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Research Article

Management implications of the influence of biological variability of invasive lionfish diet in Belize

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Abstract

With a voracious appetite for juvenile fish and invertebrates, invasive alien red lionfish (*Pterois volitans*) constitute one of the greatest threats to the Caribbean's coral reefs. Although the eradication of lionfish is no longer considered possible, population suppression to site-specific densities can allow native fish populations to recover. Understanding the diet of lionfish in invaded areas is critical to understanding local impacts they pose to coral reef communities. This study explored the diet of lionfish in the northern end of the Belize Barrier Reef and tested whether biological variables (size, sex or reproductive stage) affect the diversity and/or abundance of prey species consumed. Between 2011 and 2014, 1023 lionfish were dissected and their gut contents analysed in the Bacalar Chico Marine Reserve. Gut contents analyses revealed that large sized lionfish consumed the highest abundance of prey (Mean (M)= 3.27 prey items) compared to small (M= 1.74 prey items) and medium (M= 3.15 prey items) lionfish, and that reproductive females consumed a higher abundance of prey (M= 3.66) compared to non-reproductive females of the same size (M= 2.85). As we found that medium and large lionfish are generalist predators and feed on a diverse assemblage of prey items, the effects of lionfish on the biomass of any one species may be reduced. This may enable individual prey species to have relatively stable abundances, although this hypothesis bears further testing. If management efforts are focused on improving a site-specific population of an individual prey species, such as an endemic or threatened fish, it is important to include removal efforts of small lionfish, particularly if they inhabit the same niche habitat. However, we recommend that existing lionfish focused cull dives continue using non-size discriminatory methods in order to account for site-specific, ecologically and commercially important prey items and to deter the likelihood of a successful invasion.

Key words: *Pterois volitans,* Caribbean, coral reef; invasive species, prey diversity

Introduction

Native to the Indo-Pacific, the red lionfish (*Pterois volitans* Linnaeus, 1758) is now firmly established in the waters of the Western Atlantic and Caribbean, and its range continues to expand throughout much of the tropical and subtropical western Atlantic Ocean and Caribbean Sea (Morris 2009; Schofield 2010). Following the first documented sighting in Turneffe Atoll, Belize in 2008 (Searle et al. 2012), alien lionfish have expanded their range throughout the Belize Barrier Reef Reserve System UNESCO World Heritage Site (UNESCO 1996).

The invasion of lionfish is one of the first cases in which an introduced marine fish has become a key invasive threat. As such, it has been recognized as one of the Caribbean's principal conservation concerns (Albins and Hixon 2013; Dahl and Patterson 2014; Sutherland et al. 2010). Invasive alien lionfish in New Providence, Bahamas have been reported at densities greater than 390 lionfish per hectare (Green and Côté 2008), more than eight times greater than in their indigenous range within the Red Sea (47.9 lionfish per hectare) (McTee and Grubich 2014). In other invaded areas of the Caribbean, high growth and reproduction rates have also being reported, with lionfish reproducing year round and in excess of two-million eggs per female per year (Morris 2009; Morris and Akins 2009).

The successful invasion of the lionfish has been attributed, in part, to a generalist diet (Dahl and Patterson 2014; Layman and Allgeier 2012). In their native habitat, lionfish feed primarily on fish, crabs and shrimp (Fishelson 1997; Sano et al. 1987), though occasionally on other invertebrates such as isopods and gastropods (Harmelin-Vivien and Bouchon 1976). Lionfish gut analyses in the Bahamas revealed a typical diet consisting of small reef fishes, particularly gobies (*Gobiidae*), wrass (*Labridae*) and basselets (*Grammatidae*) (Albins and Hixon 2013; Morris and Akins 2009). Other reported lionfish prey items in invaded ranges include parrotfish, an ecologically important herbivore known for preventing the dominance of algae on coral reefs (Albins and Hixon 2008; Albins and Hixon 2013; Layman and Allgeier 2012; Rotjan and Lewis 2006). Lionfish also demonstrate a range of morphometric characteristics and behaviours, such as cryptic coloration, elongated fin rays and defensive venomous spines, that are unfamiliar to native fish prey in their invasive range, giving them a competitive advantage over native piscivores (Albins 2013; Albins and Hixon 2013; Albins and Lyons 2012). The overfishing of competitor mesopredators in the West Atlantic, such as small-bodied groupers, has further contributed to the availability of potential prey species (Farmer and Karnauskas 2013; Whitfield et al. 2007).

