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Contrasting Responses in the Niches of Two Coral Reef Herbivores Along a Gradient of Habitat Disturbance in the Spermonde Archipelago, Indonesia

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Habitat modification of coral reefs is becoming increasingly common due to increases in coastal urban populations. Coral reef fish are highly dependent on benthic habitat; however, information on species-specific responses to habitat change, in particular with regard to trophic strategies, remains scarce. This study identifies variation in the trophic niches of two herbivorous coral reef fishes with contrasting trophic strategies, using Stable Isotopes Bayesian Ellipses in R, along a spatial gradient of changing coral reef habitats. In the parrotfish *Chlorurus bleekeri*, a roving consumer, the range of $\delta^{15}N$ and $\delta^{13}C$ and their niche area displayed significant relationships with the amount of rubble in the habitat. In contrast, the farming damselfish, *Dischistodus prosopotaenia*, showed a narrow range of both $\delta^{15}N$ and $\delta^{13}C$, displaying little change in niche parameters among sites. This may indicate that parrotfish vary their feeding according to habitat, while the damselfish continue to maintain their turf and invertebrate resources. Assessing isotopic niches may help to better understand the specific trophic responses to change in the environment. Furthermore, the use of isotopic niches underlines the utility of stable isotopes in studying the potential impacts of environmental change on feeding ecology.

Keywords: isotopic niche, $\delta^{13}C$, $\delta^{15}N$, Spermonde Archipelago, coral triangle, Makassar, disturbance

INTRODUCTION

The effects of terrestrially-derived disturbance gradients in marine waters across coral reefs have been noted from many parts of the world (Edinger et al., 1998; Mallela et al., 2004; Fabricius et al., 2005; Lirman and Fong, 2007; Teichberg et al., 2018). Coral reefs closer to shore are generally characterized by less hard coral abundance, an increase in fleshy algae, a general loss of habitat complexity, and by a decrease in coral and fish species diversity or even complete shifts in the sets of species (Fabricius et al., 2005; Plass-Johnson et al., 2015a, 2018). Anthropogenic impacts can alter the resource availability and predator-prey relationships on a coral reef thus affecting habitat use and the trophic niche of the biotic constituents (Jones and Syms, 1998; Syms and Jones, 2000). Thus, changes in coral reef communities along disturbance gradients may be associated

with a change in their trophic structure (Jennings et al., 1995). However, the trophic structure of coral reef communities is highly complex, and discerning the specific change of habitat use of any individual species can be challenging due to the high biological diversity on reefs (Fenner, 2012). Nevertheless, revealing trophodynamics of a coral reef community may allow for better interpretation of community change under varying environmental stress (Done, 1992) and help facilitate management decisions that break negative feedback loops (Glaser et al., 2018).

The trophic niche of an organism has been described as the bionomic portion of a specie's ecological niche, divisible to *n* dimensions based on the sum of all nutritional resource use (Hutchinson, 1978). Stable isotope ratios of a consumer are closely linked to their diet (Post, 2002) and thus are similar to the bionomic niche axis. The heavier stable nitrogen (^{15}N) and stable carbon (^{13}C) isotopes accrue in consumers with an increase in trophic level (Post, 2002). The isotopic structure of a system depends on the availability of dissolved inorganic nitrogen (DIN) and carbon (DIC) and its use by the system's primary producers (Post, 2002) which can then be reflected at higher trophic levels (Harvey and Kitchell, 2000; Post, 2002; Letourneur et al., 2013). As a result of environmental heterogeneity, seasonality and differences in physiology, primary producers may exhibit variability in isotopic signatures over space and time (Dethier et al., 2013) both within and among species. However, as long as this isotopic variability in the prey items is lower than variance resulting from dietary shifts of their consumers, which can be revealed by sampling of prey items, variance in isotopic signature of the consumers is assumed to be a robust measure of trophic niche width (Bearhop et al., 2004). Recently, multivariate, Bayesian techniques have utilized $\delta^{15}N$ and $\delta^{13}C$ data to describe the niche width of community members (Bearhop et al., 2004; Newsome et al., 2007; Jackson et al., 2011; Dromard et al., 2013).

Herbivorous fishes can remove excess macrophyte growth that might compete with corals for space and light resources (Bellwood et al., 2006; Hughes et al., 2007; Bonaldo et al., 2014), representing a group of interest with respect to variation in trophodynamics. However, herbivores are diverse in their feeding strategies, with resource preferences varying between erect macroalgae and turf algae (Choat et al., 2002, 2004). Turf algae is recognized as a potential impediment to coral reef development (Jompa and McCook, 2003; Vermeij et al., 2010; Smith et al., 2016; Ford et al., 2018) and thus, understanding how the trophic strategy of turf algae consumers responds to changing environments is important to elucidate the potential implications of environmental change for trophodynamics in reefs.

This study explores variation in the trophic niche space of two consumers of turf algae (Bay, 1999; Ledlie et al., 2007) with different trophic strategies. Individuals of the parrotfish, *Chlorurus bleekeri* (de Beaufort, 1940), and the farming damselfish, *Dischistodus prosopotaenia* (Bleeker, 1852), were collected at islands of the Spermonde Archipelago, Indonesia, representing a spatial gradient away from the urban center of Makassar. These reefs have documented variation in habitat composition with relation to disturbance (Edinger et al., 1998; Cleary and Renema, 2007), with low live coral cover and high amounts of coral rubble with increasing turf algae recruitment and abundance (Plass-Johnson et al., 2016a) at the near-shore, impacted reefs. *C. bleekeri* and *D. prosopotaenia* were both observed to persist at most of the reefs, potentially reflecting trophic variation associated with habitat structure. Species of parrotfish in the same genus as *C. bleekeri* have been shown to forage up to 130 m for food resources (Welsh and Bellwood, 2012) while *D. prosopotaenia,* a farming damselfish, continuously maintains a patch of turf algae approximately one square meter in size (Hoey and Bellwood, 2010). Both fish consume turf algae but recent work suggests that parrotfishes may not be directly targeting this source for their diet (Clements et al., 2016). The goal of the current study is not to reconstruct the diets of the two fishes, but rather to identify changes in their trophic niche, identified through stable isotopes, in association with changes in their environment. Therefore, this study examines the variation of the trophic niches of the two herbivorous fish species across an environmental gradient, assuming that variation in habitat degradation may alter their trophic niche space through modification of available benthic food items; however, it is assumed that variation in the isotopic niche will be greater in *C. bleekeri* than *D. prosopotaenia* due to the latter's predisposition to self-maintain its nutritional resources.

