



ORIGINAL
ARTICLE



Biogeography and the structure of coral reef fish communities on isolated islands

Jean-Paul A. Hobbs^{1,2*}, Geoffrey P. Jones^{1,2}, Philip L. Munday^{1,2},
Sean R. Connolly^{1,2} and Maya Srinivasan^{1,2}

¹Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville 4811, Qld, Australia,
²School of Marine and Tropical Biology, James Cook University, Townsville 4811, Qld, Australia

ABSTRACT

Aim To determine the applicability of biogeographical and ecological theory to marine species at two remote island locations. This study examines how biogeography, isolation and species geographic range size influence patterns of species richness, endemism, species composition and the abundance of coral reef fishes.

Location Christmas Island and the Cocos (Keeling) Islands in the tropical eastern Indian Ocean.

Methods Published species lists and underwater visual surveys were used to determine species richness, endemism, species composition and abundance of reef fishes at the islands. These data were statistically compared with patterns of species composition and abundance from the neighbouring 'mainland' Indonesian region.

Results The two isolated reef fish communities were species-poor and contained a distinct taxonomic composition with an overrepresentation of species with high dispersal potential. Despite low species richness, we found no evidence of density compensation, with population densities on the islands similar to those of species-rich mainland assemblages. The mix of Indian and Pacific Ocean species and the proportional representations of the various regional faunas in the assemblages were not influenced by the relative proximity of the islands to different biogeographical provinces. Moreover, species at the edge of their range did not have a lower abundance than species at the centre of their range, and endemic species had substantially higher abundances than widespread species. At both locations, endemism was low (less than 1.2% of the community); this may be because the locations are not sufficiently isolated or old enough to promote the evolution of endemic species.

Main conclusions The patterns observed generally conform to terrestrial biogeographical theory, suggesting that similar processes may be influencing species richness and community composition in reef fish communities at these remote islands. However, species abundances differed from typical terrestrial patterns, and this may be because of the life history of reef fishes and the processes maintaining isolated populations.

Keywords

Christmas Island, Cocos Islands, coral reef fishes, density compensation, endemism, island biogeography, macroecology, range edge effects.

*Correspondence: Jean-Paul A. Hobbs, Australian Research Council Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, Qld, 4811, Australia. E-mail: jean-paul.hobbs@my.jcu.edu.au

INTRODUCTION

In comparison to similar-sized mainland areas, islands tend to support fewer species and higher local abundances (MacArthur & Wilson, 1963, 1967; MacArthur *et al.*, 1972). Isolated island communities typically contain a higher proportion of local endemics (Whittaker, 1998) and a greater representation of species with good dispersal abilities (Diamond *et al.*, 1976; Whittaker, 1998). The biogeographical context of an island can also affect species composition and relative abundances. Islands near biogeographical borders contain a mix of species that is influenced by the island's position relative to the border (e.g. Wallace's Line: Wallace, 1860; Carlquist, 1965). For particular species, relative abundances in island communities can be correlated with the size of the species' range and the position of the island within this range. Species often have lower abundances near the edges of their geographic ranges (Brown, 1984; Gaston *et al.*, 1997; but see Sagarin & Gaines, 2002), and small-range species tend to be less abundant than widespread species, which contributes to the positive relationship between abundance and range size observed in many terrestrial communities (Gaston, 1994; Blackburn *et al.*, 1997; Gaston *et al.*, 1997).

Mechanisms identified as important determinants in the structure of island communities include dispersal, population maintenance, environmental conditions and the island's geological history. The number of species on an island depends on the balance of rates of colonization, local extinction and speciation (MacArthur & Wilson, 1963, 1967). Dispersal ability affects colonization (Diamond *et al.*, 1976), while rates of extinction and *in situ* speciation are influenced by an island's isolation, size, age and environmental stability (MacArthur & Wilson, 1963, 1967; Whittaker, 1998). The amount and variety of habitats may also influence speciation and extinction rates, and are critical to determining whether new arrivals can colonize an island and maintain viable populations. Species are expected to be poorly adapted to the environmental conditions present at their range edge, and therefore peripheral populations may have low abundance (Brown, 1984). However, the relatively low diversity of species on islands may mean that ecological conditions promote high abundances in other species owing to a lack of competitors (density compensation: MacArthur *et al.*, 1972).

