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REPORT

Stable isotope analysis indicates a lack of inter- and intra-specific dietary redundancy among ecologically important coral reef fishes

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Abstract Parrotfish are critical consumers on coral reefs, mediating the balance between algae and corals, and are often categorised into three functional groups based on adult morphology and feeding behaviour. We used stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) to investigate size-related ontogenetic dietary changes in multiple species of parrotfish on coral reefs around Zanzibar. We compared signatures among species and functional groups (scrapers, excavators and browsers) as well as ontogenetic stages (immature, initial and terminal phase) within species. Stable isotope analysis suggests that ontogenetic dietary shifts occurred in seven of the nine species examined; larger individuals had enriched $\delta^{13}C$ values, with no relationship between size and $\delta^{15}N$. The relationship between fish length and $\delta^{13}C$ signature was maintained when species were categorised as scrapers and excavators, but was more pronounced for scrapers than excavators, indicating stronger ontogenetic changes. Isotopic mixing models classified the initial phase of both the most abundant excavator (*Chlorurus sordidus*) as a scraper and the immature stage of the scraper *Scarus ghobban* (the largest species) as an excavator, indicating that diet relates to size rather than taxonomy. The results indicate that parrotfish may show similar intra-group changes in diet with length, but that their trophic ecology is more complex than suggested by morphology alone. Stable isotope analyses indicate that feeding ecology may differ among species within functional groups, and according to ontogenetic stage within a species.

Keywords Resource partitioning · Parrotfish · Zanzibar · $\delta^{13}C$ · $\delta^{15}N$ · Diet · Indian Ocean

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Introduction

Mechanisms of species coexistence at the community level are debated (Hubbell 2001; Connolly et al. 2003; Bellwood et al. 2005). In high-diversity ecosystems, the maintenance of diversity is generally assumed to occur through fine-scale niche partitioning by resource specialisation (Dobzhansky 1950). Resource specialists can be associated with specialised morphological structures that allow the procurement of specific resources (Shoener 1986). Previous studies on highly diverse marine and freshwater fish families have examined dietary specialisation in relation to specialised morphological identity (Cichlidae—Liem 1980; Apogonidae—Barnett et al. 2006; Labridae—Bellwood et al. 2006). Within these families, diets are commonly general despite morphological specialisation. Given this, morphology may predict feeding potential but realised feeding and/or diet may be influenced by behaviour and prey availability. These studies provide examples of how morphological identity might be a poor predictor of niche partitioning (Bellwood et al. 2006) so that the links between morphological traits and resource use are not well understood. Alternatively, in instances of shared morphologies, it might be expected that species would be similar in resource use (Ross 1986) although shared traits

can be used differently depending on the age and size of an organism (Lokrantz et al. 2008). Similarly, because resource utilisation may change with ontogenetic stage, species with different traits could display either different or similar food preferences, depending on life stage (Ricklefs and Miles 1994). This indicates that studying resource utilisation within and among taxonomically or morphologically similar groups should improve our understanding of how biodiversity is maintained in high-diversity systems.

Diet can vary over a species' lifetime due to morphological, environmental and physiological changes, for example, during juvenile settlement from planktonic to benthic communities (Sale 1980), development of jaw structure and musculature (Wimberger 1991; Bonaldo and Bellwood 2008; Lokrantz et al. 2008) and sexual maturation (Johnsson and Johnsson 1993; Bruggemann et al. 1994b). Size-related morphological changes in foraging technique can alter the prey-specific foraging ability of an individual and result in variation in the exploitation of food resources (e.g. Mullaney and Gale 1996; Alwany et al. 2009). Additionally, because ontogeny can involve changes in dietary requirements, inter- and intra-specific competition, and vulnerability to predation (e.g. Holbrook and Schmitt 1988), it can lead to changes in microhabitat use (Sale 1980; Francini-Filho et al. 2010). Finally, changes in the structure and composition of a habitat can lead to changes in the availability of resources and subsequent changes to the diet of consumers (Winemiller 1989).

Parrotfish of the family Labridae are an important group of consumers on tropical coral reefs around the world (e.g. Mumby 2006; Bellwood et al. 2012) because they can feed off hard surfaces with their beak-like jaw. Their unique oral morphology makes them important in carbonate turnover and the clearing of reef surface area for the settlement of new sessile organisms (Bellwood 1995; Hoey and Bellwood 2008). Jaw morphology differs among the parrotfish and has been used to relate species taxonomically and to classify them into functional groups. These groups have been reviewed by Bellwood and Choat (1990) and Bellwood (1994), but in short for the Indo-Pacific region, the scrapers are composed of the genera *Scarus* and *Hipposcarus*, the excavators include *Chlorurus*, *Bolbometopon* and *Cetoscarus,* and the browsing group is composed of *Calatomus* and *Leptoscarus*. Most species are found within the *Scarus* and *Chlorurus* genera with the former having a reduced jaw that allows them to scrape the substratum and the latter having the most robust jaw, which allows them to take deeper excavating bites from hard surfaces. Lastly, the browsers have teeth that allow clipping from algae. Parrotfishes grow continuously throughout their lives (van Rooij et al. 1995), and most species go through significant ontogenetic changes with juvenile (or immature; IM), initial (IP; usually female) and terminal (TP; male) phases (Robertson et al. 1982). Many of the ontogenetic changes seen within parrotfishes are either directly associated with diet (food choice and growth) or indirectly affected by diet, such as defence of reproductive mates (Choat 1991; Bruggemann et al. 1994a, b).

This combination of shared and differing morphologies within and amongst genera, respectively, distinct ontogenetic stages, and different feeding techniques among the parrotfishes make them a good candidate to explore inter- and intra-specific dietary resource partitioning. There are inherent problems in the identification of gut contents from parrotfishes, because of their preferred foods (detritus and filamentous algae) and a high level of mechanical processing (Choat et al. 2002; Cocheret de la Morinière et al. 2003). These can be partly overcome by using chemical trophic tracers such as stable isotopes, which show predictable fractionation between trophic levels (Fry and Sherr 1984) and provide an index of diet assimilation over integrated time periods (Post 2002).

