

The use of specialisation indices to predict vulnerability of coral-feeding butterflyfishes to environmental change

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1 **Abstract**

2 In the absence of detailed assessments of extinction risk, ecological specialisation is often
3 used as a proxy of vulnerability to environmental disturbances and extinction risk. Numerous
4 indices can be used to estimate specialisation; however, the utility of these different indices to
5 predict vulnerability to future environmental change is unknown. Here we compare the
6 performance of specialisation indices using coral-feeding butterflyfishes as a model group.
7 Our aims were to (i) quantify the dietary preferences of 3 butterflyfish species across habitats
8 with differing levels of resource availability; (ii) investigate how estimates of dietary
9 specialisation vary with the use of different specialisation indices; (iii) determine which
10 specialisation indices best inform predictions of vulnerability to environmental change; and
11 (iv) assess the utility of resource selection functions to inform predictions of vulnerability to
12 environmental change. The relative level of dietary specialisation estimated for all three
13 species varied when different specialisation indices were used, indicating that the choice of
14 index can have a considerable impact upon estimates of specialisation. Specialisation indices
15 that do not consider resource abundance may fail to distinguish species that primarily use
16 common resources from species that actively target resources disproportionately more than
17 they are available. Resource selection functions provided the greatest insights into the
18 potential response of species to changes in resource availability. Examination of resource
19 selection functions, in addition to specialisation indices, indicated that *Chaetodon trifascialis*
20 was the most specialised feeder, with highly conserved dietary preferences across all sites,
21 suggesting that this species is highly vulnerable to the impacts of climate-induced coral loss
22 on reefs. Our results indicate that vulnerability assessments based on some specialisation
23 indices may be misleading and the best estimates of dietary specialisation will be provided by
24 indices which incorporate resource availability measures, as well as assessing responses of
25 species to changes in resource availability.

26

27 **Keywords:** Chaetodontidae, dietary specialisation, ecological versatility, extinction risk,
28 resource selectivity.

29

30 **Introduction**

31 With limited funding and constrained resources, there is limited capacity to effectively protect
32 the increasing number of species at risk of extinction due to environmental change, habitat
33 loss and other anthropogenic disturbances (James et al.1999; Bottrill et al. 2008).

34 Identification of species or populations that face the greatest risk of extinction is therefore
35 necessary to prioritise conservation efforts. For many species, assessment of extinction risk or
36 vulnerability to predicted environmental change is costly, time-consuming and often
37 impractical. This has lead to widespread efforts to identify factors correlated with high
38 extinction risk or vulnerability across a wide range of taxa (e.g. McKinney 1997; Purvis et al.
39 2000a) that can be used in the absence of detailed assessments to predict which species are
40 likely to be most vulnerable to future environmental change (Purvis et al. 2000b; Dulvy, et al.
41 2003).

42

43 One factor often correlated with high extinction risk and vulnerability is ecological
44 specialisation (McKinney 1997; Fisher and Owens 2004; Colles et al. 2009). Ecological
45 specialists are thought to be more vulnerable to environmental changes and disproportionately
46 affected by changes in resource availability compared to generalist counterparts. Studies
47 across both terrestrial and aquatic organisms and a range of specialisation types support this
48 prediction (e.g. nesting cavity specialisation: Aitken and Martin 2008; habitat specialisation:
49 Kotze and O'Hara 2003; Munday 2004; Fisher et al. 2003; dietary specialisation: Charrette et
50 al. 2006; Graham 2007; dietary and habitat specialisation: Harcourt et al. 2002) suggesting

51 that in many cases ecological specialisation is a key driver of extinction risk. Thus,
52 identifying species that are ecological specialists can provide a useful starting point to predict
53 likely vulnerability and prioritise conservation actions. However, binary classifications of
54 species as either specialists or generalists can mask interspecific variation in ecological
55 versatility. This is of critical importance if specialisation is used as a vulnerability proxy as
56 grouping specialists into a single category assumes equal vulnerability among all specialists,
57 whereas recent research suggests that vulnerability increases with increasing specialisation
58 (Pratchett et al. 2008). Furthermore, the use of different specialisation indices can result in
59 different estimates of specialisation, even when the same data are considered (DeVictor et al.
60 2010). As biodiversity becomes increasingly threatened by the combined effects of climate
61 change and anthropogenic disturbances (Chapin et al. 2000; Thomas et al. 2004), there is a
62 need for greater focus on the way that specialisation is assessed and interpreted to estimate
63 vulnerability.

64
65 A variety of approaches are used to quantify ecological specialisation. The most basic
66 measures report the number of different resource categories which are used by a particular
67 species or population and conclude that a species is specialised if they are only using
68 resources from a few categories (e.g. Eeley and Foley 1999; Owens and Bennett 2000). More
69 commonly, specialisation is quantified using niche breadth indices such as the Simpsons
70 index or the Shannon-Wiener diversity index, which provide estimates of specialisation based
71 on richness and evenness of resource use (e.g. Munday 2004; Christensen and Kleindorfer
72 2009). While these types of analyses provide very general information about the degree of
73 specialisation, if resources are not equally available they can result in misleading estimates of
74 specialisation as species using resources in proportion to their availability may appear to have
75 narrower niches than more specialised species (Petraitis 1979). A number of studies have