MATERIALS AND METHODS

Study Site Description

This study was conducted in November 2014, at six islands of the Spermonde Archipelago, Indonesia varying in distance from the city of Makassar (**Figure 1**). Samalona (SA; 05°07′S, 119°20′E, 7 km distance) was the closest site to the mainland, followed by Barrang Lompo (BL; 05°02′S, 119°19′E, 11 km distance), Bonetambung (BO; 05°01′S, 119°16′E, 14 km distance), Badi (BA; 04°57′S, 119°16′E, 19 km distance), Karang Kassi (KS; 04°53′S, 119°09′E, 27 km distance) and Kapoposang (KP; 04°41′S, 118°57′E, 55 km distance; **Figure 1**). November represents the end of a 4-month dry season, thus minimizing small-scale, temporal variation of nutrient inputs available to primary producers in each community. The benthic community assessment and the fish and algal collections were conducted at the northwest corner of each island to standardize the sampling sites among reefs, except for KP. The western side of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest is shallow (∼3 m) and the slope reaches down to 15 m. The last study site, KP, is located on the outer shelf wall of the archipelago and is exposed to deep oceanic waters, contributing to well-developed coral reefs with high biodiversity. Work at KP was conducted at the northeast side of the island at the edge of the carbonate shelf, which was more consistent with the structural conditions at the other sites.

Benthic Community Assessment

Benthic communities were quantified in parallel with Teichberg et al. (2018) and Plass-Johnson et al. (2018). At each island there were 50 photographic quadrats per 50 m transect. Three replicate transects were assessed per site at 5 m depth, 2 m below

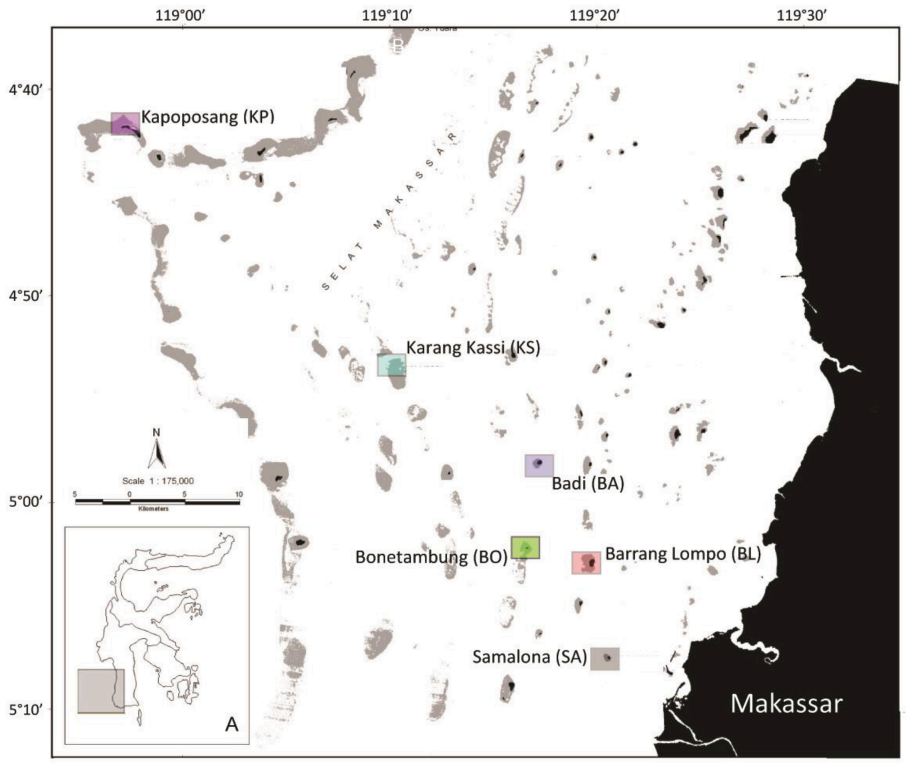

FIGURE 1 | Map of the Spermonde Archipelago with inset **(A)** indicating the islands' location in reference to Sulawesi, Indonesia. Squares indicate the sampling sites and the in-text acronym is given in parentheses. Colors correspond with **Figures 5, 6**.

the reef crest, because this represented a common habitat for both of the sampled species of fish. Photographs were taken at 1 m (standardized with a measuring pole) above the substratum, every 2 m along each transect. A photograph was taken on both sides of the transect tape, with a section of the tape within the photo to identify total area of the photograph. Analysis of the photographs was conducted with Coral Point Count with Excel extensions (CPCe; Kohler and Gill, 2006) using fifty randomized points per photograph for complementary descriptors of structure and biotic groups (Brown et al., 2004). The biotic groups included: ascidians, sponges, soft corals, crustose coralline algae (CCA), other invertebrates, cyanobacteria, macroalgae, turf algae, and live hard coral; however groups with <1% of total cover were dropped from subsequent analysis assuming that fishes' dietary and behavioral changes would largely be a product of the most abundant benthic groups. The selection of benthic categories was based on English et al. (1997). Biotic groups comprised any epi-growth irrespective of the surface structure type. To complement this, physical surface structure was also identified. Structural groups were categorized as being comprised of sand, rubble or pavement (defined as any flat, low-relief or sloping solid benthic space). Rugosity was the third measurement of the benthic habitat, and this was assessed with the linear distance-fitted chain method (Risk, 1972). The chain length used was 20 m, and measurement was conducted once per transect, starting at the first 10 m point.

