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Stable isotope and stomach content evidence of trophic overlap between invasive lionfish and native mesopredatory reef fishes in the Mexican Caribbean

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The invasive lionfish (*Pterois volitans/miles*) has become a dominant mesopredator on Caribbean reefs, potentially altering trophic interactions with native species. This study compared lionfish trophic ecology with that of three native reef mesopredators, *Scorpaena plumieri* (spotted scorpionfish), *Cephalopholis cruentata* (graysby grouper), and *Lutjanus apodus* (schoolmaster snapper) in the Puerto Morelos Reef National Park using stomach content and stable isotope analyses. Lionfish exhibited a lower proportion of empty stomachs (18%) than native mesopredators (> 60%) and consumed diverse crustaceans and reef-associated fishes. PERMANOVA revealed significant differences in diet composition among mesopredators and lionfish size classes, reflecting ontogenetic shifts from crustacean to piscivory. All species were classified as generalist secondary consumers, with trophic positions ranging from 3.2 to 3.9. Isotopic niche metrics indicated broad isotopic niches and substantial trophic overlap between lionfish and native mesopredators, particularly with *S. plumieri* (75%) and *L. apodus* (61%). Stable isotope analyses also revealed a significant relationship between lionfish body size and $\delta^{15}N$ values, indicating ontogenetic increases in trophic position. Bayesian mixing models suggested that lionfish integrate multiple trophic pathways associated with crustaceans and reef fishes. Together, these findings highlight broad resource use, high trophic plasticity, and substantial niche overlap, potentially increasing competitive interactions and altering trophic dynamics in Caribbean reef ecosystems.

Keywords: Diet overlap, Invasive mesopredators, Secondary consumers, Trophic ecology, Trophic interactions.

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El pez león invasor (*Pterois volitans/miles*) se ha convertido en un mesodepredador dominante en los arrecifes del Caribe, con potencial de alterar las interacciones tróficas con especies nativas. En este estudio se comparó la ecología trófica del pez león con la de tres mesodepredadores arrecifales nativos, *Scorpaena plumieri* (escorpión manchado), *Cephalopholis cruentata* (cherna criolla) y *Lutjanus apodus* (pargo amarillo), en el Parque Nacional Arrecife de Puerto Morelos, mediante análisis de contenido estomacal e isótopos estables. El pez león presentó una menor proporción de estómagos vacíos (18%) que los mesodepredadores nativos (> 60%) y consumió diversos crustáceos y peces asociados al arrecife. Los análisis de PERMANOVA revelaron diferencias significativas en la composición de la dieta entre mesodepredadores y las clases de talla del pez león, reflejando cambios ontogenéticos desde el consumo de crustáceos hacia la piscivoría. Todas las especies fueron clasificadas como consumidores secundarios generalistas, con posiciones tróficas entre 3.2 y 3.9. Las métricas de nicho isotópico indicaron nichos amplios y un importante traslape trófico entre el pez león y los mesodepredadores nativos, particularmente con *S. plumieri* (75%) y *L. apodus* (61%). Los análisis de isótopos estables revelaron una relación significativa entre el tamaño corporal del pez león y los valores de $\delta^{15}N$, indicando incrementos ontogenéticos en la posición trófica. Los modelos bayesianos de mezcla sugirieron que el pez león integra múltiples vías tróficas asociadas con crustáceos y peces arrecifales. En conjunto, estos hallazgos destacan un amplio uso de recursos, alta plasticidad trófica y un importante traslape de nicho, con el potencial de incrementar las interacciones competitivas y alterar la dinámica trófica en los ecosistemas arrecifales del Caribe.

Palabras clave: Consumidores secundarios, Depredadores invasores, Ecología trófica, Interacciones tróficas, Solapamiento de dieta.

INTRODUCTION

Interspecific competition is a crucial aspect of invasive species ecology, with significant implications for native species and communities (Strayer *et al*., 2006). When a novel invader depletes shared resources, exploitative competition can compel native organisms to rely on suboptimal dietary sources and habitats (Park, 1954; Petren, Case, 1996; Bøhn, Amundsen, 2001), potentially resulting in reduced fitness or physiological condition, or limiting the population growth of the native competitor (Park, 1954; Schoener, 1982; Petren, Case, 1996). Successful invaders may entirely displace native species, leading to local extinctions and biodiversity loss (Mandrak, Cudmore, 2010). Conversely, some studies have not observed invaders affecting the density or species richness of their competitors (Elise *et al*., 2015; Chevalier-Monteagudo, 2017). Other studies found no evidence that invasive predators significantly affected the density, richness, composition, diversity, or structure of prey fish populations (Hackerott *et al*., 2017; Chevalier-Monteagudo, 2017; Cobián-Rojas *et al*., 2018a). For instance, Elise *et al*. (2015) observed a consistent reduction in prey abundance within reef systems where predatory invaders were present, compared to those where they were absent. However,

the impact of a new invader is likely to vary significantly among localities; this could be influenced by factors such as the initial characteristics of the reef fish assemblage, the traits of the invading predator, the time since invasion, the availability of prey resources, and the ecological structure of the invaded area, among others (Levine, D'Antonio, 1999; Elise *et al*., 2015). One significant knowledge gap lies in understanding the synergistic effects of invasive species with existing stressors in coral reefs, such as eutrophication, sedimentation, rising water temperatures, coral bleaching, overfishing, and the influx of sargassum (Fabricius, 2005; Eakin *et al*., 2019; Rodríguez-Martínez *et al*., 2019). Alternatively, adaptation can drive niche partitioning as species optimize the use of new resources to mitigate the impacts of competition (Schoener, 1974; Ross, 1986; Cherel *et al*., 2008). Thus, studying the nature and outcomes of competitive interactions between invasive and native species is crucial for predicting the long-term effects of biological invasions and informing subsequent management efforts.

Pterois volitans/miles, native to the Indo-Pacific region, has now established itself along the southeastern coast of the United States and throughout the Great Caribbean (Schofield, 2010). *Pterois volitans* and *P. miles* are morphologically very similar in the invaded region; therefore, the only way to accurately identify them in their non-native distribution range is through molecular analysis (Morris, Whitfield, 2009; Burford-Reiskind *et al*., 2019). The use of the *P. volitans/miles*, or simply "lionfish" from now on, is preferred to refer to the two species that are present in the Western Atlantic and the Caribbean Sea. The presence of these invasive species represents one of the most significant anthropogenic influences on Caribbean reef ecosystems. Their rapid spread and predatory habits have drawn considerable attention, suggesting an impact on the reduction of biodiversity within affected ecosystems (Bellard *et al*., 2016). The success of lionfish as invasive species can be attributed, at least in part, to their adaptable feeding behavior, prolific reproductive capacity, and the absence of natural predators within their introduced range (Whitfield *et al*., 2017; Del Río *et al*., 2023).

Reports indicate that lionfish prey on a wide range of species, primarily invertebrates and fishes, as demonstrated by stomach content and stable isotope studies conducted in invaded regions (Muñoz *et al*., 2011; Cure *et al*., 2012; Layman, Allgeier, 2012; Côté *et al*., 2013; Arredondo-Chávez *et al*., 2016; Cobián-Rojas *et al*., 2016). These studies suggest that lionfish may exhibit broader trophic niches in invaded ecosystems than in their native range (Cure *et al*., 2012; Priyadharsini *et al*., 2013). However, relatively few studies have simultaneously evaluated dietary composition, isotopic niche breadth, ontogenetic trophic shifts, and resource overlap with native mesopredators using both stable isotope and stomach-content analyses within the same reef system.

Lionfish demonstrate a remarkable ability to adapt to refuge areas and prey on new species (Cure *et al*., 2012; Lönnstedt, McCormick, 2013; Arredondo-Chávez *et al*., 2016). Their voracious appetites and lack of natural predators have raised concerns about their ability to outcompete native species for resources (Andradi-Brown, 2019). They pose a potential threat as competitors to native mesopredators such as snappers (Lutjanidae), groupers (Serranidae), and stonefish (Scorpaenidae) (O'Farrell *et al*., 2014; Murillo-Pérez *et al*., 2020), and have even been observed displacing them (Albins, Hixon, 2008; Molina, 2009; Albins, Hixon, 2011; Green *et al*., 2012; Layman, Allgeier, 2012; Pantoja-Echeverría *et al*., 2017). Even species of commercial value have been recorded in their diet (Muñoz *et al*., 2011; Arredondo-Chávez *et al*., 2016), representing both ecological and economic risks (Albins, Hixon, 2011).

