Biol Invasions
https://doi.org/10.1007/s10530-018-1720-5

ORIGINAL PAPER

Feeding ecology of invasive lionfish (*Pterois volitans* and *Pterois miles*) in the temperate and tropical western Atlantic

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Received: 11 September 2017 / Accepted: 28 March 2018
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Abstract Numerous location-based diet studies have been published describing different aspects of invasive lionfish (*Pterois volitans and Pterois miles*) feeding ecology, but there has been no synthesis of their diet composition and feeding patterns across regional gradients. 8125 lionfish stomachs collected from 10 locations were analyzed to provide a generalized description of their feeding ecology at a regional scale and to compare their diet among locations. Our regional data indicate lionfish in the western Atlantic are opportunistic generalist carnivores that consume at least 167 vertebrate and invertebrate prey species across multiple trophic guilds, and carnivorous fish and shrimp prey that are not managed fishery species and not considered at risk of extinction by the International Union for Conservation of Nature disproportionately dominate their diet. Correlations between lionfish size and their diet composition indicate lionfish in the western Atlantic

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Published online: 11 April 2018

transition from a shrimp-dominated diet to a fish-dominated diet through ontogeny. Lionfish total length (TL) (mm) was found to predict mean prey mass per stomach (g) by the following equation *mean prey mass* $=0.0002*TL^{1.6391}$, which can be used to estimate prey biomass consumption from lionfish length-frequency data. Our locational comparisons indicate lionfish diet varies considerably among locations, even at the group (e.g., crab) and trophic guild levels. The Modified Index of Relative Importance developed specifically for this study, calculated as the frequency of prey *a* $\times$ the number of prey *a,* can be used in other diet studies to assess prey importance when prey mass data are not available. Researchers and managers can use the diet data presented in this study to make inference about lionfish feeding ecology in areas where their diet has yet to be described. These data can be used to guide research and monitoring efforts, and can be used in modeling exercises to simulate the potential effects of lionfish on marine food webs. Given the large variability in lionfish diet composition among locations, this study highlights the importance of continued location-based diet assessments to better inform local management activities.

Keywords Cumulative prey curves · Feeding ecology · Food webs · Indices of prey importance · Invasive species · *Pterois volitans* · *Pterois miles* · Regional diet trends

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Introduction

Indo-Pacific lionfish (*Pterois volitans* and *Pterois miles*, Linnaeus, 1758) have become an abundant and ubiquitous mesopredator throughout the temperate and tropical western Atlantic (hereafter western Atlantic) (Morris Jr. 2012). Their range expansion and proliferation is attributed to a variety of biological characteristics including their environmental tolerances, reproductive output, defense from predation, diet composition, and feeding behavior (Côté et al. 2013). Several small-scale studies suggest invasive lionfish have the potential to negatively affect local reef communities through predation on native species (e.g., Albins and Hixon 2008; Green et al. 2012; Albins 2015), and may possibly affect native fish populations at regional scales (Ballew et al. 2016). Understanding lionfish feeding ecology is therefore important for understanding their ecological role and potential effects on marine food webs in the invaded range (Meister et al. 2005; Ruiz-Carus et al. 2006).

Morris and Akins (2009) first described lionfish diet in The Bahamas in 2009. Since then, over 15 additional location-based studies have been published describing different aspects of their feeding ecology (e.g., Dahl and Patterson 2014; Eddy et al. 2016) and foraging behavior (e.g., Green et al. 2011; Green and Côté 2014). Lionfish diet composition and feeding patterns are, however, likely to differ among locations due to differences in local environmental factors including habitats and prey assemblages (Muñoz et al. 2011). Using the stomach contents of over 8000 lionfish collected from 10 locations throughout the western Atlantic, the goals of this study were to provide a generalized description of lionfish feeding ecology at a regional scale and to compare lionfish diet composition among locations. Our specific objectives were to produce a centralized list of the prey consumed and the relative contributions and importance of each to lionfish diet, assess the diversity of their diet composition, describe general diet trends, identify potential ontogenetic diet shifts, and describe key dietary differences among locations. The diet compositions and patterns described in this study can be used to make inference about lionfish feeding ecology in areas where their diet has yet to be described, inform research and monitoring efforts, and to model and predict the effects of lionfish on invaded reefs (e.g., Chagaris et al. 2017).

Methods

Data description

Lionfish diet data were collated from eight published and seven unpublished datasets (Appendix 1). In total, data were obtained on 8125 lionfish collected from Bermuda, North Carolina, The Bahamas, southeastern Florida (Florida), the northeastern Gulf of Mexico (neGoM), the northwestern Gulf of Mexico (nwGoM), the Yucatan Peninsula (Mexico), Belize, Costa Rica, and the United States Virgin Islands (USVI) (Appendix 1). Samples collected within each location were pooled across environmental gradients (e.g., depths and habitats) to represent the general area. Data collected for each sample included lionfish length (mm) and mass (g) and the mass/volume and length (mm) of each prey. Lionfish standard length was converted to total length (TL) as needed using the conversion equation in Fogg et al. (2013). Prey volume was converted to mass (g) as needed using the 1:1 conversion ratio in Swedberg and Walburg (1970).

The number of samples per location ranged from 299 to 1481 with an average of 812 ± 405 (mean ± SD). The lionfish used in this study ranged in total length from 15 to 461 mm with an average of 252.7 ± 73.4. The Shapiro–Wilk test indicated lionfish size (n = 8125) was not normally distributed (W = 0.99797, $p < 0.000$), but examination of a size frequency histogram and a normal quantile–quantile plot indicated relative normality (Fig. 1). At the locational level, one-way ANOVA and Tukey HSD indicated lionfish size (mean ± SD) was significantly different among locations (ANOVA, $F_{9,5409} = 283.38$, $p < 0.000$) (Fig. 1). Of the 8125 stomachs collected, 2251 (27.7%) were empty resulting in a total of 17,365 prey items for analysis. Of the stomachs containing identifiable prey, 2658 (45.3%) contained 8607 prey items (49.6% of all available prey items) for which mass data were available.

Prey categorization

Prior to analysis, prey were categorized into family and species, nine prey groups, four trophic guilds, seven conservation statuses, three fishery importance levels, and four fishery statuses (see Appendix 2). Conservation statuses were derived from the IUCN Red List of Threatened Species in December 2016 (http://www.iucnredlist.org/). Trophic guild categories were based on the best available information in the literature detailed in Appendix 2. Only species managed by the National Marine Fisheries Service (NMFS) and the South Atlantic, Gulf, and Caribbean Fishery Management Councils (FMCs) were considered as fishery species in this study. Although the species managed by NMFS and the FMCs do not encompass all managed species within the invaded range, this approach provided a standardized way to categorize prey using the fishery importance [e.g., species incorporated into NMFS Fishery Stock Sustainability Index (FSSI)] and fishery status (e.g., stocks/complexes considered "overfished") designations used by NMFS. The importance levels and statuses were derived from the December 2016 NMFS Stock Status Update (NMFS 2016). Additional detail on prey categorization is available in Appendix 2.

Prey metrics and indices of importance

The relative contribution of each prey category to lionfish diet was calculated using three relative metrics of prey quantity including percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by mass (%W) (Hyslop 1980; Bowen 1996). The relative importance of each prey category was calculated using three commonly used indices of importance and one novel index of importance (i.e., Modified Index of Relative Importance):

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

$$IRI_a = F_a * (N_a + M_a)$$

2. Index of Importance (IOI) (Gray et al. 1997; Hunt et al. 1999)

$$IOI_a = \frac{100 * (F_{a+}M_a)}{\sum_{a=1}^{s}(F_a + M_a)}$$

3. Index of Preponderance (IOP) (Natarajan and Jhingran 1961)

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

4. Modified Index of Relative Importance (MIRI)

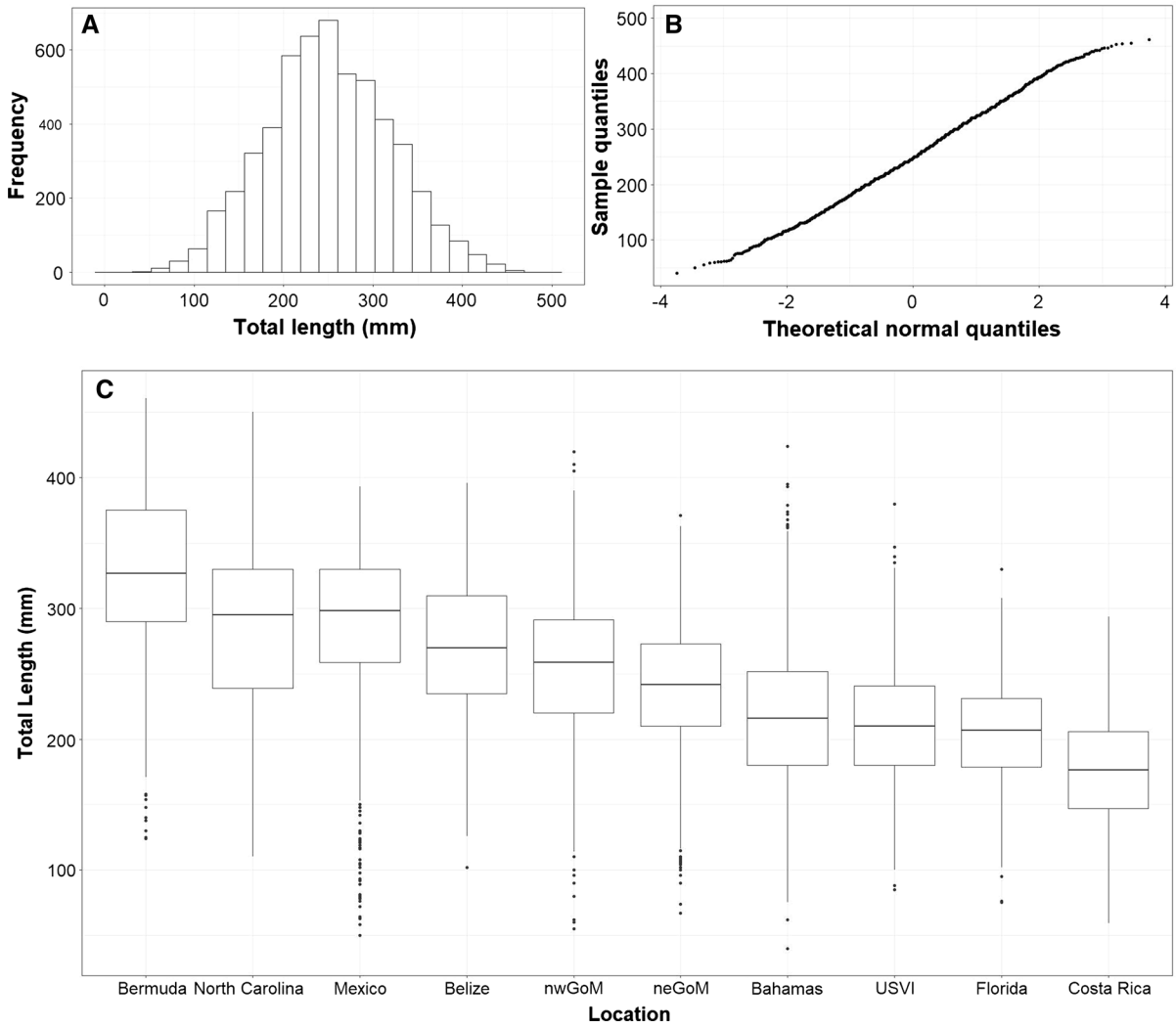


Fig. 1 Size frequency histogram (**a**) and normal quantile–quantile plot (**b**) of the combined datasets containing 8125 samples. Boxplots of lionfish size in each location (**c**)

$$MIRI_a = F_a * N_a$$

where a is the group, family, species, trophic guild, conservation status, fishery importance level or fishery status of interest, F_a is the frequency of occurrence of a, M_a is contribution of a to the total prey mass, N_a is the contribution of a to the total number of prey items, and s is the total number of each prey category for which the index was calculated.

