



Coral reef degradation alters the isotopic niche of reef fishes

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Received: 17 August 2017 / Accepted: 20 November 2017 / Published online: 28 November 2017
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Abstract

The degradation of coral reefs is widely reported, yet there is a poor understanding of the adaptability of reef fishes to cope with benthic change. We tested the effects of coral reef degradation on the feeding plasticity of four reef fish species. We used isotopic niche sizes and mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of each species in two coral reefs that differed in benthic condition. The species chosen have contrasting feeding strategies; *Chaetodon lunulatus* (corallivore), *Chrysiptera rollandi* (zooplanktivore), *Halichoeres melanurus* (invertivore) and *Zebрасoma velifer* (herbivore). We predicted that the corallivore would have a lower mean $\delta^{15}\text{N}$ value and a smaller isotopic niche size in the degraded reef, that the herbivore and the invertivore might have a larger isotopic niche size and/or a different mean $\delta^{13}\text{C}$ value, whereas the zooplanktivore might be indifferent since the species is not linked to coral degradation. Some results matched our predictions; *C. lunulatus* had a smaller niche size on the degraded reef, but no difference in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, and *H. melanurus* displayed an increase in niche size and a lower mean $\delta^{15}\text{N}$ value on the degraded reef. Some other results were contrary to our predictions; whereas *Z. velifer* and *C. rollandi* had smaller mean $\delta^{13}\text{C}$ values but no difference in niche size. Our findings suggest there may be feeding plasticity to maintain a similar diet despite contrasting habitat characteristics, with different amplitude depending on species. Such findings suggest that certain species guilds would probably adapt to changes linked to habitat degradation.

Introduction

Coral reefs are threatened by several natural and human-driven disturbances. These disturbances differ in scale and frequency, and are causing substantial economic and ecological changes (Hoegh-Guldberg 1999; Hughes et al. 2003; Wilson et al. 2006, 2010; Graham et al. 2008, 2014; Mora

et al. 2011; Riegl and Purkis 2015; Cinner et al. 2016). The long-term persistence of coral reefs is even at risk in the face of global climate change (Roff et al. 2014; Hoey et al. 2016). As pointed out by Sale et al. (2014), “ever-expanding human impacts are continuing a substantial decline in the capacity of coastal marine ecosystems to provide crucial goods and services”. It is, therefore, critical and urgent to better assess how and through what mechanisms species or functional groups can adapt and cope with changing environmental conditions (Graham et al. 2013, 2015; Mumby et al. 2016).

One way to assess these dynamic properties is to look at the feeding plasticity of coral reef organisms, as it at least partly reflects their potential to persist under changing environments. However, due to the high diversity of organisms (Hixon 2011) and complex food webs (McMahon et al. 2015; Briand et al. 2016), it remains difficult to clearly capture dynamic energetic processes on coral reefs (Harmelin-Vivien 2002; Graham et al. 2017). The ecological niche theory (Elton 1927; Odum 1959), applied to feeding processes, offers the possibility to better evaluate energetics on coral reefs through a focus on selected species.

Stable isotopes are a powerful tool to investigate feeding plasticity of organisms (Wyatt et al. 2012; Letourneur et al. 2013; McMahon et al. 2015; Briand et al. 2015, 2016);

Responsible Editor: K.D. Clements.

Reviewed by C. Bradley and an undisclosed expert.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00227-017-3272-0>) contains supplementary material, which is available to authorized users.

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both carbon and nitrogen ratios have the great advantage of providing information on time-integrated assimilated food (Fry 1988; Vander Zanden and Rasmussen 1999). $\delta^{13}\text{C}$ can provide insights on the origin of the ingested organic material (De Niro and Epstein 1978; Wada et al. 1991; Sweeting et al. 2007a), whereas $\delta^{15}\text{N}$ can be used to define the trophic level of organisms (Minagawa and Wada 1984; Post 2002; Sweeting et al. 2007b). One way to use the bi-dimensional space constituted by both ratios is to quantify the isotopic niche size; the intra-specific variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values that captures feeding plasticity for a given species in a given habitat (Newsome et al. 2007).

Here, we test if differences in coral reef habitat conditions are reflected in the dietary niches of reef fishes, with implications for the capacity to use resources. Four species with different feeding strategies were chosen: an obligate corallivore species (*Chaetodon lunulatus*), a micro-zooplanktivore (*Chrysiptera rollandi*), an invertivore (*Halichoeres melanurus*) and a herbivore (*Zebrasoma velifer*). These species may display contrasting feeding responses to coral reef degradation, and therefore, present different mean isotopic values and/or isotopic niche sizes between reefs. For instance, a decrease of *C. lunulatus*' isotopic niche size in the degraded reef might be expected due to the strong link of this species with living coral (Harmelin-Vivien and Bouchon-Navarro 1983; Pratchett et al. 2004; Pratchett 2005), which in turn implies strong dietary specialization. Conversely, as a degraded reef is most often characterized by higher algal cover (Letourneur 1996), a larger isotopic niche size may be expected for the herbivore *Z. velifer* in the degraded reef. *H. melanurus* might also be affected by habitat change because the invertebrate community on which the species feed possibly responded to habitat characteristics. Finally, we would predict *C. rollandi* to be relatively indifferent to reef-health condition and thus have similar isotopic niche sizes on both reef types.