Documenting the dietary composition and trophic interactions of lionfish is essential for understanding their feeding habits and ecosystem dynamics, as well as for assessing their ecological impacts, particularly in the context of invasive species and native fauna, to develop effective management strategies (Albins, Hixon, 2011; Albins, 2012; Morris, Green, 2013; Arredondo-Chávez *et al*., 2016; Cobián-Rojas *et al*., 2018b).

Stomach content analysis provides valuable insights into the types and relative abundance of prey species consumed, elucidating dietary preferences, patterns of predation, and prey selection (Davis *et al*., 2012; Svanbäck *et al*., 2015). However, stomach content analysis alone may not capture the full breadth of the diet, particularly regarding the assimilation of different prey items over time. Stable isotope analysis complements stomach content analysis by offering a retrospective view of the dietary habits and trophic position of species over an extended period. By measuring the signatures of stable carbon and nitrogen isotopes in tissues such as muscle, we can infer the assimilation of different prey items and assess the species trophic position within the food web (Fry, 2006; Layman *et al*., 2012).

These two methods are complementary, providing valuable information on the long-term feeding ecology of a species, including their reliance on specific prey groups and potential shifts in trophic dynamics across different habitats or ontogenetic development (Pilger *et al*., 2010; Hill *et al*., 2015).

In this study, we compared the trophic ecology of invasive lionfish with three native reef mesopredators (*Cephalopholis cruentata*, *Lutjanus apodus* and *Scorpaena plumieri*) in the Mexican Caribbean. Using stomach content analysis, we evaluated population-level diet composition, feeding strategy, niche breadth, dietary overlap and ontogenetic dietary shifts among mesopredators. Stable isotope analysis was used to estimate trophic position, isotopic niche width, isotopic overlap, and ontogenetic trophic variation. In addition, exploratory Bayesian stable isotope mixing models were conducted to evaluate potential trophic pathways supporting reef mesopredators. By integrating these complementary approaches, we aimed to assess trophic interactions, resource overlap, trophic differentiation, ontogenetic trophic shifts, and potential competition interactions among invasive lionfish and native reef mesopredators.

MATERIAL AND METHODS

Sample collections. Mesopredatory fish specimens were collected at 33 sites across the Puerto Morelos Reef National Park (PMRNP), located in the northern Mexican Caribbean (Fig. 1). Sampling was conducted during one week of fieldwork each month between August 2014 and September 2015. Fish were collected in shallow reef habitats at depths ranging from 3 to 30 m using SCUBA. Surveys were performed during daytime, twilight (dusk and dawn), and nighttime periods using multi-pronged pole spears. Mesopredator collections were conducted at the same sites and during the same sampling periods to ensure comparable sampling effort. Due to the venomous nature of lionfish and *S. plumieri*, individuals were handled using puncture-resistant gloves and placed in secure containers immediately after capture. Additional collection methods included the use of hand nets and an anesthetic eugenol solution (1:5 ratio eugenol: ethanol) to facilitate the capture of smaller individuals.

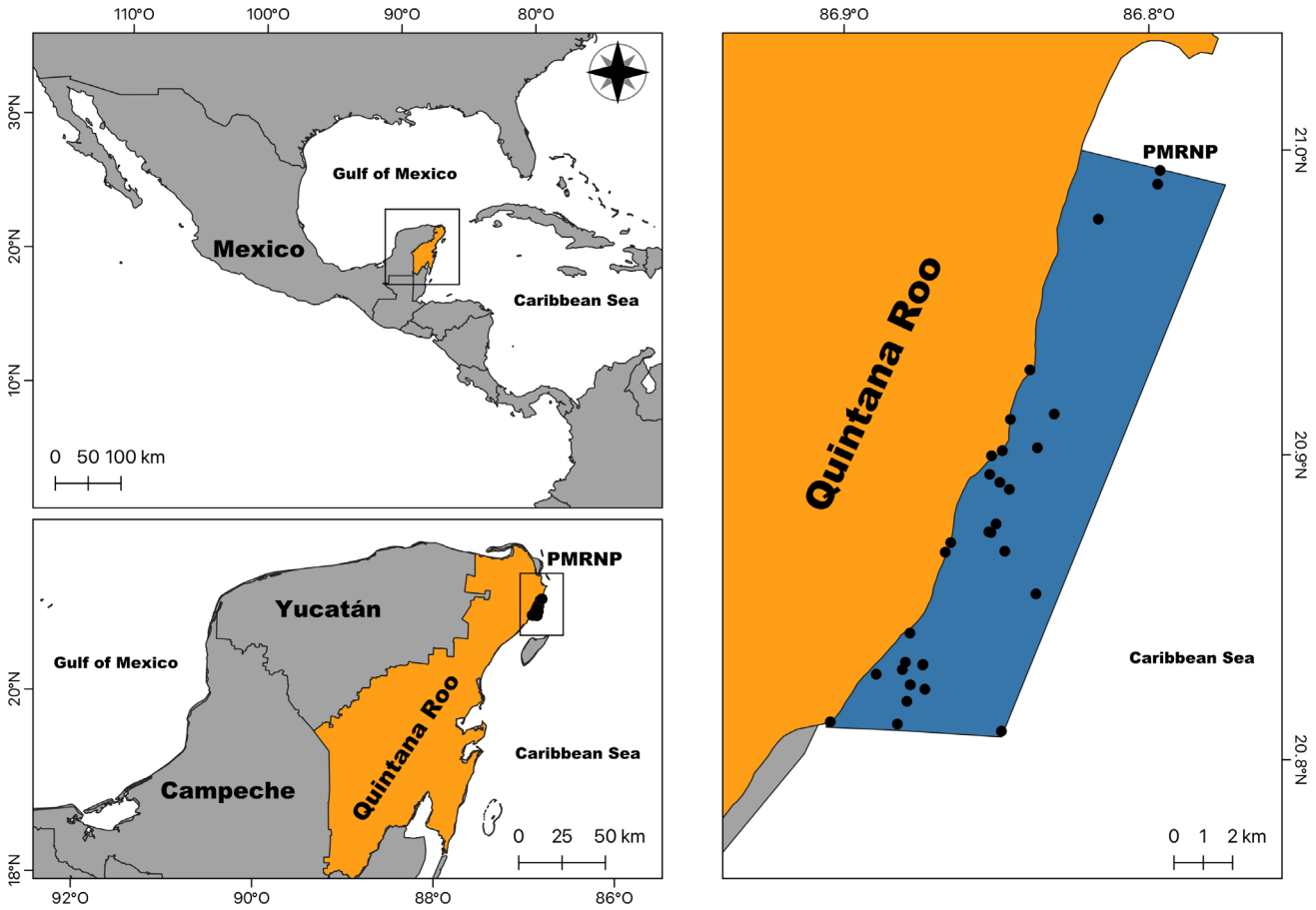

FIGURE 1 | Location of the Puerto Morelos Reef National Park. Blue color represents the polygon of the National Park. Black circles represent the collection sites.

Stomach content analyses. Stomach content analysis was conducted for all collected individuals of the four mesopredator species. Four hundred and thirty stomachs were examined, including 124 lionfish, 134 *C. cruentata*, 155 *L. apodus*, and 17 *S. plumieri*. Empty stomachs were included in the estimation of stomach fullness and feeding activity but excluded from prey composition analyses. After collection, the fish were refrigerated and transported to the laboratory, where their standard length (in millimeters) and wet weight (in grams) were recorded. Subsequently, the fish were dissected, and the length of the intestine (mm) and the weight of the stomach contents (mg) were measured. Prey items were identified to the lowest possible taxonomic level using a stereomicroscope (AmScope SZMT2) and specialized keys for fish and crustaceans (Abele, Kim, 1986; McEachran, Fechhelm, 1998; Huffard *et al*., 2008; Froese, Pauly, 2014; Robertson *et al*., 2015). Prey species were counted and individually weighed to the nearest 0.01 mg. Some prey items were grouped into higher-level taxonomic categories or classified as unidentified prey due to difficulties in species-level identification.

Stomach fullness was visually estimated based on the relative volume of prey items and classified into four categories: full (stomach completely packed with prey), mostly full (50–100% fullness), partially full (1–50% fullness), and empty (no identifiable prey remains). This qualitative classification has been widely used in stomach content studies

to describe recent feeding activity and allows comparisons among mesopredators (Hyslop, 1980; Arredondo-Chávez *et al*., 2016; Amundsen, Sánchez-Hernández, 2019).