MIRI was developed specifically for this study so samples without prey mass data could be included. Different forms of MIRI and the standard IRI (Pinkas et al. 1971) were calculated at the group, family, and species levels, and the resulting ranks were correlated. The MIRI used was chosen because its prey importance rankings were highly correlated with the importance rankings of the standard IRI when both indices were calculated on each taxonomic level ($r = 0.99, p < 0.001$). Prey categories were ultimately ranked based on the average rankings of all four indices of importance, which provided for a more robust assessment (Morris and Akins 2009).

Similar to other studies (e.g., Efron 1979; Jiang and Jorgensen 1996; Tirasin and Jorgensen 1999), the prey metrics and indices of importance were calculated using a sub-sampling and bootstrapping approach.

Table 1 The relative contributions and importance of prey to lionfish diet in the temperate and tropical western Atlantic

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Group							
Fish	70.5	58.8	89.6	1	1	1	1
Shrimp	29.5	29.5	6.0	2	2	2	2
Crab	5.4	3.0	2.5	3	3	3	3
Other invertebrate	1.9	1.0	0.4	4	4	4	4
Lobster	1.0	1.1	0.1	5	5	5	5
Squid	0.2	0.1	0.2	6	6	6	6
Snail	0.1	0.0	0.0	7	7	7	7
Octopus	0.1	0.0	0.0	8	8	8	8
Trophic guild							
Carnivore	23.8	16.2	36.8	1	1	1	1
Omnivore	9.7	7.2	9.7	2	2	2	2
Herbivore	6.7	4.0	5.8	3	3	3	4
Detritivore	6.8	5.4	0.1	4	4	4	3
Conservation status							
Least concern	12.2	7.6	17.6	1	1	1	1
Not assessed	8.4	6.9	0.8	2	3	3	2
Vulnerable	1.9	1.3	8.1	3	2	2	3
Data deficient	0.1	0.0	0.1	4	4	4	4
Near threatened	0.0	0.0	0.1	5	5	5	5
Endangered	0.0	0.0	–	–	–	–	6
Fishery importance							
Non-managed	17.9	13.7	12.1	1	1	1	1
FFSI	1.9	1.0	8.2	2	2	2	3
Non-FFSI	1.9	1.2	6.4	3	3	3	2
Fishery status							
Non-managed	17.9	13.7	12.1	1	1	1	1
Not subject to overfishing	3.2	2.0	14.6	2	2	2	2
Approaching/overfished	0.4	0.2	0.0	3	3	3	3
Subject to overfishing	0.1	0.0	0.1	4	4	4	4
Family							
Labridae	6.1	3.9	5.3	1	1	1	2
Pomacentridae	4.9	2.2	5.7	2	2	2	3
Serranidae	3.2	1.8	5.0	4	5	3	4
Lutjanidae	1.6	0.8	8.8	5	3	4	10
Haemulidae	1.7	2.0	7.1	6	4	5	8
Rhynchocinetidae	5.6	4.5	0.1	3	6	15	1
Scaridae	2.4	1.6	2.7	7	7	6	6
Gobiidae	2.5	1.8	1.0	8	9	9	5
Blenniidae	2.2	1.6	1.2	9	10	8	7
Carangidae	1.0	0.8	3.8	10	8	7	14
Apogonidae	1.3	0.7	1.5	11	11	10	11

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Penaeidae	1.6	1.1	0.6	12	12	12	9
Acanthuridae	1.0	0.7	1.2	13	13	11	15
Monacanthidae	1.2	0.7	0.8	14	14	13	12
Portunidae	1.1	0.7	0.5	15	16	16	13
Galatheidae	0.6	0.8	–	–	–	–	16
Synodontidae	0.7	0.3	1.0	16	15	14	19
Holocentridae	0.6	0.4	0.5	17	17	17	18
Hippolytidae	0.7	0.5	0.1	18	20	20	17
Grammatidae	0.5	0.3	0.4	19	19	18	21
Palaemonidae	0.6	0.3	–	–	–	–	20
Atherinidae	0.4	0.3	0.1	20	22	25	22
Calappidae	0.4	0.2	0.2	21	21	24	23
Scorpaenidae	0.3	0.2	0.4	23	23	21	27
Mullidae	0.2	0.1	0.8	22	18	19	38
Paralichthyidae	0.3	0.2	0.2	24	26	26	24
Bothidae	0.2	0.2	0.4	25	25	23	28
Triglidae	0.3	0.1	0.3	26	24	22	30
Percnidae	0.2	0.2	–	–	–	–	29
Gonodactylidae	0.3	0.1	0.2	27	28	27	35
Labrisomidae	0.2	0.1	0.2	29	30	29	33
Chaetodontidae	0.3	0.2	0.1	30	32	36	26
Mysidae	0.2	0.3	0.0	28	37	39	25
Sparidae	0.1	0.1	0.3	31	27	28	44
Sciaenidae	0.1	0.1	0.3	32	29	30	42
Xanthidae	0.2	0.1	0.1	33	35	34	32
Opistognathidae	0.2	0.1	0.2	34	31	31	39
Solenoceridae	0.2	0.1	0.1	35	34	33	37
Loliginidae	0.1	0.0	0.2	36	33	32	45
Scyllaridae	0.2	0.1	0.1	38	39	38	34
Alpheidae	0.2	0.2	0.0	37	42	48	31
Chriostylidae	0.2	0.1	0.0	39	40	43	36
Priacanthidae	0.1	0.0	0.2	40	36	35	51
Squillidae	0.1	0.1	0.1	41	41	40	41
Gerreidae	0.1	0.0	0.1	43	38	37	48
Sicyoniidae	0.1	0.1	0.1	42	43	42	40
Balistidae	0.1	0.1	0.0	44	44	44	43
Clupeidae	0.0	0.1	–	–	–	–	46
Stenopodidae	0.1	0.0	0.0	45	45	49	47
Mithracidae	0.0	0.0	0.1	46	46	41	58
Pempheridae	0.0	0.0	–	–	–	–	49
Aulostomidae	0.1	0.0	0.0	47	51	46	53
Majidae	0.1	0.0	0.0	49	47	51	50

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Syngnathidae	0.1	0.0	0.0	48	48	50	52
Grapsidae	0.0	0.0	0.1	50	50	45	60
Palinuridae	0.0	0.0	0.1	51	49	47	64
Chaenopsidae	0.1	0.0	0.0	52	55	54	55
Axiidae	0.1	0.0	0.0	54	52	56	56
Menippidae	0.1	0.0	0.0	56	53	55	57
Octopodidae	0.1	0.0	0.0	53	54	61	54
Cirrhitidae	0.0	0.0	0.0	55	57	52	59
Tetraodontidae	0.0	0.0	0.0	57	56	53	65
Inachidae	0.0	0.0	0.0	58	60	57	63
Pomacanthidae	0.0	0.0	0.0	59	58	60	62
Lysiosquillidae	0.0	0.0	–	–	–	–	61
Amphiuridae	0.0	0.0	0.0	61	59	62	66
Tripterygiidae	0.0	0.0	0.0	60	65	59	67
Parthenopidae	0.0	0.0	0.0	64	62	62	69
Panopeidae	0.0	0.0	0.0	62	61	58	78
Pleuronectidae	0.0	0.0	0.0	63	63	62	74
Inachoididae	0.0	0.0	0.0	66	64	62	72
Gammaridae	0.0	0.0	0.0	65	66	62	76
Porcellanidae	0.0	0.0	0.0	67	67	62	75
Clinidae	0.0	0.0	–	–	–	–	68
Diogenidae	0.0	0.0	0.0	68	68	62	77
Lysianassidae	0.0	0.0	–	–	–	–	70
Antennariidae	0.0	0.0	–	–	–	–	71
Marginellidae	0.0	0.0	–	–	–	–	73
Species							
Cinetorhynchus manningi	3.6	2.8	–	–	–	–	1
Rhomboplites aurorubens[a,b,c]	1.2	0.7	8.0	1	1	1	4
Thalassoma bifasciatum	2.0	1.4	1.4	2	3	3	3
Haemulon aurolineatum[a]	0.9	0.7	4.8	3	2	2	5
Cinetorhynchus rigens	2.0	1.7	0.1	4	4	7	2
Munida simplex	0.6	0.8	–	–	–	–	6
Selar crumenophthalmus	0.5	0.3	1.6	5	5	4	10
Halichoeres bivittatus	0.6	0.4	0.6	6	6	5	9
Centropristis ocyurus[a]	0.5	0.2	0.7	7	7	6	12
Halichoeres garnoti	0.6	0.4	0.2	8	11	13	8
Stegastes variabilis	0.3	0.2	0.8	10	8	8	20
Stegastes partitus	0.4	0.2	0.4	13	10	10	17
Gramma loreto	0.4	0.2	0.4	12	12	11	15
Portunus anceps	0.3	0.3	–	–	–	–	13
Chromis multilineata	0.3	0.1	0.7	11	9	9	24
Coryphopterus personatus[a,c]	0.5	0.5	0.1	9	19	20	7
Paranthius furcifer	0.3	0.3	–	–	–	–	14

