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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 $\delta^{13}C$ and $\delta^{15}N$ data and explore whether fish body size is a driver of trophic position based on $\delta^{15}N$. 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 $\delta^{13}C$ 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. $\delta^{15}N$ tended to increase with body mass in most species, and at community level, the linear $\delta^{15}N$–$\log_2$ 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 $\delta^{15}N$–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.

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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 Ferrier-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 ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) 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 ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) 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 $\delta^{13}C$ and $\delta^{15}N$ 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 δ^{15}N 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 δ^{15}N–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
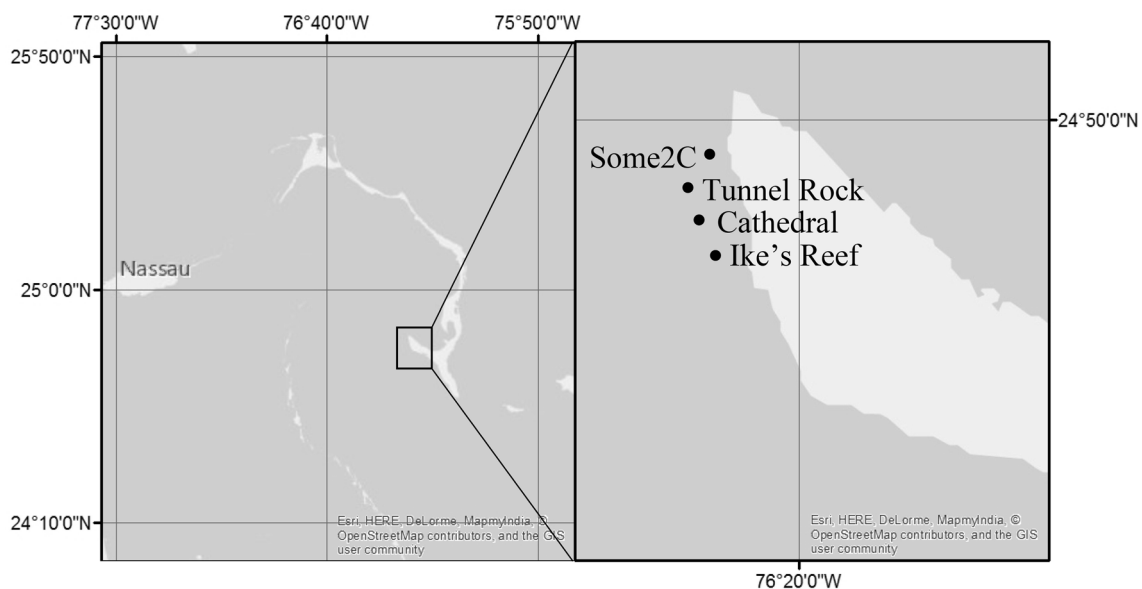

Fig. 1 Map of survey sites at Cape Eleuthera (the Bahamas)

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:

$$M = a \times L^b \tag{1}$$

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, or L was 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 ($r_L = L_{SIA\ sample}$ range/L_{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 whirlpack 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 ($\delta^{13}C = -21.6 \pm 0.1‰$, $\delta^{15}N = 7.6 \pm 0.1‰$), with quality control check samples IA-R042, IA-R038 ($\delta^{13}C = -25.0 \pm 0.1‰$, $\delta^{15}N = -0.4 \pm 0.1‰$), a mixture of IA-R006 ($\delta^{13}C = -11.7 \pm 0.0‰$) and IA-R046 ($\delta^{15}N = 21.9 \pm 0.2‰$). 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, $\delta^{13}C = -18.9 \pm 0.0‰$, $\delta^{15}N = 12.9 \pm 0.1‰$) were also used for future reference. The precision of analysis for $\delta^{13}C$, $\delta^{15}N$, %C and %N was $\pm 0.1‰$, $\pm 0.2‰$, $\pm 4\%$ and $\pm 1\%$, 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_{max}) (Humann and DeLoach 1989), UVC total length range (L_{UVC}), mean trophic position ± 1 SE (Froese and Pauly 2017), SIA sample size (n), SIA sample total length range (L_{SIA}), size range cover ratio r_L, mean $\delta^{15}N$ and $\delta^{13}C \pm 1$ SE

