

Coral reef degradation alters the isotopic niche of reef fishes

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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 melannurus* (invertivore) and *Zebrasoma 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. melannurus* 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 $\delta^{13}\text{C}$

35 values but no difference in niche size. Our findings suggest there may be feeding
36 plasticity to maintain a similar diet despite contrasting habitat characteristics, with
37 different amplitude depending on species. Such findings suggest that certain species
38 guilds would probably adapt to changes linked to habitat degradation.

39

40 **Key-words**

41 Bi-dimensional space, feeding strategies, trophic niche, stable isotopes, carbon and
42 nitrogen, New Caledonia

43

44

45 **Introduction**

46

47 Coral reefs are threatened by several natural and human-driven disturbances.
48 These disturbances differ in scale and frequency, and are causing substantial economic
49 and ecological changes (Hoegh-Guldberg 1999; Hughes et al. 2003; Wilson et al. 2006,
50 2010; Graham et al. 2008, 2014; Mora et al. 2011; Riegl and Purkis 2015; Cinner et al.
51 2016). The long-term persistence of coral reefs is even at risk in the face of global
52 climate change (Roff et al. 2014; Hoey et al. 2016). As pointed out by Sale et al. (2014),
53 *“ever-expanding human impacts are continuing a substantial decline in the capacity of*
54 *coastal marine ecosystems to provide crucial goods and services”*. It is therefore critical
55 and urgent to better assess how and through what mechanisms species or functional
56 groups can adapt and cope with changing environmental conditions (Graham et al. 2013,
57 2015; Mumby et al. 2016).

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

66 Stable isotopes are a powerful tool to investigate feeding plasticity of organisms
67 (Wyatt et al. 2012; Letourneur et al. 2013; McMahon et al. 2015; Briand et al. 2015,
68 2016); both carbon and nitrogen ratios have the great advantage of providing
69 information on time-integrated assimilated food (Fry 1988; Vander Zanden and
70 Rasmussen 1999). $\delta^{13}\text{C}$ can provide insights on the origin of the ingested organic

71 material (De Niro and Epstein 1978; Wada et al. 1991; Sweeting et al. 2007a), whereas
72 $\delta^{15}\text{N}$ can be used to define the trophic level of organisms (Minagawa and Wada 1984;
73 Post 2002; Sweeting et al. 2007b). One way to use the bi-dimensional space constituted
74 by both ratios is to quantify the isotopic niche size; the intra-specific variation in $\delta^{15}\text{N}$
75 and $\delta^{13}\text{C}$ values that captures feeding plasticity for a given species in a given habitat
76 (Newsome et al. 2007).

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

93

94 **Material and methods**

95

96 ***Conceptual framework***

97

98 This work derives from the ecological niche theory (Elton 1927; Odum 1959).
99 Compared to a given presumably "normal" state, an ecological niche's size/volume can
100 remain stable (no apparent change), decrease or increase after one or several events.
101 For instance, poor habitat quality, high intra- or inter-specific competition, or a high
102 predation rate might generate a decrease in niche size/volume (Figure 1a). Conversely,
103 good juvenile recruitment, high nutrient quality, or low predation or competition rates
104 might generate an increase (Figure 1b). The dimensions of the ecological niche may
105 concern major ecological factors like habitat and feeding preferences for instance (e.g.
106 two-dimensional biplots).

107 The isotopic niche concept is, to some degree, a simple transposition of the
108 ecological niche concept into two particular dimensions (Newsome et al. 2007), giving
109 information on a consumer position within a trophic network. Coral degradation may
110 lead to four potential responses from the species studied:

111 (1) the absence of any perceptible change, i.e. the isotopic niche size remains
112 similar (the dark full line in figure 1c does not move) and the mean C and N isotopic
113 values remain unchanged;

114 (2) an increase or decrease of the isotopic niche size but without any significant
115 change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ mean values (the small and large dotted lines in figure 1c);

116 (3) significant changes in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ mean values without any increase or
117 decrease in isotopic niche size (the white or black arrows in figure 1d);

118 (4) an increase or decrease of the isotopic niche size associated with significant
119 changes in $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ mean values (the grey arrows in figure 1d).