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Parablennius marmoreus	0.5	0.2	0.2	14	16	15	11
Apogon pseudomaculatus	0.3	0.2	0.4	15	14	12	19
Atherinomorus stipes	0.4	0.3	–	–	–	–	16
Sparisoma aurofrenatum[a,b]	0.3	0.2	–	–	–	–	18
Clepticus parrae	0.3	0.1	0.3	16	18	17	21
Halichoeres bathyphilus	0.1	0.1	0.6	17	13	14	33
Entomacrodus nigricans	0.1	0.1	0.3	19	21	19	26
Coryphopterus glaucofraenum	0.2	0.2	–	–	–	–	22
Chromis scotti	0.1	0.0	0.6	18	15	16	39
Percnon gibbesi	0.2	0.2	–	–	–	–	23
Sargocentron coruscum	0.1	0.2	0.2	22	27	23	28
Pleoticus robustus[a,b]	0.2	0.1	0.1	23	26	27	29
Cryptosoma bairdii	0.2	0.1	–	–	–	–	27
Pseudupeneus maculatus[a]	0.1	0.0	0.6	20	17	18	58
Stegastes fuscus	0.1	0.0	0.4	21	22	21	50
Stegastes leucostictus	0.1	0.0	0.2	26	25	22	42
Sparisoma radians	0.1	0.1	0.2	25	29	29	32
Chromis cyanea	0.2	0.1	0.1	24	33	35	25
Sparisoma atomarium	0.2	0.1	–	–	–	–	31
Apogon maculatus	0.1	0.0	0.3	28	24	24	48
Xyrichtys novacula	0.1	0.0	0.2	29	28	25	46
Opistognathus macrognathus	0.1	0.1	0.2	31	30	30	38
Coryphopterus eidolon[c]	0.2	0.1	0.1	27	36	37	30
Scarus iserti	0.1	0.0	0.2	30	35	32	40
Monacanthus tuckeri	0.2	0.1	0.1	34	37	41	34
Schultzea beta	0.1	0.0	0.2	35	32	33	47
Xyrichtys martinicensis	0.1	0.0	0.2	33	31	31	57
Holocentrus rufus[a]	0.1	0.0	0.3	32	23	26	71
Serranus baldwini	0.1	0.0	0.1	37	39	40	43
Diplectrum bivittatum	0.1	0.0	0.2	38	38	36	51
Malacoctenus triangulatus	0.1	0.1	0.1	42	46	45	41
Chaetodon ocellatus	0.1	0.0	–	–	–	–	45
Litopenaeus setiferus	0.1	0.1	0.0	43	52	55	36
Stegastes adustus	0.0	0.0	0.5	36	20	28	103
Halichoeres maculipinna	0.1	0.1	0.0	44	49	65	35
Serranus tigrinus	0.1	0.0	0.1	40	41	39	74
Stegastes planifrons	0.1	0.0	–	–	–	–	49
Malacoctenus macropus	0.1	0.0	0.1	47	51	47	54
Neogonodactylus curacaoensis	0.0	0.0	0.2	41	40	38	82
Trachurus lathami	0.0	0.0	0.2	39	34	34	94
Acanthurus chirurgus[a]	0.1	0.0	0.1	51	50	48	52
Decapterus punctatus	0.1	0.0	0.1	45	44	44	68
Stenopus hispidus	0.1	0.0	0.0	50	48	63	44

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Serranus subligarius	0.1	0.0	0.1	49	47	46	64
Abudefduf saxatilis	0.1	0.0	0.1	46	43	42	76
Stephanolepis hispidus	0.1	0.1	0.0	48	45	81	37
Liopropoma carmabi	0.1	0.0	0.0	53	53	57	53
Pempheris schomburgkii	0.0	0.0	–	–	–	–	56
Liopropoma rubre	0.1	0.0	0.1	54	62	49	61
Bodianus rufus[a]	0.1	0.0	0.0	56	63	51	59
Achelous ordwayi	0.1	0.0	0.0	55	55	52	69
Achelous spinicarpus	0.1	0.0	0.0	57	58	58	65
Chromis enchrysurus	0.1	0.0	0.0	58	64	64	60
Acanthurus coeruleus[a]	0.1	0.0	0.0	62	57	74	55
Portunis sayi	0.1	0.0	0.0	61	59	67	62
Aulostomus maculatus	0.1	0.0	0.0	59	70	60	67
Apogon binotatus	0.0	0.0	0.0	66	67	61	79
Synodus synodus	0.0	0.0	0.1	63	65	53	93
Serranus phoebe	0.0	0.0	0.1	67	60	59	88
Acanthurus bahianus[a]	0.1	0.0	0.0	68	66	69	72
Nicholsina usta	0.0	0.0	0.1	64	61	56	98
Anisotremus surinamensis	0.0	0.0	0.1	65	54	54	106
Phaeoptyx pigmentaria	0.1	0.0	–	–	–	–	70
Farfantepenaeus duorarum	0.1	0.0	0.0	70	68	84	66
Scarus taeniopterus[a,b]	0.1	0.0	–	–	–	–	73
Diplectrum formosum	0.0	0.0	0.2	52	42	43	155
Apogon townsendi	0.1	0.0	0.0	73	81	78	63
Mycteroperca venenosa[a,b,c]	0.0	0.0	0.1	60	56	50	129
Hypleurochilus geminatus	0.0	0.0	0.0	72	72	71	81
Chaetodon capistratus	0.0	0.0	–	–	–	–	75
Coryphopterus dicrus	0.0	0.0	0.0	74	77	72	86
Haemulon flavolineatum[a]	0.0	0.0	–	–	–	–	78
Holocentrus adscensionis[a]	0.0	0.0	0.1	69	69	62	113
Squilla empusa	0.0	0.0	0.0	77	75	77	92
Menippe mercenaria	0.1	0.0	0.0	83	74	90	80
Halichoeres pictus	0.0	0.0	0.1	71	71	66	121
Amblycirrhitus pinos	0.0	0.0	0.0	82	87	79	83
Callinectes sapidus	0.0	0.0	0.0	81	85	82	85
Synodus intermedius	0.0	0.0	0.0	76	76	73	108
Malacoctenus boehlkei	0.0	0.0	0.0	78	82	75	100
Elacatinus oceanops	0.0	0.0	–	–	–	–	84
Lucayablennius zingaro	0.0	0.0	0.0	84	88	91	77
Panulirus argus[a]	0.0	0.0	0.0	75	73	68	125
Lysmata grabhami	0.0	0.0	–	–	–	–	87
Neogonodactylus oerstedii	0.0	0.0	0.0	88	79	85	102
Chromis insolata	0.0	0.0	–	–	–	–	89

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Haemulon plumieri[a]	0.0	0.0	0.0	80	80	76	122
Lysiosquilla scabricauda	0.0	0.0	–	–	–	–	90
Gramma melacara	0.0	0.0	0.0	89	90	86	101
Paralichthys albigutta	0.0	0.0	0.0	87	95	93	91
Canthigaster rostrata	0.0	0.0	0.0	86	84	83	115
Plagusia depressa	0.0	0.0	0.0	79	78	70	145
Haemulon chrysargyreum	0.0	0.0	0.0	85	83	80	130
Sepioteuthis sepioidea	0.0	0.0	–	–	–	–	95
Stenorhyncus seticornis	0.0	0.0	0.0	90	102	94	96
Gobiosoma grosvenori	0.0	0.0	0.0	93	86	97	107
Brachycarpus biunguiculatus	0.0	0.0	–	–	–	–	97
Monacanthus ciliatus	0.0	0.0	0.0	92	89	88	120
Alpheus armatus	0.0	0.0	–	–	–	–	99
Rimapenaeus similis	0.0	0.0	0.0	95	93	97	117
Ophiothrix purpurea	0.0	0.0	0.0	96	91	97	119
Sargocentron vexillarium	0.0	0.0	–	–	–	–	104
Canthidermis sufflamen[a,b]	0.0	0.0	0.0	91	92	87	146
Scorpaenodes caribbaeus	0.0	0.0	–	–	–	–	105
Holacanthus tricolor	0.0	0.0	0.0	98	96	96	131
Ophioblennius atlanticus	0.0	0.0	0.0	101	97	97	126
Pterois volitans	0.0	0.0	0.0	100	98	97	128
Gonodactylus smithii	0.0	0.0	0.0	97	100	92	136
Cryptotomus roseus	0.0	0.0	0.0	99	99	97	132
Elacatinus prochilos[c]	0.0	0.0	0.0	102	101	97	127
Bellator brachychir	0.0	0.0	0.0	94	94	89	152
Coryphopterus thrix[c]	0.0	0.0	–	–	–	–	109
Planes minutus	0.0	0.0	–	–	–	–	110
Aluterus schoepfii	0.0	0.0	0.0	104	103	97	138
Calappa flammea	0.0	0.0	–	–	–	–	111
Hypoplectrus puella	0.0	0.0	–	–	–	–	112
Anasimus latus	0.0	0.0	0.0	105	104	97	148
Mithraculus forceps	0.0	0.0	–	–	–	–	114
Porcellana sigsbeiana	0.0	0.0	0.0	107	105	97	154
Chromis flavicauda	0.0	0.0	–	–	–	–	116
Priolepis hipoliti	0.0	0.0	0.0	106	106	97	158
Anarchopterus criniger	0.0	0.0	0.0	108	108	97	156
Pareques acuminatus	0.0	0.0	–	–	–	–	118
Sparisoma viride[a,b]	0.0	0.0	0.0	103	107	95	167
Clibanarius tricolor	0.0	0.0	0.0	110	109	97	162
Halichoeres radiatus[a]	0.0	0.0	0.0	109	110	97	165
Epinephelus striatus[a]	0.0	0.0	–	–	–	–	123
Chaetodon aculeatus	0.0	0.0	–	–	–	–	124
Starksia occidentalis	0.0	0.0	–	–	–	–	133

Table 1 continued

Prey categories	Prey metrics			Indices of importance			
	%F	*%N*	*%W*	*IRI*	*IOI*	*IOP*	*MIRI*
Paraclinus fasciatus	0.0	0.0	–	–	–	–	134
Ophioblennius macclurei	0.0	0.0	–	–	–	–	135
Apogon affinis	0.0	0.0	–	–	–	–	137
Scarus vetula[a,b]	0.0	0.0	–	–	–	–	139
Eurythenes gryllus	0.0	0.0	–	–	–	–	140
Starksia ocellata	0.0	0.0	–	–	–	–	141
Emblemaria pandionis	0.0	0.0	–	–	–	–	142
Scyllarides nodifer	0.0	0.0	–	–	–	–	143
Epinephelus adscensionis[a,b]	0.0	0.0	–	–	–	–	144
Opistognathus aurifrons	0.0	0.0	–	–	–	–	147
Mulloidichthys martinicus[a]	0.0	0.0	–	–	–	–	149
Volvarina albolineata	0.0	0.0	–	–	–	–	150
Heteropriacanthus cruentatus	0.0	0.0	–	–	–	–	151
Calappa ocellata	0.0	0.0	–	–	–	–	153
Cantherhines pullus	0.0	0.0	–	–	–	–	157
Xyrichtys splendens	0.0	0.0	–	–	–	–	159
Stephanolepis setifer	0.0	0.0	–	–	–	–	160
Microspathodon chrysurus	0.0	0.0	–	–	–	–	161
Ocyurus chrysurus[a,b]	0.0	0.0	–	–	–	–	163
Lutjanus synagris[a,b,c]	0.0	0.0	–	–	–	–	164
Cephalopholis cruentatus	0.0	0.0	–	–	–	–	166

Prey metrics are given as the means across 1000 permutations rounded to the nearest tenth of a percent. All standard deviations of the prey metrics were $\leq$ 1.8% and are omitted to reduce table clutter. Prey sub-categories are listed in descending order of importance averaged across the four indices. Bars (–) indicate prey mass data were not available for the calculation

[a]Species managed by NMFS and the FMC

[b]Species included in NMFS' FSSI

[c]Species considered at least near threatened by the IUCN

Here, 150 stomachs were randomly sampled 1000 times with replacement from each locational dataset and pooled into a regional dataset. Since data were available for 10 locations, 1500 samples were used in each of the 1000 permutations. Prey metrics and indices of importance were calculated for each permutation and then averaged across the permutations to obtain means and standard deviations. This approach standardized the number of samples used from each location and, more importantly, provided a way to estimate the variation and, therefore, the relative accuracy of our prey metrics and indices of importance. The sample size of 150 stomachs was chosen because it was half the number of samples in the smallest locational dataset, which we deemed small enough to appropriately resample each dataset, while large enough to produce an adequate sample size (n = 1500) for each permutation of the regional dataset.