Fish and Benthic Collection

A total of 64 *Chlorurus bleekeri* and 44 *Dischistodus prosopotaenia* were collected with a speargun using SCUBA. The collection was conducted at each island within a 200 m long strip, within the area described by benthic surveys, between 3 and 15 m water depth. After returning to the field lab (greatest travel time 2 h), dorsal white muscle tissue was sampled from each fish and dried at 60°C for 48 h. *D. prosopotaenia* was not present at, and therefore not sampled from, KP.

To identify variation in $\delta^{15}N$ and $\delta^{13}C$ of three different representative food items of the two fish species (Bay, 1999; Choat et al., 2002, 2004; Hoey and Bellwood, 2010), the brown calcifying algae *Padina* sp., filamentous turf algae and a mix of detritus (with the associated microphytobenthos) within the sediment were collected within the 200 m strip of reef coinciding with fish collection. It should be noted that samples of *Padina* sp. were also used as indicators of environmental condition within Teichberg et al. (2018). Collection depth was always 5 m below low tide to standardize light-associated change in plant isotopic values. Five replicates each of *Padina*, turf algae and detritus were collected along each of the transects. Individual strands of turf algae were isolated from pieces of rubble collected from outside of damselfish territories. All algal samples were cleaned of detritus and epiphytes, rinsed with distilled water, and then dried in a similar fashion to fish muscle tissue. Detritus samples for stable isotope analysis were taken from the top 2 mm of the

sediment using 2.0 ml Eppendorf tubes. Sediment samples were not collected from BL and KS due to logistical difficulties.

Fish and algae samples for stable isotope analysis were oven dried (50°C for 48 h) and ground to a homogenous powder with mortar and pestle. Subsamples of *Padina* sp., turf algae and sediment were treated with hydrochloric acid and rinsed with deionized water for analysis of organic $\delta^{13}C$, and the remaining untreated sample was used for $\delta^{15}N$ (Risk et al., 2009). Samples were analyzed for stable isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) using a Thermo Finnigan Delta Plus mass spectrometer coupled with a Flash EA 112 elemental analyzer at the Leibniz Centre for Tropical Marine Research (Bremen, Germany). Results are expressed in standard δ unit notation as:

$$\delta X(‰) = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 1000,$$

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. The analytical precision of the measurement was <0.06‰ for both carbon and nitrogen. All $\delta^{13}C$ and $\delta^{15}N$ values were reported as ‰ vs. Vienna PeeDeeBelemnite (VPDB) and air, respectively, and normalized to the internal standards of wheat flour (carbon [$\delta^{13}C$]; −27.21‰) and atmospheric nitrogen (nitrogen [$\delta^{15}N$]; 2.85‰), and calibrated to the International Atomic Energy reference materials of IAEN N1 and N2 (nitrogen) and USGS 24 and NBS 22 (carbon).

Data Analysis

Benthic habitat characteristics (biotic composition, structure and rugosity) were square root transformed and analyzed with principle component analysis (PCA) to identify differences among sites. To determine the within-site trophic niches of *C. bleekeri* and *D. prosopotaenia*, their $\delta^{15}N$ and $\delta^{13}C$ values were evaluated with SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011) from the SIAR (Stable Isotope Analysis in R; Parnell and Jackson, 2013) package in R (R Core Team, 2015). SIBER was supported with further quantitative population metrics (Layman et al., 2007) for each species, allowing for a comparison of trophic structure among sites. Metrics included nitrogen (δNR) and carbon (δCR) ranges detailing the total range of nitrogen and carbon values of exploited sources; mean distance to the centroid (CD), providing a description of trophic diversity; standard deviation of nearest neighbor distance (SDNND), which provides a measure of trophic evenness; and standard ellipse area (SEA), which provides a bivariate measure of the core isotopic niche (Layman et al., 2007; Jackson et al., 2011). The calculation of SEA allows for subsequent analysis of the degree of niche overlap (%) which can then be used as a quantitative measure of dietary similarity among sites (Jackson et al., 2012; Jackson and Britton, 2013). A small sample size correction (SEA_C) for improving accuracy of SEA values was applied as suggested in Jackson et al. (2011). All metrics, excluding SEA_C, were bootstrapped ($n = 100{,}000$) to allow for comparisons among sites (Jackson et al., 2011). Layman's metrics were plotted against benthic categories to explore fish trophic-benthic relationships. Significant linear relationships were based on Pearson Product-Moment Correlation Coefficients for the applicable degrees of freedom ($df = n-2$). Furthermore, differences among sites in fish isotope values were determined with permutational analysis of variance (PERMANOVA) with Primer (v7) +PERMANOVA software. Pair-wise comparisons were performed with 9999 permutations based on a Euclidean distance matrix. PERMANOVA was selected because it is robust in instances of uneven sample sizes and when variance is heterogeneous (Anderson et al., 2008).

Each individual food was tested for differences in isotopic values among sites with one-way analysis of variance (ANOVA). In addition, Levene's test was applied to identify significant differences in the variance of isotopic values among sites. ANOVA and Levene's tests were performed with the base package of R.