76 addressed this issue through the use of specialisation indices such as Smiths niche breadth
77 measure or chi square log likelihood statistics that incorporate estimates of resource
78 availability (e.g. Gardiner and Jones 2005; Pratchett 2007). An alternative approach to
79 quantifying specialisation is to use measures of among-individual specialisation. In contrast to
80 specialisation indices which determine the niche of the population as a whole, among-
81 individual specialisation indices provide information about how variation in resource use is
82 spread between individuals within a population (e.g. Araujo and Gonzaga 2007; Araujo et al.
83 2008). These metrics compare the niche size of individuals within a population to the overall
84 population niche to estimate the degree that resource use differs between individuals (Bolnick
85 et al. 2003). Further information on ecological specialisation can also be provided by resource
86 selection functions. In contrast to specialisation indices, which provide a single measure of
87 specialisation integrated across all resources categories, resource selection functions calculate
88 selectivity for individual resource categories (e.g. Dirnwoeber and Herler 2007; Graham
89 2007). These functions determine whether an individual resource is used significantly more or
90 less than expected based on its availability (Manly et al. 2002), potentially enabling
91 predictions of how species may respond to changes in resource availability and allowing the
92 detection of key resources that may be critical to species persistence.

93

94 Here, we compare the performance of specialisation indices using coral-feeding
95 butterflyfishes as a model group. Using a single dataset, levels of dietary specialisation in
96 three species of coral-feeding butterflyfishes (Chaetodontidae) around Lizard Island in the
97 Northern Great Barrier Reef, Australia, are calculated using four different indices of
98 specialisation - a count of the total number of prey types consumed, the Shannon-Wiener
99 diversity index, a chi-square log likelihood index that incorporates a measure of resource
100 availability, and an among-individual specialisation index. We then calculate resource

101 selection functions to investigate how individual resources are used in relation to their
102 availability. To investigate how spatial variation in resource availability may affect estimates
103 of specialisation, we compared levels of dietary specialisation and resource selection
104 functions for each species across three sites in exposed front reef habitats and three sites in
105 sheltered back reef habitats that differ in the composition and abundance of scleractinian
106 corals which these fish feed on. Unlike many other organisms for which dietary composition
107 has to be inferred through stomach content analysis or scat analysis, the dietary composition
108 of butterflyfishes can be directly quantified via in-situ observations of feeding behaviour,
109 allowing highly accurate and detailed estimation of dietary specialisation. Furthermore, the
110 availability of dietary resources can be directly measured with ease at the same locations
111 where feeding is observed (Pratchett 2005). Previous research has shown that coral-feeding
112 butterflyfishes vary in their level of dietary specialisation (e.g. Pratchett 2005, 2007) and in
113 their response to changes in resource availability, with specialised butterflyfishes showing the
114 greatest declines in abundance following coral loss on reefs (e.g. Pratchett et al. 2004;
115 Pratchett et al. 2006; Graham 2007; Wilson et al. 2006). These characteristics make coral-
116 feeding butterflyfishes appropriate models for general principles of ecological specialisation.
117

118 Our aims were to (i) quantify the dietary preferences of 3 butterflyfish species across habitats
119 with differing levels of resource availability; (ii) investigate how estimates of dietary
120 specialisation vary with the use of different specialisation indices; (iii) determine which
121 specialisation indices best inform predictions of vulnerability to environmental change; and
122 (iv) assess the utility of resource selection functions to inform predictions of vulnerability to
123 environmental change. We expected that the level of dietary specialisation calculated for each
124 species would vary between exposed and sheltered sites that differed in the availability of

125 coral prey resources. We also expected estimates of specialisation to vary between the four
126 different specialisation indices for each species.

127

128 **Methods**

129 **STUDY SITES**

130 This study was carried out in November 2008 at Lizard Island (14°40'S, 145°27'E), in the
131 northern section of the Great Barrier Reef, Australia. Sampling was conducted across six sites
132 around the island, representative of exposed front reef and sheltered back reef habitats. Lizard
133 Head, Bird Islet, and South Island are directly exposed to the prevailing winds and represent
134 front reef habitats. Corner Beach, Osprey Islet and Vickies are relatively sheltered, large patch
135 reefs, representative of back reef habitats. Sampling was conducted in 2 – 5m depth along the
136 reef crest at front reef sites, and along the tops of reefs in 3 – 6m depth at back reef sites.

137

138 **RESOURCE AVAILABILITY**

139 Variation in the availability of coral prey was assessed using 50m point intercept transects. At
140 each site, five replicate transects were randomly placed along the reef crest or reef top in the
141 same area where feeding observations took place. For each transect, the substrate directly
142 beneath 50 sampling points was recorded to species level for corals, and to broad categories
143 for all other substrate types (e.g., reef substrate, macroalgae). Variation in coral cover and
144 community composition among sites was assessed using a nested MANOVA, which
145 compared the mean abundance of the most common corals (grouped into 9 taxa) between sites
146 nested within habitat types. Data were arc-sin transformed to satisfy assumptions of
147 multivariate homogeneity and normality. Pillai's trace statistic was used to determine the
148 significance of MANOVA results. Patterns in the coral composition at each site were
149 explored using a canonical discriminant analysis (CDA). To assist with interpretation of the

150 CDA, structural co-efficients of the 9 coral taxa were plotted as vectors to indicate the
151 predominant taxa at each site.

