



# Stable Isotope Ecology of Invasive Lionfish (*Pterois volitans* and *P. miles*) in Bermuda

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Over the past three decades, lionfish (*Pterois volitans* and *Pterois miles*) from the Indo-Pacific have invaded the northwest Atlantic Ocean, Caribbean Sea, and the Gulf of Mexico. As generalist predators with a broad diet, they could pose a major threat to economically and ecologically important species and, therefore, the overall health of coral reef ecosystems and the communities that rely on them. In Bermuda, the lionfish invasion appears to be progressing at a slower rate than elsewhere in the invaded range, providing an opportunity to study their ecological impact at an early stage. This study used stable isotope analysis of lionfish, their major prey, and their competitors to investigate the feeding ecology of lionfish in Bermuda and provide a more complete evaluation of their potential impacts on community structure and trophic interactions. Results suggest that lionfish in Bermuda primarily derive resources from the plankton-based food web, with only a small contribution from food chains supported by macroalgae. Further, it appears that lionfish resource use overlaps substantially with other similarly sized sympatric mesopredators, in particular the coney grouper (*Cephalopholis fulva*), a species commonly targeted by local commercial fisheries. This visualization of Bermuda's demersal ecosystem in two-dimensional isotope space, the first of its kind, will help track the ecological impact of lionfish over time, predict potential changes in community structure, and better inform developing control strategies for this invasive species.

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## INTRODUCTION

Since lionfish (*Pterois volitans* and *Pterois miles*) were first documented in the western Atlantic Ocean in 1985 (Whitfield et al., 2002), growing evidence suggests that they could have a substantial ecological impact across their invaded range (Albins and Hixon, 2008; Lesser and Slattery, 2011; Green et al., 2012). The generalist and opportunistic feeding habits of lionfish are well-recognized (Peake et al., 2018), and their broad diet, comprising a wide variety of teleost and crustacean species, could lead to ecosystem impacts *via* predation. The ecological impacts that lionfish may cause through resource competition have been explored to a lesser degree, as have other ecological

characteristics such as trophic position and niche (but see Muñoz et al., 2011; Layman and Allgeier, 2012; Albins and Hixon, 2013; O'Farrell et al., 2014).

During the past several decades, ecologists have been using stable isotope analysis (SIA) to gain valuable insights into the diet and trophic relationships of populations, communities, and even entire ecosystems (Fry, 2006; Boecklen et al., 2011). Stable isotope ratios (e.g.,  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) in predators directly reflect those of their prey, often in a predictable manner (Peterson and Fry, 1987; Hobson and Clark, 1992; Hobson, 1999), so these isotope ratios can be used to better understand trophodynamics and predator-prey interactions across diverse systems. The relative ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  ( $\delta^{15}\text{N}$ ) typically increases in a stepwise fashion with each trophic level (DeNiro and Epstein, 1981; Minagawa and Wada, 1984) and has thus been used to estimate the relative trophic position of a species within a community or ecosystem (DeNiro and Epstein, 1981; Peterson and Fry, 1987). In contrast, the relative ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  ( $\delta^{13}\text{C}$ ), which can vary substantially among primary producers (Layman et al., 2007), has been used to reliably determine the source of primary production at the foundation of an animal's specific trophic web (DeNiro and Epstein, 1978; Peterson and Fry, 1987).

More recently, SIA has proven to be an effective complement to stomach content analysis (SCA) in studies that aim to determine complex trophic relationships (Boecklen et al., 2011). Because an animal's isotopic composition reflects its diet over a long period of time, SIA provides a more integrated view of an animal's trophic ecology when compared to the simple "snapshot" of its feeding history that SCA provides (Hesslein et al., 1993). In addition, SIA will also more accurately reflect the contribution of rapidly digesting or otherwise unidentifiable diet items that might go unrecorded in SCA (Muñoz et al., 2011).

Recognizing that the isotopic ratios found in tissues represent the long-term accumulated feeding behavior of an animal (Hobson and Clark, 1992; Hesslein et al., 1993), SIA has been used to investigate a species' trophic niche (Bearhop et al., 2004; Newsome et al., 2007), which represents the overall trophic role of a species through the accumulation of its trophic interactions (Elton, 1927; Leibold, 1995; Layman et al., 2007). The trophic niche space of a species, reflecting both ( $\delta^{15}\text{N}$ ) and ( $\delta^{13}\text{C}$ ) in two-dimensional isotopic space (i.e.,  $\delta$ -space; Newsome et al., 2007), has been used to describe community-wide trophic relationships by comparing isotopic niche space and position relative to other species in a given food web (Layman et al., 2007; Turner et al., 2010). Taken together, the isotopic niche overlap among species provides a novel approach to explore dietary similarity among consumers (Jackson et al., 2012), which can, to some degree, be used to indicate competition.

Despite being the first location outside of United States waters where non-indigenous lionfish were reported, overall lionfish densities in Bermuda are typically lower than those in other locations within the invaded range (Eddy, 2016), suggesting that the invasion is progressing more slowly there than elsewhere. This provides an important opportunity to investigate the ecological characteristics of lionfish (e.g., trophic position and niche) at an early stage of the invasion, before

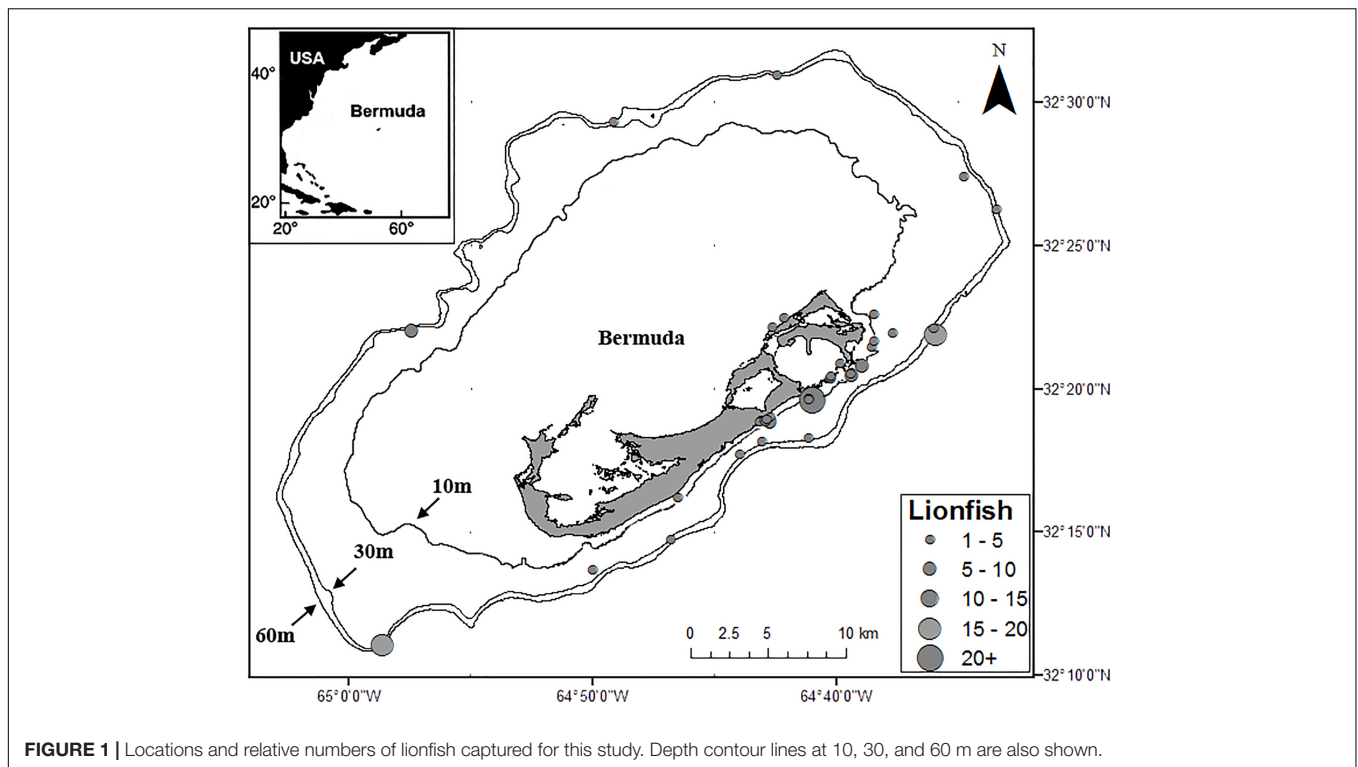
a population "explosion" occurs and potential impacts on community structure arise. As reported throughout the western Atlantic (Peake et al., 2018), the diet of lionfish in Bermuda is known to be diverse (Eddy et al., 2016), which may ultimately have an impact on Bermuda's reef ecosystem. Recognizing that SIA provides an opportunity to evaluate the degree to which their diverse prey contributes to the isotopic values of lionfish, this study measured the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for lionfish, a suite of other consumers (including potential lionfish competitors and known prey species), and primary producers, to determine the trophic structure of the invasive lionfish population and the community of coral reef fishes along Bermuda's coastline as a means to illustrate overall community structure and explore potential impacts.

