

# Trophic plasticity in an obligate corallivorous butterflyfish

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**ABSTRACT:** Changes in the abundance and/or taxonomic composition of corals are having direct impacts on the structure of reef fish assemblages, with those species that rely directly on live coral for food or shelter being most affected. Despite this, many specialist coral feeders persist on reefs where preferred coral taxa are rare. We examined feeding selectivity of the obligate corallivorous butterflyfish *Chaetodon octofasciatus*, a species known to feed predominantly on *Acropora* spp. corals, between a heavily urbanized coral reef system (Singapore) with low *Acropora* spp. cover, and a relatively intact reef system containing high *Acropora* spp. cover (Pulau Tioman, eastern Peninsular Malaysia). Both reef systems supported similar densities of *C. octofasciatus*, with live coral dominating the diet in both locations. In Pulau Tioman, *C. octofasciatus* fed on 14 genera (27.45% of available coral genera), with over a third of bites on *Acropora* spp. In contrast, *C. octofasciatus* on Singaporean reefs fed on 26 genera (45% of available coral genera), with only 4% of bites on *Acropora* spp. Despite specialist corallivores being viewed as highly susceptible to reductions in their preferred dietary coral taxa, this research highlights the potential importance of diet plasticity in sustaining populations.

**KEY WORDS:** Coral reef · Corallivore · *Chaetodon octofasciatus* · Feeding · Plasticity · *Acropora* · Behaviour

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## INTRODUCTION

Environmental change, resulting from both natural and anthropogenic impacts, often results in rapid changes in the abundance, diversity and composition of biological communities (McCauley et al. 2015, Webb & Mindel 2015, Hughes et al. 2018). Although considerable research has focussed on the numerical response of populations to changes in resource availability, such changes may also have a substantial impact on the behaviour of individuals (Forsman 2015, Wong & Candolin 2015). This may be particularly relevant for species that are reliant on a limited suite of resources (Brooker et al. 2014). Indeed, the

ability of individuals to shift patterns of resource use in response to changes in the availability of their preferred resources (Chown & Terblanche 2006, Sih et al. 2011) may ensure population persistence under changing environmental conditions.

Within coral reef systems, the response of individual species to changes in the abundance of trophic or habitat resources has often been related to the degree of resource dependency (Hoey et al. 2016). Species that use a wide range of resources for diet or shelter (i.e. generalists) are predicted to be relatively insensitive to changes in resource availability, whereas species that rely on a limited array of resource types (i.e. specialists) are predicted to be more

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sensitive to changes in the abundance of their preferred resource (Feary 2007). Nonetheless, there is increasing evidence from other ecosystems of apparent resource specialists exhibiting plasticity in their resource use following reductions in their preferred resource (Wong & Candolin 2015). Such resource plasticity may contribute to the insensitivity of some specialist coral reef fishes to reductions in the availability of their preferred resources (Berumen et al. 2005, Berumen & Pratchett 2008).

The eightband butterflyfish *Chaetodon octofasciatus* is a ubiquitous corallivore throughout Southeast Asia (Froese & Pauly 2016) where it feeds predominantly on *Acropora* spp. (Abdul Ghaffar et al. 2006, Madduppa et al. 2014). The apparent reliance of this species on *Acropora* has led to *C. octofasciatus* being proposed as a useful 'indicator species' for coral degradation (Madduppa et al. 2014). The objective of this study was to examine how the feeding ecology of this specialist corallivore differs with coral species

composition. Specifically, we compared bite rates and feeding selectivity of *C. octofasciatus* populations between Pulau Tioman, an island off eastern Peninsular Malaysia where *Acropora* spp. dominate shallow coral reefs (Guest et al. 2012), and reefs off Singapore, where *Acropora* spp. are relatively uncommon and reefs are dominated by massive, foliose and encrusting coral taxa (Guest et al. 2016).

