaling constants of $a = 0.0129$ and

$b = 3.201$ obtained from Fishbase (www.fishbase.org) for *Dendrochirus brachypterus* in our calculations of body mass for individuals of the two *Dendrochirus* species (*D. brachypterus* and *D. zebra),* observed on Kenyan reefs. To calculate the body mass of *Pterois* spp. individuals, we used values of $a = 0.00497$ and $b = 3.291$ reported by Green et al. (in review) for Bahamian *Pterois volitans.* Transect-specific biomass was then calculated as the sum of the body mass of individual lionfish encountered on that transect.

We calculated average lionfish size and body mass per site from estimates of all individuals encountered within each region. In these cases, pooling of data across transects and sites was justified because there were no difference in either variable among sites within region (size: Kenyan sites, $F_{df = 5,64} = 0.74$, $P = 0.59$; Bahamian sites: $F_{df = 12,226} = 1.49$, $P = 0.13$; body mass: Kenyan sites, $F_{df = 5,64} = 1.11$, $P = 0.36$; Bahamian sites: $F_{df = 12,226} = 1.32$, $P = 0.21$). By contrast, we calculated average lionfish density and biomass per unit area for each site by averaging the values obtained across the multiple transects conducted at that site. Both density and biomass were expressed per ha. We then compared site-averaged estimates of lionfish density and total lionfish biomass, and pooled estimates of size and individual body mass between Kenyan and Bahamian reefs using parametric *t* tests. When variances were unequal, we adjusted the degrees of freedom using the Welsh modification. We used chi-squared tests to compare the proportion of active and inactive individuals of *P. miles*, *P. volitans* and the lionfish assemblage on Kenya reefs.

Results

On Kenyan reefs, we observed 70 lionfish of five species: *Pterois antennata*, *P. miles*, *P. radiata*, *Dendrochirus brachypterus*, and *D. zebra* (Table 1). On Bahamian reefs, we observed 239 individual lionfish. Given the result of genetic analyses of Bahamian lionfish (Freshwater et al. 2009; Morris et al. 2009), it is likely that most or all were *Pterois volitans,* although some may have been *P. miles*, a sister species that is visually identical to *P. volitans*. The average density of *P. volitans* on Bahamian reefs (101.7 ± 103.0 individuals ha^{-1}) was nearly five times higher than the density of its ecological equivalent, *P. miles,* on Kenyan reefs ($t_{df = 16.8} = 2.4$, $P = 0.03$; Table 1; Fig. 1). However, the density of *P. volitans* in the Bahamas was not significantly higher than the combined density of the five lionfish species on Kenyan reefs (mean $\pm$ SD: 71.7 ± 90.1 individuals ha^{-1}; $t_{df = 18} = 0.6$, $P = 0.55$; Fig. 1).

Bahamian *P. volitans* (mean $\pm$ SD: 23.0 ± 6.5 cm) were ~ 1.5 times longer than both the average Kenyan *P. miles* ($t_{df = 259} = 5.2$, $P < 0.0001$; Table 1; Fig. 2a) and the average of all lionfishes (five species) on Kenyan reefs (TL: 14.0 ± 4.4 cm; $t_{df = 163.5} = 13.2, P < 0.0001$; Fig. 2a). *Pterois volitans* in the Bahamas (194.5 ± 159.2 g) was three times heavier than *P. miles* ($t_{df = 46.5} = 7.3$, $P < 0.0001$; Table 1; Fig. 2b), and over 4.5 times heavier than the average lionfish (all species combined) on Kenyan reefs (41.5 ± 44.6 g; $t_{df = 306.7} = 13.2$, $P < 0.0001$; Fig. 2b). Overall, the total biomass of lionfish on Bahamian reefs (19.2 ± 21.3 kg ha^{-1}) was 13 times higher than the biomass of

Table 1 Activity levels, density, size, body mass and site biomass of five lionfish species on their native Kenyan reefs ($N = 7$ reefs). Values are presented as mean $\pm$ standard deviation (minimum value—maximum value)