Assessing diet diversity

Cumulative prey curves were used to determine whether the families and species identified in this study represent all families and species consumed by lionfish in the western Atlantic. Linear regressions were fit to the mean number of cumulative prey from the last four stomachs on each prey curve and the slopes of the lines were compared to lines with slopes of zero using Student *t* tests (Bizzarro et al. 2007). Slopes that did not differ significantly from zero (i.e., $p \geq 0.05$) indicated that this study identified all of the

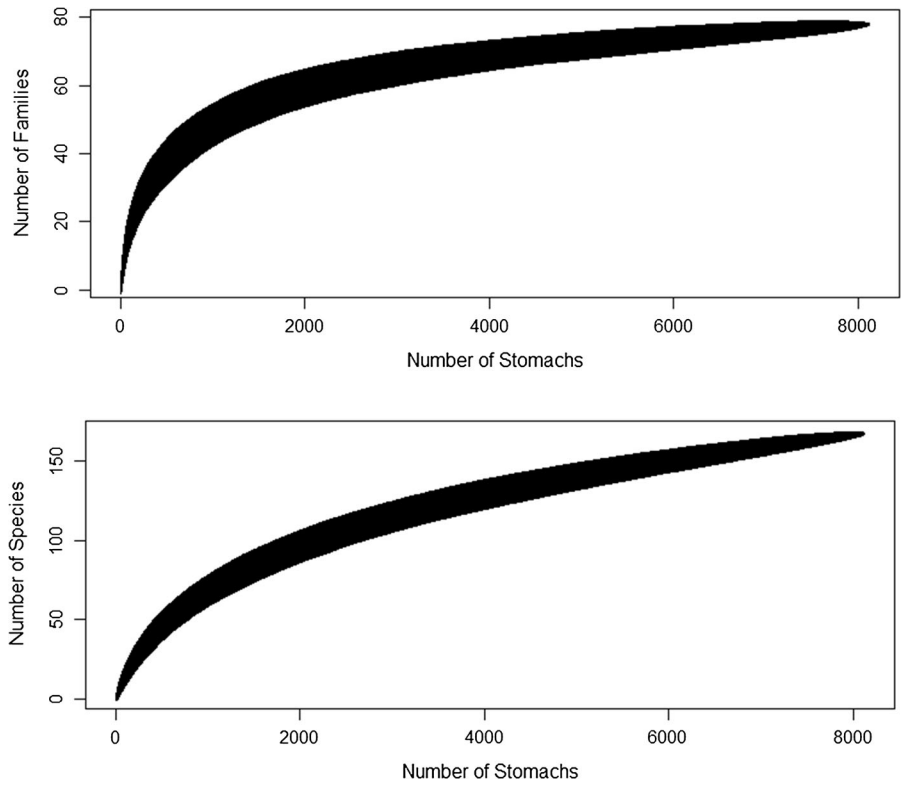


Fig. 2 Cumulative prey curves. The curves appear solid black due to the large number of samples

families or species consumed by lionfish in the western Atlantic. Cumulative prey curves were constructed using the vegan package in R version 3.4.0 (R Core Team 2017).

Trends in diet composition

Correlations between lionfish TL and 26 diet metrics were examined using Pearson's correlation coefficient (see Table 2). For each permutation produced from the bootstrapping (n = 1000), all samples (n = 1500) were binned into nine size classes. Due to low sample sizes, the first bin included all samples $\leq$ 120 mm and the last bin included all samples $\geq$ 400 mm. The remaining bins were 40 mm size classes. The means and standard deviations of each metric were calculated across the permutations in each size class. Due to the random sampling from the regional dataset, the number of samples per size class differed among permutations. To correct for this, pooled means and pooled standard deviations were used (Cohen 1988). Correlations were calculated on the pooled data (mean $\pm$ SD), which fit the assumptions of normality. The p values were adjusted using the Bonferroni post hoc correction and an a priori α-level ≤ 0.05 was considered significant. To provide a general region-wide metric for estimating prey biomass consumption from lionfish length-frequency data, the relationship between lionfish TL and mean prey mass per stomach was described using a power function.

Comparisons among locations

Lionfish diet was compared among locations at the group, trophic guild, family, and species levels. Only %N, %F and MIRI were used due to the low and varying numbers of prey with available mass data in each location. Because lionfish size differed among locations (Fig. 1) and because data were pooled to represent each general area, prey metrics and MIRI were calculated for each permutation of the bootstrapping and then averaged across the permutations to obtain means and standard deviations for each location. This approach helped balance and minimize size

Table 2 Correlations between lionfish total length (mm) and the contributions of their prey

Prey metrics	Pearson's correlation		
	Value range	|r|	*p value*
Carnivores			
%F	15.1–39.6	0.95	0.000
%N	7.5–26.6	0.88	0.000
%W	17.3–44.2	0.86	0.000
Herbivores			
%F	2.7–14.4	0.97	0.000
%N	1.2–7.2	0.97	0.000
%W	10.5–2.7	− 0.15	0.027
Detritivores			
%F	3.0–23.8	0.86	0.000
%N	2.4–17.3	0.84	0.000
%W	1.0–0.0	0.13	0.030
Omnivores			
%F	17.0–7.1	− 0.30	0.017
%N	17.3–4.3	− 0.33	0.015
%W	23.1–5.5	− 0.40	0.011
Fish			
%F	46.7–75.5	0.87	0.000
%N	25.7–69.4	0.87	0.000
%W	59.6–98.7	0.86	0.000
Shrimp			
%F	39.0–25.0	− 0.38	0.012
%N	64.2–20.1	− 0.83	0.000
%W	32.3–0.7	− 0.87	0.000
Crab			
%F	1.8–12.2	0.81	0.000
%N	0.7–8.0	0.79	0.000
%W	0.4–7.9	0.71	0.002
Per stomach metrics			
Prey	1.9–3.8	0.72	0.001
Families	0.3–1.0	0.90	0.000
Species	0.1–0.6	0.97	0.000
Prey mass (g)	0.4–5.9	0.91	0.000
Prey length (mm)	14.0–38.5	0.61	0.003

$|r|$ values < 0.60 were not considered strong correlations

and environmental related effects in each location. Non-metric multidimensional scaling (NMDS) was used to illustrate diet composition dissimilarity at the family and species levels. NMDS was not needed to describe differences at the group and trophic guild levels due to the magnitude of the estimated prey metric values. NMDS was performed on a Bray–Curtis dissimilarity matrix of the mean MIRI values of the top 10 families and species in each location using the metaMDS function of the vegan package in R version 3.4.0 (R Core Team 2017). Excluding families and species beyond the top 10 allowed for a more focused assessment on the most important prey and, therefore, key differences in diet composition. A total of 33 families and 67 species were compared among locations. Data were transformed with a Wisconsin-square-root transformation prior to scaling following the procedures in the vegan package. Both prey categories converged after 20 tries, with stresses of 0.04 for species and 0.12 for families. Locations were plotted in 2-dimensional taxa-space where the distance between locations reflected the dissimilarity in diet composition.

Results

Regional diet characteristics

In total, 167 species belonging to 108 genera and 78 families were identified in the 5874 stomachs containing 17,365 identifiable prey (Table 1). Of the species identified, 128 were fish, 15 were shrimp, 17 were crab, and three were lobster. The largest prey consumed was 48% of the TL of the lionfish that consumed it, and as many as five families, six species, and 87 identifiable prey items were found within individual stomachs.

Our cumulative prey curve analysis indicated the families ($p = 0.020$) and species ($p = 0.004$) identified in this study do not represent the full diversity of lionfish diet composition in the western Atlantic (Fig. 2). Using the slopes of the linear regressions fit to each curve, we estimate an additional 417 and 102 stomachs would have been needed to identify one new family and species in their diet.

Our regional data indicated carnivorous fish and shrimp that are not managed fishery species and have the lowest risk of extinction disproportionately dominate lionfish diet in the western Atlantic (Table 1). All standard deviations of the estimated prey metrics were $\leq 1.8\%$ indicating a high level of precision. The most important families to lionfish diet were, in order of decreasing importance, wrasses (Labridae), damselfishes (Pomacentridae), and sea basses (Serranidae), and the most important species were

Table 3 Prey metrics and rankings by location

	Bahamas			Belize			Bermuda			Costa Rica			Florida		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
Group															
Fish	81	67	1	66	51	1	61	51	1	80	45	1	58	51	1
Shrimp	31	30	2	47	37	2	39	30	2	30	54	2	18	18	2
Crab	1	1	4	4	1	3	12	8	3	2	1	3	–	–	–
Other inverts	2	1	3	3	2	4	1	0	5	–	–	–	1	2	3
Lobster	–	–	–	0	0	8	7	7	4	–	–	–	–	–	–
Squid	–	–	–	1	0	5	0	0	7	–	–	–	–	–	–
Snail	0	0	5	0	0	6	0	0	8	–	–	–	–	–	–
Octopus	0	0	6	0	0	7	0	0	6	–	–	–	–	–	–
Trophic guild															
Carnivore	25	16	1	16	9	1	29	20	1	16	8	2	16	11	1
Omnivore	9	8	2	4	2	3	13	12	3	17	7	1	3	4	3
Herbivore	6	3	3	8	4	2	7	5	4	8	5	3	–	–	–
Detritivore	1	0	4	1	0	4	22	18	2	–	–	–	6	4	2
Families															
1	Gobiidae			Labridae			Rhynchocinetidae			Acanthuridae			Palaemonidae		
2	Labridae			Pomacentridae			Labridae			Pomacentridae			Atherinidae		
3	Grammatidae			Monacanthidae			Galatheidae			Labridae			Gobiidae		
4	Scaridae			Scaridae			Scaridae			Gobiidae			Hippolytidae		
5	Apogonidae			Gobiidae			Serranidae			Blenniidae			Haemulidae		
6	Pomacentridae			Synodontidae			Blenniidae			Gonodactylidae			Lutjanidae		
7	Labrisomidae			Clupeidae			Portunidae			Serranidae			Labridae		
8	Monacanthidae			Serranidae			Holocentridae			Opistognathidae			Apogonidae		
9	Serranidae			Rhynchocinetidae			Calappidae			Sciaenidae			Monacanthidae		
10	Haemulidae			Acanthuridae			Haemulidae			Holocentridae			Serranidae		
11	Atherinidae			Labrisomidae			Gobiidae			Priacanthidae			Stenopodidae		
12	Chaenopsidae			Scorpaenidae			Paralichthyidae			Gerreidae			–		
13	Holocentridae			Sparidae			Percnidae			Chaetodontidae			–		
14	Stenopodidae			Calappidae			Chaetodontidae			Apogonidae			–		
15	Acanthuridae			Cirrhitidae			Apogonidae			Haemulidae			–		
16	Penaeidae			Blenniidae			Synodontidae			–			–		

