Aquatic Invasions (2011) Volume 6, Issue 3: 347–353
doi: 10.3391/ai.2011.6.3.11
© 2011 The Author(s). Journal compilation © 2011 REABIC

Open Access

Research Article

Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras

Christopher R. Biggs and Julian D. Olden*
School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA
E-mail: crbiggsy@gmail.com (CRB), olden@uw.edu (JDO)
**Corresponding author*

Received: 24 June 2010 / Accepted: 15 April 2011 / Published online: 11 May 2011

Abstract

The Indo-Pacific lionfish species [*Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828): Family Scorpaenidae] are the first non-native marine fishes to establish in the Western North Atlantic and Caribbean Sea. Despite the continued documentation of its range expansion and highly publicized invasion (including public-driven removal efforts) there remains a paucity of basic information on lionfish ecology. This knowledge gap limits effective long-term management. In this study we conducted a multi-scale investigation of habitat occupancy of a newly established population of lionfish in Roatan, Honduras. Based on field surveys and citizen sightings in Roatan Marine Park we found that lionfish occurred more frequently on aggregate coral reef habitats (54% of sightings) compared to patch reef habitats (30%) and sea grass lagoons (16%). In general, these aggregate and patch reef habitats contained adults (mean total length =118.9 mm and 114.7mm, respectively) whereas sea grass habitats contained juveniles (mean total length=89.5 mm). At the micro-habitat scale lionfish occupied areas dominated by hard coral and overhanging structure; the same microhabitats containing native fishes of concern – grouper (Nassau grouper, *Epinephelus striatus*; yellow fin grouper, *Mycteroperca venenosa*) and snapper (dog snapper, *Lutjanus jocu*; mutton snapper, *Lutjanus analis*). Results from this study contribute information on basic habitat requirements of lionfish and inform current management removal efforts focused on containing spread and mitigating their impacts on native species.

Key words: lionfish, habitat occupancy, microhabitat

Introduction

Invasive species are recognized as a leading threat to marine biodiversity (Carlton and Geller 1993; Ruiz et al. 1997; Grosholz 2002; Kappel 2005). In a recent synthesis of non-native species in marine environments, Molnar et al. (2008) lamented the numerous, and often, large knowledge gaps in our current understanding of the basic ecology for many species. This is particularly the case for coral reefs, which have been identified as a neglected research area in invasion biology (Coles and Eldridge 2002). Fundamental ecological data that is lacking for many introduced marine species include habitat occupancy; a strong indicator of potential spread and impact (Grosholz and Ruiz 1996), including coral reef fishes (Kane et al. 2009).

The lionfish [*Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828): Family Scorpaenidae] are the first non-native marine fish species to establish in the Western North Atlantic and Caribbean Sea (Whitfield et al. 2002; Schofield 2009, 2010). Native to the Indo-Pacific, there have been both confirmed and unconfirmed records of lionfish off the coast of Florida (USA) since 1980s; a likely result of intentional aquarium releases (Padilla and Williams 2004; Morris and Whitfield 2009). Since their initial introduction, lionfish have spread rapidly. Populations have been documented from North Carolina (USA) to Jamaica, with individual sightings as far north as New York (USA) and as far south as Venezuela (USGS 2011). It appears that the northern range may be limited by cold winter water temperature (Kimball et al. 2004), but the southernmost established populations are spreading and currently found between Honduras and Venezuela (Schofield 2009, 2010; Aquilar-Perera and Tuz-Sulub 2010). Despite growing literature documenting range expansion there is little information on its basic habitat requirements.

The rapid establishment and spread of lionfish is the result of multiple factors, only some of which have been thoroughly investigated. There are few known predators of this species both in their native and introduced ranges (Malijković et al. 2008; Morris and Whitfield 2009), especially for adult lionfish, likely because their venomous spines (Morris 2009). The potential ecological impacts of lionfish are still unknown, although preliminary reports suggest that the invasions could have devastating effects on coral reef fish communities (Meister et al. 2005). In the Bahamas, lionfish are widespread (Smith and Sealy 2007; Green and Côté 2009) and were found to reduce recruitment of reef fish by up to 80% (Albins and Hixon 2008). Lionfish have been found in a variety of habitats ranging from wrecks and solid substrate in proximity to coral reefs (Fishelson 1997) to mangroves (Barbour et al. 2010), and our research aims to quantify their occurrence in these different habitats. Such information is paramount for guiding management actions that focus on the containment of spread and mitigation of ecological impacts via government and citizen-based removal efforts.