Scientific name	Code	Trophic guild	L_{max} (mm)	L_{UVC} (mm)	Trophic position	n	L_{SIA} (mm)	r_L	$\delta^{15}N$	$\delta^{13}C$
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 tractus	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[a]	BAVE	Benthivore	610		3.8±0.1	4	320–419	NA	7.7±0.1	−12.4±0.3
Calamus pennatula	CAPE	Benthivore	381		3.7±0.2	4	278–300	NA	8.2±0.3	−11.0±0.6
Caranx ruber	CARU	Piscivore	610	190–450	4.3±0.1	5	273–392	46%	7.9±0.1	−13.2±0.5
Cephalopholis cruentata	CECR	Piscivore	305	60–220	4.3±0.6	8	103–295	73%	8.4±0.2	−13.9±0.4
Chromis cyanea	CHCY	Planktivore	127	10–130	3.7±0.4	7	54–87	28%	5.2±0.1	−17.0±0.1
Clepticus parrae	CLPA	Planktivore	305	10–250	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	2.9±0.4	3	14–34	80%	4.0±0.1	−16.5±0.4
Elacatinus genie	ELGE	Parasitivore	44	10–40	3.4±0.3	2	25–32	23%	8.9±0.8	−12.6±1.3
Epinephelus guttatus	EPGU	Benthivore	610	100–270	3.8±0.3	5	212–336	34%	7.9±0.2	−11.7±0.3
Epinephelus striatus	EPST	Piscivore	1219	250–600	4.1±0.0	6	361–423	18%	8.7±0.2	−11.9±0.2
Gramma loreto	GRLO	Planktivore	76	10–80	3.3±0.4	4	22–35	19%	4.6±0.1	−17.0±0.2
Haemulon album	HAAL	Benthivore	762	200–320	3.1±0.1	5	321–419	0%	7.5±0.2	−10.1±0.3
Haemulon flavolineatum	HAFL	Benthivore	305	50–180	3.5±0.1	9	96–233	65%	7.0±0.2	−10.9±0.3
Haemulon plumierii	HAPL	Benthivore	457	150–350	3.8±0.0	4	231–300	35%	8.1±0.2	−12.2±0.1
Haemulon sciurus	HASC	Benthivore	457	210–350	3.5±0.2	1	275	0%	7.5	−14.0
Halichoeres bivittatus	HABI	Benthivore	229	30–100	3.8±0.1	2	120–133	0%	6.1±0.1	−10.6±0.2
Halichoeres garnoti	HAGA	Omnivore	203	10–190	3.7±0.2	5	36–135	55%	6.2±0.3	−13.7±0.3
Halichoeres maculipinna	HAMA	Benthivore	165	50–140	3.3±0.2	1	117	0%	6.7	−13.7
Halichoeres pictus	HAPI	Benthivore	76	10–100	3.5±0.4	4	16–30	16%	4.5±0.1	−17.4±0.2
Holacanthus ciliaris	HOCI	Herbivore	457	140	3.0±0.0	5	195–325	0%	5.8±0.2	−14.8±0.4
Holocentrus adscensionis[a]	HOAD	Benthivore	406		3.5±0.4	2	273–308	NA	8.4±0.2	−12.0±0.9
Holocentrus rufus	HORU	Benthivore	318	70–270	3.6±0.4	6	135–275	68%	7.2±0.2	−13.6±0.2
Lutjanus apodus	LUAP	Piscivore	610	120–460	4.3±0.4	3	202–246	13%	8.6±0.1	−12.0±0.6
Lutjanus griseus	LUGR	Piscivore	610	200–370	4.2±0.3	1	377	0%	8.7	−9.5
Lutjanus synagris[a]	LUSY	Benthivore	381		3.8±0.2	5	200–300	NA	7.8±0.5	−10.6±0.9
Ocyurus chrysurus	OCCH	Piscivore	762	160–550	4.0±0.3	9	260–378	30%	8.4±0.1	−11.9±0.4
Pomacanthus arcuatus	POAR	Herbivore	610	200–360	3.2±0.1	7	210–260	31%	6.3±0.2	−14.4±0.6
Pterois volitans	PTVO	Piscivore	381	60	4.4±0.4	11	155–400	NA	8.1±0.1	−12.2±0.4
Scarus iserti	SCIS	Herbivore	254	10–380	2.0±0.0	10	62–130	18%	4.2±0.1	−13.9±0.2