Materials and methods

Conceptual framework

This work derives from the ecological niche theory (Elton 1927; Odum 1959). Compared to a given presumably "normal" state, an ecological niche's size/volume can remain stable (no apparent change), decrease or increase after one or several events. For instance, poor habitat quality, high intra- or inter-specific competition, or a high predation rate might generate a decrease in niche size/volume (Fig. 1a). Conversely, good juvenile recruitment, high nutrient quality, or low predation or competition rates might generate an increase (Fig. 1b). The dimensions of the ecological niche may concern major ecological factors such as habitat and

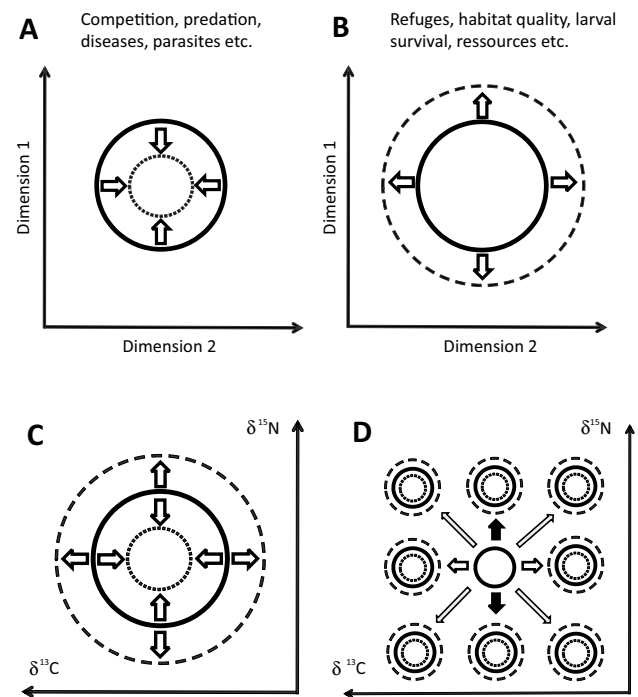


Fig. 1 The ecological niche theory; from a given ecological niche in a "normal" state (dark line, in both a and b panels), a species disturbed by an event may respond with a decrease of its niche size if the event has a negative impact (a; small-dotted line), or with an increase of its niche size if event has a positive impact (b; large-dotted line). c Transposition of the possible variations of the ecological niche size to the isotopic niche concept. Here, potential changes concern niche size, not changes in mean values of $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$. d The isotopic niche concept; from an initial isotopic niche (central position, dark line). Three main possibilities can be drawn: (1) an increase or a decrease of $\delta^{15}\text{N}$ values without change in mean $\delta^{13}\text{C}$ values (black arrows); (2) an increase or a decrease of $\delta^{13}\text{C}$ values without change in mean $\delta^{15}\text{N}$ values (white arrows); and (3) a combination of both (grey arrows). Note that for each case, the isotopic niche size can be stable (dark line), decrease (small-dotted line) or increase (large-dotted line)

feeding preferences for instance (e.g., two-dimensional biplots).

The isotopic niche concept is, to some degree, a simple transposition of the ecological niche concept into two particular dimensions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Newsome et al. 2007), giving information on a consumer position within a trophic network. Coral degradation may lead to four potential responses from the species studied:

1. the absence of any perceptible change, i.e., the isotopic niche size remains similar (the dark full line in Fig. 1c does not move) and the mean C and N isotopic values remain unchanged;
2. an increase or decrease of the isotopic niche size but without any significant change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ mean values (the small- and large-dotted lines in Fig. 1c);

3. significant changes in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ mean values without any increase or decrease in isotopic niche size (the white or black arrows in Fig. 1d);
4. an increase or decrease of the isotopic niche size associated with significant changes in $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ mean values (the grey arrows in Fig. 1d).

Study site and sampling procedures

This work was carried out in October 2014 in the southwest lagoon of New Caledonia, southwest Pacific Ocean. Two fringing reefs, close to the city of Nouméa, were studied; both reefs are shallow (0–6 m depth) and separated by approximately 1.7 km. The first, considered hereafter as “healthy” (22°19′12 S and 166°29′52 E), is located leeward, subjected to low hydrodynamic conditions and is not experiencing any significant direct anthropogenic disturbances. The second, designated hereafter as “degraded” (22°18′53 S and 166°29′84 E), is located windward, with more rigorous hydrodynamic conditions, sandy–muddy sediments occur at its base (~6 m depth) and is presumably under the influence of sporadic terrigenous runoffs from a small river (its mouth is located approximately 5–6 km northeast).