120

121 ***Study site and sampling procedures***

122

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

133 Habitat characteristics were assessed on four 30m transects at each site
134 following the method of Wilson et al. (2007). Percentage hard living coral cover, dead
135 coral, rubble, carbonate pavement and sand were estimated using point intercepts every
136 50cm along the transect tape. Structural complexity was estimated visually on a 6 point
137 scale (where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread
138 relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves, 5 =
139 exceptionally complex with numerous caves and overhangs). The number of holes <10
140 cm were estimated along a 10m² section of each transect. The abundance of the fish
141 species studied was estimated along the same transects using a 2m wide belt (i.e. 60m²,
142 x four replicates).

143 Fish were caught with a small fishing net adapted to the capture of aquarium fish.
144 In order to avoid a plausible size effect on stable isotopic signatures, only individuals
145 belonging to restricted size-classes were targeted, i.e. were caught *Chaetodon lunulatus*
146 individuals of 7-10 cm (total length, TL) (N= 24 fish), *Chysiptera rollandi* individuals of
147 4-5 cm TL (N= 61), *Halichoeres melannurus* individuals of 4-6 cm TL (N= 45), and
148 *Zebrasoma velifer* individuals of 6-12 cm TL (N= 15). Since both reefs are separated by a
149 very shallow sandy plain that is partly emerged at low tide, we therefore assumed that
150 fish movements between reefs were negligible, especially because these species are site-
151 attached or sedentary and usually have very low to moderate home range.

152 It is necessary to ensure that potential differences in fish population isotopic
153 signatures are not linked to fluctuations in organic matter (hereafter OM) source
154 isotopic values (i.e. the “baseline”), which may present significant differences even at
155 small spatial scales (Briand et al. 2015). Three replicates of algal turf and surface
156 sediments (for sedimentary organic matter, hereafter SOM) were sampled, as both
157 sources are among the most important potential OM sources on coral reefs (Vermeij et
158 al. 2010; Briand et al. 2015).

159

160 ***Stable isotope samples and analyses***

161

162 Tissues providing the most reliable isotopic values were sampled and
163 immediately frozen at -20 °C for subsequent analyses: a piece of thallus for cleaned algal
164 turf and dorsal white muscle for all fish specimens (Pinnegar and Polunin, 1999).

165 Carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analysed for all samples.
166 Sediment, algal turf and fish muscle samples were dried, then ground to a fine powder
167 with a porcelain mortar and pestle using standard protocols. Samples were weighed and
168 approximately 1 mg of powder was encapsulated for vegetal/animal tissues and 15-20
169 mg for SOM. Samples were analysed without any prior treatment, except SOM for which
170 two subsamples were analysed. The first, treated for $\delta^{13}\text{C}$ analysis, required an
171 acidification step (see details in Letourneur et al. 2013) as carbonates present higher
172 $\delta^{13}\text{C}$ than organic carbon (De Niro and Epstein 1978). The second, tested for $\delta^{15}\text{N}$, was
173 not acidified to limit alteration of nitrogen isotopes (Pinnegar and Polunin 1999).

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

177
$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$$

178 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
179 proportion of heavy to light isotope in the sample. The international standard references
180 are Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen. Measurement
181 precision, estimated using standards included in the analyses, was of 0.1 ‰ for $\delta^{13}\text{C}$ and
182 0.15 ‰ for $\delta^{15}\text{N}$.

183

184 ***Data processing***

185

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

189 Core isotopic niche area can be revealed by fitting standard ellipses to the
190 isotopic data in the bi-dimensional plot of $\delta^{13}\text{C}/\delta^{15}\text{N}$, as described in Jackson et al.
191 (2011). The standard ellipse area of a set of bivariate data is calculated from the
192 variance and covariance of x and y data and is expected to be less sensitive to sample
193 size than former methods, which enable robust estimation of the isotopic niche.