## MATERIALS AND METHODS

The feeding rate and selectivity of *Chaetodon octofasciatus* was quantified across fringing coral reefs surrounding Pulau Tioman, Malaysia, and the southern islands of Singapore (Fig. 1). Singapore has undergone extensive land reclamation and coastal development (Lai et al. 2015), resulting in high rates of sedimentation and levels of total suspended solids far exceeding those considered optimal for tropical

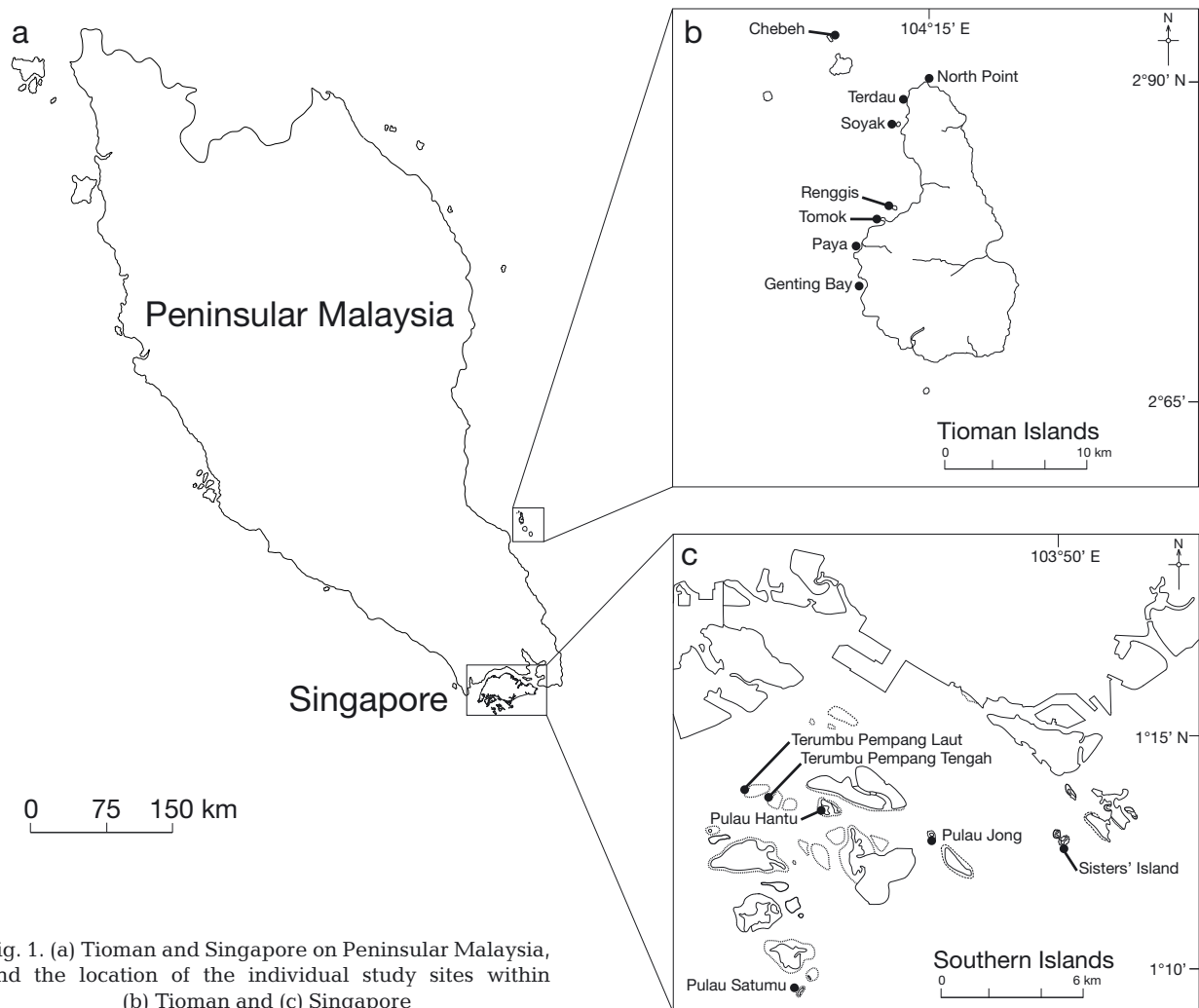


Fig. 1. (a) Tioman and Singapore on Peninsular Malaysia, and the location of the individual study sites within (b) Tioman and (c) Singapore

