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Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper

SHAY O'FARRELL,^{1,2,†} STUART BEARHOP,³ RONA A. R. MCGILL,⁴ CRAIG P. DAHLGREN,⁵
DANIEL R. BRUMBAUGH,⁶ AND PETER J. MUMBY^{1,2}

¹College of Life and Environmental Sciences, University of Exeter, Exeter EX44QD United Kingdom

²Marine Spatial Ecology Lab, School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072 Australia

³Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR109EZ United Kingdom

⁴NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre,
Scottish Enterprise Technology Park, East Kilbride G75 0QF United Kingdom

⁵Perry Institute for Marine Science, 100 N. U.S. Highway 1, Suite 202, Jupiter, Florida 33477-5112 USA

⁶Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street,
New York, New York 10024–5192 USA

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Abstract. Species invasions are a significant threat to global biodiversity and ecosystem function, and yet our knowledge of consequences for native species remains poor. The problem is exacerbated in highly speciose ecosystems like coral reefs. The invasion of the wider Caribbean by predatory lionfish (*Pterois* spp.) is one of the most successful marine colonizations ever documented, and its impact is anticipated to be substantial on native species. However, despite the ecological and commercial importance of iconic Nassau grouper (*Epinephelus striatus*), the impacts of the invasion on this IUCN Red-Listed species remain unexamined. Using data gathered from two critical habitats in the Bahamas, we investigate isotopic niche space overlap between lionfish, Nassau grouper and putative prey species. Despite their relatively small body size, we find that lionfish occupy the highest isotopic niche position on patch reefs, occupying much of the same space as the native apex predator. Contrary to expectation, lionfish trophic level ($\delta^{15}\text{N}$) does not increase with body size, contrasting with confamilials in their native range. However, we find that tissue carbon ($\delta^{13}\text{C}$) changes systematically with body size on deep forereef habitats, representing a length-specific shift in food resources, with smaller individuals partitioning resources from larger individuals in this habitat but not on shallow patch reefs. We conclude that, despite the difference in body size, lionfish are capable of directly competing for food resources with Nassau grouper, and that impacts on guilds such as planktivores and invertivores may vary systematically by habitat. Our study contributes to the growing body of research aimed at understanding how a species that is relatively rare in its native range achieved the most successful fish invasion ever documented.

Key words: apex predator; Bahamas; coral reef fish; *Epinephelus striatus*; invasive species; ontogenetic competition; *Pterois* spp.; resource partitioning; stable isotope analysis; trophic overlap.

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† **E-mail:** shay.ofarrell.ac@gmail.com

INTRODUCTION

It is widely acknowledged that invasive species represent one of the major threats to global biodiversity and ecosystem function (Vitousek et al. 1997, Sala et al. 2000, Sutherland et al. 2010). Many of the processes through which invasive species impact on native species are poorly understood and yet our ability to mitigate the impacts of invasion, and to pre-empt future invasions, is contingent upon such knowledge (Gurevitch and Padilla 2004). Even the patterns of invasion remain obscure (Vander Zanden et al. 1999) and the full magnitude and extent of threats posed by invasive species have yet to be described, because food webs are complex and the impacts of invasive species are often difficult to disentangle from other processes (Gurevitch and Padilla 2004).

The recent invasion of the wider Caribbean by predatory Indo-Pacific lionfishes, *Pterois* spp. (Scorpaenidae, L. 1758) is one of the most successful marine colonizations ever documented (Morris and Whitfield 2009, Schofield 2009), posing a significant threat to Caribbean biological diversity (Sutherland et al. 2010). The invasion probably originated in Florida in the 1980s but radiated rapidly (Whitfield et al. 2002, Freshwater et al. 2009), and the invader is now a common sight on reefs across the wider Caribbean from Venezuela to Bermuda (Morris and Whitfield 2009). The rate of invasion progress has been particularly rapid: lionfish were first sighted in the Bahamas in 2004 but within three years they were among the most abundant fishes in the archipelago and within five years populations had reached densities eight times greater than the maxima recorded within their native range, with individuals reaching larger body sizes (Green and Côté 2009, Darling et al. 2011).

It is of particular concern that Caribbean lionfish may also prey at greater rates than their Indo-Pacific relatives (Côté and Maljković 2010, Green et al. 2011). In a controlled study using experimental reef structures, Albins and Hixon (2008) found that lionfish predation reduced the abundance of juvenile fish by 79% over a five-week period. The authors also observed individual lionfish consuming up to 20 small fish in a single 30-minute period, and eating prey with body lengths two thirds of their own. Work by

Côté et al. (2013) indicates that the predator may consume more than half of the potential prey species on invaded reefs, and the impacts on native reef fish populations may yet prove to be severe. Given the intricacies of coral reef trophic interactions, such impacts can rapidly cascade to induce ecosystem-level effects, with Lesser and Slattery (2011) showing that lionfish predation is likely to be the driver of an observed phase shift from coral domination to algal domination on mesophotic reefs that may provide stability and refuge from disturbance for shallower reefs (Slattery et al. 2011).