Ethics Statement

This research was completed in Indonesian waters in accordance with permits issued by the Indonesian Ministry of Science and Technology (Kementerian Riset dan Teknologi, permit number: 3544/FRP/SM/X/2014). All work was reviewed and approved within the code of conduct for animal ethics of the Leibniz Centre for Tropical Marine Research, Germany, and the University of Hasanuddin, Indonesia. The transfer of materials was overseen by J. Jompa of the University of Hasanuddin and conducted as stated within the Memorandum of Understanding between the University of Hasanuddin and the Leibniz Centre for Tropical Marine Research.

RESULTS

Benthic Community

There was a clear grouping of the near-shore sites driven by high turf algae and rubble composition (**Table 1**, **Figure 2**). The farthest site, KP, separated from all other groups based on high CCA and live coral cover (**Table 1**, **Figure 2**). The second farthest site, KS, separated out because of high cover of sponge and cyanobacteria, and high rugosity. There was, however, a central group consisting of BA and one replicate of KS and BL each (**Table 1**, **Figure 2**) which represents intermediate conditions of high coral and CCA, but also high rubble and turf cover.

Padina sp., Turf Algae and Detritus

Nitrogen ($\delta^{15}N$) isotopic values of detritus and turf algae were significantly different among sites (**Figure 3**). Generally, $\delta^{15}N$ values were highest near the mainland and decreased with increasing distance from shore. However, the turf algae had its lowest value at BO (**Figure 3**). The only difference among sites for carbon ($\delta^{13}C$) was for detritus (**Figure 3**) with KP having the highest value (**Figure 3**). Levene's test indicated a significant difference in variation in only one instance, the $\delta^{15}N$ of turf algae (**Figure 3**). Thus, heteroscedasticity in turf algae values indicates its ANOVA results must be interpreted with caution. Within sites, the $\delta^{15}N$ and $\delta^{13}C$ of the differing foods were always significantly different (**Table 2**, **Figure 3**) while the degree of variability was only significant for $\delta^{13}C$ at BO.

Trophic Niches between Species

Stable isotopic values for *Dischistodus prosopotaenia* and *Chlorurus bleekeri* were largely differentiated based on their $\delta^{13}C$

TABLE 1 | Mean percentage benthic cover (±SE below) of primary biotic and structural groups, and rugosity.

Site	SA	BL	BO	BA	KS	KP
Distance (km)	**7**	**11**	**14**	**19**	**27**	**55**
BIOTIC GROUPS						
Macroalgae	1.41	0.53	4.17	1.35	0.58	1.88
	0.54	0.41	0.67	0.51	0.41	0.21
CCA	2.79	2.95	2.53	9.24	5.05	20.15
	0.66	0.16	0.45	0.68	0.54	3.41
Sponge	1.65	4.13	6.26	4.50	16.83	4.77
	0.27	0.60	1.66	0.40	9.10	0.01
Cyanobacteria	0.28	0.90	5.27	1.01	19.37	0.70
	0.11	0.22	0.66	0.30	6.28	0.19
Live coral	13.44	21.94	7.92	35.73	16.19	31.30
	3.34	7.32	1.18	1.37	1.37	1.94
Turf algae	60.29	44.82	57.15	34.42	26.32	20.40
	2.69	3.59	1.43	2.76	4.13	2.28
STRUCTURAL GROUPS						
Sand	7.13	13.31	10.39	3.84	4.34	9.44
	1.96	1.49	2.10	1.54	4.02	0.45
Pavement	22.24	27.19	30.44	19.98	18.83	39.07
	6.58	2.45	4.03	1.07	1.92	0.87
Rubble	35.59	23.84	32.89	29.85	18.65	10.87
	4.33	2.86	5.76	2.26	3.55	0.86
Rugosity	1.57	1.91	1.65	1.98	2.19	1.70
	0.09	0.15	0.11	0.12	0.04	0.15

Sites (SA, Samalona; BL, Barrang Lompo; BO, Bonetambung; BA, Badi; KS, Karang Kassi; KP, Kapoposang) are ordered increasing in distance from the mainland.

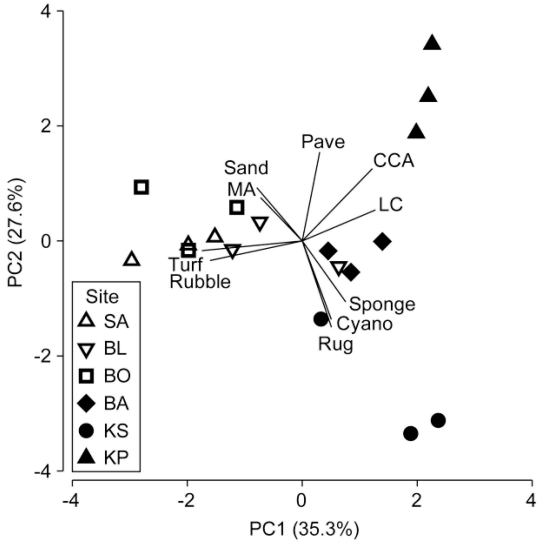

FIGURE 2 | Principal component analysis (PCA) performed on benthic biota, structure and rugosity [macroalgae (MA), crustose coralline algae (CCA), sponge, cyanobacteria (Cyano), live coral (LC), turf algae (Turf), sand, pavement (Pave), rubble and rugosity (Rug); **Table 1**]. The three sites nearest to shore a (SA, Samalona 7 km; BL, Barrang Lompo 11 km; BO, Bonetambung 14 km) are indicated with open symbols. The three sites further from shore (BA, Badi 19 m; KS, Karang Kassi 27 km; KP, Kapoposang 55 km) are indicated with closed symbols. Vectors indicate direction of separation based on specific benthic characteristics.