Table 1 (continued)

Scientific name	Code	Trophic guild	L_{max} (mm)	L_{UVC} (mm)	Trophic position	n	L_{SIA} (mm)	r_L	$\delta^{15}N$	$\delta^{13}C$
Sparisoma aurofrenatum	SPAU	Herbivore	279	10–300	2.0±0.1	6	67–400	80%	3.9±0.2	−12.5±0.8
Sparisoma viride	SPVI	Herbivore	610	10–550	2.0±0.0	1	460	0%	4.6	−11.9
Sphyraena barracuda	SPBA	Piscivore	1829	440–1150	4.5±0.6	4	853–1100	35%	9.9±0.4	−11.8±1.5
Stegastes diencaeus	STDI	Herbivore	152	40–150	2.0±0.0	7	57–85	25%	6.4±0.5	−14.0±0.7
Stegastes leucostictus	STLE	Herbivore	102	10–80	3.1±0.2	1	26	0%	5.4	−14.5
Stegastes partitus	STPA	Herbivore	102	20–70	2.0±0.0	2	67–70	6%	6.1±0.4	−14.1±0.3
Thalassoma bifasciatum	THBI	Omnivore	152	10–140	3.3±0.1	9	45–90	35%	5.4±0.1	−16.3±0.2

[a] Species sampled to represent other uncollected species on the list

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 (θ, 0°–180°) 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). θ 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). θ values close to 0° or 90° suggest dispersion in only one axis: θ values close to 0° represent relative dispersion along the x axis ($\delta^{13}C$), indicating multiple production sources, while θ values close to 90° 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_{max}) recorded by Humann and DeLoach (1989). Comparing fishes at a fixed proportion of maximum size (here $\geq 55\%$ of

Table 2 List of fishing method and targeting species

Fishing method	Targeting species	Examples of species
Hand net	Slow, approachable, small, cryptic, territorial	Gobies, damselfish, PTVO, AUMA
1 cm × 1 cm gill net	Fast, alert, non-thread shaped, schooling	J. Scarinae, A. labrids, J. haemulids, pomacentrids
BINCKE net	Fast swimming, close to substrate, schooling	J. Scarinae, labrids
Underwater fishing	Large bodied, fast swimming, cryptic, smart and alert	A. haemulids, HORU, some Scarinae, lutjanids, grouper
Line and hook	Pelagic, fast, alert	Carangids, lutjanids
Spearfishing	Fast, aggressive	A. Scarinae, acanthurids, PTVO
Surface troll	Pelagic, fast swimming individuals	Carangids, SPBA

J juvenile, *A* adult, for codes see Table 1

L_{max}) reduced the risk of comparing different life stages (Charnov 1993; Jennings et al. 2001; Galván et al. 2010).