Table 3 continued

	Bahamas			Belize			Bermuda			Costa Rica			Florida		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
17	Rhynchocinetidae			Balistidae			Acanthuridae			–			–		
18	Portunidae			Lutjanidae			Monacanthidae			–			–		
19	Opistognathidae			Chaetodontidae			Mullidae			–			–		
20	Synodontidae			Apogonidae			Pempheridae			–			–		
21	Mithracidae			Octopodidae			Pomacentridae			–			–		
22	Gerreidae			Loliginidae			Aulostomidae			–			–		
23	Mullidae			Gonodactylidae			Grapsidae			–			–		
24	Lutjanidae			Pempheridae			Hippolytidae			–			–		
25	Syngnathidae			Haemulidae			Lysiosquillidae			–			–		
26	Tripterygiidae			Bothidae			Octopodidae			–			–		
27	Aulostomidae			Portunidae			Loliginidae			–			–		
28	Alpheidae			Grammatidae			Mithracidae			–			–		
29	Tetraodontidae			Alpheidae			Penaeidae			–			–		
30	Cirrhitidae			–			Antennariidae			–			–		
31	Octopodidae			–			Clupeidae			–			–		
32	Panopeidae			–			Xanthidae			–			–		
33	Carangidae			–			Sparidae			–			–		
34	Diogenidae			–			Carangidae			–			–		
35	Blenniidae			–			Scyllaridae			–			–		
36	–			–			Palinuridae			–			–		
37	–			–			Marginellidae			–			–		
Species															
1	*C. personatus*			*S. partitus*			*C. rigens*			*T. bifasciatum*			*A. stipes*		
2	*G. loreto*			*H. bivittatus*			*M. simplex*			*O. macrognathus*			*H. aurolineatum*		
3	*H. bivittatus*			*H. garnoti*			*T. bifasciatum*			*H. rufus*			*S. baldwini*		
4	*T. bifasciatum*			*T. bifasciatum*			*P. anceps*			*A. coeruleus*			*S. hispidus*		
5	*H. garnoti*			*C. cyanea*			*P. furcifer*			*A. saxatilis*			*A. pseudomaculatus*		
6	*C. eidolon*			*C. manningi*			*H. garnoti*			*A. bahianus*			–		
7	*C. cyanea*			*S. aurofrenatum*			*P. gibbesi*			*G. grosvenori*			–		
8	*S. leucostictus*			*M. tuckeri*			*C. glaucofraenum*			*S. adustus*			–		
9	*M. macropus*			*C. personatus*			*S. aurofrenatum*			*A. maculatus*			–		

Table 3 continued

	Bahamas			Belize			Bermuda			Costa Rica			Florida		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
10	*S. hispidus*			*S.iserti*			*E. nigricans*			*N. oerstedii*			–		
11	*C. parrae*			*C. parrae*			*C. bairdii*			*A. surinamensis*			–		
12	*S. iserti*			*S. atomarium*			*S. coruscum*			–			–		
13	*A. townsendi*			*S. caribbaeus*			*H. bivittatus*			–			–		
14	*L. zingaro*			*C. flammea*			*P. marmoreus*			–			–		
15	*A. binotatus*			*A. pinos*			*H. aurolineatum*			–			–		
16	*S. hispidus*			*M. triangulatus*			*C. ocellatus*			–			–		
17	*M. triangulatus*			*M. boehlkei*			*P. schomburgkii*			–			–		
18	*C. rigens*			*A. coeruleus*			*S. hispidus*			–			–		
19	*S. tigrinus*			*A. chirurgus*			*C. capistratus*			–			–		
20	*C. dicrus*			*S. radians*			*A. maculatus*			–			–		
21	*A. bahianus*			*C. aculeatus*			*H. flavolineatum*			–			–		
22	*G. melacara*			*P. pigmentaria*			*X. martinicensis*			–			–		
23	*M. tuckeri*			*S. intermedius*			*P. maculatus*			–			–		
24	*S. partitus*			*M. chrysurus*			*S. taeniopterus*			–			–		
25	*H. adscensionis*			*S. sepioidea*			*L. grabhami*			–			–		
26	*E. striatus*			*N. curacaoensis*			*L. scabricauda*			–			–		
27	*H. pictus*			*P. schomburgkii*			*C. personatus*			–			–		
28	*H. plumieri*			*S. variabilis*			*S. sepioidea*			–			–		
29	*C. multilineata*			*L. rubre*			*P. minutus*			–			–		
30	*B. rufus*			*S. synodus*			*H. puella*			–			–		
31	*P. maculatus*			*C. pullus*			*M. forceps*			–			–		
32	*S. taeniopterus*			*C. cruentatus*			*C. flavicauda*			–			–		
33	*S. coruscum*			*C. sapidus*			*S. vexillarium*			–			–		
34	*L. rubre*			*A. armatus*			*A. pseudomaculatus*			–			–		
35	*A. chirurgus*			–			*L. rubre*			–			–		
36	*A. maculatus*			–			*A. schoepfii*			–			–		
37	*S. variabilis*			–			*A. maculatus*			–			–		
38	*L. synagris*			–			*S. synodus*			–			–		
39	*P. hipoliti*			–			*C. insolata*			–			–		
40	*C. insolata*			–			*P. depressa*			–			–		

Table 3 continued

	Bahamas			Belize			Bermuda			Costa Rica			Florida		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
41	*C. rostrata*			–			*M. martinicus*			–			–		
42	*A. saxatilis*			–			*A. townsendi*			–			–		
43	*A. pinos*			–			*C. ocellata*			–			–		
44	*S. setifer*			–			*S. nodifer*			–			–		
45	*H. radiatus*			–			*H. maculipinna*			–			–		
46	*M. boehlkei*			–			*V. albolineata*			–			–		
47	*C. glaucofraenum*			–			–			–			–		
48	*H. aurolineatum*			–			–			–			–		
49	*S. vexillarium*			–			–			–			–		
50	*H. maculipinna*			–			–			–			–		
51	*X. splendens*			–			–			–			–		
52	*C. tricolor*			–			–			–			–		
53	*O. chrysurus*			–			–			–			–		
54	*S. viride*			–			–			–			–		

	nwGoM			Mexico			North Carolina			neGoM			USVI		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
Group															
Fish	58	46	1	78	61	1	94	91	1	80	61	1	52	58	1
Shrimp	43	46	2	37	23	2	10	6	2	28	29	2	11	10	2
Crab	1	0	3	19	10	3	1	1	4	13	5	3	–	–	–
Other inverts	0	0	4	6	2	4	4	1	3	1	1	5	0	0	3
Lobster	–	–	–	0	0	5	1	1	5	2	1	4	–	–	–
Squid	0	0	5	–	–	–	–	–	–	1	0	6	–	–	–
Snail	–	–	–	–	–	–	–	–	–	0	0	7	–	–	–
Octopus	–	–	–	–	–	–	–	–	–	0	0	8	–	–	–
Trophic guild															
Carnivore	24	15	2	27	13	1	44	32	1	34	22	1	5	6	1
Omnivore	12	7	3	10	5	3	12	9	2	14	12	2	1	1	3
Herbivore	6	3	4	11	6	2	9	5	3	6	3	3	6	4	2
Detritivore	35	28	1	–	–	–	1	0	4	2	1	4	0	0	4

Table 3 continued

	nwGoM			Mexico			North Carolina			neGoM			USVI		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
Families															
1	Rhynchocinetidae			Labridae			Haemulidae			Penaeidae			Pomacentridae		
2	Labridae			Penaeidae			Serranidae			Pomacentridae			Labridae		
3	Pomacentridae			Monacanthidae			Lutjanidae			Blenniidae			Holocentridae		
4	Blenniidae			Portunidae			Carangidae			Serranidae			Palaemonidae		
5	Apogonidae			Scaridae			Scaridae			Synodontidae			Alpheidae		
6	Scaridae			Pomacentridae			Labridae			Labridae			Pomacanthidae		
7	Serranidae			Hippolytidae			Blenniidae			Gobiidae			–		
8	Gobiidae			Serranidae			Pomacentridae			Portunidae			–		
9	Acanthuridae			Mysidae			Gobiidae			Solenoceridae			–		
10	Lutjanidae			Apogonidae			Bothidae			Lutjanidae			–		
11	Carangidae			Bothidae			Scyllaridae			Carangidae			–		
12	Sciaenidae			Calappidae			Sicyoniidae			Chriostylidae			–		
13	Mysidae			Scorpaenidae			Triglidae			Apogonidae			–		
14	Labrisomidae			Mullidae			Xanthidae			Scorpaenidae			–		
15	Opistognathidae			Labrisomidae			Apogonidae			Mysidae			–		
16	Grammatidae			Sparidae			Monacanthidae			Squillidae			–		
17	Priacanthidae			Gobiidae			Balistidae			Alpheidae			–		
18	Chaenopsidae			Gonodactylidae			Synodontidae			Xanthidae			–		
19	Cirrhitidae			Haemulidae			Sparidae			Paralichthyidae			–		
20	Lysianassidae			Triglidae			Syngnathidae			Triglidae			–		
21	Chaetodontidae			Carangidae			Majidae			Loliginidae			–		
22	Clinidae			Syngnathidae			Alpheidae			Axiidae			–		
23	Alpheidae			Grammatidae			Acanthuridae			Calappidae			–		
24	–			Pomacanthidae			Amphiuridae			Scyllaridae			–		
25	–			Sicyoniidae			Mullidae			Majidae			–		
26	–			Lutjanidae			Scorpaenidae			Menippidae			–		
27	–			Tetraodontidae			Portunidae			Inachidae			–		
28	–			Blenniidae			–			Balistidae			–		
29	–			Synodontidae			–			Inachoididae			–		
30	–			Palinuridae			–			Haemulidae			–		

Table 3 continued

	nwGoM			Mexico			North Carolina			neGoM			USVI		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
31	–			Stenopodidae			–			Pleuronectidae			–		
32	–			–			–			Parthenopidae			–		
33	–			–			–			Monacanthidae			–		
34	–			–			–			Octopodidae			–		
35	–			–			–			Syngnathidae			–		
36	–			–			–			Porcellanidae			–		
37	–			–			–			Gammaridae			–		
Species															
1	*C. manningi*			*M. tuckeri*			*R. aurorubens*			*C. ocyurus*			*H. garnoti*		
2	*T. bifasciatum*			*A. ordwayi*			*H. aurolineatum*			*P. robustus*			*B. biunguiculatus*		
3	*P. marmoreus*			*C. parrae*			*S. crumenophthalmus*			*R. aurorubens*			*A. armatus*		
4	*S. variabilis*			*M. triangulatus*			*S. radians*			*A. pseudomaculatus*			*C. parrae*		
5	*C. multilineata*			*S. partitus*			*S. beta*			*L. setiferus*			*S. partitus*		
6	*S. atomarium*			*S. baldwini*			*D. bivittatum*			*H. bathyphilus*			–		
7	*C. parrae*			*T. bifasciatum*			*H. geminatus*			*C. scotti*			–		
8	*H. maculipinna*			*X. martinicensis*			*S. phoebe*			*X. novacula*			–		
9	*S. planifrons*			*L. carmabi*			*S. subligarius*			*S. fuscus*			–		
10	*A. pseudomaculatus*			*N. usta*			*M. ciliatus*			*D. punctatus*			–		
11	*S. partitus*			*N. curacaoensis*			*A. chirurgus*			*A. spinicarpus*			–		
12	*L. carmabi*			*C. sapidus*			*O. purpurea*			*P. sayi*			–		
13	*A. maculatus*			*G. smithii*			*S. baldwini*			*H. bivittatus*			–		
14	*S. aurofrenatum*			*P. maculatus*			–			*C. enchrysurus*			–		
15	*B. rufus*			*H. chrysargyreum*			–			*F. duorarum*			–		
16	*P. pigmentaria*			*G. loreto*			–			*S. subligarius*			–		
17	*G. oceanops*			*S. tigrinus*			–			*M. mercenaria*			–		
18	*H. bathyphilus*			*H. tricolor*			–			*T. lathami*			–		
19	*S. radians*			*C. rostrata*			–			*S. empusa*			–		
20	*L. rubre*			*H. garnoti*			–			*P. albigutta*			–		
21	*C. thrix*			*O. atlanticus*			–			*S. seticornis*			–		
22	*A. chirurgus*			*C. cyanea*			–			*R. similis*			–		
23	*P. acuminatus*			*S. intermedius*			–			*C. sufflamen*			–		

