



# Temporal and ontogenetic changes in the trophic signature of an invasive marine predator

Luis Malpica-Cruz · Stephanie J. Green · Isabelle M. Côté

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**Abstract** Many successful invasive species have generalist diets, but the extent to which they can track changing resources has seldom been documented. Stable isotope analysis was used to measure dietary shifts with ontogeny and over time in relation to changes in prey availability for Indo-Pacific lionfish (*Pterois* sp.). These are invasive predators that are well established throughout the western North Atlantic and Caribbean where they have caused significant decreases in native reef fish populations in some areas. Samples and observations were made off New Providence Island, Bahamas during the summers of 2008 and 2010. Lionfish  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values

increased only weakly with body length, suggesting that processes other than growth also contribute to stable isotope variability. The trophic niche of lionfish changed significantly between years, concomitant with large changes in native fish prey abundance and community structure. The trophic niche of large lionfish expanded, increasing in trophic diversity at the population level and showing lower individual trophic similarity, while that of small lionfish remained similar in size but shifted towards more  $^{15}\text{N}$ -enriched and  $^{13}\text{C}$ -depleted prey sources. The ability of lionfish to modify their diet over time may have facilitated their expansion and persistence at high densities in some areas despite local prey depletion.

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L. Malpica-Cruz · I. M. Côté  
Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

L. Malpica-Cruz  
ECOCIMATI A.C., 22800 Ensenada, Baja California, Mexico

S. J. Green  
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

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*Present Address:*

L. Malpica-Cruz (✉)  
Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, 22860 Ensenada, Baja California, Mexico  
e-mail: lmalpica@uabc.edu.mx

## Introduction

Eurytopy—the ability to thrive under a broad range of conditions—is a trait that is common among successful invaders (Ricciardi & Rasmussen, 1998; McKinney & Lockwood, 1999). Two key aspects of eurytopy are having a broad diet and showing dietary plasticity (Ribeiro et al., 2007; Falk-Petersen et al., 2011; Ruffino et al., 2011; Pagani-Núñez et al., 2016). Theory predicts that a generalist habit should facilitate prey switching to track resource availability (Charnov, 1976). For example, invasive rats (*Rattus rattus* (Linnaeus)) and cats (*Felis catus* (Linnaeus)) on tropical islands shift seasonally from targeting seabirds, their main food source, to alternative prey such as sea turtles (*Chelonia mydas* (Linnaeus)), insects, and rodents when seabirds are not nesting (Caut et al., 2008; Peck et al., 2008). Similar dietary plasticity has been noted in invasive South American cichlids (Ribeiro et al., 2007), roach (*Rutilus rutilus* (Linnaeus); Ribeiro et al., 2007; Hayden et al., 2014), Asian shore crabs (*Hemigrapsus sanguineus* (De Haan); Griffen et al., 2015), and round goby (*Neogobius melanostomus* (Pallas); Nurkse et al., 2016). These empirical examples hint that shifts in diets by invasive predators in the face of changing or depleting resources may be a general phenomenon.

Documenting dietary shifts is challenging, particularly for predators that forage sporadically over large geographic areas, and in marine habitats, which are often inaccessible. Isotopic signatures—the ratios of heavy to light carbon ( $^{13}\text{C}/^{12}\text{C}$ , expressed as  $\delta^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ , expressed as  $\delta^{15}\text{N}$ ) isotopes—and the metrics derived from them, can be a powerful way to detect changes in diet as shown in early seminal studies in this field (see DeNiro & Epstein, 1978; Deniro & Epstein, 1981; Minagawa & Wada, 1984). For example, nitrogen isotope enrichment is often observed with increasing body size within and across fish species, reflecting the fact that as fish grow, they consume larger prey at higher trophic levels (Davenport & Bax, 2002; Jennings et al., 2002; Cocheret de la Morinière et al., 2003a). In contrast, carbon isotope values generally do not vary as substantially with fish size, but when they do, it often reflects ontogenetic habitat shifts and associated changes in diet (Cocheret de la Morinière et al., 2003b). The carbon and nitrogen isotope axes can also be combined in a two-dimensional isotopic space where the area occupied by one

or more species approximates the ‘trophic niche’ of that species or community (Bearhop et al., 2004; Layman et al., 2007).

Several metrics have been proposed that describe aspects of trophic niche (Layman et al., 2007; Jackson et al., 2011). For instance, the total isotopic area occupied reflects the overall breadth of dietary resources of a species or a group of consumers (Elton, 1927; Hutchinson, 1957; Bearhop et al., 2004), while the range in nitrogen and carbon isotope values reveal vertical or horizontal trophic diversity, i.e., the trophic interactions between species and food web levels in a community (Hurtubia, 1973; Jørgensen & Svirezhev, 2004; Duffy et al., 2007; Villéger et al., 2008). In general, predators feeding on a diverse prey have larger trophic niches than specialists (Tilley et al., 2013). Changes in these niche metrics over time can reveal dietary shifts (Schmidt et al., 2007; Layman et al., 2012), including in invasive species. For example, trophic position shifts, inferred by changes in  $\delta^{15}\text{N}$  values caused by changes in diet due to prey depletion, have been reported in invaders of terrestrial [e.g., invasive argentine ants (*Linepithema humile* (Mayr)) in California Tillberg et al., 2007], and freshwater ecosystems [e.g., Louisiana swamp crayfish (*Procambarus clarkii* (Girard)) in Kenya Jackson et al., 2012].

