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Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago

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Abstract Feeding ecology of the lionfish (*Pterois volitans*), an invasive species in the Western North Atlantic, was examined by collecting stomach content data from fishes taken throughout the Bahamian archipelago. Three relative metrics of prey quantity, including percent number, percent frequency, and percent volume, were used to compare three indices of dietary importance. Lionfish largely prey upon teleosts (78% volume) and crustaceans (14% volume). Twenty-one families and 41 species of teleosts were represented in the diet of lionfish; the top 10 families of dietary importance were Gobiidae, Labridae, Grammatidae, Apogonidae, Pomacentridae, Serranidae, Blenniidae, Atherinidae, Mullidae, and Monacanthidae. The proportional importance of crustaceans in the diet was inversely related to size with the largest lionfish preying almost exclusively on teleosts. Lionfish were found to be diurnal feeders with the highest predation occurring in the morning (08:00–11:00).

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Introduction

The lionfishes, *Pterois miles* and *P. volitans*, (Hamner et al. 2007; Morris 2009) are the first non-native marine fishes to become established along the Atlantic coast of the U.S. and the Caribbean. Adult lionfish specimens are now found along the U.S. East Coast from Cape Hatteras, North Carolina, to Florida, and in Bermuda, the Bahamas, and throughout the Caribbean, including the Turks and Caicos, Haiti, Cuba, Dominican Republic, Puerto Rico, St. Croix, Belize, and Mexico (Schofield et al. 2009). The first documented capture of lionfish in the Atlantic was in 1985 off Dania Beach, Florida (J. Bohnsack, NOAA NMFS, pers. comm.). Additional sightings occurred in 1992 following an accidental release of six lionfishes from a home aquarium into Biscayne Bay, Florida (Courtenay 1995). Many other reports of lionfish were documented in southeast Florida between 1999 and 2003 by Semmens et al. (2004), who attributed many of these sightings to releases by home aquarists.

Recreational divers reported the first sightings of lionfish in the Bahamas in 2004 (REEF 2009). Snyder and Burgess (2007) published the first record of lionfish in the Bahamas, suggesting that lionfish were widely distributed throughout Little Bahama and

Grand Bahama Banks. It is uncertain if lionfish invaded the Bahamas via larval transport by ocean currents or if their introduction was the result of additional aquarium releases. Recent genetic studies by Freshwater et al. (2009) suggest that lionfish invaded the Bahamian archipelago via larval dispersal originating from U.S. waters.

Early efforts to assess the density of lionfish off North Carolina by diver surveys and remotely operated vehicles suggested that lionfish populations were rapidly increasing, with trophic interactions with native reef fishes a concern (Whitfield et al. 2002; Hare and Whitfield 2003). Recently, densities on Bahamian reefs have been documented by Green and Côté (2009) to be in excess of 390 lionfish hectare^{-1}; almost five times higher than estimates from the native range. Albins and Hixon (2008) reported the first evidence of the impacts of lionfish on native fish communities by demonstrating that lionfish reduced recruitment of coral reef fishes on experimental reefs in the Bahamas by nearly 80%.

To date, comprehensive assessments of lionfish diets are lacking in their native and invaded ranges. Preliminary observations of lionfish feeding in their native range suggest that lionfish feed primarily on small fishes and some invertebrates (Fishelson 1975, 1997; Harmelin-Vivien and Bouchon 1976). In the Pacific Ocean, the closely related luna lionfish (*P. lunulata*) was found to feed primarily on invertebrates, including penaeid and mysid shrimps (Matsumiya et al. 1980; Williams and Williams 1986). More recently, Albins and Hixon (2008) reported a list of nine species consumed by invasive lionfish in the Bahamas. While these observations suggest general patterns in lionfish diet, quantitative assessments of lionfish feeding habits in their new range are needed to elucidate the impacts of these predators on invaded reef communities. The overall objectives of this study were to 1) assess dietary habits of lionfish collected from various habitats in the Bahamian archipelago, 2) determine the relationship between prey and predator size, and 3) document temporal feeding patterns of this invader.

