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

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Abstract

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

Introduction

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

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

One factor often correlated with high extinction risk and vulnerability is ecological specialisation (McKinney 1997; Fisher and Owens 2004; Colles et al. 2009). Ecological specialists are thought to be more vulnerable to environmental changes and disproportionately affected by changes in resource availability compared to generalist counterparts. Studies across both terrestrial and aquatic organisms and a range of specialisation types support this prediction (e.g. nesting cavity specialisation: Aitken and Martin 2008; habitat specialisation: Kotze and O'Hara 2003; Munday 2004; Fisher et al. 2003; dietary specialisation: Charrette et al. 2006; Graham 2007; dietary and habitat specialisation: Harcourt et al. 2002) suggesting
that in many cases ecological specialisation is a key driver of extinction risk. Thus, identifying species that are ecological specialists can provide a useful starting point to predict likely vulnerability and prioritise conservation actions. However, binary classifications of species as either specialists or generalists can mask interspecific variation in ecological versatility. This is of critical importance if specialisation is used as a vulnerability proxy as grouping specialists into a single category assumes equal vulnerability among all specialists, whereas recent research suggests that vulnerability increases with increasing specialisation (Pratchett et al. 2008). Furthermore, the use of different specialisation indices can result in different estimates of specialisation, even when the same data are considered (DeVictor et al. 2010). As biodiversity becomes increasingly threatened by the combined effects of climate change and anthropogenic disturbances (Chapin et al. 2000; Thomas et al. 2004), there is a need for greater focus on the way that specialisation is assessed and interpreted to estimate vulnerability.

A variety of approaches are used to quantify ecological specialisation. The most basic measures report the number of different resource categories which are used by a particular species or population and conclude that a species is specialised if they are only using resources from a few categories (e.g. Eeley and Foley 1999; Owens and Bennett 2000). More commonly, specialisation is quantified using niche breadth indices such as the Simpsons index or the Shannon-Wiener diversity index, which provide estimates of specialisation based on richness and evenness of resource use (e.g. Munday 2004; Christensen and Kleindorfer 2009). While these types of analyses provide very general information about the degree of specialisation, if resources are not equally available they can result in misleading estimates of specialisation as species using resources in proportion to their availability may appear to have narrower niches than more specialised species (Petraitis 1979). A number of studies have
addressed this issue through the use of specialisation indices such as Smiths niche breadth measure or chi square log likelihood statistics that incorporate estimates of resource availability (e.g. Gardiner and Jones 2005; Pratchett 2007). An alternative approach to quantifying specialisation is to use measures of among-individual specialisation. In contrast to specialisation indices which determine the niche of the population as a whole, among-individual specialisation indices provide information about how variation in resource use is spread between individuals within a population (e.g. Araujo and Gonzaga 2007; Araujo et al. 2008). These metrics compare the niche size of individuals within a population to the overall population niche to estimate the degree that resource use differs between individuals (Bolnick et al. 2003). Further information on ecological specialisation can also be provided by resource selection functions. In contrast to specialisation indices, which provide a single measure of specialisation integrated across all resources categories, resource selection functions calculate selectivity for individual resource categories (e.g. Dirnwoeber and Herler 2007; Graham 2007). These functions determine whether an individual resource is used significantly more or less than expected based on its availability (Manly et al. 2002), potentially enabling predictions of how species may respond to changes in resource availability and allowing the detection of key resources that may be critical to species persistence.