By investigating the stable isotope profiles ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of a wide variety of parrotfish species at different ontogenetic stages on East African coral reefs, we examine how the diet of a fish may depend not only on species identity, but also on ontogenetic stage. Our goal is to describe trophic variation within parrotfishes to clarify resource partitioning within a group that displays differing levels of taxonomic and morphological relatedness. We made comparisons among groups with differing feeding techniques, but also within morphologically similar groups for a more detailed evaluation of diets amongst and within species. Lastly, while we recognise that comparisons of diet do not test the actual ecological role of these fish, we use the term "functional group" for convenience to refer to groups of parrotfish with similar feeding techniques.

Materials and methods

Sample collection

Muscle tissue of 174 individual fish from 14 different species was analysed for both carbon and nitrogen stable isotope ratios, with a large size range within and between species (Table 1). For most species, all three stages (IM, IP and TP) were collected. Browsers were only represented by one species (*Calotomus carolinus*), while excavators and scrapers had four and nine species, respectively (Table 1).

Parrotfish and food source samples were haphazardly collected between June 2010 and February 2011 at three reefs [Ukombe (6°20′ 06″S, 39°14′ 32″E), Pwakuu (6°14′ 56″S, 39°04′ 41″E) and Nyange (6°13′ 23″S, 39°08′ 52″E)] on the western coastline of Unguja Island, Zanzibar

Table 1 Mean (±SE) and range of nitrogen and carbon stable isotope values of each ontogenetic life stage (IM = immature, IP = initial phase, TP = terminal phase) of each species

Species	*F*	Stg.	*n*	FL Range (cm)	Nitrogen ($\delta^{15}N$)		Carbon ($\delta^{13}C$)	
					Mean	Range	Mean	Range
Calotomus carolinus	B	IM	2	15.5:16.3	6.3 ± 0.2	6.1:6.5	−12.5 ± 2.1	−14.6:−10.4
		IP	2	21.4:23.1	6.9 ± 0.4	6.5:7.3	−9.8 ± 0.5	−10.3:−9.3
		TP	2	26.5:27.0	6.8 ± 0.2	6.7:7.0	−9.5 ± 0.3	−9.8:−9.1
Cetoscarus bicolor	**E**	**IM**	**5**	**10.7:19.3**	**6.4 ± 0.7**	**5.9:7.3**	**−12.7 ± 0.3**	**−13.8:−12.1**
		IP	2	20.6:32.5	6.3 ± 0.2	6.1:6.5	−10.6 ± 0.1	−10.7:−10.4
Chlorurus atrilunula	E	IP	2	12.6:23.1	6.9 ± 0.3	6.6:7.2	−14.4 ± 1.5	−15.8:−12.8
Chlorurus sordidus	**E**	**IM**	**10**	**9.5:15.6**	**6.0 ± 0.1**	**5.6:6.4**	**−13.2 ± 0.3**	**−14.7:−11.6**
		IP	**34**	**16.1:23.0**	**6.0 ± 0.1**	**4.9:7.1**	**−11.6 ± 0.2**	**−14.1:−8.9**
		TP	**5**	**22.3:25.6**	**6.6 ± 0.3**	**6.0:7.5**	**−12.6 ± 0.8**	**−13.6:−9.6**
Chlorurus strongylocephalus	E	IM	4	10.8:13.7	6.2 ± 0.3	5.5:6.8	−13.3 ± 1.4	−15.9:−9.8
		IP	**9**	**14.1:25.8**	**6.7 ± 0.2**	**5.6:7.6**	**−13.3 ± 0.5**	**−14.7:−10.3**
		TP	**13**	**14.9:30.7**	**6.4 ± 0.1**	**5.6:6.8**	**−13.9 ± 0.4**	**−15.2:−11.2**
Scarus falcipinnis	S	IP	2	17.7:20.2	5.1 ± 0.1	5.0:5.1	−12.2 ± 0.8	−13.0:−11.4
Scarus frenatus	S	IP	2	12.7:13.2	5.7 ± 0.3	5.4:6.0	−13.5 ± 0.3	−13.8:−13.2
Scarus ghobban	**S**	**IM**	**6**	**18.8:30.6**	**7.5 ± 0.2**	**6.6:8.3**	**−13.0 ± 0.7**	**−15.9:−11.1**
		IP	2	32.8:44.6	5.6 ± 0.5	5.0:6.1	−12.5 ± 3.4	−15.9:−9.1
Scarus niger	**S**	**IM**	**10**	**10.2:16.4**	**5.8 ± 0.1**	**4.8:6.5**	**−14.5 ± 0.2**	**−15.1:−13.4**
		IP	**7**	**17.4:23.4**	**5.5 ± 0.1**	**5.0:6.2**	**−12.4 ± 0.3**	**−13.6:−11.6**
		TP	**7**	**19.6:34.8**	**5.5 ± 0.2**	**5.0:6.5**	**−12.1 ± 0.3**	**−13.0:−11.0**
Scarus psittacus	S	IP	1	19.3	5.7	5.7	−12.1	−12.1
		TP	**10**	**19.5:28.5**	**5.3 ± 0.1**	**5.1:5.8**	**−11.1 ± 0.2**	**−12.0:−10.9**
Scarus russelii	**S**	**IM**	**5**	**15.6:22.4**	**5.3 ± 0.2**	**5.0:5.9**	**−13.5 ± 0.4**	**−14.4:−12.2**
		IP	3	22.5:27.5	6.2 ± 0.2	5.6:7.4	−13.3 ± 1.7	−16.6:−11.4
		TP	1	29.5	6.0	6.0	−11.5	−11.5
Scarus scaber	S	IP	2	15.7:17.7	6.1 ± 0.0	6.0:6.1	−12.1 ± 0.2	−12.3:−11.9
Scarus tricolor	**S**	**IM**	**3**	**12.9:13.9**	**7.5 ± 0.3**	**7.0:7.9**	**−16.8 ± 0.3**	**−17.3:−16.3**
		IP	**9**	**14.5:20.2**	**7.5 ± 0.2**	**6.5:8.3**	**−16.4 ± 0.2**	**−16.9:−15.0**
		TP	**4**	**16.7:22.8**	**7.0 ± 0.1**	**6.8:7.4**	**−15.5 ± 0.4**	**−15.9:−14.4**
Scarus viridifucatus	**S**	**IP**	**8**	**14.7:16.5**	**5.6 ± 0.3**	**4.0:6.4**	**–11.7 ± 0.3**	**−13.1:−10.4**
		TP	2	15.9:16.7	5.6 ± 0.2	5.4:5.7	−10.7 ± 0.6	−11.3:−10.1