Stable isotope analysis (SIA) is an ideal technique for studying the lionfish invasion at local scales that are relevant for management (e.g., Muñoz et al. 2011, Layman and Allgeier 2012). The carbon and nitrogen isotopic signatures of prey items become incorporated into the tissues of consumers (Gearing 1991), and analysis of these values allows robust inferences to be made about life histories of, and interactions among, animals. For example, Vander Zanden et al. (1999) used SIA to reveal subtle, but important, impacts of invasion. In their study system, the introduction of fishes to Canadian lakes had not caused extinction of native species, but SIA demonstrated that it had forced native trout to switch diet from littoral fish to pelagic plankton, disrupting the entire food web. In another lake study, this time in a highly perturbed system, Inger et al. (2010) used SIA not only to infer temporal shifts in the dietary composition of native lamprey (*Lampetra fluviatilis*, L. 1758), but also to show that the usually anadromous species was, in this case, entirely restricted to freshwater.

In an SIA study of lionfish in a hard-bottom reef community in North Carolina, Muñoz et al. (2011) found that prey assimilation by the novel predator shifted over time within the habitat, moving from a diet dominated by serranids and scarids in 2004 to carangids and haemulids in 2006, which the authors attribute to changes in prey availability rather than changes in specialization by the invader. Working in a back-reef habitat in the Bahamas, Layman and Allgeier (2012) found evidence of a surprisingly high degree of individual specialization in the feeding of lionfish, despite the breadth of its overall niche, and their results agreed with those of Muñoz et al. (2011) that prey selection may be

driven largely by the local abundance of various food types. The authors also found that back-reef lionfish display a high degree of site fidelity.

Although general ecological insights can be hard to draw from site-specific studies, working at this scale can provide information that directly addresses local management concerns, such as the impact of the lionfish invasion on iconic and endangered Nassau grouper (*Epinephelus striatus*). A benthic-associated generalist predator, the Nassau grouper is an important piscivore in Caribbean reef fish assemblages (Hixon and Beets 1993) that also feeds on crustaceans and mollusks (Albins et al. 2009). Nassau grouper were historically observed forming large aggregations at habitual spawning sites, with group size estimated at over 100,000 individuals (Smith 1972, Miller 1984). Juveniles settle to macroalgal beds after which they may progress to patch reefs and finally to forereefs upon reaching adulthood (Eggleston 1995), the timing of the ontogenetic shift driven by a trade-off between the relative safety of the juvenile habitat against the elevated opportunity for growth presented by the adult habitat (Dahlgren and Eggleston 2000).

Unfortunately, the tendency to spawn at specific times and locations has made Nassau grouper particularly vulnerable to overexploitation (Sadovy and Eklund 1999, Albins et al. 2009) and a fish that was one of the most widely distributed serranids in the western Atlantic and a major fisheries resource for much of the twentieth century (Jory and Iverson 1989) is now listed as endangered on the IUCN Red List of Threatened Species. The arrival of the lionfish may represent an additional threat to the beleaguered iconic species but this has not yet been addressed in the literature.

Analyzing tissue samples collected from primary food sources and fish consumers on Bahamian reefs, we use the isotopic niche space concept (Newsome et al. 2007) to characterise the niche space of lionfish on patch reefs and forereefs, which are critical habitats for Nassau grouper (Dahlgren and Eggleston 2000). The isotopic niche concept purports that the axes provided by $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and other isotopes can be viewed as indicators of resource use and, although it is not identical to the trophic niche, it is likely to be closely aligned (Jackson et al.

2011).

Our analysis is presented in three parts. (1) We first characterise the carbon and nitrogen isotopic niche space of lionfish within a shallow patch reef community to indicate trophic interactions between the invader and Nassau grouper, as well as other native fishes. (2) We then determine whether lionfish occupy different trophic positions in patch reef and forereef habitats, or as they grow larger within each habitat, as has been demonstrated in the lionfish confamilials, *Scorpaena porcus* and *S. scrofa* (Deudero et al. 2004). (3) Finally, we test whether trophic overlap between lionfish and Nassau grouper differs systemically between these habitats.