To assess whether sampling effort adequately characterized mesopredator diets, rarefaction curves were generated using EstimateS v. 9.1.0 with 500 randomizations without replacement (Colwell, 2013). Dietary richness was further evaluated using two non-parametric estimators (Chao2 and Mao-Tau). Stomach repletion index was calculated for all individuals to quantify the relative amount of food present in each stomach (Hyslop, 1980).

We calculated the percentage of a prey-specific index of relative importance (%PSIRI) to determine the dominance of prey, following the criteria outlined by Brown *et al*. (2012). The %PSIRI incorporates the percentage frequency of occurrence (%FOi = number of stomachs with prey i divided by the total number of stomachs) and the prey-specific abundance:

$$\%PA_i = \Sigma^{n}_{j=1} \%Aij/n$$

the average percentage abundance ($\%N_i$, $\%W_i$):

$$\%A_i = \Sigma^{n}_{j=1} \%Aij/n$$

where $\%A_{ij}$ is the abundance (counts or weights) of prey i in stomach sample j, n_i is the number of stomachs containing prey i, and n is the total number of stomachs. The feeding strategy was further interpreted based on the relationship between prey numerical importance (%N) and frequency of occurrence (%F), following the conceptual framework proposed by Amundsen *et al*. (1996). We used the standardized Levin's index (BI) to calculate the niche width. The BI ranges between 0 and 1, with a fish considered a specialist when the BI value is lower than 0.6, and a generalist when the BI value is greater than 0.6 (Krebs, 1989). Trophic position derived from stomach content analysis (TP_SCA) was estimated using TrophLab software (Pauly *et al*., 2000). This approach estimates mesopredator trophic position as the weighted mean trophic level of all prey items, using trophic level values from FishBase and weighting each prey item according to its relative importance in the diet. Horn's index (Krebs, 1989) was employed to compare the PSIRI index of the four mesopredators.

To classify individuals by size, we utilized the standard length of all surveyed fish and percentiles in JMP v. 6.0. Subsequently, the 11 size classes obtained were categorized into three sizes: small (1–15 cm), juveniles (15.1–22 cm), and adults (22.1–34 cm). Lionfish was the only species for which we analyzed stomach content by size, describing the PSIRI index, Levin's index, and trophic position (small: n = 39; juveniles: n = 52; adults: n = 33). For the other species, we lacked a sufficient sample size to conduct these analyses. To assess prey diversity among sizes, a Shannon-Wiener analysis was performed (Margalef, 1958). Horn's index (Krebs, 1989) was employed to compare the PSIRI index per size of lionfish with the PSIRI index of *L. apodus*, *S. plumieri*, and *C. cruentata*. Differences in diet composition among species and among lionfish size classes were evaluated using a permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities and 999 permutations. The analysis was conducted using square-root transformed %PSIRI values to reduce the influence of dominant prey categories.

Isotopic analysis. For 95 specimens of lionfish, 17 *S. plumieri*, 39 *C. cruentata*, and 37 *L. apodus*, approximately 4 g of dorsal white muscle tissue was extracted near the dorsal fin, rinsed with water, and stored in individual sterilized Whirl-Pak bags at -20 °C until analysis. Muscle tissue was selected due to its relatively slow turnover rate for $\delta^{13}C$ and $\delta^{15}N$, allowing integration of dietary information over weeks to months and reducing the influence of short-term variability in isotopic baselines (MacAvoy *et al*., 2001). In addition, isotopic composition of muscle tissue is not affected by the use of chemical anesthetics such as eugenol (Malpica-Cruz *et al*., 2019). Additional isotopic samples representing potential prey groups and basal components of the food web were also collected within the study area to characterize the trophic pathways supporting reef mesopredators. These samples included reef-associated fishes, crustaceans, macroalgae, seagrasses, phytoplankton, and other benthic organisms, including several prey taxa previously reported in lionfish diets from the Mexican Caribbean (Arredondo-Chávez *et al*., 2016). Organisms were collected during field surveys using hand nets, pole spears, and an anesthetic eugenol solution (1:5 ratio eugenol:ethanol) for small fishes and invertebrates, whereas primary producers and sessile organisms were collected manually by SCUBA divers. Samples were separated from abiotic material in situ and transported to the laboratory on ice before processing. These organisms were subsequently grouped into isotopic source categories for exploratory Bayesian mixing model analyses.

Dorsal white muscle tissue was oven-dried individually in tin trays at 62 °C for approximately 48 h until constant mass was reached. Similar drying temperatures (60–70 °C) have been widely used in stable isotope analysis of fish tissues without reported effects on $\delta^{13}C$ or $\delta^{15}N$ values (*e.g*., Barrow *et al*., 2008; Logan *et al*., 2008; Britton, Busst, 2018). All samples were processed under identical conditions to ensure methodological consistency across species and size classes.

Lipids were subsequently extracted using a chloroform–methanol solution (1:1 v/v) for 24 h to minimize potential bias in $\delta^{13}C$ values associated with variable lipid content. After air-drying for an additional 24 h, samples were homogenized and ground to a fine powder using a mortar and pestle before isotopic analysis. Samples were then weighed to 1.0 ± 0.1 mg in tin capsules (8 x 5 mm) using an Ohaus microbalance and analyzed at the UC Davis Stable Isotope Facilities. Stable isotope ratios were expressed using conventional delta notation (δ) in parts per thousand (‰) according to the equation $\delta^{15}N$ or $\delta^{13}C = \{(R_{sample} / R_{standard}) - 1\} \times 10^3$, where R represents the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Reference standards were Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric nitrogen (AIR) for nitrogen. Analytical precision was better than ±0.2‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$, based on repeated measurements of internal laboratory standards analyzed throughout the samples.

Trophic position based on stable isotopes (TP_SIA) was estimated using $\delta^{15}N$ values following the framework of Post (2002): $TP_i = [(\delta^{15}N_i - \delta^{15}N_baseline) / \Delta n] + \lambda$, where $\delta^{15}N_i$ represents the mean nitrogen isotopic value of consumer i, $\delta^{15}N_baseline$ corresponds to the isotopic value of the baseline organism, Δn is the trophic enrichment factor (2.8‰), and λ is the trophic position of the baseline organism. The isotopic baseline corresponded to primary consumers (λ = 2), represented by small benthic invertebrates and herbivorous reef fishes, using mean $\delta^{15}N$ values derived from baseline organisms sampled within the study area. This baseline was selected to reflect

the dominant trophic pathways of the reef system and to provide a consistent reference for trophic position estimation. The trophic enrichment factor used here follows the meta-analysis of Caut *et al*. (2009), which provides broadly applied estimates for aquatic consumers. A single-baseline model was considered appropriate because $\delta^{13}C$ values of mesopredators showed relatively limited dispersion, suggesting integration of similar basal carbon sources within the reef system. Although two-source models may be useful when consumers integrate isotopically distinct basal resources (*e.g*., benthic vs pelagic), the limited separation observed in $\delta^{13}C$ values among consumers in this study did not support the application of a dual-baseline approach.

Isotopic niche metrics were estimated using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson *et al*., 2011). Overall, trophic niche extent was quantified using the convex hull total area (TA), which represents the total isotopic space occupied by each mesopredator species. Core isotopic niche space was estimated as the standard ellipse area corrected for small sample size (SEAc), representing the isotopic niche occupied by approximately 40% of individuals (Curtis *et al*., 2017). Isotopic niche overlap among species and size classes was calculated as the proportional overlap between SEAc ellipses. Bayesian ellipses were estimated using 10,000 posterior iterations.

To further explore potential trophic pathways supporting reef mesopredators, exploratory Bayesian stable isotope mixing models were conducted using the package simmr in R (Parnell *et al*., 2013). Predator isotope values were analyzed separately for each species using individual $\delta^{13}C$ and $\delta^{15}N$ values. Potential food sources were grouped into five functional categories based on ecological similarity, trophic role, and isotopic characteristics to reduce source redundancy and improve model interpretability: crustaceans, herbivorous fishes, small reef fishes, phytoplankton-derived production, and macroalgae/seagrass-associated production. Source means and standard deviations were calculated from isotopic data of prey and basal resources collected within the study area. Trophic discrimination factors of 0.4 ± 0.2‰ for $\delta^{13}C$ and 3.4 ± 0.5‰ for $\delta^{15}N$ were applied following commonly used estimates for marine fishes. Models were fitted using Markov Chain Monte Carlo (MCMC) simulations, and posterior distributions were summarized as mean proportional contributions with 95% credible intervals. Because isotopic overlap among some source groups remained moderate, model outputs were interpreted as exploratory estimates of trophic pathways rather than exact dietary proportions.

