

Rarity and extinction risk in coral reef angelfishes on isolated islands: interrelationships among abundance, geographic range size and specialisation

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Abstract Determining the species most vulnerable to increasing degradation of coral reef habitats requires identification of the ecological traits that increase extinction risk. In the terrestrial environment, endemic species often face a high risk of extinction because of an association among three traits that threaten species persistence: small geographic range size, low abundance and ecological specialisation. To test whether these traits are associated in coral reef fishes, this study compared abundance and specialisation in endemic and widespread angelfishes at the remote Christmas and Cocos Islands in the Indian Ocean. The interrelationships among traits conferring high extinction risk in terrestrial communities did not apply to these fishes. Endemic angelfishes were 50–80 times more abundant than widespread species at these islands. Furthermore, there was no relationship between abundance and ecological specialisation. Endemic species were not more specialised than widespread congeners and endemics used similar resources to many widespread species. Three widespread species exhibited low abundance and some degree of specialisation, which may expose them to a greater risk of local extinction. For endemic species, high abundance and lack of specialisation on susceptible

habitats may compensate for the global extinction risk posed by having extremely small geographic ranges. However, recent extinctions of small range reef fishes confirm that endemics are not immune to the increasing severity of large-scale disturbances that can affect species throughout their geographic range.

Keywords Endemic species · Macroecology · Ecological versatility · *Centropyge* · Reef fish · Christmas Island

Introduction

The causes of rarity have long intrigued biologists (Darwin 1859) and are critical to conservation biology because rare species may experience a high intrinsic risk of extinction (Soulé 1986; Simberloff 1988). Rarity can be defined in terms of whether a species has a large or small geographic range, high or low abundance, or specialist or generalist pattern of resource use (Rabinowitz 1981). Species with small geographic ranges (endemics), low abundance or specialist patterns of resource use appear susceptible to extinction from multiple causes, including local disturbances, the demographic attributes of small populations and habitat loss (Lawton 1993; McKinney 1997; Gaston 1998; Munday 2004). Indeed, the highest rates of extinction have been recorded for endemic species on isolated islands (Frankham 1998; Whittaker 1998). Consequently, the study of island endemics is imperative to understand the processes that combine to increase extinction risk and directly affect global biodiversity.

Rare species face a greater intrinsic risk of extinction if two or more of the characteristics that threaten population persistence are associated. One of the most widely reported

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macroecological patterns is the positive relationship between geographic range size and abundance (Gaston et al. 1997). Widely distributed species tend to be abundant while small-range relatives are often scarce. This pattern is considered one of the few fundamental laws in ecology (Lawton 1999) because it has been observed across a broad array of taxa and systems, and spans a variety of spatial and temporal scales (Lawton 1993; Brown 1995; Gaston 1994, 1996; Gaston et al. 1997; McKinney 1997). As a consequence of this relationship, endemic species are expected to face a dual threat of extinction associated with either small range size or low abundance—often referred to as a double jeopardy (Gaston 1998).

Range size also tends to be positively correlated with niche breadth (Brown 1995; Lawton and May 1995; McKinney 1997). This relationship is thought to exist because a species' geographic distribution will be constrained by the distribution of its resources, and thus on average, specialist species tend to have smaller geographic ranges than generalists (Brown 1984; Gaston et al. 1997). Generalist species can potentially persist in more locations than specialist species because they can utilise a greater variety of resources (Gaston 1994; Lawton 1995; Kunin and Gaston 1997).

Not only do specialist species tend to have smaller range sizes, but they also appear to have lower abundance than generalists (Brown 1984; Hanski et al. 1993). Specialists are expected to be more vulnerable to disturbances because changes in a just a few resources can have profound effects on their abundance. Indeed specialisation is considered a fundamental trait that increases extinction risk (Foufopoulos and Ives 1999; Fisher et al. 2003; Julliard et al. 2004) and has been linked to recent and past extinctions (McKinney 1997). The potential for a positive association among specialisation, small range size and low abundance means that endemic species could face a triple jeopardy risk of extinction (Munday 2004).

The majority of published studies on extinction risk and macroecology have focussed on terrestrial communities. Determining the generality of terrestrial based patterns and theories in the marine environment is crucial for identifying marine species most at risk of extinction (Jones et al. 2002; Dulvy et al. 2003, 2004); this is an urgent priority given the recent global changes that are occurring in this system (Hughes et al. 2003; Orth et al. 2006; Bruno and Selig 2007). For example, an estimated 20% of the world's coral reefs have recently been seriously degraded and a further 50% is in decline (Wilkinson 2004). The loss of coral cover has caused significant changes in the abundance and community structure of reef associated species, including coral reef fishes (Jones et al. 2004; Graham et al. 2006; Pratchett et al. 2008). The greatest impact has been on those species with specialist habitat (Munday 2004;

Wilson et al. 2006, 2008) or dietary requirements (Pratchett et al. 2006; Graham 2007), particularly those dependent on live branching corals. If these specialists also have restricted ranges and low abundance then this will greatly increase their intrinsic risk of extinction (Munday 2004).