METHODS

Fieldwork was conducted in the Bahamas at two patch reef sites and nine forereef sites (Table 1). Patch reefs are shallow habitats with relatively sparse coral heads scattered across sandy benthos, and play an important role as habitat for many juvenile reef fishes. As is commonly the case, our sites were adjacent to beds of *Thalassia testudinum* and *Syringodium filiforme* seagrasses, and it may be expected that seagrass carbon would make an important contribution to the food web. Forereef sites are deeper, ours being located at depths of 8–12 m. More exposed than patch reefs, they tend to have higher productivity with commensurately greater abundance of plankton and planktivorous fishes.

Some of our study species, such as Nassau grouper and parrotfishes (Scaridae), are of high conservation value and so all species but lionfish were sampled non-lethally. Fin clippings were taken from all fish, as the carbon and nitrogen isotopic values compare very well with lethally sampled muscle tissue (Kelly et al. 2006). Clippings were taken from the posterior portion of the dorsal fin rather than the tail fin, as terminal phase males often display elaborately adorned tail fins, which may be assumed to have meaning in courtship. In exploratory samplings, fish did not appear to suffer discomfort from the removal of clippings, and a number of sampled fish were subsequently re-sighted during the course of the study and did not appear to be impaired relative to non-sampled conspecifics.

Table 1. Habitat types and GPS coordinates of study sites in Exuma Cays, Bahamas. Coordinates are given in decimal degrees.

Site number	Habitat type	Longitude	Latitude
1	Patch reef	-76.089731	23.775172
2	Patch reef	-76.083038	23.764444
3	Forereef	-76.675119	24.426508
4	Forereef	-76.685731	24.431735
5	Forereef	-76.684922	24.429487
6	Forereef	-76.747344	24.508513
7	Forereef	-76.815016	24.779700
8	Forereef	-76.801074	24.689917
9	Forereef	-76.100638	23.782663
10	Forereef	-76.089731	23.775172
12	Forereef	-76.083038	23.764444

Tissue sampling

Lionfish were caught using pole spears but other fish species (Table 2) were caught using traps, seine nets, hand nets, and/or quinaldine (2-methylquinoline) anesthetic mixed with equal parts ethanol (95%). Algal samples were collected at each site from *Dictyota* spp., *Lobophora* spp., *Cladophora* spp. and algal turfs (various taxa). The seagrasses *Syringodium filiforme* and *Thalassia testudinum* were also sampled adjacent to patch reefs. All plant samples were thoroughly cleaned of epiphytes. Phytoplankton were sampled using a towed net and fractionated through a 105- μ m sieve. Samples were arranged on clean plastic trays, which were covered to prevent contamination. After drying to a constant weight (approximately four hours, fan assisted), samples were individually placed into numbered vials and silica gel beads were added to each before being sealed.

Sample processing

Fin clippings are composed of a mixture of tissue types (skin and ray), which reflect different periods of assimilation, will have different biochemical compositions and different trophic discrimination factors (Pinnegar and Polunin 1999). Due to mass constraints, samples were taken from the edge distal to the margin of each fin clipping so that all samples were a homogenized mixture of skin and ray tissue. The desiccated clippings were snipped to fine particles that were then scooped into tin capsules (5×3.5 mm) and weighed to 0.7 mg ($\pm 10\%$) on a microbalance. Algae and seagrasses were pulverized and weighed to 3 mg ($\pm 10\%$). Carbon

and nitrogen isotope values of samples were determined at the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility, East Kilbride, Scotland.

Data analysis

The most commonly used data in SIA trophic studies are the ratios of heavy to light stable isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$), which are converted to δ -values by comparison with the ratios of international standards (Post 2002). The nitrogen isotope ratio ($\delta^{15}\text{N}$) in consumer tissues changes by a relatively predictable factor for each trophic level (Pinnegar & Polunin 1999) allowing the trophic position of the consumer to be elucidated from the enrichment of ^{15}N relative to that of primary producers. Conversely, the carbon isotope ratio ($\delta^{13}\text{C}$) in consumer tissues changes little with trophic level, creating a characteristic signal from which the photosynthetic origins of the carbon may be traced (Pinnegar and Polunin 2000). By measuring these isotope ratios, trophic niche widths of species can robustly be estimated (Bearhop et al. 2004) and even the 'isotopic niche space' of entire communities can be recreated (Newsome et al. 2007).