152

153 FEEDING OBSERVATIONS

154 Feeding observations were conducted for three common and widespread species of
155 butterflyfishes; *Chaetodon citrinellus*, *C. lunulatus*, and *C. trifascialis*. *Chaetodon citrinellus*
156 is a facultative corallivore, consuming hard corals in addition to soft corals, other macro-
157 invertebrates and non-coral prey items, while *C. trifascialis* and *C. lunulatus* are obligate
158 corallivores, both feeding almost exclusively on hard (scleractinian) corals (Pratchett 2005).
159 The dietary preferences and proportional use of different prey types for each species were
160 determined from field observations of feeding behaviour across the six sites. Individual
161 butterflyfishes were randomly selected and followed at a distance of 2 - 5 metres for a 3-
162 minute period. The total number of bites taken from each species of coral, other non-coral
163 macro-invertebrates, and non-coral substrata during each observation was recorded, following
164 Pratchett (2005). Twenty observations for each species were conducted on adult fish
165 throughout the day at each site. Every effort was made to ensure that individual fish were not
166 observed more than once. Variation in dietary composition of the three species was analysed
167 using a nested multivariate analysis of variance (MANOVA), which simultaneously compared
168 the mean number of bites taken from each of 15 major prey types at each site, nested within
169 habitat type. Pillai's trace statistic was used to determine the significance of MANOVA
170 results.

171

172 DIETARY SPECIALISATION AND SELECTIVITY

173 To investigate how different specialisation indices may vary in their estimates of
174 specialisation, dietary specialisation for each species at each site was assessed using four

175 different indices – a simple count of the total number of different prey types consumed, the
176 Shannon-Wiener diversity index (Zar 1999), the Chi square log likelihood statistic X_{L2}^2
177 (Manly et al. 2002) and an index of among-individual dietary specialisation (Araujo et al.
178 2008). For calculation of the Shannon-Wiener diversity index, the log likelihood statistic and
179 among-individual dietary overlap, all dietary items were grouped into 15 major prey
180 categories (listed in Table 3) and indices were calculated based on these categories. Dietary
181 selectivity for each species at each site was assessed using resource selection functions
182 (Manly et al. 2002), which were also calculated based on 15 major prey categories.

183

184 The Shannon-Wiener diversity index assesses specialisation based on the number and
185 evenness of different prey categories consumed and was calculated using the formula:

186

187 k

188 $H' = - \sum_{i=1}^k p_i \log p_i$ eqn 1.

189 $i=1$

190

191 where k is the number of prey categories and p_i is the proportional use of each prey category
192 (Zar 1999). Values of H' can range from zero to one, with lower values indicating increasing
193 specialisation.

194

195 The Chi square log-likelihood statistic X_{L2}^2 , was calculated following Manly et al. (2002). As
196 data were collected on selection of resource units by individual animals, but resource
197 availability was assessed at the population level, Model Design II with Sampling Protocol A
198 was used (Manly et al. 2002, eq 4.27). X_{L2}^2 was calculated using the formula:

199

200
$$n \quad I$$

201
$$X_{L2}^2 = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e \{ u_{ij} / E(u_{ij}) \} \quad \text{eqn 2.}$$

202

203

204 where u_{ij} is the proportional use of each prey type (i) by each individual (j) and $E(u_{ij})$ is the
 205 expected number of bites taken from prey type i by the jth individual if use is proportional to
 206 availability (Manly et al. 2002). The resulting value of X_{L2}^2 was compared to the chi-squared
 207 distribution with $n(I-1)$ degrees of freedom (where I is the total number of prey categories) to
 208 determine the significance of selectivity exhibited by each butterflyfish species at each site.
 209 Higher values of X_{L2}^2 indicate increasing specialisation.

210

211 Variation in dietary composition between individual butterflyfishes (among-individual
 212 specialisation) was assessed using an individual niche overlap network following Araujo et al.
 213 (2008). For each species at each site a niche overlap network was defined using the
 214 programme DIETA1.0 (Araujo et al. 2008) in which the nodes of the network represented
 215 individual fishes and the connections between nodes measured the degree of dietary overlap
 216 among pairs of individuals. Each connection was assigned a weight (w_{ij}) ranging from 0 for
 217 no overlap to 1 for total overlap ($0 < w_{ij} < 1$) as a measure of the pairwise dietary overlap
 218 between individuals i and j. Among-individual dietary variation (E) was then measured as the
 219 average density of all connections in the network, quantified as $E = 1 - \bar{w}_{ij}$. Low values of E
 220 indicate that there is little individual dietary specialisation, with E equal to 0 when all
 221 individuals have identical diets; high values of E indicate that individual dietary specialisation
 222 is high, with E equal to 1 when each individual uses a unique resource. If individual-level
 223 specialisation is high, then species-level specialisation is generally low. Monte Carlo
 224 bootstrap simulations were run using DIETA1.0 for each species at each site to test the null

225 hypothesis that any observed dietary variation arose from individuals sampling stochastically
226 from a shared distribution (Araujo et al. 2008). In these simulations each individual was
227 reassigned the same number bites that it was observed taking, drawn randomly from the
228 observed distribution of the population diet via multinomial sampling. 10,000 such
229 populations were simulated and among individual dietary variation, E , was recalculated for
230 each simulated population. The null hypothesis was rejected if the empirical (observed value)
231 E was higher than 95% of the E values of the simulated populations.

232

233 To investigate dietary selectivity and determine which prey corals were used significantly
234 more or less frequently than expected, resource selection functions were calculated for major
235 prey corals for each species at each site following Manly et al.'s (2002) Model Design II,
236 Sampling Protocol A, using the formula:

237

$$238 \quad n$$
$$239 \quad w_i = \left\{ \sum_{j=1}^n u_{ij} / p_i \right\} / n \quad \text{eqn 3.}$$
$$240 \quad j=1$$

241

242 where u_i is the proportional use of prey category i by the j th individual, n is the number of
243 individuals sampled and p_i is the proportional availability of each prey category within each
244 site. These functions allow for sampling of resource use at the individual level and resource
245 availability at the population level (Manly et al. 2002, eq 4.29). Bonferroni corrected 95%
246 confidence intervals were calculated around each selection function such that the use of a
247 particular prey was deemed to be significantly disproportionate to its availability if the 95%
248 confidence interval did not encompass one (Manly et al. 2002). Selection functions
249 significantly greater than one indicated selection (i.e. coral prey was consumed significantly

250 more than expected based on availability); selection functions significantly less than one
251 indicated avoidance (i.e. coral prey was consumed significantly less than expected based on
252 availability).

