Fish stable isotope community structure of a Bahamian coral reef

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Abstract
Stable isotopes have provided important insight into the trophic structure and interaction in many ecosystems, but to date have scarcely been applied to the complex food webs of coral reefs. We sampled white muscle tissues from the fish species composing 80% of the biomass in the 4–512 g body mass range at Cape Eleuthera (the Bahamas) in order to examine isotopic niches characterised by δ13C and δ15N data and explore whether fish body size is a driver of trophic position based on δ15N. We found the planktivore isotopic niche was distinct from those of the other trophic guilds suggesting the unique isotopic baseline of pelagic production sources. Other trophic guilds showed some level of overlap among them especially in the δ13C value which is attributable to source omnivory. Surprising features of the isotopic niches included the benthivore Halichoeres pictus, herbivores Acanthurus coeruleus and Coryphopterus personatus and omnivore Thalassoma bifasciatum being close to the planktivore guild, while the piscivore Aulostomus maculatus came within the omnivore and herbivore ellipses. These characterisations contradicted the simple trophic categories normally assigned to these species. δ15N tended to increase with body mass in most species, and at community level, the linear δ15N–log2 body mass relationship pointing to a mean predator–prey mass ratio of 1047:1 and a relatively long food chain compared with studies in other aquatic systems. This first demonstration of a positive δ15N–body mass relationship in a coral reef fish community suggested that the Cape Eleuthera coral reef food web was likely supported by one main pathway and bigger reef fishes tended to feed at higher trophic position. Such finding is similar to other marine ecosystems (e.g. North Sea).

Introduction
In coral reef food webs, fishes are typically categorised into strict trophic guilds (e.g. Hiatt and Strasburg 1960; Jennings et al. 1995; Polunin 1996; McClanahan et al. 1999; Hughes et al. 2003; MacNeil et al. 2015; D’Agata et al. 2016; Graham et al. 2017; Stamoulis et al. 2017; Hadi et al. 2018; Moustaka et al. 2018). Yet this may overlook trophoplasticity, where many species feed across trophic boundaries (e.g. Robertson 1982; Chen 2002) and thus their trophic functions and the overall functioning of the reef (Mouillot et al. 2014). Inaccurate trophic information jeopardises comprehensive understanding of these food webs. Traditional gut contents analysis gives detailed dietary information; however, this typically has high temporal and spatial variability (Jennings et al. 2001) and it might include items accidently ingested (e.g. eDNA in gut contents DNA bar coding; Leal and Ferrer-Pagès 2016). Stable isotopes provide a time-integrated signal of what has been assimilated from the diet (Jennings et al. 2001). The stable isotope ratio of carbon (13C/12C, expressed as δ13C) is commonly used to distinguish production sources such as benthic and pelagic autotrophs (Tieszen et al. 1983; Bearhop et al. 2004), whereas the stable isotope ratio of nitrogen (15N/14N, expressed as δ15N) is used as a proxy for trophic position (TP) because it has a higher trophic enrichment factor (TEF) (DeNiro and Epstein 1978, 1981; McCutchan et al. 2003; Strieder Philippsen and Benedito 2013) and shows less variation at the baseline (Hesslein et al. 1991) than does carbon. Combining δ13C and δ15N delineates ‘isotopic niches’ (Leibold 1995; Newsome et al. 2007) which inform feeding strategies and trophic

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Robertson 1982; Chen 2002) and thus their trophic functions and the overall functioning of the reef (Mouillot et al. 2014). Inaccurate trophic information jeopardises comprehensive understanding of these food webs. Traditional gut contents analysis gives detailed dietary information; however, this typically has high temporal and spatial variability (Jennings et al. 2001) and it might include items accidently ingested (e.g. eDNA in gut contents DNA bar coding; Leal and Ferrer-Pagès 2016). Stable isotopes provide a time-integrated signal of what has been assimilated from the diet (Jennings et al. 2001). The stable isotope ratio of carbon (13C/12C, expressed as δ13C) is commonly used to distinguish production sources such as benthic and pelagic autotrophs (Tieszen et al. 1983; Bearhop et al. 2004), whereas the stable isotope ratio of nitrogen (15N/14N, expressed as δ15N) is used as a proxy for trophic position (TP) because it has a higher trophic enrichment factor (TEF) (DeNiro and Epstein 1978, 1981; McCutchan et al. 2003; Strieder Philippsen and Benedito 2013) and shows less variation at the baseline (Hesslein et al. 1991) than does carbon. Combining δ13C and δ15N delineates ‘isotopic niches’ (Leibold 1995; Newsome et al. 2007) which inform feeding strategies and trophic
interactions (Post 2002) at species, trophic guild and community levels (France et al. 1998; Jennings et al. 2001, 2002a, b; Al-Habsi et al. 2008). Combining these levels of data can explain a species’ trophic ecology including how strict it is and what potential source(s) it is utilising with the latter being very important because trophic interactions among omnivorous species within the same community remain understudied in coral reefs.