We combined data collected by citizen scientists with our own field surveys to provide an examination of habitat occupancy by a newly established population of lionfish in Roatan, Honduras. First, we quantified occupancy among major macro-habitat types of aggregate reef, patch reef and lagoon/sea grass. Second, we evaluated micro-habitat use of lionfish within macro-habitat types, focusing specifically on substrate composition and the availability of overhanging structure. Patterns of lionfish abundance were compared to two native taxa species of concern – grouper [Nassau grouper, *Epinephelus striatus* (Bloch, 1792); yellow fin grouper, *Mycteroperca venenosa* (Linnaeus, 1758)] and snapper [dog snapper, *Lutjanus jocu* (Bloch and Schneider, 1801); mutton snapper, *Lutjanus analis* (Cuvier in Cuvier and Valenciennes, 1828)].

Methods

Study region

Roatan is the largest and most populated of the Bay Islands, located on the north coast of Honduras in the western Caribbean Sea. It is 200 km^2 (50 km long and 2–4 km wide) in area and is primarily surrounded by fringing and barrier reefs, with extensive mangrove wetlands on the east end. The fringing reef provides a wide spectrum of habitats including lagoons containing turtle grass (*Thalassia testudinum*), patch reef (an isolated, comparatively small reef outcrop surrounded by sand or sea grass) and aggregate sloping reef (a grouping of 3–10 patch reefs of various sizes that share a common area of surrounding sand or sea grass). The study region consists of approximately 12 km along the northwest coast, including 8 km in Roatan Marine Park. The marine park has strict regulations against fishing or harvesting animals (with the exception of removing lionfish) and regulates boat use and recreational diving.

Field surveys

We conducted twenty-one visual surveys partitioned equally between three macro-habitat types – aggregate reef (n=7), patch reef (n=7) and lagoon/sea grass (n=7) – over a two-week period from January 23 to February 5, 2010 during daylight hours of 09:00–15:00. We surveyed aggregate and patch reefs by SCUBA diving and sea grass sites by snorkeling. Each survey consisted of a single 50-m transect positioned parallel to the shoreline and included 5 equally spaced quadrats where habitat was categorized in a 2 m^2 area according to the percentage cover of hard coral, soft coral, sponge, sand, sea grass, rock, algae and overhead environment. The transect length was measured with the use of a reel with markings every 10 meters or with fin cycles (4 cycles/10 meters) when the use of a reel was not possible. A second diver conducted surveys at the same site for 30 minutes using the roving diver technique (RDT) (see Schmitt and Sullivan 1996) to locate lionfish, grouper (collectively *Epinephelus striatus* and *Mycteroperca venenosa*) and snapper (collectively *Lutjanus jocu* and *Lutjanus analis*) by freely roving in a given area and recording fish. For each fish sighting we recorded percent cover in a 2 m^2 area.

Marine Park data

We collated data on the presence and estimated total body length of lionfish within Roatan Marine Park for a 9-month period (May 22, 2009 to March 12, 2010) from sightings reported by recreational divers at locations throughout the marine park (geo-referenced to the dive site: http://www.roatanmarinepark.com/lionfish/).
Because macro-habitats do not change greatly over time, the 21 survey sites were classified as

aggregate reef, patch reef and lagoon/sea grass using Google Earth. Field-based macro-habitat assignments of the 21 sites conducted during the field surveys were compared to macro-habitat classifications according to this method. We found 100% correspondence between the two classification methods. Total available macro-habitat in the marine park was estimated by calculating the area (length × width) for each habitat using the distances provided by Google Earth. To account for the additional area along the wall of aggregate reefs, a secondary calculation (depth × length) was added to the total area for aggregate habitat. Patch reef (39%) and sea grass habitats (37%) were the dominant macro habitats, aggregate reef was third most abundant (24%) and wrecks composed less than 1% of available habitat and thus are not considered further. We recognize two limitations of using this data source. First, recreational diver effort may not be randomly distributed across major macro-habitat types. Divers may have a greater tendency to visit reef habitats due to elevated marine biodiversity, although the proximity (and hence, ease of access) of lagoon/sea grass dive sites also attracts dive activity. Second, we acknowledge a number of methodological errors and biases associated with visual census techniques, including that estimates of total body length represent an approximation because they relied on untrained recreational divers without the use of a measuring device (Bell et al. 1985). Objects appear larger in water and this can lead to over-estimation of size without proper training and experience. However, all sight occurrences are checked for accuracy by Roatan Marine Park (as well as prior to our analysis); therefore clearly erroneous data was omitted.