Functional groups (F): *B* browsers, *E* excavators, *S* scrapers. Sample size (*n*) and their length range (*FL* = for fork length) are also given. Bold type indicates that the stage (*Stg.*) was used in the isotopic bi-plots and mixing model

(United Republic of Tanzania), in the western Indian Ocean. Care was taken to ensure that individual food sources and fish species were sampled from each reef to provide representative mean isotope signatures. Fish were collected with a speargun using SCUBA. Immediately after collection, fish were individually marked and stored on ice for return to the field laboratory where they were photographed, and length, species and life history stages were recorded. Although regional variation can exist (Choat et al. 2003), we used length at maturity as described in the published literature as a guide (Choat and Robertson 1975, 2002; Robertson et al. 1982; Page 1998) to differentiate immature from initial phase individuals, while initial phase (IP) and terminal phase (TP) were distinguished by colouration. Where present, the gonads were examined using a dissecting microscope to confirm gender. This allowed us to test for possible sex-associated changes in diet that occurred prior to colour change. IP primary males were rare, so that differences in diet from female IP fish could not be established, and they were grouped with IP females. Dorsal white muscle samples were collected for isotope analysis. Species identification was based on descriptions

by Randall and Bruce (1983). Additional fish were obtained from one fish landing site within Stone Town and a second 10 km farther south (Mizingani). These fish were caught by artisanal fishers using "dema", or fish traps made of stiff reeds baited using green algae (*Ulva* spp.) and checked daily. These landing sites were chosen because they were supplied from reefs where food samples were collected or other reefs within approximately 2 km.

In situ selection for our study was based on local abundance and availability of food sources (Plass-Johnson personal observations). Identified food sources for parrotfish include live coral, macroalgae, turfing algae and detritus (Bruggemann et al. 1994a; Wilson et al. 2003). Individual coral heads that showed signs of feeding by parrotfish (Bonaldo and Bellwood 2009) were sampled using a chisel and hammer to remove pieces of approximately 15 × 15 cm. Parrotfish show regional variation in coral species preference, and *Porites* spp. were selected because many species feed on this genus (Cole et al. 2008), and for practicality in sampling and analyses. Because coral isotope signatures can vary with light conditions, the top-most, horizontal lying part of the colony was sampled (Maier et al. 2010). Selection of macroalgae was opportunistic and based on availability. Coral rubble and intact coral heads with turfing algae were sampled if they were seen to be fed on by parrotfish or showed feeding scars. Detritus was vacuumed (Texsport Double Action Hand Pump, 2.0 l volume) from areas of rubble, dead and live coral heads after feeding was observed. After collection, coral, rubble and algae were rinsed with distilled water and then placed in individually marked freezer bags. Detritus samples were expelled from the pump into marked 1.5 l plastic bottles after evacuation between samples. Samples from each dive were put on ice at the surface (boat travel from the farthest reef (Ukombe) took approximately 2 h) and frozen at the field station (University of Dar es Salaam, Institute of Marine Science, Stone Town) until processed.

Thawed coral tissue was removed from the skeleton with an airbrush connected to a diving regulator and tank, using approximately 20 ml of distilled water. Coral homogenate was allocated to Eppendorf tubes (2 ml) and centrifuged (Eppendorf Centrifuge 5402 R) for 15 min at 14,000 rpm (at 4 °C) to separate zooxanthellae from coral tissue. The supernatant was decanted and centrifuged a second time to ensure separation of all zooxanthellae. Supernatant was decanted and passed through pre-combusted glass-fibre filters (GFFs; Advantec 47 mm, GF-75) with a hand vacuum pump (MityVac MV8010). The filters and remaining precipitate (i.e. zooxanthellae pellet) were then oven-dried. Dried filter paper with coral tissue was checked for residual zooxanthellae using a dissecting microscope. Coral polyps and zooxanthellae were separated because they can have significantly different isotope signatures and assimilation of plant and animal tissue can differ depending on the consumer.

Thawed rubble with turfing algae was rinsed in distilled water multiple times to remove epiphytes and detritus. The surface of the rubble was then scraped with a stainless steel scalpel, and scrapings were oven-dried in Eppendorf tubes. Samples were ground with a mortar and pestle and dried. Half of the sample was acidified using 1 N HCL and re-dried (Kolasinski et al. 2008). After stable isotope analysis, acidified samples were compared with untreated ones to identify possible changes in nitrogen. This comparison indicated no effect of acidification (ANOVA: $n = 4$, $F_{1,6} = 0.16$, $p = 0.71$). Detritus samples were thawed, re-suspended through mechanical shaking and then passed through pre-combusted GFFs using a hand pump. Filter papers were oven-dried and acidified as above. After isotope analysis, they were compared to untreated samples to identify possible changes in nitrogen (ANOVA: $n = 5$, $F_{1,8} = 1.52$, $p = 0.25$). Macroalgae were thawed and rinsed with distilled water and identified based on Oliveira et al. (2005).

All GFFs (coral tissues and detritus), zooxanthellae, fish tissue, macroalgae, and turf algae isotope samples were oven-dried at 60 °C for 48 h, then ground to fine powder and placed in tin capsules (OEA Laboratories, C11470.250P, pressed tin capsules 8 × 5 mm) for stable isotope analysis.

Stable isotope analysis

Following Post et al. (2007), lipids were not removed from parrotfish tissues because C:N ratios were always <4. Samples were analysed for stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) using a continuous flow Isotopic Ratio Mass Spectrometer (Europa Scientific Integra IRMS), at the IsoEnvironmental Laboratory, Rhodes University, Grahamstown, South Africa. Results are expressed in standard δ unit notation as:

$$\delta X(‰) = \left[\left(R_{\text{sample}}/R_{\text{reference}}\right) - 1\right] \times 1{,}000$$

where X is ^{13}C or ^{15}N, and R is the ratio of $^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for nitrogen. Ammonium sulphate, beet sugar and casein were used as standards, calibrated against multiple International Atomic Energy reference standards. Precision of replicate determinations for carbon was in the range ±0.03–0.25 ‰ and for nitrogen ±0.08–0.28 ‰.