In addition, lionfish invasions can impact community structure. Bahamian reefs invaded by lionfish displayed significantly lower native coral reef fish community recruitment rates compared to uninvaded reefs (Albins 2013). The presence of lionfish caused a reduction in native reef fish abundance—2.5 times that of a similarly sized native piscivores—as well as a reduction in reef fish species richness (Albins 2013). In addition, in these same reef systems, a single lionfish reduced native coral reef fish recruitment rates by up to 79% in five weeks (Albins and Hixon 2008). Such a decline in reef fish populations could in turn lead to declines in commercially important fish species such as groupers, snappers and goatfishes (Albins and Hixon 2013), or a shift in the diet of lionfish to other prey items such as invertebrates (Layman et al. 2014).

The first confirmed report of a red lionfish in Belize was in December 2008 (Schofield 2009). Although accurate estimates of the lionfish population in Belize are deficient, lionfish sighting data collected from the Bacalar Chico Marine Reserve (BCMR), in the northern end of the Belize Barrier Reef, since 2010 suggest that lionfish are firmly established in the BCMR and have increased in size and abundance during four subsequent years of monitoring (Chapman et al. 2016).

The additional threat to fish and invertebrate populations posed by lionfish is particularly concerning to the BCMR ecosystem. The overall reef health in the BCMR is considered to be "poor" (Chapman 2013). A combination of decreased mean hard coral cover (18% in 2004 (Garcia-Salgado et al. 2008) to 9% in 2013 (Chapman 2013), dominance of fleshy macro algae (23% in 2013), critically low long-spined sea urchin (*Diadema* sp.) populations (key reef grazers and bioeroders) (Chapman 2013) and low reef fish diversity (Chapman 2013) has placed the BCMR on alert status since 2004 (Garcia-Salgado et al. 2008).

Given the outstanding ecological and economic value of the Belize Barrier Reef and its resources, there is an urgent need to develop systems for the effective management of invasive alien lionfish (Barbour et al. 2011; Gongora 2012). The total estimated value of fisheries, tourism and shoreline protection services in Belize's coral reef and mangroves is US$ 395–559 million per year (2008 value) (Nuenninghoff et al. 2015). Belize attracts up to 294,000 tourists annually (2013 data), (World Bank 2016), many of whom visit the Belize Barrier Reef, making tourism the greatest foreign exchange earner in the country (CIA 2015; Diedrich 2007).

Existing lionfish removal efforts in many invaded ecosystems centre around culls conducted by recreational SCUBA divers who target lionfish with spears or hooks (Nuttall 2014; Pitt and Tammy 2013). Although many dive operations take part in controlled culls, they often lack sufficient time, funds or labour to conduct removals at a level that is ecologically effective (Pitt and Tammy 2013). In addition, lionfish residing in deeper, mesophotic habitats remain below the limit of recreation SCUBA divers (Nuttall 2014). Although eradication of lionfish is no longer considered possible due to the broad geographic extent of the invasion, population suppression to site-specific threshold densities can protect native fish communities from lionfish-induced community biomass declines (Green et al. 2014). If lionfish populations are to be suppressed in the long term, a more efficient management approach is required.

This study explores the diet of lionfish in the BCMR in order to understand the local impacts posed to coral reef communities. The aim of this study is to identify the diversity and abundance of prey species targeted by lionfish in Belize and to test whether prey consumption varies with lionfish size, sex, or reproductive stage.