Statistical analysis

Macro-habitat occupancy by lionfish in Roatan Marine Park was examined using an adaptation of Manly's selectivity index (Manly et al. 2002). This index was chosen because it does not fluctuate with inclusion or exclusion of seldom-used habitats (Manly et al. 2002) and is considered more versatile than other selection preferences indexes (Garshelis 2000). The equation for selectivity is:

$$w_i = u_i/(h_i \times u_{it})$$

where u_i= the count of type *i* habitat used by all lionfish, h_i= the proportion of available habitat *i*, and u_{it}= the total count of all lionfish for all habitats. The values were normalized using the equation $S_{norm} = w_i/\sum w_i$, where w_i is the selectivity value which varies from 0 to 1 for any macro-habitat type, and takes on the value of 0.33 if habitat selection is random in the case of our study. A log-likelihood chi-squared analysis (recommended by Manly et al. 2002) was conducted to determine if the observed distribution between macro habitats was different from the total available habitat. A student's t–test was used to compare micro-habitat characteristics between sites with and without lionfish, groupers and snappers, as well as to test for differences in lionfish size distributions between macro-habitats.

Results

A total number of 531 sightings of lionfish were reported by recreational divers in Roatan Marine Park during the 9-month period. Lionfish occupied aggregate reefs in over half the sightings (54%), followed by patch (30%) and sea grass habitats (16%). According to Manly's index of selectivity there was a non-random pattern of macro-habitat occupancy (log-likelihood χ^2 =21.4, df = 2, P≤ 0.001). Aggregate reefs were more likely to be occupied by lionfish (P=0.006), occurrences in patch reefs did not differ from random (P=0.108) and sea grass habitats contained lower numbers of lionfish than expected based on its availability in the park (P≤0.001) (Figure 1). These results may be influenced by non-random patterns of diving activities in the park; however, occupancy percentages correspond to those based on our field survey (see below).

Body length distribution of 511 lionfish (out of 531 sightings) observed by recreational divers in Roatan Marine Park varied between macro-habitat types, ranging between 25 mm and 381 mm (mean=113.1 mm, SD=51.5 mm). Average body length was significantly smaller in sea grass habitats (mean=89.5 mm, SD=39.5 mm, n=86) compared to both aggregate reefs (mean=118.9 mm, SD=54.3 mm, n=255) (t=5.40, df= 201, P≤ 0.001) and patch reefs (mean=114.7 mm, SD=48.5 mm, n=138) (t=4.24, df= 207, P≤ 0.001).

Lionfish were found in 7 out of the 21 survey localities (29% frequency of occurrence), which included 4 aggregate reef sites (57% of occupied sites), 1 patch reef site (14%) and 2 sea grass sites (29%). Across these macro-habitat types,

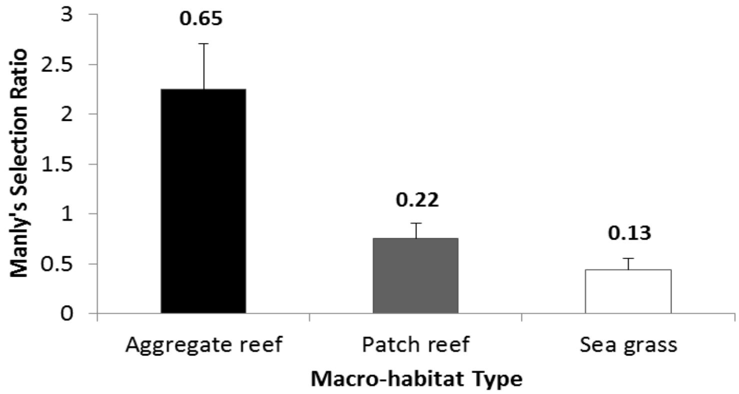

Figure 1. Manly's selection ratio for lionfish macro-habitat occupancy in Roatan Marine Park. Bars represent 1 standard error, and values represent standardized selection ratios.