Here, we compare the performance of specialisation indices using coral-feeding butterflyfishes as a model group. Using a single dataset, levels of dietary specialisation in three species of coral-feeding butterflyfishes (Chaetodontidae) around Lizard Island in the Northern Great Barrier Reef, Australia, are calculated using four different indices of specialisation - a count of the total number of prey types consumed, the Shannon-Wiener diversity index, a chi-square log likelihood index that incorporates a measure of resource availability, and an among-individual specialisation index. We then calculate resource
selection functions to investigate how individual resources are used in relation to their availability. To investigate how spatial variation in resource availability may affect estimates of specialisation, we compared levels of dietary specialisation and resource selection functions for each species across three sites in exposed front reef habitats and three sites in sheltered back reef habitats that differ in the composition and abundance of scleractinian corals which these fish feed on. Unlike many other organisms for which dietary composition has to be inferred through stomach content analysis or scat analysis, the dietary composition of butterflyfishes can be directly quantified via in-situ observations of feeding behaviour, allowing highly accurate and detailed estimation of dietary specialisation. Furthermore, the availability of dietary resources can be directly measured with ease at the same locations where feeding is observed (Pratchett 2005). Previous research has shown that coral-feeding butterflyfishes vary in their level of dietary specialisation (e.g. Pratchett 2005, 2007) and in their response to changes in resource availability, with specialised butterflyfishes showing the greatest declines in abundance following coral loss on reefs (e.g. Pratchett et al. 2004; Pratchett et al. 2006; Graham 2007; Wilson et al. 2006). These characteristics make coral-feeding butterflyfishes appropriate models for general principles of ecological specialisation.

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

Methods

STUDY SITES

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

RESOURCE AVAILABILITY

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

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

DIETARY SPECIALISATION AND SELECTIVITY
To investigate how different specialisation indices may vary in their estimates of specialisation, dietary specialisation for each species at each site was assessed using four
different indices – a simple count of the total number of different prey types consumed, the
Shannon-Wiener diversity index (Zar 1999), the Chi square log likelihood statistic $X_{L^2}$
(Manly et al. 2002) and an index of among-individual dietary specialisation (Araujo et al.
2008). For calculation of the Shannon-Wiener diversity index, the log likelihood statistic and
among-individual dietary overlap, all dietary items were grouped into 15 major prey
categories (listed in Table 3) and indices were calculated based on these categories. Dietary
selectivity for each species at each site was assessed using resource selection functions
(Manly et al. 2002), which were also calculated based on 15 major prey categories.

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

\[ H' = -\sum_{i=1}^{k} p_i \log p_i \]  

\text{eqn 1.}

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

The Chi square log-likelihood statistic $X_{L^2}$, was calculated following Manly et al. (2002). As
data were collected on selection of resource units by individual animals, but resource
availability was assessed at the population level, Model Design II with Sampling Protocol A
was used (Manly et al. 2002, eq 4.27). $X_{L^2}$ was calculated using the formula:
where \( u_{ij} \) is the proportional use of each prey type (i) by each individual (j) and \( E(u_{ij}) \) is the expected number of bites taken from prey type i by the jth individual if use is proportional to availability (Manly et al. 2002). The resulting value of \( X_{L2}^2 \) was compared to the chi-squared distribution with \( n(I-1) \) degrees of freedom (where I is the total number of prey categories) to determine the significance of selectivity exhibited by each butterflyfish species at each site. Higher values of \( X_{L2}^2 \) indicate increasing specialisation.

Variation in dietary composition between individual butterflyfishes (among-individual specialisation) was assessed using an individual niche overlap network following Araujo et al. (2008). For each species at each site a niche overlap network was defined using the programme DIETA1.0 (Araujo et al. 2008) in which the nodes of the network represented individual fishes and the connections between nodes measured the degree of dietary overlap among pairs of individuals. Each connection was assigned a weight \( w_{ij} \) ranging from 0 for no overlap to 1 for total overlap \((0 < w_{ij} > 1)\) as a measure of the pairwise dietary overlap between individuals i and j. Among-individual dietary variation (E) was then measured as the average density of all connections in the network, quantified as \( E = 1 - \bar{w}_{ij} \). Low values of E indicate that there is little individual dietary specialisation, with E equal to 0 when all individuals have identical diets; high values of E indicate that individual dietary specialisation is high, with E equal to 1 when each individual uses a unique resource. If individual-level specialisation is high, then species-level specialisation is generally low. Monte Carlo bootstrap simulations were run using DIETA1.0 for each species at each site to test the null
hypothesis that any observed dietary variation arose from individuals sampling stochastically
from a shared distribution (Araujo et al. 2008). In these simulations each individual was
reassigned the same number bites that it was observed taking, drawn randomly from the
observed distribution of the population diet via multinomial sampling. 10,000 such
populations were simulated and among individual dietary variation, E, was recalculated for
each simulated population. The null hypothesis was rejected if the empirical (observed value)
E was higher than 95% of the E values of the simulated populations.