Ontogenetic variation in isotopic composition was evaluated using the same size classes defined for stomach content analyses. Differences in $\delta^{13}C$ values, $\delta^{15}N$ values, and trophic position among mesopredator species and size classes were tested using Kruskal-Wallis analyses due to non-normal data distribution, as assessed with Kolmogorov-Smirnov and Lilliefors test. When significant differences were detected ($p < 0.05$), post hoc Tukey-HSD tests were applied. Mean isotopic values and standard deviations were calculated. In addition, the relationship between body size and $\delta^{15}N$ values was evaluated using linear regression analyses to further assess ontogenetic trophic shifts. A bivariate plot of mean isotopic values (±1 SD) was constructed to visualize trophic relationships among mesopredator species in $\delta^{13}C$-$\delta^{15}N$ space.

RESULTS

Population-level diet composition and feeding activity. Four hundred and thirty specimens of the four mesopredatory species were collected. *Scorpaena plumieri* was represented by 17 individuals, with standard length (SL) ranging from 12 to 33.5 cm (mean = 24.1 ± 1.5 cm) and weights ranging from 35.6 to 854.7 g (mean = 376.7 ± 63.1 g). *Cephalopholis cruentata* comprised 134 individuals, with SL ranging from 7.5 to 30 cm (mean = 19.5 ± 0.4 cm) and weights ranging from 5.5 to 525.3 g (mean = 130.3 ± 6.8 g). *Lutjanus apodus* included 155 individuals, with SL ranging from 5 to 30.5 cm (mean = 18.1 ± 0.4 cm) and weights ranging from 9 to 497.7 g (mean = 131.8 ± 9.1 g). Lionfish included 124 individuals, with SL ranging from 4.5 to 34 cm (mean = 18.6 ± 0.5 cm) and weights ranging from 1 to 620 g (mean = 118.0 ± 11.4 g).

A high proportion of empty stomachs was observed in native mesopredators. In *S. plumieri*, 12 out of 17 stomachs were empty (71%), leaving only five stomachs with identifiable prey. Similarly, 91 of 134 stomachs in *C. cruentata* (68%) and 98 of 155 stomachs in *L. apodus* (63%) were empty. In contrast, lionfish showed a markedly lower proportion of empty stomachs, with only 22 out of 124 stomachs lacking prey remains (18%) (Fig. 2A).

We identified 35 prey items in the stomachs of lionfish, representing 16 families and 23 genera (Tab. **S1**). When prey were grouped into functional categories based on the %PSIRI index, lionfish diet was dominated by cleaner shrimps (43.3%) and benthic shrimps (30.8%). Other crustacean groups were comparatively less important, including crabs (1.6%), stomatopods (0.1%), and other benthic decapods (3.8%). Fish prey was represented mainly by mobile reef carnivorous fishes (9.1%), herbivorous reef fishes (5.9%), territorial damselfishes (2.6%), pelagic or water-column fishes (1.1%), and cryptobenthic fishes (0.8%) (Fig. 2B; Tab. **S2**).

In *C. cruentata*, 24 prey items belonging to 15 families and 18 genera were identified (Tab. **S1**). Functional group analysis showed a relatively balanced trophic contribution of crustaceans and fishes. Stomatopods constituted the most important crustacean group (28.8%), followed by cleaner shrimps (10.3%), other benthic decapods (4.2%), benthic shrimps (3.9%), and crabs (3.4%). Fish prey consisted mainly of mobile reef carnivorous fishes (13.4%), herbivorous reef fishes (12.3%), pelagic/water-column fishes (8.1%), and cryptobenthic fishes (1.3%) (Fig. 2B; Tab. **S2**).

For *L. apodus*, 17 prey items belonging to 14 families and 11 genera were recorded (Tab. **S1**). Its diet was dominated by amphipods and other small crustaceans (76.9%), with secondary contributions from crabs (7.4%), benthic shrimps (7.1%), cleaner shrimps (5.2%), and other benthic decapods (1.1%). Fish prey represented only minor components, including herbivorous reef fishes (0.3%) and cryptobenthic fishes (0.3%) (Fig. 2B; Tab. **S2**). In contrast, the diet of *S. plumieri* was dominated by crabs (33.3%), followed by cleaner shrimps (16.7%) and mobile reef carnivorous fish (16.7%), and pelagic/water-column fishes (16.7%) (Fig. 2B; Tabs. **S2**, **S3**).

PERMANOVA revealed significant differences in diet composition among mesopredator species (pseudo-F = 2.5, R^2 = 0.3, p = 0.001). Pairwise comparisons indicated that *L. apodus* differed significantly from lionfish and *C. cruentata*, mainly due to the dominance of amphipods in its diet. Despite these overall differences, Horn's index indicated moderate dietary overlap between lionfish and *C. cruentata* (0.54), as well as between *S. plumieri* and *C. cruentata* (0.43) (Tab. 1).

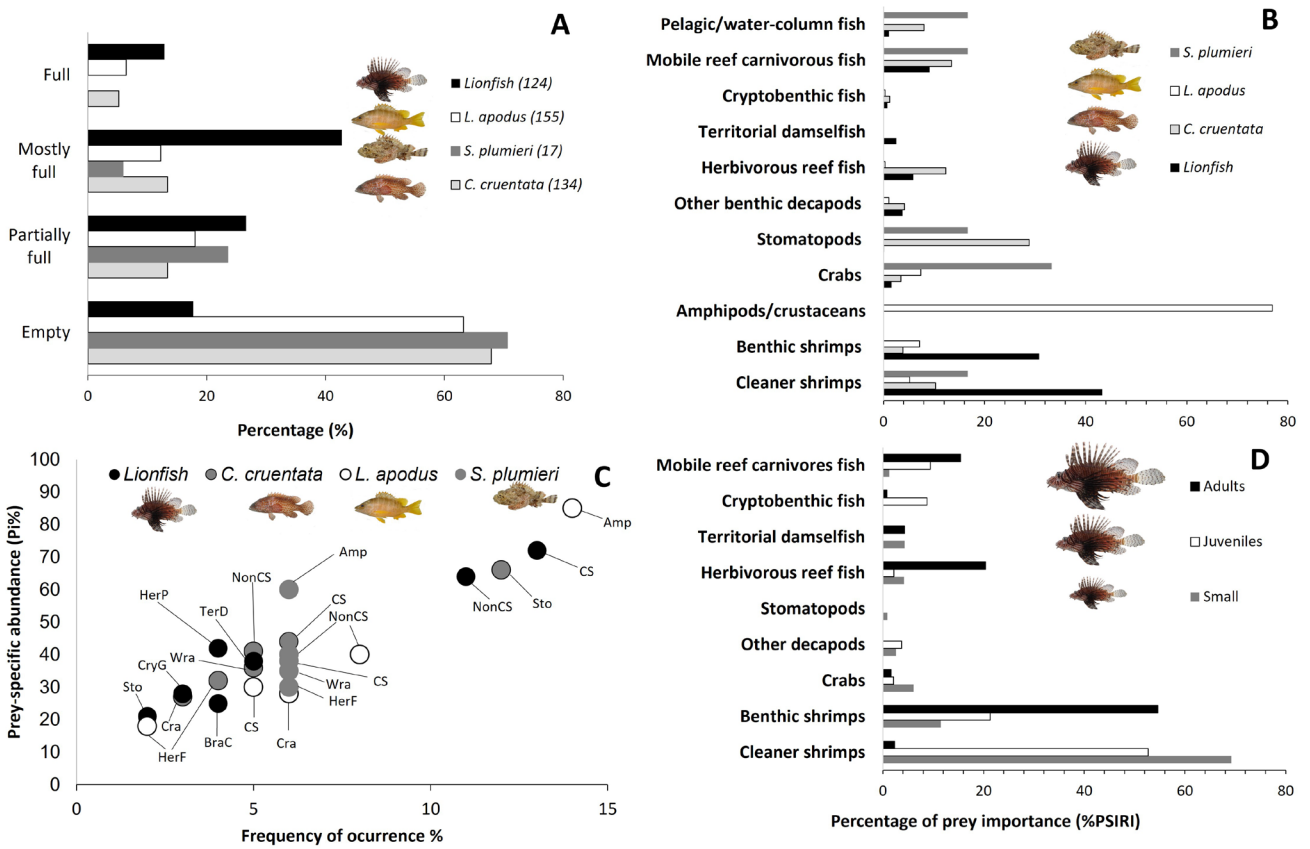

FIGURE 2 | Feeding patterns of the four mesopredatory reef fishes based on stomach content analyses. **A.** Stomach fullness categories expressed as the percentage of individuals for each predator species; total sample sizes are shown in parentheses after each species name. The number of individuals in each category is indicated after the bars. **B.** Diet composition expressed as percentage of the prey-specific index of relative importance (%PSIRI), grouped by functional prey categories for each predator species. **C.** Amundsen graphical analysis of feeding strategy based on prey-specific abundance (Pi) and frequency of occurrence (Fi) for the main prey functional groups across predator species. **D.** Ontogenetic variation in diet composition of Lionfish, showing the %PSIRI contribution of functional prey groups for small, juvenile, and adult size classes. Abbreviations of prey functional groups are as follows: Amp = amphipods (*Gammarus* spp.); CS = cleaner shrimps; NonCS = non-cleaner benthic shrimps; Sto = stomatopods; Cra = crabs; HerF = herbivorous reef fishes; Wra = wrasses (mobile reef carnivorous fishes).