Indo-Pacific lionfish (*Pterois* sp. (Oken)) are high-profile marine invasive predators that have become established in the western North Atlantic, Caribbean, and Gulf of Mexico (Schofield, 2009, 2010; Fogg et al., 2013; Callicó Fortunato & Avigliano, 2014; Nuttall et al., 2014; Ferreira et al., 2015; Trégarot et al., 2015). Lionfish have reached high densities in some parts of the invaded range (Whitfield et al., 2007; Green & Côté, 2009; Darling et al., 2011), and at some sites, their presence has been associated with marked reductions in native reef fish recruitment, biomass, and diversity (Albins & Hixon, 2008; Albins, 2012; Green et al., 2012; Benkwitt, 2014; Green et al., 2014; Albins, 2015; Benkwitt, 2016a; Smith et al., 2017), but see Hackerott et al. (2017). Their broad diet includes many invertebrate and fish species, with an ontogenetic shift from more of the former to more of the latter (Morris & Akins, 2009; Muñoz et al., 2011; Layman & Allgeier, 2012; Côté et al., 2013; Dahl & Patterson, 2014; Peake et al., 2018). It is of interest to understand whether dietary plasticity plays a role in the persistence of lionfish at high population densities, where

the potential for local prey depletion is high and intraspecific competition is strong (Benkwitt, 2013, 2016b).

Our main aims were (1) to explore size-related variation in carbon and nitrogen stable isotope signatures of lionfish, and (2) to examine whether the diet of lionfish has shifted, as inferred from changes in trophic niche metrics, over a period during which local prey fish biomass has declined by 65%, on average (Green et al., 2012). We test for the first time whether these declines were concomitant with substantial shifts in species composition. We predicted that the trophic niche area of lionfish would either expand (if lionfish shift to consume a broader range of prey species from the altered community, sensu Tilley et al., 2013) or contract (if lionfish preferentially exploit specific prey species and thus have a reduced prey set available, sensu Fanelli et al., 2015). We also expected to see an increase in niche partitioning—as reflected by lower overlap of trophic niches (Evangelista et al., 2014)—between lionfish of different competitive abilities (e.g., small vs large individuals) over time, which may be caused by an increase in intraspecific competition following prey depletion (Araujo et al., 2011; Benkwitt, 2016b). Moreover, any shifts in prey assemblages towards species that use different basal resources (e.g., pelagic vs. benthic) or feed at different trophic levels would be reflected in shifts in the core of the lionfish trophic niche along the carbon and nitrogen isotope axes, respectively. This is the first study to assess changes through time in the trophic niche of lionfish in their invaded range.

## Methods

### Study sites and sample collection

We surveyed lionfish prey communities and collected lionfish specimens at nine sites along a continuous coral reef wall bordering the Tongue of the Ocean Trench, off southwest New Providence, The Bahamas in 2008 and 2010. Sites were 10–20 m deep, marked by a mooring buoy, each separated by at least 1 km. We collected lionfish in summer 2008, 4 years after initial reports of lionfish in New Providence, and again in summer 2010. In 2008, lionfish density was already very high ( $> 390$  fish  $\text{ha}^{-1}$ ; Ribeiro et al., 2007; Green & Côté, 2009). While some removals of lionfish

by recreational divers occurred, there was no systematic culling at these sites in the following 2 years. Therefore, lionfish densities in 2010 were similar to those in 2008 (Green et al., 2012).

We collected lionfish for stable isotope analysis using one of two methods. Some lionfish were collected with hand nets and euthanized at the surface in a clove oil and seawater solution. Others were speared with a prong paralyzer underwater, placed in a water-filled dry bag, and then brought to the surface. All specimens were kept on ice until brought into the laboratory. We measured the total length (TL, to the nearest mm) of each lionfish captured. The collection and handling of all lionfish specimens for this study was approved by the Simon Fraser University Animal Care Committee and met Canadian Council on Animal Care animal usage guidelines and policies (Permit 947B-09).

### Prey fish abundance

To estimate prey fish abundance on each reef, we also conducted underwater surveys during the summers of 2008 and 2010 on the same reefs from which lionfish were collected. We surveyed 6–12  $30 \text{ m} \times 2 \text{ m}$  transects laid parallel to the crest reef at each site, carefully searching crevices and overhangs. We recorded the number and estimated TL (to the nearest 1 cm) of each potential lionfish prey encountered. We considered as potential fish prey all fish  $< 15$  cm TL: because of the well-documented generalist feeding habit of lionfish (Peake et al., 2018) and because this is the maximum prey size for gape-limited lionfish at these sites (Green & Côté, 2014). Lastly, we revised available stomach content data from 567 lionfish collected in 2008 originally reported by Green et al. (2012) to estimate prey percentage contribution to overall lionfish diet.

### Stable isotope processing

We removed a portion of dorsal muscle from 106 individual lionfish in 2008 (size range 115 to 374 mm TL) and 78 fish in 2010 (size range 158 to 399 cm TL). Each sample was cleaned, labeled, and stored frozen (Arrington & Winemiller, 2002), in individual containers. Samples were then dried at  $60^\circ\text{C}$  for 24–48 h and 0.5–1.0 mg of finely ground tissue was placed in pre-cleaned tin capsules. We did not extract lipids

from muscle tissue because the C:N ratios indicated a low lipid content (mean  $\pm$  SD  $3.22 \pm 0.12$ ; see Post et al., 2007). Samples were sent to the UC Davis Stable Isotope Facility where C and N stable isotope ratios were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer. The long-term standard deviations of the laboratory's internal standard (sucrose and ammonium sulfate) were  $\pm 0.20\%$  for  $^{13}\text{C}$  and  $\pm 0.30\%$  for  $^{15}\text{N}$ , respectively.

We elected to sample fish muscle instead of other tissues because muscle has a relatively slow carbon and nitrogen isotopic turnover rate, with a reported half-life of 49–173 days for other fish species (summer flounder *Paralichthys dentatus* (Linnaeus), Buchheister & Latour, 2010); bluegill *Lepomis macrochirus* (Rafinesque), largemouth bass *Micropterus salmoides* (Lecépède), and yellow perch *Perca flavescens* (Mitchill), Weidel et al., 2011). A slow turnover rate tissue should dilute any short-term variability in baseline producers (e.g., brief pulses due to seasonal oceanographic processes and micro-scale individual movements; O'Reilly et al., 2002; Montoya, 2007). Additionally, muscle stable isotope composition is not affected by the use of chemical anesthetics such as the clove oil used to euthanize captured individuals (Nahon et al., 2017).

