Diet shifts in a native mesopredator across a range of invasive lionfish biomass

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ABSTRACT: In marine ecosystems, little is known about how competition with invasive fishes may affect the resource use of native predators. Throughout the western Atlantic, invasive Indo-Pacific lionfishes (*Pterois* spp.) are likely to compete with native mesopredators such as the graysby *Cephalopholis cruentata*, an ecologically similar serranid. In conjunction with a before-after-control-impact lionfish removal experiment, this study measured whether graysby population size, diet, and condition varied in relation to cohabitant lionfish biomass. Lionfish, graysby, and prey populations were surveyed and sampled along a contiguous reef ledge in Biscayne National Park, south Florida. Mesopredator diet was measured with stable isotope (δ^{13}C and δ^{15}N) and gut content analyses, and isotopic niches were used to compare patterns of inter- and intraspecific resource use diversity. The isotopic niches of graysby and lionfishes overlapped by 67%, suggesting similar population-level resource use. On sites with higher lionfish biomass, graysby isotopic niche was 34% smaller and overlapped 47% less with that of lionfishes, possibly indicating both a narrower breadth of resource use and associated interspecific niche segregation. Although gut content analyses suggested that graysby may consume less fishes on high lionfish biomass sites, prey fish populations did not vary accordingly, potentially inferring interference by lionfishes on graysby foraging behavior. However, graysby condition was not related to lionfish biomass, so the 2 species ultimately did not fit the classic definition of competitors. By discussing potential influences of lionfishes on graysby resource use, our research contributes useful information to the study of how invasive lionfishes may affect native predator communities.

KEY WORDS: Diet breadth · Niche variation · Interference competition · Habitat exclusion · SIBER analysis · Reef ecology

INTRODUCTION

Interspecific competition is a critical component of invasive species ecology, and can impart broad, long-lasting effects on native species and communities through multiple mechanisms (Zavaleta et al. 2001, Strayer et al. 2006). When a novel invader depletes common resources, exploitative competition can force native organisms to rely on sub-optimal dietary sources and habitat (Park 1954, Petren & Case 1996, Bøhn & Amundsen 2001). Invasive species can also preclude access to preferred resources through non-consumptive interactions, constituting interference competition (Brian 1956, Schoener 1982, Warnock & Rasmussen 2013). Both forms of competition by definition can lead to reductions in fitness, physiological condition, or population growth of the native competitor (Park 1954, Schoener 1982, Petren & Case 1996). In extreme cases, successful invaders can completely displace indigenous species, causing local extirpations and losses of biodiversity (Mandrak & Cudmore 2010, Morales et al. 2013). Alternatively, adaptation can drive niche partitioning as species optimize the use of new resources to ameliorate the

effects of competition (Schoener 1974, Ross 1986, Cherel et al. 2008). Studying the nature and outcome of competitive interactions between invasive and native species is therefore key to predicting the long-term effects of biological invasions and informing subsequent management efforts.

In marine ecosystems, little is known about how competition may shape the resource use of native fishes following the establishment of an invasive species. As prominent marine invaders, Indo-Pacific lionfishes *Pterois miles* and *P. volitans* (hereafter, lionfish) have received considerable attention from both the scientific community and the public following their precipitous spread throughout the western Atlantic. Owing to their high consumption rates, lionfish can reduce the abundance and diversity of native prey (Albins & Hixon 2008, Green et al. 2014, Albins 2015), potentially resulting in exploitative competition with similarly sized native predatory fishes. Lionfish diet has been found to overlap with that of native predators (Layman & Allgeier 2012, O′Farrell et al. 2014), a necessary precursor of exploitative competition. Additionally, lionfish occupy a broad range of habitats, including seagrass beds (Jud & Layman 2012), mangrove roots (Morris & Akins 2009), artificial structures (Dahl & Patterson 2014), patch reefs (Layman & Allgeier 2012), and complex contiguous reefs (Albins 2015), and thus are likely to encounter a wide diversity of commercially and ecologically important species. Given that lionfish can engage in aggressive, territorial behavior (Fishelson 1975) and may trigger avoidance in other predators (Raymond et al. 2015), interspecific interactions also have the potential to result in interference competition. Despite the high likelihood for competitive interactions, only Albins (2013) has examined the physiological conse-quences of cohabitation between invasive lionfish and a native predator, a necessary component of any attempt to determine whether 2 species are undergo-ing competition (Birch 1957). That study found no effect of the invasive species on the growth rate of coney *Cephalopholis fulva*, but the author noted that the duration of the experiment may have been too short to allow detection of the long-term effects of interspecific competition. To date, no study has measured population-level variation in the diet and condition of predators native to the western Atlantic across a gradient of lionfish biomass.

One likely competitor with lionfish throughout much of the invaded range is the graysby *Cephalo-pholis cruentata*, a reef-dwelling serranid with simi-lar maximum size, habitat use, diet, and life history patterns to the invasive species (Nagelkerken 1979,

Sluka et al. 1998, Morris & Akins 2009). In the Red Sea, native lionfish densities increased following re-moval of *Cephalopholis* spp., suggesting competition with graysby congeners (Shpigel & Fishelson 1991). As mesopredators, graysby can mediate the abun-dance and behavior of other reef species, particularly through top-down effects on prey density and diver-sity (Stallings 2008, Feeney et al. 2012). Any influ-ence of lionfish on graysby could therefore disrupt invaded communities, especially in southeast Florida where graysby are among the most abundant grouper species (Sluka et al. 1998). Thus, under-standing how the lionfish invasion can affect graysby and other mesopredators is a pertinent objective for resource managers and conservation ecologists.

This study examined whether graysby population metrics, diet, and physiological condition varied across naturally occurring and experimentally in-duced gradients of lionfish biomass, allowing assess-ment of the potential effects of interspecific competi-tion. We compared lionfish and graysby diet via stable isotope analysis (SIA), a useful tool for describ-ing resource use overlap between 2 species and thus determining the plausibility of interspecific competi-tion (Bearhop et al. 2004, Jackson et al. 2011, Knickle & Rose 2014). We also applied a combination of SIA and gut content analyses to assess whether graysby diet composition related to ambient lionfish biomass. Concurrent measurements of graysby condition allowed us to discuss how changes in diet were reflected in population-level physiology, and thus whether lionfish and graysby could be classified as competitors in the study area.