values. *C. bleekeri* ranged in δ^{13}C from −8.5‰ to −12‰ while *D. prosopotaenia* ranged from −13‰ to −16‰ (**Figures 4**, **5**). δ^{15}N values of *D. prosopotaenia* were within the range of the most enriched *C. bleekeri* values, with the former ranging from 5.7‰ to 7.3‰ and the latter from 4.3‰ to 7.3‰ (**Figures 4**, **5**). The stable isotope metrics of *D. prosopotaenia* and *C. bleekeri* showed that the damselfish trophic niches (SEA_c) were approximately half the size of that of the parrotfish (**Table 3**). This was reflected in both the range of resources (δCR) and trophic levels (δNR) which were smaller for *D. prosopotaenia* (**Table 3**). Concurrently, the damselfish also showed lower CD (trophic diversity) and SDNND (trophic evenness) values than the parrotfish (**Table 3**). At no point did the trophic niches of the two fishes overlap (**Figure 5**).

Trophic Niches across Sites

SIBER indicated no statistical differences among sites in SEAc for either fish, except that BO was significantly smaller than BL and KS for the damselfish ($p < 0.05$). There was, however, a clear increase in the range (δCR) in the parrotfish (**Table 3**), with values increasing from 1.67 to 2.64 between SA and KS. KP had a slightly lower δCR value (2.40) than the next site closer to shore (KS). Mean δ^{13}C and δ^{15}N values of the parrotfish were significantly different among sites [δ^{13}C: Pseudo-$F_{(5,58)} = 5.577$, $p < 0.001$; δ^{15}N: Pseudo-$F_{(5,58)} = 9.731$, $p < 0.001$]. SA and KS had significantly lower mean δ^{13}C values than other sites (**Figure 4**). A clear pattern was not evident in the δNR; however SA samples were enriched in ^{15}N by ∼1‰ compared to the other sites (**Figure 4**). Samples from SA, BO and BA had the widest δNR, while those from the two farthest sites had half that range (**Figure 3**). There was more overlap of isotopic niche width between sites in the parrotfish than the damselfish (**Table 4**).

Patterns in Layman's metrics and mean corrected isotope values were less clear for the damselfish. δNR was highest at BA and lowest at BO (**Figure 3**). Mean δ^{13}C and δ^{15}N values were also significantly different among sites for the damselfish [δ^{13}C: Pseudo-$F_{(5,38)} = 3.689$, $p < 0.01$; δ^{15}N: Pseudo-$F_{(5,38)} = 4.074$, $p < 0.01$]. The low values at BO were relatively low in δ^{15}N and high in δ^{13}C (**Figure 5**), however this site also had the lowest sample size. δCR was particularly high at BL, but mean δ^{13}C values showed few differences among sites (**Figure 5**).

The relationship between isotopic niche metrics and benthic categories was only significant between *C. bleekeri* and for rubble. Both the δNR ($R^2 = 0.89$, $p < 0.05$) and SEA_C ($R^2 = 0.81$, $p < 0.05$) were positively correlated (**Figures 6A,C**), while the δCR ($R^2 = 0.82$, $p < 0.05$) was negatively correlated with rubble (**Figure 6B**).

DISCUSSION

Localized disturbances to coral reef ecosystems can involve important alterations to the habitat, and consequently, to the

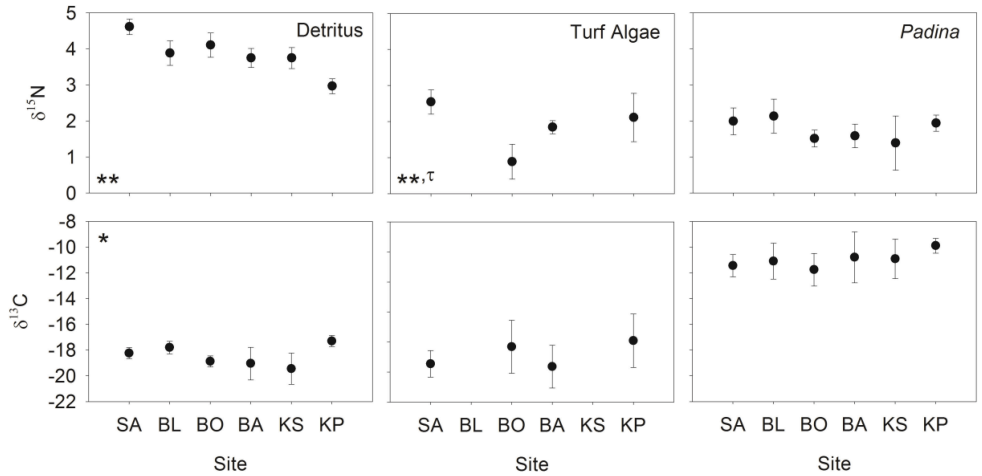

FIGURE 3 | Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ of detritus, turf algae and *Padina*. Sites are ordered left to right increasing in distance from the mainland. Asterisks indicate significance level in ANOVA (*$p < 0.01$, **$p < 0.001$) and tau indicates significance in the Levene's test (τ: $p < 0.05$).

TABLE 2 | Differences in values (ANOVA) and variance (Levene's test) of food sources within sampling sites.

Site	δ	DF	ANOVA		Levene's	
			F	*p*	*F*	*p*
SA	N	2.13	94.89	<0.001*	0.471	0.634
	C		121.4	<0.001*	1.391	0.286
BL	N	1.8	45.31	<0.001*	1.825	0.214
	C		104.6	<0.001*	7.732	0.024
BO	N	2.13	108.8	<0.001*	3.325	0.071
	C		39.73	<0.001*	8.662	0.005*
BA	N	2.13	106.3	<0.001*	1.437	0.273
	C		38.72	<0.001*	0.811	0.467
KS	N	1.8	19.88	<0.001*	0.133	0.725
	C		39.70	<0.001*	0.871	0.378
KP	N	2.13	55.32	<0.001*	1.400	0.284
	C		527.5	<0.001*	0.573	0.579

A significant p-value in either test is represented with an asterisk (*).