## Statistical analyses

### *Changes in prey community structure*

To assess changes in prey fish community structure between 2008 and 2010, we calculated a Bray–Curtis similarity across sites of mean prey fish species abundance standardized by transect area. We estimated similarity matrices and ran an analysis of similarities (ANOSIM) in fish communities between years. ANOSIM generates an R statistic, which varies between 0 (samples are as similar across groups as they are within group) and 1 (all samples within groups are more similar to each other than to any sample across groups) and is tested for difference from 0 with a permutation test (in this study,  $N = 999$  permutations). We graphically represent the differences in prey fish assemblages through time using a non-metric multidimensional scaling (nMDS) plot in which sites that are more similar in community composition appear closer together than more

dissimilar sites. Stress values of  $< 0.1$  suggest that distances among sites on an MDS plot accurately reflect the extent of community differences (Clarke & Warwick, 2001). We applied the similarity percentage (SIMPER) routine to estimate the contribution of individual fish species to dissimilarity between years. We deemed species to be important to differences between years if their individual dissimilarity contribution was 1.8% or more, which is twice the expected value if dissimilarity were evenly partitioned among all species in the analysis (i.e., 100% divided by 109 prey fish species, multiplied by 2). We used the “vegan” package in R (Oksanen et al., 2016) to run all community structure analyses.

### *Ontogenetic changes in stable isotope ratios*

We used linear regressions to test the relationships between carbon and nitrogen stable isotope ratios and lionfish TL separately for 2008 and 2010. Visual model diagnostics were implemented to assess homogeneity of variance and normality (Zuur et al., 2010; Harrison et al., 2018). Linear regression analyses were performed in R (R Core Team, 2016).

### *Estimating trophic niche changes*

Because there was some evidence of  $^{15}\text{N}$  and  $^{13}\text{C}$  enrichment with lionfish body size (see “Results”; see also (Dahl & Patterson, 2014; O'Farrell et al., 2014; Curtis et al., 2017), we followed the size-based analytical approach of O'Farrell et al. (2014) to further explore our data. We only used data from lionfish spanning similar size ranges ( $> 150$  mm) across the 2 years for an overall size range studied 150–399 mm TL. We divided this normally distributed sample into two size classes (i.e., ‘small’ and ‘large’), separated around the median length of the pooled sample (i.e., 263 mm). Small and large classes comprised 93 and 86 individuals, respectively. These two classes were then used in comparisons of trophic niche metrics between years.

We calculated various isotope niche metrics proposed by Layman et al. (2007) to assess temporal changes in trophic niche of lionfish. For each year, we first estimated (1) total niche area (TA), i.e., the total amount of niche space occupied by lionfish along the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  axes, as estimated by the maximum convex hull, (2) the carbon range (CR; maximum–

minimum  $\delta^{13}\text{C}$  values), and (3) the nitrogen range (NR; maximum–minimum  $\delta^{15}\text{N}$  values), using the R package “SIAR” (Parnell & Jackson, 2013). We then used a Bayesian procedure using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011), also within the R package “SIAR” (Parnell & Jackson, 2013), to estimate changes in two metrics between the 2 years: (1) standard ellipse area corrected for small samples ( $\text{SEA}_C$ ), i.e., the core isotopic niche space occupied, and (2) Bayesian estimates of standard ellipse area ( $\text{SEA}_B$ ). We also implemented the nested linear models and residual permutation procedure (RPP) by Turner et al. (2010) to compare (1) the difference in centroid location (CL), which is the mean position of all the points in the convex hull, (2) the mean distance to centroid (CD), which provides a measure of the average degree of trophic diversity at the population level, (3) the mean nearest-neighbor distance (NND), which describes the degree of trophic similarity among individuals, and (4) eccentricity ( $E$ ), which describes departure from isotopic scatter in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  dimensions for each year. In addition to RPP, we used Hotellings’  $T^2$  test to examine differences in CL between years. The approach by Turner et al. (2010) tests two sets of null hypotheses: (1) the Euclidean distance between each pair of centroids

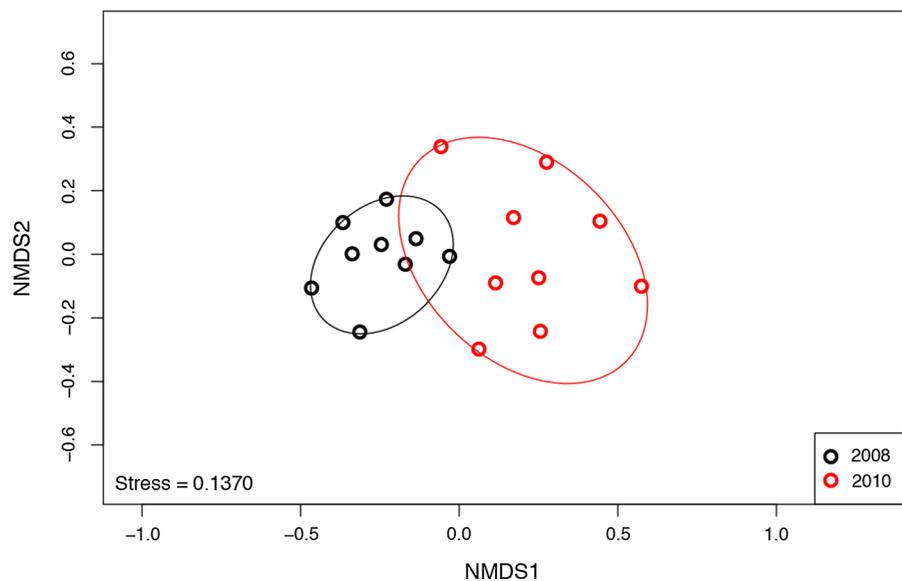
over time does not differ from zero, and (2) the absolute value of the difference in estimates of CD, NND, and  $E$  between years does not differ from zero.