MATERIALS AND METHODS

Study region and sites

Our study was performed along the eastern boundary of Biscayne National Park (BNP) in south-east Florida (Fig. 1), where a complex, contiguous reef ledge consisting of a diverse array of soft corals, stony corals, and sponges provides habitat for com-parable densities of lionfish and graysby (Harlem et al. 2012). We collected data from 18 sites, each measuring 1000 m² (20 to 25 m depth), distributed along 25 km of reef as part of an associated lionfish removal experiment (Stallings & Albins 2013). Sites differed in shape, as they were designed to follow the boundary of the ledge in selected locations, but were comparable in relief and topography based on visual assessments and stratified depth measure-
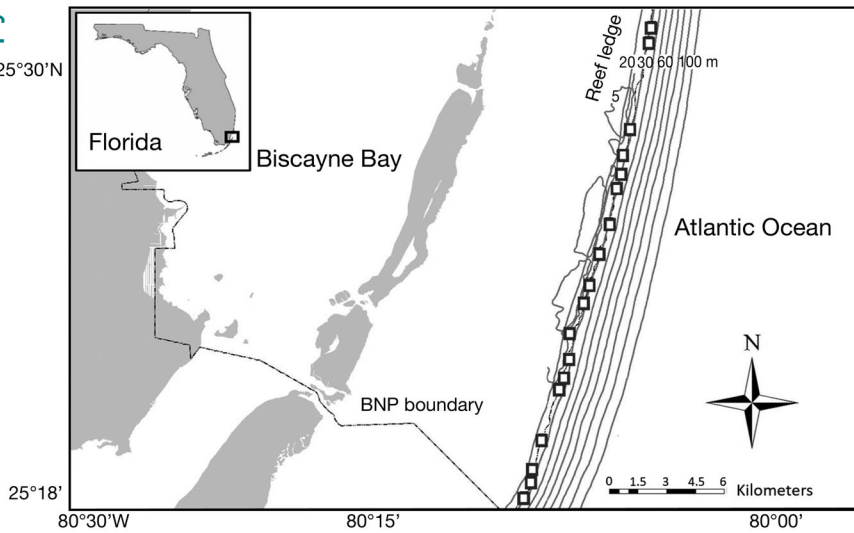
Fig. 1. Study area along the reef ledge of Biscayne National Park (BNP). The dashed line is the portion of the BNP boundary that is included in the frame. The solid grey lines are isobaths at 5 m, as well as subsequent 10 m increments from 10 to 100 m depth

over the entire site using a roving protocol designed to enhance lionfish detection (Green et al. 2013). Subsequently, 2 divers estimated abundance and length of all native fishes along adjacent permanent strip transects (25 × 2 m). Although these surveys included fishes of all sizes, they were conducted slowly and methodically, and with a particular emphasis on the assessment of abundance and diversity of small and cryptic species. By avoiding the tendency of more traditional, rapid fish community surveys to under-represent species that are difficult to detect, these methods enabled more accurate comparisons of the potential prey community among our sites. All surveys took place from 08:00 to 19:00 h and were directed into the prevailing current.

ments. Each site was randomly assigned to 1 of 3 levels of a lionfish removal treatment: control (no removal, n = 6 sites); tri-annual removal (n = 6 sites); and monthly removal (n = 6 sites). Sites were surrounded by a 500 m buffer zone where lionfish were not removed for the duration of the experiment. Although recreational anglers had unrestricted access to the sites, creel surveys suggest that the catch of lionfish and graysby was extremely low along BNP's reef ledge during the study period (S. Moneysmith unpubl. data).

Surveys and removals

The accompanying 2 yr removal experiment used a before-after-control-impact (BACI) study design, with 1 yr of surveys before (January, May, July, September 2014) and after (December 2014, and May, July, September 2015) the initiation of lionfish removal in late September 2014. No data from May 2014 were included for analysis, as inclement weather prevented the completion of surveys. The BACI study structure allowed for potential analyses of graysby diet and condition both across natural (spatial) gradients of lionfish biomass and removal driven (temporal) gradients. On each sampling trip, scientific SCUBA divers measured populations of lionfish, native predators, and native prey on all sites. Estimates of abundance and length of lionfish and native predators, including graysby, were made

Lionfish removals were performed by BNP scientific staff, following the completion of visual surveys in months when the 2 activities overlapped. On removal sites, all individuals detected by divers were collected with a polespear, placed on ice, frozen at the end of the day, and eventually transported to the University of South Florida (USF) for further analysis. Although a small number of lionfish may have avoided detection and capture by hiding in the complex reef habitat, divers involved in culling efforts were adeptly trained and highly experienced in the BNP environment, and therefore likely to find and effectively remove the majority of individuals from each site. At the conclusion of the study, all detected lionfish were collected from every site, including those in the control treatment. Graysby were sampled during July and September of both years after the completion of seasonal native fish surveys. To avoid causing local depletion or strongly affecting graysby population dynamics, a maximum of 3 individuals per sampling effort were removed from each site prior to the final survey of the experiment. Graysby were collected via polespear, when necessary with the assistance of a 20% solution of quinaldine ($C_{10}H_9N$), a commonly used fish anesthetic (Gibson 1967). Sampled graysby were stored on ice after each dive and dissected the same day. Specimen collections were made under the auspices of the USF Institutional Animal Care and Use Committee (protocol W4193) with approval from the US National Park Service (permit BISC-2014-SCI-0025).

Dissections

Before dissection, all frozen lionfish were thawed at room temperature. Thawing was not required for graysby, which were dissected on the day of capture. Standard length (cm), total length (cm), and total mass (g) of each individual were measured. The viscera of each fish were then removed from the anterior end of the esophagus to the posterior end of the digestive tract and weighed. When intact, the liver was separated and weighed, followed by the eviscerated soma of each fish. Graysby viscera were preserved in a 30% formalin solution for a minimum of 48 h before transfer to a 50% isopropanol solution. Lionfish viscera were frozen for future analyses not included in this study.