Methods

Collections

Lionfish were collected from the Bahamian archipelago (Fig. 1) between January 2007 and May 2008. All specimens were collected by fisheries professionals and trained volunteers while snorkeling or using SCUBA gear at sites (n=134) comprised of high profile coral reefs, patch reefs, artificial reefs, mangroves, and man-made canals ranging in depth from 1 to 30 m. Sampling sites were chosen opportunistically to optimize sampling success. Most collections utilized hand nets and vinyl collection bags, although some were collected by pole spear. Live captures from nets and bags were euthanized by excess anesthesia in a bath of eugenol (Borski and Hodson 2003). Only two lionfish regurgitated stomach contents during ascension; therefore, stomach content retention measures were unnecessary. Lionfish were placed on ice and dissected the same day as capture.

Lionfish were collected every month of the calendar year ($\overline{X} = 111 \pm 28$ individuals per month), with the smallest sample size collected during June (n=10) and the largest collected during February (n=368). Collections of lionfish were achieved from 07:00 to 21:00; the majority of collections (99.1%) occurred between 08:00 and 17:00.

Cumulative prey curve

A cumulative prey curve was used to assess sample size sufficiency of lionfish stomachs containing identifiable prey. Prey taxa were grouped by family and cumulative numbers of novel prey were determined following 1,000 randomizations (Bizzarro et al. 2007). Mean and standard deviation of the cumulative number of novel prey was calculated and sufficiency of sample size was assessed statistically using the linear regression method of Bizzarro et al. (2007) that compares the slope from a regression of the last four stomach samples to a slope of zero using a Student's t-test of equality of two population regression coefficients (Zar 1999). A p-value >0.05 was considered to demonstrate sampling sufficiency. To determine the minimum number of stomach samples (with identifiable prey) required to adequately describe lionfish diet, one sample was removed sequentially until the Student's t-test p-value fell below 0.05 indicating that asymptote was not achieved.

Stomach content analyses

Stomach contents were identified to lowest possible taxon (without fixation), counted, and measured for