reefs. Average underwater visibility has declined from ~10 m in the 1960s to <5 m in the mid-1990s (with local temporally ephemeral [from several minutes up to 1–2 d] reductions of visibility associated with passing ship traffic and high wind-driven currents reducing visibility to ~2 m) (Chou 1996). In comparison, Pulau Tioman has limited coastal development, and underwater visibility is typically >10 m. The prey preference (feeding substrata used) and bite rates (number of bites over a distinct time period) of *C. octofasciatus* were estimated using focal individual observations across 6 and 8 replicate sites in Singapore and Pulau Tioman, respectively (Fig. 1). Specifically, we selected areas within the 2 locations that were as similar as possible in terms of abiotic conditions, with all work undertaken in 5–7 m depth on the upper reef slope, where the complexity of the reefs between regions was similar (following Polunin & Roberts 1993). Potential competitors of *C. octofasciatus* were relatively scarce throughout both regions (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m605p165\\_supp.pdf](http://www.int-res.com/articles/suppl/m605p165_supp.pdf)).

An individual *C. octofasciatus* was haphazardly selected and its total length estimated to the nearest cm. After a short (~20 s) acclimation period, the individual was followed at a distance of 2–5 m for 3 min, during which all bites and feeding substrata were recorded. All feeding observations were undertaken within short temporal windows (~1 wk in the field) of relatively high underwater visibility. Observations were aborted if fish displayed any adverse reactions to diver presence (<1% of individuals). Feeding observations were recorded for a minimum of 5 ind. site<sup>-1</sup>, with a total of 68 and 209 individuals recorded within Pulau Tioman and Singapore, respectively. Individuals observed for feeding showed no significant difference in mean size between locations (ANOVA,  $F_{1,14} = 1.4$ ,  $p = 0.251$ ; mean  $\pm$  SE total length [TL], Singapore:  $8.06 \pm 0.19$  cm, Pulau Tioman:  $7.86 \pm 0.16$  cm).

The majority of individuals observed were very small (~8–10 cm TL). Although much smaller individuals (and no individuals larger than this body size) were apparent on reefs (usually 2–3 cm TL), their abundance was so low (<5 ind. seen across both sites combined) that any confidence in the patterns of diet use and bite number of this very small size class was deemed to be too low to use effectively.

Within sites where feeding selectivity of *C. octofasciatus* populations were recorded, the density of individuals was visually estimated within 30 m  $\times$  2 m belt transects ( $n = 8$ ). A single observer recorded all individuals within each transect. Low visibility in Singapore necessitated the use of the narrow belt transects.

Mean size (TL) of focal fish did not differ between locations (ANOVA,  $F_{1,276} = 3.661$ ,  $p = 0.06$  Singapore:  $7.71 \pm 0.11$  cm, Pulau Tioman:  $7.28 \pm 0.13$  cm).

Benthic communities were surveyed within the same 8 transects, using point-intercept methods recording the substratum directly below the transect tape at 0.5 m intervals (61 points transect<sup>-1</sup>). Substratum types included hard (scleractinian) corals (identified to genus), soft corals, macroalgae, rock, pavement, rubble, epilithic algal matrix (turf algae) and sand. A power analysis on point-intercept transects from Singapore reefs showed that using an  $\alpha$ -value of 0.05 and a desired power of 0.8, the number of replicate transects required to detect a significant difference was approximately  $n = 7.33$  transects. Therefore, the number of point-intercept transects used (8 transects, 61 points each) in this study sufficiently characterized the benthic assemblages, including coral genera (not species) present on each reef (Jokiel et al. 2015).

All statistical analyses were performed in R. To compare the composition of (1) benthic communities and (2) coral communities between Singapore and Pulau Tioman, separate non-metric multidimensional scaling (nMDS) ordinations were used (Clarke & Warwick 2001). The nMDS were based on Bray-Curtis dissimilarities of square root transformed site-mean data for each benthic category and coral genus. To test the effect of location on both factors, separate 1-factor permutational multivariate ANOVAs (PERMANOVAs) with 9999 permutations were used. Similarity percentage (SIMPER) analyses were then performed to identify the contribution of benthic taxa and coral genera to community dissimilarity.

To examine the relationship between bite rate of *C. octofasciatus* and the fixed factors of location and coral genera, a series of hierarchical models with a Poisson link function were performed using *lmer* in the package 'lme4' (Bates et al. 2015). Within the model, site (nested within location) and individual were included as random effects. The step function in R was used to develop the most parsimonious model, and Akaike's information criterion (AIC) values of that model were compared with those from a null model (i.e. only the random structure). The significance of factors in impacting bite rate was examined using separate likelihood ratio tests, comparing a full model (with the fixed effects) against a reduced model; a fixed effect was deemed significant if the difference between the likelihood of these 2 models was significant. Assumptions of normality and homoscedasticity were validated by visual inspection of the residual plots for all models.