Trophodynamics can be size based. In aquatic systems, large individuals generally feed at higher TPs (Jennings et al. 2001, 2002b; Al-Habsi et al. 2008; Romanuk et al. 2011). This is a result of ontogenetic dietary shifts, morphometric changes including increasing gape size, post-maturity factors and greater predator ability that influence foraging (Peters 1986; Jennings et al. 2001; Munday 2001; Jennings et al. 2002b; Al-Habsi et al. 2008; Newman et al. 2012; Robinson and Baum 2015; Ríos et al. 2019). However, some large fishes forage at lower TPs due to dietary shifts (e.g. Chen 2002; Layman et al. 2005), seasonality effects (Bronk and Glibert 1993; Rolff 2000) and human disturbance (Pastorok and Bilyard 1985). TPs of some species remain relatively unchanged with increasing body size (e.g. herbivores; Plass-Johnson et al. 2013; Dromard et al. 2015). Size-based feeding remains almost unstudied in coral reef ecosystems (Robinson and Baum 2015) where large herbivores contribute greatly to the biomass.

Investigating TP to body mass relationships at community level can improve understanding of predator to prey relationships and energetic pathways (Romanuk et al. 2011; Robinson and Baum 2015) and of changes in community trophic composition (Graham et al. 2017). Where a positive TP relationship with body mass exists, the predator–prey mass ratio (PPMR) can be calculated. This reflects constraints on community structure (Trebilco et al. 2013) and can be used to evaluate general food web properties such as food chain length (Jennings and Warr 2003) and food chain transfer efficiency (Jennings et al. 2002c; Barnes et al. 2010) across different aquatic systems (Jennings et al. 2001, 2002c; Bode et al. 2003, 2006; Al-Habsi et al. 2008). The great diversity of production sources and trophic partitioning by consumers on coral reefs suggest that the PPMR may be smaller and food chains longer than in many other marine ecosystems. But to date, the community-level δ15N to body mass relationship and the PPMR have not been reported for a coral reef, so important insights such as measures of food chain length cannot be gained.

Here, underwater visual census and stable isotope data were used to explore the role of body size and trophic interactions among fish species in structuring a coral reef fish community at Cape Eleuthera (the Bahamas). Specifically, the study aimed to: (1) define isotopic niches at species and trophic guild levels in order to understand the principal energy pathways supporting them; and (2) assess whether there are positive δ15N–body mass relationships at the species and community levels and if so, derive an average predator–prey biomass ratio (PPMR).

Materials and methods

Study site

Four accessible and conservation-protected reef sites (Fig. 1) on the Exuma side of Cape Eleuthera (the Bahamas) with

![Fig. 1 Map of survey sites at Cape Eleuthera (the Bahamas)](image-url)
relatively high structural complexity and a diverse fish community were selected for visual surveys and fish sampling. These sites were close to each other and to shore and represented both bommies and patch reefs. In spite of the conservation status of the study sites, the reefs have been subject to chronic overfishing and otherwise impacted by cyclones and coral bleaching episodes.

**Fish survey**

Underwater visual census (UVC) was conducted by two divers using eight single-sweep 30 m × 5 m transects at each site to record fish species, individual total length ($L$, to nearest cm) and numbers of individuals. Surveyors’ length estimation precision was repeatedly measured by conducting underwater fish-shaped object length estimation training (Bell et al. 1985) to minimise error (± 5%). Transects ran parallel to each other to avoid intersection. Transects were carried out in the morning (9:30–11:30) or afternoon (14:00–16:00), while swimming at a steady speed for 30 min. Highly mobile transient individuals (e.g., sharks and jacks) were excluded since they had large home range and were not necessarily reef associated, and also large schools of fishes were excluded since they were sighted only sporadically (Ferreira et al. 2001).

**Sampling for stable isotope analysis**

Abundant species were selected by their contribution to the total biomass ($B$). From UVC data, individual body mass values ($M$, g) were calculated from $L$ (cm) using:

$$M = a \times L^b$$  

with published length to weight conversion factors $a$ and $b$ (“Appendix A” in supplementary materials) from fishbase.org (Froese and Pauly 2017). Where conversion factors were linked with standard or fork length rather than $L$ org (Froese and Pauly 2017). Where conversion factors were in units other than centimetres, length was converted into appropriate units or length types using the equations in fishbase.org. All body mass data were log$_2$ transformed to remove any effects of relationship between body size and phylogeny (Freckleton 2000). For each $M$ class (2–512 g), $B$ was calculated by summing individual $M$ values. Species were ranked in order of their contribution to the $B$ of each log$_2$M interval, and those making up 80% of the $B$ were selected for the community trophic structure analysis.

Samples of selected species (Table 1) were collected through the length range recorded in the UVC to adequately describe species $\delta^{15}$N–log$_2$M relationships (Galván et al. 2010). The size range cover ratio ($r_L = L_{\text{SIA sample range}}/L_{\text{UVC range}}$) was used to check whether the sampling objective was met. Fish were collected using a variety of techniques depending on their behaviour towards divers, feeding habits and swimming patterns. Hand net, gill net (mesh size: 1 cm × 1 cm, net size: 2 m × 1 m), BINCKE net (Anderson and Carr 1998), underwater fishing hook and line, static hook and line, spearfishing (local fishermen only) and hook and line surface trolling were all used in the sampling in the survey sites and adjacent areas (Table 2). Fish were killed by spine dislocation and stored in an ice chest on board. Samples were all collected within a 1-month period and from nearby sites to reduce spatial and temporal isotopic variation (Bronk and Glibert 1993; Jennings et al. 1997; Rolff 2000; McCutchan et al. 2003).