Table 3 continued

	nwGoM			Mexico			North Carolina			neGoM			USVI		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
24	*C. eidolon*			*M. venenosa*			–			*D. formosum*			–		
25	*O. aurifrons*			*P. argus*			–			*A. latus*			–		
26	*O. macclurei*			*C. multilineata*			–			*H. aurolineatum*			–		
27	*C. insolata*			*A. saxatilis*			–			*S. synodus*			–		
28	*G. loreto*			*C. roseus*			–			*A. criniger*			–		
29	*P. furcifer*			*G. prochilos*			–			*P. sigsbeiana*			–		
30	*S. ocellata*			*S. hispidus*			–			*B. brachychir*			–		
31	*H. cruentatus*			*P. volitans*			–			–			–		
32	*E. adscensionis*			*D. bivittatum*			–			–			–		
33	*C. scotti*			–			–			–			–		
34	*E. pandionis*			–			–			–			–		
35	*A. pinos*			–			–			–			–		
36	*S. vetula*			–			–			–			–		
37	*A. affinis*			–			–			–			–		
38	*E. gryllus*			–			–			–			–		
39	*H. garnoti*			–			–			–			–		
40	*S. occidentalis*			–			–			–			–		
41	*P. fasciatus*			–			–			–			–		
42	–			–			–			–			–		
43	–			–			–			–			–		
44	–			–			–			–			–		
45	–			–			–			–			–		
46	–			–			–			–			–		
47	–			–			–			–			–		
48	–			–			–			–			–		
49	–			–			–			–			–		
50	–			–			–			–			–		
51	–			–			–			–			–		
52	–			–			–			–			–		
53	–			–			–			–			–		

Table 3 continued

	nwGoM			Mexico			North Carolina			neGoM			USVI		
	F	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*	*F*	*N*	*R*
54	–			–			–			–			–		

F % frequency, *N* % number, *R* MIRI rank. Prey metrics are given as the means across 1000 permutations rounded to the nearest percent. Bars (–) denote prey items not identified. Families and species are listed in descending order of MIRI importance

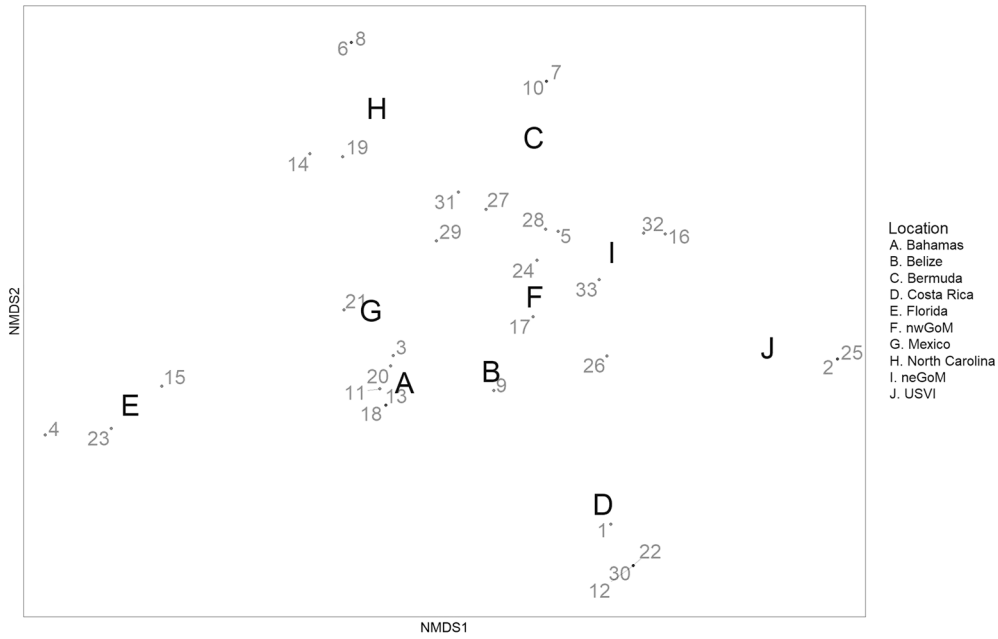
Manning hingebeak shrimp (*Cinetorhynchus manningi*), vermilion snapper (*Rhomboplites aurorubens*), and bluehead wrasse (*Thalassoma bifasciatum*) (Table 1). The most speciose families by group were Serranidae (16 spp.), Pomacentridae (15 spp.), and Labridae (12 spp.) (fish); Gonodactylidae (3 spp.) and Penaeidae (3 spp.) (shrimp); and Portunidae (5 spp.) and Calappidae (3 spp.) (crab).

Pearson's r indicated several strong (i.e., $|r| > 0.60$) and significant correlations with lionfish TL (Table 2). Mean prey mass and length significantly increased with lionfish size, as did the number of prey, families, and species per stomach. Lionfish TL (mm) predicated mean prey mass per stomach (g) by the following equation: $mean\ prey\ mass = 0.0002{*}TL^{1.6391}$, $R^2 = 0.95$. Our results also indicated a significant ontogenetic shift in lionfish diet where the number and mass of fish prey increased with lionfish size, while the number and mass of shrimp prey decreased (Table 2).

Diet variation among locations

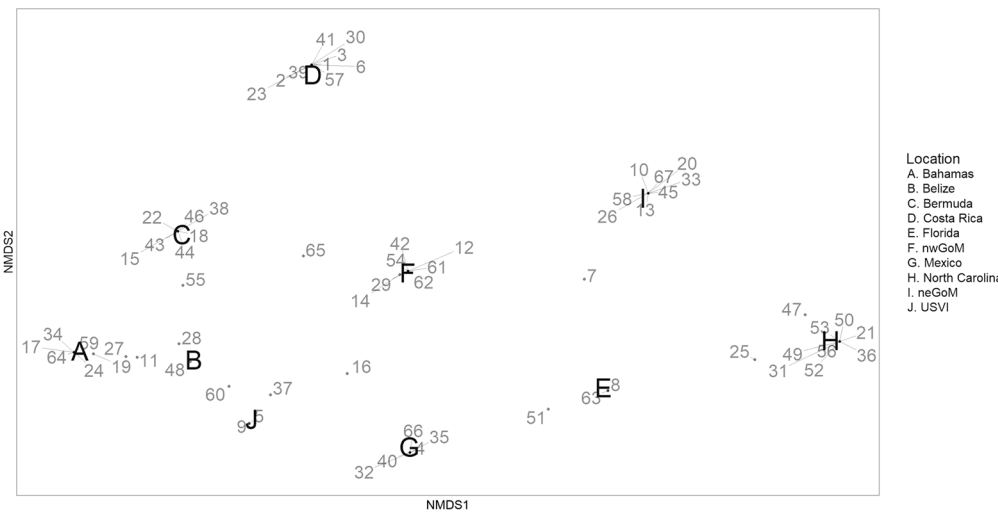
Carnivorous fish and shrimp were the most important prey and their contributions were relatively consistent among locations (Table 3). The contributions of lobster, herbivores, and omnivores were also relatively consistent, with a few exceptions (see Table 3). In contrast, the presence and contributions of crab and detritivores was highly variable among locations (Table 3). Crab were consumed in all locations except Florida and the USVI, and were small contributors by frequency (i.e., $\leq$ 4.1%) and number (i.e., $\leq$ 1.4%) in The Bahamas, Belize, Costa Rica, North Carolina, and the nwGoM, but large contributors by frequency (i.e., 13.0–19.0%) and number (i.e., 4.9–9.9%) in Bermuda, Mexico, and the neGoM. Detritivores were present in all locations except Costa Rica and Mexico, and were nominal contributors by frequency (i.e., 0.2–1.7%) and number (i.e., 0.1–1.4%) in The Bahamas, Belize, North Carolina, neGoM, and the USVI, but very large contributors by frequency (i.e., 22.4–35.3%) and number (i.e., 18.3–28.1%) in Bermuda and the nwGoM.

The composition and rankings of the top 10 most important families and species were highly variable among locations, with a few exceptions. Serranids were present in 80% of the locations, Gobies and Scarids in 60%, and Blennies and Pomacentrids in



Prey Family

1. ACANTHURIDAE	8. CARANGIDAE	15. HIPPOLYTIDAE	22. OPISTOGNATHIDAE	29. SCARIDAE
2. ALPHEIDAE	9. CLUPEIDAE	16. HOLOCENTRIDAE	23. PALAEMONIDAE	30. SCIAENIDAE
3. APOGONIDAE	10. GALATHEIDAE	17. LABRIDAE	24. PENAEIDAE	31. SERRANIDAE
4. ATHERINIDAE	11. GOBIIDAE	18. LABRISOMIDAE	25. POMACANTHIDAE	32. SOLENOCERIDAE
5. BLENNIIDAE	12. GONODACTYLIDAE	19. LUTJANIDAE	26. POMACENTRIDAE	33. SYNODONTIDAE
6. BOTHIDAE	13. GRAMMATIDAE	20. MONACANTHIDAE	27. PORTUNIDAE	
7. CALAPPIDAE	14. HAEMULIDAE	21. MYSIDAE	28. RHYNCHOCINETIDAE	



Prey Species

1. ABUDEFDUF SAXATILIS	18. CORYPHOPTERUS GLAUCOFRAENUM	35. MALACOCTENUS TRIANGULATUS	52. SERRANUS PHOEBE
2. ACANTHURUS BAHIANUS	19. CORYPHOPTERUS PERSONATUS/HYALINUS	36. MONACANTHUS CILIATUS	53. SERRANUS SUBLIGARIUS
3. ACANTHURUS COERULEUS	20. DECAPTERUS PUNCTATUS	37. MONACANTHUS TUCKERI	54. SPARISOMA ATOMARIUM
4. ACHELOUS ORDWAYI	21. DIPLECTRUM BIVITTATUM	38. MUNIDA SIMPLEX	55. SPARISOMA AUROFRENATUM
5. ALPHEUS ARMATUS	22. ENTOMACRODUS NIGRICANS	39. NEOGONODACTYLUS OERSTEDII	56. SPARISOMA RADIANS
6. APOGON MACULATUS	23. GOBIOSOMA GROSVENORI	40. NICHOLSINA USTA	57. STEGASTES ADUSTUS
7. APOGON PSEUDOMACULATUS	24. GRAMMA LORETO	41. OPISTOGNATHUS MACROGNATHUS	58. STEGASTES FUSCUS
8. ATHERINOMORUS STIPES	25. HAEMULON AUROLINEATUM	42. PARABLENNIUS MARMOREUS	59. STEGASTES LEUCOSTICTUS
9. BRACHYCARPUS BIUNGUICULATUS	26. HALICHOERES BATHYPHILUS	43. PARANTHIUS FURCIFER	60. STEGASTES PARTITUS
10. CENTROPRISTIS OCYURUS	27. HALICHOERES BIVITTATUS	44. PERCNON GIBBESI	61. STEGASTES PLANIFRONS
11. CHROMIS CYANEA	28. HALICHOERES GARNOTI	45. PLEOTICUS ROBUSTUS	62. STEGASTES VARIABILIS
12. CHROMIS MULTILINEATA	29. HALICHOERES MACULIPINNA	46. PORTUNUS ANCEPS	63. STENOPUS HISPIDUS
13. CHROMIS SCOTTI	30. HOLOCENTRUS RUFUS	47. RHOMBOPLITES AURORUBENS	64. STEPHANOLEPIS HISPIDUS
14. CINETORHYNCHUS MANNINGI	31. HYPLEUROCHILUS GEMINATUS	48. SCARUS ISERTI	65. THALASSOMA BIFASCIATUM
15. CINETORHYNCHUS RIGENS	32. LIOPROPOMA CARMABI	49. SCHULTZEA BETA	66. XYRICHTYS MARTINICENSIS
16. CLEPTICUS PARRAE	33. LITOPENAEUS SETIFERUS	50. SELAR CRUMENOPHTHALMUS	67. XYRICHTYS NOVACULA
17. CORYPHOPTERUS EIDOLON	34. MALACOCTENUS MACROPUS	51. SERRANUS BALDWINI	