lionfish (9 total individuals) inhabited particular micro-habitat substrate types (Figure 2A). We found that areas occupied by lionfish had a significantly higher percentage of hard coral ($t=2.09$, $df=112$, $P=0.038$) and overhanging structure ($t=3.56$, $df=112$, $P<0.001$), and a lower percentage of algae ($t=-2.02$, $df=112$, $P=0.045$) when compared to unoccupied areas. Groupers (29 total individuals) and snappers (49 total individuals) exhibited similar patterns of micro-habitat occupancy compared to lionfish, where individuals were more likely (but not significantly) to be sighted on hard coral and associated with overhanging structure (Figure 2B,C). For all species our limited sample size precluded an examination of micro-habitat occupancy for each macro-habitat type.

Discussion

Occupancy of lionfish along the northwest shoreline of Roatan, Honduras, was greatest in aggregate reef habitats compared to patch reefs and sea grass/lagoon habitats, and within these habitats lionfish tended to occur in areas of hard coral containing substantial amounts of overhanging structure. Hard coral may be providing opportunities for enhanced camouflage and protection compared to other substrates due to greater topography complexity (Fishelson 1997). Overhanging structure is favorable for ambush predation strategies by lionfish, which feed primarily in the morning hours 07:00 – 11:00 (Morris and Akins 2009). However, there is little information on behavior and substrate association during nocturnal periods. Preference and ability to select certain corals or areas of coral reefs based on microhabitat characteristics has been reported in other reef fish (Sale et al. 1984), and our findings can help guide future investigations and management strategies aimed at removal activities that target lionfish during daylight hours.

Given the large popularity of lionfish in the aquarium trade and its widely publicized invasion of marine ecosystems (Padilla and Williams 2004) it is surprising that limited research exists on its basic ecology. In their introduced range it has been suggested that lionfish are capable of reproducing year round with an annual fecundity of 2 million eggs (Morris et al. 2008). Our results showed that smaller individuals tended to occupy sea grass habitats compared to reef habitats; a finding also supported by Barbour et al. (2010). Lagoons composed of sea grass have long been classified as nursery grounds for many juvenile fish (Parrish 1989; Nagelkerken et al. 2002), and this may also be the case for lionfish. There is little documentation of size at time of settlement, but the smallest (and most recently settled) lionfish observed in this study was 25 mm. To obtain this size in a ~26 day larval stage (Ahrenholz and Morris 2010) would require a rate of growth of 1 mm/day from hatching at 1.5 mm (Morris et al. 2008). This would suggest that there is a relatively fast growing period to reach size at maturation from the observed size at settlement.

Morris and Whitfield (2009) found that lionfish reach sexual maturity within one year at a size of 100 mm and 180 mm for males and females, respectively. The average size of 89 mm