Less than 10% of all ecological and biodiversity studies have been conducted in the marine realm (Hendriks *et al.*, 2006; Richardson & Poloczanska, 2008). There are fundamental differences between the marine and terrestrial environments (Steele, 1985; Raffaelli *et al.*, 2005), and therefore ecological patterns observed in terrestrial systems may not be reflected in marine systems. For example, the geographic ranges of marine species tend to be larger than those of terrestrial species (Jones *et al.*, 2002), indicating that marine species may have greater dispersal and colonization abilities than terrestrial species. While dispersal and geological history (e.g. vicariance) have long been argued to be determinants of the distribution of marine species (reviewed by Briggs, 2004), evidence for the importance of these mechanisms in structuring island com-

munities remains mixed. For example, some studies indicate that the composition of marine communities on isolated islands is linked to greater dispersal ability (Hourigan & Reese, 1987; Mora *et al.*, 2003), while others have found that isolated islands contain a high proportion of endemic species (Randall, 1998; Robertson, 2001) with restricted dispersal abilities (Eble *et al.*, 2009). Moreover, in contrast to the case in many terrestrial communities (Brown, 1984; Gaston, 1994; Gaston *et al.*, 1997), endemic species are often abundant (Randall, 1998; Robertson, 2001; DeMartini & Friedlander, 2004), and some widespread species do not have low abundance at their range edge (Jones *et al.*, 2002). These contrasting results highlight the fact that the biogeographical patterns that have been proposed to be widespread on land remain unresolved in the marine environment. Therefore, the study of marine organisms can add significantly to our understanding of island biogeography by identifying differences and similarities in the processes structuring marine and terrestrial island communities (Vermeij, 2004).

In this study, we test whether reef fish communities at two isolated island locations conform to ecological patterns that have been proposed to be widespread, based principally on evidence from terrestrial systems (e.g. Carlquist, 1965; Brown, 1984; Gaston, 1994; Whittaker, 1998). The following questions were addressed.

1. Are isolated reef fish communities depauperate with a high level of endemism?
2. Does the composition of reef fish communities on isolated islands differ from that of neighbouring mainland communities by having an overrepresentation of species with greater dispersal abilities?
3. Are the composition and relative abundance of reef fishes on the Indo-Pacific biogeographical border influenced by the position of the island(s) relative to different biogeographical source regions?
4. Is there evidence of density compensation? That is, do reef fish populations on isolated islands attain higher densities than mainland populations?
5. Are reef fishes at the edge of their range less abundant than species that are at the centre of their range?
6. Are endemic reef fishes less abundant than species with broad geographic ranges?

The coral reef fish communities of the Cocos Islands and Christmas Island, in the eastern Indian Ocean, provide an excellent natural laboratory in which to address these questions. Coral reef fishes have been a model system in marine biogeographical research (Bellwood & Hughes, 2001; Mora *et al.*, 2003; Sandin *et al.*, 2008) because of their high species diversity and association with islands and habitat patches of varying size, degrees of isolation and biogeographical positions. The geographic distributions of reef fishes are among the best documented for marine species, and there is much information on their dispersal abilities. Furthermore, they are likely to provide important insights into ecological generalizations about island community structure because they have provided examples that contrast with terrestrial patterns (e.g.

Randall, 1998; Robertson, 2001; Jones *et al.*, 2002; DeMartini & Friedlander, 2004). Christmas Island and the Cocos Islands are ideal study locations not only because they are isolated, but also because they lie on the Indo-Pacific biogeographical border. This border represents the junction of the world's two largest tropical marine biogeographical provinces (Indian and Pacific Oceans), and probably arose from land bridge formations in Indonesia inducing vicariance during recent geological periods of low sea level (Randall, 1998; Rocha *et al.*, 2007; Hobbs *et al.*, 2009). As a consequence of their isolation and biogeographical position, the reef fish communities at Christmas Island and the Cocos Islands contain a mix of species from the Indian and Pacific Oceans, as well as endemics, and widespread species at the edges of their geographic ranges (Allen & Smith-Vaniz, 1994; Allen *et al.*, 2007; Hobbs & Salmond, 2008).