SIA

For SIA in both lionfish and graysby, approximately 1 cm^3 of tissue was removed from the musculature posterior to the dorsal fin, the same location used in previous measurements of lionfish stable isotopes (Layman & Allgeier 2012). Freezing was chosen as the preferred method for fish tissue storage, as it does not impart preservation-driven offsets in stable isotope values (Stallings et al. 2015). We measured the 2 stable isotopes most commonly used in diet studies: ^{13}C, which reflects basal resource use of the sampled organism; and ^{15}N, which describes relative food web positioning and increases with trophic level (Fry 2006). Overlap in the values of these stable isotopes between 2 species is typically interpreted as similarity in resource use, a potential precursor to competition (Bearhop et al. 2004, Jackson et al. 2011). Muscle tissue was freeze-dried at −40°C for at least 36 h and mechanically ground until homogenized. For analysis, 400 to 1000 μg of material was collected and weighed on a Mettler-Toledo precision micro-balance, wrapped in tin capsules, and loaded into a Costech Technologies Zero-Blank Autosampler. Samples were combusted at 1050°C in a Carlo-Erba NA2500 Series-II Elemental Analyzer coupled in continuous-flow mode to a Finnigan Delta Plus XL isotope ratio mass spectrometer. Measurements of molar C:N ratio were calibrated and isotopic measurements were normalized to the atmospheric air and Vienna PeeDee Belemnite scales, respectively, using NIST 8573 and NIST 8574 L-glutamic acid standard reference materials. Measurements were expressed in units per mille (‰) using δ notation, where δ = [($R_{sample}/R_{standard}$) − 1] × 1000, and R is the isotopic ratio of interest (e.g. ^{13}C:^{12}C). Analytical precision, estimated by replicate measurements of a working standard (NIST 1577b, bovine liver, n = 176) was ±0.16‰ (δ^{15}N), ±0.13‰ (δ^{13}C), and ±0.27‰ (C:N). For each fish, 2 replicate samples were analyzed and the results were averaged for further statistical comparison. The mean difference (±SD) between replicate samples was 0.00 ± 0.15‰ for both δ^{15}N and δ^{13}C, indicating a high degree of consistency among isotopic measurements of the same material.

Stomach contents

SIA provides an integrated measurement of isotopic input from diet over the turnover period of sampled tissue, which for fish muscle takes weeks to months (Trueman et al. 2005, Ankjærø et al. 2012). Therefore, it is also informative to consult stomach contents to obtain a snapshot of feeding trends and ground-truth stable isotope data (Knickle & Rose 2014, Condini et al. 2015). However, to robustly compare fine-scale patterns in consumption, larger sample sizes are usually required than were available for this study (Ferry & Cailliet 1996). Additionally, delays between capture and dissection led to stomach contents frequently being digested beyond the point of high taxonomic resolution. Therefore, we limited our analysis to quantification of the presence/absence of invertebrate and teleost prey, which was performed via examination of graysby gut contents under a dissecting microscope.

Condition indices

In order to determine whether lionfish biomass was correlated with a decrease in graysby physiological condition, a necessary component of the classic definition of competition (Birch 1957), we consulted 4 different metrics: Ricker's condition index, the hepatosomatic index (HSI), muscle C:N ratios, and gut fullness. Ricker's condition index can be applied to readily compare the condition of 2 populations experiencing different environmental regimes (Weatherley 1972). We chose this index over the computationally simpler Fulton's K because the Ricker's condition index does not assume a cubic growth law, and thus may allow for more refined and species-specific comparisons of weight-at-length values among 2 conspecific populations (Froese 2006). Ricker's index is described by the equation $K = W/aL^b$, where $W =$

observed weight (g), L = length (cm), and a, b are species-specific growth parameters (Le Cren 1951). Parameters for graysby (a = 0.0079, b = 3.22) were calculated using non-linear least squares regression on morphometric data measured in specimens collected for this experiment (Fig. A1 in the Appendix). The HSI describes energy reserves and fish condition, as teleost livers are a primary site for lipid deposition (Delahunty & De Vlaming 1980, Stallings et al. 2010). HSI values were calculated as $100 \times (W_l/W_s)$, where W_l = liver weight and W_s = somatic weight, or weight of the fish after removal of the viscera (Jensen 1979). As graysby were collected only in the summer, relative comparisons of HSI values were assumed to be unaffected by seasonal fluctuations, which can influence lipid deposition and confound analyses of condition (Adams & McLean 1985). Measurements of muscle C:N ratios can also serve as a proxy for lipid content (Post et al. 2007), and were calculated as a component of SIA. Samples with larger C:N ratios are higher in fat content, as lipids are richer in carbon than the amino acids predominant in lean muscle (Woodland & Secor 2011). Graysby stomach fullness was assessed to link physiological condition indices to the ecological process of foraging, and was measured using a metric described by Haram & Jones (1971). Each stomach was assigned a fullness value based on the following rubric: 0 (completely empty stomach), 0.5 (trace of food present), 1 (1/4 full), 2 (1/2 full), 3 (3/4 full), 4 (full), 5 (stomach completely distended). Despite the frequent occurrence of heavily digested material that precluded identification of prey to the species level, comparison of the relative amount of material in the stomach was still readily achievable.

Statistical analysis

For all frequentist analyses in this study, statistics were calculated with distribution-free, non-parametric tests derived from the Fathom Toolbox for MATLAB (Jones 2015). Significance was assessed using p-values calculated by comparing the position of test statistics derived from the original data relative to a distribution of the same statistic calculated from n = 1000 randomized permutations of the dataset (Moore et al. 2009). Statistics that were more extreme than 95% of permuted values (2-tailed) were considered to be significant (α = 0.05). Although these methods allowed us to relax some of the strict assumptions of parametric statistical tests, particularly that of normally distributed errors, they can be sensitive to the inclusion of dependent or spatially structured data (Anderson 2001). Therefore, for tests involving multiple individuals collected from the same study site, which represent subsamples rather than independent replicates, randomization was constrained to within study sites (Legendre & Legendre 1998, Økland 2007).

To measure evidence of potential interspecific habitat exclusion or population declines driven by competitive interactions, we examined trends among site-averaged lionfish and graysby population metrics (density and biomass) with 2-sided tests of Pearson's correlation coefficient. In order to avoid including any potential influence of systematic culling on interspecific population dynamics, these correlations were only performed on data collected before the initiation of lionfish removals. Both density and biomass values were estimated based on information from visual diver surveys.