## MATERIALS AND METHODS

### Sample Collection

Samples of lionfish, lionfish prey, and potential lionfish competitors were collected from multiple locations on the Bermuda platform from 2012 through 2015 by fishermen, snorkelers, SCUBA divers, researchers, and commercial fishermen using pole spears, collecting nets, experimental lionfish traps, and as bycatch in commercial lobster traps (Figure 1). Each specimen was measured for total length (TL), weighed, then either placed on ice to be dissected the same day or frozen whole ( $-10^{\circ}\text{C}$ ) for up to 4 weeks before being thawed and dissected. To prepare samples for SIA, myotomal muscle samples ( $\sim 2$  g, taken from the area immediately posterior to the operculum) from lionfish and potential lionfish competitors were collected, placed in 2-ml centrifuge tubes, and frozen ( $-10^{\circ}\text{C}$ ). Samples of teleost prey species were prepared similarly where possible, while smaller fish and non-teleost prey species were placed in 2-ml centrifuge tubes and frozen whole ( $-10^{\circ}\text{C}$ ). Minimally digested prey items (i.e., easily and rapidly identifiable) found in the stomach contents of lionfish were also collected, placed in 2-ml centrifuge tubes, and immediately frozen ( $-10^{\circ}\text{C}$ ). Prey items were identified in a concurrent SCA (Eddy et al., 2016). Potential lionfish competitors were considered to be any species whose size, habitat use, and feeding preferences (as indicated by previous studies) are similar to those of lionfish in Bermuda (Eddy, 2016; Eddy et al., 2016). While searching for lionfish, SCUBA divers collected samples ( $\sim 2$  g) of two common macroalgal genera (*Dictyota* spp. and *Laurencia* spp.), which were rinsed with fresh water, placed into 50-ml tubes, and frozen ( $-10^{\circ}\text{C}$ ) prior to processing and analysis. Stable isotope ratios for seagrass and other macroalgae in Bermuda were taken from Fourqurean et al. (2015) and Burgett et al. (2018). Stable isotope ratios for plankton<sup>1</sup>, dissolved nutrients, and particulate matter were taken from Altabet (1989), Gruber et al. (2002), Knapp et al. (2005), Landrum et al. (2011), and McMahon et al. (2013).

<sup>1</sup>It is important to acknowledge here that plankton includes detritus and zooplankton and should not strictly be considered a source of primary production, but instead a primary food source.



## Sample Analysis

Myotomal muscle samples for lionfish, potential competitors, and prey were dehydrated at 60°F for at least 48 h (Muñoz et al., 2011; Layman and Allgeier, 2012). Small prey specimens, collected either from stomach contents or using collecting nets, were dehydrated whole at 60°F for at least 48 h after their heads and viscera were removed. Dehydrated muscle samples and whole animals were homogenized using a mortar and pestle, and ~0.85 mg of each was sealed separately in tin capsules. Dried macroalgae were cut into small pieces (~1 mm<sup>3</sup>) using scissors, and ~0.85 mg of each was also sealed separately in tin capsules.

Samples were processed by continuous-flow isotope-ratio mass spectrometry (CF-IRMS) using a GV IsoPrime to determine <sup>15</sup>N/<sup>14</sup>N and <sup>13</sup>C/<sup>12</sup>C ratios. These ratios (R) were transformed to δ<sup>15</sup>N and δ<sup>13</sup>C values by:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000\text{‰}$$

where X is the heavy isotope of nitrogen (δ<sup>15</sup>N) or carbon (δ<sup>13</sup>C), R<sub>sample</sub> is the isotopic ratio of the sample, and R<sub>standard</sub> is the ratio of an accepted reference material [i.e., Pee Dee Belemnite (PDB) for δ<sup>13</sup>C and atmospheric N<sub>2</sub> gas for δ<sup>15</sup>N]. The mass spectrometer was interfaced to an elemental analyzer for automated online combustion and purification of sample nitrogen and carbon. Every 10th sample was repeated, and a standard sample of dehydrated and homogenized mahi-mahi (*Coryphaena hippurus*) myotomal muscle (~0.85 g) was analyzed every 12th sample as a quality control measure and to monitor and compensate for potential analyzer drift. The estimated analytical precision for the isotopic measurements was better

than ±0.1%. The minimal lipid content (C:N < 3.5) of all samples precluded any potential bias due to a high lipid content, thus lipids were not extracted and the data were not normalized (Post et al., 2007).

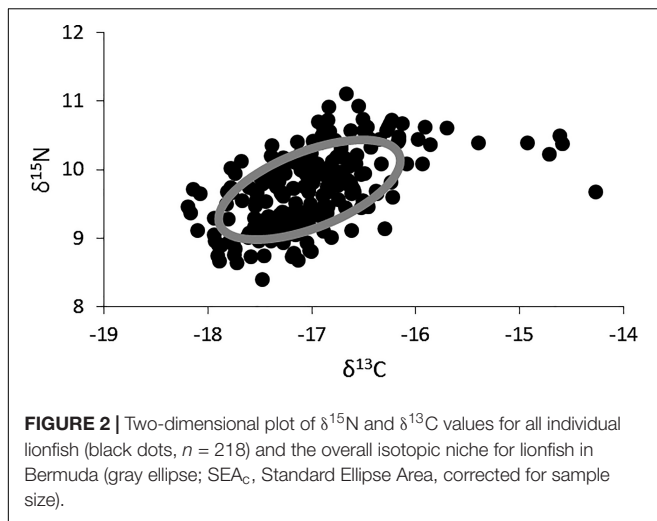
The ratio of stable carbon isotopes (δ<sup>13</sup>C) differs between pelagic and benthic systems and was used to indicate the base of the lionfish food web (France, 1995; Post, 2002). Following Post (2002), relative trophic position (TP) was estimated using δ<sup>15</sup>N values by:

$$TP = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta n$$

where λ is the TP of the organism used to estimate δ<sup>15</sup>N<sub>base</sub>, Δn is the lionfish-specific enrichment in <sup>15</sup>N per trophic level [i.e., trophic discrimination factor (TDF)] calculated experimentally (Eddy, 2019), δ<sup>15</sup>N<sub>consumer</sub> is the direct measurement of δ<sup>15</sup>N for the target species (i.e., lionfish), and δ<sup>15</sup>N<sub>base</sub> was obtained from juvenile Atlantic creolefish (*Paranthias furcifer*), a sympatric zooplanktivore (i.e., primary consumer) with an assumed TP of 2.25 (Jacobsen and Bennett, 2013) and an important diet item of lionfish in Bermuda (Eddy et al., 2016).