To determine whether *C. octofasciatus* showed a preference for any coral genera within each location, Manly's selectivity ratio ( $Wi$ ) with Bonferroni-adjusted confidence limits was calculated based on design I (resource use and availability are measured at the population level, animals are not individually identified; Manly et al. 1993). Analyses were performed using *widesI*, in the R package 'adehabitatHS', with Manly's design I used (Calenge 2006). The function tests resource selection with the  $\chi^2$  of Pearson and log-likelihood  $\chi^2$  (recommended, see Manly et al. 1993). The Manly selectivity measure (selection ratio = used/available) is computed, the preference/avoidance is tested for each location, and the differences between selection ratios are computed and tested between locations (Calenge 2006). Manly's selectivity ratios ( $Wi$ ) of  $>1$  indicate positive selection (preference),  $Wi < 1$  indicates avoidance, and  $Wi$  that includes 1 indicates that the coral genus was used in proportion to its availability.

## RESULTS

Benthic community composition differed significantly between Singapore and Pulau Tioman (Fig. 2a, pseudo- $F_{1,13} = 4.94$ ,  $p < 0.0001$ ), driven mainly by the higher cover of rock in Pulau Tioman and macroalgae in Singapore (Table S2 in the Supplement). Despite these differences, live hard coral were the dominant benthic organisms at both locations (Table S2)

Coral composition differed significantly between locations (Fig. 2b, pseudo- $F_{1,13} = 9.17$ ,  $p < 0.001$ ). Pulau Tioman coral communities were composed of 37 genera, but were dominated by *Acropora* spp. In comparison, Singapore sites had a more taxonomically rich coral community (42 genera), with no one dominant genus, and near complete absence of *Acropora* (Figs. 2b & 3a,b, Table S3 in the Supplement).

Average population density (mean  $\pm$  SE) of *Chaetodon octofasciatus* did not substantially differ between locations (per 150 m<sup>2</sup>: Singapore: 1.27  $\pm$  0.21 ind., Pulau Tioman: 1.55  $\pm$  0.22 ind.,  $p > 0.05$ ) and was positively correlated with live coral cover (Singapore:  $r = 0.53$ ,  $p < 0.001$ ; Pulau Tioman:  $r = 0.34$ ,  $p = 0.006$ ). Average feeding rates between locations were non-

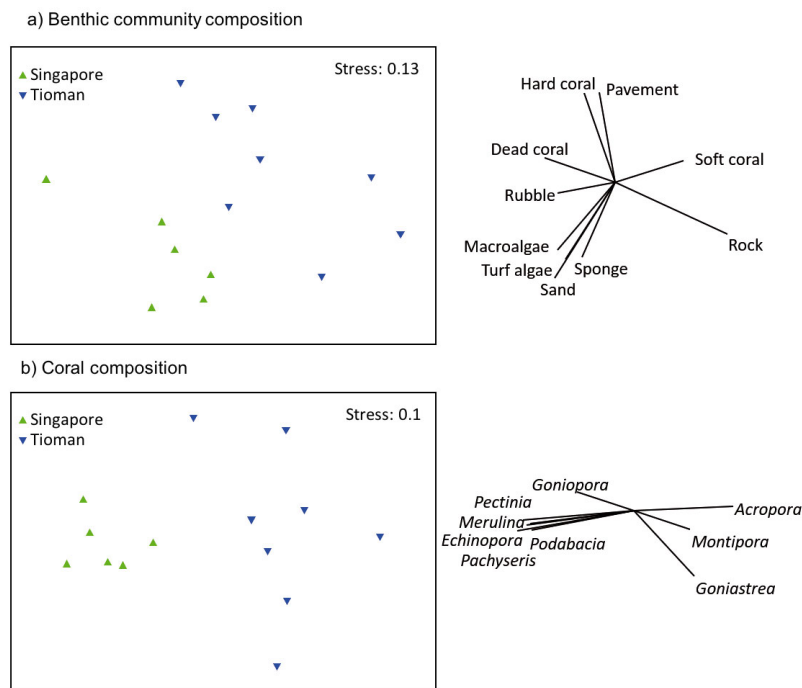


Fig. 2. Non-metric multidimensional scaling (nMDS) plots showing the relationship among (a) benthic community composition and (b) coral composition across reefs throughout Singapore and Tioman. Analyses were based on the Bray-Curtis distances of square-root transformed abundance data. Vectors represent the partial regression coefficients of the original variables in the 2 dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient

significant (ANOVA,  $F_{1,12} = 0.101$ ,  $p = 0.756$ ; Singapore, 12.25  $\pm$  3.2; Pulau Tioman 12.54  $\pm$  2.5), with hard coral being the dominant feeding substratum in both Singapore (96.47% of bites) and Pulau Tioman (95.52% of bites) (Fig. 3c,d). Despite this, there were significant differences in the coral genera comprising diets between populations ( $\chi^2(25) = 36.96$ ,  $p < 0.05$ ). *Acropora* comprised  $>60\%$  of the diet of *C. octofasciatus* in Pulau Tioman (average bites per 3 min observation: 6.14  $\pm$  1.16, Fig. 3d), while no single genus numerically dominated the diet within Singapore (Table S4 in the Supplement, Fig. 3c). In addition, *C. octofasciatus* populations in Singapore fed on almost twice the number of coral genera (26 genera, 44.82% of available genera, Fig. 3c) than populations in Pulau Tioman (14 genera, 27.45% of available genera, Fig. 3d). Within both locations, rare genera were used but their contribution to species diet was so low (on the order of 1–2 bites across the whole dataset, total bites  $n = 1112$ ) that they were excluded from further analysis.

Feeding selectivity of *C. octofasciatus* populations differed between the 2 locations, with populations on