To map the isotopic niche space of the study species, carbon and nitrogen isotope values were used as dimensions within which the means and standard deviations of the δ -values were plotted. When comparing overlapping isotopic niche space of lionfish and Nassau grouper, SIBER (Jackson et al. 2011) was used to plot standard ellipses, which are the two-dimensional equivalents of standard deviations. To investigate variation in tissue isotope values as a function of changes in habitat or body size, linear regressions, ANOVAs or t-tests were conducted, the last being used when sample sizes were unbalanced. Approximation of normality in the distribution of model residuals was confirmed using quantile-quantile plots of standardized residuals versus fitted values (Crawley 2007).

RESULTS

Lionfish position in patch reef community isotope space

The data for putative prey and competitor species were classified into functional groups

Table 2. Taxa, number of tissue samples and, where appropriate, functional groups of biota contained in the stable isotope dataset.

Tissue item	No. samples	Functional group
Phytoplankton	13	...
<i>Thalassia testudinum</i>	12	...
<i>Syringodium filiforme</i>	11	...
<i>Cladophora</i> spp.	12	...
<i>Dictyota</i> spp.	10	...
<i>Lobophora</i> spp.	6	...
Algal turfs	8	...
Lionfish	17 (patch reefs)	Lionfish
(<i>Pterois</i> spp.)	37 (forereefs)	
Nassau grouper	14	Apex predator
(<i>Epinephelus striatus</i>)		
Coney	1	Mesopredator
(<i>Cephalopholis fulva</i>)		
Red hind	2	Mesopredator
(<i>Epinephelus guttatus</i>)		
French grunt	16	Benthic invertivore†
(<i>Haemulon flavolineatum</i>)		
White grunt	1	Benthic invertivore†
(<i>Haemulon plumieri</i>)		
Spotted goatfish	2	Benthic invertivore†
(<i>Pseudupeneus maculatus</i>)		
Longspine squirrelfish	1	Benthic invertivore†
(<i>Holocentrus rufus</i>)		
Bluehead wrasse	7	Planktivore‡
(<i>Thalassoma bifasciatum</i>)		
Sergeant major	5	Planktivore‡
(<i>Abudefduf saxatilis</i>)		
Blue tang	10	Turf grazer
(<i>Acanthurus coeruleus</i>)		
Ocean surgeon	8	Turf grazer
(<i>Acanthurus bahianus</i>)		
Striped parrotfish	19	Algal scraper
(<i>Scarus iseri</i>)		
Queen parrotfish	2	Algal scraper
(<i>Scarus vetula</i>)		
Princess parrotfish	1	Algal scraper
(<i>Scarus taeniopterus</i>)		
Redband parrotfish	10	Algal excavator
(<i>Sparisoma aurofrenatum</i>)		
Stoplight parrotfish	3	Algal excavator
(<i>Sparisoma viride</i>)		

† Habituate reefs but forage for invertebrates in seagrass benthos.

‡ Aggregate around coral heads, feeding on zooplankton.

(Table 2). When the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patch reef data are plotted, the groups assemble in ecologically coherent δ -space (Fig. 1). Lionfish, Nassau grouper and mesopredators (coney, *Cephalopholis fulva*, L. 1758; red hind, *Epinephelus guttatus*, L. 1758) occupy the highest (most ^{15}N enriched) positions in the trophic system, with lionfish at the very top. The body size of patch reef Nassau grouper had a mean value of 29 cm, lionfish mean was 22 cm, and mesopredator mean was 20 cm. The next highest group is the 'benthic invertivores' that forage in seagrass beds, consisting of two grunts (*Haemulon flavolineatum*, Desmarest 1823; *H. plumieri*, Lacépède, 1801), a goatfish (*Pseudupeneus maculatus*, Bloch 1793)

and a squirrelfish (*Holocentrus rufus*, Walbaum 1792), and is offset rightwards in Fig. 1 towards the higher $\delta^{13}\text{C}$ values of seagrasses (mean $\delta^{13}\text{C}$: $-5.2 \pm 0.7\text{‰}$). The planktivore group consists of a wrasse (*Thalassoma bifasciatum*, Bloch 1791) and a damselfish (*Abudefduf saxatilis*, L. 1758), and is offset leftwards in Fig. 1 towards the lower $\delta^{13}\text{C}$ isotopic values of phytoplankton (mean $\delta^{13}\text{C}$: $-16.4 \pm 3.3\text{‰}$) and benthic algae (mean $\delta^{13}\text{C}$: $-14.4 \pm 2.1\text{‰}$).