## Results

### Changes in fish community structure

Prey fish community structure differed significantly between the 2 years (ANOSIM,  $R = 0.20$ ,  $P = 0.002$ ), and there was little overlap in fish assemblages between 2008 and 2010 (Fig. 1; stress = 0.137). A three-dimensional nMDS plot yielded a lower stress value (stress = 0.091) but the same clear pattern (Fig. S1). Reductions in abundance of seven species between 2008 and 2010 contributed disproportionately to community dissimilarity between years (SIMPER analysis, Table 2). These species were masked goby (*Coryphopterus personatus* (Jordan & Thompson)), creole wrasse (*Clepticus parrae* (Bloch & Schneider)), silverside (*Atherinomorus* sp. (Fowler)), boga (*Haemulon vittatum* (Poey)), blue chromis (*Chromis cyanea* (Poey)), bigeye scad (*Selar crumenophthalmus* (Bloch)), and bluehead wrasse (*Thalassoma bifasciatum* (Bloch)), all of which are

**Fig. 1** Non-metric multidimensional scaling (nMDS) plot of lionfish prey fish community structure (< 15 cm TL), based on mean prey fish density and species identity surveyed at nine reef sites off New Providence, The Bahamas, in 2008 and 2010. Each point is a coral reef site



documented lionfish prey items (Morris & Akins, 2009; Green et al., 2012). Additionally, four of these species (masked goby, blue chromis, bluehead wrasse, and creole wrasse) comprised  $\sim 54\%$  of prey in lionfish stomach contents assessed in 2008 (Table S1).

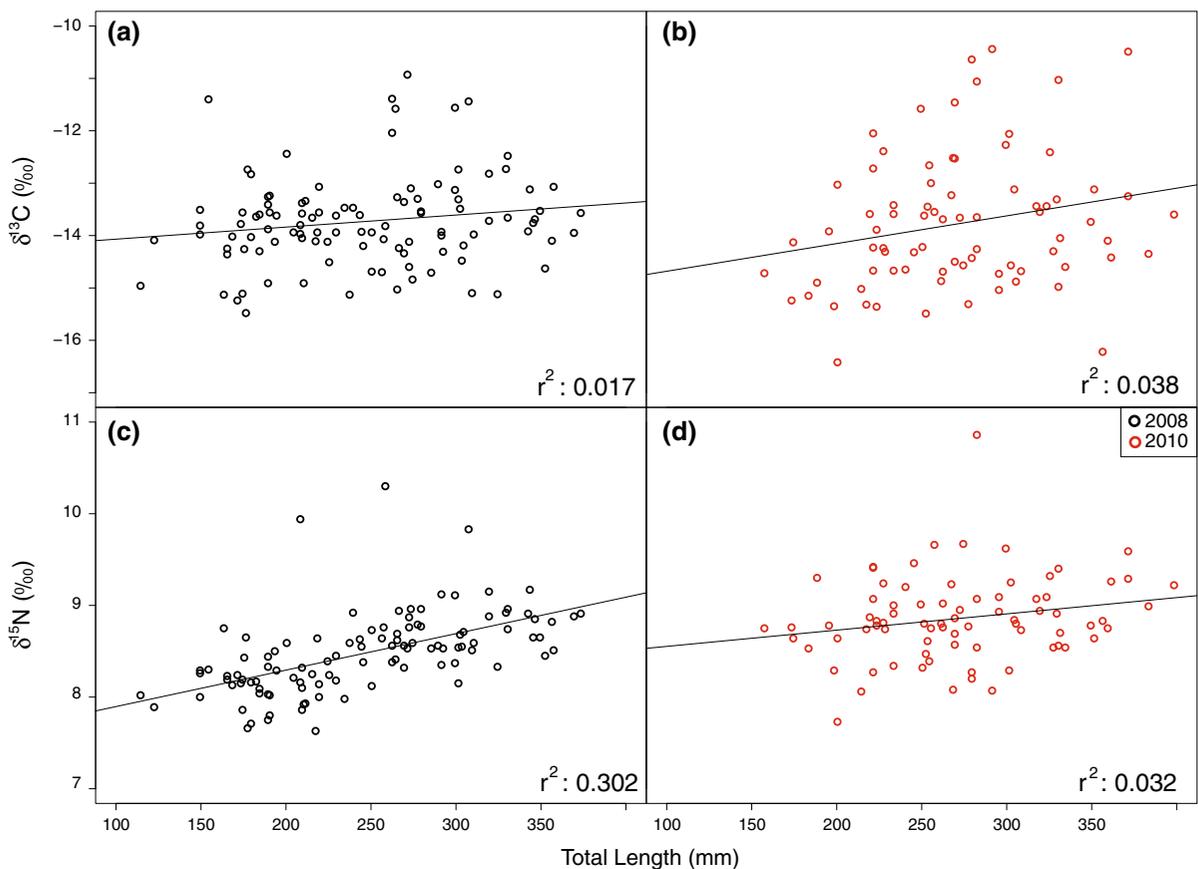
#### Ontogenetic changes in lionfish isotope signatures

The values of  $\delta^{15}\text{N}$  increased with lionfish length on New Providence reefs, although the relationship was marginally non-significant in 2010 (2008:  $F_{(1,104)} = 46.48$ ,  $P < 0.001$ ; 95% CI = 0.0023–0.0051,  $r^2 = 0.30$ ; 2010:  $F_{(1, 76)} = 3.52$ ,  $P = 0.06$ ; 95% CI =  $-0.0001$  to 0.0037,  $r^2 = 0.03$ ; Fig. 2a, b). The values of  $\delta^{13}\text{C}$  for New Providence lionfish also increased significantly with fish length in 2010 ( $F_{(1, 76)} = 4.04$ ,  $P = 0.04$ ; 95% CI = 0.00004–0.01,  $r^2 = 0.04$ ; Fig. 2d) but only modestly

in 2008 ( $F_{(1, 104)} = 2.82$ ,  $P = 0.09$ ; 95% CI =  $-0.0004$  to 0.005,  $r^2 = 0.02$ ; Fig. 2c). Linear models were checked to conform to assumptions of normality and homoscedasticity (Fig. S2).