194 Layman metrics, based on the elaboration of convex hulls in the bi-dimensional
195 $\delta^{13}\text{C}/\delta^{15}\text{N}$ plot, were developed with the purpose to describe with precision the isotopic
196 niche of a species or assemblage of several species (Layman et al. 2007; Cucherousset
197 and Villeger 2015). Finally and for each species, the following metrics were calculated
198 with the SIBER package (Jackson et al. 2011) to compare each species between the two
199 reef sites, i.e. healthy vs. degraded:

200 (i) TA- Total Area of the ellipse; measuring the whole trophic diversity of
201 individuals of a given species in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ biplot;

202 (ii) SEAc- Corrected Standard Ellipse Area; representing the averaged isotopic
203 niche of the group of individuals, but including a correction factor that takes into
204 account the sample size and is thus more robust than non-corrected standard ellipse
205 area (in particular for samples with small number of individuals);

206 (iii) SEAb- Bayesian Standard Ellipse Area; the Bayesian assessment of the
207 standard ellipse calculated with SEAc, performed with 10^4 iterations, allows to minimize
208 uncertainties linked to SEAc calculated with small sample size. Values close to TA and
209 SEAc are good indicators of the relevance of these metrics.

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

213

214 **Results**

215

216 ***Habitat and fish population parameters***

217

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

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

227

228 ***Organic matter sources and fish isotopic ratios***

229

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

234 For each species, $\delta^{13}\text{C}$ values were slightly higher in the healthy reef, and the
235 opposite was found for $\delta^{15}\text{N}$, except for *H. melannurus* (Table 4). Differences in mean
236 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between healthy and degraded reefs for each species were non-
237 significant in most cases (Mann-Whitney U test, $p > 0.05$); only *C. rollandi* ($p = 0.024$) and
238 *Z. velifer* ($p = 0.021$) presented significantly C-depleted values in the degraded reef, and
239 *H. melannurus* ($p = 0.044$) revealed significantly N-depleted ratios in the degraded reef.
240 Among fish, *Chaetodon lunulatus* showed the highest mean $\delta^{13}\text{C}$ values and *Chrysipetra*
241 *rollandi* and *Zebrasoma velifer* the lowest (Table 4). Finally, *Z. veliferum* displayed the
242 lowest $\delta^{15}\text{N}$ mean value whereas *Halichoeres melannurus* presented the highest.

243

244 ***Metrics and patterns of isotopic niches***

245

246 *H. melannurus* and *Z. velifer* respectively showed the highest and lowest TA in
247 both reefs (Table 5). The differences between reefs were relatively high for *C. lunulatus*

248 and *Z. velifer* (although the latter species should be cautiously considered due to a low
249 N) whereas *C. rollandi* and *H. melannurus* revealed similar values. Trends in SEAc
250 slightly differed from TA results and differences were generally smoothed because the
251 sample size was taken into account. For instance, the highest and lowest values of SEAc
252 were obtained for *C. lunulatus* and *C. rollandi* respectively in the healthy reef and *H.*
253 *melannurus* and *C. lunulatus* in the degraded reef (Table 5). *C. lunulatus* and *Z. velifer*
254 displayed contrasted values of SEAc between both reefs, with a ~2-fold higher value in
255 the healthy reef, whereas the opposite trend was found for *H. melannurus*. All species
256 displayed moderate to low SEAc/TA ratio values (i.e. SEAc 2 to 3 times lower than TA),
257 except *Z. velifer* (especially in the degraded reef) indicating a relatively important
258 individual variability in their $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$. SEAc/TA ratios remained close on both
259 reefs for *C. lunulatus* and *C. rollandi* indicating a similar individual variability, whereas
260 an increase was observed for *H. melannurus* and *Z. velifer* in the degraded reef indicating
261 a trend towards a decrease in individual variability.