After landing, approximately 2 g of dorsal white muscle tissue near the dorsal fin were dissected, rinsed with water and stored in individual whirlock bags in a −20 °C freezer, and algal samples were only rinsed and stored in a freezer. All samples were dried in individual tin trays in an oven at 40 °C for ~ 12 h until fully dried and then in individual sealed Eppendorf tubes in zip-lock bags.

**Stable isotope analysis preparation**

All dried samples were imported to Newcastle University, freeze dried and then manually ground with mortar and pestle. Fish samples were weighed to 1.0 ± 0.1 mg in tin capsules with a Mettler MT5 microbalance. The prepared samples were analysed by Iso-Analytical Ltd (Crewe, UK) by Elemental Analysis-Isotope Ratio Mass Spectrometry (EA-IRMS). The $^{15}$N/$^{14}$N ratio ($\delta^{15}$N) was expressed relative to N$_2$ in air for nitrogen, while that of $^{13}$C/$^{12}$C ($\delta^{13}$C) was relative to Pee Dee Belemnite (PDB) of CO$_2$. Reference material used for this analysis was IA-R042 ($\delta^{13}$C = −21.6 ± 0.1‰, $\delta^{15}$N = 7.6 ± 0.1‰), with quality control check samples IA-R042, IA-R038 ($\delta^{13}$C = −25.0 ± 0.1‰, $\delta^{15}$N = −0.4 ± 0.1‰), a mixture of IA-R006 ($\delta^{13}$C = −11.7 ± 0.0‰) and IA-R046 ($\delta^{15}$N = 21.9 ± 0.2‰). IAR042 and IA-R038 were calibrated against and traceable to IAEA-CH-6 ($\delta^{13}$C = −10.4‰) and IAEA-N-1 ($\delta^{15}$N = 0.4‰), IA-R006 to IAEA-CH-6 and IA-R046 to IAEA-N-1. External standards (fish white muscle tissue, $\delta^{13}$C = −18.9 ± 0.0‰, $\delta^{15}$N = 12.9 ± 0.1‰) were also used for future reference. The precision of analysis for $\delta^{13}$C, $\delta^{15}$N, %C and %N was ± 0.1‰, ± 0.1‰, ± 4% and ± 1%, respectively. For individual samples, no lipid extraction was needed because their C/N ratios were less than 3.7 (Fry et al. 2003; Sweeting et al. 2006).

**Data analysis**

All data were tested for normality and homogeneity of variance prior to analysis and analysed in R 3.24 (R Core Team 2016) using the package siar (Parnell and Jackson 2013) between $\delta^{13}$C and $\delta^{15}$N data, linear regression (Wilkinson and Rogers 1973; Bates et al. 1992) between $\delta^{15}$N and log$_2$
Table 1  List of sampled species of reef fish at Cape Eleuthera (the Bahamas), with scientific name, common name, species code, trophic guild (Froese and Pauly 2017), maximum total length ($L_{\text{max}}$) (Humann and DeLoach 1989), UVC total length range ($L_{\text{UVC}}$), mean trophic position ± 1 SE (Froese and Pauly 2017), SIA sample size (n), SIA sample total length range ($L_{\text{SIA}}$), size range cover ratio $r_L$, mean δ15N and δ13C ± 1 SE