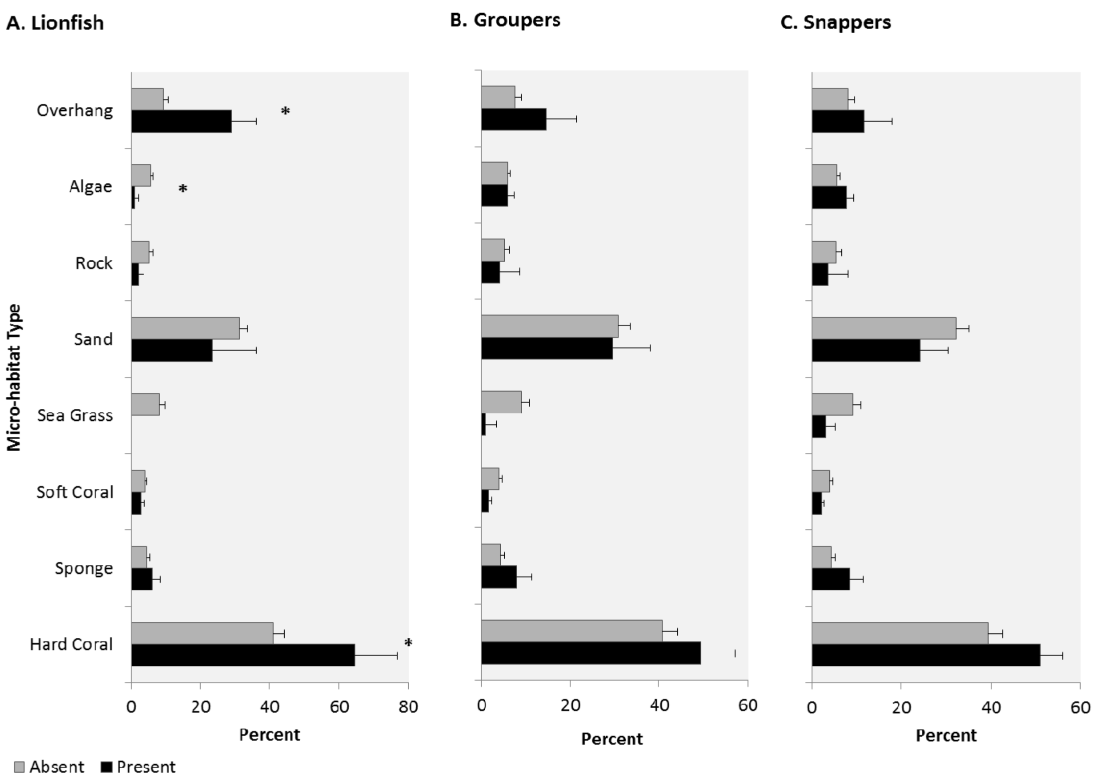

Figure 2. Micro-habitat substrate composition of presences versus absences for (A) lionfish, (B) groupers and (C) snappers. Bars represent 1 standard error. Statistically significant differences are indicated by * (P<0.05).

for lionfish in sea grass habitats indicates that fewer individuals are sexually mature in these areas compared to aggregate and patch reefs. These findings have direct relevance to current management strategies that are actively controlling lionfish throughout their introduced range. For example, in the Bahamas, current efforts focusing on the removal of lionfish include spearfishing and live capture by recreational divers, biologists and anglers on reef habitats and by island residents in shallow sea grasses. Targeting removal efforts in sea grass habitats containing juvenile lionfish may be beneficial for the long-term control of populations because these individuals are unlikely to have reached maturity and therefore have not contributed to the effective population. In support of this, recent population modeling results emphasized the importance of targeting juveniles as well as adults in removal efforts (Morris et al. 2010).

Lionfish have been shown to significantly affect the recruitment of juvenile reef fish (Albins and Hixon 2008), and previous studies between Florida and North Carolina have also found them to be equally abundant as grouper and snapper (Whitfield et al. 2007). Our survey found that two species of grouper (mean of 1.4 fish per transect) and two species of snapper (2.3) out-numbered lionfish (0.4), however longer term data suggests that grouper/snapper in Roatan are being depleted (Gobert et al. 2005). Nassau Grouper occupy similar settlement sites as lionfish, specifically around coral heads in lagoon areas (Eggleston 1995). This would put them in direct competition for food and other resources during the juvenile life stage. As adults, lionfish and grouper have many of the same habitat preferences, including overhang areas or crevices which provide protection or cover (this study, Sadovy and Eklund 1999); therefore, we expect that predatory effects of lionfish on sensitive grouper species may also be prevalent.