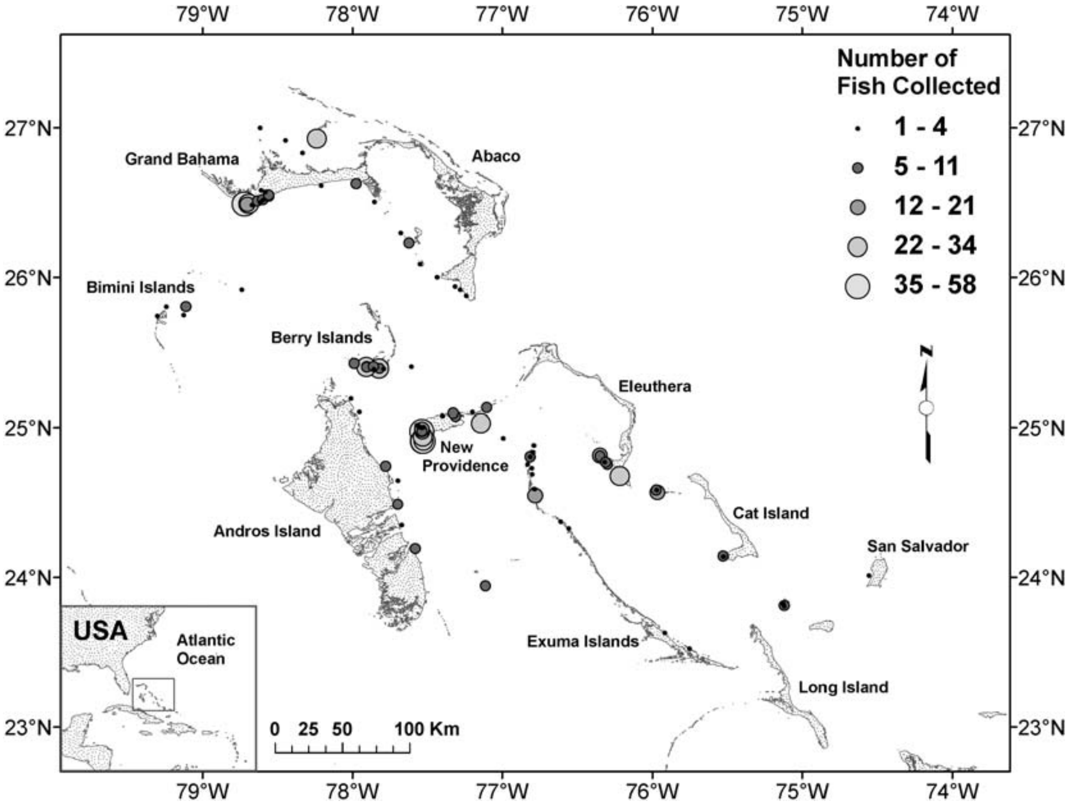

Fig. 1 Sampling locations and number of lionfish collected along the Bahamian archipelago

total length (TL). No adjustment of prey TL due to partial digestion was performed, thus the estimated prey sizes are potentially underestimated. Volumes of diet items taken from contents were measured by water displacement in a graduated cylinder. The contribution of each prey taxon to the overall diet was assessed using the following three relative metrics of prey quantity: percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by volume (%V) (Hyslop 1980; Bowen 1996). Variations in prey size and diet composition across lionfish sizes were examined statistically by conducting a significance test on the slope of a linear regression. An α-level $\leq$0.05 was considered significant.

Dietary importance indices or hybrid diet indices have been widely-employed in the study of fish food habits (Bowen 1996), yet their specific use has been criticized (Windell and Bowen 1978) and subject to controversy (Hyslop 1980; Cortés 1997; Hansson 1998). For a robust assessment of prey importance, three indices of importance were calculated:

(1) the Index of Relative Importance (IRI) (Pinkas et al. 1971),

$$IRI_a = F_a \cdot (N_a + V_a)$$

(2) the Index of Importance (IOI_a) (Gray et al. 1997; Hunt et al. 1999),

$$IOI_a = \frac{100 \cdot (F_a + V_a)}{\sum_{a=1}^{s}(F_a + V_a)}$$

(3) the Index of Preponderance (IOP) (Natrajan and Jhingran 1962; Sreeraj et al. 2006),

$$IOP_a = \frac{F_a \cdot V_a}{\sum_{a=1}^{s}(F_a + V_a)}$$

where s is the number of prey types, F_a is the frequency of occurrence of species a, V_a is the percent composition by volume of species *a*, and N_a is the percent composition by number of species *a*.

Results

The size of lionfish ranged from 62 to 424 mm TL with a mean size (±SE) of 217±7 mm. A total of 1,876 prey items from 1,069 stomachs were assigned to taxa. Volumetric measurements of prey by taxon were determined for 699 stomachs. Lionfish were sampled from diverse habitat types including high profile coral reefs (68%), canals (11%), artificial reefs (9%), other (predominately blue holes) (5%), patch reefs (4%), and mangrove habitats (3%). Cumulative prey curve analysis indicated sample size sufficiency reached asymptote for stomachs with identifiable prey ($p>0.58$). A large number of stomachs were required to attain sufficient sample size as $p<.05$ occurred at sample 706.

Prey composition

Twenty-one families of teleosts, four families of crustaceans, and one family of mollusks were represented in the diets of lionfish (Table 1). Teleost fishes dominated lionfish diet comprising 78% by volume (%V), 71.2% by number (%N), and 61.6% by occurrence (%F). Crustaceans were also represented at 14.4%V, 28.5%N, and 24.7%F, while mollusks comprised <.01%V, %N, and %F. Approximately 21% ($n=225$) of the stomachs were empty.

Teleost prey included 41 species and exhibited a wide-range of body shapes and morphological characteristics (Table 1). The families with the greatest number of species included Labridae (8), Pomacentridae (6), Gobiidae (5), and Serranidae (4). Eight families comprised 38% of lionfish diet by volume and 48% of the volume of identifiable teleosts. These included Pomacentridae (7.2%), Labridae (6.7%), Mullidae (5.5%), Grammatidae (5.0%), Serranidae (4.3%), Gobiidae (4.2%), Apogonidae (3.6%), and Blenniidae (1.1%). Unidentified prey accounted for 42.1%N, 38.1%V, and 36.5%F of all food items. The following teleost families had the greatest representation in percent number: Gobiidae (8.4%), Labridae (4.4%), Grammatidae (4.3%), Apogonidae (3.1%), Pomacentridae (1.8%), Serranidae (1.5%), Blenniidae (1%), and Atherinidae (1%). In terms of %F, the same familial order applied with only minor changes in the percentages.