| Scientific name                   | Code | Trophic guild | $L_{\text{max}}$ (mm) | $L_{\text{UVC}}$ (mm) | Trophic position | n     | $L_{\text{SIA}}$ (mm) | $r_L$ | δ15N     | δ13C     |
|-----------------------------------|------|---------------|------------------------|------------------------|------------------|-------|------------------------|-------|----------|----------|
| Acanthurus chirurgus              | ACCH | Herbivore     | 381                    | 40–100                 | 2.1 ± 0.1        | 1     | 280                    | 0%    | 5.6      | −12.4    |
| Acanthurus coeruleus              | ACCO | Herbivore     | 381                    | 30–380                 | 2.0 ± 0.0        | 3     | 81–168                 | 25%   | 4.7 ± 0.3 | −16.5 ± 0.8 |
| Acanthurus trachus                | ACTR | Herbivore     | 381                    | 90–210                 | 2.0 ± 0.0        | 9     | 84–280                 | 100%  | 5.1 ± 0.2 | −13.6 ± 0.5 |
| Aulostomus maculatus              | AUMA | Piscivore     | 914                    | 240–430                | 4.3 ± 0.6        | 2     | 145–530                | 100%  | 5.9 ± 0.6 | −14.9 ± 0.2 |
| Balistes vetula                   | BAVE | Benthivore    | 610                    | 3.8 ± 0.1              | 4     | 320–419                | NA    | 7.7 ± 0.1 | −16.4 ± 0.3 |
| Calamus pennatula                 | CAPE | Herbivore     | 381                    | 3.7 ± 0.2              | 4     | 278–300                | NA    | 8.2 ± 0.3 | −11.0 ± 0.6 |
| Caranx ruber                      | CARU | Herbivore     | 610                    | 3.8 ± 0.1              | 4     | 273–392                | 46%   | 7.9 ± 0.1 | −13.2 ± 0.5 |
| Cephalopholis cruentata           | CECR | Herbivore     | 305                    | 3.7 ± 0.4              | 8     | 103–295                | 73%   | 8.4 ± 0.2 | −13.9 ± 0.4 |
| Chromis cyanea                    | CHCY | Herbivore     | 381                    | 3.7 ± 0.4              | 7     | 54–87                  | 28%   | 5.2 ± 0.1 | −17.0 ± 0.1 |
| Clepticus parrae                  | CLPA | Herbivore     | 305                    | 3.4 ± 0.2              | 8     | 71–113                 | 18%   | 5.4 ± 0.2 | −17.2 ± 0.1 |
| Coryphopterus glaucofraenum       | COGL | Herbivore     | 64                     | 2.7 ± 0.4              | 1     | 34                     | NA    | 3.9      | −10.9     |
| Coryphopterus personatus          | COPE | Herbivore     | 38                     | 10–30                  | 3.0 ± 0.1        | 3     | 14–34                  | 80%   | 4.0 ± 0.1 | −16.5 ± 0.4 |
| Epinephelus guttatus              | EPGU | Piscivore     | 610                    | 3.8 ± 0.3              | 5     | 212–336                | 34%   | 7.9 ± 0.2 | −11.7 ± 0.3 |
| Epinephelus striatus              | EPST | Piscivore     | 1219                   | 4.1 ± 0.0              | 6     | 361–423                | 18%   | 8.7 ± 0.2 | −11.9 ± 0.2 |
| Gramma loreto                     | GRLO | Herbivore     | 76                     | 3.3 ± 0.4              | 4     | 22–35                  | 19%   | 4.6 ± 0.1 | −17.0 ± 0.2 |
| Haemulon album                    | HAAL | Herbivore     | 762                    | 3.1 ± 0.1              | 5     | 321–419                | 0%    | 7.5 ± 0.2 | −10.1 ± 0.3 |
| Haemulon flavolineatum            | HAPL | Benthivore    | 305                    | 3.5 ± 0.1              | 9     | 96–233                 | 65%   | 7.0 ± 0.2 | −10.9 ± 0.3 |
| Haemulon plumierii                | HAPL | Benthivore    | 457                    | 3.8 ± 0.0              | 4     | 231–300                | 35%   | 8.1 ± 0.2 | −12.2 ± 0.1 |
| Haemulon sciuroid                 | HASC | Benthivore    | 457                    | 3.5 ± 0.2              | 2     | 275                    | 0%    | 7.5      | −14.0     |
| Holichoreus bivittatus            | HABI | Benthivore    | 229                    | 3.8 ± 0.1              | 2     | 120–133                | 0%    | 6.1 ± 0.1 | −10.6 ± 0.2 |
| Holichoreus garnotii              | HAGA | Omnivore      | 203                    | 3.7 ± 0.2              | 5     | 36–135                 | 55%   | 6.2 ± 0.3 | −13.7 ± 0.3 |
| Holichoreus maculipinnna          | HAMA | Benthivore    | 165                    | 3.3 ± 0.2              | 1     | 117                    | 0%    | 6.7      | −13.7     |
| Holichoreus pictus                | HAPI | Benthivore    | 76                     | 3.5 ± 0.4              | 4     | 16–30                  | 16%   | 4.5 ± 0.1 | −17.4 ± 0.2 |
| Holacanthus ciliaris              | HOCI | Herbivore     | 457                    | 3.0 ± 0.0              | 5     | 195–325                | 0%    | 5.8 ± 0.2 | −14.8 ± 0.4 |
| Holocentrus adacensionis          | HOAD | Herbivore     | 406                    | 3.5 ± 0.4              | 2     | 273–308                | NA    | 8.4 ± 0.2 | −12.0 ± 0.9 |
| Holocentrus rufus                 | HORU | Benthivore    | 318                    | 3.6 ± 0.4              | 6     | 135–275                | 68%   | 7.2 ± 0.2 | −13.6 ± 0.2 |
| Lutjanus apodus                   | LUAP | Benthivore    | 610                    | 4.3 ± 0.4              | 3     | 202–246                | 13%   | 8.6 ± 0.1 | −12.0 ± 0.6 |
| Lutjanus griseus                  | LUGR | Benthivore    | 610                    | 4.2 ± 0.3              | 1     | 377                    | 0%    | 8.7      | −9.5      |
| Lutjanus synagris                 | LUSY | Benthivore    | 381                    | 3.8 ± 0.2              | 5     | 200–300                | NA    | 7.8 ± 0.5 | −10.6 ± 0.9 |
| Ocyurus chrysurus                 | OCCH | Benthivore    | 762                    | 4.0 ± 0.3              | 9     | 260–378                | 30%   | 8.4 ± 0.1 | −11.9 ± 0.4 |
| Pomacanthus arcuatus              | POAR | Benthivore    | 610                    | 3.2 ± 0.1              | 7     | 210–260                | 31%   | 6.3 ± 0.2 | −14.4 ± 0.6 |
| Pterois volitans                  | PTVO | Benthivore    | 381                    | 4.4 ± 0.4              | 11    | 155–400                | NA    | 8.1 ± 0.1 | −12.2 ± 0.4 |
| Scarus iserti                     | SCIS | Herbivore     | 254                    | 2.0 ± 0.0              | 10    | 62–130                 | 18%   | 4.2 ± 0.1 | −13.9 ± 0.2 |
body mass and mvtnorm to simulate values from a bivariate normal distribution. Results were visualised using ggplot2 (Wickham and Chang 2016). The assumptions of the ordinary least squares linear regression analyses were assessed with QQ plots, histograms of standardised residuals and plots of standardised residuals versus fitted values. Pearson’s correlation coefficient was used to test correlations between variables. Significance was set at $p = 0.05$ in all cases. All errors are reported as ± 1SE unless otherwise stated.