After a review of preliminary results, we determined that there was too much variability in the success of lionfish removals for temporal comparison of graysby diet and condition; not enough sites showed rapid and persistent decreases in the density or biomass of lionfish for statistically powerful comparison using the BACI study structure. Therefore, sites were grouped into lionfish biomass categories (LBCs) for analyses examining diet and condition. Estimates of lionfish and graysby biomass were derived from visual diver surveys based on the same weight–length relationship used to calculate Ricker's condition index ($W = aL^b$). Growth parameters for lionfish (a = 0.0082, b = 3.18) were derived from local specimens collected through BNP's lionfish removal program (Stallings & Albins 2015, unpubl. data). To compare graysby diet and condition across extremes of interaction with lionfish, only the 6 sites with the highest and lowest average lionfish biomass were categorized into LBCs (Fig. 2). The remaining 6 sites, with lionfish biomass values closest to the average for the study area, were excluded from LBC-based analyses. The choice of 6 sites per LBC was based on a need to ensure a comparable geographic range of constituent sites, as well as to provide appropriate sample sizes of both species for subsequent measurements. We tested the difference in lionfish biomass between the 2 LBCs using a mixed effects generalized linear model with survey period as a random effect and a compound Poisson-gamma distribution (log link, Tweedie family with p = 1.61). Based on the best fitting model, lionfish biomass in the high category (25.29 kg ha^{-1}, 95% CI: 20.24 to 31.60) was about 2 times greater than lionfish biomass in the low
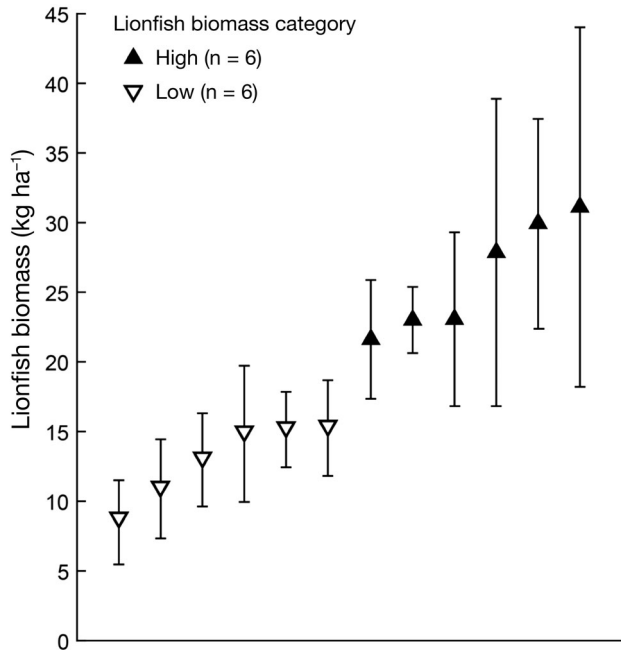
Fig. 2. Mean lionfish biomass (±SE) on study sites in the low lionfish biomass category (LBC; ▽) and high LBC (▲) in ascending order

category (12.75 kg ha^{-1}, 95% CI: 9.94 to 16.36). To ensure that the size structure of collected individuals did not systematically vary between LBCs, we used a 2-way Kolmogorov-Smirnov test to compare distributions of standard lengths of both species. There was no evidence that the size distributions of either lionfish (K-S statistic = 0.13, p = 0.383) or graysby (K-S statistic = 0.07, p = 0.997) differed between LBCs.

Relationships between stable isotope values and standard lengths were assessed using linear regressions to measure trophic trends with growth of both species. Patterns of change in stable isotope values related to size are inconsistent in marine fishes, but can be associated with ontogenetic shifts in diet and habitat (Cocheret de la Morinière et al. 2003, Nakamura et al. 2008), an important component of resource use to understand in the context of an invasive predator such as lionfish (Layman & Allgeier 2012, Dahl & Patterson 2014). Comparisons of mean stable isotope values were made with non-parametric *t*-tests, and 95% confidence intervals were calculated for differences among means via bootstrapping with n = 1000 permutations (Moore et al. 2009).

In addition to calculating mean stable isotope values, we compared the dispersion of lionfish and graysby isotopic measurements to provide information on inter- and intraspecific patterns of resource use diversity (Bearhop et al. 2004, Layman et al. 2007). Analyses of isotopic variation have previously

been used to assess population-level diet in terrestrial and marine species (Fry et al. 1978, Knickle & Rose 2014), including lionfish (Layman & Allgeier 2012). Comparing the relative position and amount of overlap between lionfish and graysby isotopic niches can help indicate the extent to which the 2 species share prey and habitat, a precursor to competition if those resources become limiting (Tilman 1977, Cherel et al. 2008, O'Farrell et al. 2014). Assessing differences in graysby isotopic niche width across a range of lionfish biomass may additionally suggest whether interaction with the invasive species can affect the breadth of graysby resource use.

Lionfish and graysby stable isotope dispersions were quantified using stable isotope Bayesian ellipses in R (SIBER) analysis, which describes aspects of a population's isotopic niche by plotting and measuring the bi-variate standard deviation, or standard ellipse area (SEA), of isotope bi-plots (Jackson et al. 2011). The value used for statistical comparisons of isotopic niche width was SEA_B, or the mode of n = 20000 standard ellipses generated via Bayesian permutation, with a significance cutoff for the test set at Bayesian probability = 95%. Above a threshold of approximately n = 30 (Syväranta et al. 2013), these measurements are not biased by sample size, allowing comparisons of isotopic niche width even among datasets derived from vastly different numbers of individuals (e.g. n = 294 lionfish vs. n = 151 graysby). SIBER analysis was also used to measure the amount of overlap between isotopic niches. In previous studies of diet, an overlap of 60% was used as the threshold of biological significance (Smith 1985). Before applying SIBER analysis, multivariate outliers were identified via the MVN package in R, using a Mahalanobis measure of distance from the multivariate centroid (Korkmaz et al. 2014). As isotopic outliers can still yield important information about individual foragers (Layman et al. 2007), only the most extreme values (Mahalanobis distance >10) were removed from SIA calculations. In total, 4 lionfish and 2 graysby were excluded as multivariate isotopic outliers. Additionally, for comparisons of lionfish and graysby stable isotope values and dispersions within the low LBC, 1 site was excluded from which there were no available lionfish samples for isotopic analysis.

To assess how lionfish biomass may relate to resource availability in BNP, we performed linear regressions of prey density and species richness with lionfish biomass across all study sites. Although all native fishes were surveyed, only individuals ≤10 cm total length were classified as potential prey, as

larger teleosts do not contribute substantially to the diet of either lionfish (Morris & Akins 2009, Muñoz et al. 2011) or graysby (Nagelkerken 1979, Stallings 2008). Predator and prey community compositions were also compared across LBCs using 1-way non-parametric MANOVAs.

Proportions of full (fullness index ≥4) and empty (fullness index ≤0.5) graysby stomachs, as well as the proportions of graysby stomachs containing teleost and invertebrate prey, were compared between LBCs using a Pearson's 2 × 2 chi-squared test. Although digestion rates and the composition of stomach contents can be influenced by time of day, fish size, water temperature, and a suite of other environmental and biological factors, graysby were collected randomly with respect to the categorization of sites into LBCs. Therefore, there was no systematic bias introduced by the collection and dissection process that would have affected comparison of the amount or identity of material in graysby stomachs across LBCs. Additionally, we restricted analyses of gut contents to an intraspecific comparison (graysby vs. graysby), thereby avoiding any confounding variability that could stem from different species-specific rates of digestion (Ferry & Cailliet 1996). Mean condition indices of graysby from each LBC were compared using non-parametric t-tests.