The majority of crustacea prey were identified as shrimps: 25.5%N, 22.1%F, and 12.7%V of the total prey. Of the remaining crustacean prey, 3%V, %F, and %N were represented by four families (Corallanidae, Squillidae, Rhynchocinetridae, Stenopodidae) along with items from the categories of unidentified crab, and unidentified crustaceans (Table 1).

Rankings of importance indices

The same ten families of teleosts ranked as the top ten for all three indices (IRI, IOI, IOP) (Table 2). Top three rankings (gobiids, labrids, and grammatids) occurred in the IRI and IOP lists; whereas, the IOI ranked labrids, pomacentrids, and gobiids as most important of the teleost prey.

Diet composition and size of lionfish

The importance of teleosts in the diet of lionfish increased significantly with size in all three dietary metrics (%F $R^2=0.86$, $p=0.0003$; %N $R^2=0.55$, $p=0.02$; %V $R^2=0.76$, $P=0.005$) (Fig. 2). The mean sizes of teleosts and crustaceans in the diet increased with the size of lionfish (teleost prey $R^2=0.46$, $p=.01$; crustacean prey $R^2=0.36$, $P=0.002$) (Fig. 3). The maximum number of crustacean prey per lionfish was 50, whereas the maximum number of teleost prey was 21. The mean ratio of prey size (TL) to lionfish size (TL) was 14.5%±0.003 standard error of the mean. The maximum prey size was 48% of the total length of lionfish, whereas the minimum prey size was 0.02%.

Feeding activity

Stomachs of lionfish contained the highest volume of prey during the morning hours of 07:00–11:00 with a significant decrease in mean prey volume towards the evening ($R^2=-0.39$, $P=.01$) (Fig. 4). Few lionfish were collected at dusk or immediately after dark; therefore the prevalence of feeding at this time is uncertain.

Discussion

In the Bahamian archipelago, invasive lionfish feed predominantly on teleosts and crustaceans. The large

Table 1 Identifiable lionfish prey sorted by taxa

	Frequency (stomachs)	%F (*n*=1,069)	%N (*n*=926)	%V (*n*=699)
Mollusca	3			
Unidentfied spp.	2	0.2	0.2	
Octopodidae				
Octopoda	1	0.1	0.1	
Crustacea	264			
Unidentified crustacean	2	0.2	0.2	
Unidentified shrimp	236	22.1	25.5	13.8
Unidentified crab	8	0.7	0.9	0.5
Corallanidae	3	0.3	0.3	
Stenopodidae				
Stenopus hispidus	4	0.4	0.4	
Rhynchocinetidae				
Rhynchocinetes rigens	5	0.5	0.5	1.0
Squillidae	6	0.6	0.6	0.2
Teleosts	659			
Unidentified fish	390	36.5	42.1	41.3
Atherinidae	9	0.8	1.0	0.6
Lutjanidae				
Ocyurus chrysurus	1	0.1	0.1	
Labridae	4	0.4	0.4	0.3
Thalassoma bifasciatum	13	1.2	1.4	0.6
Halichoeres pictus	2	0.2	0.2	0.7
Halichoeres bivittatus	3	0.3	0.3	1.1
Clepticus parrae	4	0.4	0.4	2.6
Halichoeres garnoti	13	1.2	1.4	1.9
Halichoeres maculipinna	1	0.1	0.1	0.1
Bodianus rufus	1	0.1	0.1	
Xyrichtys sp.	1	0.1	0.1	
Opistognathidae	3	0.3	0.3	0.3
Gobiidae	20	1.9	2.2	1.1
Coryphopterus personatus/hyalinus	39	3.6	4.2	1.6
Coryphopterus eidolon	14	1.3	1.5	1.5
Coryphopterus dicrus	3	0.3	0.3	0.4
Coryphopterus glaucofraenum	1	0.1	0.1	
Priolepis hipoliti	1	0.1	0.1	
Scaridae	2	0.2	0.2	
Scarus iserti	3	0.3	0.3	
Scarus viride	1	0.1	0.1	0.1
Blenniidae	1	0.1	0.1	
Lucayablennius zingaro	4	0.4	0.4	0.1
Malacoctenus triangulatus	4	0.4	0.4	0.8
Malacoctenus boehlkei	1	0.1	0.1	0.3
Tripterygidae				
Enneanectes sp.	1	0.1	0.1	0.1