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

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

273

274 **Overlap in fish isotopic niches**

275

276 The overlap of *Chaetodon lunulatus* isotopic niche between both reefs is 18%; a
277 percentage representing 46% of the degraded reef SEAc area and 25% of the healthy
278 reef (Table 6). A similar overlap was obtained for *Chrysiptera rollandi*, but with an equal
279 SEAc area overlap of ~30% in both reefs. *Halichoeres melannurus* was different, with the
280 highest overlap found (25%) and an opposite trend for overlapping between reefs, i.e. a
281 lower percentage overlap in the degraded reef (Table 6). The last species, *Z. velifer*, has
282 shown the lowest overlap between isotopic niches from both reefs. Overall, these
283 overlap differences illustrate a clear displacement of the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-dimensional

284 space from one reef to the other. It also clearly indicates a low to moderate (i.e. 9 to
285 25%) overlap of the isotopic niche of each species between reef types and thus
286 reinforces the previous pattern of isotopic niche displacements towards more $\delta^{13}\text{C}$
287 and/or $\delta^{15}\text{N}$ depleted isotopic niches from a healthy to a degraded reef (Figure 2).

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

292

293 **Discussion**

294

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

303 The responses to habitat degradation of the four studied fishes were different in
304 terms of mean isotopic values and/or isotopic niche size, and only partly fit with our
305 initial expectations. All species displayed a modest overlap in their isotopic niche size
306 (25% at best, for *H. melannurus*), strongly supporting a clear change in feeding
307 characteristics between both reefs. Thus, the discrepancies in isotopic niches between
308 both reef types likely reflect a potential for feeding plasticity enabling the four studied
309 species to fit in contrasted habitat constrains.

310 *Chaetodon lunulatus*, a species usually considered as having a highly specialized
311 diet on corals (Harmelin-Vivien and Bouchon Navaro 1983; Harmelin-Vivien 1989;
312 Pratchett et al. 2004), showed some capacity for feeding versatility. Despite similar
313 mean isotopic ratios on both reefs, the isotopic niche size of the obligate corallivore in
314 the degraded reef was substantially smaller, with displacement towards more C-
315 depleted values. However, it should be borne in mind that the degraded reef still had
316 30% live coral cover, so the findings may be quite different in an even more degraded
317 habitat. There is likely a theoretical minimal value of live coral cover or threshold of the
318 isotopic niche size for *C. lunulatus* under which feeding plasticity is not enough to permit
319 maintenance in a severely degraded reef. The fact that this species had a very narrow

320 isotopic niche size in the degraded reef, associated with the highest probability of having
321 lower SEAb in the degraded reef than in the healthy reef (Table 6), might thus reflect
322 increasing difficulties in its condition resulting from a combination of its feeding
323 specialization with degraded habitat characteristics.

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

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

349 Finally, the invertivore *Halichoeres melannurus* demonstrated 3 interesting
350 changes on the degraded reef; an increase in mean density, a decrease in mean $\delta^{15}\text{N}$
351 values (lower trophic level) and, mainly, an increase in isotopic niche size. Overall, these
352 results suggest that *H. melannurus* may feed successfully on degraded habitats, likely
353 benefiting from excess algal resources and associated small benthic invertebrates,
354 despite lower habitat complexity. In such conditions, *H. melannurus* may express its
355 feeding plasticity towards a larger diversity of prey-types supporting the population and

356 not only numerous small benthic prey. We could also assume that these various prey
357 rely on more numerous C-depleted OM sources and/or on lower trophic level prey,
358 explaining respectively the niche displacement towards more negative $\delta^{13}\text{C}$ values and a
359 decrease in mean trophic levels for *H. melannurus* on the degraded reef. Another
360 possible explanation might be related to a shift within the invertebrate prey from a diet
361 at least partially influenced by planktonic sources, such as filter feeding bivalves on the
362 healthy reef; to one more dominated by the benthic algae cover with a larger makeup of
363 isopods. Such a shift following reef degradation has been demonstrated in meso-
364 predatory reef fish on the Great Barrier Reef (Hempson et al. 2017). However, this
365 hypothesis needs to be further explored as we do not have data to support it in our
366 study.