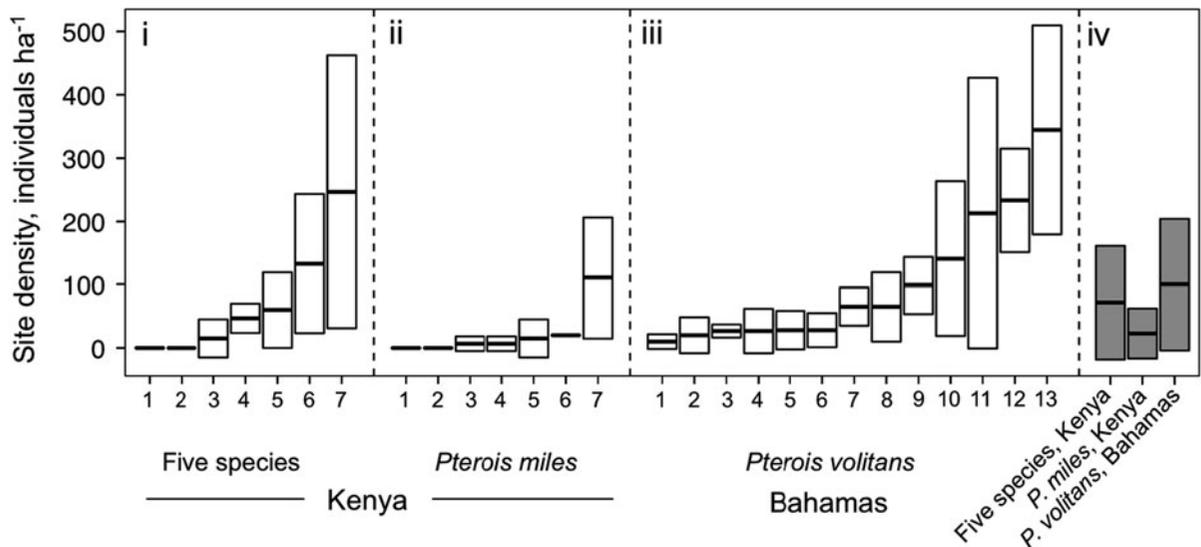| Species	No. individuals (no. sites present)	No. active individuals	Total length (cm)	Body mass (g)	Site density, individuals ha^{-1}	Site biomass, kg ha^{-1}
Dendrochirus brachypterus	10 (2)	0	11.8 ± 2.1 (8–15)	38.0 ± 19.9 (10.0–75.0)	12.6 ± 30.6 (0–81.8)	0.5 ± 1.1 (0–3.0)
Dendrochirus zebra	2 (1)	0	16.5 ± 4.9 (13–20)	118.0 ± 99.7 (47.5–188.5)	1.9 ± 5.0 (0–13.3)	0.2 ± 0.6 (0–1.6)
Pterois antennata	27 (4)	1	12.9 ± 3.2 (5–20)	27.1 ± 19.1 (1.0–95.1)	28.5 ± 29.3 (0–72.7)	0.8 ± 0.9 (0–2.2)
Pterois miles	22 (5)	7	15.5 ± 6.2 (7–27)	65.5 ± 68.0 (3.0–255.3)	25.1 ± 45.7 (0–110.5)	1.5 ± 2.4 (0–6.7)
Pterois radiata	9 (1)	0	15.9 ± 2.5 (10–19)	47.9 ± 18.8 (9.7–80.3)	8.6 ± 22.7 (0–60.0)	0.4 ± 1.1 (0–2.9)

Fig. 1 Densities of lionfish on native (Kenyan) and invaded (Bahamian) reefs. *i* Total density of five lionfish species on Kenyan reefs, *ii* density of *Pterois miles* on Kenyan reefs, *iii* density of *Pterois volitans* on Bahamian reefs, *iv* comparison of overall averages between Kenya and the Bahamas. Sites are ordered by increasing values within each panel. Means (*thick horizontal bands*) and standard deviations (*top and bottom of boxes*) are given

P. miles on Kenyan reefs ($t_{df = 12.5} = 3.1$, $P = 0.01$; Table 1; Fig. 2c) and over six times higher than the biomass of all lionfish species on Kenyan reefs (3.0 ± 3.7 kg ha^{-1}; $t_{df = 13.3} = 2.8$, $P = 0.02$; Fig. 2c).