This study tests extinction risk theory in the marine environment by examining whether endemic reef fishes from isolated islands also have lower abundances and are more specialised than their widespread congeners. This study examines reef fishes at the remote Christmas and Cocos Islands in the northeastern Indian Ocean. The assemblage of angelfishes at these islands contains both endemic and geographically widespread species, which offers an ideal opportunity to compare patterns of abundance and specialisation among geographically restricted and widespread species. The specific aims of this study were to test whether:

1. Island endemics are less abundant than widespread relatives
2. Island endemics use a narrower range of resources than widespread relatives
3. Specialists are less abundant than generalists
4. Island endemics exploit different niches to widespread species
5. Island endemics face a triple jeopardy risk of extinction

Methods

Study location and study species

This study focussed on pygmy angelfishes (genus *Centropyge*), which are found on coral reefs worldwide, typically inhabiting depths between 0–80 m (Allen et al. 1998). There are 31 species of pygmy angelfishes, with a centre of diversity in the Indonesia-Philippines region (Allen et al. 1998). The study locations, Christmas Island (10°30' S, 105°40' E) and the Cocos (Keeling) Islands (12°12' S, 96°54' E) are situated approximately 350 and 1,000 km southwest of Indonesia. Nine species of pygmy angelfishes have been recorded at Christmas Island and seven at the Cocos Islands (Allen and Smith-Vaniz 1994; Allen et al. 2007; Hobbs et al. 2007).

Geographic range

The extent of occurrence (sensu Gaston 1994) was calculated as a proxy for range size using published distributions for all but one of the pygmy angelfish species at Christmas and Cocos Islands (Allen et al. 1998). The estimated range sizes of study species were: *Centropyge bicolor* (32,000 km²),

C. bispinosa (48,000 km²), *C. eibli* (27,000 km²), *C. flavicauda* (43,000 km²), *C. flavissima* (1,000 km²), *C. jocular* (1,000 km²), *C. tibicen* (24,000 km²) and *C. vroloki* (32,000 km²). *C. colini* is only found deeper than 60 m at Christmas and Cocos Islands and was not included in this study because it is beyond the limits of safe SCUBA diving. *C. flavissima* (Indian Ocean subspecies) and *C. jocular* are endemic to Christmas and Cocos Islands, whereas the other six study species are more widely distributed throughout the Indian and/or Pacific Oceans (Allen et al. 1998). The Indian Ocean subspecies of *C. flavissima* is separated by more than 3,000 km from the Pacific Ocean subspecies, and this distance combined with different facial markings and colouration suggests that it is a separate species (Allen et al. 1998).

Three of the study species (*C. bicolor*, *C. tibicen* and *C. vroloki*) are distributed throughout the west Pacific and the Indonesian–Philippines region with Christmas and Cocos Islands representing the western edge of their range. Two widespread species (*C. bispinosa* and *C. flavicauda*) are distributed throughout the Indian and Pacific Oceans and Christmas and Cocos Islands occur close to the centre of their range. The study islands also occur near the centre of the geographic range of *C. eibli*, which is distributed from Sri Lanka to the Western Australian coastline.

Abundance

Densities of each angelfish were estimated by underwater visual censuses on the outer reef slope at 12 sites at the Cocos Islands and 14 sites at Christmas Island in November and December 2002. At each site, densities of angelfish were attained using four replicate 50 × 6 m strip transects at 20 m depth. This depth was chosen because this is close to the mean depth range used by all study species (see “Results”). Surveys were also conducted at 5 m depth, but only one species was observed (*C. flavissima*), and therefore these data were not analysed. Preliminary observations at 40 m depth only found two species, and only one species was common (*C. jocular*). The density of *C. flavissima* at 5 m and *C. jocular* at 40 m was similar to their density at 20 m. Due to unequal variances, a Mann–Whitney *U* test was used to compare the mean abundance of endemic and widespread pygmy angelfishes.

Resource use

Patterns of resource use were determined for endemic and widespread angelfishes at Christmas Island in May and June 2005. Three aspects of resource specialisation considered important to reef fishes were examined: depth range, microhabitat use and diet. Observations and collections were undertaken while SCUBA diving at survey

sites on the outer reef slopes on the eastern, northern and western sides of the island.

Depth range

The depth range of each study species was estimated at Christmas Island by recording the depth at which individuals were encountered while swimming up the reef slope from 40 to 0 m at north coast sites. Preliminary observations revealed that most individuals of the study species occur above 40 m, and the limitations of SCUBA diving also prevented detailed surveys below 40 m. While swimming up the reef, care was taken to make sure equal time was spent surveying across all depths. Surveys were repeated at several sites until a minimum cumulative total of 20 individuals was achieved for each species. A total of 20 individuals was chosen because of the time required to locate 20 individuals of the rarer species. Observations on 84 individuals of a common species (*C. jocular*) indicated that estimates based on 20 individuals was a reliable representation of depth range. The number of individuals encountered per species varied from 20 to 84, and to allow for effective statistical comparison of depth ranges, 20 individuals were randomly subsampled from the more common species. Regression analysis was used to test for a relationship between geographic range size and depth range. For depth range, the mean deviation was used as a measure of niche breadth, and this was calculated by taking the average of the absolute deviations from the mean depth inhabited by a species (based on 20 individuals).