The 'turf grazers' (Burkepile and Hay 2010), namely blue tangs (*Acanthurus coeruleus*, Bloch & Schneider 1801) and ocean surgeonfish (*A. bahianus*, Castelnau 1855), represent the lowest (most left-set) $\delta^{13}\text{C}$ of any of the sampled fish

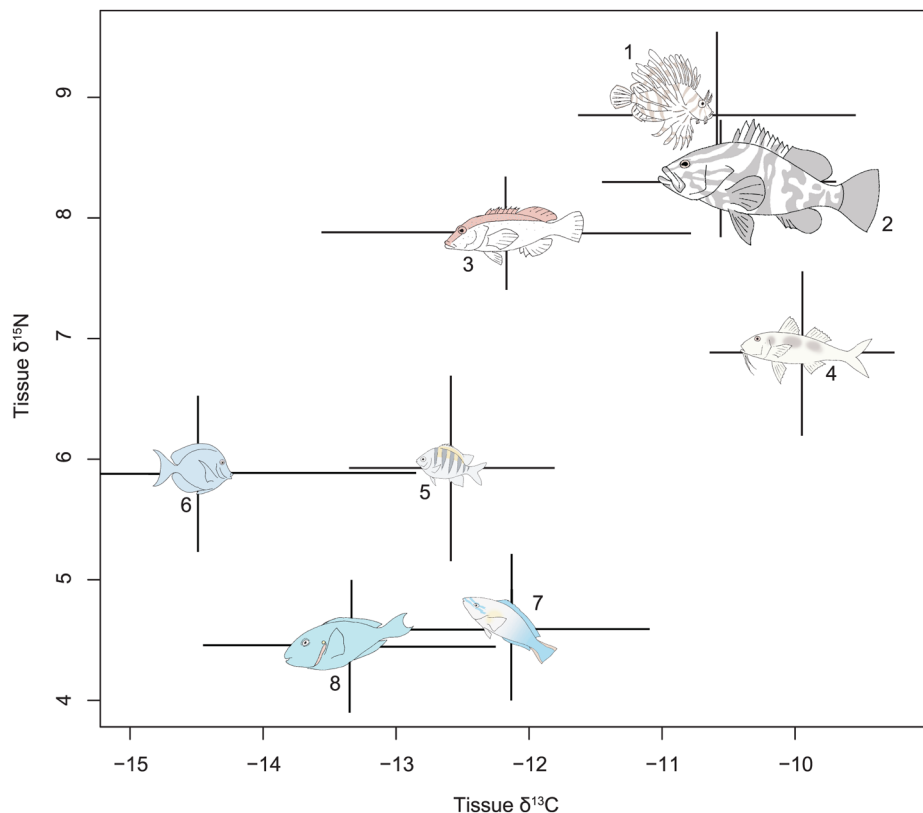


Fig. 1. Isotopic niche space of lionfish and putative competitor and prey groups, classified by taxonomic and/or functional similarity. Icons show representative species from each group. 1, Lionfish; 2, Nassau grouper; 3, Mesopredators; 4, Benthic invertivores; 5, Planktivores; 6, Turf grazers (*Acanthurus* spp. surgeonfishes); 7, Algal scrapers (*Scarus* spp. parrotfishes); 8, Algal excavators (*Sparisoma* spp. parrotfishes).

species. They are enriched in ^{15}N compared to the other herbivores, the parrotfishes, which comprise the two groups with lowest $\delta^{15}\text{N}$ values: the ‘algal excavators’ and the ‘algal scrapers’. The algal excavators (stoplight parrotfish, *Sparisoma viride*, Bonnaterre 1788; redband parrotfish, *Sp. Aurofrenatum*, Valenciennes 1840) can feed heavily on macroalgae (Randall 1967, Mumby 2006) and have more similar $\delta^{13}\text{C}$ values to these food sources (mean $\delta^{13}\text{C}$: $-14.2 \pm 1.9\text{‰}$) than do the algal scrapers (queen parrotfish, *Scarus vetula*, Bloch & Schneider 1801; princess parrotfish, *Sc. taeniopterus*, Lesson 1829; striped parrotfish, *Sc. iseri*, Bloch 1789), whose $\delta^{13}\text{C}$ values are more similar to the algal turfs (mean $\delta^{13}\text{C}$: $-11.8 \pm 1.3\text{‰}$) on which they specialize (Burkepile and Hay 2010).