The introduction and spread of lionfish into coral reef systems provides an opportunity for more inclusive management strategies that involve the public. The incorporation of citizen science is especially attractive with regards to lionfish because coral reefs attract tourism and in many cases, the local economy relies on the preservation of the coral reef ecosystem. Citizen science has proven to be useful in monitoring both the distribution and range expansion of non-native species such as Asian shore crabs [*Hemigrapsus sanguineus* (De Haan, 1853)] (Delaney et al. 2007) and the overall biodiversity of aquatic environments (Goffredo et al. 2010). Removal efforts are generally lacking within these programs and there have been very few assessments as to the efficacy of non-native removal efforts by citizen scientists. Lionfish seem to be an exception where citizen-removal programs are becoming increasingly common, including in Roatan Marine Park (http://www.roatanmarinepark.com/news/lionfish-derby/). For example, the data being collected by the Roatan Marine Park on lionfish occurrence and size illustrate a powerful form of citizen science, yet it could be augmented by integrating a protocol with the goal of recording lionfish absences. Data on the absence of lionfish is crucial in determining broad-scale habitat relationships and it provides the greatest opportunity to develop powerful ecological niche models that predict the secondary spread of invasive species for management purposes (Vander Zanden and Olden 2008). The Reef Environmental Education Foundation (REEF) has set up a program to utilize recreational SCUBA divers in this way. They have developed a survey for divers to perform during their dives to record information on the presence of lionfish and other species as well as certain habitat characteristics. We urge REEF to also consider the inclusion of species absence in their surveys. This kind of program would be a powerful addition to current lionfish management strategies aimed at deploying early detection and rapid response.

Acknowledgements

We would like to thank the Roatan Marine Park and Matt Nawrocki for the use of their data set, and Diane Faulkner, Ian Drysdale and Reef Gliders dive shop for their assistance in the field. This paper benefited greatly from the reviews of three anonymous referees. Helpful guidance throughout the project was provided by members of the Olden Lab.

References

Aquilar-Perera A, Tuz-Sulub A (2010) Non-native, invasive red lionfish [*Pterois volitans* (Linnaeus, 1758): Scorpaenidae], is first recorded in the southern Gulf of Mexico, off the northern Yucatan Peninsula, Mexico. *Aquatic Invasions* 5: S9–S12, doi:10.3391/ai.2010.5.S1.003

Ahrenholz DW, Morris JA (2010) Larval duration of the lionfish, *Pterois volitans*, along the Bahamian Archipelago. *Environmental Biology of Fishes* 88: 305–309, doi:10.1007/s10641-010-9647-4

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* 367: 233–238, doi:10.3354/meps07620

Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. *Marine Ecology Progress Series* 401: 291–294, doi:10.3354/meps08373

Bell JD, Craik GJS, Pollard DA, Russell BC (1985) Estimating length frequency distributions of large reef fish underwater. *Coral Reefs* 4: 41–44, doi:10.1007/BF00302203

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261: 78–82, doi:10.1126/science.261.5117.78

Coles SL, Eldredge LG (2002) Nonindigenous species introductions on coral reefs: a need for information. *Pacific Science* 56: 191–209, doi:10.1353/psc.2002.0010

Delaney DG, Sperling CD, Adams CS Leung B (2007) Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions* 10: 117–128, doi:10.1007/s10530-007-9114-0

Eggleston DB (1995) Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series* 124: 9–22, doi:10.3354/meps124009

Fishelson L (1997) Experiments and observations on food consumption, growth and starvation in *Dendrochirus brachypterus* and *Pterois volitans* (Pteroinae, Scorpaenidae). *Environmental Biology of Fishes* 50: 391–403, doi:10.1023/A:1007331304122

Garshelis DL (2000) Delusions in habitat evaluation: Measuring use, selection, and importance. In: Boitani L, Fuller TK (eds), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, pp 111–164

Gobert B, Berthou P, Lopez E, Lespagnol P, Turcios MDO, Macabiau C, Portillo P (2005) Early stages of snapper-grouper exploitation in the Caribbean (Bay Islands, Honduras). *Fisheries Research* 73: 159–169, doi:10.1016/j.fishres.2004.12.008

Goffredo S, Pensa F, Neri P, Orlandi A, Scola Gagliardi M, Velardi A, Piccinetti C, Zaccanti F (2010) Unite research with what citizens do for fun: "recreational monitoring" of marine biodiversity. *Ecological Applications* 20: 2170–2187, doi:10.1890/09-1546.1

Green SJ, Côté IM (2008) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28: 107, doi:10.1007/s00338-008-0446-8

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab (*Carcinus maenas). Biological Conservation* 78: 59–66, doi:10.1016/ 0006-3207(94)00018-2

Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27, doi:10.1016/S0169-5347(01)02 358-8

Kane CN, Brooks AJ, Holbrook SJ, Schmitt RJ (2009) The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. *Environmental Biology of Fish* 84: 1–10, doi:10.100 7/s10641-008-9377-z