The Amundsen graphical analysis indicated a mixed feeding strategy for lionfish, characterized by a generalist pattern combined with partial specialization on dominant crustacean prey, particularly cleaner shrimps and non-cleaning shrimps. In contrast, *L. apodus* exhibited a more specialized feeding strategy, strongly associated with amphipod consumption. *C. cruentata* showed an intermediate opportunistic strategy with moderate reliance on multiple crustacean and fish prey types. Interpretation for *S. plumieri* should be treated cautiously due to the limited number of stomachs containing prey (Fig. 2C).

Trophic position estimates based on stomach content (TP_SCA) and stable isotopes (TP_SIA). The Levin index indicated that all four mesopredator species exhibited generalist feeding habits: lionfish (BI = 0.7), *C. cruentata* (BI = 0.6), *L. apodus* (BI = 0.6), and *S. plumieri* (BI = 0.8). Trophic position estimates derived from stomach content analysis (TP_SCA) classified all mesopredators as secondary consumers, with

TABLE 1 | Trophic overlaps among predator species and lionfish size classes based on dietary composition and stable isotope niche metrics. Values outside parentheses represent dietary overlap estimated using Horn's index calculated from %PSIRI values derived from stomach content analysis. Values in parentheses represent proportional isotopic niche overlap based on standard ellipse areas corrected for small sample size (SEAc) obtained from stable isotope analyses. Higher values indicate greater trophic similarity among predators at short-term (dietary) and longer-term (isotopic) temporal scales. Lf: Lionfish, Cc: *Cephalopholis cruentata*, La: *Lutjanus apodus*, Sp: *Scorpaena plumieri*.

	Lf	Cc	La	Sp	Lf small	Lf juvenils	Lf adults
Lf	1	(0.23)	(0.61)	(0.75)	-	-	-
Cc	0.54	1			0.52	0.43	0.54
La	0.29	0.23	1		0.26	0.26	0.26
Sp	0.29	0.43	0.19	1	0.25	0.36	0.37

values of 3.7 ± 0.6 for lionfish, 3.9 ± 0.6 for *C. cruentata*, 3.6 ± 0.6 for *L. apodus*, and 3.9 ± 0.6 for *S. plumieri* (Fig. 3A). Significant differences in TP_SCA were detected between *L. apodus* and lionfish ($p < 0.005$).

Stable isotope analyses included 188 muscle tissue samples: 95 lionfish, 17 *S. plumieri*, 39 *C. cruentata*, and 37 *L. apodus*. Mean isotopic values were $\delta^{13}C$ = -13.5 ± 1.0‰ and $\delta^{15}N$ = 9.6 ± 0.5‰ for lionfish; $\delta^{13}C$ = -14.0 ± 0.5‰ and $\delta^{15}N$ = 10.1 ± 0.4‰ for *C. cruentata*; $\delta^{13}C$ = -13.0 ± 0.9‰ and $\delta^{15}N$ = 10.5 ± 0.8‰ for *L. apodus*; and $\delta^{13}C$ = -13.4 ± 0.6‰ and $\delta^{15}N$ = 9.7 ± 0.6‰ for *S. plumieri* (Fig. 3C).

Trophic position estimates derived from stable isotopes (TP_SIA) ranged from 3.2 to 3.6, categorizing all mesopredators as secondary consumers (Tab. 2; Fig. 3A). Significant differences in trophic position were detected among species (Kruskal-Wallis, $p = 0.001$), with lionfish exhibiting the lowest TP_SIA values (3.2 ± 0.2) and *L. apodus* the highest (3.6 ± 0.3).

Trophic niche width and overlap. The isotopic niche breadth of lionfish ranged from $\delta^{13}C$ = -16.2 to -11.2‰ and $\delta^{15}N$ = 8.5 to 10.8‰. For *C. cruentata*, values ranged from $\delta^{13}C$ = -14.7 to -12.7‰ and $\delta^{15}N$ = 9.4 to 11.3‰. *L. apodus* exhibited a range from $\delta^{13}C$ = -16.0 to -11.4‰ and $\delta^{15}N$ = 8.9 to 12.9‰, whereas *S. plumieri* ranged from $\delta^{13}C$ = -14.6 to -12.2‰ and $\delta^{15}N$ = 8.2 to 10.5‰ (Fig. 3B).

Kruskal-Wallis analyses detected significant differences in isotopic values among species. Post hoc comparisons showed that lionfish and *S. plumieri* did not differ significantly in $\delta^{13}C$ ($p = 0.6$) or $\delta^{15}N$ values ($p = 0.2$). However, lionfish differed significantly from *C. cruentata* ($\delta^{13}C$: $p = 0.01$; $\delta^{15}N$: $p = 0.001$) and *L. apodus* ($\delta^{13}C$: $p = 0.01$; $\delta^{15}N$: $p = 0.001$). Lionfish exhibited lower $\delta^{15}N$ values than both species. *Cephalopholis cruentata* and *L. apodus* also differed significantly in $\delta^{13}C$ values ($p = 0.001$), with *C. cruentata* exhibiting higher mean $\delta^{13}C$ values. Although *S. plumieri* and *L. apodus* did not differ significantly in $\delta^{13}C$ values ($p = 0.2$), significant differences were detected in $\delta^{15}N$ values ($p = 0.007$), with *L. apodus* exhibiting higher mean $\delta^{15}N$ values.

Isotopic niche metrics revealed that *L. apodus* exhibited the largest total isotopic niche area (TA = 10.3), followed by lionfish (TA = 8.3), whereas *S. plumieri* (TA = 3.7) and *C. cruentata* (TA = 2.5) occupied smaller isotopic spaces (Fig. 3B). Similarly, *L.*