Habitat characteristics were assessed on four 30 m transects at each site following the method of Wilson et al. (2007). Percentage hard living coral cover, dead coral, rubble, carbonate pavement and sand were estimated using point intercepts every 50 cm along the transect tape. Structural complexity was estimated visually on a 6-point scale (where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves, 5 = exceptionally complex with numerous caves and overhangs). The number of holes < 10 cm were estimated along a 10 m² section of each transect. The abundance of the fish species studied was estimated along the same transects using a 2-m wide belt (i.e., 60 m², \times four replicates).

Fish were caught with a small fishing net adapted to the capture of aquarium fish. To avoid a plausible size effect on stable isotopic signatures, only individuals belonging to restricted size-classes were targeted, i.e., were caught *Chaetodon lunulatus* individuals of 7–10 cm (total length, TL) ($N = 24$ fish), *Chrysiptera rollandi* individuals of 4–5 cm TL ($N = 61$), *Halichoeres melanurus* individuals of 4–6 cm TL ($N = 45$), and *Zebbrasoma velifer* individuals of 6–12 cm TL ($N = 15$). Since both reefs are separated by a very shallow sandy plain that is partly emerged at low tide, we, therefore, assumed that fish movements between reefs were negligible, especially because these species are site-attached or sedentary and usually have very low to moderate home range (Nash et al. 2015; Green et al. 2015).

It is necessary to ensure that potential differences in fish population isotopic signatures are not linked to fluctuations

in organic matter (hereafter OM) source isotopic values (i.e., the “baseline”), which may present significant differences even at small spatial scales (Briand et al. 2015). Three replicates of algal turf and surface sediments (for sedimentary organic matter, hereafter SOM) were sampled, as both sources are among the most important potential OM sources on coral reefs (Vermeij et al. 2010; Briand et al. 2015).

Stable isotope samples and analyses

Tissues providing the most reliable isotopic values were sampled and immediately frozen at $-20\text{ }^{\circ}\text{C}$ for subsequent analyses: a piece of thallus for cleaned algal turf and dorsal white muscle for all fish specimens (Pinnegar and Polunin, 1999). Carbon- and nitrogen-stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analysed for all samples. Sediment, algal turf and fish muscle samples were dried, then ground to a fine powder with a porcelain mortar and pestle using standard protocols. Samples were weighed and approximately 1 mg of powder was encapsulated for vegetal/animal tissues and 15–20 mg for SOM. Samples were analysed without any prior treatment, except SOM for which two subsamples were analysed. The first, treated for $\delta^{13}\text{C}$ analysis, required an acidification step (see details in Letourneur et al. 2013) as carbonates present higher $\delta^{13}\text{C}$ than organic carbon (De Niro and Epstein 1978). The second, tested for $\delta^{15}\text{N}$, was not acidified to limit alteration of nitrogen isotopes (Pinnegar and Polunin 1999).

The $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ ratios were measured by continuous-flow isotope-ratio mass spectrometry. Isotope ratios were expressed as parts per 1000 (‰) differences from a standard reference material:

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

where X is ^{13}C or ^{15}N , R is the corresponding ratio ($^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$) and δ is the proportion of heavy to light isotope in the sample. The international standard references are Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen. Measurement precision, estimated using standards included in the analyses, was of 0.1‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{15}\text{N}$.

Data processing

Variances of organic matter sources (i.e., SOM and algal turf), habitat parameters and fish density were heterogeneous (Levene test). Therefore, non-parametric Mann–Whitney U tests were run to compare means.

Core isotopic niche area can be revealed by fitting standard ellipses to the isotopic data in the bi-dimensional plot of $\delta^{13}\text{C}/\delta^{15}\text{N}$, as described in Jackson et al. (2011). The standard ellipse area of a set of bivariate data is

calculated from the variance and covariance of x and y data and is expected to be less sensitive to sample size than former methods, which enable robust estimation of the isotopic niche.

Layman metrics, based on the elaboration of convex hulls in the bi-dimensional $\delta^{13}\text{C}/\delta^{15}\text{N}$ plot, were developed with the purpose to describe with precision the isotopic niche of a species or assemblage of several species (Layman et al. 2007; Cucherousset and Villéger 2015). Finally, and for each species, the following metrics were calculated with the SIBER package (Jackson et al. 2011) to compare each species between the two reef sites, i.e., healthy vs. degraded:

- (i) TA—total area of the ellipse; measuring the whole trophic diversity of individuals of a given species in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ biplot;
- (ii) SEAc—corrected standard ellipse area; representing the averaged isotopic niche of the group of individuals, but including a correction factor that takes into account the sample size and is thus more robust than non-corrected standard ellipse area (in particular for samples with small number of individuals);
- (iii) SEAb—Bayesian standard ellipse area; the Bayesian assessment of the standard ellipse calculated with SEAc, performed with 10^4 iterations, allows to limit the effect of the sample size and then minimize uncertainties linked to SEAc calculated with small sample size. Values close to TA and SEAc are good indicators of the relevance of these metrics.