On Kenyan reefs, 23% of the 22 *P. miles* and 11% of all 70 lionfish individuals were active upon encounter during the daytime. *Pterois miles* was significantly more active than the four other species of lionfish ($\chi^2 = 13.7$, $P = 0.008$; Table 1). We did not observe any hunting lionfishes on Kenyan reefs. On Bahamian reefs, about one-quarter (27%, N = 56) of the 208 lionfish observed were active. Of these lionfish, 23 individuals were observed hunting. There was no difference in the proportion of active *P. volitans* in the Bahamas and *P. miles* in Kenya ($\chi^2 = 0.06$, $P = 0.8$), although a higher proportion of *P. volitans* in the Bahamas were active compared to the overall lionfish assemblage in Kenya ($\chi^2 = 6.3$, $P = 0.01$).
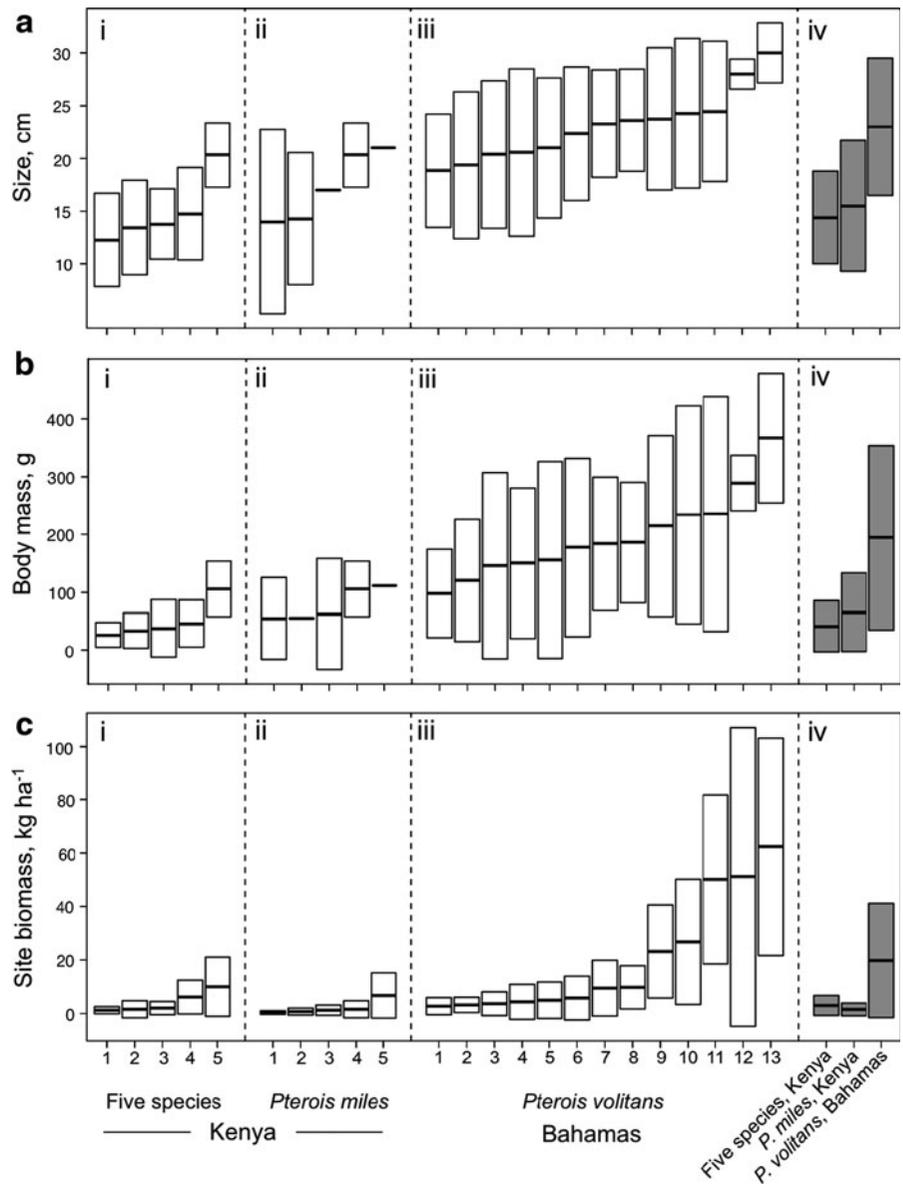
Discussion

We present the first direct comparisons of lionfish density, body size, biomass and behaviour across native and invaded coral reefs using the same, lionfish-focused survey method. On invaded Bahamian reefs, the Indo-Pacific lionfish *Pterois volitans* (and perhaps also some

P. miles) occurred at higher densities than its ecological equivalent, *P. miles*, on native reefs, although the average combined density of all five lionfish species on Kenyan reefs was similar to that of *P. volitans* in the Bahamas. Bahamian lionfish were significantly larger and achieved higher overall biomass than either *P. miles* or the total lionfish assemblage in Kenya.