Inter-habitat variation in lionfish isotope position as a function of size

As the size of predators and their prey often scale with each other (Dörner et al. 2007), it is an intuitive hypothesis that a generalist predator should systematically feed higher in the food web as it grows (Deudero et al. 2004). However, analyzing the lionfish data as a function of body length does not support the hypothesis, and no consistent enrichment in ^{15}N with body size was found either on patch reefs (Fig. 2A; $F_{1,15} = 1.807$; $P = 0.198$) or on forereefs (Fig. 2B; $F_{1,19} = 0.01$; $P = 0.946$). No significant shift in the carbon isotope ratio ($\delta^{13}\text{C}$) was observed on patch reefs, either (Fig. 2C; $F_{1,15} = 0.378$; $P = 0.548$) although $\delta^{13}\text{C}$ exhibited a strong shift with body size on forereefs (Fig. 2D; $F_{1,19} = 17.45$; $P < 0.001$; $r^2 = 0.45$).

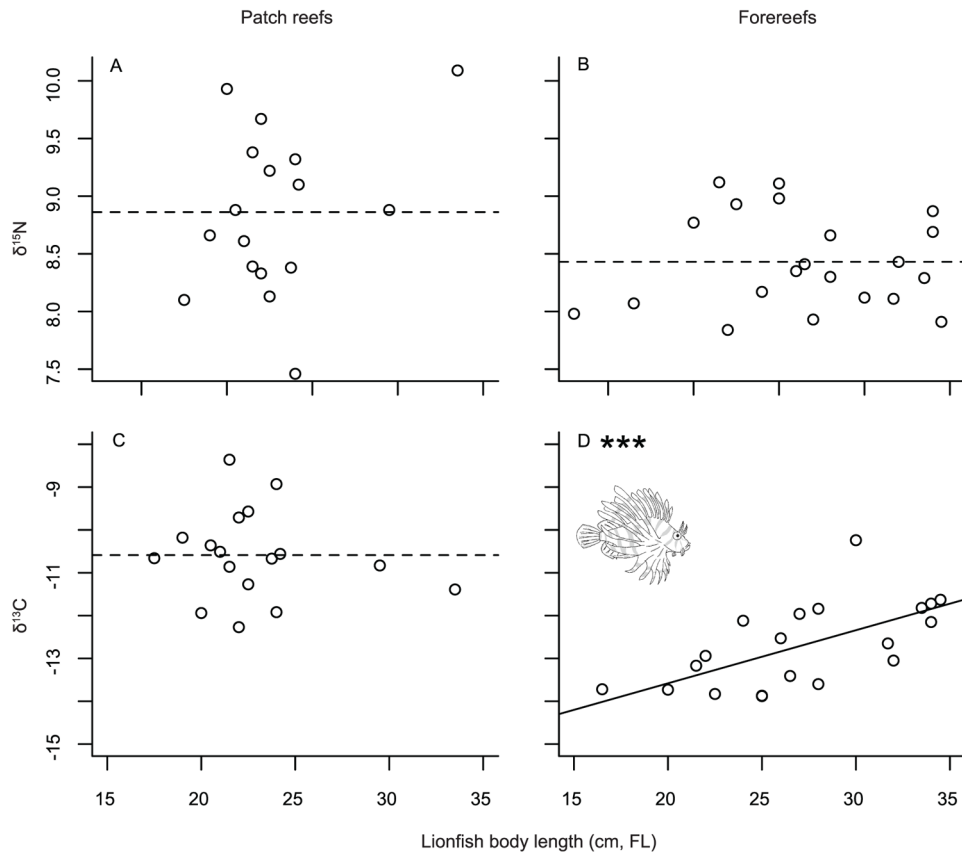


Fig. 2. Tissue isotope signals as a function of lionfish body size across two habitats, shallow patch reef and deeper forereef. Lines show linear model fits to each subset of data. No significant trend was observed in $\delta^{15}\text{N}$ with body size in either habitat (panels A and B). There was a significant $\delta^{13}\text{C}$ increase with size in forereef habitats (panel D) but not in patch reefs.

Inter-habitat variation in isotopic overlap of lionfish and Nassau grouper

Lionfish and Nassau grouper overlap considerably in δ -space on patch reefs (Fig. 1) and, although the invader is positioned slightly higher (^{15}N -enriched) than the native predator, it is likely that they compete for food resources. To determine whether competition is likely to be more intense in one habitat or another, δ -space overlap between the two species was examined for habitat-specific shifts.

Within each habitat, the lionfish data are divided into two groups by body size, 'small' and 'large', around the median length of the pooled data for the habitat: 26.5 cm. Plotting the δ -space of the lionfish size classes in each habitat against the δ -space of Nassau grouper shows a shift in trophic overlap across habitats (Fig. 3).

On shallow patch reefs, small and large lionfish share almost identical δ -space (Fig. 3A) and both overlap considerably with Nassau grouper. On forereefs, however, the isotopic niche spaces of small and large lionfish are partitioned (Fig. 3B) with a small lionfish showing significantly lower $\delta^{13}\text{C}$ values ($t_{17} = 3.835$; $P < 0.001$).