Kappel CV (2005) Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. *Frontiers in Ecology and the Environment* 3: 275–282, doi:10.1890/ 1540-9295(2005)003[0275:LPOTPT]2.0.CO;2

Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Marine Ecology Progress Series* 283: 269–278, doi:10.3354/meps283269

Maljković A, Van Leeuwen TE, Cove SN (2008) Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* 27: 501, doi:10.1007/s00338-008-0372-9

Manly B, McDonald L, Thomas DL, Thomas TL, Erickson WP (2002) Resource selection by animals, statistical design and analysis for field studies, 2nd edn. Springer, London, 240 pp

Meister H, Wyanski DM, Loefer JK, Ross SW, Quattrini AM, Sulak KJ (2005) Further evidence for the invasion and establishment of *Pterois volitans* (Teleostei: Scorpaenidae) along the Atlantic Coast of the United States. *Southeastern Naturalist* 4: 193–206, doi:10.1656/ 1528-7092(2005)004[0193:FEFTIA]2.0.CO;2

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485–492, doi:10.1890/070064

Morris JA, Akins JL, Barse A, Cerino D, Freshwater DW, Green SJ, Munoz RC, Paris C, Whitfield PE (2008) Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. Proceedings of the 61st Gulf and Caribbean Fisheries Institute, November 10–14, 2008. Gosier, Goudeloupe, French West Indies, pp 409–414

Morris JA, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes* 86: 389–398, doi:10.10 07/s10641-009-9538-8

Morris JA, (2009) The biology and ecology of invasive Indo-Pacific lionfish. Ph.D. Dissertation. North Carolina State University, Raleigh, NC, USA, 168 pp

Morris JA, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum NOS NCCOS 99, 57 pp

Morris JA, Shertzer KW, Rice JA (2010) A stage-based matrix population model of invasive lionfish with implications for control. *Biological Invasions* 13: 7–12, doi:10.1007/s10530-010-9786-8

Nagelkerken I, Roberts CM, van der Velde G, Dorenbosch M, van Riel MC, Cocheret de la Moriniere E, Niehuis PH (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244: 299–305, doi:10.3354/meps244299

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2: 131–138, doi:10.1890/1540-9295(2004) 002[0131:BBWAAO]2.0.CO;2

Parrish JD (1989) Fish communities of interacting shallow water habitats in tropical oceanic regions. *Marine Ecology Progress Series* 58: 143–160, doi:10.3354/meps 058143

Roatan Marine Park (2010) Lionfish Sighting Database. Roatan, Honduras, http://www.roatanmarinepark.com (Accessed 10 January 2010)

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *American Zoologist* 37: 621–632

Sadovy Y, Eklund A (1999) Synopsis of biological data on the Nassau grouper, *Epinephelus striatus,* and the Jewfish, *E. itajara*. NOAA Technical Report NMFS 146. FAO Fisheries synopsis 157

Sale PF, Douglas WA, Doherty PJ (1984) Choice of microhabitats by coral reef fishes at settlement. *Coral Reefs* 3: 91–99, doi:10.1007/BF00263759

Schofield PJ (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. *Aquatic Invasions* 4: 473–479, doi:10.3391/ai.2009.4.3.5

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 Sea and Gulf of Mexico. *Aquatic Invasions* 5, Supplement 1: S117–S122, doi:10.3391/ai.2010. 5.S1.024

Schmitt EF, Sullivan KM (1996) Analysis of a volunteer method for collecting fish presence and abundance data in the Florida Keys. *Bulletin of Marine Science* 59: 404–416

Smith N, Sealy KS (2007) The lionfish invasion in the Bahamas. *Bahamas Naturalist and Journal of Science* 2 (2): 35–39

[USGS] United States Geological Survey (2011) Nonindigenous Aquatic Species. http://www.usgs.gov (Accessed 10 February 2011)

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Science* 65: 1512–1522, doi:10.1139/F08-099

Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish (*Pterois volitans)* along the Atlantic coast of North America. *Marine Ecology Progress Series* 235: 289–297, doi:10.3354/meps235289

Whitfield PE, Hare J, David AW, Harter S, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biological Invasions* 9: 52–64, doi:10.1007/s10530-006-9063-z