RESULTS

Population measurements

Before the initiation of culling, there was no correlation at our study sites between lionfish and graysby density (n = 18, r = −0.11, p = 0.633) or biomass (n = 18, r = −0.01, p = 0.962). Importantly, there was also no evidence of a difference in graysby density (t_{10} = 0.40, p = 0.358) or biomass (t_{10} = 0.27, p = 0.403) between LBCs. Given comparable population sizes, the strength of intraspecific interaction would not be expected to vary, suggesting that whatever influence graysby may have had on conspecific diet or condition should not have systematically affected our analyses of resource use and condition across LBCs.

SIA

Both lionfish and graysby $\delta^{15}N$ values were positively related to length (lionfish: n = 311, F = 134, R^2 = 0.30, p = 0.001; graysby: n = 170, F = 31.6, R^2 = 0.16, p = 0.001; Fig. 3). Using a bootstrap analysis (n = 1000

permutations), we determined that the 95% confidence intervals of regression slopes overlapped between lionfish and graysby (lionfish 95% CI: 0.028 to 0.037‰ cm⁻¹; graysby 95% CI: 0.022 to 0.048‰ cm⁻¹), and therefore the rate of increase of $\delta^{15}N$ values with size was not significantly different between species. However, the relationship of $\delta^{13}C$ values with size was not consistent between species. Lionfish $\delta^{13}C$ values were lower in larger individuals (n = 311, F = 28.5, R^2 = 0.09, p = 0.001), while graysby $\delta^{13}C$ values were not related to standard length (n = 170, F = 0.02, R^2 <0.01, p = 0.891; Fig. A2 in the Appendix). Although the regression was significant, lionfish size explained <10% of variation among $\delta^{13}C$ values, limiting its usefulness for describing population-level trends in basal resource use with growth.

Examining all sampled individuals, mean $\delta^{13}C$ was 0.33‰ higher in lionfish than in graysby (95% CI = 0.23 to 0.40, t_{443} = 6.82, p = 0.001). However, the magnitude of this difference was small relative to the range of measured stable isotope values (Table 1). Although mean lionfish $\delta^{15}N$ was 0.07‰ lower than
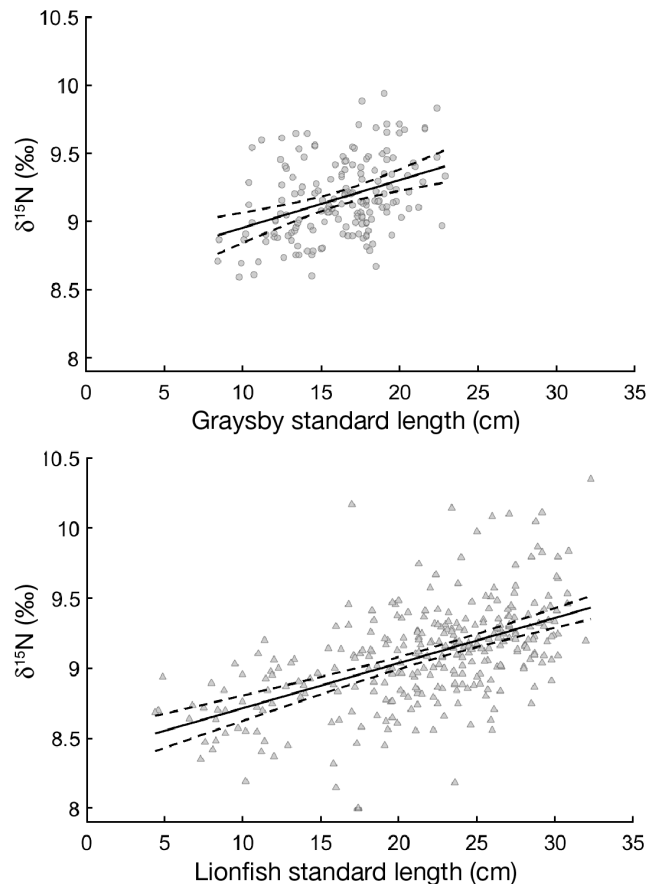

Fig. 3. Regressions of graysby (top) and lionfish (bottom) $\delta^{15}N$ with standard length (solid lines). Dashed lines are 95% confidence bands for the regression

Table 1. Stable isotope (δ^{13}C, δ^{15}N) means (±SE) and ranges from graysby and lionfish across sites, and separated between low and high lionfish biomass categories (LBCs)

Variable	n	δ^{13}C	δ^{13}C (min.)	δ^{13}C (max.)	δ^{15}N	δ^{15}N (min.)	δ^{15}N (max.)
Graysby — all sites	151	−15.05 ± 0.03	−15.92	−13.92	9.17 ± 0.02	8.59	9.94
Lionfish — all sites	294	−14.72 ± 0.03	−16.32	−13.13	9.10 ± 0.02	8.00	10.35
Graysby — low LBC	52	−14.91 ± 0.06	−15.90	−13.92	9.21 ± 0.03	8.69	9.94
Lionfish — low LBC	78	−14.67 ± 0.06	−15.89	−13.64	9.21 ± 0.04	8.45	10.14
Graysby — high LBC	49	−15.14 ± 0.04	−15.92	−14.59	9.13 ± 0.04	8.60	9.65
Lionfish — high LBC	94	−14.73 ± 0.05	−16.32	−13.34	9.11 ± 0.04	8.14	10.35

in graysby (95% CI = 0.01 to 0.13, t_{443} = −2.03, p = 0.017), this difference was smaller than instrumentation error. Overall, SIBER analysis measured a 67.5% overlap in graysby isotopic niche with that of lionfish (Fig. 4).

Stable isotope values on low LBC sites showed similar trends to those measured in the full dataset (Table 1). On average, lionfish δ^{13}C values were 0.25‰ higher than measured in graysby (95% CI = 0.07 to 0.43, t_{120} = −2.57, p = 0.019) and SIBER analysis measured a 63.6% interspecific isotopic niche overlap (Fig. 5). In contrast, data from high LBC sites showed potential signs of resource use differentiation between the 2 species. Although the interspecific difference in mean δ^{13}C was still small (difference = 0.41‰, 95% CI = 0.26 to 0.57, t_{141} = −4.89, p = 0.001), its magnitude increased by 65% relative to low LBC sites. In addition, the amount of isotopic niche overlap between lionfish and graysby was 47% lower on high LBC sites (0.178‰²) than on low LBC sites (0.336‰²). Although within graysby neither mean δ^{13}C (t_{99} = 2.86, p = 0.109) nor δ^{15}N (t_{99} = 1.36, p = 0.177) values differed between LBCs, graysby isotopic niche width was 33.4% smaller on high LBC sites (low SEA$_B$ = 0.425‰², high SEA$_B$ = 0.283‰², probability = 97.9%; Fig. 6). Conversely, lionfish isotopic niche width did not differ between low and high LBCs (low SEA$_B$ = 0.511‰², high SEA$_B$ = 0.585‰², probability = 80.6%).