◀**Fig. 3** NMDS plots

50%. Bluehead wrasse were present in 60% of the locations, yellowhead wrasse (*Halichoeres garnoti*) in 40%, and twospot cardinalfish (*Apogon pseudomaculatus*), creole wrasse (*Clepticus parrae*), and bicolor damselfish (*Stegastes partitus*) in 30% of the locations (Table 3). Non-metric multidimensional scaling (NMDS) indicated several strong dissimilarities at the family and species levels (Fig. 3). The dissimilarity was more evident at the species level than at the family level. At both the family and species levels, diet in Florida, Costa Rica, and the USVI was considerably different from the other locations. Diet in the neGoM and North Carolina was also different from the other locations, but only at the species level. Diet in The Bahamas, Belize, Bermuda, Mexico, and the nwGoM was relatively similar at both the family and species levels.

Discussion

Numerous location-based studies have described different aspects of lionfish feeding ecology, yet there has been no regional synthesis of their diet to describe general trends or to compare their diet among locations. Through the analysis of 8125 stomachs, this study provides a comprehensive description of lionfish feeding ecology in the western Atlantic to inform research and monitoring. Our regional data indicate lionfish are generalist carnivores that consume at least 167 vertebrate and invertebrate prey species across multiple trophic guilds (Fig. 2, Table 1). When combined with the broad geographic distributions and commonality of the top 10 most important prey, this general feeding behavior suggests lionfish are opportunistic predators at a regional scale, which is consistent with location-based reports (e.g., Muñoz et al. 2011; Layman and Allgeier 2012; Eddy et al. 2016). Our regional data also show lionfish transition from a shrimp-dominated diet to a fish-dominated diet through ontogeny (Table 2). This ontogenetic shift in diet from crustacean to teleost prey has been reported at local scales (e.g., Morris and Akins 2009; Eddy et al. 2016) and appears to be consistent with other scorpaenids (Harmelin-Vivien and Bouchon 1976). Our locational comparisons indicate lionfish diet composition and the relative contributions of prey varies considerably among locations, even at the group and trophic guild levels (Fig. 3, Table 3). This is a particularly interesting finding and further highlights the potential variability in lionfish diet among locations since it is less likely for prey assemblages and, therefore, the diets of opportunistic generalists to vary significantly among locations at higher taxonomic categories (i.e., assemblages less likely to vary considerably among locations at the group level compared to the species level).

The general opportunistic feeding behavior of lionfish is an important, but sometimes overlooked, characteristic when interpreting invasive predator diets and their potential direct effects on native prey populations. The importance of prey to an opportunistic generalist and the risk of them causing prey extirpations through consumption is strongly governed by prey availability. The risk of causing prey extirpations is considerably lower for opportunistic generalists than it is for specialized predators because opportunistic generalists consume the most abundant and readily available prey. Specialists on the other hand target specific prey and exert stronger direct effects on fewer species (Rilov 2009). Since lionfish diet composition and prey importance are most likely a direct function of prey availability (Muñoz et al. 2011; Layman and Allgeier 2012; Eddy et al. 2016), the overall risk of prey extirpations occurring due to lionfish predation is likely to be low at a regional scale. Our findings do not refute the hypothesis that individual lionfish and local populations can be dietary specialists (Layman and Allgeier 2012). Specializations are more likely to be observed at local scales and may largely depend on local prey assemblages (Layman and Allgeier 2012; Muñoz et al. 2011). Robust large-scale studies comparing prey availability and lionfish diet composition are needed to better elucidate the potential for individual and population level specializations and whether specializations result in negative effects on native prey populations. Efforts could first focus in the nwGoM and Mexico given the disproportionately large contributions of detritivores and crabs in these locations (Table 3).

Our regional data show that, collectively and at the species level, species at risk of extinction (e.g., endangered species), economically important fishery species (e.g., FSSI species), and threatened fishery species (e.g., overfished species) contribute little to lionfish diet at a regional scale (Table 1). Since

lionfish are opportunistic generalists, the low contributions of these prey are likely due to their low population abundances. Depending on local predator communities, lionfish predation could increase predation mortality on these already stressed populations. Of the top 55 most important species to lionfish diet, which constitutes 33% of the species identified, seven are managed [i.e., vermillion snapper, tomtate (*Haemulon aurolineatum*), bank seabass (*Centropristis ocyurus,* managed as an ecosystem component species), redband parrotfish (*Sparisoma aurofrenatum*), royal red shrimp (*Pleoticus robustus*), spotted goatfish (*Pseudupeneus maculatus*), and longspine squirrelfish (*Holocentrus rufus*)] and three are considered vulnerable to extinction (i.e., vermillion snapper, masked goby (*Coryphopterus personatus)*, and pallid goby (*Coryphopterus eidolon*). Three of the fishery species are FSSI (i.e., vermillion snapper, redband parrotfish, and royal red shrimp) and one is threatened [i.e., redband parrotfish, as part of the Caribbean Parrotfishes Complex, are approaching an overfished state (NMFS 2016)]. While research and monitoring is warranted for all fishery species and species at risk of extinction, future studies should first consider focusing on the populations/complexes identified within the top 55 given their relatively large contribution to lionfish diet and their high economic importance and conservation status. Particular attention should be given to redband parrotfish (FSSI and approaching an overfished state), vermillion snapper (FSSI and considered vulnerable to extinction), and tomtate [managed species and evidence suggests lionfish have caused a decline in their abundance in the southeast U.S. (Ballew et al. 2016)].

It is important to note that the primary justification by the IUCN for classifying two of the three (i.e., *C. personatus* and *C. eidolon)* vulnerable species in the top 55 as such is due to their susceptibility to predation by lionfish and the findings in Green et al. (2012). Green et al. (2012) documented a 65% decline in total prey biomass on a single Bahamian reef tract over a 2-year study period. First, no known studies have indicated lionfish have a functional effect on these species at local or regional scales. Second, by this classification reasoning, a majority of the 167 species identified in this study would likely be considered as vulnerable to extinction by the IUCN, which is unfounded. It is unknown if these species would still be considered as vulnerable to extinction, which is one classification level below endangered, if the potential effects of lionfish were not considered. Species-specific studies are needed to determine whether lionfish have a functional effect on populations at conservation and management scales prior to their risk assessment. This is especially true since a majority of the studies reporting a negative effect of lionfish have been based on short-term, small-scale, uncontrolled, and/or unreplicated data (e.g., Albins and Hixon 2008; Albins 2013, 2015; Layman et al. 2014; Green et al. 2012; Lesser and Slattery 2011; Ingeman 2016; Kindinger and Albins 2017). In contrast, only one regional scale study has suggested an effect (e.g., Ballew et al. 2016) while two other regional scale studies suggest lionfish do not have an effect (e.g., Elise et al. 2014; Hackerott et al. 2017). The species identified as the top 10 most important provide a good starting point for research and monitoring to inform conservation status classifications (Table 1).

Without major technological advances for large-scale control, lionfish will continue to be a permanent component of marine food webs throughout the western Atlantic. While the direct effects of lionfish on native prey populations are uncertain at conservation and management scales (Ballew et al. 2016; Elise et al. 2014; Hackerott et al. 2017), lionfish are widely distributed and relatively abundant throughout the western Atlantic. When combined with their diverse diet and the potential to consume large quantities of prey (e.g., 87 identifiable prey were identified in a single stomach in this study), lionfish may cause substantial and long-term indirect effects on native food webs. Using Ecopath-with-Ecosim, Chagaris et al. (2017) suggest lionfish may indirectly affect, in both positive and negative ways, the west Florida shelf food web over the next 30 years through trophic cascades, competitive release, and predation release. Our diet compositions show lionfish consume a variety of prey that are also common prey for many native species (Table 1). The data provided in this study can be used in similar modeling exercises that require lionfish diet data.

While based on small-scale and/or unreplicated data, Lesser and Slattery (2011) and Kindinger and Albins (2017) suggest lionfish may indirectly affect algal communities through predation on herbivores, which could have considerable consequences for overall reef health (e.g., Mumby 2006). Our data show that herbivorous prey, at both the species and

trophic guild levels, contribute very little to lionfish diet at a regional scale (Table 1). Even when combined with omnivorous prey, the contributions of herbivores were still considerably lower than carnivorous prey alone. Regional scale declines in the herbivore community appear to be unlikely given the low contribution of these prey to lionfish diet. Our results do not preclude local or even regional effects on populations of herbivorous species especially since the contributions of herbivores was not uniform among locations (Table 3). Herbivorous fish have been historically overfished in the Caribbean (e.g., Hughes 1994), which could explain why these prey were not better represented in this study. Depending on local fishing pressures and predator communities, lionfish predation could increase total mortality on stressed populations. Robust studies at conservation and management scales are needed to determine whether lionfish are negatively affecting the herbivore community and their functional role as grazers on invaded reefs.

The sub-sampling and bootstrapping approach and the Modified Index of Relative Importance (MIRI) are two methods that may be applicable in other diet studies. The sub-sampling and bootstrapping prevented a single locational dataset from dominating the regional dataset, providing a more balanced depiction of lionfish diet in the western Atlantic. This approach also allowed us to calculate means and standard deviations of the prey metrics, which provided an indication of the accuracy of the regional analysis. This was particularly important in our study since lionfish diet varies considerably among locations. The low standard deviations for the estimated prey metrics (i.e., 0.0–1.8%) suggest the differences in diet compositions among locations had a nominal effect on the regional diet. This approach also helped balance and minimize the effects of different size distributions and environmental factors in our locational comparisons. A similar approach may be valuable in other studies that combine data across environmental gradients and/or aim to statistically compare prey metrics between depths, habitats, years, or even species. The MIRI was developed so samples without prey mass data could be analyzed. The resulting MIRI values were naturally different from the standard IRI values, but the final prey rankings were highly correlated. The MIRI ranks were also very consistent with the IOI and IOP ranks at the group, trophic guild, conservation, and both fishery levels (see Table 1). This suggests our MIRI may be a valid index for assessing prey importance when prey mass data are not available. Future diet studies should consider reporting MIRI and IRI ranks to determine its application across datasets.