253

254 **Results**

255 CORAL COVER AND COMPOSITION

256 Cover and community composition of scleractinian corals varied among habitat types and
257 sites. Cover of scleractinian corals was highest at exposed sites, covering 51% (± 3.7) of hard
258 substrate at South Island, and 41% (± 3.0) and 40% (± 0.9) of hard substrate at Lizard Head
259 and Bird Islet respectively. At sheltered sites, cover of scleractinian corals was highest at
260 Osprey Islet (32% ± 3.5 of hard substrate) and Vickies (32% ± 4.5 of hard substrate), and
261 lowest at Corner Beach (29% ± 5.6 of hard substrate). Variation in coral community
262 composition was highly significant among habitats (MANOVA, Pillai's trace=14.1, df = 9,16,
263 $P < 0.001$) and sites (MANOVA, Pillai's trace=2.6, df = 36,76, $P < 0.001$). Exposed sites were
264 characterised by a high abundance of tabular and digitate *Acropora* corals, while sheltered
265 sites were dominated by soft corals (family Alcyonacea) (Fig. 1).

266

267 DIETARY COMPOSITION

268 *Chaetodon citrinellus* fed predominantly on hard corals at each site (taking between 39 to
269 75% of all bites from hard corals), but also supplemented its diet with small amounts of soft
270 corals, other non-coral macro invertebrates and bites on reef substrates (Table 1).

271 Consumption of hard corals was highest at exposed sites where hard corals were more
272 abundant. Both *C. lunulatus* and *C. trifascialis* fed almost exclusively on hard corals at all
273 sites. *Chaetodon lunulatus* took between 96 to 99% of all bites from hard corals, while *C.*
274 *trifascialis* took 100% of all bites from hard corals at all sites except Lizard Head (Table 1).

275 Dietary composition varied significantly (MANOVA, $P < 0.05$) for all three species between
276 habitats and sites (Table 2).

277

278 DIETARY SPECIALISATION AND SELECTIVITY

279 The number of prey types consumed was similar for *C. citrinellus* and *C. lunulatus* and both
280 species consumed a greater number of prey types at exposed sites compared to sheltered sites
281 (Fig. 2). *Chaetodon trifascialis* consumed almost the same number of prey types at both
282 sheltered and exposed sites and consumed fewer types than both *C. citrinellus* and *C.*
283 *lunulatus*. Dietary evenness (indicated by the Shannon Wiener index) was relatively high for
284 both *C. citrinellus* and *C. lunulatus*, but was low for *C. trifascialis* (Fig. 2). For all three
285 species, dietary evenness varied between sites. Evenness was higher at exposed sites for *C.*
286 *citrinellus*, comparable across all sites for *C. lunulatus* and higher at sheltered sites for *C.*
287 *trifascialis*.

288

289 Based on significant differences in the proportional consumption versus availability of
290 different coral prey, all three species showed highly significant dietary selectivity at each site
291 ($P < 0.001$ for all species, Table 3). Patterns of dietary selectivity indicated by the Chi square
292 log-likelihood statistic (X_{L2}^2) were different to patterns of dietary evenness indicated by the
293 Shannon Wiener index and levels of specialisation estimated using a count of total number of
294 prey categories consumed. *Chaetodon trifascialis* was the most selective, closely followed by
295 *C. lunulatus*, while *C. citrinellus* was the least selective. Selectivity was higher at sheltered
296 sites compared to exposed sites for all three species (Fig. 2).

297

298 *Chaetodon citrinellus* showed a high degree of dietary versatility, consuming a number of
299 different hard coral taxa at each site (Table 1) and resource selection functions indicated that

300 *C. citrinellus* was a fairly generalised feeder (Table 3). Significant selectivity or avoidance
301 was only shown for a few prey categories and most categories were consumed in proportion
302 to their availability (Table 3).

303

304 Although overall dietary selectivity (X_{L2}^2) was high for *C. lunulatus* at each site and
305 comparable to that of *C. trifascialis* (Fig. 2), resource selection functions for individual coral
306 taxa indicated that *C. lunulatus* was a much more generalised feeder (Table 3). *Chaetodon*
307 *lunulatus* consumed a large number (between 25 and 34) of different hard coral taxa at each
308 site (Table 1) and only showed avoidance of non hard coral prey categories (Table 3). At
309 exposed sites *C. lunulatus* exhibited significant feeding selectivity for *Acropora* corals and
310 *Pocillopora* corals, but fed on most hard coral prey categories in proportion to their
311 availability across both exposed and sheltered sites.

312

313 In contrast, *C. trifascialis* had much more specialised feeding preferences, consuming 17 or
314 fewer different hard coral taxa at each site (Table 1) and never using a large number of hard
315 coral taxa across all sites, regardless of their availability (Table 3). *Chaetodon trifascialis* only
316 fed on corals from three genera – *Acropora*, *Pocillopora* and *Montipora* – and only showed
317 selectivity for *Acropora* corals (Table 3), taking more than 90% of all bites from *Acropora*
318 corals at each site. Particularly strong selectivity was exhibited for *Acropora hyacinthus*, with
319 *C. trifascialis* taking between 45 and 78% of all bites from this species at each site.