Data analysis

Isotope signature: total length relationship

To investigate possible changes in diet in relation to fish size, length was linearly regressed against carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signatures separately for each

species and a two-tailed t test performed to test the null hypothesis that slope $\neq 0$. Only species with more than five samples were analysed. For species with significant regressions, homogeneity of slopes based on covariance was tested to compare slopes of species within and between functional groups. Species with a significant slope and R^2 were pooled within functional groups and checked for differences in slopes amongst groups with length as the continuous independent variable. Because of unbalanced sample sizes, the test for homogeneity of slopes was performed using type-III sums-of-squares. Homogeneity of variance was checked using Levene's test. If heteroscedasticity was detected, the results were interpreted conservatively or not at all depending on the alpha level.

Comparison of ontogenetic isotope signatures amongst and within species

To compare the diets of ontogenetic stages (IM, IP and TP) within species, stages were plotted on an isotopic bi-plot, omitting stages with less than three individuals, a δ^{15}N standard error (SE) >0.5 or a δ^{13}C SE > 1.0 because of the lack of replication or to be conservative when interpreting isotopic diet position. On the bi-plots, individual stages were compared with functional groups by defining a functional group's envelope using the mean and SE for each constituent species across all life stages. *Scarus tricolor* and *S. ghobban* means and SE were not used in the definition of the scraper functional group envelope because of their exceptionally different isotopic signatures when compared to other scrapers.

Food source contribution and comparison

Stable Isotope Analysis in the R environment (SIAR; Parnell and Jackson 2010) was run as a nine-source mixing model to estimate the proportional source contributions to parrotfish diets (for constituents see Table 3). Although *Halimeda* has been recognised as a food source of parrotfish (Mantyka and Bellwood 2007), it was not sampled in the field and values added to the model were taken from studies in comparable environments (Yamamuro et al. 1995; Cocheret de la Morinière et al. 2003; Lugendo et al. 2006). No C:N ratio was provided for *Halimeda* spp. in reported studies. *Udotea* sp. and *Ulva* sp. were grouped as "green algae" because, subjectively, they had similar signatures to each other, but different from the other green algae. For parrotfish, the groups used were those from the isotopic bi-plot. Mill et al. (2007) suggest a δ15 N fractionation value for herbivorous fish of 4–5 ‰, while Kolasinski et al. (2009), based on Post (2002), used an δ15 N enrichment value of 2.3 ‰ for *Mulloidichthys flavolineatus*, which, like parrotfish, has a diet consisting of both high- and low-protein foods. Given the similarity in diet and digestive system (Choat et al. 2002, 2004), we adopted a fractionation value of 2.3 ‰ for δ15 N. A fractionation value of 0.5 ‰ was used for δ^{13}C. The model was based on 3,000 iterations for each food source by fish stage. To compare the relatedness of fish stages based on their diet proportions (model output), a cluster analysis was performed on the means of the food source iterations. The cluster analysis was based on Euclidean distance and clusters were created using group averages. Significance and groupings were confirmed with a MANOVA and Fisher's LSD post hoc test, respectively. All statistical tests were performed using StatSoft Statistica 6, R (v. 2.12.2) and Primer 6.

Results

Isotope signature × total length relationship

There was a significant, positive linear relationship between total length and δ^{13}C for seven of the ten species tested, although some of the R^2 values were low. The relationship was significant for all excavators and the scrapers *Scarus ghobban*, *S. niger*, *S. psittacus and S. tricolor* but not for the browser, *Calotomus carolinus* (Table 2). The models had particularly strong correlations for *Cetoscarus bicolor*, *S. ghobban*, *S. niger* and *S. psittacus*, with R^2 values near to or above 0.50. No species showed a significant relationship between δ^{15}N and length (Table 2).

With the exception of the single browser species, there was a positive relationship between length and δ^{13}C signature within functional groups. The slopes for scrapers and excavators were significantly different from zero (scrapers: $t_{56} = 7.22$, $p < 0.001$; excavators: $t_{77} = 3.37$, $p = 0.001$) and also from each other ($F_{1,1} = 12.61$, $p < 0.001$); the slope for scrapers was nearly double that for the excavators (scrapers: $\delta^{13}C = 0.23 \times \text{Length}—18.3$, $R^2 = 0.48$, $p < 0.01$; excavators: $\delta^{13}C = 0.12 \times \text{Length}—14.9$, $R^2 = 0.13$, $p < 0.01$). Within groups, there were no significant differences among the δ^{13}C signatures of excavator species ($F_{2,1} = 0.98$, $p = 0.381$) or those scrapers with slopes significantly different from zero (Table 2; $F_{3,1} = 1.18$, $p = 0.325$). When slopes of individual scraper species were compared to the slope of the excavators as a group, only *S. tricolor* showed no difference ($F_{3,1} = 1.55$, $p = 0.208$), while all individual excavators were significantly ($p < 0.05$) different from the scraper group.

Comparison of ontogenetic isotope signatures among and within species

Most individual ontogenetic stages grouped with their appointed functional group (Fig. 1) with the exception of

the IM and IP stages of *Chlorurus sordidus* (excavator), which were positioned more closely to the scraper group. The TP stage of *Scarus tricolor* fell within the excavator group boundaries, while the other stages of this species were the most depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$. The level of $\delta^{15}N$ enrichment in the IM stage of *S. ghobban* separated it from all other stages and groups.

Food source contribution and comparison

The nine food sources used in the mixing model covered a wide range of ratios for both elements (Table 3). The algae *Halimeda* spp. were the most depleted in both $\delta^{13}C$ and $\delta^{15}N$. Coral tissue had the highest enrichment in $\delta^{15}N$ and *Dictyosphaeria cavernosa* in $\delta^{13}C$. Coral tissue and detritus had the lowest C:N ratios, while *Sargassum* spp. had the highest and was double that of the next highest, *D. cavernosa.* Macro- and turfing algae all had similar C:N ratios.