Gut contents

Among stomachs containing identifiable items, the proportion of gut contents containing teleost prey was 25% lower on high LBC sites than on low LBC sites, although the difference was only marginally significant (χ^2 = 2.80, p = 0.095). The proportion of stomachs containing invertebrate prey did not differ between LBCs (χ^2 = 0.27, p = 0.596), nor did the proportion of full (χ^2 = 0.17, p = 0.682) or empty (χ^2 = 0.19, p = 0.889) graysby stomachs.
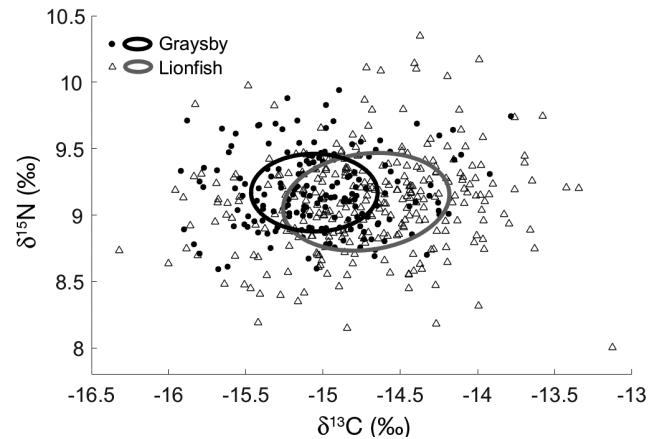

Fig. 4. Stable isotope bi-plot of all sampled graysby (●) and lionfish (△). Standard ellipses created by SIBER analysis (SEA$_B$) are overlaid on the data. The graysby SEA$_B$ (0.392‰²) is depicted as a black line, the lionfish SEA$_B$ (0.561‰²) as a grey line. Interspecific SEA$_B$ overlap was 67.5%, indicating a similar isotopic niche
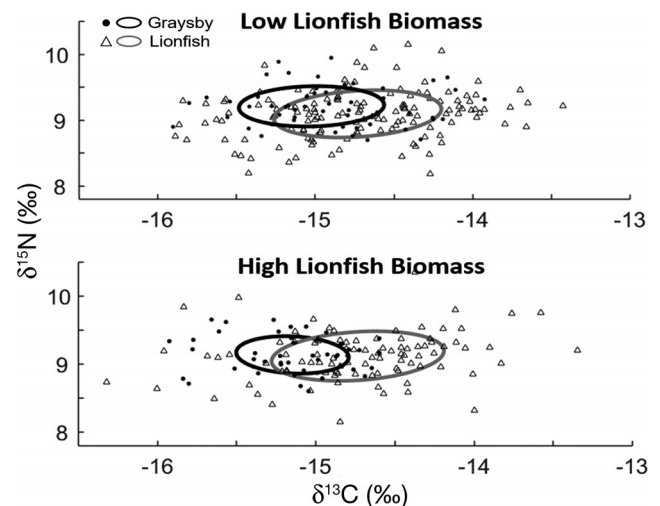

Fig. 5. Stable isotope bi-plot of graysby (●) and lionfish (△) from low (top) and high lionfish biomass sites (bottom). Standard ellipses created by SIBER analysis (SEA$_B$) are overlaid on the data. The graysby SEA$_B$ (low: 0.283‰²; high: 0.425‰²) is depicted as a black line, the lionfish SEA$_B$ (low: 0.511‰²; high: 0.585‰²) as a grey line. The amount of interspecific isotopic niche overlap was 47% lower on high LBC (0.178‰²) than low LBC sites (0.336‰²)
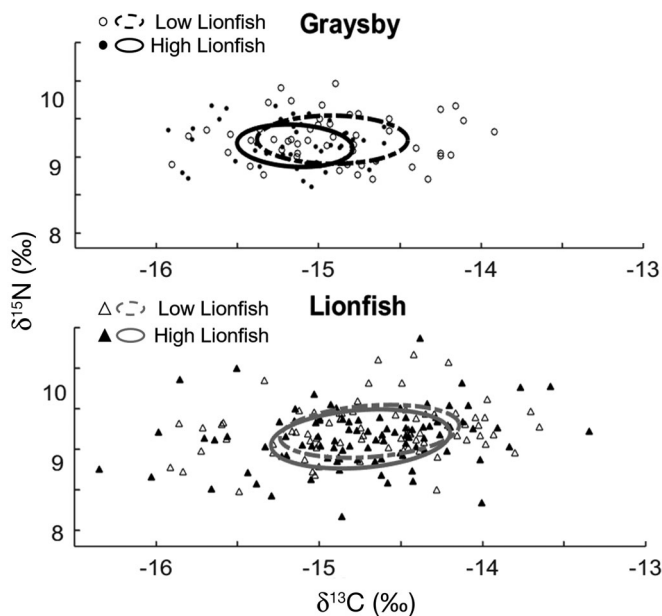
Fig. 6. Stable isotope bi-plots of graysby (top, circles) and lionfish (bottom, triangles) from low (open) and high (filled) lionfish biomass categories (LBCs). Standard ellipses created by SIBER analysis (SEA$_B$) are overlaid on the data (low LBC = dashed line, high LBC = solid line). Graysby SEA$_B$ was 34% smaller on high vs. low LBC sites (probability = 97.9%). Lionfish SEA$_B$ did not differ between LBCs (probability = 80.6%)

Prey and predator communities

Across all study sites, neither prey fish density (n = 18, F = 0.29, p = 0.607) nor species richness (n = 18, F = 0.50, p = 0.480) were related to lionfish biomass. Additionally, non-parametric MANOVAs measured no difference in the community composition of prey ($F_{1,11}$ = 1.35, p = 0.236) or predatory fishes ($F_{1,11}$ = 0.27, p = 0.998) between LBCs. Overall, graysby were by far the most abundant mesopredator on our surveys, and were counted more frequently than all other predatory fishes combined.