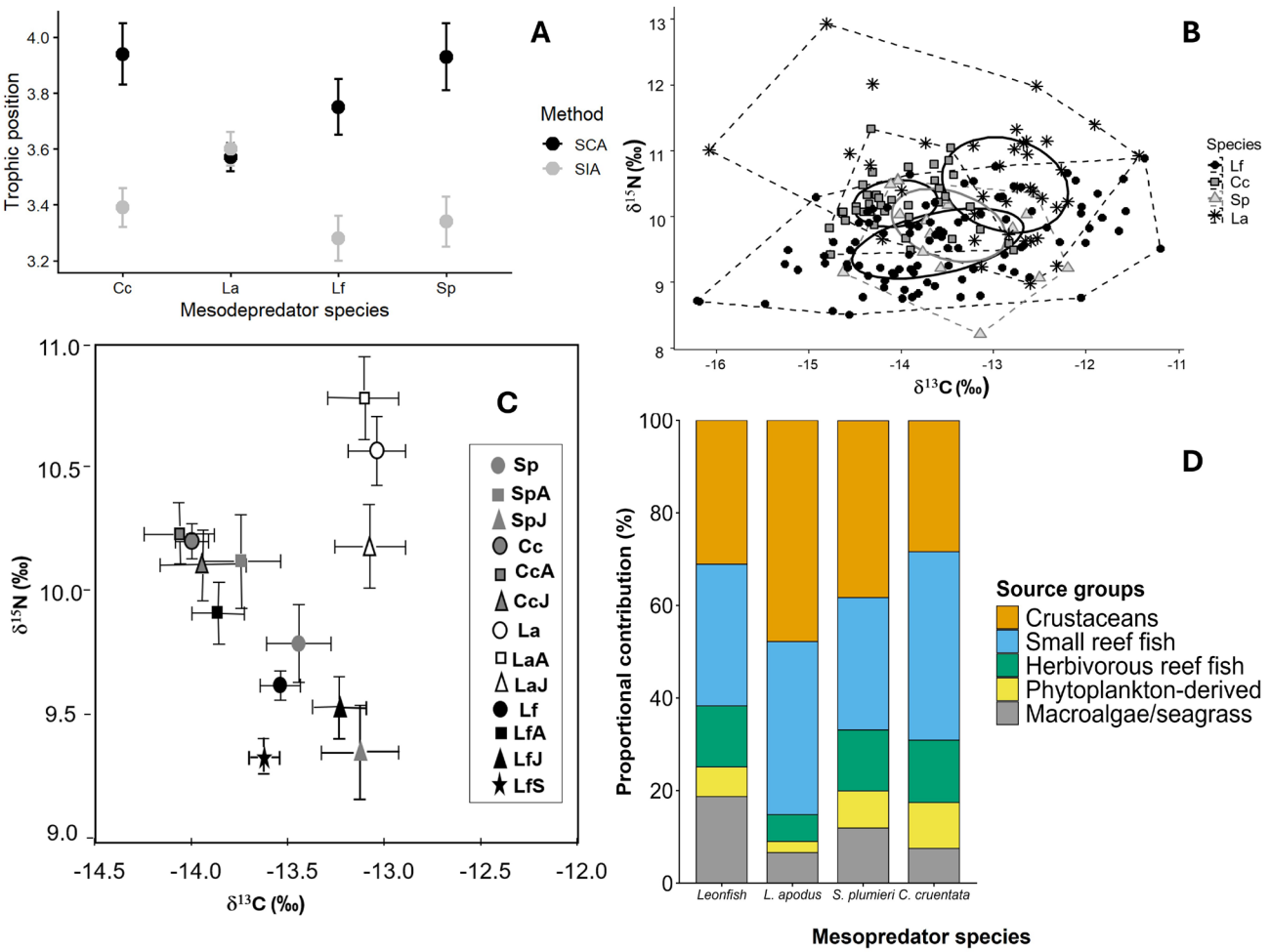

FIGURE 3 | A. Trophic position estimates of the four mesopredator species (Lionfish, *Lutjanus apodus*, *Scorpaena plumieri*, and *Cephalopholis cruentata*) obtained from stomach content analysis (SCA) and stable isotope analysis (SIA). Points represent mean values, and vertical lines indicate standard deviation. **B.** Isotopic niche space ($\delta^{13}C$ *vs.* $\delta^{15}N$) of mesopredator species based on muscle tissue samples. Solid ellipses represent the Bayesian standard ellipse area corrected for small sample size (SEAc), whereas dashed polygons represent the total isotopic niche area (TA). **C.** Mean isotopic values (± SD) for each mesopredator species separated by size class (juveniles and adults for native species; small, juvenile, and adult for lionfish), illustrating ontogenetic variation in isotopic niche position. **D.** Estimated proportional contribution (%) of major trophic pathways to mesopredator isotopic signatures based on exploratory Bayesian stable isotope mixing models. Contributions are shown for grouped isotopic source categories: crustaceans, small reef fish, herbivorous reef fish, phytoplankton-derived production, and macroalgae/seagrass-associated production. Abbreviations: Lf = *Pterois volitans/miles* (lionfish); LfS = small lionfish; LfJ = juvenile lionfish; LfA = adult lionfish; Cc = *Cephalopholis cruentata*; CcJ = juvenile *C. cruentata*; CcA = adult *C. cruentata*; Sp = *Scorpaena plumieri*; SpJ = juvenile *S. plumieri*; SpA = adult *S. plumieri*; La = *Lutjanus apodus*; LaJ = juvenile *L. apodus*; LaA = adult *L. apodus*.

apodus showed the largest core isotopic niche (SEAc = 2.3), followed by lionfish (SEAc = 1.6), *S. plumieri* (SEAc = 1.4), and *C. cruentata* (SEAc = 0.7) (Tab. 2). Isotopic niche overlap analyses indicated 61% overlap between *L. apodus* and lionfish, and 75% overlap between lionfish and *S. plumieri*.

Ontogenetic trophic shifts. Stomach content analysis showed that small lionfish individuals consumed 15 prey items belonging to 10 families and eight genera (Tab. **S4**). According to the %PSIRI index, their diet was strongly dominated by cleaner shrimps (69%), whereas fish prey represented only minor contributions (Fig. 2D). Juvenile lionfish consumed 18 prey items distributed among 12 families and 14 genera. Cleaner shrimps (53%) and benthic shrimps (21%) represented the dominant prey groups (Fig. 2D). Adult lionfish consumed 17 prey items distributed among 12 families and 12 genera. In adults, benthic shrimps constituted the dominant prey category (52%), followed by herbivorous reef fishes (20%) and mobile reef carnivorous fishes (15%) (Fig. 2D; Tab. **S2**).

PERMANOVA analysis revealed significant differences in diet composition among lionfish size classes (pseudo-F = 2.4, R^2 = 0.15, p = 0.03). This shift was mainly associated with an increase in fish consumption and a reduction in shrimp dominance in larger individuals.

According to Levin's index, large adults exhibited the greatest niche breadth (BI = 0.6), followed by small adults (BI = 0.4) and juveniles (BI = 0.4). Shannon-Wiener analyses indicated that juveniles showed the highest prey diversity (1.98 bits/ind), followed by large adults (1.9 bits/ind) and small adults (1.3 bits/ind). Horn's index indicated moderate dietary overlap between small (0.52), juveniles (0.43) and large adult lionfish (0.54) and *C. cruentata* (Tab. 1).

Stable isotope analyses showed no significant differences in $\delta^{13}C$ values among lionfish size classes (p = 0.06) and *L. apodus* size classes (p = 0.7). Similarly, no significant differences in $\delta^{15}N$ values were observed among size classes of *C. cruentata* (p = 0.4) (Tab. 2). However, significant differences in $\delta^{13}C$ values were detected among size classes of *C. cruentata* (p = 0.0001) and *S. plumieri* (p = 0.008). Tukey post hoc comparisons indicated that juvenile *C. cruentata* exhibited higher $\delta^{13}C$ values, whereas juvenile *S. plumieri* exhibited lower $\delta^{13}C$ values (Tab. 2). Significant differences in $\delta^{15}N$ values were also detected among size classes of lionfish (p = 0.007), *L. apodus* (p = 0.001), and *S. plumieri* (p = 0.01). Tukey post hoc comparisons revealed that adults exhibited higher $\delta^{15}N$ values than smaller individuals (Tab. 2). In addition, a significant positive relationship between body size and $\delta^{15}N$ values was observed in lionfish (R^2 = 0.1, p = 0.02), indicating an ontogenetic increase in trophic position. A similar but weaker trend was detected in *L. apodus*, whereas no clear relationship between body size and $\delta^{15}N$ values was observed in *C. cruentata*.

Significant differences in trophic position were detected among lionfish size classes (p = 0.0001). Tukey post hoc comparisons indicated that small adults exhibited the lowest trophic position values (Tab. 2). However, no significant differences in trophic position were observed among size classes of *C. cruentata* (p = 0.4), *L. apodus* (p = 0.5), or *S. plumieri* (p = 0.1). All size classes of the four mesopredator species were categorized as secondary consumers (Tab. 2).

TABLE 2 | Isotopic values (media ± SD) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰), trophic position (TP_SIA) and core isotopic niche width (SEAc, ‰²) for mesopredatory fishes and their size classes. LfS = lionfish small, LfJ = lionfish juvenile, LfA = lionfish adult, CcJ = *Cephalopholis cruentata* juvenile, CcA = *C. cruentata* adult, LaJ = *Lutjanus apodus* juvenile, LaA = *L. apodus* adult, SpJ = *Scorpaena plumieri* juvenile, SpA = *S. plumieri* adult. Kruskal-Wallis tests were used to evaluate differences among size classes within each species. Different superscript letters within each species indicate significant differences among size classes based on post hoc comparisons ($p < 0.05$). *Significant differences. TP_SIA values between 3 and 4 indicate secondary consumer trophic positions according to the trophic classification proposed by Post (2002).