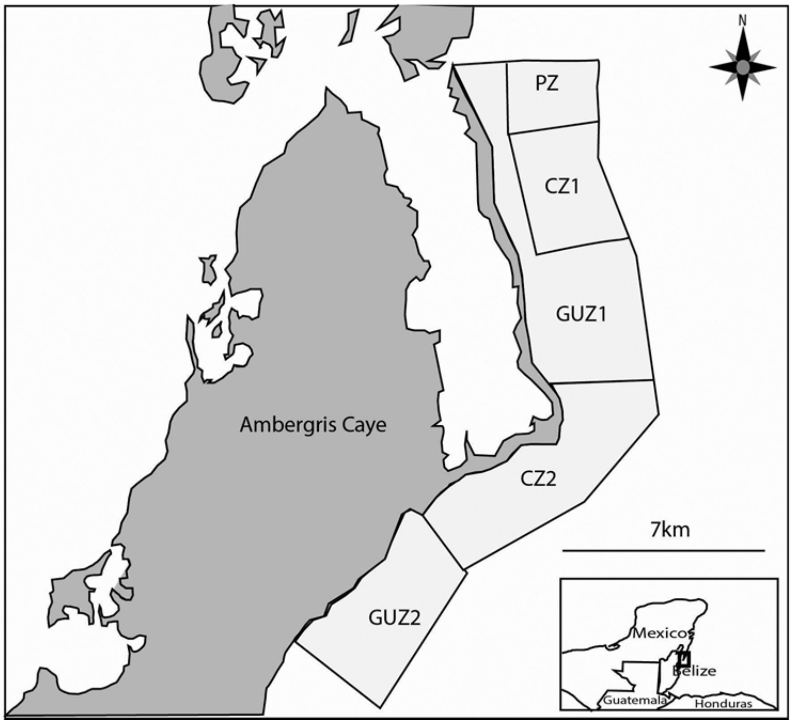

Figure 1. Map of the Bacalar Chico Marine Reserve (BCMR) Showing Preservation Zone (PZ); Conservation Zone 1(CZ1); General Use Zone 1 (GUZ1); Conservation Zone 2 (CZ2); General Use Zone 2 (GUZ2).

Methods

Ethics statement

Blue Ventures has a research permit under the Belize Fisheries Department, and Blue Ventures' staff hold lionfish hunting licenses that permit research on and culling of lionfish on SCUBA dives within the Bacalar Chico Marine Reserve (BCMR). All lionfish were culled as part of a control program, and culled specimens were used post hoc for research.

Study site

The BCMR is located in north Belize bordering Mexico and on the east coast of Ambergris Caye (18º08′28″N; 87º51′47″W) (Figure 1). The reserve is one of seven Marine Protected Areas in the Belize Barrier Reef Reserve System UNESCO World Heritage Site (UNESCO 1996) and is a biodiversity hotspot as a part of the Mesoamerican Barrier Reef system (Vásquez-Yeomans et al. 2011).

Opportunistic lionfish sightings and collection

Between 2011 and 2014, on every scientific dive (n = 2033) within the BCMR (e.g. including non-lionfish related surveys or training dives), opportunistic sightings of lionfish were recorded and their size estimated for total length (TL, mouth to tip of tail) to the nearest 10 mm. All dives took place between the hours of 06:30 and 18:00 during every month of the calendar year between 2011 and 2014, including both the wet (June to November) and dry (December to May) seasons. Dives took place within 24 dive sites throughout the BCMR to a maximum depth of 30m. During a portion (n = 199) of the sighting dives, all encountered lionfish were culled. Following culls, lionfish were kept cool and dissected within six hours of death.

The dive sites represented a variety of habitat types within the following four management zones (Figure 1): Preservation Zone (PZ), completely protected, no commercial or recreational activities permitted; Conservation Zone 1 (CZ1), no-take, all forms of fishing banned, no catch and release however recreational activities (snorkelling and SCUBA) allowed; Conservation Zone 2 (CZ2), no-take however catch and release sport fishing and other recreational activities such as snorkelling and SCUBA; and General Use Zone 2 (GUZ), extractive fishing permitted however must obtain license to fish (no gill nets or long lines).

Lionfish dissection and gut analysis

Staff used protocols in Green et al. (2012b) to dissect lionfish. Body size (TL, to the nearest mm) and gut contents were recorded. The length of whole prey items were also measured and visually identified to the lowest possible taxonomic level (e.g. blue headed wrasse (*Thalassoma bifasciatum* Bloch, 1791)); Wrasse (*Labridae*); vertebrate). Prey items were only identified to the lowest taxonomic level if they were fully intact, or had minor to substantial degradation to external structures (e.g. scale pigmentation or fin rays) in accordance with recommendations in Green et al. (2012b). Majorly degraded prey items were identified to the vertebrate/invertebrate level. For prey items that were too digested to discern body shape, length was not measured (Green et al. 2012b).

In 2012, the presence or absence of reproductive ovaries (denoting spawning capability) in lionfish was recorded and used to identify reproductively mature female lionfish. When reproductive ovaries were lacking, sex was undetermined. After 2012, lionfish sex was identified using the gonad staging key in Green et al. (2012b). Testes were largely indistinguishable from immature ovaries in immature lionfish and may have resulted in visual misidentification in specimens smaller than 180 mm TL (Green et al. 2012b). Therefore, only lionfish over 180 mm were sexed during dissections in order to avoid gender misidentification.

Data analysis

All data were entered by field staff and/or volunteers and verified through a double entry and checking system built in Visual Basic (VBA).

The following lionfish size categories were established: small: <180 mm; medium: 181 mm to 280 mm; and large: >281 mm. Our size categories are within previously reported ranges of "large" lionfish from populations found in the Gulf of Mexico (Dahl and Patterson 2014) and the Caribbean (Tamburello and Cote 2015).