Condition indices

Despite an apparent difference in graysby resource use associated with higher lionfish biomass, graysby condition did not vary accordingly. Neither Ricker's condition index (t_{100} = 0.21, p = 0.434), the HSI (t_{64} = 0.63, p = 0.252), C:N values (t_{100} = 1.46, p = 0.098), nor gut fullness index (t_{100} = 0.29, p = 0.527) were different between graysby collected from high and low LBC sites.

DISCUSSION

The strength and outcome of competition between lionfish and native predators is an important, yet relatively unexplored, aspect of this marine fish invasion. The results of this study are the first to describe changes in the resource use of a native mesopredator across a range of lionfish biomass, and can provide insight into the possible consequences and mechanisms of interaction among lionfish and ecologically similar predatory fishes.

The biomass and density of lionfish and graysby were not related across the study region, and thus did not show the negative trend expected under a strong competitive regime (Hardin 1960, Bøhn et al. 2008). One possible caveat is that this result may not reflect shifts in microhabitat use or small-scale spatial distribution that could have followed interspecific interactions, which would not have materialized as site-level correlations in biomass or density (Eagle et al. 2001). Still, it does not appear from these data that the size of the lionfish population affected that of graysby in the setting of the BNP reef ledge.

Despite the lack of a relationship in population size, the high amount of isotopic overlap between lionfish and graysby suggests a similarity in population-level resource use that may drive competition in a resource-limited environment (Tilman 1977, Bearhop et al. 2004, Layman et al. 2007). Additionally, both lionfish and graysby δ^{15}N values rose similarly with size, measuring comparable growth-driven increases in trophic level that could result in overlapping resource use across multiple life stages and size classes (France et al. 1998). This result matches descriptions of dietary transitions from invertebrate to teleost prey based on gut content analyses both in lionfish (Morris & Akins 2009, Muñoz et al. 2011) and graysby (Nagelkerken 1979), as well as stable isotope measurements previously made in some populations of lionfish (Dahl & Patterson 2014) and other serranids (Condini et al. 2015).

The observed change in graysby isotopic dispersion across LBCs could provide insight on how invasive lionfish may affect the resource use of native mesopredators. Based on the reduced amount of interspecific isotopic overlap on high LBC sites, graysby appear to differentiate diet or habitat use from that of lionfish where populations of the invasive species are larger. This result resembles findings from other systems, which have been similarly interpreted as niche segregation in response to interspecific interactions (Cherel et al. 2008, Páez-Rosas et al. 2014). Additionally, graysby isotopic niche width was 34% smaller

on high LBC sites, possibly reflecting a narrowing of resource use diversity in the presence of larger populations of lionfish. Although lionfish are not the only mesopredator that may have affected the resource use of graysby, other native predators were comparatively uncommon on our study sites, and their community composition did not differ across LBCs.

Lower dispersion of graysby stable isotope values on sites with presumably stronger interspecific interaction is consistent with the niche variation hypothesis (NVH) (Van Valen 1965). According to the NVH, release from interspecific competition at the population level should lead to niche expansion, whereas increased interspecific interactions should cause niche contraction (Araújo et al. 2011, Kernaléguen et al. 2015). The mechanism driving the NVH is the degree of individual diet specialization, which is expected to increase as intraspecific interactions become more dominant following weakened interspecific competition (Araújo et al. 2011). In the Bahamas, Layman & Allgeier (2012) found that lionfish, usually described as a generalist forager, displayed a surprisingly high capacity for individual specialization. Therefore, similar individual specialization of graysby resource use, which has not yet been empirically measured, may play a role in shaping the response of the species to habitat or diet overlap with invasive lionfish.

We measured a lower proportion of graysby stomachs containing fish material on high LBC sites, although the result was only marginally significant. Additionally, the primary difference in graysby isotopic distributions between LBCs was the presence of graysby with relatively high $\delta^{13}C$ values (−14 to −14.5‰) on low LBC sites (Fig. 6). In combination, these results suggest that reduced consumption of prey fishes in the benthic food web, which is less depleted in ^{13}C than planktonic food webs (Fry 2006), may be a potential outcome for graysby in areas heavily invaded by lionfish. Site depth may have been a confounding variable for this result, as the 2 low LBC sites where the majority of graysby with high $\delta^{13}C$ values were captured were also among the shallowest in the study area (Muscatine et al. 1989, Radabaugh et al. 2013). However, had depth-driven $\delta^{13}C$ gradients contributed to patterns in graysby stable isotope values, lionfish isotopic dispersion should have changed similarly across LBCs, which we did not observe. Furthermore, the same 2 shallow sites of interest contained among the lowest lionfish densities in the study region, maintaining at least an association of high graysby $\delta^{13}C$ values with smaller lionfish populations. Refined measurements of $\delta^{13}C$ values in a variety of taxa, especially primary producers, would have to be made across our study area to elucidate how spatial variables such as depth may have influenced graysby stable isotope dispersions.

If the observed difference in graysby resource use between LBCs was in fact a response to a greater presence of lionfish, the lack of a relationship between lionfish biomass and teleost prey communities among study sites could allow us to infer a potential mechanism of interspecific interaction (exploitative vs. interference). If intense foraging by lionfish had depleted fish communities on high LBC sites, which our data did not indicate, preferred prey species would likely have become unavailable for graysby consumption, constituting exploitation (Park 1954, Birch 1957, Petren & Case 1996). It is worth noting, however, that our daytime surveys of fish communities likely underestimated nocturnal prey taxa that may have been reduced by lionfish foraging. Although invertebrate communities were not surveyed, the consistency in the proportion of graysby stomachs containing invertebrate prey suggests that lionfish may not influence the opportunity for consumption of non-teleost taxa. Occupation of preferred habitat by lionfish would also be considered exploitation if shelter were a limiting resource (Park 1954, Petren & Case 1996), but the complex reefs on our sites likely offered enough space for any potentially displaced graysby. Given the apparent lack of exploitation of any obviously limiting resource, lionfish could have more strongly affected graysby diet by altering patterns of foraging behavior, either through passive avoidance of the invasive species (Raymond et al. 2015) or aggressive, territorial interactions (Fishelson 1975, Nagelkerken 1979), both of which would constitute interference (Brian 1956).