Table 1 (continued)

	Frequency (stomachs)	%F (*n*=1,069)	%N (*n*=926)	%V (*n*=699)
Serranidae	5	0.5	0.5	1.0
Epinephelus striatus	2	0.2	0.2	0.6
Serranus tigrinus	4	0.4	0.4	0.9
Hypoplectrus sp.	1	0.1	0.1	1.4
Liopropoma rubre	3	0.3	0.3	0.8
Grammatidae	1	0.1	0.1	0.1
Gramma loreto	36	3.4	3.9	5.2
Gramma melacara	3	0.3	0.3	0.1
Synodontidae	3	0.3	0.3	0.4
Pomacentridae	4	0.4	0.4	
Chromis insolata	1	0.1	0.1	
Chromis cyanea	7	0.7	0.8	0.6
Chromis multilineata	2	0.2	0.2	5.1
Stegastes partitus	1	0.1	0.1	0.2
Stegastes leucostictus	1	0.1	0.1	
Stegastes variabilis	1	0.1	0.1	1.9
Apogonidae	21	2.0	2.3	3.1
Apogon townsendi	4	0.4	0.4	0.1
Apogon binotatus	4	0.4	0.4	0.6
Tetradontidae				
Canthigaster rostrata	1	0.1	0.1	
Syngnathidae	2	0.2	0.2	0.1
Acanthuridae				
Acanthurus bahianus	2	0.2	0.2	
Monacanthidae	2	0.2	0.2	0.1
Monacanthus tuckeri	3	0.3	0.3	0.4
Holocentridae				
Sargocentron vexillarium	1	0.1	0.1	
Cirrhitidae				
Amblycirrhitus pinos	1	0.1	0.1	0.2
Aulostomidae				
Aulostomus maculates	1	0.1	0.1	0.3
Mullidea				
Pseudupeneus maculatus	2	0.2	0.2	5.9

number of teleostean families in lionfish diet indicates that lionfish feed upon a wide variety of available prey, but feed primarily on abundant teleosts and crevice dwelling species. The proportion of teleosts in the diet was size-dependent, with larger lionfish feeding more heavily on teleosts. Smaller size classes of lionfish had a higher proportion of crustaceans in their diet, primarily shrimps.

The amount of prey in lionfish stomachs over the course of the day suggest that lionfish feeding is highest in the morning (07:00–11:00), or the hours prior, with a decrease in feeding activity throughout the day. Diurnal visual observations of lionfish feeding further support this conclusion (L. Akins, S. Green, unpubl. data). Fishelson (1975) reported that lionfish (*Pterois volitans*) in the Red Sea are primarily

Table 2 Rankings of importance indices for each fish family for each importance index

Rank	IRI	IOP	IOI
1	Gobiidae	Gobiidae	Labridae
2	Labridae	Labridae	Pomacentridae
3	Grammatidae	Grammatidae	Gobiidae
4	Apogonidae	Apogonidae	Grammatidae
5	Pomacentridae	Pomacentridae	Mullidea
6	Serranidae	Serranidae	Serranidae
7	Blenniidae	Blenniidae	Apogonidae
8	Atherinidae	Atherinidae	Blenniidae
9	Mullidea	Mullidea	Atherinidae
10	Monacanthidae	Monacanthidae	Monacanthidae