The lack of mass data for half the prey items likely affected the final prey rankings. The effects appear to be stronger at the family and species levels due to the increased variability in the MIRI ranks compared to the other indices (Table 1). However, the IRI, IOP, and IOI ranks were also more variable at these taxonomic levels. Given the overall consistencies in the rankings, the low standard deviations of the prey metrics, and since prey were ultimately ranked based on the average of the four indices, it is unlikely that the final prey ranks would change considerably, perhaps only a few places, had mass data been available for all prey.

A portion of the variability in lionfish diet among locations could have been due to potentially incomplete diet compositions in the USVI and Florida. At least ten families were identified and compared in all locations except the USVI (n = 6) and at least ten species were identified and compared in all locations except the USVI (n = 5) and Florida (n = 5). NMDS in this study plotted each location in space based on differences in diet composition. By nature, it is not surprising that locations with fewer than 10 families or species were found to vary from the other locations. It is possible that the diet compositions described for Florida (n = 299) and the USVI (n = 494) are not comprehensive (i.e., not all families and species consumed were identified) due to the relatively low number of samples in each location. However, if they are comprehensive and the families and species compared in this study constitute the full breadth of their diet in each location, then the lower number of families and species did not negatively affect the NMDS results. More robust diet descriptions are needed for these locations to determine the relative accuracy of the diets compared in this study.

This study serves as the most comprehensive description of invasive lionfish feeding ecology in the western Atlantic to date. It is the first known study to describe their diet composition and feeding patterns at a regional scale and to compare their diet composition among locations. Researchers and managers can use the diet compositions, diet patterns, and methods described in this study to (1) make inference about

lionfish diet in areas where lionfish diet has not been described, (2) inform and prioritize research and monitoring into the direct effects of lionfish at regional scales, particularly for management and conservation purposes, (3) estimate prey biomass consumption from lionfish length-frequency data, (4) investigate the potential indirect effects of lionfish on native communities through modeling simulations, (5) assess prey importance when prey mass data are unavailable, and (6) determine the relative accuracy of stomach content analyses for large datasets that combine data across environmental gradients. Given the variability in lionfish diet among locations, this study highlights the importance of continued location-based diet composition studies to better inform local management. Caution should be used when assuming these data in a location where lionfish diet has not been previously described. The regional diet composition, or the locational diet compositions from nearby areas, should only be used until location-based data become available.

Acknowledgements We appreciate the thoughtful comments provided by K. Shertzer, S. Gittings, T. Kellison, A. Hohn, A. Chester, and two anonymous reviewers. We thank NOAAs National Centers for Coastal Ocean Science, NOAAs Office of Education, and the Earnest F. Hollings Scholarship Program for providing support for this project. We are grateful to all who helped collect the data that were used in this study including N. Van Der Haar, M. Doodey, G. Lotz-Cador, the Caribbean Oceanic Restoration and Education Foundation (CORE), UVI CHE 495 students, New Wave Ltd. fishing co., the Bermuda Lionfish Culling Program, C. Buckel, C. Coy, B. Degan, W. Freshwater, J. Hoyt, D. Kesling, M. Lacroix P. Maddi, T. Potts, C. Shemanski, J. Styron, G. Taylor, L. Akins, NOAA Sanctuaries divers, divers from Texas A&M University Galveston, the MV FLING, the Fish Conservation Lab at Texas A&M University Corpus Christi, staff and volunteers of Blue Ventures Expeditions in Belize, D. Kennedy, C. Retherford, S. Bartel, B. Clark, A. Clark, J. Tarnecki, J. Mostowy, and S. Stockton-Teleske.

Author's contribution Statement of authorship: J.A.M. and A.K.B. conceived and designed the study; A.K.B. & J.P. conducted the study and wrote the manuscript; all authors contributed stomach content data and revised the manuscript. Authors after C.A.L are listed alphabetically by institution.

Appendix 1: Metadata. References for data are available in the reference section of the main text

Location	Samples	Sampling date(s)	Depths (m)	Lionfish total length (mm)	Lionfish mass (g)	Empty stomachs (%)	Total prey mass (g)	Number of prey	Number of families	Number of species	Reference or data source
Bahamas	1481	2003 2007–2015	–	40–424	0.3–1380	35	1044	2426	35	54	N. Higgs (unpub.) Layman and Allgeier (2012) Morris and Akins (2009)
Bermuda	1097	2007–2010 2013–2015	1–22	124–461	10–1370	35	485	2268	37	46	Eddy et al. (2016)
Costa Rica	371	2011	0–7	59–300	2–444	29	378	841	15	11	Sandel et al. (2015)
Belize	1336	2011–2015	–	102–445	20–999	32	–	2978	30	34	Blue Ventures Belize (unpub.)
Florida	299	2010–2013	1–10	75–330	5–382	30	–	469	11	5	Ellis and Faletti (2016) J. Morris (unpub.)
nwGoM	837	2011–2015	18–40	45–420	1–1016	19	–	1923	23	41	M. Johnston (unpub.)
Mexico	785	2010 2013 2015	4–30	15–393	1–1000	28	941	1860	31	32	A. Bogdanoff (unpub.), Villaseñor-Derbez and Herrera-Pérez (2014)

Location	Samples	Sampling date(s)	Depths (m)	Lionfish total length (mm)	Lionfish mass (g)	Empty stomachs (%)	Total prey mass (g)	Number of prey	Number of families	Number of species	Reference or data source
North Carolina	495	2004–2006 2008–2010	30–45	110–450	23–1380	27	1452	1264	27	13	Muñoz et al. (2011) J. Morris (unpub.)
neGoM	930	2013–2014	–	67–377	10–780	18	1234	2604	37	30	Dahl and Patterson (2014)
US Virgin Islands	494	2011 2014	–	63–380	2–624	9	–	732	5	6	B. Castillo and K. Reale-Munroe (unpub.)

Appendix 2: Additional detail on prey categorization

Prey were categorized into family, species, group (e.g., fish, shrimp, crab, lobster, squid, snail, octopus, unidentifiable mass, and other invertebrate), trophic guild (e.g., carnivore, herbivore, omnivore, and detritivore), conservation status (e.g., not assessed, data deficient, least concern, near threatened, vulnerable, endangered, and critically endangered), fishery importance (e.g., non-managed, FSSI, and non-FSSI), and fishery status (e.g., non-managed, not subject to overfishing, subject to overfishing, and approaching an overfished state/overfished). The prey group 'unidentifiable mass' was included for relative purposes and was not considered a formal group in the analysis. The group 'other invertebrates' included unidentifiable invertebrate prey pieces and invertebrate groups with extremely low representation in the diet (e.g., amphipods). Trophic guilds and conservation statuses were determined at the species level to minimize generalizations at higher taxa. Conservation statuses were derived from the IUCN Red List of Threatened Species in December 2016 (http://www.iucnredlist.org/). Trophic guild categories were based on the best available information in the literature (e.g., Albertoni et al. 2003; Bardach 1959; Böhlke and Chaplin 1993; Bullock and Smith 1991; Burgess 2002; Carter 2002; Cartes 1993; Cervigón 1993; Chande and Mgaya 2005; Claro and Lindeman 2008; Corredor 1978; Darnell 1962; Davenport 2009; de Boer 1980; Doncel and Paramo 2010; Emery 1978; Floeter et al. 2004; Franks and VanderKooy 2000; Frick et al. 2004; Gibran 2007; Gladfelter and Johnson 1983; Gloeckner and Luczkovich 2008; Gomon 1978; Halpern and Floeter 2008; Hazlett 1981; Heemstra and Randall 1993; Heemstra et al. 2002; Hughes and Elner 1989; Humann and Deloach 2004; Iversen et al. 1986; Johnson and Ruben 1988; Katsuragawa and Ekau 2003; Lavalli et al. 2007; Lieske and Myers 1994; Link 1980; Matsuura 2002; McEachran 2009; McEachran and Fechhelm 2005; Medeiros et al. 2011; Puccio et al. 2006; Randall 1967, 1996, 2002; Randall et al. 1964; Reed 1954; Robertson 1981; Romero et al. 2004; Roux and Conand 2000; Ryan 1956; Samson et al. 2007; Sedberry and Cuellar 1993; Sharp et al. 2007; Snyderman and Wiseman 1996; Squatriglia 2001; Starck et al. 1978; Sterrer 1992; Sterrer and Schoepfer-Sterrer 1986; Whiteman and Côté 2004;

Whiteman et al. 2007; Woods and Greenfield 1978; Zhang et al. 1998). Full references for these citations are available in the main document. Only species managed by the National Marine Fisheries Service (NMFS) and the South Atlantic, Gulf, and Caribbean Fishery Management Councils (FMCs) were considered in our assessment of fishery species. We understand that certain species not managed by NMFS and the FMCs are managed in other locations inhabited by lionfish, and that lionfish also consume species managed at state and/or local levels. However, this approach provided a standardized way to categorize each species using the fishery importance and fishery status designations used by NMFS. The fishery categories used in this study were derived from the fishery importance and status designations issued in the December 2016 NMFS Stock Status Update (NMFS 2016).The fishery importance and fishery status category "non-managed" includes species not managed by NMFS and the FMCs. The fishery importance category 'FSSI' includes species incorporated into NMFS Fishery Stock Sustainability Index (FSSI), which is an indexing metric used by NMFS to assess overall performance of U.S. fish stocks. FSSI species are selected because of their "high importance and value" to commercial and recreational fisheries. Specific criteria used by NMFS for including species in the FSSI can be found at (www.nmfs.noaa.gov/sfa/fisheries_eco/status_of_fisheries/archive/2013/methodology.pdf). The category "non-FSSI" includes species not included in the FSSI. The fishery status category "not subject to overfishing" includes species whose stock mortality rates are not above threshold levels. The category "subject to overfishing" includes species whose stock mortality rates are above threshold levels. The category "approaching/overfished" includes species whose stocks are expected to become overfished within the next 2 years or whose stock biomass levels are already below threshold levels. Each species in this study was categorized based on the fishery status designations given to the stock(s) or complex(es) to which they belong. Several species are part of multiple stocks, and some stock statuses are known while others are not. For example, the overfishing status of tomtate (*Haemulon aurolineatum*) as part of the Puerto Rico, St. Croix, and St. Thomas/St. John Grunt Complexes is known, whereas their status as part of the South Atlantic Grunt Complex is unknown. In these cases, which also included yellowfin grouper (*Mycteroperca venenosa*), lane snapper (*Lutjanus synagris*), long spine squirrelfish (*Holocentrus rufus*), squirrelfish (*Holocentrus adscensionis*), rock hind (*Epinephelus adscensionis*), and white grunt (*Haemulon plumierii*), each species was categorized based on the known designation (see NMFS 2016). Similarly, more severe designations were chosen when the statuses differed (e.g., one stock is subject to overfishing while the other(s) is/are not). This was applicable to ocean triggerfish (*Canthidermis sufflamen*), Caribbean spiny lobster (*Panulirus argus*) and Nassau grouper (*Epinephelus striatus*), which were herein categorized as subject to overfishing, subject to overfishing, and approaching/overfished, respectively. The designations given to the remaining fishery species by NMFS were consistent between stocks and did not require generalizations for this study.

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