## Back-Calculation of Resource Pools

Experimentally derived TDFs (Eddy, 2019), annotated as Δ<sup>15</sup>N and Δ<sup>13</sup>C, were used to back-calculate the estimated position in δ-space where lionfish may derive their resources (i.e., the base of the trophic web). These estimated resource pools were compared to those of primary and secondary consumers, but lacking species-specific TDFs, and the back-calculation for consumers was done using global averages of Δ<sup>15</sup>N and Δ<sup>13</sup>C (Post, 2002: ΔN = 3.4‰, ΔC = 0.4‰; Caut et al., 2009: ΔN = 2.8‰, ΔC = 0.8



and to mean values calculated specifically from myotomal muscle samples of marine teleosts ( $\Delta\text{N} = 3.2\text{‰}$ ,  $\Delta\text{C} = 2.2\text{‰}$ ; data provided in **Supplementary Table S1** of Caut et al., 2009).

## Data Analysis

Differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values between lionfish and competitors, as well as among competitors, were tested using non-parametric tests (i.e., Kruskal–Wallace  $H$ -test and Dunn's  $t$ -test). Isotopic space (i.e.,  $\delta$ -space) for the lionfish food web was visualized by plotting the mean isotope values of each species'  $\delta^{15}\text{N}$  ( $y$ -axis) and  $\delta^{13}\text{C}$  ( $x$ -axis) (Genner et al., 1999; Newsome et al., 2007). Variations in diet as a function of habitat (i.e., depth) and total length (i.e., ontogenetic change) were analyzed using linear regressions, ANOVAs, and/or  $t$ -tests. The size and position of isotopic niche space among lionfish, potential competitors, prey species, and primary producers were compared by generating standard ellipses (i.e., two-dimensional equivalents of isotope value standard deviations) using SIBER in the statistical package R (Jackson et al., 2011). These ellipses ( $\text{SEA}_c$  = Standard Ellipse Area, corrected for sample size) were

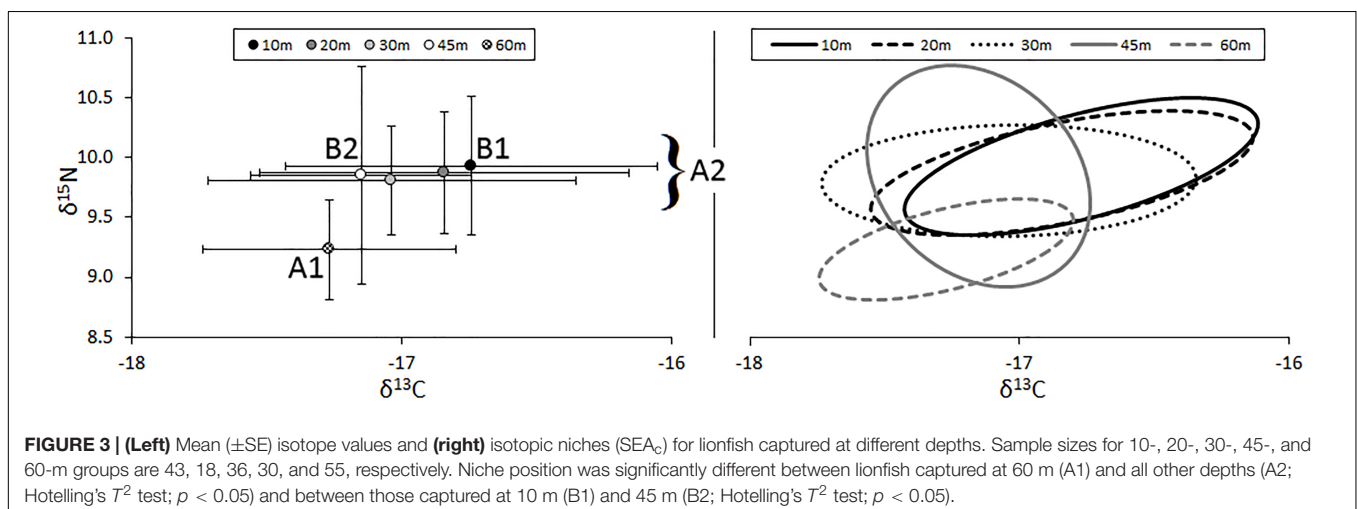
then plotted in  $\delta$ -space, as representations of isotopic niche, to investigate niche overlap and the potential for competition between lionfish and other mesopredators (i.e., small- to medium-sized predators) occupying similar habitats. Several metrics of community trophic structure (e.g., niche position and niche width) were determined following calculations outlined in Layman et al. (2007) and statistically analyzed following Turner et al. (2010) using the statistical software R.

## RESULTS

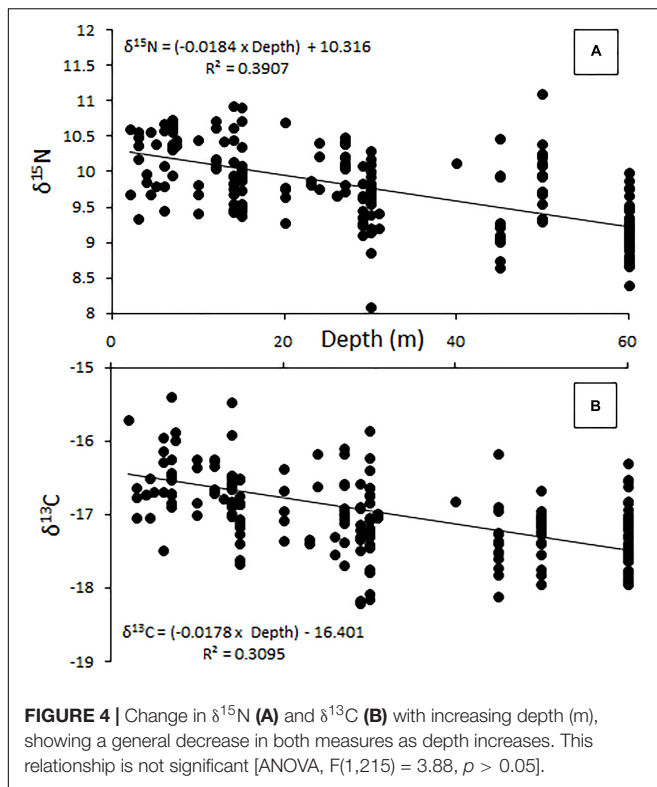
### Lionfish Isotope Ecology

The  $\delta^{15}\text{N}$  values for lionfish ranged from 8.4 to 11.1‰ (mean  $\pm$  SE:  $9.7 \pm 0.04$ ,  $n = 219$ ), and the  $\delta^{13}\text{C}$  values ranged from -18.2 to -14.3‰ (mean  $\pm$  SE:  $-17.0 \pm 0.04$ ,  $n = 219$ ; **Figure 2**). The highest  $\delta^{13}\text{C}$  values (i.e.,  $> -15\text{‰}$ ), which fell outside of the standard ellipse area, were found in lionfish captured in shallow, inshore areas. The isotopic niche width for lionfish was 1.62 (**Figure 2**).