In addition, the ratio SEAc/TA was calculated to obtain an idea of the individual variability within the group. The lower SEAc/TA is, the higher is the difference between TA and SEAc and thus the higher is the individual variability.

Table 1 Mean percentages (\pm SD) of living coral cover and non-coral habitats, index of structural complexity and number of holes < 10 cm per 60 m² in the two fringing reefs studied ($n = 4$)

	Healthy reef	Degraded reef
Live coral cover	79.6 \pm 7.1	32.5 \pm 10.8
Rubble	0.4 \pm 0.8	0.4 \pm 0.8
Dead coral	13.3 \pm 5.3	38.8 \pm 20.7
Carbonate pavement	2.5 \pm 1.0	1.3 \pm 2.5
Sand	2.1 \pm 2.1	24.6 \pm 11.3
Structural complexity	2.8 \pm 0.3	1.8 \pm 0.6
No of holes < 10 cm	355.0 \pm 71.9	130.0 \pm 74.7

Results

Habitat and fish population parameters

Except for rubble and carbonate pavement cover, all habitat parameters showed strong significant differences between reefs (Mann–Whitney U test, $p < 0.05$, Table 1). For instance, structural complexity and total live coral cover were both substantially greater on the healthy reef compared to the degraded reef. Conversely, dead coral and sand cover were 3- and 12-fold higher in the degraded reef, respectively.

Fish displayed similar (i.e., *Zebrasoma velifer*) or non-significantly different densities (e.g., *Chaetodon lunulatus*) on both reefs, except for *Halichoeres melanurus* that was approximately twofold more numerous on the degraded reef (Mann–Whitney U test, $p < 0.05$, Table 2).

Organic matter sources and fish isotopic ratios

Both OM sources, i.e., algal turf and SOM, revealed very similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values between healthy and degraded reefs (Mann–Whitney U test, $p > 0.05$, Table 3). Ratios were slightly C- and N-depleted in algal turf compared to SOM, and were very close to values found by Briand et al. (2015) in neighbouring fringing reefs.

For each species, $\delta^{13}\text{C}$ values were slightly higher in the healthy reef, and the opposite was found for $\delta^{15}\text{N}$, except for *H. melanurus* (Table 4). Differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between healthy and degraded reefs for each

Table 2 Mean densities (\pm SD) of the four targeted species per 60 m² in the two fringing reefs studied ($n = 4$)

	Healthy reef	Degraded reef
<i>Chaetodon lunulatus</i>	2.3 \pm 2.6	1.3 \pm 1.5
<i>Chrysiptera rollandi</i>	6.0 \pm 3.4	6.5 \pm 7.8
<i>Halichoeres melanurus</i>	4.0 \pm 0.8	9.0 \pm 1.8
<i>Zebrasoma velifer</i>	0.5 \pm 0.6	0.5 \pm 0.6

Table 3 Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (expressed in ‰) in the healthy and degraded fringing reefs for two major potential organic matter sources, i.e., the algal turf and the sedimentary organic matter (SOM) ($n = 3$)

	Healthy reef	Degraded reef
Algal turf		
$\delta^{13}\text{C}$	- 17.64 \pm 0.12	- 17.67 \pm 0.11
$\delta^{15}\text{N}$	2.58 \pm 0.05	2.62 \pm 0.04
SOM		
$\delta^{13}\text{C}$	- 15.54 \pm 0.14	- 15.61 \pm 0.17
$\delta^{15}\text{N}$	3.48 \pm 0.04	3.51 \pm 0.05

Table 4 Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (expressed in ‰) in the healthy and degraded fringing reefs for the four studied species

	Healthy reef	Degraded reef
<i>Chaetodon lunulatus</i>		
$\delta^{13}\text{C}$	-14.63 ± 0.46	-14.82 ± 0.32
$\delta^{15}\text{N}$	7.58 ± 0.31	7.68 ± 0.45
N	12	12
<i>Chrysiptera rollandi</i>		
$\delta^{13}\text{C}$	-18.51 ± 0.27	-18.73 ± 0.33
$\delta^{15}\text{N}$	7.77 ± 0.36	7.80 ± 0.34
N	26	35
<i>Halichoeres melanurus</i>		
$\delta^{13}\text{C}$	-16.61 ± 0.57	-16.83 ± 0.89
$\delta^{15}\text{N}$	8.13 ± 0.24	7.97 ± 0.21
N	21	24
<i>Zebrasoma velifer</i>		
$\delta^{13}\text{C}$	-18.47 ± 0.51	-19.06 ± 0.65
$\delta^{15}\text{N}$	5.64 ± 0.20	5.69 ± 0.15
N	8	7