320

321 All three species showed significant among-individual dietary variation at each site ($P < 0.001$,
322 Monte Carlo simulations). Both *C. citrinellus* and *C. lunulatus* showed high levels of among
323 individual dietary variation across all sites ($E > 0.5$, Individual niche overlap network), while

324 *C. trifascialis* showed some among individual dietary variation at sheltered sites and low
325 levels of among individual dietary variation at exposed sites (Fig. 2).

326

327 **Discussion**

328 The strengths and weaknesses of different specialisation indices have been reviewed several
329 times, and most recently by DeVictor et al. (2010), but this is the first study to directly
330 compare the performance of such indices using the same dataset. Similarly, the link between
331 specialisation and vulnerability has been explored in depth (e.g. Colles et al. 2009), but there
332 has been little consideration of how the measurement of specialisation may affect estimates of
333 vulnerability. To our knowledge this is the first study to investigate the utility of different
334 specialisation indices within the context of predicting vulnerability to environmental change.
335 We found that the level of dietary specialisation estimated for all three butterflyfish species
336 varied when different specialisation indices were used, indicating that the choice of index can
337 have a considerable impact upon estimates of the degree of specialisation. These impacts are
338 likely to be less important for generalist species. For example patterns of dietary
339 specialisation for *C. citrinellus*, the most generalist of the three study species, were similar
340 between all four specialisation indices. But for species that are neither true generalists nor
341 extreme specialists, indices based solely on patterns on resource use (e.g. Shannon-Wiener
342 index) may give somewhat different estimates of specialisation to indices which incorporate
343 resource availability (e.g. Chi square selectivity index). *Chaetodon lunulatus* feeds almost
344 exclusively on hard corals and therefore could be considered to have a specialised diet, yet it
345 feeds across a broad range of hard coral species and is considered more of a generalist feeder
346 within the butterflyfishes that are obligate corallivores (Pratchett 2005; 2007). Specialisation
347 levels estimated by the Shannon Wiener index for *C. lunulatus* were similar to those of the

348 generalist *C. citrinellus*, while specialisation levels estimated by the Chi square index (which
349 considers resource availability) were more similar to those of the specialist *C. trifascialis*.

350

351 The importance of incorporating resource availability into specialisation estimates has long
352 been recognised by ecologists (Hurlbert 1978; Petraitis 1979). Although the use of indices
353 which only evaluate patterns of resource use is no longer as widespread as it once was (see
354 MacNally 1995), many current studies continue to use these types of indices to measure
355 specialisation (e.g. Kotze and O'Hara 2003; Munday 2004; Charrette et al. 2006; Julliard et
356 al. 2006; Christensen and Kleindorfer 2009). Specialisation indices which ignore resource
357 availability may be highly misleading as a species that uses only a few resources will be
358 classified as a specialist, even if those resources are highly abundant (Hurlbert 1978). In
359 contrast, when specialisation indices incorporating measures of resource availability are used,
360 a species will only be classified as a specialist if resources are used disproportionately to their
361 availability. Some may believe this distinction is a somewhat semantic issue and may argue
362 that regardless of whether or not resource availability is considered, any type of specialisation
363 index will always classify extreme specialists as such. However, resource use may actually
364 reflect patterns of resource availability rather than specialisation per se. Specialisation indices
365 that do not consider resource availability will be unable to distinguish between a species using
366 a few commonly available resources and one that uses a narrow subset of available resources.
367 Both types of species will be classified as extreme specialists, even though the first species
368 may actually have a generalised ecology and utilise a large number of resources in cases
369 where it is not limited by resource availability (e.g. Pampas fox, Varela et al. 2008). While
370 any species using resources which are threatened will be at risk of extinction, in the context of
371 predicting vulnerability, a species that uses resources disproportionately to their availability is
372 much more likely to be vulnerable to changes in the abundance of those resources than a

373 species that uses a few commonly available resources. Therefore, the use of specialisation
374 indices that incorporate measures of resource availability is preferable if specialisation is used
375 as a proxy for vulnerability.

376

377 Consideration of several locations or time periods is also essential when quantifying
378 ecological specialisation in order to understand responses to changes in resource availability
379 (Devictor et al. 2010). The degree of specialisation estimated for all three species in this study
380 varied between individual sites and habitats. Consideration of specialisation patterns at only a
381 single site (e.g. Pratchett 2007) may have resulted in specialisation estimates that were not
382 reflective of the true versatility of each species. It is possible that species classified as
383 specialists based on studies in a single location may only be functioning as specialists on a
384 local scale, and across their entire geographic range these species may in fact have generalised
385 ecologies (Fox and Morrow 1981). For example, on the south coast of Japan two species of
386 decorator crab (*Micippa platipes* and *Tiarinia cornigera*) were highly selective in their
387 preferences for algae, but on the north coast both species showed no selectivity (Hultgren et
388 al. 2006). Consideration of temporal and spatial variation in specialisation is crucial in
389 systems where resources can become depleted (e.g. Pratchett et al. 2006) or where the
390 availability of resources may vary seasonally (e.g. Varela et al. 2008) in order to accurately
391 determine specialisation and predict vulnerability.

392

393 Understanding how ecological specialisation varies between individuals within a population
394 may also be important in predicting how a species will respond to changes in resource
395 availability. A population of individuals each specialising on a different resource may still
396 look like a “generalist” species by some measures, but such a population may respond
397 differently to resource depletion than another population composed of individual generalists.