For each species, the $\delta^{15}N$–$\log_2 M$ relationship was generated using linear regression, the slope and intercept values being used to calculate $\delta^{15}N$ values of individuals of the same species with other body mass values. To derive the community relationship between $\delta^{15}N$ and $\log_2 B$ (B was used instead of M to differentiate the community-level analysis from the species-level analysis), the mean weighted $\delta^{15}N$ value of each $\log_2 B$ class was derived by calculating (1) the mass ratio (r) of each individual (i) in each $\log_2 B$ class, using $r_i = M_i / \sum_{i=1}^{n} M_i$, where n is the total number of individuals in the $\log_2 B$ class; and (2) mean weighted $\delta^{15}N$ for each $\log_2 B$ class j of the whole community as $\delta^{15}N_j = \sum_{i=1}^{n} \delta^{15}N_i \times r_i$ (Al-Habsi et al. 2008). The $\delta^{15}N$ of each individual ($\delta^{15}N_i$) was either calculated using the species-level linear $\delta^{15}N$–$\log_2 M$ relationship if it is significant or equivalent to the mean $\delta^{15}N$ of the species if not.

Because of the species richness of these reefs and limitation of fishing techniques, not all species could be sampled. To obtain $\delta^{15}N$ values of such species, several methods were used (full details in "Appendix B" supplementary materials): (1) using samples from similar species within the same genus if possible (order of priority: same genus, family, site, trophic position, diet and feeding habit from fishbase.org) by comparing 3 criteria: (a) length to weight conversion factors, (b) dietary similarities and (c) their feeding behaviours in this area; and (2) using existing data in the literature from nearby locations or elsewhere in the Caribbean with baseline adjustment (*D. cavernosa* to *D. cavernosa* if possible, otherwise *D. cavernosa* to turf algae) to reduce temporal and/or spatial baseline variations (Cabana and Rasmussen 1996).

Predator–prey mass ratio

The mean PPMR was calculated using the slope (b) of the regression line of the TP–$\log_2 B$ relationship as PPMR $= 2^{1/b}$. TP was calculated using the additive framework as

$$TP = TP_{base} + \frac{\delta^{15}N_{fish} - \delta^{15}N_{base}}{\Delta\delta^{15}N} \tag{2}$$

where the $\Delta\delta^{15}N$ is assumed constant and equal to 3.4‰ (DeNiro and Epstein 1981; Minagawa and Wada 1984). TP_{base} was indicated by the striped parrotfish (*S. iserti*, $\delta^{15}N_{base} = 4.2 \pm 0.1$‰; $TP_{base} = 2.0$) 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–$\log_2 B$ relationship was obtained from the slope (s) of $\delta^{15}N$–$\log_2 B$ relationship where $b = s/3.4$. Thus, the PPMR is calculated as

$$PPMR = 2^{3.4/s}. \tag{3}$$

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 $\Delta\delta^{15}N$ 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 $\delta^{15}N$, 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_L) ranged from 0 to 100% (mean = 31.0 ± 5.0). Mean species $\delta^{13}C$ ranged from -17.4 ± 0.2‰ (*Halichoeres pictus*) to -9.5 ± 0.0‰ (*Lutjanus griseus*), while mean $\delta^{15}N$ ranged from 3.9 ± 0.8‰ (*S. aurofrenatum*) to 9.9 ± 1.5‰ (*Sphyraena barracuda*). $\delta^{15}N$ values were significantly but weakly correlated with $\delta^{13}C$ ($p < 0.05$, $r^2_{adjusted} = 0.29$) at the species level