N is the number of fish per studied species and per reef

species were non-significant in most cases (Mann–Whitney U test, $p > 0.05$); only *C. rollandi* ($p = 0.024$) and *Z. velifer* ($p = 0.021$) presented significantly C-depleted values in the degraded reef, and *H. melanurus* ($p = 0.044$) revealed significantly N-depleted ratios in the degraded reef. Among fish, *Chaetodon lunulatus* showed the highest mean $\delta^{13}\text{C}$ values and *Chrysiptera rollandi* and *Zebrasoma velifer* the lowest (Table 4). Finally, *Z. veliferum* displayed the lowest $\delta^{15}\text{N}$ mean value, whereas *Halichoeres melanurus* presented the highest.

Metrics and patterns of isotopic niches

H. melanurus and *Z. velifer*, respectively, showed the highest and lowest TA in both reefs (Table 5). The differences between reefs were relatively high for *C. lunulatus* and *Z. velifer* (although the latter species should be cautiously considered due to a low N), whereas *C. rollandi* and *H. melanurus* revealed similar values. Trends in SEAc slightly differed from TA results and differences were generally smoothed because the sample size was taken into account. For instance, the highest and lowest values of SEAc were obtained for *C. lunulatus* and *C. rollandi*, respectively, in the healthy reef and *H. melanurus* and *C. lunulatus* in the degraded reef (Table 5). *C. lunulatus* and *Z. velifer* displayed contrasted values of SEAc between both reefs, with a ~ two-fold higher value in the healthy reef, whereas the opposite trend was found for *H. melanurus*. All species displayed moderate to low SEAc/TA ratio values (i.e., SEAc 2–3 times lower than TA), except *Z. velifer* (especially in the degraded

Table 5 Corrected standard ellipses (SEAc, in ‰²), total areas (TA, in ‰²) and ratio SEAc/TA calculated for the four studied species in the healthy and degraded fringing reefs

	Healthy reef	Degraded reef
<i>Chaetodon lunulatus</i>		
SEAc	0.464	0.250
TA	1.005	0.555
SEAc/TA	0.461	0.450
<i>Chrysiptera rollandi</i>		
SEAc	0.311	0.332
TA	0.881	0.991
SEAc/TA	0.353	0.335
<i>Halichoeres melanurus</i>		
SEAc	0.435	0.621
TA	1.288	1.395
SEAc/TA	0.338	0.445
<i>Zebrasoma velifer</i>		
SEAc	0.387	0.197
TA	0.566	0.209
SEAc/TA	0.684	0.942

reef) indicating a relatively important individual variability in their $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$. SEAc/TA ratios remained close on both reefs for *C. lunulatus* and *C. rollandi* indicating a similar individual variability, whereas an increase was observed for *H. melanurus* and *Z. velifer* in the degraded reef indicating a trend towards a decrease in individual variability.

C. lunulatus' TA and SEAc were clearly higher in the healthy reef (Table 5; Fig. 2), but a lower $\delta^{15}\text{N}$ and more negative $\delta^{13}\text{C}$ was also apparent. This latter pattern also appeared for *C. rollandi*, although TA and SEAc displayed similar expansion (Fig. 2). For *H. melanurus*, a trend to the extension of TA and SEAc towards more negative $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values in the degraded reef was shown (Fig. 2). *Z. velifer* seemed to have more negative $\delta^{13}\text{C}$ values on the degraded reef even if the modest number of individuals prevented any robust description.

SEAb values for each species and both reefs were globally close to those of TA and SEAc (Fig. 3), indicating the relevance of TA and SEAc metrics in our study. The only exception was *Z. velifer* in the degraded reef, but relatively large credibility intervals are likely linked to low numbers of individuals.

Overlap in fish isotopic niches

The overlap of *Chaetodon lunulatus* isotopic niche between both reefs is 18%; a percentage representing 46% of the degraded reef SEAc area and 25% of the healthy reef (Table 6). A similar overlap was obtained for *Chrysiptera rollandi*, but with an equal SEAc area overlap of ~ 30% in