Cluster analysis based on the nine-source mixing model identified four different groups of fish based on their diets (Fig. 2). Overall, fish fell within their recognised functional groups with a few exceptions. Group A consisted of a single species (*S. tricolor* (IP)), group B represented excavators (except *Chlorurus sordidus* (IP)), and the

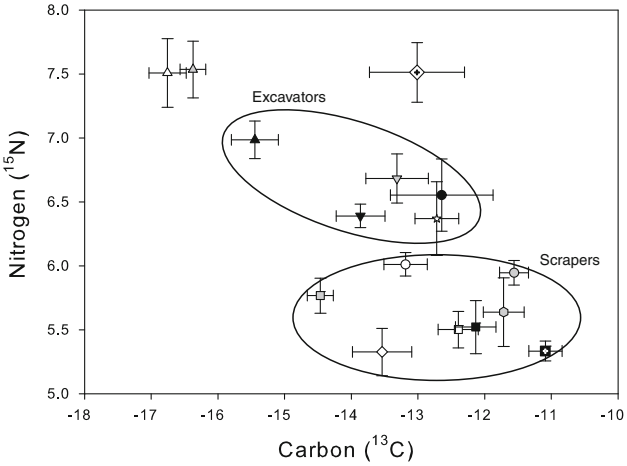

Fig. 1 $\delta^{13}C$ and $\delta^{15}N$ signatures of selected ontogenetic stages of parrotfish (stages with $n < 3$, $\delta^{15}N$ SE > 0.5 or $\delta^{13}C$ SE > 1.0 were not included). Stages are compared to functional group envelopes (functional groups defined by the mean ± SE of each constituent species across all life stages). *Scarus tricolor* and *S. ghobban* were excluded from defining the envelope for scrapers due to their extremely different signatures. Ontogenetic stages include IM (*white*), IP (*grey*) and TP (*black*). *Cetoscarus bicolor—star*; *Chlorurus sordidus—circle*; *C. strongylocephalus—down-triangle*; *Scarus ghobban—diamond with cross*; *S. niger—square*; *S. psittacus—square with cross*; *S. russelii—diamond*; *S. tricolor—up-triangle*; *S. viridifucatus—hexagon*. Functional group envelopes are indicated in the *graph*

Table 2 Results from regression analyses applied to carbon and nitrogen stable isotopic signatures of individual species with life stages (IM, IP and TP) grouped

Species	F.G.	Stable isotope	Slope	*y*-Intercept	R^2	*p*
Calotomus carolinus	B	$\delta^{13}C$	0.27	−16.5	0.44	0.151
($n = 6$)		$\delta^{15}N$	0.04	0.8	0.05	0.335
Cetoscarus bicolor	E	$\delta^{13}C$	0.15	−15.0	0.75	**0.012**
($n = 7$)		$\delta^{15}N$	−0.03	6.9	0.15	0.392
Chlorurus sordidus	E	$\delta^{13}C$	0.15	−15.0	0.21	**0.003**
($n = 49$)		$\delta^{15}N$	0.02	0.4	0.02	0.174
Chlorurus strongylocephalus	E	$\delta^{13}C$	0.14	−16.4	0.26	**0.009**
($n = 26$)		$\delta^{15}N$	−0.00	6.6	0.00	0.802
Scarus ghobban	S	$\delta^{13}C$	0.21	−18.7	0.61	**0.038**
($n = 8$)		$\delta^{15}N$	−0.04	8.4	0.18	0.350
Scarus niger	S	$\delta^{13}C$	0.21	−16.9	0.78	**0.001**
($n = 24$)		$\delta^{15}N$	−0.01	5.9	0.03	0.455
Scarus psittacus	S	$\delta^{13}C$	0.17	−15.2	0.49	**0.025**
($n = 11$)		$\delta^{15}N$	0.01	5.1	0.03	0.643
Scarus russelii	S	$\delta^{13}C$	0.19	−17.4	0.28	0.144
($n = 9$)		$\delta^{15}N$	0.03	4.9	0.05	0.568
Scarus tricolor	S	$\delta^{13}C$	0.13	−18.4	0.23	**0.015**
($n = 16$)		$\delta^{15}N$	0.09	5.9	0.18	0.115
Scarus viridifucatus	S	$\delta^{13}C$	0.12	−13.7	0.01	0.846
($n = 8$)		$\delta^{15}N$	−0.22	9.1	0.03	0.700

A significant value ($p < 0.05$; in Bold) indicated the slope $\neq 0$, tested with a Student's *t*-test. Functional group (F.G.): *B* browser, *E* excavators and *S* scrapers

Table 3 The nine food sources, including sample size (*n*), mean (±SE), range and carbon-to-nitrogen ratios used in the mixing model to reconstruct the diet of parrotfishes in Fig. 1

Food source	*n*	Nitrogen (δ^{15}N)		Carbon (δ^{13}C)		C:N ± SE
		Mean	Range	Mean	Range	
Coral tissue	18	4.8 ± 0.2	2.1:6.2	−15.0 ± 0.3	−18.4:−12.9	6.3 ± 0.3
Detritus	9	3.5 ± 0.2	2.5:4.3	−16.1 ± 0.8	−19.5:−12.8	8.3 ± 0.5
Green algae	14	4.4 ± 0.3	2.7:6.3	−18.0 ± 0.4	−20.4:−14.8	13.2 ± 0.8
Padina sp.	6	2.6 ± 0.6	0.7:5.4	−11.6 ± 0.5	−13.9:−10.9	15.6 ± 1.2
Turfing algae	9	3.4 ± 0.3	2.0:5.1	−10.1 ± 0.9	−13.3:−6.2	16.8 ± 1.1
Dictyota spp.	10	4.7 ± 0.1	4.1:5.5	−15.8 ± 0.6	−20.7:−13.3	17.5 ± 0.8
Dictyosphaeria cavernosa	3	4.1 ± 0.2	3.8:4.4	−5.6 ± 1.3	−7.6:−3.1	18.3 ± 1.7
Sargassum spp.	9	3.7 ± 0.4	1.8:6.5	−14.1 ± 1.2	−19.4:−10.9	35.9 ± 3.2
Halimeda sp.	4	2.1 ± 0.1	1.8:2.3	−20.5 ± 1.3	−24.2:−17.3	NA