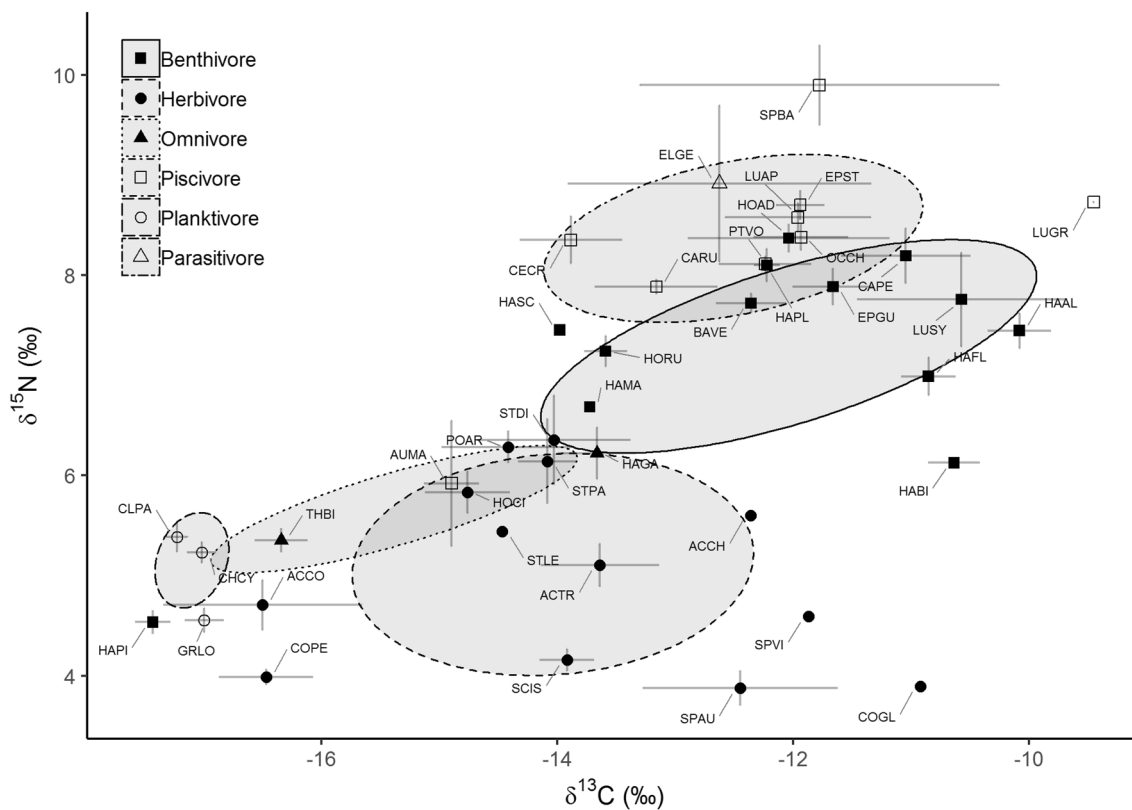**Fig. 2** Plot of bulk $\delta^{15}N$ against $\delta^{13}C$ (mean ± SE) of all sampled fish species (for codes see Table 1) and standard ellipses (solid line-ellipses) for five trophic guilds (and one species of parasitivore, ELGE) of fish at Cape Eleuthera (the Bahamas)

(Fig. 2). Some species had large SE values in $\delta^{13}C$ (≥ 1‰) (e.g. *S. barracuda*) or $\delta^{15}N$ (≥ 0.5‰) (e.g. *Aulostomus maculatus*), or both $\delta^{13}C$ and $\delta^{15}N$ (e.g. *Elacatinus genie*). Mean $\delta^{13}C$ and $\delta^{15}N$ values of strict pelagic planktivores (e.g. *Chromis cyanea*, TP = 3.7, $\delta^{13}C = -17.0 \pm 0.1$‰, $\delta^{15}N = 5.2 \pm 0.1$‰) and strict benthivores of similar TP (e.g. *B. vetula*, TP = 3.8, $\delta^{13}C = -12.4 \pm 0.3$‰, $\delta^{15}N = 7.7 \pm 0.1$‰) 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 $\delta^{13}C$ 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.

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 (‰^{2})	E	θ (°)	SEA_B (‰^{2})	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			
Omnivore	0.00	0.77		
Piscivore	0.57	0.00	0.00	
Planktivore	0.00	0.00	0.03	0.00

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 ($\theta < 45°$), while that of the planktivores was more vertically spread ($\theta > 45°$). 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 ($r^2_{\text{adjusted}} = 0.12$, $p < 0.05$; Fig. 3a) and δ^{13}C data ($r^2_{\text{adjusted}} = 0.17$, $p < 0.05$; Fig. 3b). The δ^{15}N values of several species did not scale positively with $\log_2 M_{\max}$ (e.g. *E.*