To determine if there were significant size differences between lionfish opportunistically sighted and those that were culled, a Welch F test was used. To test if culled lionfish size differed between the wet (June to November) and dry (December to May) season, a student T-Test was used. Only lionfish that had prey items were included in the following analyses. Differences in the proportion of invertebrate and vertebrate prey items consumed by lionfish of different size classes were tested using a Chi-Square test. Non-parametric Kruskal-Wallis tests were used to test for differences in prey diversity between male and female lionfish, reproductive and non-reproductive lionfish and small, medium and large lionfish with Tukey post-hoc tests used to identify pair-wise differences in prey diversity between size class groups. Finally a Mann-Whitney U test was performed to test for differences in the number of prey items consumed by small and large lionfish, female and male lionfish, and to test for differences in the number of prey items consumed by reproductive and non-reproductive females of the same size category. Statistical analyses were carried out using the statistical software Past3 and R 3.23.

Results

Size class frequency

In total, 1023 lionfish were culled and dissected (n = 2011:251; 2012:459; 2013:122; 2014:191), the majority of which (76%) were over 180 mm and considered sexually mature (Morris 2009; Green et al. 2012b). In total, 4158 lionfish were opportunistically sighted and sized in the water (n = 2011:861; 2012:1389; 2013:1324; 2014:584). The majority of opportunistically sighted lionfish (75%) were also over 180 mm. The size structure of culled lionfish did not significantly differ from the size structure of lionfish sighted in the water (Blue Ventures unpublished data; $t= -1.99$, $df= 14$, $p= 0.07$). Although this p-value is close to the significance cut-off value, it implies that culled lionfish provide a relatively good representation of the size structure of the invasive population. Therefore for the purpose of this study, culled individuals were considered representative of the wider lionfish population.

The peak size class frequency for culled lionfish was between 241 and 300 mm throughout 2011 to 2014, bar 2013, which saw a peak in the 310–360 mm size category (Figure 2). There was no significant difference in the size structure of lionfish between years ($F = 1.02$, $df = 14.38$, $p = 0.41$), however the proportion of 361–420 mm lionfish in the population increased from 0% in 2011 to 7% in 2014 (n = 191). There were no significant seasonal differences between lionfish of different size classes ($t = 0.50$, $df = 5$, $p = 0.64$)

Prey item abundance

Of the 1023 lionfish dissected, the mean number of prey items per lionfish was 2.09 (range 0–18, SD = 2.67). A total of 372 lionfish (36% of total lionfish dissected) had no prey items found within their guts. The mean number of prey items found in lionfish that had a minimum of one prey item in its gut was 3.12 (range 1–18, SD = 2.75). Of those lionfish that had at least one prey item present, there was a significant difference between the number of prey items consumed by small (<180 mm), (Mean (M) = 1.74) and large (>280 mm), (M = 3.27) lionfish