398 Theory suggests that populations of individual specialists may be more stable and open to
399 future evolutionary diversification (Bolnick et al. 2003; Kendall and Fox 2002, 2003).
400 Furthermore, niche variation within a population may help to buffer against loss of particular
401 habitats or resources and provide genetic variation needed to adapt to changing environments
402 (Bolnick et al. 2003; Durell 2000). In cases where estimation of resource availability is not
403 possible, measurement of among-individual variation in resource use may provide additional
404 information about ecological specialisation and vulnerability to that gained from the use of
405 traditional niche breadth measures. As highly specialised species are likely to have low levels
406 of among-individual variation due to their narrow niche breadth, use of among-individual
407 specialisation indices may be most informative when comparing vulnerability of species with
408 more generalised ecologies.

409

410 Resource selection functions provide fine scale information on ecological specialisation,
411 enabling greater insights into the potential response of species to changes in resource
412 availability, and therefore vulnerability to future environmental changes, than can be gained
413 from overall estimates of specialisation. Although overall levels of dietary specialisation
414 estimated by the Chi square selectivity index were similar for *C. lunulatus* and *C. trifascialis*,
415 resource selection functions indicated that the diet of *C. trifascialis* was much more
416 specialised and its feeding preferences were more conserved, both in the terms of the number
417 of resources it showed selectivity for and in the spatial variation of its selectivity.

418 Consequently, *C. trifascialis* is likely to be highly vulnerable to changes in resource
419 availability, particularly to changes in the abundance of the *Acropora* corals that it
420 preferentially feeds on (Pratchett 2005; 2007). In contrast, *C. lunulatus* utilised a large
421 number of resources at each site and selectivity of specific dietary items varied between sites
422 which also varied in their resource availability. These findings suggest that even though *C.*

423 *lunulatus* has a reasonably specialised diet, it is likely to be fairly resilient to changes in
424 resource availability. Such responses to changes in resource availability have already been
425 reported for both species. In French Polynesia, the abundance of *C. trifascialis* declined by
426 almost 100% following declines in the abundance of its preferred *Acropora* corals (Berumen
427 and Pratchett 2006), while on the Great Barrier Reef, *C. lunulatus* has been shown to alter its
428 diet in response to a loss of some coral taxa (Pratchett et al. 2004). These responses highlight
429 the predictive value of resource selection functions and provide justification for their use in
430 the identification of key resources which may be critical to a species' persistence.

431
432 In addition to current threats, effective conservation strategies need to consider future threats
433 to habitats and the potential resultant habitat composition. For coral reefs, the frequency of
434 mass bleaching events, disease and mortality are predicted to increase as a result of
435 anthropogenic climate change (Hoegh-Guldberg et al. 2007). As the dietary preferences of *C.*
436 *trifascialis* are highly conserved - the same coral prey was selected at each site regardless of
437 availability - we can predict that this species is likely to have a very low capacity to respond
438 to changes in the availability of coral prey. Acroporid corals, including *Acropora hyacinthus*,
439 the preferred prey of *C. trifascialis*, are highly susceptible to bleaching (Marshall and Baird
440 2000), and the abundance of these corals is likely to decline in the future with increased
441 frequency of bleaching events. Consequently, the vulnerability of *C. trifascialis* to the impacts
442 of climate change on coral reefs is only likely to increase and this species should be assigned
443 a high extinction risk based on its level of dietary specialisation.

444
445 While the example presented here comes from a single family of coral reef fishes, we believe
446 the butterflyfishes are useful models for understanding more general trends and that these
447 findings reflect ecological principles that transcend the system. Calculating the four

448 specialisation indices from the same dataset removes any variation that might have resulted
449 from simply comparing the findings of several independent studies. Consequently, we are
450 confident that the differences in the levels of specialisation estimated by each of the four
451 indices reflect actual differences and not sampling effects. The three species we included in
452 our analysis displayed a range of specialisation levels, from generalist to extreme specialist,
453 and provide an indication of how these indices are likely to perform across species with
454 varying levels of specialisation. Moreover, the comparison of two differing habitats illustrates
455 how estimates of specialisation may be affected by temporal or spatial differences in resource
456 availability.

457

458 CONCLUSIONS

459 This is the first study to compare the effects of using different indices on estimates of
460 ecological specialisation and predictions of vulnerability. While we recognise realistic
461 limitations of decision makers in conducting extensive assessments, our results demonstrate
462 that vulnerability assessments based on a single specialisation index may be misleading and
463 the best estimates of specialisation will be provided by indices which incorporate resource
464 availability measures. Furthermore, the use of resource selection functions in addition to
465 overall specialisation indices will provide a more accurate picture of ecological versatility and
466 therefore vulnerability to future environmental changes. For example, the highly conserved
467 dietary preferences and high specialisation values estimated for *C. trifascialis* in this study
468 suggest that this species is likely to be highly vulnerable to the impacts of climate-induced
469 coral loss on reefs.

470

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478

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Table 1

Dietary composition of *Chaetodon citrinellus*, *C. lunulatus* and *C. trifascialis* at 3 exposed front reef sites (Bird Islet, Lizard Head, South Island) and 3 sheltered back reef sites (Corner Beach, Osprey Islet, Vickies) at Lizard Island, Great Barrier Reef.