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 ($p < 0.05$)
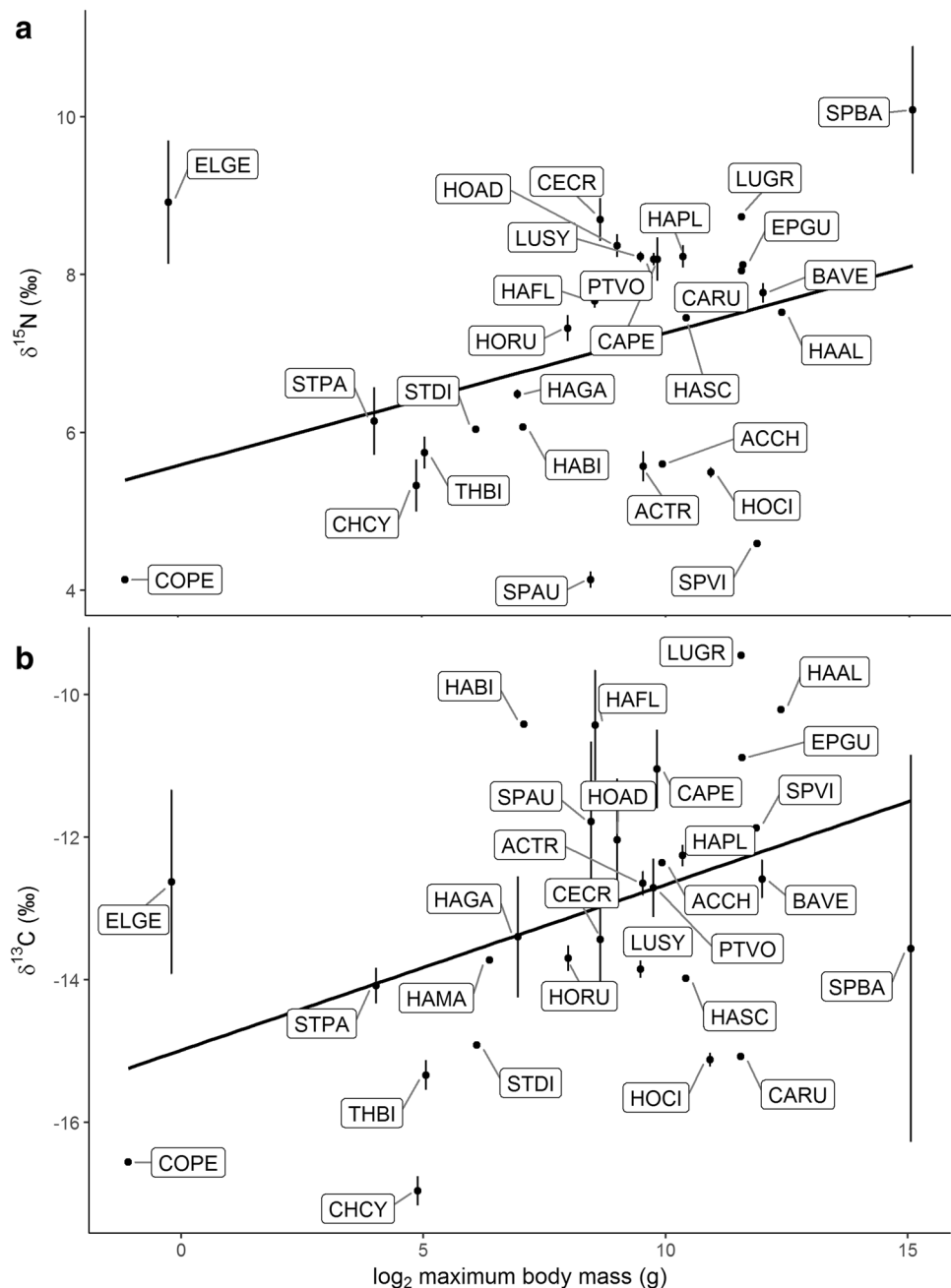
genie, *Sparisoma viride*, *Scarus iserti* and *S. aurofrenatum*). The SE values of $\delta^{13}C$ were generally higher than those of $\delta^{15}N$ regardless of M_{max}. $\delta^{15}N$ tended to vary with $\log_2 M$ for 29 species (Fig. 4) with $n \geq 3$; of these 24 relationships were positive (significantly so, e.g. *C. cyanea*), while five were negative (significantly so, e.g. *Pomacanthus arcuatus*, "Appendix C" supplementary materials). There was considerable variability around the regression line for nine species ($r^2_{adjusted} < 0.5$, 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 $\delta^{15}N$ and $\log_2 B$, the regression equation being $\delta^{15}N = 0.34 \pm 0.04 \log_2 B + 4.03 \pm 0.24$ ($r^2_{adjusted} = 0.64$, $p < 0.05$, Fig. 5). The slope value of TP–$\log_2 B$ was $b = 0.10$ ($r^2_{adjusted} = 0.80$, $p < 0.05$), and the PPMR estimates were 1047:1 (Table 5).