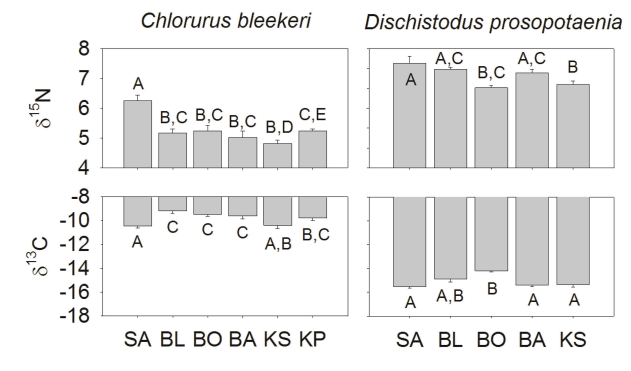

FIGURE 4 | Isotopic values at each site and for each species of fish (mean ± SE). Sites are listed from left to right increasing in distance from the mainland. Lettering indicates homogenous subgroups as identified by PERMANOVA. Lettering is independent for each species × isotope.

ecological niches of the associated fish communities. Our results agree with previous studies in the Spermonde Archipelago (Edinger et al., 1998, 2000; Sawall et al., 2012; Plass-Johnson et al., 2015a, 2016a,b), where the three sites closer to shore were characterized by low coral cover, higher rubble and higher abundances of turf algae. Cross-shelf variation in these benthic components are related to isotopic metrics of the parrotfish, *Chlorurus bleekeri*. A positive relationship between rubble and SEA_c and δNR, and a negative relationship with δCR suggest change in resource use and the trophic niche for *C. bleekeri* while little change in isotopic metrics was observed for the damselfish *Dischistodus prosopotaenia*.

Given the many sources of variation in isotope values, an increase in δCR of a consumer could be due to the consumption of more food sources across a range of distinct ^{13}C values or it could be due to increasing variation in the ^{13}C values of each of the food sources. Here, we show that the variability in the $\delta^{13}C$ values of individual food sources (turf algae and detritus) and other benthic constituents (*Padina* sp.) do not differ significantly among sites. With the exception of BO, these three groups do differ from each other within sites. This among-site similarity within food, and within-site difference among foods, suggests that the increased δCR is most likely a product of an increasingly diverse diet. Further differences in trophic responses of the two fishes are reflected in the size of their trophic niche (SEA_c) with *D. prosopotaenia*'s being half the size of *C. bleekeri*. Smaller SEA_c, δCR and δNR indicate the damselfish had a much more restricted diet than the parrotfish.

Although parrotfishes are known to feed from turf algae, their diet also includes detritus, endolithic algae and invertebrates (Choat et al., 2002; Plass-Johnson et al., 2013; Dromard et al.,

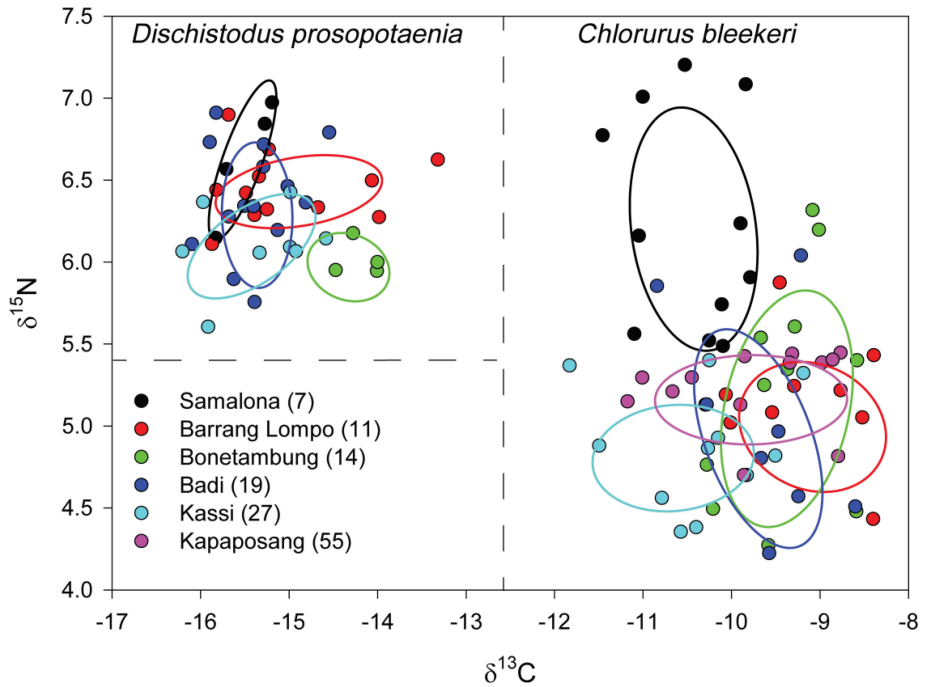

FIGURE 5 | $\delta^{15}N$ and $\delta^{13}C$ bi-plot of fish values with corrected standard ellipse areas (SEA_C) representing the core niche space of *C. bleekeri* and *D. prosopotaenia* by site. Dashed lines are a visual aid to identify differing niche areas of the two fish species. Sites are listed in order of increasing distance from Makassar, with distance (km) given in brackets.

TABLE 3 | SIBER and Layman's isotopic niche metrics for both species of herbivorous fishes.