DISCUSSION

Our results indicate that lionfish feed at higher trophic levels than their body length may suggest, overlapping considerably with the isotopic niche space of larger bodied Nassau grouper. The effects of body size on lionfish diet were also counterintuitive, with the invader showing no increase in trophic level ($\delta^{15}\text{N}$ value) as it grows larger. However, lionfish appear to

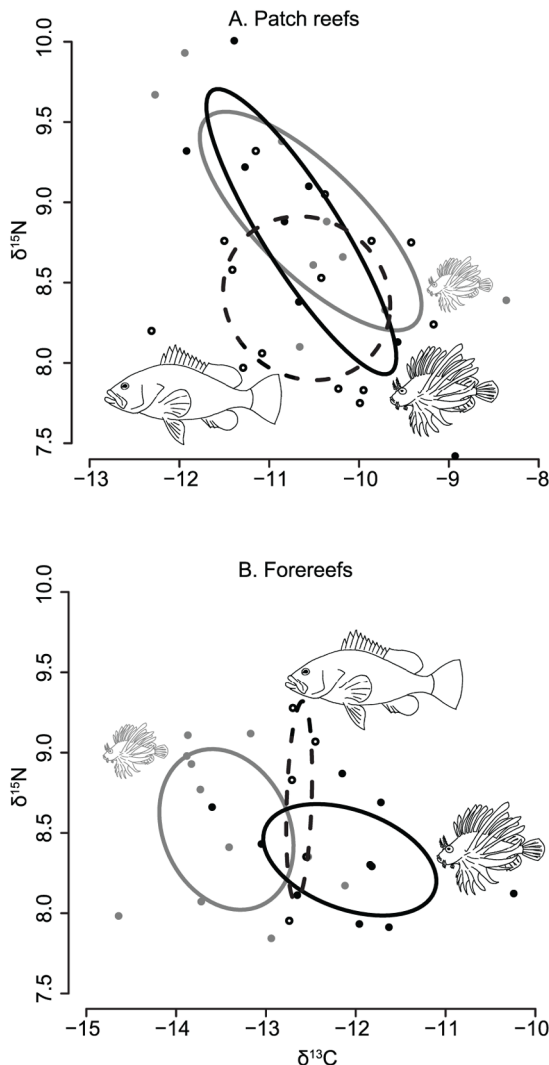


Fig. 3. Changes in the overlap in isotopic niche space of small lionfish (solid lines, gray), large lionfish (solid lines, black) and Nassau grouper (dashed lines) across two habitat types: shallow, low-productivity patch reefs (panel A) and deeper, high-productivity forereefs (panel B). Points represent tissue isotope data from individual fish, overlaid with standard ellipses that may be considered analogous for bivariate data to standard deviations in univariate data. Note that the horizontal scale varies.

undergo an ontogenetic shift in the $\delta^{13}\text{C}$ values on forereefs, with smaller individuals partitioning resources from larger individuals in this habitat but not on shallow patch reefs. We discuss these results in the context of competition

with Nassau grouper and ontogenetic changes in predation on native prey.

The body size of animal predators tends to scale with the size of their prey (Döerner et al. 2007), a rule that generally applies across disparate taxa, from invertebrates (e.g., Warren and Lawton 1987) to vertebrates (e.g., Cohen et al. 1993). This paradigm suggests that lionfish should increase their trophic level as they grow larger (Deudero et al. 2004) and overlap most in food resources with similarly sized predators such as red hind, *Epinephelus guttatus*, and coney, *Cephalopholis fulva* (e.g., Albins 2013).

We found that, contrary to expectation, the trophic level ($\delta^{15}\text{N}$ value) of Bahamian lionfish remains relatively constant as they grow, although we acknowledge that the range of body sizes in our data is limited and ontogenetic increases in trophic level may have occurred during sub-adult stages. It was also counterintuitive that lionfish would share so much trophic overlap with much larger bodied Nassau grouper, and that they appear to be positioned higher in isotopic niche space than the native apex predator.