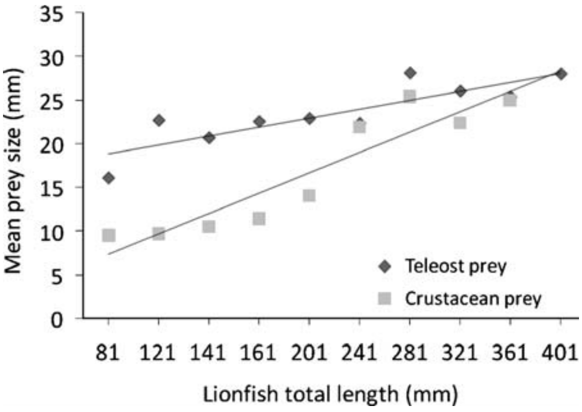

Fig. 3 Mean teleost and crustacean prey size consumed by lionfish. Lionfish size displayed in 40 mm total length size classes

nocturnal and become active during crepuscular periods of dawn and dusk. Given the lack of samples in this study from the hours of 21:00 to 07:00, feeding activity during the late night hours (or nocturnal period) is unknown.

Lionfish are suction feeders, a common teleostean feeding technique comprised of rapid expansion of the buccal and opercular cavities coupled with quick forward motion (Van Leeuwen and Muller 1984). Lionfish also use a variety of feeding strategies, including ambush predation and corralling prey with their large, frilly pectoral fins. Lionfish also use their pectoral fins to flush benthic invertebrates from the substrate by palpation (Fishelson 1975). Specialized bilateral swim bladder muscles in lionfish provide novel control of their pitch in the water column,

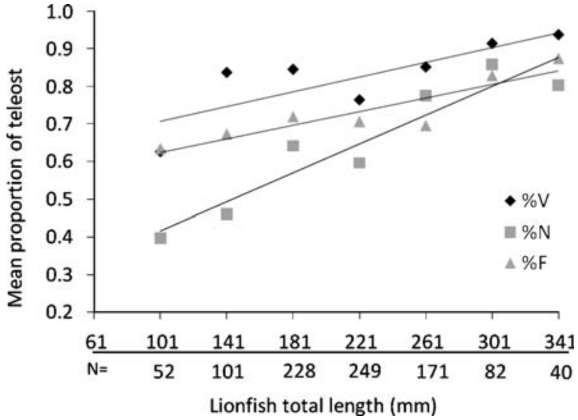

Fig. 2 Mean proportion of lionfish diet comprised of teleosts by lionfish 40 mm total length size classes

which allows lionfish to alter their center of gravity and provides fine-tuning of position prior to striking prey (Hornstra et al. 2004). Lionfish also use this mechanism to orient and hover; they are frequently observed in an up-side-down position under ledges and on the lateral face of structure. Hovering behavior, hunting, ambush predation, and the flushing of prey from the benthos enable lionfish to employ a diverse array of feeding strategies well-suited for feeding on benthically-associated and cryptic fauna.

The relative importance of teleost families in the stomachs of lionfish was similar among the three indices of importance, suggesting a high degree of confidence in the rankings of the top ten teleost prey (Table 2). Similar rankings of the top two families (gobiids and labrids) among all three indices is evidence that these fishes are of highest importance in the diet of lionfish.

All three indices used here engage at least two of the dietary metrics %F, %N, and %V, but place different weight on the importance of each metric. The IRI, for example, places equal weight on %N and %V, and higher weight on %F. The IOI does not include %N and increases bias towards high volume, but infrequently found prey items. The IOP also does not incorporate %N, but employs a weighted mean approach. The IRI and IOP indices resulted in identical rankings. The IOI reported a different ranking order when compared to the IRI and IOP. The teleost family exhibiting the highest difference in ranking was Mullidae (ninth in the IRI and IOP and fifth in the IOI), probably because of its low %N and %F, but relatively high %V. The IRI and IOP are the