Microhabitat use

Underwater observations were conducted to compare the variety of microhabitats used by endemics and widespread congeners. To quantify microhabitat use, an individual or social group was identified and its home range determined by observing the behaviour and movements of the individual(s) for approximately 5 min. Once the home range was determined a 3-m line intercept transect was placed on the substrate through the centre of the territory and the amount of each microhabitat within the territory was recorded. Ten types of substrate microhabitat were identified (Table 1). Due to differences in abundance and spatial distribution, the number of individuals or social groups surveyed varied between species: *C. jocular* (*n* = 24), *C. flavissima* (*n* = 19), *C. bicolor* (*n* = 6), *C. eibli* (*n* = 13), *C. bispinosa* (*n* = 14), *C. tibicen* (*n* = 5), *C. flavicauda* (*n* = 14), and *C. vroloki* (*n* = 7). To determine if there was a relationship between geographic range size and the diversity of microhabitats, geographic range size of each species was correlated with the diversity of habitats in their

Table 1 Ten substrate microhabitats used by angelfishes at Christmas Island

Microhabitat	Characteristics
Calcareous algae	Encrusts the substrate and is often pink in colour
Turfing algae	Epilithic algae growing on the surface of the substrate
Branching corals	Arborescent, corymbose, columnar and digitate scleractinian corals
Massive corals	Mound shape, spherical and hemispherical scleractinian corals
Tabular corals	Plating or laminar scleractinian corals
Foliaceous corals	Thin leaf-like scleractinian corals that form whorls
Encrusting corals	Scleractinian corals growing as a thin veneer over the substrate
Sand	Silicious or calcareous grains
Bare rubble	Parts of dead coral skeletons that are not covered in live algae of coral
Soft corals	Alcyonarian corals that lack a hard calcium carbonate skeleton

Descriptions are based on Veron (1986) and Eagle et al. (2001)

home ranges. The Shannon–Weiner index, $H' = -\sum p_j \log p_j$ (where P is the proportion of each habitat used) was to estimate habitat diversity within home ranges because it accounts for both the number and evenness of different habitats used.

Diet

The diet of endemic and widespread angelfish was estimated by examination of gut contents. At Christmas Island, haphazardly selected individuals of the eight study species were collected by spearfishing. Within 1–2 h of collection, the stomach of each fish was dissected out and placed in 10% buffered seawater-formalin solution. After fixation for 24 h, the stomach and contents were transferred to 80% ethanol for storage. Gut contents were later examined in the laboratory by cutting the stomach open and spreading the contents onto a gridded petri dish. Gut contents of each individual were examined under a stereo-dissecting microscope and quantified by recording the food type present at 10 randomly assigned point intercepts on the grid. The food types were allocated to one of 6 categories (Table 2). Gut contents were quantified for 19–21 individuals of each species. The Shannon–Weiner diversity index was used to estimate dietary specialisation of each species.

Table 2 Six diet categories used to classify food types consumed by angelfishes at Christmas Island

Diet	Characteristics
AOM	Amorphous organic matter that lacks form (detritus)
Chlorophyta	Filamentous or thallate green algae
Rhodophyta	Filamentous or thallate red algae
Sediment	Silicious or calcareous grains
Sponge	Honeycomb-like structure with perforated walls or loose spicules
Miscellaneous	Rare items such as urchin spines, invertebrate exoskeletons, fish scales, cyanobacteria

Descriptions based on Eagle and Jones (2004)

Ecological differences between endemic and widespread species

Potentially, endemic and widespread species could exhibit similar levels of specialisation but may utilise a completely different suite of resources. To determine if endemics inhabit different depths than widespread species an ANOVA was used to compare the mean depth inhabited based on 20 individuals for each species (described above).

Canonical discriminant analysis (CDA) was used to determine if endemics utilise different microhabitats compared to widespread species. CDA focuses on the variation between known groups (in this case species) and can produce a two dimensional representation of multivariate data. The closer that species are grouped together in multivariate space (displayed on a biplot), the greater the similarity in the types and frequency of microhabitats used. To examine if species overlapped in the microhabitat, 95% confidence intervals were plotted as circles around the group centroids using the formula:

$$95\% \text{ CL} = \sqrt{(\chi^2_{0.05/n})}$$

where n represents the number of replicates (Seber 1984). The structure coefficients were plotted as vectors to show the microhabitats that were important in distinguishing between species.

CDA was also used to compare the diets of endemic and widespread species. Vectors were plotted on the CDA biplot using the structure coefficients to illustrate the importance of particular food types in distinguishing between the diets of different species. The miscellaneous diet category was not included in the CDA analysis because it was present in less than 2% of the total number of individuals and was not informative in distinguishing between species.