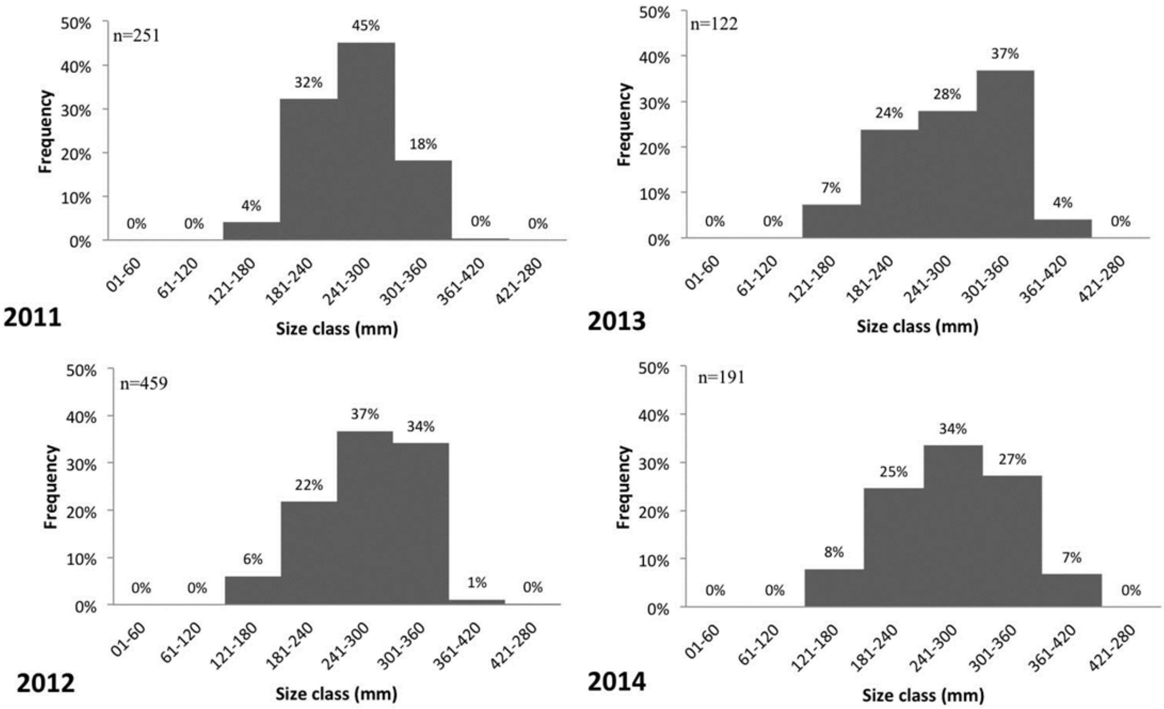

Figure 2. Total size class frequency by year of lionfish (*Pterois volitans*) collected from the Bacalar Chico Marine Reserve every month between 2011 and 2014.

($U = 1027$, $z = -2.72$, $p = 0.01$) and small and medium ($M = 3.15$) lionfish ($U = 1291.5$, $z = -2.41$, $p = 0.02$). There was no significant difference between number of prey items consumed by medium and large lionfish ($U = 16662$, $z = -0.61661$, $p = 0.54$).

Of those lionfish that had at least one prey item present, no significant difference was found between the number of prey items consumed by female ($M = 3.26$, $SD = 2.87$) compared to male lionfish ($M = 3.10$, $SD = 2.68$) ($U = 16737$, $p = 0.91$, $df = 368$). However, significantly more prey items were found in reproductive (spawning capable) females ($M = 3.66$) than non-reproductive females (immature/early developing ovaries) of the same size class (over 180 mm) ($M = 2.85$), ($U = 4147$, $z = -2.88$, $df = 205$, $p = <0.01$).

Prey diversity

Overall, 1855 prey items could be identified to the vertebrate/invertebrate level, and 1022 could be identified to an order level or below (Figure 3). A total of 176 prey items were deemed indistinguishable between invertebrate and vertebrate and were therefore excluded from this data. As only 106 prey items could be identified to the species level, order and family were selected as the most appropriate measures of prey diversity. Silverside (*Atherinidae*), ray fined-fish (*Clupeidae*) and anchovy (*Engraulidae*) were grouped together to account for similarities in identification. If two or more families were identified under the same order, the order was used to avoid over-representing prey diversity (e.g. grouper and hamlet were classified together as *Serranidae*). A total of 22 different prey orders and families were recorded across 1022 prey items.

There was a significant difference between the ratio of vertebrate and invertebrate consumption between the size classes of small, medium and large lionfish ($X^2 = 129.55$, $df = 2$, $p = <0.01$) (Figure 4). The diet of small lionfish ($n = 5$) was dominated by invertebrates (62%), the diet of medium lionfish ($n = 18$) was almost evenly mixed (51% invertebrates), and the diet of large lionfish ($n = 17$) was dominated by vertebrates (75%).

The diversity of prey consumed by female compared to male lionfish (Females: $n = 19$; Males: $n = 17$) did not differ significantly ($X^2 = 0.11$, $df = 1$, $p = 0.74$), nor was there a significant difference in the diversity of prey items in reproductive and non-reproductive females of the same size class (over 180 mm) (reproductive females: $n = 19$; non-reproductive females: 14) ($X^2 = 1.28$, $df = 1$, $p = 0.25$).