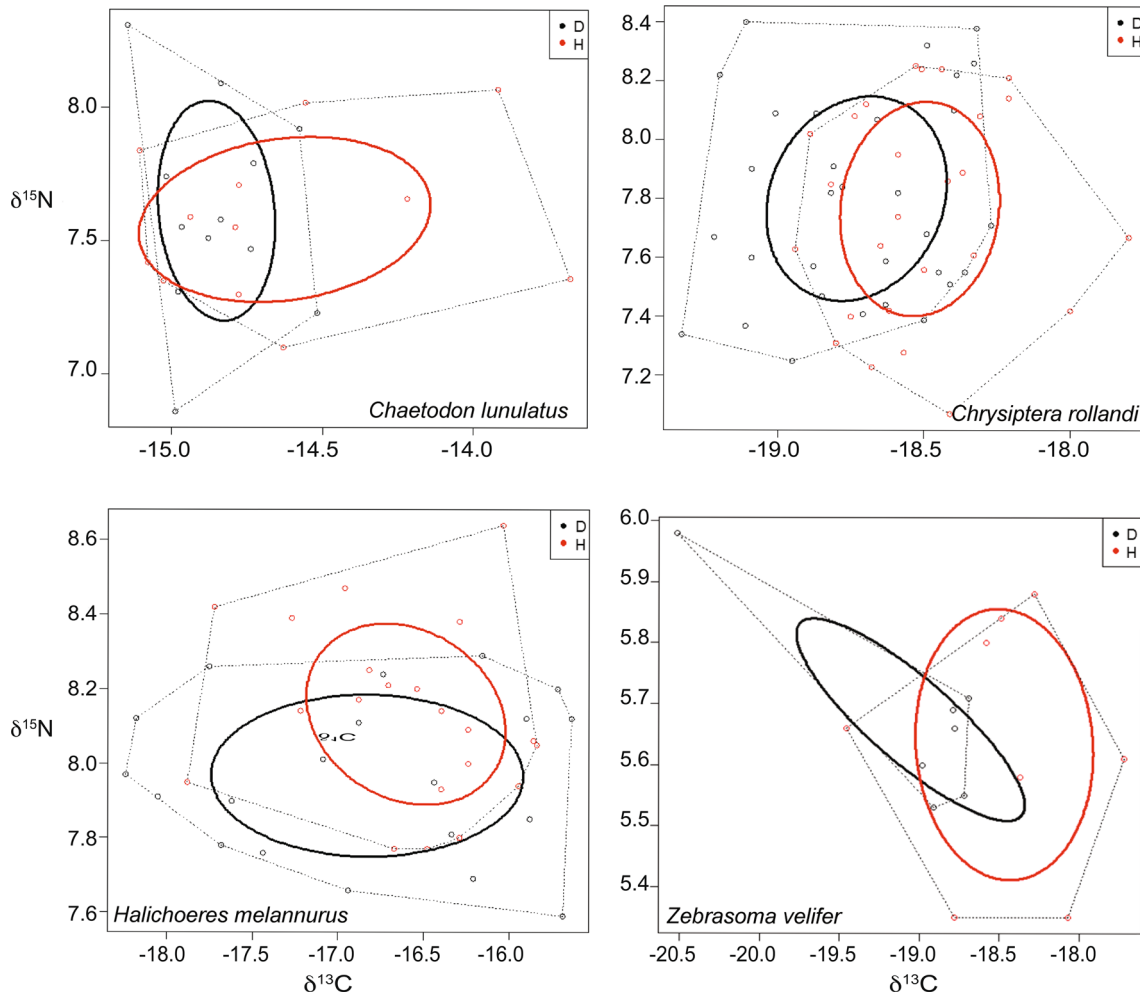


Fig. 2 Total area (TA, dotted lines) and corrected standard ellipse area (SEAc, solid lines) for *Chaetodon lunulatus* (a), *Chrysiptera rollandi* (b), *Halichoeres melanurus* (c) and *Zebrasoma velifer* (d).

Black ellipses represent the degraded reef (labelled D) and the red ellipses represent the healthy reef (labelled H)

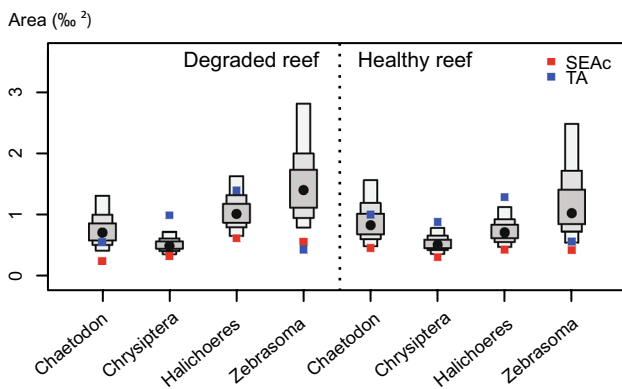


Fig. 3 Boxplots of the Bayesian standard ellipse area (SEAb, in %²) for the four studied species in the degraded and healthy reefs. Shaded boxes represent, from light to dark grey, 50, 75, and 95% Bayesian credibility intervals. Black dots represent the modes of Bayesian distribution, whereas blue and red dots represent TA and SEAc, respectively

Table 6 Overlapping percentages of different species' SEAc between reefs: indicated values represent the percentage of overlap between both reefs, and the percentage of this overlap area compared to the SEAc area of each reef

	<i>Chaetodon lunulatus</i>	<i>Chrysiptera rollandi</i>	<i>Halichoeres melanurus</i>	<i>Zebrasoma velifer</i>
Overlap	0.18	0.17	0.25	0.09
Overlap in degraded	0.46	0.31	0.43	0.38
Overlap in healthy	0.25	0.33	0.62	0.20
Probability SEAb degraded vs. healthy	0.67	0.58	0.13	0.39