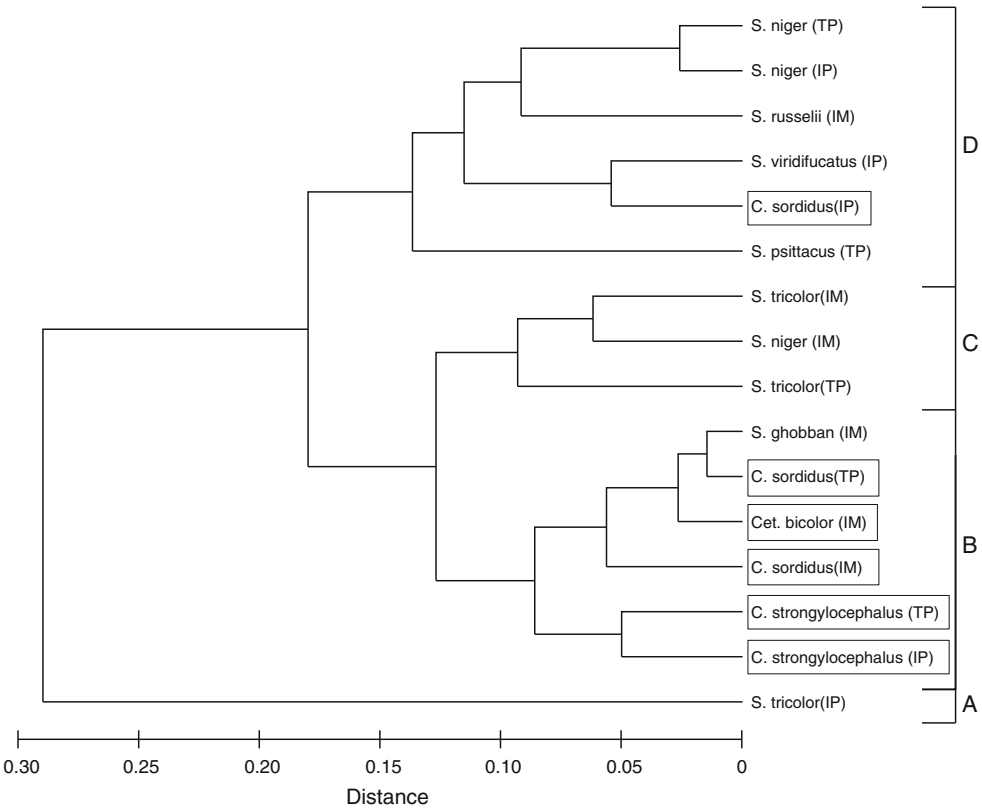

Fig. 2 Dendrogram of the cluster analysis based on the nine-source mixing model. Food sources and signatures are listed in Table 3, and fish groups are given in Table 1. *Black borders* represent the excavator functional group, and *no border* represents the scraper functional group. *Lettering* indicates groups of fishes with similar diets as identified by the cluster analysis

scrapers divided into two groups: C (closer to excavators) and D (apart from *S. ghobban* (IM)). MANOVA indicated that the groupings were significantly different ($F_{8,24} = 140.69$, $p < 0.001$). Groups A and D were different from each other and all other groups, while groups B and C did not differ significantly.

The mixing model indicated that coral tissue, detritus, green algae and *Dictyota* spp. showed similar trends for all members of each group. These four food sources occurred in high proportions in the diets of groups A, B and C (Fig. 3), but formed a smaller contribution for group D. Green algae formed a particularly high proportion for group A [*S. tricolor* (IP)], while the contribution of detritus was less variable amongst the groups. Of the remaining five dietary components, *Dictyosphaeria cavernosa* and turfing algae showed similar trends amongst the groups (Fig. 3): low for groups A and C, high for D and intermediate for group B (Fig. 3). *Padina* sp. formed a relatively high proportion for the single species group A and for group C (Fig. 3). The contribution of *Halimeda* spp. was low for group A and for *C. strongylocephalus* (IP and TP), but relatively high for the other three species in group B. *Sargassum* spp. made the least variable

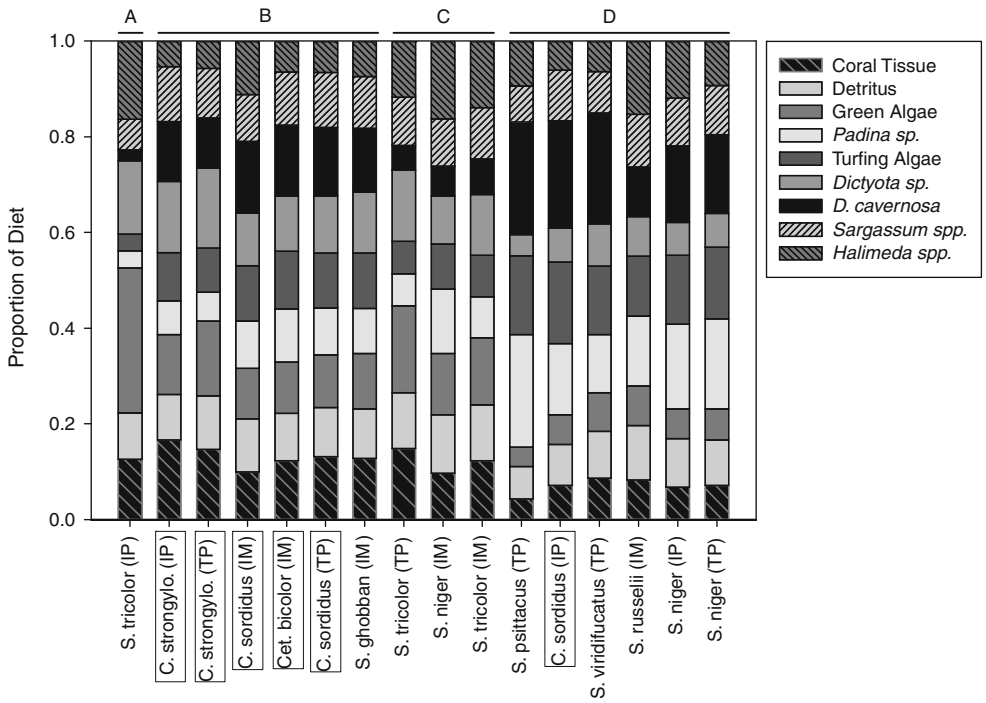

Fig. 3 Mean SIAR results for the dietary proportion of each food source and fish stage. *Boxed* fish stages belong to the excavating functional group, and *no box* represents the scraper group. *Uppercase lettering* above *graph* indicates similar sub-groups identified in the cluster analysis (Fig. 2)