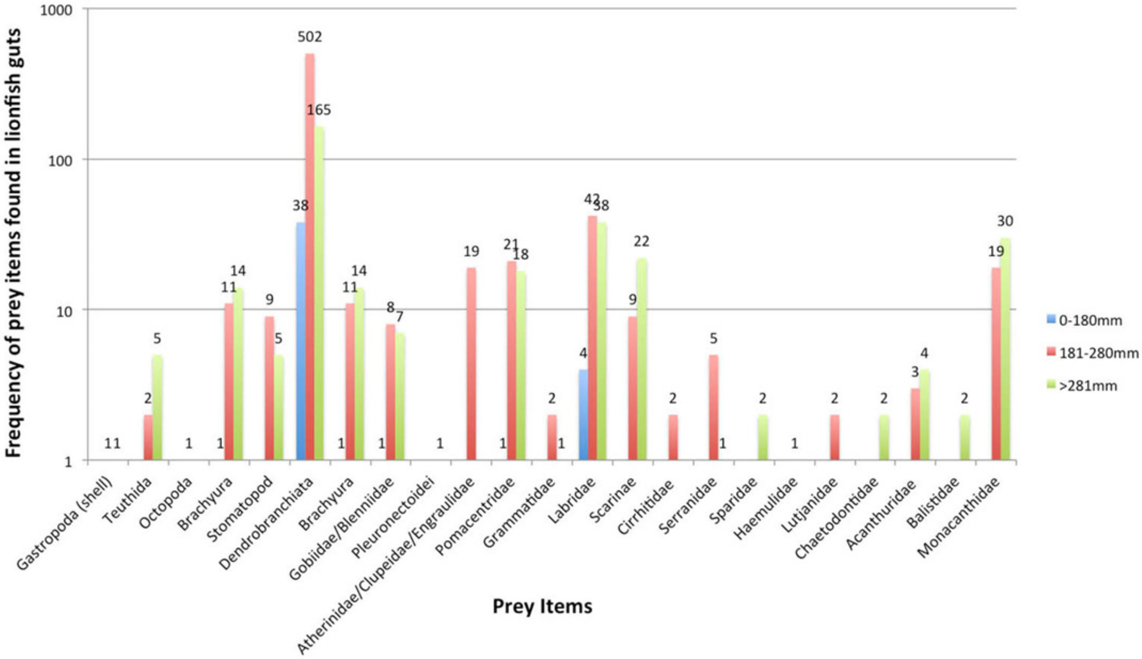

Figure 3. Prey diversity (identified to ordinal and family level) and number of prey items within three size classes of lionfish (*Pterois volitans*) collected from the Bacalar Chico Marine Reserve between 2011 and 2014 on a logarithmic scale. The total number of prey items found was 1023.

However, there was a significant difference in the diversity of prey items consumed by different size classes of lionfish (small = 5; medium = 18; large = 17), ($X^2 = 8.07$, df = 2, $p = 0.02$), driven by differences between small and medium ($p = <0.01$) and small and large lionfish ($p = 0.01$), but not medium and large lionfish ($p = 0.81$). The diet of small lionfish was dominated by prawns (*Dendrobranchiata*) (84% of prey) and to a lesser extent wrasse (*Labridae*) (16%). In contrast, the diversity of prey eaten by medium and large size classes was more diverse, typically including crabs (*Brachyura*), parrotfish (*Scarinae*), wrasse (*Labridae*), filefish (*Monacanthidae*) and damselfish/clownfish (*Pomacentridae*) (Figure 4). Butterflyfish (*Chaetodontidae*) (n = 2), flatfish (*Pleuronectoidei*) (n = 1), porgies (*Sparidae*) (n = 2) and triggerfish (*Balistidae*) (n = 2) were only consumed by the largest size class of lionfish (>281 mm). In comparison, grunts (*Haemulidae*) (n = 1), bass (*Serranidae*) (n = 1), hawkfish (*Cirrhitidae*) (n = 2), octopus *Octopoda* (n = 1), snappers *Lutjanidae* (n = 2) and Silverside (*Atherinidae*)/ray fined-fish (*Clupeidae*)/anchovy (*Engraulidae*) (n = 19) were only consumed by medium sized lionfish.

One observation of particular note was the identification of a 17 mm juvenile slipper lobster (*Scyllarides aequinoctialis* Lund, 1793) in a 310 mm lionfish in December 2014 (Figure 5).

Discussion

Invasive alien lionfish are voracious predators of both invertebrate and vertebrate prey. They have reduced the prey abundance of native fishes by up to 95% in some parts of the Caribbean (Albins 2013; Green et al. 2012a) and have been implicated in the competitive exclusion of native mesopredators (Green et al. 2011). Understanding the ecological impacts posed by the lionfish invasion in the Bacalar Chico Marine Reserve (BCMR) in Belize is therefore important in identifying and prioritising regional management measures.

Research into the diet of lionfish in invaded areas is critical to understanding the local impacts posed to coral reef communities (Dahl and Patterson 2014). The results of this study support evidence that lionfish are generalist mesopredators (Dahl and Patterson 2014; Morris and Akins 2009) and provides evidence that the abundance of prey items removed by lionfish in the BCMR is significantly higher in medium (181 mm to 280 mm) and large (>281 mm) size lionfish compared to small (<180 mm) size classes. Gut contents analyses also indicate that the diet of lionfish in the BCMR shifts towards piscivores in medium and large size classes.