The relative position of lionfish in  $\delta$ -space varied by the depth at which they were captured (**Figure 3**). The  $\delta^{15}\text{N}$  values of lionfish captured at 60 m were significantly different from the  $\delta^{15}\text{N}$  values of lionfish captured at all other depths (Student's  $t$ -test,  $p < 0.001$ ). The  $\delta^{13}\text{C}$  values of lionfish captured at 60 m were significantly different from those captured at 10 and 20 m (Student's  $t$ -test,  $p < 0.001$ ), and the  $\delta^{13}\text{C}$  values of lionfish captured at 45 m were significantly different from those captured at 10 m (Student's  $t$ -test,  $p < 0.001$ ). Overall, the isotopic position of lionfish captured at 60 m was significantly different from those of lionfish captured at all other depths (i.e., 45, 30, 20, and 10 m; Hotelling's  $T^2$ -test;  $p < 0.05$ ) and the isotopic position of lionfish captured at 45 m was significantly different from that of lionfish at 10 m (Hotelling's  $T^2$ -test;  $p < 0.05$ ). Although there was overlap in the isotopic niches of lionfish at different depths, the positions of isotopic niches moved toward lower  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values with depth (**Figure 3**). However, there was no significant linear relationship between depth and either stable







isotope [Figure 4;  $r^2 = 0.39$  and  $0.31$ , respectively, ANOVA:  $F(1,215) = 3.88$ ,  $p > 0.05$ ].

The relative position of lionfish in  $\delta$ -space was also affected by size, with larger size classes of lionfish generally having higher  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (Figure 5). However, the only significant difference in niche position was found between lionfish of 250–300 mm TL and those in the largest size classes (350–400 mm TL and >400 mm TL; Hotelling's  $T^2$ -test;  $p < 0.05$ ); other comparisons using the Hotelling's  $T^2$ -test returned non-significant values. Further, there was no statistically

significant relationship between either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  and lionfish size overall (Figure 6). Some variation in niche width can be observed (Figure 5), with the smaller size classes exhibiting narrower niches.

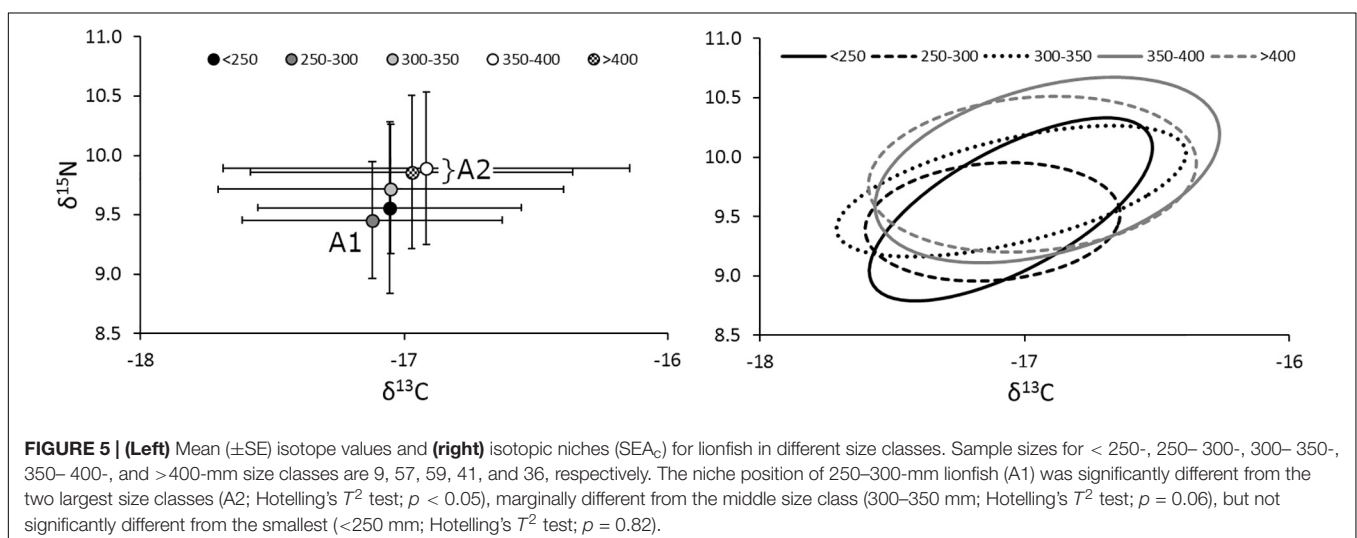
## Trophic Position

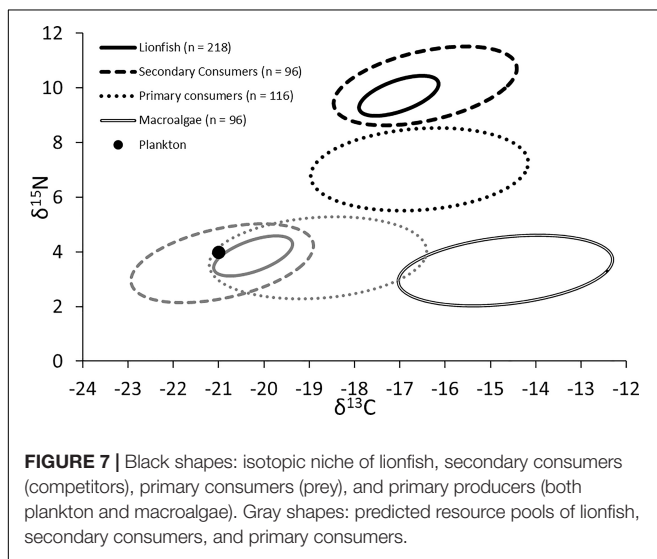
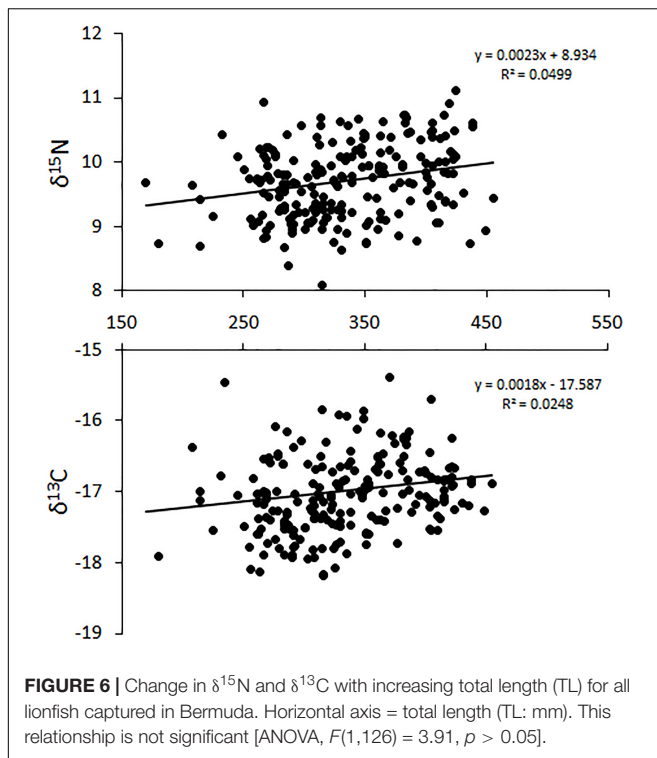
The trophic position of lionfish [using the Atlantic creolefish (*P. furcifer*) to represent the  $\delta^{15}\text{N}_{\text{base}}$ , see above] was 3.4 when applying the lionfish-specific TDF (Eddy, 2019) and 3.2 when applying a global mean  $^{15}\text{N}$  TDF (Post, 2002). The experimentally derived TDF was also used to back-calculate the position of resource pools (i.e., the base of the trophic web), suggesting that resources were drawn primarily from a plankton-based food web with a small contribution from macroalgae (Figure 7;  $\delta^{15}\text{N}$ :  $\sim 3.5$  to  $4.0\text{‰}$ ;  $\delta^{13}\text{C}$ :  $\sim -21.1$  to  $-19.5\text{‰}$ ), a similar finding to that reached by applying other TDFs for muscle samples of marine teleosts (i.e., Caut et al., 2009). By contrast, the use of global mean TDFs from Post (2002) would indicate that resources were derived nearly equally from plankton and macroalgae ( $\delta^{15}\text{N}$ :  $\sim 2.6$  to  $3.0\text{‰}$ ;  $\delta^{13}\text{C}$ :  $\sim -19.1$  to  $-17.5\text{‰}$ ).