#### Temporal changes in lionfish trophic niche

The diet of lionfish, as inferred by isotopic trophic niche metrics, changed over time, but these temporal differences varied between lionfish size classes (lionfish population studied had mean  $\pm$  SD:  $257.32 \pm 60.17$  TL; Fig. S3). Between 2008 and 2010, the range in carbon isotope values (CR) increased for both size classes of lionfish; however, the range for nitrogen values (NR) increased for large lionfish, while it decreased for small lionfish (Table 1). Standard ellipse area analysis indicates a core niche overlap ( $\text{SEA}_C$ ) between years of only 20%



**Fig. 2** Carbon (a and b) and nitrogen (c and d) stable isotope ratios as a function of total length (cm) of lionfish collected off New Providence, The Bahamas, in 2008 (a and c) and 2010

(b and d). Fitted regression lines (solid lines) and  $r^2$  values are shown for each isotope and year

**Table 1** Mean carbon and nitrogen isotope ratios and trophic niche metrics of small (< 263 mm TL) and large lionfish captured off New Providence, the Bahamas in 2008 and 2010

Size class	Metric	Year		Difference between years	RPP <i>P</i> value	Hotelling's $T^2$	Hotelling's <i>P</i> value
		2008	2010				
Small	$\delta^{13}\text{C}$	- 13.82	- 14.11	0.29			
	$\delta^{15}\text{N}$	8.31	8.79	0.48			
	CR	4.09	4.84	0.75			
	NR	2.67	1.93	0.74			
	CD	0.75	0.95	0.21	0.10		
	NND	0.15	0.24	0.08	0.15		
	<i>E</i>	0.69	0.87	0.18	0.26		
	CL			0.55	< 0.01*	29.60	< 0.001*
Large	$\delta^{13}\text{C}$	- 13.58	- 13.46	0.12			
	$\delta^{15}\text{N}$	8.73	8.92	0.19			
	CR	4.19	5.78	1.59			
	NR	1.68	2.97	1.29			
	CD	0.79	1.19	0.41	0.02*		
	NND	0.19	0.29	0.09	0.03*		
	<i>E</i>	0.91	0.87	0.04	0.53		
	CL			0.23	0.09	4.97	0.42

The trophic niche metrics include carbon range (CR), nitrogen range (NR), mean distance to centroid (CD), mean nearest-neighbor distance (NND), eccentricity (*E*), and centroid location change (CL). Significance (*P* values) of between-year differences in CD, NND, *E*, and CL was estimated based on nested linear models and residual permutation procedure (RPP) of Turner et al. (2010). Directional Hotelling's tests were also used to estimate the significance of between-year differences in CL

\*Statistically significant value ( $P < 0.05$ )

for small lionfish but 95% for large lionfish (Fig. 3). For both small and large lionfish, the Bayesian trophic niche width ( $\text{SEA}_B$ ) was larger in ~ 99% of Bayesian posterior draws in 2010 than in 2008 (Fig. 3).

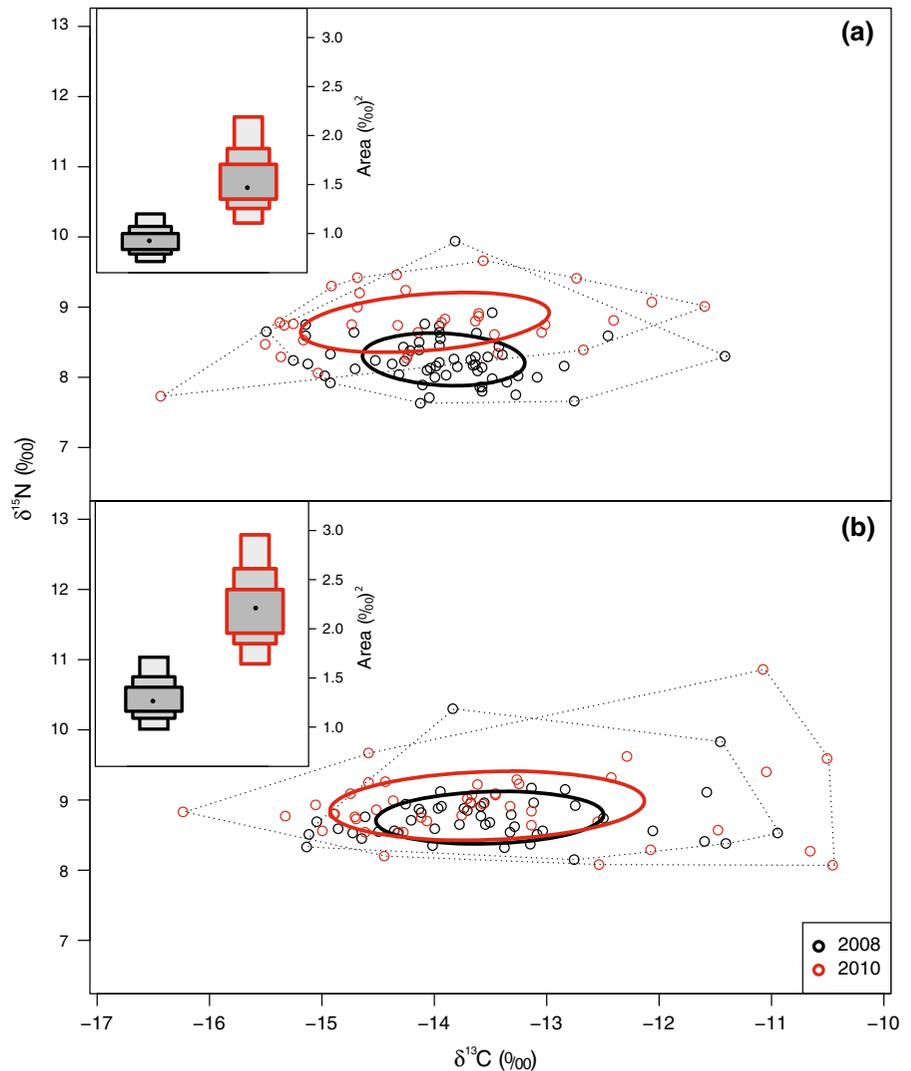
There was a significant shift between years in CL of the isotope niche of small lionfish but not of large lionfish (Table 1; Fig. 3). Population-level trophic diversity of lionfish, as estimated by CD, was significantly larger for large lionfish in 2010 than in 2008 (Table 1). NND was also larger for larger fish in the second year. Neither parameter was temporally variable for small lionfish (Table 1). Eccentricity (*E*) did not vary significantly between years or size classes (Table 1).