**Species and trophic guild stable isotope analyses**

The bulk $\delta^{13}C$ and $\delta^{15}N$ data were used to interpret $\delta^{15}N–\delta^{13}C$ relationships in each species and trophic guild (Froese and Pauly 2017). Isotopic niches of five trophic guilds (four benthic: benthivore, herbivore, omnivore and piscivore and one pelagic: planktivore) were investigated using SIBER in the siar package. This was achieved by investigating standard ellipse parameters: eccentricity ($E$) and the angle in degrees ($\theta$, $0^\circ–180^\circ$) between semi-major axis and the $x$ axis, the sample size corrected standard ellipse areas (SEA$_C$) and Bayesian standard ellipse areas (SEA$_B$) (Jackson et al. 2011). $\theta$ and $E$ values potentially distinguish among isotopic niches where different trophic guilds have similar sized SEA$_C$ but different relationships between $\delta^{13}C$ and $\delta^{15}N$ (Reid et al. 2016). $\theta$ values close to $0^\circ$ or $90^\circ$ suggest dispersion in only one axis: $\theta$ values close to $0^\circ$ represent relative dispersion along the $x$ axis ($\delta^{13}C$), indicating multiple production sources, while $\theta$ values close to $90^\circ$ highlight relative dispersion along the $y$ axis ($\delta^{15}N$), indicating feeding across multiple trophic positions from a uniform basal source. $E$ explains the variance on the $x$ and $y$ axes: low $E$ refers to similar variance on both axes with a more circular shape, while high $E$ indicates that the isotopic niche is stretched along either $x$ or $y$ axis. The overlap of the standard ellipses between guilds was calculated using “sea. overlap” using SIBER. In order to compare isotopic niche areas among trophic guilds, a Bayesian approach was used that calculated 20,000 posterior estimates of SEA$_B$ based on the data set. The mode and 95% credible intervals (CI) were reported. A significant difference among SEA$_B$ was interpreted graphically whereby if the 95% CI did not overlap, then the SEA$_B$ were deemed to be significantly different (Parnell and Jackson 2013).

**$\delta^{15}N$–body size relationship**

Cross-species relationships between stable isotope data and $M$ were analysed using linear regression between mean bulk $\delta^{13}C$ and $\delta^{15}N$ of each species and their maximum body mass ($M_{\text{max}}$) recorded by Humann and DeLoach (1989). Comparing fishes at a fixed proportion of maximum size (here ≥ 55% of
To obtain δ15N values of such species, several methods were used. Of the regression line of the TP–log2B relationship as 

\[ TP = TP_{\text{base}} + \frac{\delta^{15}N_{\text{fish}} - \delta^{15}N_{\text{base}}}{\Delta \delta^{15}N} \]

where the Δδ15N is assumed constant and equal to 3.4‰ (DeNiro and Epstein 1981; Minagawa and Wada 1984). TPbase was indicated by the striped parrotfish (S. iserti, \( \delta^{15}N_{\text{base}} = 4.2 \pm 0.1‰; TP_{\text{base}} = 2.0 \)) due to its low isotopic variation across sizes, time integration of seasonality from producers and adequate sample size (n = 10). The slope (b) of TP–log2B relationship was obtained from the slope (s) of δ15N–log2B relationship where \( b = s/3.4 \). Thus, the PPMR is calculated as

\[ \text{PPMR} = 2^{3.4/s}. \]

The uncertainty of PPMR was estimated by (1) simulating 10,000 times of independent variables s (the mean and standard deviation from the linear regression statistics) and Δδ15N values (mean and standard deviation of 3.4 ± 1.0‰; Post 2002) from a bivariate normal distribution (\( \rho = 0 \)) and (2) calculating PPMR estimates using Eq. 3. The median, 25th and 75th quantiles were reported. The same method was applied to existing studies for comparison.

### Results

#### Isotopic niches at species and trophic guild levels

In total 9055 individuals (L from 1 to 120 cm, M from 0.01 to 2742 g) were recorded in 32 UVCs over 4800 m² of reef. Of 41 fish species collected and analysed for δ15N, 11 had sample sizes under three, and three (Coryphopterus glaucofraenum, Balistes vetula, Holocentrus adscensionis) were sampled to represent certain uncollected species. The size range cover ratio (\( r_2 \)) ranged from 0 to 100% (mean = 31.0 ± 5.0%). Mean species δ13C ranged from −17.4 ± 0.2‰ (Halichoeres pectoralis) to −9.5 ± 0.6‰ (Lutjanus griseus), while mean δ15N ranged from 3.9 ± 0.8‰ (S. aurofrenatum) to 9.9 ± 1.5‰ (Sphyraena barracuda). δ15N values were significantly but weakly correlated with δ13C (\( p < 0.05, r^2_{\text{adjusted}} = 0.29 \)) at the species level.
(Fig. 2). Some species had large SE values in δ13C (≥ 1‰) (e.g., *S. barracuda*) or δ15N (≥ 0.5‰) (e.g., *Aulostomus maculatus*), or both δ13C and δ15N (e.g., *Elacatinus genie*). Mean δ13C and δ15N values of strict pelagic planktivores (e.g., *Chromis cyanea*, TP = 3.7, δ13C = −17.0 ± 0.1‰, δ15N = 5.2 ± 0.1‰) and strict benthivores of similar TP (e.g., *B. vetula*, TP = 3.8, δ13C = −12.4 ± 0.3‰, δ15N = 7.7 ± 0.1‰) were significantly different.