## Community Structure

The isotopic position of secondary consumers, which may compete with lionfish for food, varied in  $\delta$ -space (Figure 8A, with details in Supplementary Table S1), with mean  $\delta^{15}\text{N}$  values ranging from  $8.1\text{‰}$  for hogfish, *Lachnolaimus maximus*, to  $10.7\text{‰}$  for porgy, *Calamus calamus*, and mean  $\delta^{13}\text{C}$  values ranging from  $-18.6\text{‰}$  for red hind, *Epinephelus guttatus*, to  $-13.2\text{‰}$  for Lane snapper, *Lutjanus synagris*. Within a species, the largest variations of  $\delta^{15}\text{N}$  ( $\pm 2.2\text{‰}$ ) and  $\delta^{13}\text{C}$  ( $\pm 2.2\text{‰}$ ) were observed among juvenile Galapagos sharks, *Carcharhinus galapagensis*, and gray snapper, *Lutjanus griseus*, respectively, and the smallest variations in  $\delta^{15}\text{N}$  ( $\pm 0.5\text{‰}$ ) and  $\delta^{13}\text{C}$  ( $\pm 0.6\text{‰}$ ) were observed among red hinds and Lane snapper, respectively.

The position of primary consumers, many of which are lionfish prey (Eddy et al., 2016), also varied in  $\delta$ -space (Figure 8B,





with details in **Supplementary Table S1**), with  $\delta^{15}\text{N}$  values ranging from 5.2‰ for the box crab, *Cryptosoma bairdii*, to 8.7‰ for goldspot goby, *Gnatholepis thompsoni*, and mean  $\delta^{13}\text{C}$  values ranging from -13.5‰ for goldspot goby to -20.6‰ for spotfin butterflyfish, *Chaetodon ocellatus*. In contrast, mean ( $\pm$ SE)  $\delta$ -values among all crustacean prey, invertivorous prey, and zooplanktivorous prey varied more narrowly, with  $\delta^{15}\text{N}$  values of 6.2‰ ( $\pm 0.2$ ‰,  $n = 25$ ), 7.0‰ ( $\pm 0.3$ ‰,  $n = 20$ ), and 6.9‰ ( $\pm 0.2$ ‰,  $n = 17$ ) and mean  $\delta^{13}\text{C}$  values of -15.8‰ ( $\pm 0.5$ ‰,  $n = 25$ ), -16.8‰ ( $\pm 0.6$ ‰,  $n = 20$ ), and -18.9‰ ( $\pm 0.2$ ‰,  $n = 17$ ), respectively.

The niche positions in  $\delta$ -space for primary producers (**Figure 8C**), primary consumers, and secondary consumers were significantly different (Hotelling's  $T^2$  test;  $p = 0.001$ ), while the niche position of lionfish was contained within the overall niche for secondary consumers (**Figure 7**). The size of the niche (i.e., width) for primary producers was not significantly different from that for primary consumers (Hotelling's  $T^2$  test,  $p = 0.529$ ). The niche positions of most potentially competing secondary consumers in  $\delta$ -space differed significantly from that of lionfish (Hotelling's  $T^2$  test;  $p < 0.05$ ; **Table 1** and **Figure 9**). The size of isotopic niches among these potential competitors varied, and approximately half of them were significantly different in size from others (**Table 2**). Yellowtail snapper (*Ocyurus chrysurus*) had the widest isotopic niche (5.34) and Lane snapper had the narrowest (0.52). Among known prey species, the detritivorous red night shrimp (*Cinetorhynchus rigens*; Manning, 1961) had the widest niche (6.85) and the zooplanktivorous juvenile Atlantic creolefish had the narrowest niche (0.16; **Figure 9**). The niche of macroalgae was very broad (9.17).

## Resource Competition

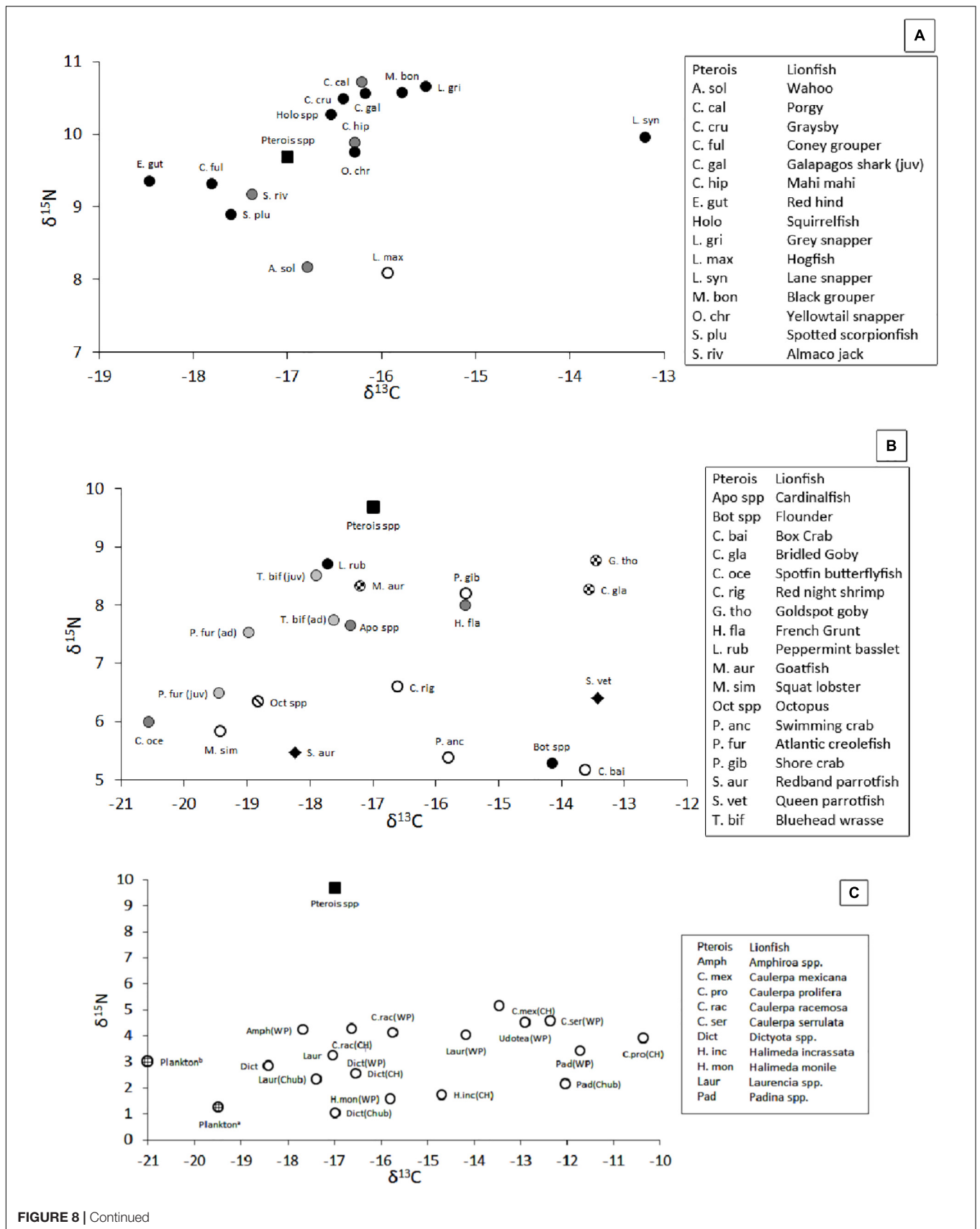
Mean  $\delta^{15}\text{N}$  values differed significantly between lionfish and likely competitors (**Figure 8A**, **Supplementary Table S1**; Kruskal-Wallis  $H$ -test:  $p < 0.001$ ), and the pairwise comparisons between lionfish ( $9.7 \pm 0.04$ ‰) and most potential competitors (i.e., juvenile Galapagos shark:  $10.6 \pm 0.2$ ‰; gray snapper:  $10.7 \pm 0.2$ ‰; coney grouper:  $9.3 \pm 0.1$ ‰; red hind:  $9.4 \pm 0.1$ ‰; black grouper:  $10.6 \pm 0.3$ ‰), as well as between several of these competitors, were significantly different (**Table 3**; Dunn's  $t$ -test:  $p < 0.05$ ).