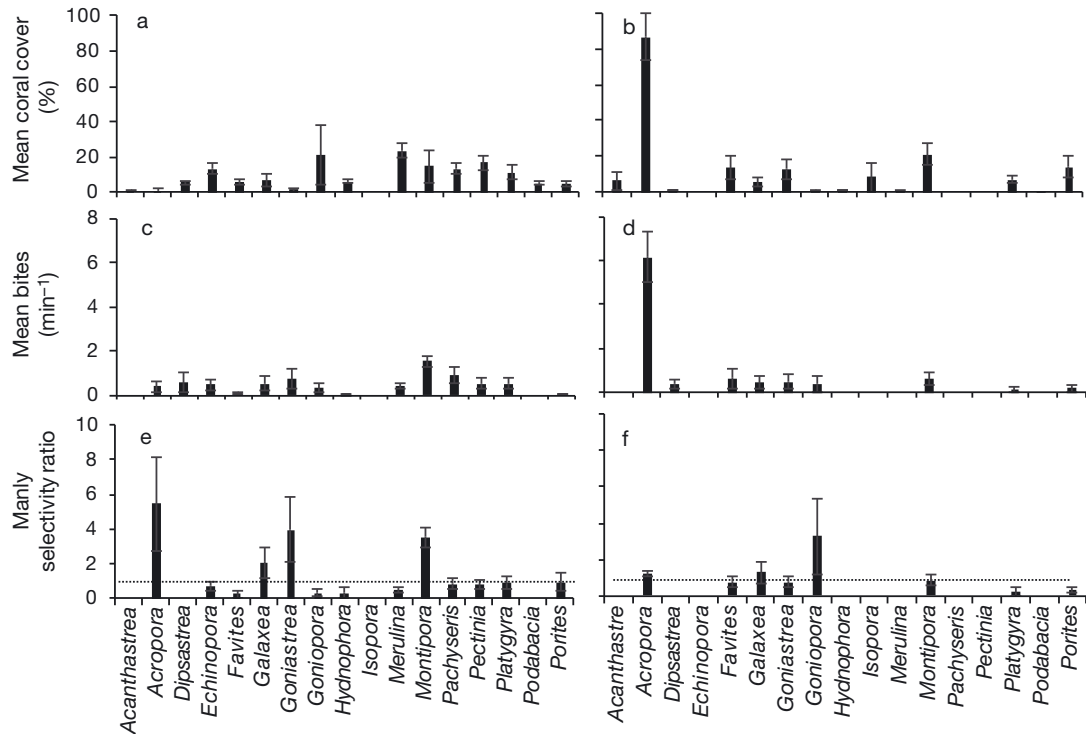


Fig. 3. Mean ( $\pm$ SE) % cover (% of the total coral cover), number of bites  $\text{min}^{-1}$  and selectivity ratios of *Chaetodon octofasciatus* for (a,c,e) Singapore and (b,d,f) Tioman. All coral genera showing  $<5\%$  mean percent coral cover within both locations were excluded. For feeding, selectivity ratios ( $W_i$ )  $> 1$  indicate positive selection for coral genera (preference), and  $W_i < 1$  indicates negative selection (avoidance). Selection ratios  $\pm$  SE that encompassed 1 indicate that the coral genus was used in proportion to its availability

Singaporean reefs selecting for *Acropora*, *Montipora*, *Goniastrea* and *Galaxea*, avoiding *Favites*, *Goniopora*, *Hydnophora*, and *Merulina*, but using several other genera in proportion to their availability (Fig. 3e). In contrast, in Pulau Tioman, *C. octofasciatus* actively selected *Goniopora* and used several other genera (including *Acropora*) in proportion to their availability (Fig. 3f), while avoiding *Porites* and *Platygyra*.

## DISCUSSION

Given the unprecedented scale and rate of human-induced changes to coral reef ecosystems globally, it is critical to understand how coral reef species may adjust to changing resource availability. Using the specialist corallivore *Chaetodon octofasciatus* as a model species, we show that trophic plasticity may allow populations to persist in areas with different trophic resource composition. Although the abundance and feeding rates of *C. octofasciatus* did not differ between Singapore and Pulau Tioman, the composition of prey corals and selectivity of feeding

differed between locations. In Singapore, *C. octofasciatus* populations fed on a wide range of coral taxa, incorporating nearly half of the available genera at this location, with no single coral genus dominating their diet. In contrast, *C. octofasciatus* fed on less than a third of the available coral genera on Pulau Tioman reefs, with  $>60\%$  of their feeding concentrated on *Acropora* spp. Interestingly, *C. octofasciatus* actively selected 4 coral genera (*Acropora*, *Montipora*, *Goniastrea* and *Galaxea*) in Singapore, but only selected a single genus (*Goniopora*) at Pulau Tioman. Such differences in trophic resource use between locations indicates substantial plasticity in coral trophic use within Singapore populations.

Dietary specialisation can be a successful trophic strategy when preferred prey is abundant, but is a risky trophic strategy when the preferred prey is sensitive to environmental conditions. In Pulau Tioman, *C. octofasciatus* populations focussed their feeding on a specific coral genus (*Acropora*), using it in proportion to its high availability within coral communities. In contrast, *Acropora* spp. were rare in Singapore, but were preferred as a feeding substratum by *C. octofasciatus*. These results confirm that *Acropora*

spp. are an important food source for this species (Abdul Ghaffar et al. 2006, Madduppa et al. 2014), but not essential. Such feeding plasticity may allow *C. octofasciatus* to persist despite low abundances of *Acropora* on Singaporean reefs.

Broad reductions in coral cover have been associated with dramatic declines in the density and diversity of resident obligate corallivores (Pratchett et al. 2006, 2011), predominantly due to the sensitivities of their preferred corals (e.g. *Acropora*, *Pocillopora*) to disturbances and environmental change. Despite this, the obligate corallivore *C. octofasciatus* appears to be less sensitive to the taxonomic composition of local coral assemblages, showing near identical abundance between Singapore reefs, where their preferred coral taxon (*Acropora*) is relatively rare (Bauman et al. 2015), and Pulau Tioman reefs where *Acropora* are abundant (Guest et al. 2012). As coral communities shift from being dominated by stress-sensitive taxa to those more tolerant of stressors (Bento et al. 2016, Hughes et al. 2017), understanding the role of trophic plasticity in sustaining associated fish communities may be vital in determining the future configuration of coral reef ecosystems. Predicted changes in species composition within coral reefs should not only consider the degree of species specialisation but also species-specific trophic plasticity (Nagelkerken & Munday 2016).