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

378 Substantial modifications in habitat characteristics between the two reefs might
379 explain the variation in density obtained for *C. lunulatus*, which strongly depends on
380 living coral (Harmelin-Vivien 1989; Pratchett et al. 2004). Surprisingly, the herbivorous
381 *Z. velifer* did not display any significant difference in density, despite *a priori* more
382 favorable conditions for algal coverage in the degraded reef. Overall, and irrespective of
383 fish densities, our results most clearly highlighted that the four studied species do better
384 in one or other of the reef conditions, suggesting that they either encounter different
385 types of food resources or similar food resources but in different quantities. From a
386 broad assessment of their diet (i.e. stomach content, Table S1), *Chrysiptera rollandi* and
387 *Halichoeres melannurus* seem to consume similar prey in both reefs, in more or less
388 comparable proportions for major items. However, both species showed some
389 variations in prey consumption between reefs, such as for calanoid copepods or isopods.
390 Strong inter-individual variability is also suggested by high SD values.

391 Futuyma and Moreno (1998) suggested that trophic niche size and specialization
392 were the results of complex interactions between biological traits and local constraints,
393 generating difficulties to disentangle the respective effects of each characteristic. Our
394 findings strongly suggest that there is an interaction between food availability and
395 trophic niche size of coral reef fish, but several other biological traits or environmental
396 characteristics remain to be investigated, such as individual size and reef location at
397 different spatial scales for instance. Balance between different traits and characteristics
398 may lead to different responses (Bolnick et al. 2010) and thus influence feeding
399 plasticity in response to changes of resource availability. To better assess the role of
400 feeding plasticity during reef degradation, it is thus necessary to undertake further
401 research on more numerous species with differing life-spans, including a wide size-
402 range, and various ecological strategies. Despite this, the data we present here are a
403 powerful indication that feeding plasticity related to habitat degradation may be
404 possible in a diverse range of reef fishes.

405

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413

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419

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563 **Figures legends**

564

565 Figure 1: The ecological niche theory; from a given ecological niche in a “normal” state
 566 (dark line, in both A and B panels), a species disturbed by an event may respond with a
 567 decrease of its niche size if the event has a negative impact (a; small dotted line), or with
 568 an increase of its niche size if event has a positive impact (b; large dotted line). (c):
 569 Transposition of the possible variations of the ecological niche size to the isotopic niche
 570 concept. Here, potential changes concern niche size, not changes in mean values of $\delta^{15}\text{N}$
 571 and/or $\delta^{13}\text{C}$. (d): The isotopic niche concept; from an initial isotopic niche (central
 572 position, dark line). Three main possibilities can be drawn: (1) an increase or a decrease
 573 of $\delta^{15}\text{N}$ values without change in mean $\delta^{13}\text{C}$ values (black arrows); (2) an increase or a
 574 decrease of $\delta^{13}\text{C}$ values without change in mean $\delta^{15}\text{N}$ values (white arrows); and (3) a
 575 combination of both (grey arrows). Note that for each case, the isotopic niche size can be
 576 stable (dark line), decrease (small dotted line) or increase (large dotted line).
 577

578 Figure 2: Total area (TA, dotted lines) and corrected standard ellipse area (SEAc, solid
 579 lines) for *Chaetodon lunulatus* (a), *Chrysiptera rollandi* (b), *Halichoeres melannurus* (c)
 580 and *Zebrasoma velifer* (d). Black ellipses represent the degraded reef (labeled D) and the
 581 red ellipses represent the healthy reef (labeled H).
 582

583 Figure 3: Boxplots of the Bayesian standard ellipse area (SEAb, in ‰^2) for the four
 584 studied species in the degraded and healthy reefs. Shaded boxes represent, from light to
 585 dark grey, 50%, 75%, and 95% Bayesian credibility intervals. Black dots represent the
 586 modes of Bayesian distribution, whereas blue and red dots represent TA and SEAc,
 587 respectively.
 588