Site	*n*	Mean length	Length range	δNR	δCR	CD	SDNND	SEA_C
D. prosopotaenia								
Samalona (7)	4	8.8	6.8–11.4	0.820	0.640	0.393	0.164	0.182
Barrang Lompo (11)	14	13.8	11.4–15.4	0.790	2.550	0.736	0.097	0.582
Bonetambung (14)	4	11.5	10.5–12.5	0.230	0.470	0.214	0.143	0.116
Badi (19)	14	15.5	13.9–17.0	1.150	1.550	0.463	0.118	0.481
Karang Kassi (27)	8	15.3	13.4–16.8	0.820	1.630	0.550	0.161	0.519
C. bleekeri								
Samalona (7)	11	24.9	19.8–28.4	1.710	1.670	0.829	0.187	1.340
Barrang Lompo (11)	9	21.9	14.2–27.5	1.440	1.670	0.665	0.174	0.878
Bonetambung (14)	12	23.1	15.8–28.0	2.050	1.710	0.764	0.249	1.262
Badi (19)	8	24.1	20.8–30.5	1.820	2.240	0.766	0.298	1.439
Karang Kassi (27)	11	19.9	16.4–24.0	1.050	2.640	0.713	0.187	1.012
Kapoposang (55)	13	22.8	17.1–27.8	0.750	2.400	0.810	0.222	0.668

Species, site with distance (km) from shore, sample size (n), average fish length and length range, and mean stable isotope metrics: δNR, $\delta^{15}N$ range; δCR, $\delta^{13}C$ range; CD, mean distance to centroid; SDNND, standard deviation of nearest neighbor distance; SEA_C, standard ellipse area corrected for small sample size.

2014; Clements et al., 2016). Our results indicate that *C. bleekeri* is assimilating foods with ^{13}C values closer to that of *Padina* sp. (**Figure 5**). While the exact food source cannot be determined, the significant relationship between δCR, SEA_C, δNR and rubble composition suggests that the alternate source may be indirectly linked to rubble. Because *C. bleekeri*'s δCR becomes narrower, its δNR becomes wider, and the SEA_C gets larger as rubble content increases, it seems that an increase in rubble reduces the number of food sources, but *C. bleekeri* begins to eat across a broader range of trophic levels. Clements et al. (2016) recently identified parrotfishes as microphages, getting their protein from cyanobacteria and other microorganisms that are (a) living either on or in calcareous substrates, (b) epiphytic on algae or (c) endosymbionts of sessile invertebrates. Nonetheless, the strong relationship between the metrics and rubble indicates that the fish is altering its diet, perhaps toward cyanobacteria

TABLE 4 | Percentage (%) of niche area (SEA) overlapping between sites for *C. bleekeri* (gray) and *D. prosopotaenia* (white).

	SA	BL	BO	BA	KS	KP
SA		5	0*	11	<1	NA
BL	<1*		<1*	25	6	NA
BO	<1	60		0*	0*	NA
BA	2*	50	87*		19	NA
KS	<1*	2	24*	34		NA
KP	<1*	37	48*	54	19	

D. prosopotaenia was not collected from Kapoposang (KP). An asterisk (*) indicates a significate difference in the standard ellipse area (SEA).

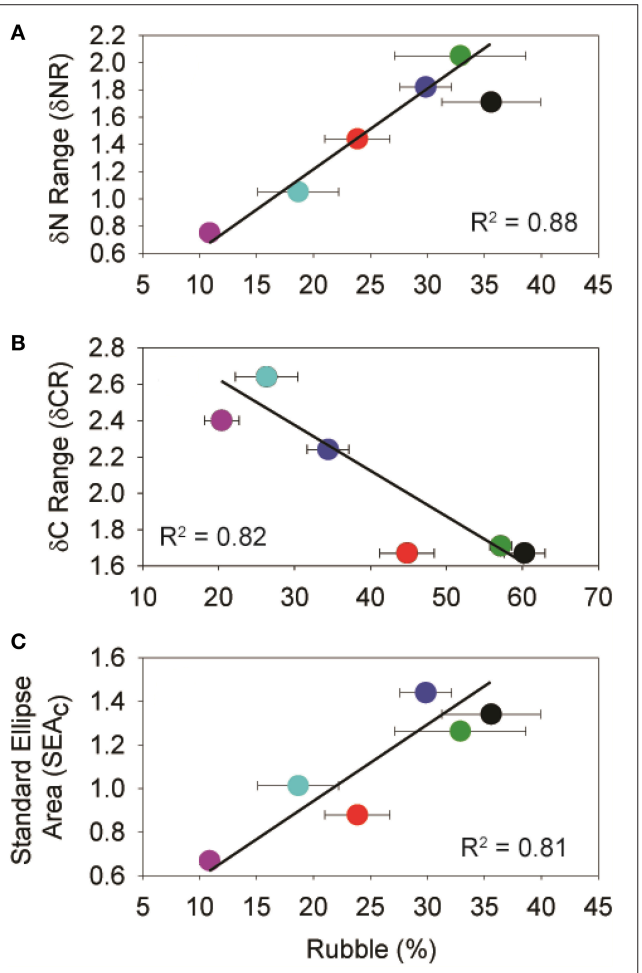

FIGURE 6 | Plots of significant isotopic niche metrics of *C. bleekeri* vs. mean (% ± SE) rubble cover. Based on the Pearson Product-Moment Correlation Coefficient, all alpha values were between 0.02 and 0.05, with 4 degrees of freedom. Colors represent the different sampling sites and correspond to **Figures 1, 5**.

and/or microorganisms associated with rubble and away from hard substrate associated biota, suggesting a degree of trophic plasticity based on changes in the habitat structure (Bellwood, 1995; Bonaldo and Bellwood, 2009).Given the reduction in the δCR at SA, it would seem that they become more focused on foods associated with rubble.