Invasive species often reach high abundance in their introduced range. This is the case for *P. volitans* in the Atlantic (Green and Côté 2009; this study). Both the mean and highest reported densities of *P. volitans* in the Bahamas ($\sim$100 individuals ha^{-1} and $\sim$340 individuals ha^{-1}, respectively; this study, see also Green and Côté 2009) were higher than the matching densities of *P. miles*, its ecological equivalent, in Kenya (25 individuals ha^{-1} and $\sim$100 individuals ha^{-1}, respectively). However, lionfish can also occur at relatively low densities on some Bahamian reefs—eight of the 13 sites had fewer than 65 individuals ha^{-1}, lower than the average of the five lionfish species in Kenya (Fig. 1)—even though all of our study sites in the Bahamas were invaded by lionfish in the same year (S. Cove, personal communication). Moreover, the native lionfish assemblage on Kenyan reefs, which is composed of five species, can reach similar average ($\sim$70 individuals ha^{-1}) and maximum densities ($\sim$250 individuals ha^{-1}) as lionfish on Bahamian reefs. Whether low-density lionfish

Fig. 2 Comparisons of **a** total length, cm, **b** body mass, g, and **c** biomass, kg ha^{-1}, of lionfish on coral reefs in native (Kenyan) and introduced (Bahamian) ranges. Each plot is divided into four panels: *i* average of five lionfish species found on Kenyan reefs, *ii Pterois miles* on Kenyan reefs, *iii P. volitans* on Bahamian reefs, and *iv* comparison of overall averages between Kenya and the Bahamas. Sites are ordered by increasing values within each panel; numbers do not indicate individual sites. The mean (*thick horizontal band*) and standard deviations (*top and bottom of box*) are given

populations in the Bahamas are still increasing and have yet to reach higher densities, or are limited by some ecological process (e.g., habitat and/or prey availability, competition, predation) requires further investigation. However, our results are consistent with the idea that *P. volitans* in its introduced range could be released from the constraints of resource partitioning, which may be occurring among lionfish species and may be maintaining low species-specific densities in the native range. A similar pattern has been noted for the peacock grouper *Cephalopholis argus*: it is more abundant in its introduced range (Hawaiian Islands) where it is the only

grouper of its size than in its native Indo-Pacific range, where it is outcompeted by several other grouper species (Dierking et al. 2009).

Lionfish on invaded Bahamian reefs are significantly larger than native lionfish in Kenya. The difference in average length between *P. volitans* and *P. miles* is striking: the former was ∼50% longer than the latter in our study, although in their native ranges (Pacific and Indian Oceans, respectively), there is little difference between the two species, at least in maximum length (38 cm total length, TL, for *P. volitans* vs. 35 cm standard length, SL, for *P. miles*; Sommer et al. 1996;

Randall et al. 1990; Froese and Pauly 2000). The maximum recorded total length of *P. volitans* in the Caribbean is 49 cm (J. Morris, personal communication). Other biological invaders have also been reported to grow larger in their non-native range. For example, introduced plants commonly attain larger sizes in their introduced than in their native range (e.g. Jakobs et al. 2004; Ebeling et al. 2008; Chun et al. 2010). Similar comparisons of animal species in their indigenous and introduced ranges are rarer, but those we have found show a similar pattern (e.g. Indian mongoose: Simberloff et al. 2000; coypu: Guichón et al. 2003). There are several non-mutually exclusive explanations. Lack of exploitation or low predation mortality in the introduced range could favour the evolution of larger body sizes and later ages at maturity (Guichón et al. 2003). For lionfish, predator diversity and abundance in the Caribbean are both low compared to the tropical Pacific (e.g. Gladfelter et al. 1980) and there is anecdotal evidence that lionfish have been traditionally fished in their native range. However, the rapidity and magnitude of the shift in body size suggest a phenotypic rather than genetic response. Ecological release from congeneric competitors (Simberloff et al. 2000), as well as introduction into areas that are more productive (perhaps exacerbated by prey naivety) could also account for the larger size of Bahamian lionfish.