Fig. 4 Plot of $\delta^{15}N$ versus $\log_2$ 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
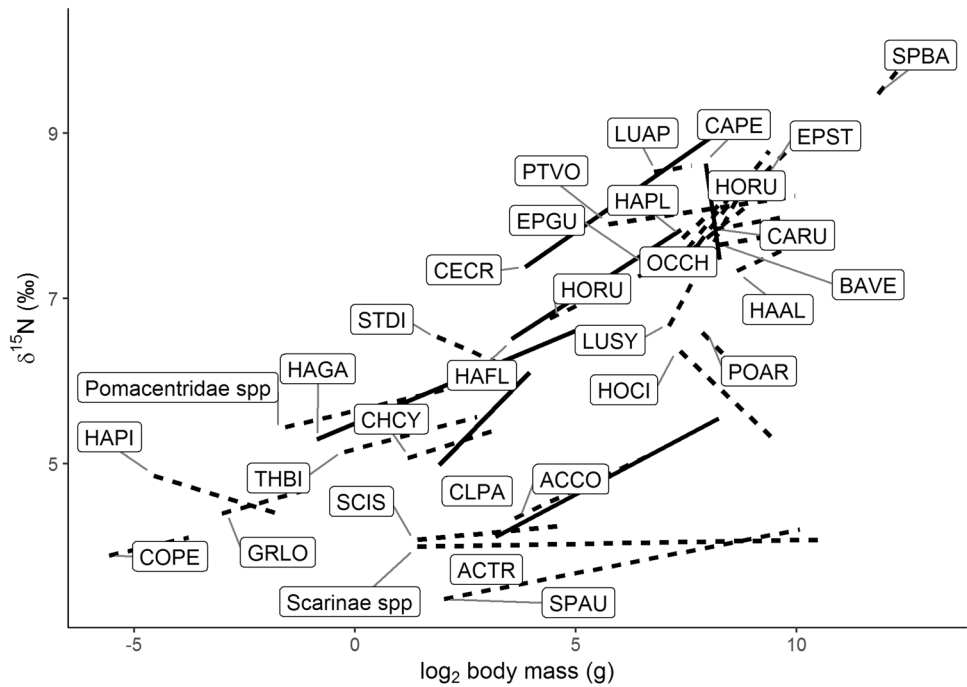

Fig. 5 Plot of combined relationship (linear regression) between $\delta^{15}N$ and $\log_2$ body mass at Cape Eleuthera (the Bahamas). Solid line: linear regression line ($p < 0.05$), long dashed line: 95% CI