Multiple threats of extinction

To determine the proportion of study species facing multiple threats of extinction required identification of species that exhibit different combinations of the three forms of rarity (small range size, low abundance and specialisation). The following definitions were used to designate species as exhibiting one of the forms of rarity. The two endemic species were classified as having a small range size (<2,000 km²). Species were deemed to have low abundance if their mean density was below 3 individuals per 300 m². The thresholds for small range size and low abundance were post hoc definitions that were determined by the distribution of these traits in the study species. Although the categories of small range size and low abundance were arbitrarily defined, they are representative of the way these terms are used to describe reef fish. To compare relative specialisation within the group of angelfishes, we identified 1–2 species that were the most specialised for any of the three components of resource use. Using this method specialist species were defined as those species that had either a depth range mean deviation less than 3.5 or a microhabitat use diversity index less than 0.5 or a diet diversity index less than 0.35.

Results

Range size–abundance

The mean abundance of endemic pygmy angelfishes was significantly higher than widespread species at both Christmas (Mann–Whitney U : $Z = 2.0$, $P < 0.05$) and Cocos Islands (Mann–Whitney U : $Z = 2.0$, $P < 0.05$). At Christmas Island, the mean density of the two endemic pygmy angelfishes (8.61 per 300 m²) was more than 50 times higher than the mean density of widespread relatives (0.16 per 300 m²). Eight widespread angelfishes from other genera (*Apolomichthys*, *Genicanthus*, *Paracentropyge*, *Pomacanthus*, *Pygoplites*) also occur at Christmas Island, and these species had low abundances (<1.02 individuals per 300 m²), or were absent in the surveys. At the Cocos Islands, the mean density of the two endemic species (6.6

per 300 m²) was more than 80 times greater than widespread congeners (0.01 per 300 m²) and other angelfishes (0.08 per 300 m²). Therefore, out of a total of 16 angelfish species recorded at Christmas and Cocos Islands, the endemic species were by far the most abundant.

Range size–specialisation

There was no relationship between the breadth of the depth range inhabited by pygmy angelfish at Christmas Island and geographic range size ($F = 1.31$, $R^2 = 0.18$, $P = 0.30$, Fig. 1a). The endemic *C. flavissima* had the broadest depth range (5–40 m), while the endemic *C. jocularis* had the third broadest depth range (12–40 m).

No relationship was found between microhabitat specialisation and geographic range size ($F = 0.21$, $R^2 = 0.034$, $P = 0.66$, Fig. 1b). Endemic angelfishes used a similar diversity of microhabitats as most of the widespread species. Seven of the eight study species exhibited habitat use diversity indices (H') between 0.76 and 0.89. The notable exception was *C. flavicauda* which is the second most widely distributed study species yet utilised a considerably narrower range of microhabitats than other species ($H' = 0.45$).

No relationship was found between dietary specialisation and geographic range size ($F < 0.001$, $R^2 < 0.001$, $P = 0.997$, Fig. 1c). The diversity of food types consumed by the endemics ($H' = 0.38$ and 0.45) was within the range exhibited by widespread congeners ($H' = 0.28$ –0.51).

Specialisation–abundance

There was no relationship between abundance and any of the resource specialisation measures: depth range ($F = 0.75$, $R^2 = 0.11$, $P = 0.42$, Fig. 2a), habitat use ($F = 0.02$, $R^2 = 0.004$, $P = 0.88$, Fig. 2b) and diet ($F = 0.001$, $R^2 = 0.0002$, $P = 0.97$, Fig. 2c). Rerunning the analyses with the two highly abundant endemic species excluded did not substantially change any of the relationships ($P > 0.2$ for all comparisons).

Ecological differences between endemics and widespread species

Not only was niche breadth similar between endemic and widespread pygmy angelfishes, but endemics also occupied the same niches as some of the widespread species. Endemic angelfishes did not occupy unique depth zones, but rather the position of their depth range overlapped considerably with most of the widespread congeners (Fig. 3). The endemic *C. flavissima* was found between depths of 5 and 40 m (mean = 21.5 ± 1.6 SE) which was similar to four widespread species, but was significantly