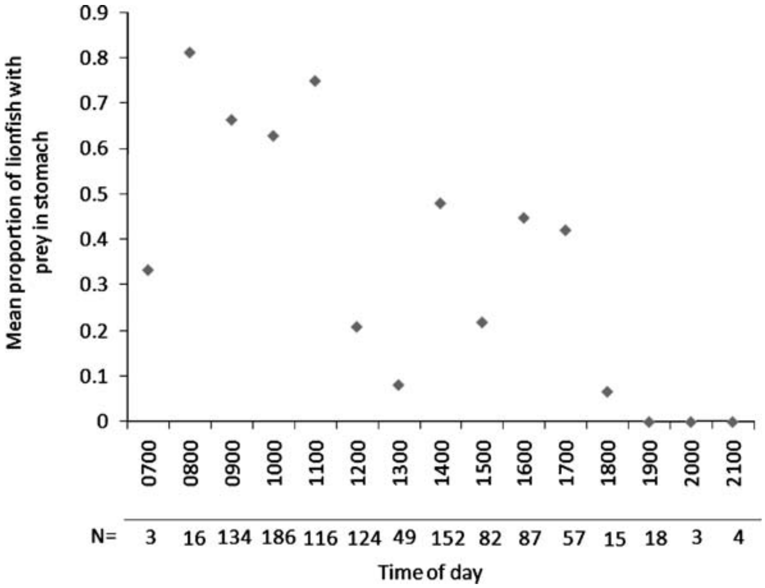

Fig. 4 Proportion of lionfish stomachs containing prey throughout the day

more appropriate indices for investigating importance of prey items in lionfish diet because these indices require prey ranked high in importance to be both high in %F and %V.

This study suggests that lionfish feed primarily upon small-bodied teleost fishes, which are an important component of the diet of many economically important fishes of the tropical and western north Atlantic such as serranids (Lindquist et al. 1994; Eggleston et al. 1998) and lutjanids (Rooker 1995; Duarte and García 1999; Ouzts and Szedlmayer 2003). The diet of lionfish is diverse and includes 21 families and 41 species of teleosts. Direct predation by lionfish on economically-important species, including yellowtail snapper (*Ocyurus chrysurus*) and Nassau grouper (*Epinephelus striatus*), was observed, but these specific species were in relative low frequency.

The scale of ecological or economic impact of lionfish predation is uncertain and multiple scenarios are plausible: 1) prey are abundant because many top-level predators are removed by fishing, thus lionfish could have no direct impact; 2) lionfish will reduce prey communities causing a diminution of prey for native predators; 3) reduced levels of prey will slow, but not inhibit, stock rebuilding efforts for native fishes; and 4) lionfish predation on economically important species will cause direct impacts and possibly cascading effects. Although the likelihood of any of these scenarios occurring is unknown, lionfish appear to be steadily increasing in both abundance and distribution. Recent evidence suggests that lionfish are capable of removing significant proportions (78%) of the prey community on isolated patch reefs (Albins and Hixon 2008). Future studies that quantify the biomass of the prey community and the seasonality of their abundance are needed to clarify direct and indirect impacts of lionfish on native species.

Our sampling did not include quantitative assessments of the prey communities; therefore prey preference cannot be derived from this study. Further, it is possible that lionfish diet may shift over time if predation by lionfish reduces or alters the abundance of the prey fish communities. Seasonal bias could also be present in our sampling as our sample size did vary among months and tropical reef fish recruitment is known to vary seasonally (Luckhurst and Luckhurst 1977; McFarland et al. 1985). Future assessments of the seasonality of lionfish diet, coupled with assessments of native reef fish recruitment across locales in the Southeast U.S., Caribbean, and Gulf of Mexico are needed to further elucidate the trophic impacts of lionfish. Additional research directed towards understanding the metabolic demands of lionfish coupled with dietary analysis and prey density surveys could quantify consumptive removal of native species by lionfish. These efforts would then allow scaling trophic impacts of lionfish at the individual and population level.

Conclusion

This study provides the first comprehensive assessment of feeding habits of the invasive lionfish (*Pterois volitans*) in the tropical Western North Atlantic. Future research is needed to quantify the impacts of lionfish on forage fish communities in various habitats. Given the ecological and economical importance of higher trophic level predators such as serranids, increased efforts to remove lionfish through fishery development and/or control strategies are needed to mitigate the present and future impacts of lionfish.

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