These results support observations elsewhere in the Caribbean suggesting lionfish have a preference

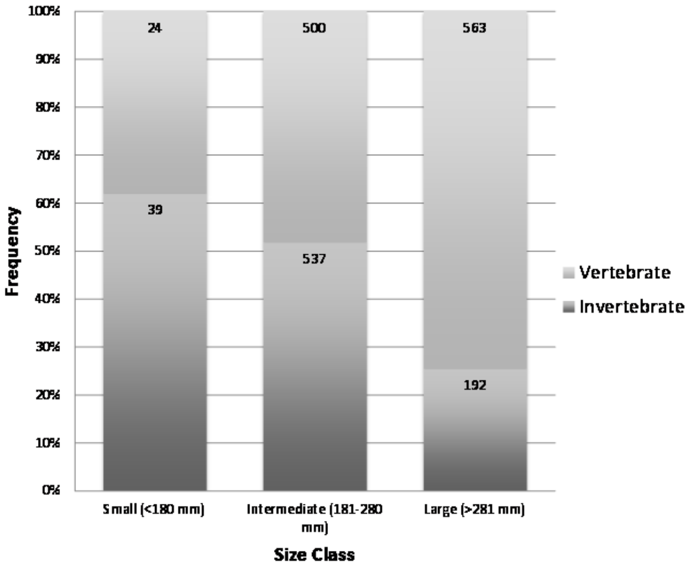

Figure 4. Frequency of vertebrate and invertebrate prey items by lionfish (*Pterois volitans*) size class collected from the Bacalar Chico Marine Reserve between 2011 and 2014. The total number lionfish dissected was 1023, and the total number prey items was 1855.

for reef fish prey (e.g. Gobiidae, Labridae and Scarinae in both Belize and the Bahamas) throughout their invasive range (Albins and Hixon 2008; Dahl and Patterson 2014; Morris and Akins 2009; Muñoz et al. 2011; Rocha et al. 2015). However, there is also evidence to suggest that both invasive and native lionfish adapt their diets to exploit locally abundant prey. For example, gut-analyses of invasive lionfish on artificial reef habitats in Mexico revealed a diet of non-reef associated prey, while those found on natural reefs in Mexico consisted of predominantly reef-associated demersal fishes (Dahl and Patterson 2014). In addition, native lionfish in Madagascar were found to eat an almost equal amount of fish and brachyurans (Harmelin-Vivien and Bouchon 1976). It is therefore evident that lionfish exhibit a plastic predation response to take advantage of novel habitats.

Reports indicate that reef health in the BCMR is poor and show a reduction in hard coral and an increase in macroalgae cover since 2012 (Kramer et al. 2015). Community shifts such as these have often been considered symptomatic of a reduction in herbivorous fishes caused by an abundance of meso-predators, both as a result of the introduction of lionfish and overfishing of other top predators (Albins and Hixon 2013; Stallings 2009). However, the proportion of herbivorous fishes (Monacanthidae, Scarinae, and Pomacentridae) found in lionfish guts in this study was relatively low, accounting for only 6.85% of the prey items. Given that some parrotfish and damselfish are not entirely herbivorous, this proportion may actually be lower but could also be representative of their abundance on the reef. Given the low number of herbivorous fish found in lionfish in the BCMR, it is unlikely that lionfish presence is impacting coral and macroalgal coverage.

Invertebrates dominate the diet of small lionfish

Although our results indicate a piscivorous diet among larger lionfish, invertebrate prey items dominated the diet of smaller lionfish, reflecting similar trends observed in lionfish populations in the Gulf of Mexico (Dahl and Patterson 2014) and the Bahamas (Morris and Akins 2009). Small/medium sized lionfish (≤ 256 mm) have small home ranges (<10 m) (Jud and Layman 2012) and are more likely to have site fidelity to a reef crevice or cave (Tamburello and Côté 2015). Such habitats offer higher protection and may also be shared with cave-dwelling invertebrate species (Curtis-Quick et al. 2013) and may explain their association with invertebrate prey.

The consumption of invertebrates by juvenile lionfish does not yet appear to pose a threat to Belize's fisheries, as the two most commercially important target species (conch and lobster) were notably absent from lionfish gut analysis. However, the presence of a slipper lobster (*Scyllaridae*), the first lobster to be found in a lionfish stomach in Belize, does present an initial concern. Given that the Caribbean spiny lobster (*Panularis argus* Latreille, 1804) is the most dominant wild catch fishery in Belize (Palomares and Pauly 2011), the impact of lionfish consuming small lobsters has the potential to

Figure 5. The first slipper lobster (*Scyllarides aequinoctialis* Lund, 1793) (top of ruler) to be found within the stomach of a lionfish (*Pterois volitans*) in Belize in December 2014.

be devastating to Belize's fisheries. With that said, the gregarious nature and defensive capabilities of the Caribbean spiny lobster, which include long, armoured, mobile antennae, are believed to make the species less vulnerable to predation compared to the slipper lobster (Mizrahi 2015; Parsons 2003). This should not, however, lead to complacency, and the diet of small lionfish in the vicinity of Caribbean spiny lobster fisheries should be carefully monitored due to possible dietary shifts at different stages of the invasion.