The probability that the SEAb of fish species are smaller in the degraded reef than in the healthy reef (based on 10⁴ iterations) is also indicated

both reefs. *Halichoeres melanurus* was different, with the highest overlap found (25%) and an opposite trend for overlapping between reefs, i.e., a lower percentage overlap in the degraded reef (Table 6). The last species, *Z. velifer*, has shown the lowest overlap between isotopic niches from both reefs. Overall, these overlap differences illustrate a clear displacement of the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-dimensional space from one reef to the other. It also clearly indicates a low to moderate (i.e., 9–25%) overlap of the isotopic niche of each species between reef types and thus reinforces the previous pattern of isotopic niche displacements towards more $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ depleted isotopic niches from a healthy to a degraded reef (Fig. 2).

Finally, *Chaetodon lunulatus* and *C. rollandi* revealed a high probability of having lower SEAb in the degraded reef than in the healthy reef ($p = 0.67$ and 0.58 , respectively, Table 6). The two other species, *H. melanurus* and *Z. velifer* displayed opposite results ($p = 0.13$ and 0.39 , respectively).

Discussion

Coral reefs are exposed to a diversity of local and global pressures, which are leading to substantial benthic degradation (McClanahan et al. 2011; De'ath et al. 2012). Here, we have shown how all four species of fishes, with contrasted feeding strategies (an obligate corallivore, a micro-zooplanktivore, an invertivore and a herbivore), changed in feeding habits according to benthic condition on reefs; some conforming to expectations while others differed. Clearly, the influence of reef degradation on coral reef fishes will be variable, and the capacity for species to alter diets will dictate their responses.

The responses to habitat degradation of the four studied fishes were different in terms of mean isotopic values and/or isotopic niche size, and only partly fit with our initial expectations. All species displayed a modest overlap in their isotopic niche size (25% at best, for *H. melanurus*), strongly supporting a clear change in feeding characteristics between both reefs. Thus, the discrepancies in isotopic niches between both reef types likely reflect a potential for feeding plasticity enabling the four studied species to fit in contrasted habitat constrains.

Chaetodon lunulatus, a species usually considered as having a highly specialized diet on corals (Harmelin-Vivien and Bouchon-Navaro 1983; Harmelin-Vivien 1989; Pratchett et al. 2004; Pratchett 2005), showed some capacity for feeding versatility. Despite similar mean isotopic ratios on both reefs, the isotopic niche size of the obligate corallivore in the degraded reef was substantially smaller, with displacement towards more C-depleted values. However, it should be borne in mind that the degraded reef still had 30% live coral cover, so the findings may be quite different in an even more

degraded habitat. There is likely a theoretical minimal value of live coral cover or threshold of the isotopic niche size for *C. lunulatus* under which feeding plasticity is not enough to permit maintenance in a severely degraded reef. The fact that this species had a very narrow isotopic niche size in the degraded reef, associated with the highest probability of having lower SEAb in the degraded reef than in the healthy reef (Table 6), support the hypothesis that reef degradation will decrease feeding habits for that species and is a strong signal of impact of change in benthic conditions. That might thus reflect increasing difficulties in *C. lunulatus* condition resulting from a combination of its feeding specialization with degraded habitat characteristics.

As expected, the micro-zooplanktivore *Chrysiptera rollandi* may have a similar feeding plasticity on both reefs as their isotopic niche size did not drastically vary, despite a decrease in mean $\delta^{13}\text{C}$ values in the degraded reef. Another non-exclusive hypothesis is that this relative niche stability may reflect their capacity to maintain a similar diet in a more or less wide range of resource conditions and habitat characteristics. Although mostly based on copepods, *C. rollandi* demonstrated a relatively eclectic but consistent diet on both reefs (Table S1), and therefore, unchanged feeding plasticity. Strongly site-attached (Lieske and Myers 1994), *C. rollandi* remains globally indifferent to coral degradation for the amplitude measured here and despite a decrease of structural complexity and number of available holes as potential refuges.

The herbivore *Zebrasoma velifer*, a species for which a larger isotopic niche was expected in poorer reef habitat conditions, had more C-depleted values and surprisingly a lower niche size (SEAc) in the degraded reef. Species living in large schools such as many herbivorous fish may display higher isotopic niche sizes than non-schooling species because this behavioural trait enables them to easily reach their feeding resources. *Z. velifer* only rarely forms large schools and is most often encountered in small groups or even solitary, an ecological trait suggesting that *Z. velifer* has a smaller foraging influence than other aggregating herbivorous species (Lawson et al. 1999). It is thus unclear why this species displayed a narrower isotopic niche size in the degraded reef despite environmental conditions that are a priori more favourable. Although more individuals would permit a more robust statistical comparison, complementary work should be done on algal community structures on both reefs to investigate if the most consumed algae are abundant on the degraded reef. Alternatively, we cannot exclude that the density of the preferred algae for that species decreased on the degraded reef despite higher overall algal cover.