Species (size class)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SEAc(‰)	TP_SIA
Lionfish (total)	95	-13.5±0.1	9.6±0.5	1.6	3.2
LfS	29	-13.7±0.1	9.3±0.1[a]		3.1[a]
LfJ	43	-13.3±0.2	9.7±0.0[b]		3.2[b]
LfA	24	-13.9±0.2	9.8±0.1[b]		3.2[b]
Kruskal-Wallis Pv		p = 0.0641	p = 0.0079*		p = 0.0001*
***C. cruentata* (total)**	39	-14.0±0.5	10.1±0.4	0.7	3.4
CcJ	20	-13.9±0.1[a]	10.0±0.0		3.4
CcA	19	-14.0±0.1[b]	10.3±0.1		3.3
Kruskal-Wallis Cc		p = 0.0001*	p = 0.4776		p = 0.4961
***L. apodus* (total)**	37	-13.0±0.9	10.5±0.8	2.3	3.6
LaJ	19	-13.1±0.1	10.1±0.1[a]		3.6
LaA	18	-13.1±0.3	10.8±0.2[b]		3.6
Kruskal-Wallis *La*		p = 0.7989	p = 0.0012*		p = 0.5104
***S. plumieri* (total)**	17	-13.4±0.6	9.7±0.6	1.4	3.3
SpJ	8	-13.1±0.2[a]	9.3±0.2[a]		3.3
SpA	9	-13.7±0.1[b]	10.1±0.1[b]		3.3
Kruskal-Wallis Sp		p = 0.0086*	p = 0.0112*		p = 0.1279

Bayesian mixing model analyses. Exploratory Bayesian stable isotope mixing models revealed differences in the relative contribution of trophic pathways among mesopredators (Fig. 3D; Tab. **S5**). Invasive lionfish exhibited relatively balanced contributions from crustaceans (31.1 ± 5.1%) and small reef fish pathways (30.6 ± 5.0%), with lower contributions from macroalgae/seagrass-associated pathways (18.7 ± 2.5%), herbivorous reef fish pathways (13.2 ± 5.3%), and phytoplankton-derived production (6.4 ± 2.2%). In contrast, *L. apodus* showed stronger associations with crustacean-derived (47.9 ± 11.0%) and small reef fish pathways (37.4 ± 8.7%), whereas *C. cruentata* was primarily associated with small reef fish pathways (40.7 ± 5.2%) and crustaceans (28.3 ± 6.1%). *Scorpaena plumieri* displayed a more even contribution pattern, including crustaceans (38.2 ± 12.8%), small reef fish pathways (28.6 ± 10.0%), herbivorous reef fish pathways (13.2 ± 8.4%), and macroalgae/seagrass-associated pathways (11.9 ± 5.3%). All models showed satisfactory convergence (R-hat ≈ 1). Although isotopic overlap among some source groups warrants cautious interpretation, these exploratory analyses support trophic differentiation among mesopredators while also indicating substantial sharing of reef-associated energy pathways.

DISCUSSION

An issue of paramount concern in Caribbean reefs is the invasion of the lionfish, given its potential impact on ecosystems (Albins, Lyons, 2012; Elise *et al*., 2015; Smith, Côté, 2021). Extensive research has highlighted the negative repercussions of this invader on native species in Caribbean coral reefs, potentially leading to ecological breakdowns (Arredondo-Chávez *et al*., 2016; Acero *et al*., 2019; Murillo-Pérez *et al*., 2020; Del Río *et al*., 2023).

A major contribution of our study is the integration of stomach content and stable isotope analysis conducted at the same spatial and temporal scale. These complementary approaches provide distinct temporal and ecological perspectives: stomach content analysis offers fine-scale taxonomic resolution of recent feeding events, whereas stable isotope analysis (via $\delta^{15}N$ and $\delta^{13}C$) integrates dietary information over longer temporal scales and allows broader inference on trophic position and carbon source use (Hyslop, 1980; Vander Zanden, Rasmussen, 2001; Post, 2002).

This study contributes to a more comprehensive and comparative understanding of trophic interactions and potential competition between lionfish and native reef mesopredators (*S. plumieri*, *C. cruentata*, and *L. apodus*), providing valuable insights into the trophic ecology on Caribbean reefs, particularly within the Puerto Morelos Reef National Park. However, feeding patterns in *S. plumieri* should be treated cautiously because the relatively small sample size and high proportion of empty stomachs may limit the representativeness of population-level dietary patterns and influence estimates of feeding strategy and niche breadth. Such limitations are common in reef fish diet studies, where intermittent feeding behavior, rapid digestion of soft-bodied prey, and diel differences in foraging activity can reduce the detectability of stomach contents and potentially bias dietary inference (Hyslop, 1980; Amundsen *et al*., 1996; Amundsen, Sánchez-Hernández, 2019).

All four mesopredator species examined in this study were classified as secondary consumers with carnivorous and generalist feeding habits. Stomach contents analysis identified lionfish as a generalist, opportunistic carnivore capable of consuming a broad diversity of prey items, particularly shrimps such as *Periclimenes* and *Pleoticus*, as well as reef fishes including *Sparisoma* and *Stegastes*. Similar prey patterns have been documented in previous studies for three of the four species analyzed here, with lionfish consistently described as a generalist predator capable of exploiting a wide diversity of reef prey. However, prey composition often varies according to habitat characteristics and predator ontogeny (Heck, Weinstein, 1989; Nagelkerken *et al*., 2000; Morris, Akins, 2009; Muñoz *et al*., 2011; Arredondo-Chávez *et al*., 2016; Murillo-Pérez *et al*., 2020; Rosas-Luis, Elias-Valdez, 2021; Del Río *et al*., 2023; Martínez-Juárez *et al*., 2024).

The broad trophic niche observed in lionfish is consistent with previous studies documenting high trophic plasticity in invaded Caribbean reefs (Cure *et al*., 2012; Layman, Allgeier, 2012; Côté *et al*., 2013). Such patterns have been interpreted as evidence of trophic expansion and ecological release, whereby invasive predators exploit a wider range of prey resources in novel environments. The integration of stomach content analyses, isotopic niche metrics, and ontogenetic dietary variation in this study further supports the hypothesis that trophic flexibility enhances the ecological success and potential competitive advantage of lionfish relative to native mesopredators (Albins, Hixon, 2008; Cure *et al*., 2012; Green *et al*., 2012). Exploratory

Bayesian mixing models further supported these patterns by indicating that lionfish integrate multiple trophic pathways, including both crustacean- and reef fish-derived energy sources. Lionfish showed relatively balanced contributions among different prey-associated pathways, consistent with their generalist feeding behavior and trophic flexibility (Albins, Hixon, 2008).

Ontogenetic dietary shifts were observed in lionfish, with smaller individuals feeding primarily on crustaceans and larger individuals showing increased piscivory. Such ontogenetic trophic shifts are common among reef predators, and stable isotope analyses supported this pattern in lionfish by revealing a significant increase in $\delta^{15}N$ values with body size, indicating a progressive rise in trophic position throughout ontogeny. This size-dependent trophic shift suggests that lionfish expand their resource use during development, potentially increasing competitive interactions with multiple native mesopredators while exerting predation pressure on a broader range of reef prey (Layman, Allgeier, 2012). Our stomach-content results also suggest trophic similarities among lionfish across ontogenetic stages with *C. cruentata* (0.43–0.54). We also documented significant isotopic niche overlap between lionfish and native mesopredators, particularly with *S. plumieri* (75%) and *L. apodus* (61%), while stomach content results indicated a moderate dietary overlap between lionfish and *C. cruentata* (0.54), as well as between *S. plumieri* and *C. cruentata* (0.43), indicating considerable resource sharing among these species. According to Resource Competition Theory (MacArthur, Levins, 1967), high niche overlap may increase the potential for resource competition when species exploit similar prey resources.

Trophic position estimates derived from stomach content analysis (TP_SCA) were generally higher than those estimated from stable isotope analysis (TP_SIA) for lionfish, *C. cruentata* and *S. plumieri*, whereas *L. apodus* exhibited more consistent trophic position estimates between both approaches. These differences likely reflect temporal variation in prey consumption, feeding periodicity, and differences between recently ingested prey and assimilated dietary signals. In contrast, the relatively consistent isotopic values observed in *L. apodus* suggest a more stable trophic integration over time.

The trophic differences, trophic position, and overlaps observed among mesopredators may also be partially explained by variation in hunting strategies. Lionfish and native scorpaeniform mesopredators, such as *S. plumieri*, typically rely on ambush predation, remaining motionless and exploiting cryptic or benthic prey through rapid suction feeding (Albins, Hixon, 2011; Cure *et al*., 2012). Similarly, serranids such as *C. cruentata* combine ambush tactics with short active pursuits within structurally complex reef habitats (Randall, 1967; Nagelkerken *et al*., 2000). In contrast, snappers such as *L. apodus* exhibit more mobile foraging behavior and wider spatial movements while searching for prey (Starck, Schroeder, 1971; Nagelkerken *et al*., 2000). These behavioral differences may influence prey encounter rates, resource partitioning, and trophic niche breadth, thereby contributing to the observed patterns of isotopic niche overlap and dietary variability.