Neither lionfish nor Nassau grouper are exclusively piscivorous, each consuming invertebrates as well as fishes (Dahlgren and Eggleston 2000, Morris and Akins 2009) and it is clear from our data that the two occupy a similar (although changing) isotopic niche space on both forereefs and patch reefs. A limitation of our study is that it represents a static picture of isotopic niche space, and we cannot know whether the niches of lionfish and Nassau grouper have overlapped since the arrival of the invader, have converged as a result of lionfish foraging altering the prey community, or may subsequently diverge through the same mechanism. The arrival of lionfish at a reef has been shown capable of altering the composition of the native community through the consumption of large numbers of small-bodied individuals, reducing both local recruitment rates (Albins and Hixon 2008) and species richness (Albins 2013). Lionfish have also been shown capable of switching prey in response to changes in the abundance of preferred prey (Muñoz et al. 2011). A time-series of stable isotope data could reveal whether the isotopic overlap between the two predators is in fact dynamic, and shifts systematically over time

as a result of lionfish foraging.

Although lionfish do not show a consistent enrichment in ^{15}N with body size in either habitat, the clear correlation in tissue $\delta^{13}\text{C}$ with body size in forereef lionfish is particularly interesting, especially as this effect is not seen on patch reefs. In our data, the $\delta^{13}\text{C}$ value of planktivores is lower than that of invertivores on patch reefs and so the observed ^{13}C enrichment with lionfish body size is consistent with an ontogenetic shift in diet from small planktivores to larger invertivores when living on outer forereefs.

Both of these prey groups are represented in both habitats, and systematic differences between habitats in the body sizes of the two guilds could explain the observed shift in lionfish $\delta^{13}\text{C}$. Many invertivores use patch reefs as an intermediate nursery habitat between seagrass beds or mangroves and outer forereefs, tending to occur at smaller, sub-adult sizes in the patch reef habitat and reaching larger sizes when they migrate to the forereef (Mumby et al. 2004). Analysis of visual census data for the study sites (Fig. 4; P. J. Mumby, *unpublished data*) confirms that the average body size of invertivores on our forereef study sites is $\sim 40\%$ larger than on patch reefs, with respective means of ~ 14 cm and ~ 10 cm ($t_{107} = 3.048$; $P = 0.003$). Conversely, the average size of planktivores is slightly smaller on forereefs than on patch reefs with respective means of ~ 3.5 cm and ~ 4 cm ($t_{342} = 2.0783$; $P = 0.038$). On patch reefs, there will therefore be less of a difference between the body sizes of planktivores and invertivores than on forereefs and, as they grow, patch reef lionfish may continue to forage on a mixture of the two prey guilds because a lack of large invertivores reduces the opportunity to switch diet to larger bodied prey. On forereefs, on the other hand, small lionfish may prey on the abundant small planktivores in this high productivity system, switching diet as they grow in order to target the larger-bodied invertivores that migrate ontogenetically to the forereef habitat. Although we feel that this explanation is plausible, field evidence of changing foraging behaviour or study of stomach contents data would be required to corroborate our stable isotope results.

The speed and scale of the lionfish colonization (Lesser and Slattery 2011, Morris and Whitfield

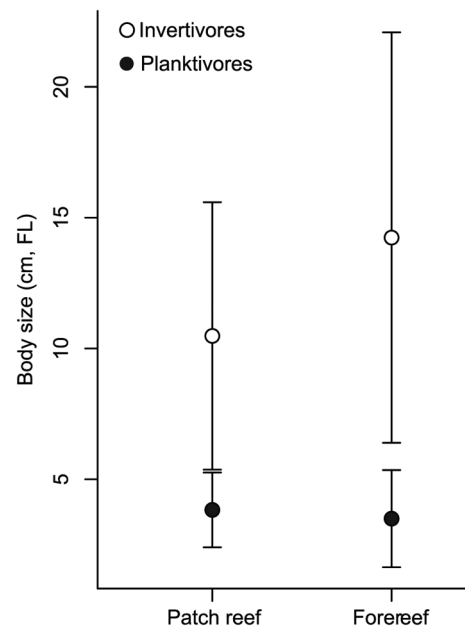


Fig. 4. Body-size mean values and standard deviations of two guilds of putative lionfish prey items across the two Bahamian habitats in which stable isotope analysis was conducted. On deeper forereefs, the mean body size and size range of invertivores are both greater than they are on shallow patch reefs. The stable isotope data used in the present work indicate that forereef lionfish increasingly focus their feeding on invertivores as they grow, which may result from the elevated availability on forereefs of larger-bodied invertivorous prey.

2009) is surprising given the low densities in which it occurs in its natural distribution (Green and Côté 2009). However, the species is relatively unstudied in its home range, hampering attempts to understand how it so readily invaded Caribbean fish communities, or how it may affect individual species. Despite the differences in body sizes between the two species, our results demonstrate that lionfish may be impacting directly on apex-predatory Nassau grouper in the Bahamas and we hope that the study may prove valuable to reef managers tasked with protecting this critically endangered Caribbean icon.

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