## Discussion

We found weak evidence of size-related  $^{15}\text{N}$  enrichment in lionfish sampled on coral reefs of New Providence, suggesting that processes that are not size-related contribute to variation in diet composition

between individuals. We also found evidence of lionfish trophic niche changes over a 2-year period during which the composition and biomass of reef fishes also changed significantly, with substantial decreases in known lionfish prey items. While the isotopic niche of all lionfish increased over time, the direction and magnitude of the shift differed between small (150–263 mm TL) and large lionfish (> 263 cm TL). The isotopic niche of small lionfish became larger over time due to a broadening of the carbon isotope range, and the location of its centroid shifted to become more enriched in nitrogen and less enriched in carbon. The isotopic niche of large lionfish also increased, due to widening of both CR and NRs, but its CL did not shift. Instead, the broader dispersion of individual isotopic signatures suggests an increase in trophic diversity (i.e., larger mean CD) at the population level, and a decrease in trophic similarity between individual lionfish (i.e., larger mean NNDs). Our results suggest that lionfish exhibit high degrees of dietary plasticity across size classes, potentially allowing them to shift diet in the face of changing

**Fig. 3** Isotopic trophic niche width of **a** small (< 263 mm TL) and **b** large lionfish sampled off New Providence, The Bahamas, in 2008 (open black dots) and 2010 (open red dots). The solid lines delimit the standard ellipse areas corrected for small samples ( $SEA_C$ ) and the black dotted lines, the total area (TA) of the isotopic niches of lionfish, as determined by convex hull. The insets show density plots of posterior draws from Bayesian standard ellipse area ( $SEA_B$ ), where the black points correspond to the mean standard ellipse areas while the gray boxed areas reflect 95, 75, and 50% confidence intervals



resource availability—a trait that might have contributed to their invasion success in the wider Caribbean region. However, it is important to note that we could not establish the stable isotope signatures of the prey base in either year, which means that caution is needed in interpreting our results.

#### Changes in prey community structure

Lionfish have had a major impact on native reef fish communities on some Caribbean reefs. Studies of lionfish predation on artificial and natural reefs at specific locations in The Bahamas show that they can significantly decrease native reef fish recruitment, biomass, and diversity (Albins & Hixon, 2008; Albins,

2012; Green et al., 2012). Here, we document that significant alterations of fish community structure occurred over time, concomitant with the large prey abundance declines reported by Green et al. (2012) on the same reefs.

A number of factors could cause variation in reef fish communities. For example, studies have reported marked seasonal shifts in reef fish community dynamics, mainly related to larvae settlement and recruitment (e.g., Sale, 2004). In our study area, fish recruitment predominantly occurs in summer (Robertson & Kaufmann, 1998); we therefore surveyed reef fish communities and lionfish tissues only during the summer months to minimize this well-known seasonal effect. Moreover, Green et al. (2012) suggested that

**Table 2** Individual and cumulative contributions of individual species to dissimilarity in prey fish community structure between 2008 and 2010 on Bahamian reef sites invaded by Indo-Pacific lionfish

Family	Species name	Mean abundance 2008	Mean abundance 2010	Individual contribution ( $\pm$ SD)	Cumulative contribution
Gobiidae	<i>Coryphopterus personatus</i> <sup>a</sup>	14.18	10.65	0.09 (0.07)	0.17
Labridae	<i>Clepticus parrae</i> <sup>a</sup>	7.88	2.22	0.09 (0.07)	0.33
Atherinidae	<i>Atherinomorus</i> sp. <sup>a</sup>	5.93	1.5	0.05 (0.10)	0.42
Haemulidae	<i>Haemulon vittatum</i> <sup>a</sup>	6.57	0	0.04 (0.09)	0.50
Pomacentridae	<i>Chromis cyanea</i> <sup>a</sup>	4.04	1.15	0.03 (0.02)	0.56
Carangidae	<i>Selar crumenophthalmus</i>	2.26	0	0.02 (0.04)	0.61
Labridae	<i>Thalassoma bifasciatum</i> <sup>a</sup>	2.93	1.35	0.02 (0.01)	0.65

Only species that contributed disproportionately (i.e., > 1.8%; see “Methods” in main text) are shown

<sup>a</sup>Denotes species that have been confirmed as prey of lionfish at our study sites during the study period through analyses of lionfish stomach contents

interannual differences in disease, predation by native predators, and oceanographic conditions were unlikely to have affected prey fish recruitment between 2008 and 2010, leaving lionfish predation as the most likely factor involved in changes in native fish community abundance.

This conclusion appears to be supported by the fact that prey species targeted by lionfish have largely driven the observed changes in fish assemblages (Fig. 1; Table 2). Of the 7 prey species that drove community changes, 6 (86%) were reported in the stomach contents of lionfish from these same sites and time period (Green et al., 2012), 4 likely contributed in a high proportion ( $\sim$  54%) to the overall lionfish diet in 2008 (Table S1), and all possessed morphological and behavioral characteristics that make them vulnerable to lionfish predation (Green & Côté, 2014). By comparison, only 41% of prey species that were not disproportionately important to between-year differences in fish community structure were confirmed prey of lionfish. Therefore, it appears likely that lionfish have had an impact not only on reef fish abundance and recruitment but also on community structure, which suggests changes in availability of prey to lionfish over time. Indeed, predator-mediated changes in community structure have been documented for other invasive species such as the Nile perch (*Lates niloticus* (Linnaeus)) in Lake Victoria, the sharptooth catfish (*Clarias gariepinus* (Burchell)) in rivers in the Eastern Cape, South Africa, and different species in stocking efforts worldwide (Hughes, 1986; Eby et al.,

2006; Kadye & Booth 2012; but see Hackerott et al., 2017).