Species	Site	Hard corals (%)	Soft corals (%)	Other macro invertebrates (%)	Imperceptible items ¹ (%)	Total number hard coral species consumed
<i>C. citrinellus</i>	Bird Islet	75.3	1.1	2.4	21.1	23
	Lizard Head	55.9	6.8	3.1	34.2	21
	South Island	74.9	1.3	2.5	21.3	29
	Corner Beach	39.1	3.0	2.5	55.5	18
	Osprey Islet	49.6	0.0	0.0	50.4	12
	Vickies	59.5	11.8	1.6	27.1	28
<i>C. lunulatus</i>	Bird Islet	98.6	0.4	0.5	0.5	34
	Lizard Head	99.6	0.0	0.0	0.4	25
	South Island	99.0	0.2	0.0	0.8	27
	Corner Beach	99.2	0.0	0.0	0.8	26
	Osprey Islet	100.0	0.0	0.0	0.0	26
	Vickies	96.2	0.0	3.4	0.4	26
<i>C. trifascialis</i>	Bird Islet	100.0	0.0	0.0	0.0	15
	Lizard Head	99.4	0.0	0.0	0.6	14
	South Island	100.0	0.0	0.0	0.0	17

Corner Beach	100.0	0.0	0.0	0.0	15
Osprey Islet	100.0	0.0	0.0	0.0	14
Vickies	100.0	0.0	0.0	0.0	15

¹ Refers to bites taken on reef pavement, sand and rubble. It was assumed that these bites were targeting small motile invertebrates such as polychaetes and crustaceans.

Table 2

MANOVA results for dietary composition of *Chaetodon citrinellus*, *C. lunulatus* and *C. trifascialis* among habitats (exposed front reef and sheltered back reef) and sites (Bird Islet, Lizard Head, South Island, Corner Beach, Osprey Islet, Vickies) nested within habitats at Lizard Island, Great Barrier Reef.

Species	Source	Pillai's trace	d.f.	P
<i>C. citrinellus</i>	Habitat	4.29	15, 100	<0.001
	Site (Habitat)	1.52	60, 412	<0.05
<i>C. lunulatus</i>	Habitat	5.52	15, 100	<0.001
	Site (Habitat)	2.82	60, 412	<0.001
<i>C. trifascialis</i>	Habitat	5.77	9, 106	<0.001
	Site (Habitat)	1.60	36, 436	<0.02

Table 3

Dietary selectivity of *Chaetodon citrinellus*, *C. lunulatus* and *C. trifascialis* at 3 exposed front reef sites (Bird Islet, Lizard Head, South Island) and 3 sheltered back reef sites (Corner Beach, Osprey Islet and Vickies) at Lizard Island, Great Barrier Reef for 15 major prey categories. +: prey category used significantly more than expected (selected); -: prey category used significantly less than expected (avoided); U: prey category unused (strongly avoided); NA: prey category not available; blank cells indicate prey categories that were used in proportion to availability (neither selected nor avoided).

	X_{L2}^2	d.f	P	<i>Acropora hyacinthus</i>	<i>A. muricata</i>	<i>A. nasuta</i>	Staghorn <i>Acropora</i>	Other <i>Acropora</i>	<i>Pocillopora damicornis</i>	Other <i>Pocilloporidae</i>	<i>Montipora</i> sp.	<i>Porites</i> sp.	<i>Favidae</i>	<i>Isopora</i> sp.	Other hard corals	Soft coral	Reef substrate ^a	Other
<i>C. citrinellus</i>																		
Exposed																		
Bird Islet	2103	220	<0.001	U	U		+		+							-	-	
Lizard Head	1520	220	<0.001	NA			NA	+	+				-					
South Island	1557	240	<0.001	U								-				-	-	
Sheltered																		
Corner Beach	1602	180	<0.001		-		+		NA			U	NA	U	-		+	
Osprey Islet	2227	180	<0.001				U	+	NA		-		NA	U	U	U	+	U
Vickies	2261	280	<0.001													-		
<i>C. lunulatus</i>																		
Exposed																		

Bird Islet	2731	220	<0.001	+	U		+	+		+		-	-	-
Lizard Head	3390	180	<0.001		NA	NA	+	+				U	-	U
South Island	1869	200	<0.001	+	U		+	+				-	-	U
Sheltered														
Corner Beach	3928	180	<0.001		+		+	NA		NA		U	-	U
Osprey Islet	2950	180	<0.001					NA		NA		U	U	U
Vickies	2782	240	<0.001							+		U	-	

C. trifascialis

Exposed

Bird Islet	3693	80	<0.001	+	U	U				U	U	U	U	U	U	U	U
Lizard Head	3146	100	<0.001	+	NA	NA		-		U	U	U	U	U	U	-	U
South Island	1969	100	<0.001	+	U			+		U	U	U	U	U	U	U	U

Sheltered

Corner Beach	3810	80	<0.001	+		-		-	NA	NA	U	U	NA	U	U	U	U
Osprey Islet	4357	120	<0.001	+				+	NA		U	U	NA	U	U	U	U
Vickies	2879	100	<0.001	+					U	U	U	U	U	U	U	U	U

^a Includes reef pavement, sand and rubble. It was assumed that bites on reef substrates were targeting small motile invertebrates such as polychaetes and crustaceans.

Figure Legends

Fig. 1

Canonical discriminant analysis showing coral assemblages at three exposed front reef sites (BI: Bird Islet; LH: Lizard Head; SI: South Island) and three sheltered back reef sites (OI: Osprey Islet; CB: Corner Beach; VI: Vickies) around Lizard Island, Great Barrier Reef. Circles plotted represent 95% confidence intervals around the group centroid for each site (unfilled circles: exposed sites; filled circles: sheltered sites). Vectors are structural coefficients indicating the relative abundance of the major coral taxa among the 6 sites.