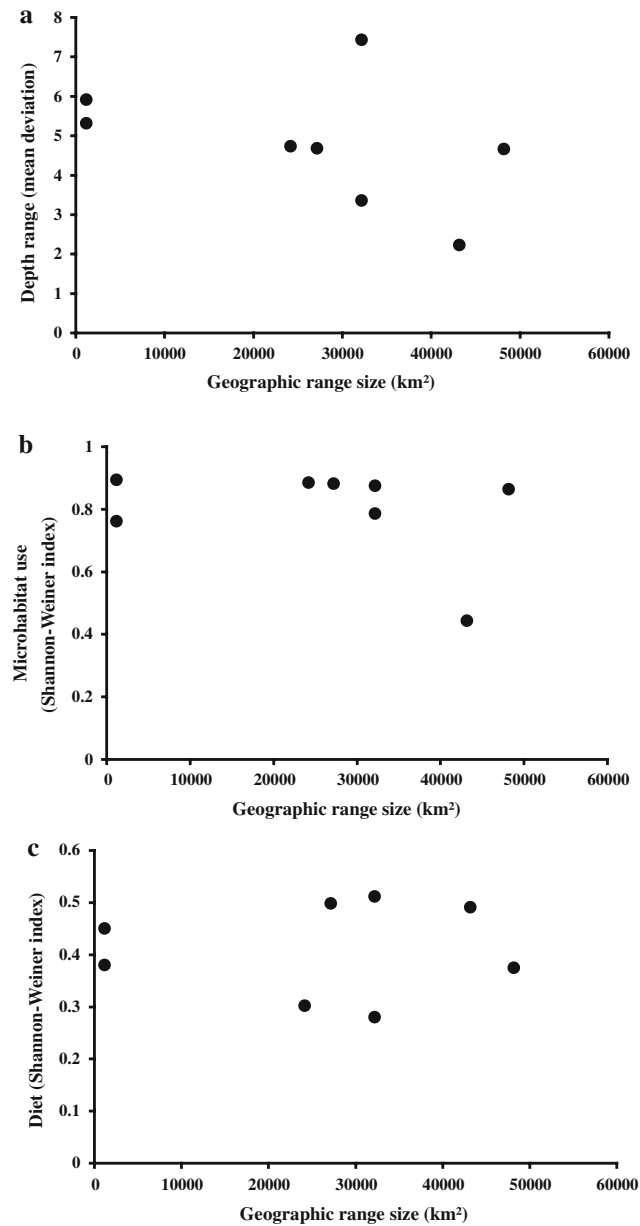


Fig. 1 The relationship between geographic range size (km²) and resource use for pygmy angelfishes at Christmas Island. Resource use includes: **a** depth range (mean deviation), **b** microhabitat use (Shannon–Weiner index) and **c** diet (Shannon–Weiner index)

shallower than the mean depths inhabited by *C. tibicen* and *C. flavicauda*. The endemic *C. jocular* inhabited depths between 12 and 40 m (mean = 28.0 ± 1.8 SE) and this was similar to all species, except *C. vroloki*, which occupied shallower water. Although there was variation among species in the mean depth inhabited (one-way ANOVA: $F = 10.1$, $df = 7$, $P < 0.001$, Fig. 3), Tukey's test revealed most of the significant differences ($P < 0.05$) were due to two widespread species, *C. vroloki* and *C. tibicen*, that occupied depths that were shallower and deeper (respectively) than the rest of the species.

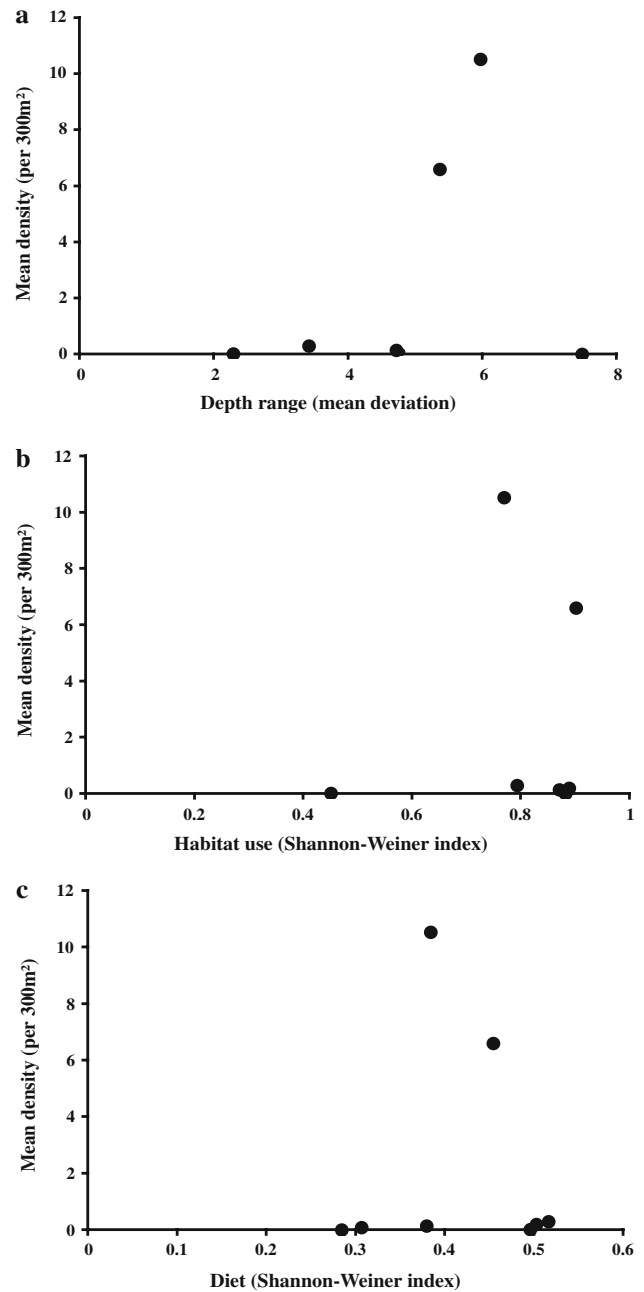
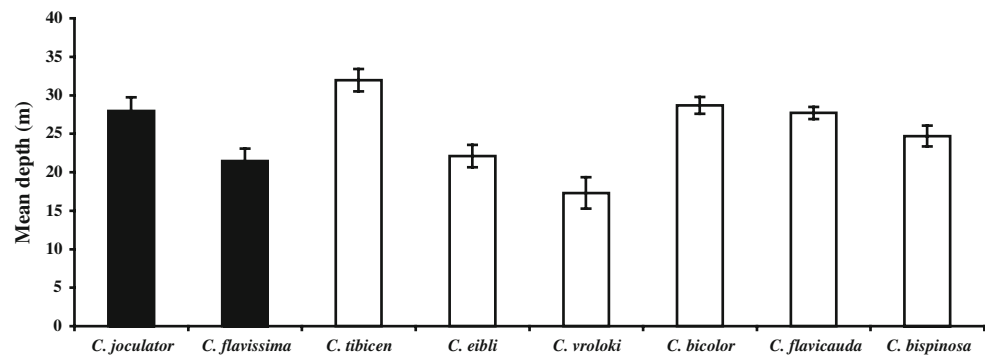