The herbivore and benthivore guilds had the largest isotopic niches, followed by the piscivore guild, and then the omnivore guild; the planktivore guild had an isotopic niche significantly smaller than others (Table 3). The planktivore guild had a lower δ13C than others and was separated from the herbivore, benthivore and piscivore trophic guilds (Fig. 2, Table 4). The isotopic niche of the omnivores overlapped with those of the herbivores and planktivores as did those of the benthivore and piscivore (Table 4). The isotopic niche of the herbivores was vertically separated from those of the benthivores and piscivores. *E* and θ values differed among trophic guilds (Table 3); the herbivore guild had the lowest *E* (0.77), while the omnivores had the highest (0.98). The benthivore (0.94) and planktivore (0.79) trophic guilds had *E* values very similar to those of the omnivore and herbivore trophic guilds, respectively.

**Fig. 2** Plot of bulk δ15N against δ13C (mean ± SE) of all sampled fish species (for codes see Table 1) and standard ellipses (solid line-ellipses) for five trophic guilds (and one species of parasitivore, ELGE) of fish at Cape Eleuthera (the Bahamas).

**Table 3** Isotopic niche area (% ‰2) estimates and parameters [eccentricity (*E*), the angle in degree between the semi-major axis of the standard ellipse and the x axis (θ)] for five trophic guilds (benthivore, herbivore, omnivore, piscivore and planktivore) of coral reef fish at Cape Eleuthera (the Bahamas)

| Trophic guild | SEA_c (%) | *E* | θ (°) | SEA_B (%) | SEA_B 95% CI |
|---------------|-----------|-----|------|-----------|--------------|
| Benthivore    | 5.30      | 0.94| 20.96| 5.19      | 3.96–6.93    |
| Herbivore     | 5.90      | 0.77| 6.29 | 5.73      | 4.32–7.53    |
| Omnivore      | 1.83      | 0.98| 19.17| 1.77      | 1.05–3.14    |
| Piscivore     | 3.91      | 0.89| 14.36| 3.81      | 2.88–4.04    |
| Planktivore   | 0.46      | 0.79| 75.69| 0.41      | 0.26–0.66    |

Estimates of isotopic niche areas are given as (SEA_c) and the mode of the Bayesian standard ellipse area (SEA_B) estimates. Upper and lower 95% credible intervals (CI) indicate the uncertainty in the SEA_B estimates.

**Table 4** Standard ellipse overlap (% ‰2) among the five trophic guilds

| Trophic guild | Benthivore | Herbivore | Omnivore | Piscivore |
|---------------|------------|-----------|----------|-----------|
| Herbivore     | 0.00       | 0.77      | 0.00     | 0.00      |
| Omnivore      | 0.00       | 0.77      | 0.00     | 0.00      |
| Piscivore     | 0.57       | 0.00      | 0.00     | 0.00      |
| Planktivore   | 0.00       | 0.00      | 0.03     | 0.00      |

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The θ values of the δ^{15}N versus δ^{13}C relationships of all the trophic guilds were positive; the herbivores had the lowest θ (6°), while the planktivores had the highest (76°). Among the benthivore, omnivore, piscivore and herbivore trophic guilds, the isotopic niche was spread along the x axis (θ < 45°), while that of the planktivores was more vertically spread (θ > 45°). Some species (the benthivore *H. pictus*, herbivores *Acanthurus coeruleus* and *Coryphopterus personatus* and omnivore *Thalassoma bifasciatum*) had isotopic coordinates close to the ellipse of the planktivore trophic guild, and one piscivore (*A. maculatus*) had an isotopic coordinate within the standard ellipse of the herbivore trophic guild.

### δ^{15}N–body mass relationships at species and community levels and PPMR

There were significant but weak relationships across species between log_{2}M_{max} (maximum body mass) and both δ^{15}N (r_{adj}^{2} = 0.12, p < 0.05; Fig. 3a) and δ^{13}C data (r_{adj}^{2} = 0.17, p < 0.05; Fig. 3b). The δ^{15}N values of several species did not scale positively with log_{2}M_{max} (e.g. *E.*