Mean  $\delta^{13}\text{C}$  values also differed significantly between lionfish and potentially competing species (**Figure 8A**, **Supplementary Table S1**; Kruskal-Wallis  $H$ -test:  $p < 0.001$ ), and the pairwise comparisons between lionfish ( $-17.0 \pm 0.04$ ‰), juvenile Galapagos shark, and all members of the grouper snapper complex examined were significantly different (**Table 4**; Dunn's  $t$ -test:  $p < 0.05$ ). The pairwise comparisons between several of these competitors were also significantly different (**Table 4**).

The overlap of isotopic niches of secondary consumers, a potential indicator of resource competition, varied considerably among mesopredators that occupy similar habitats as lionfish and presumably compete for both space and resources (**Figure 10** and **Table 5**). The greatest overlap occurred between lionfish and coney grouper, where 54% of the coney grouper niche is included in that of lionfish, while there is no overlap between lionfish and Lane snapper (**Figure 10** and **Table 5**). The niche of squirrelfishes overlapped 92% of the lionfish niche, but lionfish overlapped that of squirrelfishes by only 23% (**Figure 10** and **Table 5**).

## DISCUSSION

By applying isotope measures of community structure (Layman et al., 2007; Turner et al., 2010), we offer the first glimpse of Bermuda's marine ecosystem in two-dimensional isotopic space (i.e.,  $\delta$ -space). This approach allows the investigation of isotopic



**FIGURE 8 | (A)** Position of mesopredators in  $\delta$ -space (i.e., potential competitors, pelagic piscivores, and demersal invertivores). Black square = lionfish. Black circle = demersal piscivores. Gray circle = pelagic piscivores. White circle = demersal invertivore. **(B)** Position of prey species, most of which are primary consumers, in  $\delta$ -space. Black square = lionfish. Black circle = invertivore/piscivore. Dark gray circle = invertivore. Light gray circle = zooplanktivore. Checkered circle = detritivore/invertivore. Circle with diagonal line = Octopus. White circle = crustacean. Black diamond = herbivore. **(C)** Position of primary producers in  $\delta$ -space (Fourqurean et al., 2015; Burgett et al., 2018). Black square = lionfish. White circle = macroalgae. Lined circle = plankton. WP = Walsingham Pond. CH = Castle Harbor. Chub = Chub Head.  $\delta$ -values not shown:  $\delta^{13}\text{C}$  for dissolved inorganic carbon ranged from 1 to 1.6‰,  $\delta^{15}\text{N}$  for suspended particles and zooplankton were 2.0 and 3.8‰, respectively, and  $\delta^{15}\text{N}$  for total dissolved inorganic and organic nitrogen was  $\sim$ 3.9‰. Sample sizes and standard errors for panels **(A,B)** are provided in **Supplementary Table S1**. Sample sizes and standard errors are not provided for panel **(C)** because the values were collected from the literature.

**TABLE 1 |** Results of Hotelling's  $T^2$  test comparing niche position between competitors.

	C. gal	L. gri	L. syn	C. ful	E. gut	O. chr	M. bon
<i>Pterois</i>	0.001	0.001	0.001	0.002	0.001	0.032	0.001
C. gal		0.070	0.001	0.001	0.001	0.029	0.395
L. gri			0.001	0.001	0.001	0.006	0.751
L. syn				0.001	0.001	0.001	0.001
C. ful					0.080	0.001	0.001
E. gut						0.001	0.001
O. chr							0.042

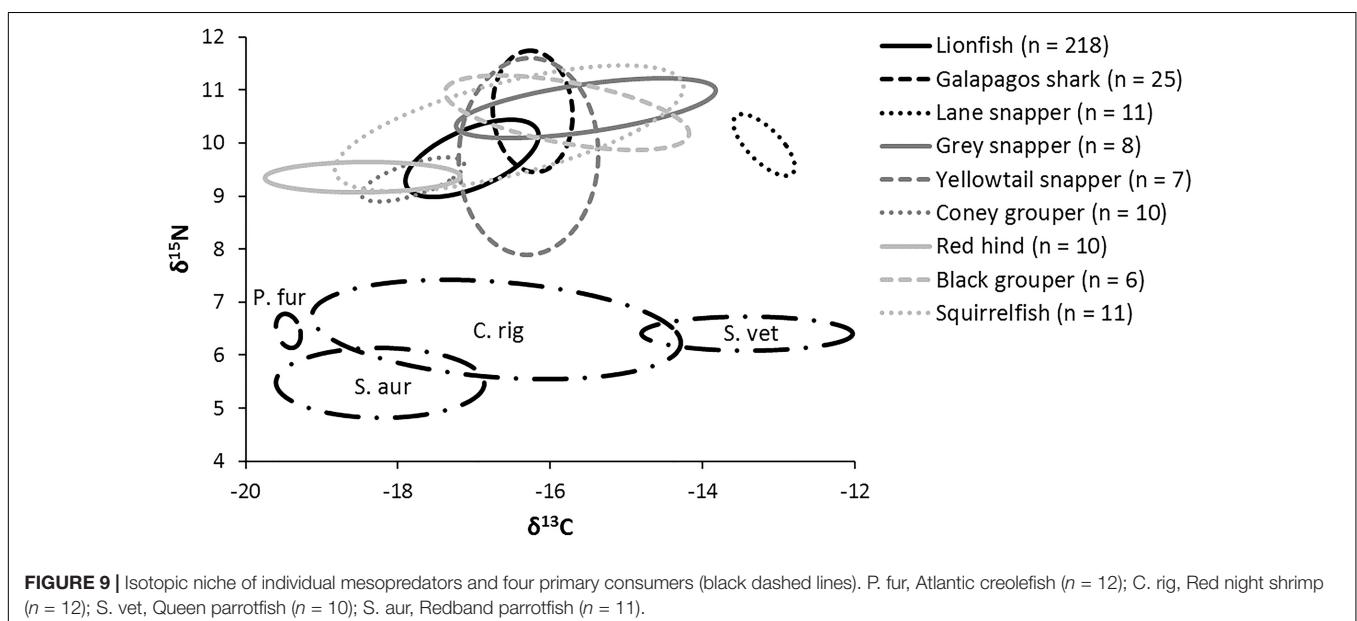
Shaded cells indicate where niche positions were not significantly different ( $p > 0.05$ ).

niche position and size and the opportunity to explore dietary resource use and competition between the invasive lionfish and native species.

Among demersal piscivores of similar size, lionfish are a top predator in Bermuda and occupy a trophic position of 3.4. The wide  $\delta$ -space occupied by lionfish highlights a broad isotopic niche characteristic of a generalist predator feeding from a varied resource base, in agreement with stomach contents analyses (Peake et al., 2018) and similar work using SIA (Muñoz et al., 2011; Layman and Allgeier, 2012; O'Farrell et al., 2014). Stomach contents analyses also typically show a subtle dietary shift through ontogeny (Morris and Akins, 2009; Eddy et al.,

2016; Peake et al., 2018). While our new findings do not show a significant change in either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  with increased body length, the niche position of the second smallest size class was significantly different from all larger size classes, and a significant difference in the niche position of the smallest size class (<250 mm;  $n = 9$ ) might have been detected if a larger sample size were available. Further, given that lionfish, at least at the population level, are generalist predators feeding opportunistically upon dozens of species (Eddy et al., 2016; Peake et al., 2018), their diet is unlikely to change in any distinct way with additional growth after maturity.