Fig. 2 The relationship between mean density (per 300 m² ± SE) and resource use for pygmy angelfishes at Christmas Island. Resource use includes: **a** depth range (mean deviation), **b** microhabitat use (Shannon–Weiner index) and **c** diet (Shannon–Weiner index)

Patterns of microhabitat use were compared using a CDA that explained 85.4% in the first two canonical axes (CV1 = 69.7% and CV2 = 15.7%). The types of microhabitats utilised by endemics were broadly similar to those used by most of the widespread species (Fig. 4a). The endemic *C. jocular* used the same microhabitats as the widespread species *C. bicolor*, and the endemic *C. flavissima* inhabited similar microhabitats as the widespread

Fig. 3 The mean depth ($m \pm SE$) of water inhabited by endemic (black bars) and widespread (white bars) pygmy angelfishes at Christmas Island



species *C. eibli* and *C. bispinosa*. Neither of the endemics was associated with live branching corals. Three of the widespread species, *C. flavicauda*, *C. tibicen* and *C. vroloki*, utilised microhabitats that were distinct from the other species. *C. flavicauda* was found in microhabitats dominated by calcareous and turfing algae, *C. tibicen* inhabited areas rich in sand, while *C. vroloki* occupied areas containing relatively high amounts of tabular and branching corals.

Similarities in the diet of the study species were examined using CDA and the resulting biplot explained 87.3% of the variance ($CV1 = 66.2\%$ and $CV2 = 21.1\%$). Endemic species did not feed on unique resources, but rather their diet overlapped with some of the widespread species (Fig. 4b). The diet of the endemic *C. jocularator* overlapped with that of the widespread *C. bispinosa* and was characterised by relatively high amounts of amorphous organic matter and low amounts of sponge. The endemic *C. flavissima* consumed food types similar to the widespread species *C. bicolor* and *C. eibli* and their diets typically contained relatively high amounts of chlorophyta and low amounts of sediment. The widespread species *C. tibicen*, *C. flavicauda* and *C. vroloki* each had diets that were distinct from the rest of the study species.

Multiple extinction threats

Examining the interrelationships among range size, abundance and specialisation revealed that none of the angelfish species at Christmas and Cocos Islands faced a triple jeopardy (i.e., no species had small range size, low abundance and was a resource specialist) (Fig. 5). Three of the widespread species (*C. flavicauda*, *C. tibicen* and *C. vroloki*) had dual threats of extinction associated with low local abundance at Christmas and Cocos Islands and a relatively high degree of specialisation. Endemic species, however, did not have low abundance or specialised patterns of resource use, and therefore, their greatest risk comes from having a small range size. The remaining three widespread species had a single threat of extinction associated with low abundance at Christmas and Cocos Islands.

Discussion

This study of coral reef angelfishes at two isolated islands did not find support for positive associations among small geographic range, low abundance or ecological specialisation evident for many terrestrial organisms. In fact, some opposite patterns appeared to hold, with endemics being 50–80 times more abundant than widespread species, and being among the more generalist species in terms of depth range, diet and habitat use. These factors are expected to partially compensate for any global extinction risk posed by their small range and geographic isolation. In contrast, some widespread species exhibited a combination of specialisation and low abundance and this may expose them to a local extinction risk at these isolated islands, although they are unlikely to be at risk of global extinction due to their large geographic ranges.

The positive relationship between range size and abundance is regarded as “one of the most general and robust patterns in nature” (Gaston et al. 1997), yet the inverse relationship was found in this study. Endemic reef fishes have also been found to have relatively high abundances in other locations (Fishelson 1977; Hourigan and Reese 1987; Randall 1998; Allen et al. 1998; Jones et al. 2002; DeMartini 2004; DeMartini and Friedlander 2004). A large proportion of endemic reef fishes are found on remote islands (Jones et al. 2002), and in the terrestrial environment, the few cases where endemic species are abundant also occurs in isolated habitats or locations (Blackburn et al. 1997; Päävinen et al. 2005; Reif et al. 2006). Isolation may allow endemics to become better adapted to local conditions, thereby enabling them to exploit unoccupied niches or out-compete other species (Hourigan and Reese 1987; Thiollay 1997; Reif et al. 2006). However, in this study, the highly abundant endemic angelfishes used the same resources as widespread relatives, and often coexisted with congeners in overlapping territories with no signs of competitive interactions (cohabiting angelfish have also been reported elsewhere: Eagle et al. 2001). Potentially, endemic species may be more efficient at exploiting the same resources used by widespread congeners.