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

\[ w_i = \frac{\sum_{j=1}^n u_{ij} / p_i}{n} \]  

\text{eqn 3.}

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

Results

CORAL COVER AND COMPOSITION

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

DIETARY COMPOSITION

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

Consumption of hard corals was highest at exposed sites where hard corals were more
abundant. Both C. lunulatus and C. trifascialis fed almost exclusively on hard corals at all
sites. Chaetodon lunulatus took between 96 to 99% of all bites from hard corals, while C.
trifascialis took 100% of all bites from hard corals at all sites except Lizard Head (Table 1).
Dietary composition varied significantly (MANOVA, P<0.05) for all three species between habitats and sites (Table 2).

DIETARY SPECIALISATION AND SELECTIVITY

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

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

*Chaetodon citrinellus* showed a high degree of dietary versatility, consuming a number of different hard coral taxa at each site (Table 1) and resource selection functions indicated that
C. citrinellus was a fairly generalised feeder (Table 3). Significant selectivity or avoidance was only shown for a few prey categories and most categories were consumed in proportion to their availability (Table 3).

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

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

All three species showed significant among-individual dietary variation at each site (P<0.001, Monte Carlo simulations). Both C. citrinellus and C. lunulatus showed high levels of among individual dietary variation across all sites (E >0.5, Individual niche overlap network), while...
C. trifascialis showed some among individual dietary variation at sheltered sites and low levels of among individual dietary variation at exposed sites (Fig. 2).

**Discussion**

The strengths and weaknesses of different specialisation indices have been reviewed several times, and most recently by DeVictor et al. (2010), but this is the first study to directly compare the performance of such indices using the same dataset. Similarly, the link between specialisation and vulnerability has been explored in depth (e.g. Colles et al. 2009), but there has been little consideration of how the measurement of specialisation may affect estimates of vulnerability. To our knowledge this is the first study to investigate the utility of different specialisation indices within the context of predicting vulnerability to environmental change.

We found that the level of dietary specialisation estimated for all three butterflyfish species varied when different specialisation indices were used, indicating that the choice of index can have a considerable impact upon estimates of the degree of specialisation. These impacts are likely to be less important for generalist species. For example patterns of dietary specialisation for C. citrinellus, the most generalist of the three study species, were similar between all four specialisation indices. But for species that are neither true generalists nor extreme specialists, indices based solely on patterns on resource use (e.g. Shannon-Wiener index) may give somewhat different estimates of specialisation to indices which incorporate resource availability (e.g. Chi square selectivity index). Chaetodon lunulatus feeds almost exclusively on hard corals and therefore could be considered to have a specialised diet, yet it feeds across a broad range of hard coral species and is considered more of a generalist feeder within the butterflyfishes that are obligate corallivores (Pratchett 2005; 2007). Specialisation levels estimated by the Shannon Wiener index for C. lunulatus were similar to those of the
generalist *C. citrinellus*, while specialisation levels estimated by the Chi square index (which considers resource availability) were more similar to those of the specialist *C. trifascialis*.

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

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

Understanding how ecological specialisation varies between individuals within a population may also be important in predicting how a species will respond to changes in resource availability. A population of individuals each specialising on a different resource may still look like a “generalist” species by some measures, but such a population may respond differently to resource depletion than another population composed of individual generalists.
Theory suggests that populations of individual specialists may be more stable and open to future evolutionary diversification (Bolnick et al. 2003; Kendall and Fox 2002, 2003). Furthermore, niche variation within a population may help to buffer against loss of particular habitats or resources and provide genetic variation needed to adapt to changing environments (Bolnick et al. 2003; Durell 2000). In cases where estimation of resource availability is not possible, measurement of among-individual variation in resource use may provide additional information about ecological specialisation and vulnerability to that gained from the use of traditional niche breadth measures. As highly specialised species are likely to have low levels of among-individual variation due to their narrow niche breadth, use of among-individual specialisation indices may be most informative when comparing vulnerability of species with more generalised ecologies.