The isotopic composition of Bermuda's lionfish varied more noticeably with depth. Lionfish from mesophotic reefs at 60 m had lower  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  than those from shallow reefs (10–20 m), with fish from 45 m showing overlapping characteristics. These differences between depth zones reflect changes in overall reef community structure across a range of taxa (Goodbody-Gringley et al., 2019; Stefanoudis et al., 2019a,b) and thus in the prey items available to an opportunistic generalist predator such as the lionfish. For example, juvenile Atlantic creolefish (*P. furcifer*) and small squat lobster (*Munida simplex*), both common prey items for lionfish (Eddy et al., 2016), are common at 60 m but absent at shallow depths (Sterrer, 1985; Eddy, 2016). Importantly, as macroalgae and seagrass are less common in deep water around Bermuda (Manuel et al., 2013), and those macroalgal species that are present at depth tend to be less





**TABLE 2** | Results of Hotelling's  $T^2$  test comparing niche width between competitors.

	C. gal	L. gri	L. syn	C. ful	E. gut	O. chr	M. bon
<i>Pterois</i>	0.008	0.001	0.241	0.627	0.119	0.001	0.025
C. gal		0.062	0.013	0.053	0.878	0.005	0.524
L. gri			0.002	0.002	0.086	0.339	0.447
L. syn				0.688	0.057	0.001	0.012
C. ful					0.126	0.001	0.048
E. gut						0.009	0.469
O. chr							0.095

Shaded cells indicate where niche widths were not significantly different ( $p > 0.05$ ).

**TABLE 3** | Results of Dunn's test comparing  $\delta^{15}\text{N}$  between predators.

	C. gal	L. gri	L. syn	C. ful	E. gut	O. chr	M. bon
<i>Pterois</i>	0	0	0.092	0.022	0.028	0.352	0.002
C. gal		0.131	0.105	0	0	0.009	0.242
L. gri			0.025	0	0	0.002	0.399
L. syn				0.008	0.009	0.125	0.064
C. ful					0.470	0.153	0
E. gut						0.170	0
O. chr							0.008

Shaded cells indicate where  $\delta^{15}\text{N}$  values were not significantly different ( $p > 0.05$ ).

**TABLE 4** | Results of Dunn's test comparing  $\delta^{13}\text{C}$  between predators.

	C. gal	L. gri	L. syn	C. ful	E. gut	O. chr	M. bon
<i>Pterois</i>	0	0.005	0	0.002	0.001	0.016	0.006
C. gal		0.316	0.026	0	0	0.246	0.437
L. gri			0.027	0	0	0.424	0.41
L. syn				0	0	0.019	0.063
C. ful					0.38	0	0
E. gut						0	0
O. chr							0.345

Shaded cells indicate where  $\delta^{13}\text{C}$  values were not significantly different ( $p > 0.05$ ).

palatable (Goodbody-Gringley et al., 2019; Stefanoudis et al., 2019b),  $\delta^{13}\text{C}$  values among teleosts and crustaceans decrease with depth as the carbon sources become more planktonic and pelagic. Although horizontal distances between deep water (i.e., 60 m) and shallow water areas (i.e., 10 m) around Bermuda can be as little as 1.5 km, this is still enough to segregate shallow carbon sources from deep carbon sources. This is particularly true for species with small ranges, such as lionfish (Jud and Layman, 2012; Tamburello and Côté, 2015), at least on the temporal scales at which stable isotopes are integrated by predators.

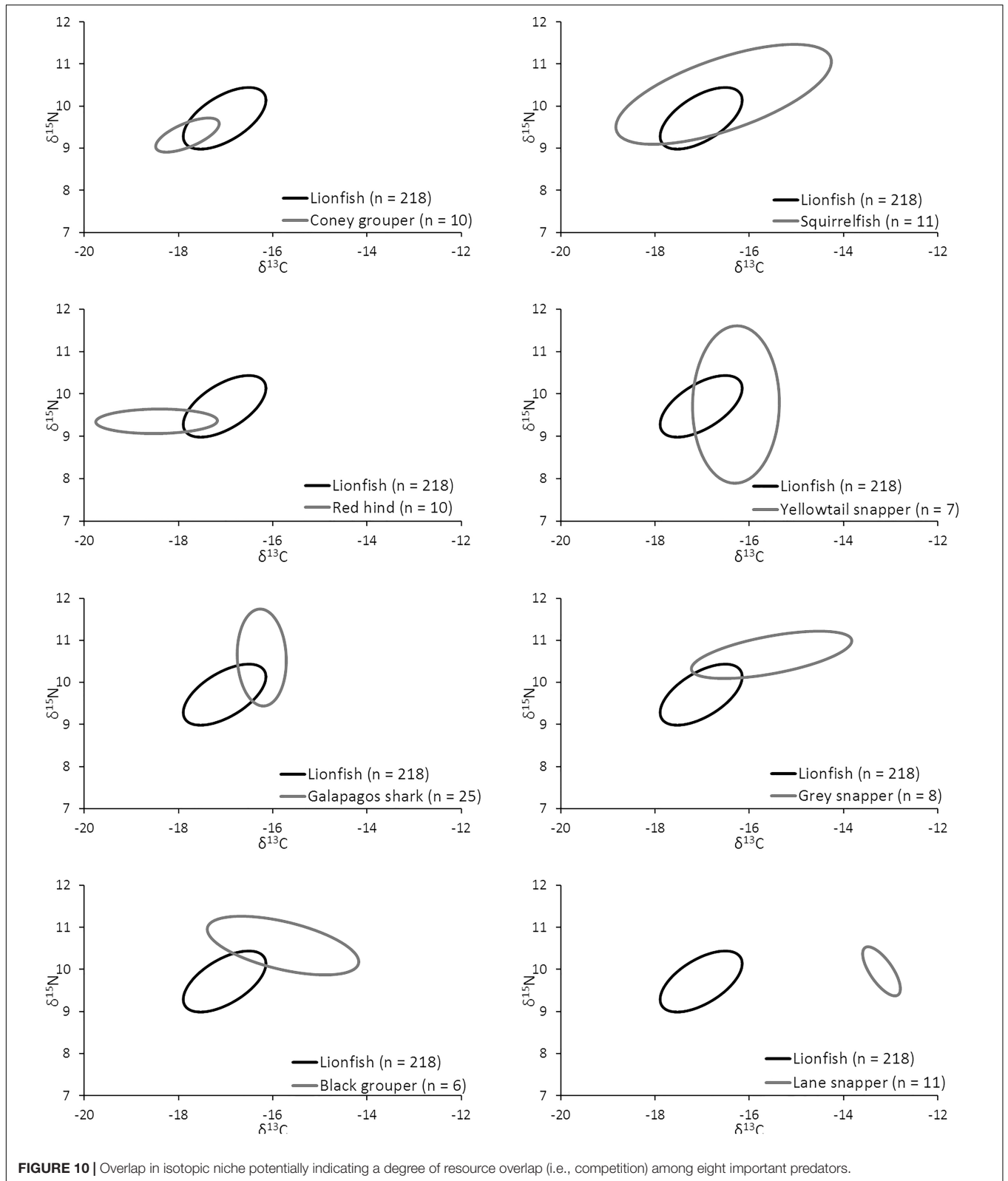
The predictable changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  between trophic levels (i.e., isotope enrichment rates or TDFs; DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; McCutchan et al., 2003; Caut et al., 2009) provide an opportunity to estimate the relative isotopic position of the resource pools from which lionfish and other consumers within the reef community derive their energy, thus identifying the theoretical base of these animals' food webs.