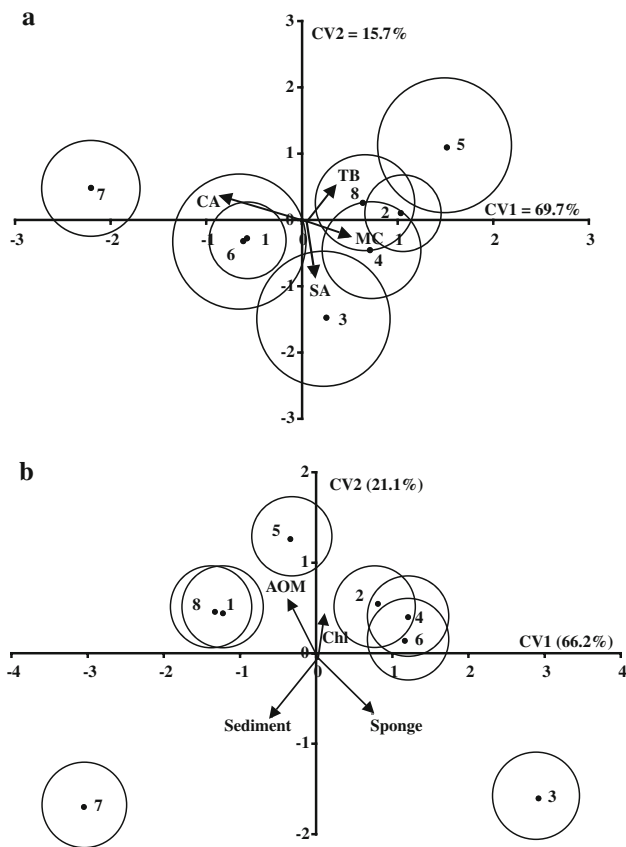


Fig. 4 **a** A canonical discriminant analysis (CDA) of microhabitat use of pygmy angelfishes at Christmas Island. The first two canonical variates explained 69.7% (CV1) and 15.7% (CV2) of the variation. Mean group centroids are plotted for each species with circles representing 95% confidence limits. Habitat types important to distinguishing between diets of the study species are shown as vectors (CA calcareous algae, MC massive corals, SA sand, TB tabular corals). Species labelled 1 and 2 are the endemic *Centropyge jocularis* and *C. flavissima*, respectively. Widespread species are numbered in order from 3 to 8: *C. tibicen*, *C. eibli*, *C. vroloki*, *C. bicolor*, *C. flavicauda* and *C. bispinosa*. **b** A canonical discriminant analysis (CDA) of the diets of pygmy angelfishes at Christmas Island. The first canonical variates explained 66.2% (CV1) and 21.1% (CV2) of the variation. Mean group centroids are plotted for each species with circles representing 95% confidence limits. Food types important to distinguishing between diets of the study species are shown as vectors (AOM amorphous organic matter, Chl chlorophyta). Species labelled 1 and 2 are the endemic *Centropyge jocularis* and *C. flavissima*, respectively. Widespread species are numbered in order from 3 to 8: *C. tibicen*, *C. eibli*, *C. vroloki*, *C. bicolor*, *C. flavicauda* and *C. bispinosa*

Alternatively, other ecological or life history traits, not associated with resource use, may be responsible for high abundances. Given the highly variable recruitment characteristic of most reef fishes (Doherty and Williams 1988; Doherty 1991), possessing an ability to maintain high abundances would be critical to increase the persistence time (McKinney 1997). Endemic reef fishes without such adaptive traits will have low abundances and therefore are

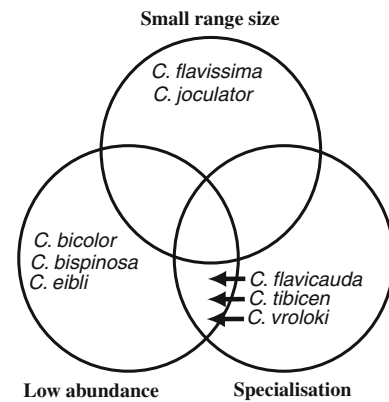


Fig. 5 A Venn diagram illustrating the number of pygmy angelfishes that have multiple threats of extinction associated with small range size (<2,000 km²), low abundance (<3 individuals per 300 m²) and specialisation (depth range mean deviation <3.5, or microhabitat use index <0.5, or diet index <0.35)

unlikely to be present in a community because they have already gone extinct (“extinction filtering” see Gaston 1998; Johnson 1998).