#### Ontogenetic changes in lionfish isotopic signatures

The size-related <sup>15</sup>N enrichment results we observed mirror those of Dahl & Patterson (2014) for lionfish from natural and artificial reefs from the northern Gulf of Mexico. This is despite the fact that reefs in that area are ecologically dissimilar from our study sites in terms of depth (24–35 m), species composition, and trophic structure (Dance et al., 2011). In contrast, the nitrogen signature of lionfish from a Bahamian forereef environment similar to the one we sampled did not change with body size (O’Farrell et al., 2014), perhaps owing to the small sample size ( $N = 21$ ) and the restricted size range of lionfish examined. Indeed, a larger sample size stemming from lionfish sampled in forereefs off Florida also suggested a positive relationship with length (Curtis et al., 2017).

It is now well documented that lionfish undergo a marked ontogenetic dietary shift. Based on dietary and/or stable isotope analysis, several studies suggest that a diet shift—generally an increase in piscivory and reduction in the intake of invertebrates—occurs for “larger”-sized lionfish (> 240–265 mm; Morris & Akins, 2009; Muñoz et al., 2011; Dahl & Patterson, 2014; O’Farrell et al., 2014), which would generally result in <sup>15</sup>N enrichment with increasing body size. However, this apparent shift is associated with local resource availability, with specific cases reporting that

the prevalence of other prey groups, such as invertebrates, might delay this expected ontogenetic dietary shift (Peake et al., 2018).

Although carbon signatures might not necessarily covary with fish size, such a relationship might occur in lionfish for a number of reasons. For example, smaller lionfish might settle and forage in shallow-water,  $^{13}\text{C}$ -enriched habitats (e.g., seagrass beds and shallow reef crest) before moving to deeper,  $^{13}\text{C}$ -depleted reefs (Barbour et al., 2010; Claydon et al., 2012; Byron et al., 2014; Pimiento et al., 2015). However, there is little evidence of ontogenetic habitat shifts in lionfish (Pimiento et al., 2015). In addition, juvenile lionfish exhibit density-dependent growth and a competition-related propensity to forage in non-reef habitats, especially seagrass (Benkwitt, 2013). Even in the absence of differential, size-related foraging habitat use,  $\delta^{13}\text{C}$  values could still increase with body size if the prey of smaller lionfish depend on a different primary producer baseline than those of larger lionfish (France, 1995; Marra et al., 1998; Cocheret de la Morinière et al., 2003a). O'Farrell et al. (2014), for example, suggested that the carbon-depleted signature of small lionfish stemmed from their consumption of planktivorous fishes instead of the benthic invertebrates and demersal fishes consumed by larger conspecifics. Given that stomach contents were not available for analysis, we cannot attribute our findings to a specific process.

In all cases except  $\delta^{15}\text{N}$  in 2008, the coefficients of determination were very low ( $r^2 < 0.04$ ), suggesting that processes other than growth contribute to stable isotope variability among individual lionfish. Given the generalist diet of lionfish (Muñoz et al., 2011; Layman & Allgeier, 2012; Côté et al., 2013), great isotopic variability is expected spatially and temporally. Moreover, prey depletion as a result of predation (Albins & Hixon, 2008; Albins, 2012; Green et al., 2012), coupled with high lionfish densities (Whitfield et al., 2007; Green & Côté, 2009; Darling et al., 2011), can lead to strong intraspecific competition (Benkwitt, 2013) and individual dietary specialization (Layman & Allgeier, 2012), all of which can increase isotopic variability at the population level.

#### Temporal changes in lionfish trophic niche

Concomitant with large changes in native fish prey abundance (Green et al., 2012) and significant changes

in community structure (this study), the trophic niche of lionfish changed between 2008 and 2010. Across both lionfish classes, the isotopic niche area broadened, which is a common response to resource depletion in trophically flexible consumers (Chapman et al., 1989; Peck et al., 2008). However, the isotopic niches of small and large lionfish changed differently. Taken together, the various isotope niche metrics suggest that the niche of large lionfish has simply expanded, increasing in trophic diversity at the population level and shrinking in trophic similarity among individuals, while that of small lionfish has shifted towards more  $^{15}\text{N}$ -enriched and  $^{13}\text{C}$ -depleted prey sources.

Size-dependent shifts in lionfish trophic niche between years could be explained by several alternative ecological processes. In particular, size-dependent differences in isotopic niche trajectories might have been driven by intra-specific competition. Indeed, intra-specific competition in controlled mesocosm experiments and in observational studies has been found to impact a range of ecological phenomena, including community dynamics, trophic interactions, and breeding success, in different species (Goubault et al., 2005; Damijan, 2006; Marques et al., 2013; Holdridge et al., 2016). In our study, larger lionfish appear to have broadened their resource base (in terms of carbon sources), increasing overlap (and thus potential competition) with smaller size classes of lionfish in 2010, which they may have been able to outcompete for prey resources (and have higher total consumption rates of prey). Between 2008 and 2010, lionfish densities were high on the reefs studied (Green & Côté, 2009; Green et al., 2012), creating scope for competition. There is little evidence for direct interference competition in lionfish (personal observations); however, intraspecific exploitation competition is the most likely mechanism behind the density-dependent growth rates of lionfish on artificial reefs (Benkwitt, 2013, 2016b). Furthermore, size-based dominance in competitive interactions is a common phenomenon in marine fishes (Brown & Maurer, 1986; Hin & Roos, 2019). This process has been invoked in the partitioning of isotopic niche space between large and small lionfish in a snapshot study on Bahamian forereefs (O'Farrell et al., 2014), as well as the lower site fidelity of small than large lionfish on patch reefs (Tamburello & Côté, 2015). Low prey availability coupled with dominance by

larger individuals may force smaller lionfish to exploit a different pool of prey over time, resulting in the isotopic niche shifts observed in our study.