In the case of the damselfish, *D. prosopotaenia*, there was little consistent change in its trophic niche in relation to the environment or distance from shore. Furthermore, there were no significant relationships between benthic components and the Layman's metrics of the damselfish. The farming damselfish feed on their cultivated algae but also on the invertebrate communities and detritus that become established within the algal mat (Wilson and Bellwood, 1997; Dromard et al., 2013), suggesting two possible sources of variability; the invertebrate community and the algae. Recent studies have shown that in the Spermonde Archipelago there is significant variation in invertebrate recruitment in relation to distance from shore (Plass-Johnson et al., 2016a). Undoubtedly variation in invertebrate composition may contribute to some differences in the damselfish values (i.e., BO), however, differences in the species composition of the turf algae among farmed territories may also contribute to variability. Although the sampling for this study attempted to isolate sources of variability in the values of the consumers, further explanation of *D. prosopotaenia's* trophic niche may need to include a more specific investigation that integrates dietary and behavioral variation (Helfman, 1989).

The mechanisms of species co-existence in highly diverse systems at a small spatial scale are generally maintained via fine-scale niche partitioning by resource specialization (Dobzhansky, 1950). Interestingly, there was never an overlap in the isotopic niche space between the two species at any site. Farming damselfish aggressively defend their territory from other herbivores (Ceccarelli et al., 2005) including parrotfish (Ceccarelli et al., 2011), and the lack of isotopic overlap between *D. prosopotaenia* over *C. bleekeri* suggests that the latter may not feed often within the territory of the damselfish. This is further supported by the ∼3‰ difference between the fishes in their ^{13}C values indicating they may be assimilating completely different foods associated with their diets which is also in line with parrotfishes as microphages (Clements et al., 2016). In nearly every instance however, at any site, the Layman's metrics of the parrotfish were greater than those of the damselfish, likely reflecting their contrasting trophic strategies and also evolutionary history. For instance, the capacity of the parrotfish to forage at greater distances may enable them to target a diversity of resources that is only limited by their home range (Welsh and Bellwood, 2012). While wider foraging ranges may conversely result from reliance on specific, rare resources, their robust jaw morphology (Bellwood, 1994) and a gut able to process high sediment loads (Choat et al., 2002) support the first interpretation, as they allow the fish to process more foods with differing isotopic values. In contrast, farming damselfish actively select the composition of their $1m^2$ territories (Hata and Kato, 2004; Ceccarelli et al., 2005) which counterintuitively can also lead to higher diversity via intermediate disturbance (Gochfeld, 2010). Their restricted niche values suggest that they are reduced in the number of food sources that they assimilate in comparison to the parrotfish. As a result, the SEA_C values and the isotopic ranges (δCR and δNR) of the parrotfish were ∼10× and ∼1.5-2×,

respectively, greater than those of the damselfish. Furthermore, the mean values of the parrotfish were nearly two trophic levels (one trophic level = 3.4‰; Post, 2002) higher for ^{15}N and 2–3‰ for ^{13}C than the damselfish. Thus, although *D. prosopotaenia* and *C. bleekeri* are similar in their diets, morphological and behavioral specialization allow them to occupy distinctive dietary niches while coexisting (Cowman et al., 2009).

The occurrence of local and global disturbance to coral reefs is increasing because of climate change and human resource use (Burke et al., 2011). These disturbances result in modifications of the coral reef habitat, and this will have important effects on the associated fish species. In the worst case scenarios, a coral-dominated reef can transition to macroalgal, sponge or other non-coral dominance (Norström et al., 2009). The maintenance of micro—habitat by *D. prosopotaenia*, a fish that selects specific groups of algae and invertebrates (Hoey and Bellwood, 2010), guarantees resource availability despite a change in the greater environment. In contrast, the ability of *C. bleekeri* to vary resource utilization across differing habitat compositions is a different response allowing persistence in the face of environmental change. The ability to adapt resource utilization according to a changing habitat seems particularly important given that the species may actively avoid some altered coral reef conditions (Hoey and Bellwood, 2011; Welsh and Bellwood, 2015). Understanding species-specific responses to changed habitat will allow to better predict changes in community due to local and global disturbances.

The analysis of stable isotopes in coral reef food webs offers a powerful tool in elucidating trophic variation among consumers (Cocheret de la Moriniere et al., 2003; Carassou et al., 2008; Kolasinski et al., 2009; Greenwood et al., 2010; Dromard et al., 2013, 2014; Plass-Johnson et al., 2013, 2015b), however further clarification of sources of variability is needed to successfully apply this method within highly diverse systems. In our study, turf algae was more abundant at the degraded sites, however, the parrotfish *C. bleekeri* may have altered its feeding behavior because of specific structural (rubble) preferences for finding foods with ^{13}C values closer to *Padina* sp. This is further supported by a recent study that identifies cyanobacteria and microorganisms as their target food sources (Clements et al., 2016). Nonetheless, the trophodynamics of parrotfish are still being uncovered (Plass-Johnson et al., 2014; Clements et al., 2016) and the description of the actual feeding capacity of any species will likely take much more work. For parrotfishes, revealing specific diets through isotopes will require the isolation and sampling of endolithic organisms. At the same sites, the farming damselfish *D. prosopotaenia* was able to maintain its trophic niche, suggesting successful defense of its algal community-related resources. These findings help understand both the intra- and inter-specific capacity of two coral reef fishes to change or maintain their trophic relationship within the context of a changing environment. As the effect of environmental degradation on the trophic strategies still remains poorly understood for many species, the current study helps to identify the capacity of some fishes to respond to habitat loss by employing different trophic niches.

AUTHOR CONTRIBUTIONS

All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

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