Resource specialists are often viewed as most likely to show declines in population abundance within habitats where preferred resources are rare; this research highlights the potential importance of resource plasticity in sustaining species within such environments (Chown & Terblanche 2006, Sih et al. 2011, Hoey et al. 2016). To better manage and conserve biodiversity into the future, understanding the limits of such plasticity will be vital (Wong & Candolin 2015, Nagelkerken & Munday 2016). Consequently, there is a need to understand whether a broad trophic niche is a local population character or a broader characteristic of a given species. Understanding when, and potentially how, individual coral reef fish may adjust their phenotype, and whether such traits are inherent within species when faced with low resource availability, will be vital in determining the role of trophic plasticity in structuring coral reef fishes within an increasingly changing ecosystem.

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#### LITERATURE CITED

- Abdul Ghaffar M, Ng MY, Abdul Adziz KA, Arshad A (2006) Linking the feeding regime of *Chaetodon octofasciatus* to the coral health in Redang Island, Malaysia. *Coast Mar Sci* 30:276–282
- ✦ Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- ✦ Bauman AG, Guest JR, Dunshea G, Low J, Todd PA, Steinberg PD (2015) Coral settlement on a highly disturbed equatorial reef system. *PLOS ONE* 10:e0127874
- ✦ Bento R, Hoey AS, Bauman AG, Feary DA, Burt JA (2016) The implications of recurrent disturbances within the world's hottest coral reef. *Mar Pollut Bull* 105:466–472
- ✦ Berumen ML, Pratchett MS (2008) Trade-offs associated with dietary specialization in corallivorous butterflyfishes (Chaetodontidae: *Chaetodon*). *Behav Ecol Sociobiol* 62:989–994
- ✦ Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Mar Ecol Prog Ser* 287:217–227
- ✦ Brooker RM, Munday PL, Brandl SJ, Jones GP (2014) Local extinction of a coral reef fish explained by inflexible prey choice. *Coral Reefs* 33:891–896
- ✦ Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- Chou LM (1996) Response of Singapore reefs to land reclamation. *Galaxea* 13:85–92
- ✦ Chown SL, Terblanche JS (2006) Physiological diversity in insects: ecological and evolutionary contexts. *Adv Insect Physiol* 33:50–152
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2<sup>nd</sup> edn. PRIMER-E, Plymouth Marine Laboratory, Plymouth
- ✦ Feary DA (2007) The influence of resource specialization on the response of reef fish to coral disturbance. *Mar Biol* 153:153–161
- ✦ Forsman A (2015) Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity* 115:276–284
- Froese F, Pauly D (2016) FishBase. [www.fishbase.org](http://www.fishbase.org) (accessed 13 January 2016)
- ✦ Guest JR, Baird AH, Maynard JA, Muttaqin E and others (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLOS ONE* 7:e33353
- ✦ Guest JR, Tun K, Low J, Vergés A and others (2016) 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. *Sci Rep* 6:36260
- ✦ Hoey AS, Howells E, Johansen JL, Hobbs JPA and others (2016) Recent advances in understanding the effects of climate change on coral reefs. *Diversity* 8:12

- Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG and others (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373–377
- Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. *Nature* 556:492–496
- Jokiel PL, Rodgers KS, Brown EK, Kenyon JC, Aeby G, Smith WR, Farrell F (2015) Comparison of methods used to estimate coral cover in the Hawaiian Islands. *PeerJ* 3: e954
- Lai S, Loke LHL, Hilton MJ, Bouma TJ, Todd PA (2015) The effects of urbanisation on coastal habitats and the potential for ecological engineering: a Singapore case study. *Ocean Coast Manage* 103:78–85
- Madduppa HH, Zamani NP, Subhan B, Aktani U, Ferse SC (2014) Feeding behavior and diet of the eight-banded butterflyfish *Chaetodon octofasciatus* in the Thousand Islands, Indonesia. *Environ Biol Fishes* 97:1353–1365
- Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London
- McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: animal loss in the global ocean. *Science* 347:1255641
- Nagelkerken I, Munday PL (2016) Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob Change Biol* 22:974–989
- Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100:167–176
- Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of *Chaetodon* butterflyfishes following extensive coral depletion. *J Fish Biol* 69:1269–1280
- Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in the biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3:424–452
- Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evol Appl* 4:367–387
- Webb TJ, Mindel BL (2015) Global patterns of extinction risk in marine and non-marine systems. *Curr Biol* 25: 506–511
- Wong BBM, Candolin U (2015) Behavioral responses to changing environments. *Behav Ecol* 26:665–673

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