Although lionfish and *Scorpaena plumieri*, both members of the family Scorpaenidae, exhibit relatively similar trophic positions ($\delta^{13}C$ and $\delta^{15}N$ values) and isotopic niche overlap, these patterns raise questions about the degree of ecological redundancy between the two species. Ecological theory predicts that closely related species with overlapping distributions may occupy similar ecological niches (Hutchinson, 1959; Chase, 2003; Peterson *et al*., 2011). Despite these similarities, lionfish showed substantially lower

stomach vacuity rates than *S. plumieri*, with only 18% of lionfish stomachs empty compared to 71% in *S. plumieri*. This pattern suggests higher feeding activity and broader prey exploitation by lionfish. Such differences may increase the potential for asymmetric resource use and competitive interactions between these mesopredators, particularly in reef habitats with reduced structural complexity.

Beyond individual species interactions, lionfish may exert broader ecosystem-level effects through their generalist feeding behavior and wide prey spectrum. By consuming a diverse array of crustaceans and reef-associated fishes, lionfish may alter prey availability for native mesopredators and influence patterns of resource use within reef food webs. These effects are consistent with ecological theory predicting that invasive predators can modify trophic interactions and energy flow in ecosystems where mesopredators play important functional roles (Ripple *et al*., 2016).

Lionfish also exhibit specialized predatory tactics that, together with their cryptic behavior and mimicry, may contribute to their ecological dominance (Cure *et al*., 2012; Layman, Allgeier, 2012; Pantoja-Echeverría *et al*., 2017; Rojas-Vélez *et al*., 2019). They use their elongated fins to corner prey, effectively directing them toward the mouth, where prey are rapidly engulfed by powerful suction feeding (Albins, Hixon, 2011; Cure *et al*., 2012; Rojas-Vélez *et al*., 2019; Peterson, McHenry, 2022; Del Río *et al*., 2023). As an invasive species, the lionfish and its predatory behavior represent a novel threat within Caribbean ecosystems. Native prey may have limited ability to recognize lionfish as predators, increasing their vulnerability to predation and potentially contributing to the species' high prey consumption rates (Albins, Lyons, 2012; Berchtold, Côté, 2020). This interpretation is further supported by the low proportion of empty stomachs observed in lionfish (<18%) compared with native mesopredators (>60%). But confirming this hypothesis would require comparable data on stomach fullness from populations within the species' native distribution, where a higher proportion of empty stomachs would be expected relative to invaded habitats. Although previous studies have already suggested that the invasive lionfish consume a greater daily prey biomass than in their native distribution range (Cure *et al*., 2012).

From a functional perspective, lionfish consume a broader range of ecologically important prey groups on Caribbean reefs than native mesopredators, including cleaner organisms (*e.g*., *Periclimenes pedersoni*), territorial benthic fishes (*e.g*., *Stegastes* spp.), and herbivorous reef fishes such as parrotfishes (*Sparisoma*) and surgeonfishes (*Acanthurus*). The high consumption of cleaner shrimp may indicate a disruption of cleaning symbioses resulting from the lack of coevolution between the predator and the symbiont. Consequently, lionfish may not be recognized as a threat, while cleaner shrimp may not be identified as symbionts (Côté *et al*., 2013; Álvarez *et al*., 2014; Leung *et al*., 2015).

Pomacentrids are a highly territorial group of fish that assess potential threats within their territories and decide whether to attack or avoid intruders according to perceived level of risk (Helfman, Winkelman, 1997; Holmes, McCormick, 2006). Therefore, the greater consumption of *Stegastes* species by lionfish, relative to native mesopredators, may suggest that lionfish are not recognized as a potential predator, thereby increasing the vulnerability of these fishes to predation. Previous studies have further reported that predation on fishes of the genus *Stegastes* by lionfish occurs only within the invaded range and not within the species' native range (Cure *et al*., 2012). Predation on territorial damselfishes may also alter benthic community dynamics by reducing the abundance of

species that shape algal assemblages through the aggressive defense of feeding territories (Helfman, Winkelman, 1997; Holmes, McCormick, 2006).

Our findings further indicate that lionfish frequently consume herbivorous reef fishes, including ecologically important taxa such as *Sparisoma atomarium* and *Acanthurus* spp. These herbivorous functional groups play a crucial role in reef maintenance by controlling macroalgal growth and facilitating coral recruitment and resilience (Kindinger, Albins, 2017; Del Río *et al*., 2023). Similar patterns of herbivorous fish consumption by lionfish have been reported in other Caribbean studies (Arredondo-Chávez *et al*., 2016; Chappell, Smith, 2016; Chevalier-Monteagudo, 2017; Pantoja-Echeverría *et al*., 2017), but not within the species' native range (Cure *et al*., 2012). Predation on these functional groups may reduce grazing pressure and disrupt herbivory-mediated regulation of algal communities, thereby increasing the likelihood of reef degradation and phase shifts from coral- to algae-dominated states (Kindinger, Albins, 2017; Berchtold, Côté, 2020). Moreover, the trophic impacts of lionfish may interact synergistically with other stressors affecting Mexican Caribbean reefs, including nutrient enrichment, overfishing, pollution, coral bleaching, and habitat degradation, further promoting macroalgal proliferation (Albins, Hixon, 2008; Arredondo-Chávez *et al*., 2016; Rodríguez-Martínez *et al*., 2019; Del Río *et al*., 2023). In reef ecosystems already affected by overfishing and declining structural complexity, the trophic plasticity and broad niche breadth of lionfish may further destabilize predator-prey dynamics and reduce reef resilience (Green *et al*., 2012; Côté *et al*., 2013). Although these synergistic effects were not directly quantified in this study, our findings suggest that lionfish invasion may amplify existing ecological pressures in Caribbean reef systems.

Another major concern is the predation by lionfish on commercially valuable reef-associated species, including snappers, groupers, crabs, and shrimp (Morris, Akins, 2009; Arredondo-Chávez *et al*., 2016; Dahl *et al*., 2017; Sancho *et al*., 2018). Sustained predation on juvenile stages of these organisms could reduce recruitment into adult populations, thereby negatively impacting local fisheries and associated livelihoods (Morris, Akins, 2009; Morris, Green, 2013). In addition, reef degradation linked to trophic imbalances may further affect species that depend on coral reef habitats for shelter, feeding, and reproduction (Valdez-Moreno *et al*., 2012; Arredondo-Chávez *et al*., 2016; Cobián-Rojas *et al*., 2018b; Del Río *et al*., 2023).

This study highlights the ecological implications of lionfish as a generalist predator in the Mexican Caribbean, emphasizing their broad trophic niche, trophic flexibility, substantial overlap with native mesopredators, and predation on ecologically important groups. These characteristics may facilitate resource sharing and increase the potential for competitive interactions within reef food webs. Conversely, several studies suggest that the impact of lionfish on fish and invertebrate populations may not be as severe as initially proposed (Elise *et al*., 2015; Chevalier-Monteagudo, 2017; Hackerott *et al*., 2017; Cobián-Rojas *et al*., 2018b). Nevertheless, evaluating the full ecological impact of lionfish on reef communities remains challenging because multiple interacting factors must be considered, including local predator-prey dynamics, time since invasion, and the ecological structure of the invaded habitat, among others, to accurately assess their effects on native fish and invertebrate populations (Levine, D'Antonio, 1999; Fabricius, 2005; Elise *et al*., 2015; Eakin *et al*., 2019; Rodríguez-Martínez *et al*., 2019).

To mitigate potential ecological impacts, management strategies should prioritize targeted lionfish removals, particularly in reef habitats where trophic overlap with

native mesopredators is pronounced. Further research is needed to evaluate the long-term effects of lionfish predation on reef ecosystem structure and function and to support the development of ecosystem-based management approaches that incorporate the conservation and recovery of native reef communities. By integrating resource competition, niche partitioning, stomach content analyses, stable isotopes, and trophic dynamics, this study contributes to a broader understanding of the ecological impacts of invasive lionfish in Mexican Caribbean reef ecosystems.

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ETHICAL STATEMENT

All procedures involving fish were conducted in accordance with national and institutional guidelines for the use of animals in research in Mexico. Specimen collection was authorized under fishing permit Nº DGOPA.08990.031111.3073, and all efforts were made to minimize animal stress and suffering during sampling and handling. No additional ethical committee approval was required for this study.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

AI STATEMENT

Generative artificial intelligence tools were used exclusively for language editing and improvement of clarity and grammar in the manuscript text. No AI-assisted technologies were used for data analysis, figure preparation, interpretation of results, or generation of scientific content. All analyses, interpretations, and conclusions are the sole responsibility of the authors.

COMPETING INTERESTS

The author declares no competing interests.

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