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**Fig. 3** Plots of bulk δ^{15}N (a) and bulk δ^{13}C (b) (mean ± SE) versus log_{2} maximum body mass for all collected fish species (for codes see Table 1) at Cape Eleuthera with mean isotope values of individuals bigger than 55% of their *L_{max}*. Solid line: linear regression line (p < 0.05)
genie, Sparisoma viride, Scarus iserti and S. auroprena-tum). The SE values of δ13C were generally higher than those of δ15N regardless of $M_{\text{max}}$. δ15N tended to vary with log₂M for 29 species (Fig. 4) with $n \geq 3$; of these 24 relationships were positive (significantly so, e.g. C. cyanea), while five were negative (significantly so, e.g. Pomacentrus arcuatus, “Appendix C” supplementary materials). There was considerable variability around the regression line for nine species ($r^2_{\text{adjusted}} < 0.5$, e.g. S. barracuda), whereas this was not the case for others (e.g. Clepticus parrae, Calamus pennatula, Halichoeres garnoti). At the community level, the combined isotope data demonstrated a strong positive linear relationship between mean δ15N and log₂B, the regression equation being $\delta^{15}N = 0.34 \pm 0.04\log_{2}B + 4.03 \pm 0.24$ ($r^2_{\text{adjusted}} = 0.64$, $p < 0.05$, Fig. 5). The slope value of TP–log₂B was $b = 0.10$ ($r^2_{\text{adjusted}} = 0.80$, $p < 0.05$), and the PPMR estimates were 1047:1 (Table 5).

Fig. 4 Plot of $\delta^{15}N$ versus log₂ body mass (linear regression) of all sampled species at Cape Eleuthera (the Bahamas). Solid line: significant relationship ($p < 0.05$), dashed line: non-significant relationship. For codes see Table 1.

Fig. 5 Plot of combined relationship (linear regression) between $\delta^{15}N$ and log₂ body mass at Cape Eleuthera (the Bahamas). Solid line: linear regression line ($p < 0.05$), long dashed line: 95% CI.
Table 5  Mean PPMR values of different communities from the literature using the additive framework

| Community            | PPMR estimates | Reference               |
|----------------------|----------------|-------------------------|
| Central North Sea    | 104:1          | Jennings et al. (2002a, b) |
| Northern North Sea   | 1037:1         | Jennings et al. (2001)   |
| Cape Eleuthera       | 1047:1         | Present study            |
| Puget Sound          | 4320:1         | Reum et al. (2015)       |
| North Sea            | 8349:1         | Jennings and Warr (2003) |
| Western Arabian      | 8935:1         | Al-Habsi et al. (2008)   |
| Iberian Peninsula    | 2.02×10^3:1    | Bode et al. (2006)       |

Discussion

Species and trophic guild tropodynamics

Stable isotope data at both species and trophic guild levels indicated that at the Cape Eleuthera site there were large differences in trophic ecology within and among species, and species utilising a range of production source types were common.

High within-species variability in δ^{13}C and δ^{15}N values for some species suggested the existence of individual specialisation (Matthews and Mazumder 2004) in the food web where different individuals of the same species were consistently sampling different production sources. For example, similarly sized individuals of the apex predator S. barracuda had similar δ^{15}N values but differed greatly in δ^{13}C values. The δ^{13}C value of approximately −16‰ was close to that within the planktivore trophic guild, while the δ^{13}C value of −10‰ was more consistent with the piscivore trophic guild. Trophic position omnivory indicated by differences in δ^{15}N also occurs, for example, in the parasitivore E. genie which feeds on parasites from fish at different trophic positions.

The SIBER analysis indicated at least two types of production sources, namely benthic (e.g. algae) and pelagic (e.g. plankton), and mixed-feeding patterns for some species that are typically regarded as relying solely on single types of source materials (e.g. herbivorous fish; Plass-Johnson et al. 2013; Dromard et al. 2015). In this study, isotopic niche areas of the planktivores were significantly smaller than other guilds even though plankton can have highly variable isotopic signatures (McClelland and Montoya 2002; Kürtén et al. 2013), which indicated a level of dietary strictness or consistency. High θ, low E and low SEA values of the planktivore guild nevertheless suggested TP omnivory, with these fish feeding at different TPs albeit from the same type of pelagic source (e.g. phytoplankton and zooplankton). The omnivore guild had high E, low θ and SEA values, the δ^{13}C data indicating that the two species are supported by plankton and benthic algae with similar δ^{15}N baselines. Although based on only two species, the omnivores may be connecting these two pathways to some extent (McMeans et al. 2016). The benthivore, piscivore and herbivore trophic guilds, which share mostly benthic production sources, had similar isotopic niche areas which were much greater than those of the planktivores and omnivores, with their isotopic niches spread along the x axis as indicated by E and θ values, suggesting source omnivory within the benthic producer category. Overlapping isotopic niches among the trophic guilds (e.g. piscivore and benthivore) suggested that they might share dietary resources to some extent; for example, some lutjanids are both piscivorous and feed on zoobenthos (Allen 1985; Kulbicki et al. 2005; Layman and Allgeier 2012). The vertical distribution in the isotopic niches for the four benthic trophic guilds reflected the herbivorous fish feeding at low trophic positions, while the omnivores, benthivores and piscivores utilised a wider range of energy sources from different TPs. There were species with stable isotope values outside the isotopic niches of their assumed trophic guilds, which suggested feeding on different food sources than previously known or those derived from snapshot diet studies. For example, the four benthic feeders (H. pICTus, A. coereTiles, C. personatus and T. bifasciatau) were likely relying on plankton sources, and the piscivore A. maculatus might be preying on smaller herbivores. Some herbivores came partly within the isotopic niches of other trophic guilds, indicating feeding on food sources in addition to algae such as invertebrates or planktivore faeces (Robertson 1982; Wulff 1997; Dunlap and Pawlik 1998; Chen 2002; Plass-Johnson et al. 2013). This can only be confirmed with detailed dietary analysis including baseline variation (i.e. during the 3–6 months isotopic turn over period).