Considering the diversity of known lionfish prey items and a general lack of isotopic data by which to describe them, it would not be appropriate to use a multiple-source mixing model (i.e., Vander Zanden and Rasmussen, 2001) to reconstruct the diet of lionfish. Therefore, back-calculating resource pools using TDFs is a more suitable approach. However, the use of different TDFs generates considerable variability in the identification of carbon resource pools. Using global mean TDFs from Post (2002) suggested that lionfish food webs derived resources nearly equally from plankton and macroalgae. However, species- and location-specific TDFs are thought to provide more accurate and reliable results. Our approach, using global means (Post, 2002) for 1.0 trophic level [i.e., the number of trophic steps between primary producers (TP = 1) and consumers] together with lionfish-specific TDFs (Eddy, 2019) for 1.2 trophic levels (i.e., the number of trophic steps between primary consumers and lionfish), suggests most of the resources used by lionfish in Bermuda are derived from a plankton-based food web, with a less substantial contribution from macroalgae. Use of mean values for other marine teleosts (i.e., Caut et al., 2009) produces a similar finding for potential competitors, indicating that this applies more broadly across reef fish species in Bermuda, at least among the species included in this study. Indeed, planktonic productivity is important in Bermuda's oligotrophic mid-oceanic location where terrestrial nutrient inputs to reef environments are relatively low (Smith et al., 2013). The importance of planktonic production to the base of demersal food webs has also been described by Davenport and Bax (2002) for a reef ecosystem off southeastern Australia.

As lionfish are a recognized threat to marine ecosystems across their invaded range, with demonstrated ecological impacts (Albins and Hixon, 2008; Green et al., 2012; Lesser and Slattery, 2011), it is important to understand the various mechanisms through which these impacts occur. While the impact of lionfish predation is well established, the impact caused by resource competition is less understood, but the use of stable isotope ecology provides new ways to investigate community structure and explore how lionfish may affect the resource use of other teleosts. This approach shows substantial overlap between the isotopic niches of lionfish and certain ecologically and economically important native meso-predators (Figure 10), which may be indicative of resource competition.

It appears that lionfish in Bermuda compete most with coney groupers (*Cephalopholis fulva*), squirrelfishes<sup>2</sup> (Holocentridae), and red hind (*Epinephelus guttatus*), eclipsing 54, 23, 22%, respectively, of the niche space of these species. This is supported by the known feeding habits of these species, previously identified by SCA (Randall, 1967). Similarly, Hackerott et al. (2013) suggested coney grouper, red hind, and graysby (*Cephalopholis cruentata*) would be the most likely competitors of lionfish based on their similar foraging habitats and known prey items. As graysby is not abundant in Bermuda, we did not collect

<sup>2</sup>Our analysis of squirrelfish is assumed to include multiple species because samples provided from fishermen often were only identified with the common name, "squirrelfish". With that in mind, the isotopic niche of the family (Holocentridae) used in this study (6.47) should not be used to compare to a single competing species.



**FIGURE 10** | Overlap in isotopic niche potentially indicating a degree of resource overlap (i.e., competition) among eight important predators.

a sufficient number of samples to calculate a reliable estimate of its trophic niche (Jackson et al., 2011) and thus cannot comment on this potential interaction. In contrast, lionfish

eclipse a smaller portion of the niches belonging to gray snapper (*L. griseus*, 11%) and Bermuda's black grouper (*Mycteroperca bonaci*, 4%) and have no isotopic niche overlap with Lane

**TABLE 5** | Isotopic niche width of eight potential competitors and the overlap in niche with lionfish.

Species	Niche Width	Niche Overlap	%Pterois	%Comp
<i>Pterois</i> spp.	1.62	–	–	–
<i>Cephalopholis fulva</i>	0.65	0.35	21.73	54.29
Holocentridae <sup>a</sup>	6.47	1.49	92.26	23.09
<i>Epinephelus guttatus</i>	1.15	0.25	15.28	21.57
<i>Ocyurus chrysurus</i>	5.34	1.00	61.61	18.69
<i>Carcharhinus galapagensis</i>	1.87	0.35	21.53	18.64
<i>Lutjanus griseus</i>	2.44	0.26	16.15	10.72
<i>Mycteroperca bonaci</i>	2.93	0.12	7.23	4.00
<i>Lutjanus synagris</i>	0.52	0.00	0.00	0.00

%Pterois, percentage of lionfish niche occupied by competitor niche; %Comp, percentage of competitor niche occupied by lionfish niche; a, individuals from multiple squirrelfish species were combined in this analysis.

snapper (*L. synagris*), a species that forages over open sandy areas where lionfish do not typically hunt (Biggs and Olden, 2011; C. Eddy, personal observation). At first glance, it may appear counterintuitive that lionfish eclipse 19% of the isotopic niche of juvenile Galapagos sharks (*C. galapagensis*). However, they are known to feed on similar species, including a variety of mid-sized herbivores and planktivores (C. Eddy, unpublished data), so although different size classes are targeted, the prey species in question are unlikely to undergo substantial ontogenetic shifts in diet or isotope profiles. Altogether, it should be recognized that competitive interactions between lionfish and native species across the invaded region will vary according to the species composition of a given community, which may vary spatially, both horizontally and with depth, and also seasonally.

Considering the degree of trophic overlap between lionfish and several co-occurring mesopredators (Figure 10 and Table 5), it is important to consider the possible impacts of such competition on ecosystem structure and function. Depletion of certain prey items by lionfish may cause changes in the diet of other mesopredators, which could respond by choosing lower quality prey and/or modifying their feeding behavior, which may in turn expose them to greater predation risks during novel feeding events (Hrabik et al., 1998; Jackson, 2002; Albins, 2013). Consequences could potentially include reductions in growth, reproduction, and overall fitness of these competing species, or increased mortality, all of which could then lead to a reduction in abundance (Hrabik et al., 1998; MacRae and Jackson, 2001; Jackson, 2002; Hixon and Jones, 2005; Albins, 2015). Additionally, Hrabik et al. (1998) suggests that competition may decrease the strength of entire year classes, with subsequent impacts on community structure as well as population size and dynamics. As mesopredators have a direct influence on the abundance of smaller reef fishes, any effect that lionfish may have upon them, *via* exploitative competition could very well disrupt community structure and function.

Our data suggest that, in Bermuda, the coney grouper is likely to sustain the greatest competitive impact from lionfish. This could be compounded by the fact that the annual fishery landings of coney grouper, and thus their mortality rates, have increased considerably since 1990 (Trott and Luckhurst, 2008).

Future research to monitor potential changes in diet (including isotopic niche), growth, reproduction, and abundance of coney grouper, as well as other potentially competing mesopredators (e.g., squirrelfish and red hind), could indicate interspecific impacts and ecosystem effects of exploitative competition.

This study demonstrates that SIA and isotopic niches provide a valuable tool to recognize and highlight the ecological role of lionfish and the potential impact they may exert *via* resource competition. Recognizing this concern, our results provide a foundation for resource managers to estimate the impact of lionfish upon competitors, model ecosystem-wide effects of the invasion, and design or alter fisheries management plans to account for that. Furthermore, in the absence of baseline isotopic data for Bermuda prior to the arrival of lionfish, our results provide a benchmark by which future changes in trophic ecology and trophodynamics can be measured across the entire ecosystem.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all animals used in this research were collected and examined in Bermuda. Ethical review and approval were not required by Bermuda's Department of Environment and Natural Resources, which does not have an animal ethics committee.

## AUTHOR CONTRIBUTIONS

CE and JP executed the fieldwork and collected data. CE, JL, and MA analyzed the data. All authors developed the concept for this study and contributed to writing of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00435/full#supplementary-material>

**TABLE S1** | Sample sizes,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and standard errors for species mentioned in **Figures 8A,B**.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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