contribution, varying from ~0.09 to 0.11 and contributed minimally to group A (Fig. 3).

Discussion

Ideally, stable isotopes data should be complemented by analyses of gut contents. For parrotfish, this is difficult as the gut contents can be highly processed or consist of foods that are difficult to identify such as detritus (Choat et al. 2002, 2004; Cocheret de la Morinière et al. 2003), leading to large proportions being described as unidentifiable or simply organic matter. For example, Choat et al. (2002) found *C. sordidus* gut content to be 80 % organic matter. Numerous studies have used stable isotope signatures to identify ontogenetic dietary shifts in teleosts. Many used signatures of food sources from different habitats to demonstrate large-scale ontogenetic habitat shifts between planktonic and juvenile fishes (e.g. Cocheret de la Morinière et al. 2003; Wells et al. 2008; Kolasinski et al. 2009). Most of these studies documented isotopic shifts between pre- and early post-settlement stages associated, in the case of parrotfish, with a carnivorous, planktonic diet (Chen 2002). In contrast, our results are not explained by changes in macrohabitat, although we recognise that finer-scale shifts within macrohabitats are possible. Most parrotfish are closely associated with the coral reef habitat throughout their post-settlement life (Randall et al. 1997), so our results indicate ontogenetic changes in diet, possibly associated with habitat selection within the reef (for example, reef base, slope, and crest, and back-reef).

Isotope signature, length and functional groups

The relationship between length and $\delta^{13}C$ in most individual species as well as within the scraper and excavator functional groups as a whole indicates a dietary shift in resource selection related to length, while the lack of a relationship between $\delta^{15}N$ and length suggests that the link between trophic position and size is more complicated than suspected. Although most food sources used in the mixing model fell within the normal $\delta^{15}N$ fractionation range (2.3 ‰ per trophic level), they had statistically significant differences.

The relationship between $\delta^{13}C$ and length was consistent amongst species within functional groups, suggesting that changes in food sources are similar amongst similar species. The gentler slope for excavators presumably reflects their robust jaw morphology (Bellwood 1994), which would allow even early stage fish access to a wide variety of food sources with different isotope signatures (for example, foods within the reef's carbonate framework such as infauna and bacteria). For scrapers, an increase in length

would lead to increased food accessibility as gape size and muscle mass increase. The regression lines of the two groups converged at ~30 cm body length, suggesting that scraper and excavator food sources become similar at this size. In fact, the scraper *Scarus ghobban*, with the greatest average length, had an isotope signature more consistent with that of an excavator.

The trends seen in this study must be considered within the context of sample size. Galván et al. (2010) showed that to improve the ability of linear models to predict sized-based dietary changes in $\delta^{15}N$ signatures, greater than 40 % of the L_{MAX} should be sampled. Within each species, samples within the current study were taken from a broad range of sizes, and predictions beyond the sampled lengths are not made. Although we are confident in our findings because of the consistency found amongst species, an increase in sample size would help increase the predictability of models of size-based changes in diet.

Inter- and intra-specific dietary comparisons

None of the three species for which all three life stages were represented in the mixing model (*Chlorurus sordidus*, *Scarus tricolor* and *S. niger*) showed a consistent ontogenetic trend in diet. Both *C. sordidus* and *S. tricolor* had IM and TP stages that fed on similar sources with very different diets at the IP stage. The IP and TP stages of *S. niger* had similar diets, but both differed from the IM stage. Comparable IM and TP diets seem anomalous as growth and energy demands are greatest at the IM stage, while sperm production in the TP stage is energetically relatively inexpensive. Bruggemann et al. (1994a, b) and van Rooij et al. (1995) reported diets that were lower in energy and protein for *Sparisoma viride* IP individuals compared with other stages. This accords with our study. We found that both IM and TP stage *C. sordidus* relied proportionally more on foods high in energy or those with the lowest C:N ratios (e.g. coral tissue and detritus) than the IP stage individuals. This was surprising as Lokrantz et al. (2008) found no change in bite frequency on corals with change in *C. sordidus* size. This may indicate dissociation between behaviour and physiology where fish feed in the same manner throughout their life, but metabolism causes changes in food assimilation. Similar to *S. viride*, *C. sordidus* IP stage had a very high reliance on *Dictyosphaeria cavernosa*, the source with the second highest C:N ratio.

The situation is more complicated for the scraper *Scarus tricolor*, for which green algae and *Halimeda* spp. were important diet components across all stages. The $\delta^{13}C$ and $\delta^{15}N$ signatures for all stages of *S. tricolor* were very different to those of both scrapers and excavators, implying the use of resources unavailable to other scrapers. Given similar morphology to other scrapers, the distinctly different signature in *S. tricolor* may represent resource partitioning based on alternate sources, effectively reducing competition with other species that share similar dietary needs. This may also be a strategy utilised by the scraper *S. ghobban*, which had $\delta^{15}N$ signatures similar to those of *S. tricolor*, suggesting that these fish feed at a similar trophic level not shared within other scrapers. While the existence of two distinct scraper groups (*S. tricolor* and *S. ghobban* with high $\delta^{15}N$ signatures versus all other scrapers with lower signatures) requires confirmation, this suggests resource partitioning between species in the same functional group.