Resource selection functions provide fine scale information on ecological specialisation, enabling greater insights into the potential response of species to changes in resource availability, and therefore vulnerability to future environmental changes, than can be gained from overall estimates of specialisation. Although overall levels of dietary specialisation estimated by the Chi square selectivity index were similar for C. lunulatus and C. trifascialis, resource selection functions indicated that the diet of C. trifascialis was much more specialised and its feeding preferences were more conserved, both in the terms of the number of resources it showed selectivity for and in the spatial variation of its selectivity. Consequently, C. trifascialis is likely to be highly vulnerable to changes in resource availability, particularly to changes in the abundance of the Acropora corals that it preferentially feeds on (Pratchett 2005; 2007). In contrast, C. lunulatus utilised a large number of resources at each site and selectivity of specific dietary items varied between sites which also varied in their resource availability. These findings suggest that even though C.
*lunulatus* has a reasonably specialised diet, it is likely to be fairly resilient to changes in resource availability. Such responses to changes in resource availability have already been reported for both species. In French Polynesia, the abundance of *C. trifascialis* declined by almost 100% following declines in the abundance of its preferred *Acropora* corals (Berumen and Pratchett 2006), while on the Great Barrier Reef, *C. lunulatus* has been shown to alter its diet in response to a loss of some coral taxa (Pratchett et al. 2004). These responses highlight the predictive value of resource selection functions and provide justification for their use in the identification of key resources which may be critical to a species’ persistence.

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

While the example presented here comes from a single family of coral reef fishes, we believe the butterflyfishes are useful models for understanding more general trends and that these findings reflect ecological principles that transcend the system. Calculating the four
specialisation indices from the same dataset removes any variation that might have resulted
from simply comparing the findings of several independent studies. Consequently, we are
confident that the differences in the levels of specialisation estimated by each of the four
indices reflect actual differences and not sampling effects. The three species we included in
our analysis displayed a range of specialisation levels, from generalist to extreme specialist,
and provide an indication of how these indices are likely to perform across species with
varying levels of specialisation. Moreover, the comparison of two differing habitats illustrates
how estimates of specialisation may be affected by temporal or spatial differences in resource
availability.

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

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McKinney ML (1997) Extinction vulnerability and selectivity: Combining ecological and


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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Hard corals (%)</th>
<th>Soft corals (%)</th>
<th>Other macro invertebrates (%)</th>
<th>Imperceptible items (%)</th>
<th>Total number hard coral species consumed</th>
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<td>75.3</td>
<td>1.1</td>
<td>2.4</td>
<td>21.1</td>
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<td>6.8</td>
<td>3.1</td>
<td>34.2</td>
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<tr>
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<td>74.9</td>
<td>1.3</td>
<td>2.5</td>
<td>21.3</td>
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<tr>
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<td>3.0</td>
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<td>11.8</td>
<td>1.6</td>
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<td>Vickies</td>
<td>96.2</td>
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<td>3.4</td>
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<td>0.0</td>
<td>0.0</td>
<td>15</td>
<td></td>
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</tbody>
</table>

\(^1\) 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.

<table>
<thead>
<tr>
<th>Species</th>
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<th>Pillai’s trace</th>
<th>d.f.</th>
<th>P</th>
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<td>15, 100</td>
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<td>Site (Habitat)</td>
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<td>15, 100</td>
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<td>Site (Habitat)</td>
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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).

<table>
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<th>Staghorn Acropora</th>
<th>Other Acropora</th>
<th>Pocillopora damicornis</th>
<th>Other Pocilloporidae</th>
<th>Montipora sp.</th>
<th>Porites sp.</th>
<th>Favidae</th>
<th>Isopora sp.</th>
<th>Other hard corals</th>
<th>Soft coral</th>
<th>Reef substrate^a</th>
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**C. lunulatus**

Exposed

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</table>

\* 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, $X_{1,2}^2$; and (D) among-individual dietary variation, E. Data are means for each habitat type ± 1SE.
Figure 1
Figure 2