As a result of both higher abundance and larger body size, the total biomass of lionfish on Bahamian reefs was 13 times higher than the biomass of *P. miles* on Kenyan reefs, and more than six times higher than the biomass of all lionfish species on Kenyan reefs. Lionfish now make up a significant proportion of the fish biomass on many invaded reefs (Green et al. in review). This, combined with the facts that lionfish have a generalist diet (Morris and Akins 2009) and few predators owing to their venomous spines (Morris and Whitfield 2009), has serious implications for energy flow on invaded reefs. Although mesopredators by size, lionfish may effectively be apex predators in their introduced range, shortening food chain length, with consequences for ecosystem functioning (reviewed by Vander Zanden and Fetzer 2007).

Lionfish have become successfully established on reefs in the Bahamas (see also Green and Côté 2009) and are continuing to spread throughout the western Atlantic and Caribbean (Schofield 2009, 2010; Ahrenholz and Morris 2010). Further comparisons across the native and invaded ranges are required to identify the ecological processes that may limit lionfish populations in both areas. Identifying these mechanisms, and at which life history stage these processes act on, is crucial information for management decisions that aim to control populations of invasive lionfish.

References

Ahrenholz DW, Morris JA (2010) Larval duration of the lionfish, *Pteros volitans* along the Bahamian Archipelago. Environ Biol Fish 88:305–309

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

Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. Mar Ecol Prog Ser 401:291–294

Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. PLoS One 3:e295

Chun YJ, Kim C-G, Moloney KA (2010) Comparison of life history traits between invasive and native populations of purple loosestrife (*Lythrum salicaria*) using nonlinear mixed effects model. Aquat Bot 93:221–226

Côté IM, Maljković A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. Mar Ecol Prog Ser 404:219–225

Dierking J, Williams ID, Walsh WJ (2009) Diet composition and prey selection of the introduced grouper species peacock hind (*Cephalopholis argus*) in Hawaii. Fish Bull 107:464–476

Ebeling SK, Hensen I, Auge H (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. Divers Distrib 14:225–233

Freshwater D, Hines A, Parham S, Wilbur A, Sabaoun M, Woodhead J, Akins L, Purdy B, Whitfield PE, Paris CB (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

Friedlander M, Parrish JD, DeFelice RC (2002) Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian bay. J Fish Biol 60:48–68

Froese R, Pauly D (2000) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños 344 p

Gladfelter WB, Ogden JC, Gladfelter EH (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61:1156–1168

Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. Coral Reefs 28:107

Green SJ, Dulvy ND, Cooper AB, Côté IM (in review) Past, present and future impacts of an invasive marine predator on high diversity fish communities

Grubich J, Westneat M, McCord C (2009) Diversity of lionfishes (Pisces: Scorpaenidae) among remote coral reefs of the Palau Archipelago. Coral Reefs 28:807

Guichón M, Doncaster CP, Cassini MH (2003) Population structure of coypus (*Myocastor coypus*) in their region of origin and comparison with introduced populations. J Zool 261:265–272

Jakobs G, Weber E, Edwards PJ (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. Divers Distrib 10:11–19

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

Morris JAJ, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environ Biol Fish 86:389–398

Morris JAJ, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum NOS NCCOS 99

Morris JAJ, Akins JL, Barse A, Cerino D, Freshwater DW, Green SJ, Munoz RC, Paris C, Whitfield PE (2009) Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. In: Proceedings of the 61st Gulf and Caribbean Fisheries Institute, vol 61, pp 1–6

Randall JE, Allen GR, Steene RC (1990) Fishes of the Great Barrier Reef and Coral Sea. University of Hawaii Press, Honolulu 506 p

REEF (2010) Reef environmental education foundation volunteer survey project database. World Wide Web electronic publication. www.reef.org. Accessed Dec 2010

Schofield P (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. Aquat Invasions 4:473–479

Schofield P (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5:S117–S122

Simberloff D, Dayan T, Jones C, Ogura G (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81:2086–2099

Sommer C, Schneider W, Poutiers J-M (1996) FAO species identification guide for fishery purposes. The living marine resources of Somalia. FAO, Rome, p 376

Vander Zanden MJ, Fetzer WW (2007) Global patterns of aquatic food chain length. Oikos 116:1378–1388