Despite a change in resource use associated with higher lionfish biomass, graysby condition did not vary between LBCs. As competition must involve a negative physiological effect on involved species (Birch 1957, Schoener 1982, Petren & Case 1996), our results do not allow unequivocal classification of lionfish and graysby as competitors. Possibly, the ratio of consumer demand to prey and habitat availability was low enough to preclude any interspecific overlap in resource use from manifesting as competition. The maximum lionfish density on our study sites was 113 per hectare, substantially lower than the 400 to 1500 per hectare reported elsewhere in the invaded range (Albins & Hixon 2013, Dahl & Patterson 2014). Also, graysby were sampled during the summer, a season featuring high recruitment of juvenile fishes to coral reefs (Williams & Sale 1981), plausibly elevating prey densities past the point of resource limitation. Finally,

the structural complexity of BNP's rugose reef ledge may have effectively reduced the strength of interspecific interaction by providing unexploited space for occupation by lionfish, graysby, and prey species (Almany 2004). Studies of native mesopredator diet and condition in an environment with higher lionfish biomass, more depleted prey, and less complex habitat could help identify the environmental and ecological thresholds at which resource use overlap with invasive lionfish may transition into empirically demonstrable interspecific competition.

An assumption for our analyses and interpretations is that both lionfish and graysby were resident species that moved and foraged similarly within the 1000 m^2 study sites. Graysby dwell in home ranges comparable in scale to the size of our sites and demonstrate high site fidelity (Popple & Hunte 2005), meeting both criteria. Although the size of our sites was selected based on previous descriptions of lionfish as having high site fidelity (e.g. Jud & Layman 2012), rapid and broad translocations by some individuals have been recently observed (Bacheler et al. 2015, Tamburello & Cote 2015). Indeed, throughout our study lionfish frequently followed divers across the 100 m site length during predator surveys (K.R.W. pers. obs.). Thus, lionfish have a demonstrated capacity to move and forage on a larger spatial scale than considered in the design of this study, potentially weakening our categorization of sites into LBCs. However, our estimates of lionfish biomass on each site were based on 7 surveys over 2 yr, which should have provided an accurate enough approximation of average lionfish population size for crude classification into low and high categories. Additionally, the numbers and sizes of lionfish removed by BNP staff from study sites days after our surveys were generally similar to those measured in our visual censuses, further suggesting that our biomass estimates were not completely undermined by broader-scale movements. Regardless, future measurement of invasive lionfish foraging ranges and site fidelity remains a critical research objective that could not only clarify our findings but also inform predictions of the spatial scale of resource use overlap with resident native mesopredators.

CONCLUSIONS

Considering the extent and severity of the lionfish invasion, total eradication of the species across the invaded range is unrealistic. Measuring the non-consumptive effects of lionfish on native species as they continue to integrate into western Atlantic ecosystems is therefore necessary for concerned resource managers and conservation scientists. We did not detect a change in graysby condition associated with lionfish biomass, and thus our work cannot be used to ascribe competition between the 2 species in BNP. Yet, as one of the only comprehensive studies to examine evidence for *in situ* competition between lionfish and an ecologically similar native mesopredator, this 'negative' result can still provide valuable information to those trying to understand and predict consequences of the invasion on contiguous reef habitat. Importantly, the high amount of interspecific overlap in stable isotope distributions suggests that competition between these 2 species, and possibly other reef predators, remains plausible in more resource-limited environments. Additionally, we found a reduction of graysby isotopic niche width and an interspecific diversification of resource use coincident with larger lionfish populations, possibly associated with interference on foraging patterns or habitat occupation of the native predator. Future studies in environments with more depleted resources or higher lionfish biomass (or both) could reveal whether these species undergo classic competition when subjected to more extreme ecological circumstances. Furthermore, characterization of graysby habitat association and behavior along a gradient of lionfish population size may demonstrate whether the invasive species does in fact interfere with native mesopredator foraging patterns. Finally, comparative studies of movement in lionfish and species such as graysby could indicate the spatial scale of resource use overlap among lionfish and native predators, critical information for managers designing removal programs intended to alleviate the effects of lionfish on invaded ecosystems.

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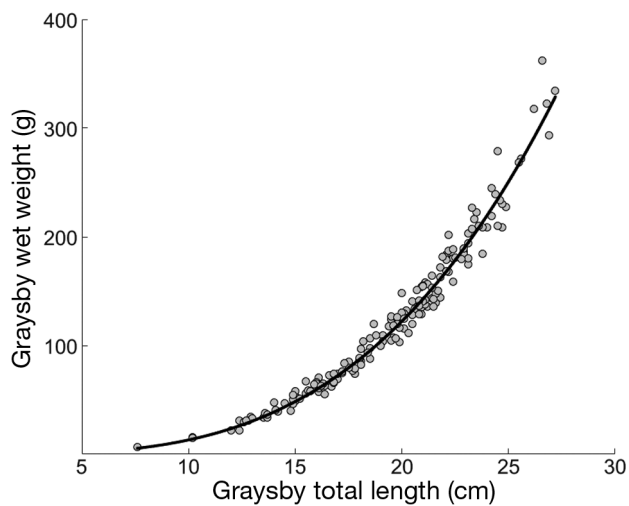
Appendix. Additional data

Fig. A1. Graysby total length vs. wet weight. The fitted curve was used to calculate parameters for the equation $W = aL^b$ ($a = 0.0079$, $b = 3.22$) using non-linear least squares regression
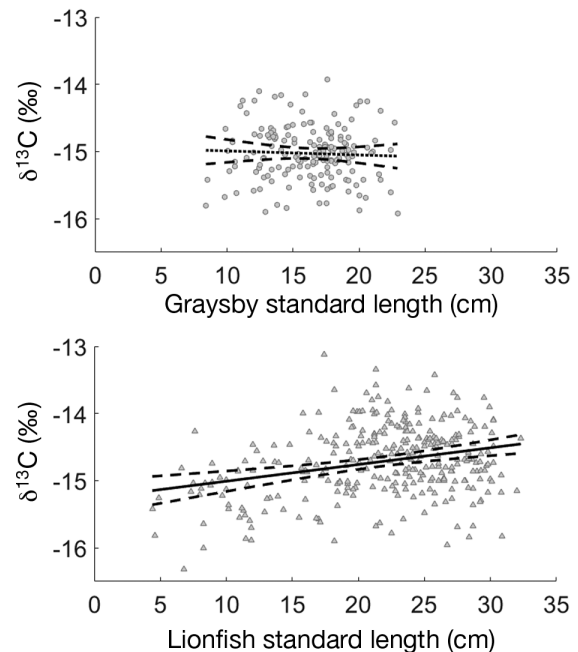

Fig. A2. Regressions of graysby (top) and lionfish (bottom) $\delta^{13}C$ with standard length. Solid and dashed trendlines respectively indicate statistically significant and non-significant regressions ($p \leq 0.05$). Curved, dashed lines are 95% confidence bands for the regressions