Changes observed in trophic niche metrics might also be attributed to factors other than changes in lionfish trophic interactions. For example, seasonal oceanographic processes and terrestrial inputs can shift carbon and nitrogen baselines in coastal marine systems (Montoya, 2007; El-Sabaawi et al., 2012; McMahon et al., 2013). In addition,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  gradients related to isotopic baseline differences exist within and between ecosystems (Radabaugh et al., 2013). Hence, isotopic baseline changes between years could alter isotopic signatures of consumers at low trophic levels, with repercussions at higher levels (Goering et al., 1990; Vizzini & Mazzola, 2003). We lack local isotopic baseline data from our study site; however, nearby Atlantic reef sites off Florida show only slight seasonal variability in basal (particulate organic matter) N and no variability in C stable isotopes (Lamb & Swart, 2008). Ward-Paige et al. (2005), on the other hand, found nitrogen isotopic enrichment over time in the tissues of gorgonians from Florida reefs but only at sites impacted by sewage discharges, which is not a persistent impact in our study area (Dahlgren et al., 2014). Furthermore, if the trophic niche changes observed were solely the result of a system-wide process that altered isotopic baselines, we would have expected both size classes of lionfish to be affected similarly, which was not the case.

Recent larval settlement (Herzka & Holt, 2000) or ontogenetic movements between mangroves, shallow and deep reefs (Cocheret de la Morinière et al., 2003b) could also have contributed to isotopic differences between years. However, the size range we studied (150–399 mm TL) was well above lionfish settlement size (estimated at 12 mm TL; Hare & Whitfield, 2003), and most individuals would have been mature (size at maturity 100–200 mm TL; Morris, 2009; Gardner et al., 2015). The size range was also similar across years. As stated earlier, there is little evidence of habitat shifts related to growth and maturation in lionfish (Pimiento et al., 2015).

Changes in the isotopic composition of prey tissues could also contribute to the observed changes in lionfish isotopic niche. Ontogenetic diet shifts and changes in basal resources of prey can influence prey isotopic composition, which in turn would lead to

confounded variation in the isotopic composition of their predators. However, there is little evidence to date for marked seasonal or annual variability in stable isotope signatures of reef fish. For example, analysis of C and N stable isotopes in multiple tissues (i.e., to discriminate dietary sources via differences in tissue turnover rates) from various species in the families Haemulidae, Siganidae, and Labridae from the Indo-Pacific region showed that the isotopic composition of resident reef fish varies little through time (Davis et al., 2015). Similarly, Wyatt et al. (2012) detected no seasonal variability in isotopic composition of the tissues of different Australian reef fish species. If similar ecological processes occur in our system, it is unlikely that prey isotopic changes could be driving the lionfish niche shifts we observed. Unfortunately, we could not access prey isotopic data for our study period, and hence additional studies are needed to verify this hypothesis.

Finally, ecosystem-level perturbations on coral reefs (e.g., habitat degradation) can lead to community-wide changes in basal resource use (Morillo-Velarde et al., 2018) and in trophic interactions among consumers, which might modify the isotopic composition of mesopredators (Hempson et al., 2017). While our study reefs have experienced habitat degradation processes, similar to most other reef areas in the Caribbean region, there were no notable perturbations (e.g., hurricanes, thermal anomalies, bleaching events) during our study that would have caused a mark change in ecosystem state (Dahlgren et al., 2014). Nevertheless, stable isotope data from basal sources, prey species, and lionfish stomach content analysis are needed to test this and the other alternative hypotheses suggested here.

#### Ecological implications

Lionfish have been previously classified as a generalist predator (Muñoz et al., 2011; Layman & Allgeier, 2012; Côté et al., 2013). However, apparent diet generality at the population level can belie individual specialization (Bolnick et al., 2003; Araujo et al., 2011). Our results may support this notion. In particular, the wide isotopic niche and increase in trophic diversity of large lionfish observed over time are indicative of a generalist predator at the population level. However, the decrease in trophic similarity among large individuals, likely as a result of prey

depletion and competition between conspecifics, may suggest some level of individual specialization (Layman & Allgeier, 2012). The extent to which individual specialization is maintained in the face of changing resource availability is of concern if some lionfish target species that are rare or of conservation concern (e.g., Rocha et al., 2015; Tornabene & Baldwin, 2017). Indeed, lionfish have been shown to consume preferred prey in a density-independent manner, continuing to hunt them even when prey populations are small, which increases the risk of population loss through demographic stochasticity (Ingeman & Webster, 2015; Ingeman, 2016).

Our results suggest that ontogenetic changes in prey consumption should be taken into account when interpreting stable isotope data from invasive lionfish, either by analyzing different size class categories separately (e.g., O'Farrell et al., 2014; this study) or by controlling statistically for the effect of size (e.g., Dahl & Patterson, 2014). Future studies should focus on tissues with faster turnover rates (e.g., whole blood, plasma) to generate a better understanding of short-term processes that can influence diet, such as movements of lionfish between habitats, and dietary specialization among similar-sized conspecifics.

The evidence we provide of trophic niche changes of lionfish, as inferred by stable isotopes, gives only a partial glimpse of the ecological impacts of lionfish, given that lionfish were already well established in The Bahamas at the onset of our study (Schofield, 2009). It seems likely that much more extensive changes to native fish assemblages and to the lionfish trophic signature would be documented if baselines from earlier stages of the lionfish invasion were available. In the absence of information on stomach contents, we unfortunately cannot assess whether the trophic niche shifts observed are the result of targeting different fish prey, incorporating additional invertebrate prey and/or foraging more extensively in non-coral habitats. While it is now well established that lionfish consume a wide variety of prey (see Morris & Akins, 2009; Muñoz et al., 2011; Layman & Allgeier, 2012; Côté et al., 2013; Dahl & Patterson, 2014; Peake et al., 2018), ours is the first report that documents potential prey changes over time, at the population level. Stomach content analyses should be conducted to confirm the evidence we present based solely on stable isotope analysis. If these uphold our results, it would add weight to the idea that the dietary plasticity

of lionfish helps them to cope with changes in prey abundance and intraspecific competition, and is likely to be a factor that facilitates their continued expansion and persistence at high densities despite local prey depletion.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

#### Compliance with ethical standards

**Conflict of interest** All authors declare that they have no conflicts of interest.

**Ethical approval** All national and institutional guidelines concerning the care and use of animals were followed.

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