Range size is expected to be negatively associated with specialisation because the geographic distribution of a specialist is constrained by the distribution of a limited number of resources (Brown 1984). While some studies of reef fishes have found support for such a relationship (Hawkins et al. 2000), others studies have not (Jones et al. 2002; this study). A lack of supporting evidence could occur because the appropriate resources have not been examined. However, this study found endemic fishes were not more specialised than widespread congeners in both habitat and dietary resources, including those resources that have been found to correlate with range size in other reef fish studies (Hawkins et al. 2000). In addition, specialisation is predicted to covary across a number of resources (Brown 1995, McKinney 1997), and in this study, endemic species were generalists in all measures of resource use (depth range, microhabitat use and diet).

Abundance is predicted to be positively correlated with niche breadth (Brown 1984). While several reef fish studies have found evidence of such a relationship (Meekan et al. 1995; Bean et al. 2002; Jones et al. 2002; Munday 2004; Pratchett et al. 2008), no such support was found in this study. Abundance was not related to depth range, microhabitat use or diet. Support for this relationship is also generally lacking in the terrestrial environment and the reasons for the hypothesised relationship are not obvious (Gaston et al. 1997). If the abundance–specialisation relationship is dependent on a positive range-size abundance relationship and a positive range size–niche breadth relationship, then the predicted abundance–specialisation relationship would not be expected in this study because the other two relationships were not found.

When range size is associated with low abundances and specialisation, endemic species face an extreme risk of extinction (Angermeier 1995; Munday 2004). At least one example of such a triple jeopardy has been documented for reef fishes (Munday 2004) and instances of double jeopardy have also been reported (Jones et al. 2002). However, it is fortunate that such relationships are not universal (Hourigan and Reese 1987; Randall 1998; Allen et al. 1998; DeMartini 2004; Pratchett et al. 2008). In this study, extinction risk in endemic species due to small range size is buffered by a high abundance and a generalist pattern of resource use. Because of their high abundance and lack of specialisation, the greatest threats to endemic angelfishes are likely to be disturbances that impact on a scale that encompasses all of their geographic range.

The greatest broadscale threats to coral reef fishes are overfishing and a loss of live coral habitat due to increasing sea temperatures (Jennings et al. 1999; Dulvy et al. 2003; Pratchett et al. 2008; Munday et al. 2008). Although the endemic *C. jocularis* is collected for the aquarium fish trade, overfishing is unlikely because there is only one collector who visits a small number of sites at the Cocos Islands and the annual catch represents less than 1% of the population. Widespread loss of live coral has caused local extinctions of small reef fishes on Indian Ocean reefs (Graham et al. 2006), and further decreases in live coral habitat are predicted, particularly for the region including Christmas and Cocos Islands (Sheppard 2003). While pygmy angelfishes do not feed on live coral, they do rely on coral reef habitat for shelter sites (Allen et al. 1998), so much so, that they do not persist on reefs when habitat complexity collapses (Sano et al. 1987). Therefore, the immediate death of corals is likely to have little impact on pygmy angelfishes, however, the long-term impact (reduced habitat complexity) is likely to pose a significant threat to these small-bodied reef fishes (Sano et al. 1987; Wilson et al. 2006).

Due to the enormous diversity of marine fishes currently threatened by a multitude of impacts, there is an urgent need to identify the type of species most at risk, and therefore of greatest priority to conservation efforts (Dulvy et al. 2003). Although there has been considerable research on extinction risk in terrestrial species and large marine species (e.g., cetaceans), differences in life histories and environmental conditions make it difficult to predict extinction risk in marine fishes based on these groups. For example, marine fishes were thought to be resistant to extinction due to their large geographic ranges and high fecundities, however, it appears that their risk of extinction may be just as high as terrestrial species (Dulvy et al. 2003). In the terrestrial environment, small-bodied species are often short-lived and prone to extinction, while large, long-lived species are least likely to go extinct (Diamond 1984). In marine fishes, large

bodied species have the greatest vulnerability to fishing (Dulvy and Reynolds 2002; Reynolds et al. 2005), while small-bodied fishes appear most vulnerable to the loss of habitat complexity and shelter holes (Wilson et al. 2006). Given that endemic reef fishes tend to have smaller body sizes (Hawkins et al. 2000), we may expect endemic species to be most vulnerable to impacts that reduce habitat complexity. Determining which traits predispose marine fishes to a high risk of extinction will depend on the type of impact being considered.

Overall, this study has found that terrestrial macroecological patterns associated with extinction risk do not necessarily apply to reef fishes. Endemic angelfishes at the remote Christmas and Cocos Islands were not specialists and did not have low abundance and therefore do not face an extreme risk of extinction. The reason why endemics can reach such extraordinary abundance on isolated islands requires further investigation. Exploration of macroecological patterns in other marine taxa will be necessary to identify whether ecological factors combine to increase extinction risk. While the risk of extinction for the endemic species in this study appears to be relatively low, conservation of endemic species should remain a priority given that the greatest extinction rates in the terrestrial environment have been reported for endemics on offshore islands (Frankham 1998; Whittaker 1998), and the only known extinctions of coral reef fishes have been endemics on isolated islands (Dulvy et al. 2003). Although high abundance and generalist patterns of resource use may compensate for the risks of being restricted to a small area, it may not be sufficient to buffer endemics from the impacts of broadscale disturbance events that have been predicted to increase in ocean environments.

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