Fig. 2

Dietary specialisation shown by *Chaetodon citrinellus*, *C. lunulatus* and *C. trifascialis* across 3 exposed front reef sites (Bird Islet, Lizard Head, South Island) and 3 sheltered back reef sites (Corner Beach, Osprey Islet, Vickies) at Lizard Island, Great Barrier Reef. Dietary specialisation is calculated using (A) total number of prey categories consumed; (B) Shannon Wiener index; (C) Chi square log likelihood statistic, X_{L2}^2 ; and (D) among-individual dietary variation, *E*. Data are means for each habitat type \pm 1SE.

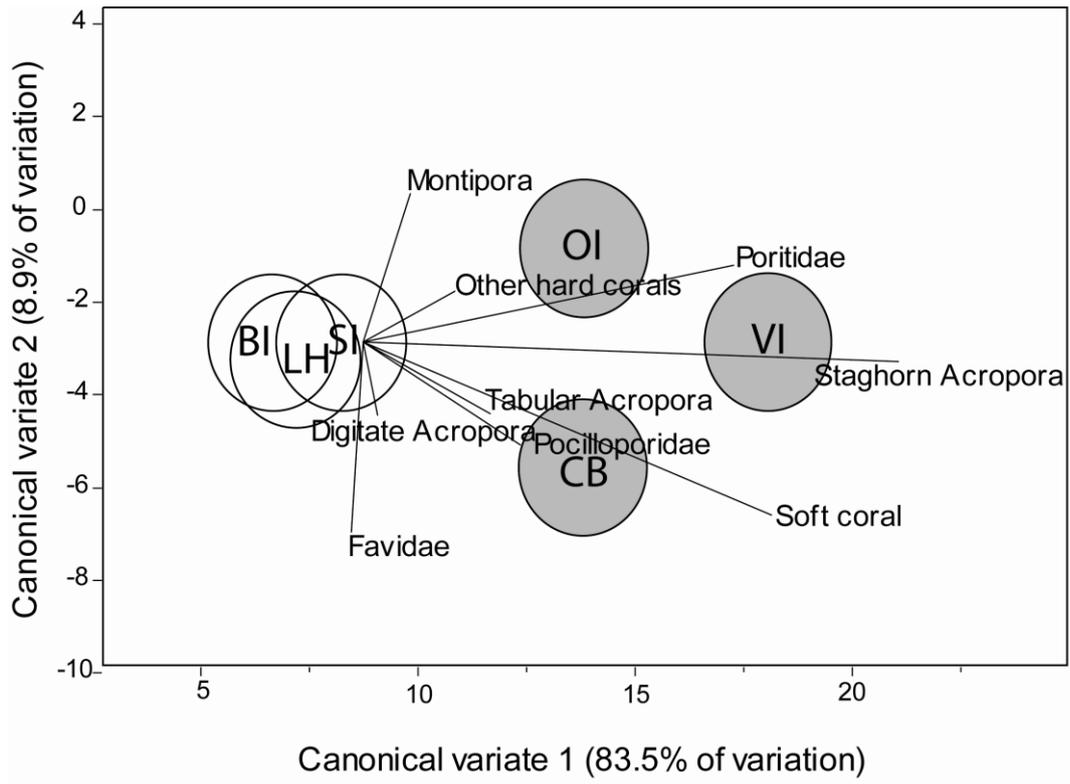


Figure 1

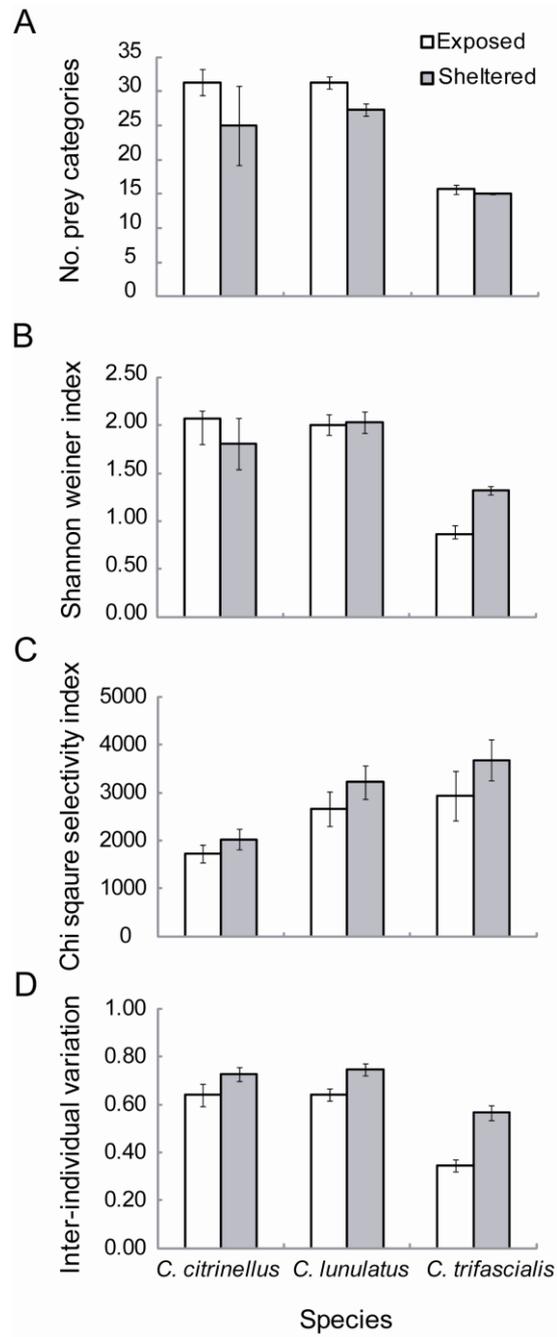


Figure 2