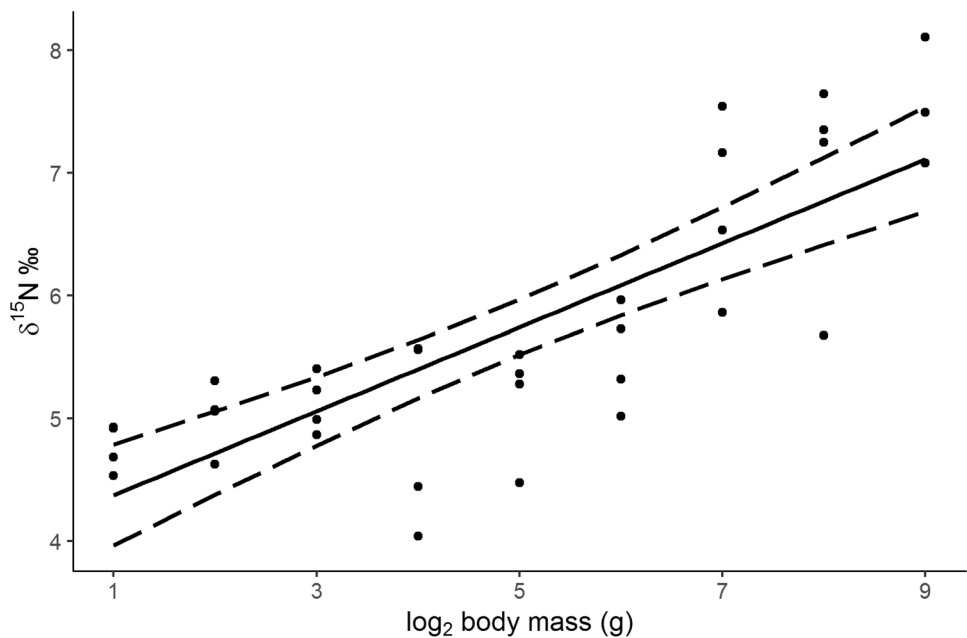**Table 5** Mean PPMR values of different communities from the literature using the additive framework

Community	PPMR estimates		Reference
	Median	25th and 75th quantiles	
Central North Sea	104:1	42 to 75:1	Jennings et al. (2002a, b)
Northern North Sea	1037:1	239 to 4503	Jennings et al. (2001)
Cape Eleuthera	1047:1	250 to 4833:1	Present study
Puget Sound	4320:1	779 to 2.71×10^4:1	Reum et al. (2015)
North Sea	8349:1	1235 to 6.73×10^4:1	Jennings and Warr (2003)
Western Arabian	8935:1	1287 to 6.60×10^4:1	Al-Habsi et al. (2008)
Iberian Peninsula	2.02×10^7:1	2.27×10^5 to 1.61×10^{10}:1	Bode et al. (2006)

Discussion

Species and trophic guild trophodynamics

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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{15}N$ values but differed greatly in $\delta^{13}C$ values. The $\delta^{13}C$ value of approximately $-16‰$ was close to that within the planktivore trophic guild, while the $\delta^{13}C$ value of $-10‰$ was more consistent with the piscivore trophic guild. Trophic position omnivory indicated by differences in $\delta^{15}N$ 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; Kürten 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 $\delta^{13}C$ data indicating that the two species are supported by plankton and benthic algae with similar $\delta^{15}N$ 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. coeruleus*, *C. personatus* and *T. bifasciatum*) were likely relying on plankton sources, and the piscivore *A. maculatus* might be predating 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).

$\delta^{15}N$–body mass relationship

The majority of species had a positive trend between $\delta^{15}N$ 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 $\delta^{15}N$–$\log_2 M$ 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 $\delta^{15}N$ and $\log_2 B$ 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 $\log_2 M_{max}$ 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 $\delta^{15}N$–$\log_2 B$ 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 fulfil 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 $\delta^{15}N$–$\log_2 M$ relationships. Low sample sizes and/or size ranges (r_L) meant that for some species, stable isotope data could not be derived across whole UVC size ranges; for these stable isotope 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 $\delta^{15}N$–$\log_2$ body mass relationship in a coral reef system, but this may not pertain to all coral reefs.

Compliance with ethical standards

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