Finally, the invertivore *Halichoeres melanurus* demonstrated three interesting changes on the degraded reef; an increase in mean density, a decrease in mean $\delta^{15}\text{N}$ values (lower trophic level) and, mainly, an increase in isotopic

niche size. Overall, these results suggest that *H. melanurus* may feed successfully on degraded habitats, likely benefiting from excess algal resources and associated small benthic invertebrates, despite lower habitat complexity (Kramer et al. 2012). In such conditions, *H. melanurus* may express its feeding plasticity towards a larger diversity of prey-types supporting the population and not only numerous small benthic prey. We could also assume that these various prey rely on more numerous C-depleted OM sources and/or on lower trophic level prey, explaining, respectively, the niche displacement towards more negative $\delta^{13}\text{C}$ values and a decrease in mean trophic levels for *H. melanurus* on the degraded reef. Another possible explanation might be related to a shift within the invertebrate prey from a diet at least partially influenced by planktonic sources, such as filter feeding bivalves on the healthy reef; to one more dominated by the benthic algae cover with a larger makeup of isopods. Such a shift following reef degradation has been demonstrated in meso-predatory reef fish on the Great Barrier Reef (Hempson et al. 2017a, b). However, this hypothesis needs to be further explored as we do not have data to support it in our study.

Without any difference between the healthy and degraded reefs, algal turf and SOM displayed very similar isotopic values to ratios obtained in neighbouring New Caledonian reefs (Briand et al. 2015). This is an important point, suggesting that any obtained difference in fish $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, niche size or niche displacement may be independent from sources of OM (at least those taken into account here), and rather depend on prey item consumption. This hypothesis is partly supported by the broad diet data obtained for *H. melanurus* and *C. rollandi* for example (Table S1). In regard to the significant decreases in $\delta^{13}\text{C}$ values for *C. rollandi* and *Z. velifer* in the degraded reef, the existence of an OM pathway ending at these fish and at least partly based on other non-sampled OM sources characterized by low $\delta^{13}\text{C}$ values (e.g., phytoplankton, particulate organic matter or macroalgae) cannot be excluded.

Substantial modifications in habitat characteristics between the two reefs might explain the variation in density obtained for *C. lunulatus*, which strongly depends on living coral (Harmelin-Vivien 1989; Pratchett et al. 2004). Surprisingly, the herbivorous *Z. velifer* did not display any significant difference in density, despite a priori more favourable conditions for algal coverage in the degraded reef. Overall, and irrespective of fish densities, our results clearly highlighted that the four studied species do better in one or other of the reef conditions, suggesting that they either encounter different types of food resources or similar food resources but in different quantities. From a broad assessment of their diet (i.e., stomach content, Table S1), *Chrysiptera rollandi* and *Halichoeres melanurus* seem to consume similar prey in both reefs, in more or less comparable proportions for

major items. However, both species showed some variations in prey consumption between reefs, such as for calanoid copepods or isopods. Strong inter-individual variability is also suggested by high SD values.

Futuyma and Moreno (1988) suggested that trophic niche size and specialization were the results of complex interactions between biological traits and local constraints, generating difficulties to disentangle the respective effects of each characteristic. Our findings strongly suggest that there is an interaction between food availability and trophic niche size of coral reef fish, but several other biological traits or environmental characteristics remain to be investigated, such as individual size and reef location at different spatial scales for instance. Balance between different traits and characteristics may lead to different responses (Bolnick et al. 2010) and thus influence feeding plasticity in response to changes of resource availability. To better assess the role of feeding plasticity during reef degradation, it is thus necessary to undertake further research on more numerous species with differing life-spans, including a wide size range, and various ecological strategies. Despite this, the data we present here are a powerful indication that feeding plasticity related to habitat degradation may be possible in a diverse range of reef fishes. Our findings also suggest that certain species guilds would probably adapt to changes linked to habitat degradation (micro-zooplanktivores and invertivores), whereas some other would be more vulnerable, such as obligatory corallivores and even some herbivores.

Acknowledgements Many thanks to Antoine Teitelbaum for his help in catching fish, to Clément Pigot for his help in preparing samples, to Gaël Guillou for running stable isotopic analyses, to the Province Sud of New Caledonia for permitting the sampling (permit no.: 3238-2014/ARR/DENV), to the University of New Caledonia for funding the field-trip of Nicholas Graham. We thank the anonymous referees for their constructive comments that allowed us to improve the article.

Compliance with ethical standards

Funding This research received no specific Grant from any funding agency, commercial or non-profit sectors.

Conflict of interest All authors declare that they have no conflict of interest.

Ethical statement All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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