δ^{15}N–body mass relationship

The majority of species had a positive trend between δ^{15}N and \log_{2}M indicating that they tend to feed at higher TPs as size increases. This could be a result of increasing gape size, predatory skill and fitness level allowing individuals to feed on higher TP prey as they grow (Peters 1986; Munday 2001; Newman et al. 2012). Those with negative or highly variable stable isotope-size relationships potentially have dietary shifts from isotopically high value production sources to
low or multi-pathway (e.g. exploitation of short food chain) feeding patterns in their sampled size ranges, or otherwise assimilating significantly different isotopic baselines across the population (Jennings et al. 2002a; Layman et al. 2005). Unlike Robinson and Baum (2015) where δ15N–log2M relationships of all individuals in two separate trophic pathways (herbivore and carnivore) were investigated, species-level and whole-community-level analyses were conducted in this study. The variation among species is attributable to differences in the trophic pathways supporting them, but to understand better how trophic pathways affect such relationships, more data are clearly needed. At community level, a positive linear relationship between δ15N and log2B across the combined sites was found, indicating that TP tended to increase with body mass regardless of taxonomy and larger coral reef fish in this Cape Eleuthera community on average fed at higher TPs.

The weak cross-species relationship between isotopic signatures and log2Mmax suggested that maximum body mass could scarcely constrain species’ trophic capabilities in this food web in which there were small-bodied benthivores and planktivores and large-bodied herbivores. The body-size structuring is similar to that of North Sea and Western Arabian Sea community data (Jennings et al. 2001; Al-Habsi et al. 2008). Here, the small size class biomass data were dominated by herbivores rather than higher TP omnivores such as Labridae (Graham et al. 2017), while the large size classes were dominated by piscivores and omnivores rather than large-bodied herbivores such as Scarinae (Hughes et al. 2007; Zhu 2019). Although the surveyed Cape Eleuthera sites are now legally protected, they were previously fished and are structurally degraded. The linearity of the δ15N–log2B relationship at Cape Eleuthera may not be generic; it could be influenced by the loss of habitat structural complexity and aspects of past overfishing (e.g. removal of large herbivores).

The present study also had limitations. All individuals were treated as if they had the same isotopic baseline, yet significant isotopic differences between benthic and pelagic sources are expected (McConnaughey and McRoy 1979; Polunin and Pinnegar 2002), whereas other baselines would have been taken into consideration when estimating the trophic positions of consumers with significantly mixed diets. Also, for some species, sample sizes failed to adequately fulfill requirements for confidently describing stable isotope changes as a function of body mass (Galván et al. 2010), yet linear regression was still applied to these species to explore their δ15N–log2M relationships. Low sample sizes and/or size ranges (r2) meant that for some species, stable isotope data could not be derived across whole UVC size ranges; for these stable isotopic data were assumed to be size invariant. For missing species, the methods used to infer stable isotope values had limitations including species within the same genus or family having ontogenetic and/or dietary differences; some not meeting all three criteria and using published data from the same species could be subject to feeding strategies varying ontogenetically (Plass-Johnson et al. 2013) or spatially (Jennings et al. 1997; Matthews and Mazumder 2004). Unlike studies using combined baselines (Mill et al. 2007), here the benthic alga D. cavernosa was the sole baseline and this might not adequately represent the whole benthic assemblage, which includes turf algae, cyanobacteria and other potential production sources.

### Predator–prey mass ratio

The mean PPMR at Cape Eleuthera indicates a relatively long food chain in this coral reef system compared with other aquatic systems (Table 5), suggesting potentially greater ecosystem size and stability (Jennings and Warr 2003). However, surveys at adjacent non-protected sites failed to show the presence of large predators there; thus, the PPMR data we report seem to be specific to the protected sites.

### Conclusions

Stable isotope data indicate more than one production source and mixed reliance on them by some coral reef fishes suggesting evidence of reef fish crossing trophic boundaries described by their trophic guilds and that current categorisations are often simplistic. Combining visual census and stable isotope data indicated that the Cape Eleuthera coral reef fish community was size structured. The relationship at this site points to body size as a driver of predator–prey relationships and trophic pathways at community level, with the isotope data suggesting that trophic position plasticity is common at species level. This is the first indication of a positive linear δ15N–log2 body mass relationship in a coral reef system, but this may not pertain to all coral reefs.

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### Author contributions

This study was designed by YZ and NVCP, the field work was carried out by YZ, the data analysis was conducted by YZ, SPN and WDKR, and the paper was written by YZ, NVCP, WDKR and SPN.

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### Compliance with ethical standards

#### Conflict of interest

The authors declare that they have no conflicts of interest.
Ethic approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The research was approved by the Newcastle University Ethics Committee and the Bahamian Department of Marine Resources under permits MAMR/FIS/17 and MAMR/FIS/34A. No coral habitat was disturbed during this research. All fish were killed in accordance with the UK Home Office Scientific Procedures (Animal) Act. All samples were imported to UK under DEFRA permit TARP/2015/210.

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