In contrast, the ontogenetic shift in diet seen in *S. niger* may be associated with a different life strategy, as this is one of the few parrotfish that are monandric. The mixing models showed that the IM stage was more reliant on detritus and coral tissue than later stages, which had high proportions of *Dictyosphaeria cavernosa* and turfing algae, indicating similar diets in IP and TP fish. Fishes that feed over the epilithic algal matrix (EAM) often consume turfing algae, macroalgae, detrital aggregates and epiphytic material (Choat et al. 2002; Wilson 2002). Although the patterns differed between species, detritus was generally not important relative to other algal material, but contributed to diet in similar proportions to coral tissue. Corallivory is documented in parrotfishes (reviewed in Cole et al. 2008), and the results from the current study provide further evidence on how it might be an important protein subsidy along with detritus, depending on the life stage. We do, however, apply caution in the interpretation of ontogeny in our results. For some of our species, IP and TP overlapped in size, so that these groupings represent a state of maturity and not necessarily individual size. This may help to explain why, in some species, no difference was found between their adult stages (for example, *S. niger* and *C. strongylocephalus*). The analyses by life history stage and size should be interpreted differently, but when combined, allow insight into ontogenetic dietary changes within these parrotfishes.

Historically, the separation of the scrapers and excavators has largely been based on the different jaw morphology and biting strategies (Bellwood and Choat 1990; Bellwood 1994). It was also believed that this morphological difference allowed ecological diversification, but studies of one *Chlorurus* and two *Scarus* species (Choat et al. 2002; Crossman et al. 2005) revealed similar dietary profiles, suggesting that different feeding strategies had little effect on their diets. Our stable isotope analyses identified broad-scale differences in the diets of the scraper and excavator functional groups where coral tissue along with *Dictyota* spp. and green algae comprised the main diet of the former and *Dictyosphaeria cavernosa* and turfing

algae that of the latter. However, this becomes more complicated when the scale of analysis is decreased to include ontogeny. The fact that two species had ontogenetic stages that grouped into different functional groups (*C. sordidus* (IP) within the scraper group and *S. ghobban* (IM) within the excavator group, see Fig. 2) and the occurrence of an intermediate group of scrapers underlines the fact that diet similarity cannot be determined based solely on morphology. This supports data from studies in the Caribbean where scrapers, browsers and excavators can all be present within the morphologically similar *Sparisoma* genus (Bruggemann et al. 1994a, b; McAfee and Morgan 1996). Thus, diet forms a continuum within species, depending on the requirements of the ontogenetic stage. Because stable isotope analysis is specific to foods that are assimilated, consumer isotopic signatures can be a result of differences in food signatures, differences within the sample population and/or variability within the consumer species itself (Vanderklift and Ponsard 2003).

The interpretation of our data involves a number of assumptions. Changes in stable isotope signatures can result from changes in diet, tissue growth or tissue repair (Vanderklift and Ponsard 2003), and because metabolism is directly related to growth (Kerrigan 1994), such changes will be greatest when growth is fastest (Fry and Arnold 1982). Although there is little information on fractionation rates in parrotfish, most show continuous growth throughout their life (Choat et al. 1996), and juvenile coral reef fishes show little relationship between growth rate and isotopic signature (Kolasinski et al. 2009). Consequently, we interpret the observed isotopic differences as an indication of dilution of the original isotopic pool by newly deposited biomass. Interpretation of isotopic data depends on how the signatures of different dietary constituents mix. For herbivores, this is influenced by the degree of fermentation and urea cycling in the gut. This problem is minimised for parrotfishes as they have a relatively short gut and a brief digestion period with reduced fermentation and urea cycling (Choat et al. 2004), which is more consistent with omnivores. Further caveats concern the use of mixing models to interpret consumer diets. These models function on the assumption that all consumers in a $\delta^{13}C/\delta^{15}N$ bi-plot will fall within a polygon, or mixing space, created by the signatures of the prey. Also, these models are only as useful as the data that go into them. When approximations are used in applying discrimination factors, this uncertainty is magnified because small changes not only change the estimated proportions of each prey, but also where the consumer fits within the mixing space. Discrimination factors have not been specifically identified for parrotfish, and because of this, we interpret the importance of individual food constituents conservatively and emphasise foods that represent a high proportion of a diet. Given the generalist feeding strategies of parrotfish, it is likely that their diets include many more foods than were used in this model. Therefore, we interpret the importance of groups of foods, rather than individual food species. Lastly, parrotfish feed over a wide variety of surfaces that are associated with very different community compositions.

Our results highlight the advantages and disadvantages of stable isotope analysis. For example, our study indicates *Sargassum* spp. contributes approximately 10 % to parrotfish diet, while previous studies (Mantyka and Bellwood 2007; Hoey and Bellwood 2009) indicate that parrotfish consume very little of this macroalgae. However, these findings were based on translocation experiments, providing information on feeding at a particular time and place. On the other hand, the causes of variation in isotope signatures can be difficult to identify as foods apart from those sampled can contribute to consumer signatures, while resource signatures can vary in time and space. The advantage of an isotope approach is integration of diet under natural conditions. Despite the shortcomings of an isotopic approach, we were able to show ontogenetic variation in the isotopic signatures of our species.

Assuming similar resource use across ontogenetic stages within individual species may not be justified as access to and use of foods will change with growth due to physiological and ecological transitions. Here, we found a strong positive relationship between $\delta^{13}C$ signature and length, which may help us to better understand resource partitioning within and across species. Indeed, we demonstrated that some life stages showed isotope ratios that more closely resembled those of other species than other stages of their own species. Some stages were so different that they did not resemble any other species or life stage within their nominal functional group. This study supports the findings of Bellwood et al. (2006) who examined many labrid species and found little room for dietary generalisation despite morphological and mechanical similarity. They suggested that morphological specialisation allows the utilisation of extreme resources, but that this is only used under unfavourable conditions. We found that trophic variation in parrotfish seemed to be most closely related to size and/or ontogenetic stage rather than jaw morphology as can be seen in *S. ghobban*. Certainly, the results here will help us to better understand trophic partitioning within and amongst these coral reef species. It seems that the life stages of a parrotfish species exist on a dietary continuum so that species are able to coexist through an ability to utilise differing resources despite minimal morphological differences.

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