Prey diversity

Our results indicate that large lionfish consume the greatest abundance of prey items, suggesting that large lionfish have the greatest impact on the number of native fish extracted. Our results also reveal that medium and large lionfish consume a significantly higher diversity of prey compared to small lionfish.

Increased prey diversity in medium and large lionfish is not necessarily more detrimental to biodiversity, as high prey diversity should essentially decrease the overall impact on prey biomass of individual species (Duffy 2002; Hillebrand and Cardinale 2004; Pintor and Sih 2011). As medium and large lionfish feed on a diverse diet, the effects of lionfish on the biomass of any one species may be limited and allow individual species to have relatively stable population abundances, although this hypothesis bears further testing. Current culling efforts are focused on larger lionfish, but if management efforts are focused on improving a site-specific population of an individual prey species, such as an endemic fish, then it is important to include efforts on removal of small lionfish, particularly if they inhabit the same niche habitat. However, we do not suggest that efforts to remove medium and large lionfish should be deterred for the following two reasons: 1) medium and large sized lionfish consume the greatest abundance of native prey; and 2) higher prey diversity in medium and large lionfish could also suggest a high abundance of edible and/or naive prey species, and thus a greater probability of a successful invasion (Sih et al. 2010). It is therefore important to remove all sizes of lionfish in order to reduce the impact on overall native prey abundance and to deter the likelihood of a successful invasion.

Prioritisation of control efforts

Although our results showed a significant difference in the abundance of prey consumed between reproductive (spawning-capable) and non-reproductive female lionfish, it is unlikely that these results will aid in the prioritization of culling efforts for these two categories as there is no peer-reviewed literature on how to identify the sex of a lionfish externally, nor determine whether it is reproductively mature. Our results will likely aid the development of lionfish population models by demonstrating the proportion of females in the BCMR that are reproductively capable and that prey diversity differs between the two.

An example where these findings could be applied is in Pelican Cayes, Belize, where the threatened endemic social wrasse (*Halichoeres socialis,*) comprises almost half of the lionfish diet in the area (Rocha et al. 2015) leading to the belief that *H. socialis* might be the world's most threatened coral reef fish (Barrat 2015). With highly specific habitat requirements, this species is restricted to Belize's inner barrier reef particularly around the Pelican Cayes (Rocha et al. 2015). The results from our diet study, including size and sex specific prey assemblages, can be used to inform future models to develop methods to prioritise lionfish control efforts in the Pelican Cayes.

Limitations of this study

A limitation of this study was that identification of prey relied on visual assessments. While this approach was economical and allowed a large sample size to be analysed, the use of DNA testing or stable isotope analyses may have allowed the identification of prey items to the species level, rather than being restricted to the order or family level (Côté et al. 2013; Muñoz et al. 2011; Vásquez-Yeomans et al. 2011). Future studies may consider DNA testing in order to gain a more robust understanding of prey item diversity at the species level.

Conclusion

With limited measures available for lionfish control efforts, it is imperative that management measures are identified and prioritised in sites where they will have the greatest impact. The results of this study demonstrate that it is unlikely to be effective to prioritise culls based on lionfish biological structure (i.e., size) alone. Future studies should aim to determine what environmental and anthropogenic variables influence lionfish prey diversity and number of prey items. For example, although lionfish have a generalist diet, they typically have more specialized diets at different life stages and in different locations, often preying upon specific assemblages due to their site fidelity (Layman and Allgeier 2012; Tilley et al. 2015). By locating the distribution of ecologically/commercially important prey items (i.e. reef grazers, IUCN listed or commercially important prey items), lionfish management efforts can be conducted more efficiently and focused on the areas of the reef that are most vulnerable.

We recommend that at this point, despite the significant ontogenetic differences in diet between juvenile and adult stages of lionfish shown in this study, existing lionfish focused cull dives should continue by participating operators in the Caribbean using non-size discriminatory methods. This approach will ensure that all sizes of lionfish are removed that prey upon both ecologically and commercially important vertebrate and invertebrate species and will also deter the likelihood of a successful invasion.

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