MATERIALS AND METHODS

Study site

Christmas Island (10°30' S, 105°40' E) and the Cocos (Keeling) Islands (12°12' S, 96°54' E) are located approximately 400 and 1000 km, respectively, south-west of Indonesia (Fig. 1a). The Cocos Islands are situated about 1000 km west of Christmas Island and are considered among the most isolated islands (i.e. greatest distance from the nearest landmass) in the tropical Indian Ocean (Briggs, 1974). The two locations are similar-sized oceanic coral reef systems (about 20 km along the longest axis); however, Christmas Island is a single high island (361 m at its highest point) whereas the Cocos Islands comprise a coral atoll with a ring of low-lying sandy islands surrounding a central lagoon (Woodroffe & Berry, 1994; Allen *et al.*, 2007). Christmas Island and the Cocos Islands have approximately 20 km² and 110 km² of coral reef habitat, respectively (Robertson & Allen, 1996), and there are no estuaries at either location.

Are isolated reef fish communities depauperate with a high level of endemism?

Species richness and endemism of fish communities at the islands were estimated using published species lists (Allen & Smith-Vaniz, 1994; Allen *et al.*, 2007), combined with extensive underwater visual surveys around all sides of the islands from 0 to 60 m depth (Hobbs *et al.*, 2007, 2010; unpublished data). Endemic species were defined as those that occur only at the Cocos Islands and/or Christmas Island. To determine whether these islands have fewer species than expected as a result of their isolation, we constructed a species–area curve by plotting the number of reef fishes (from published literature listed in Fig. 1) against the area of reef habitat (from Spalding *et al.*, 2001) for various Indian Ocean locations. We then examined the residual variation of Christmas Island and the Cocos Islands. If the residuals for these islands fall below the line (i.e. species richness is lower than expected based on the

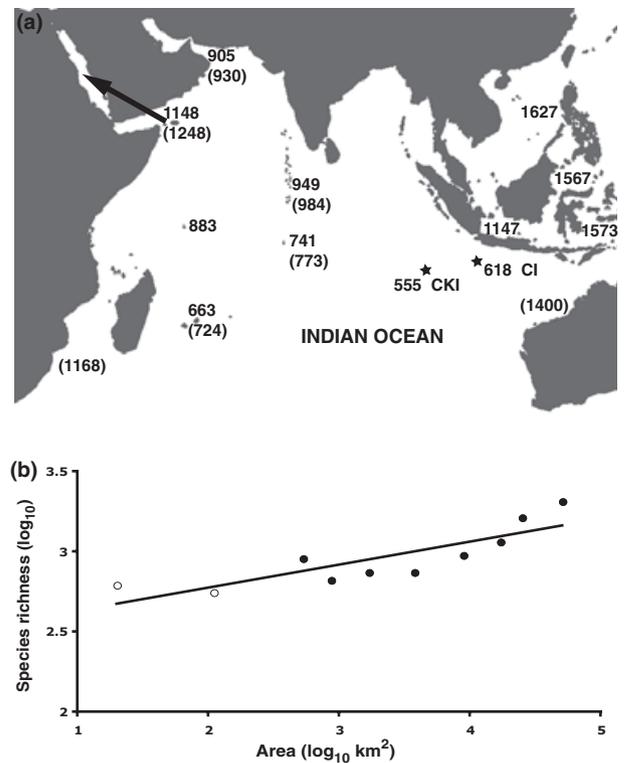


Figure 1 (a) Species richness and (b) species–area relationship ($y = 0.14x + 2.49$, $R^2 = 0.71$) for shallow reef fishes at locations across the Indian Ocean and Indonesian region. Only those places where reef fish estimates are available are plotted on the species–area relationship, and the open circles represent Christmas Island and the Cocos Islands (in increasing order of area). Area of reef habitat calculated from Spalding *et al.* (2001). Species richness values on the map are estimates for shallow reef fishes, and estimates for all marine fishes (including deepwater and pelagic) are presented in parentheses. Locations from west-to-east and north-to-south are: Red Sea, South Africa, Oman, Seychelles, Mauritius, Maldives, Chagos, Cocos Islands (CKI), Christmas Island (CI), Java (Indonesia), central Philippines, Western Australia, northern Sulawesi (Indonesia) and Molucca Islands (Indonesia). Data sources are as follows: Indonesia and Philippines, Allen (2008); Western Australia, Allen & Swainston (1988); Christmas Island and the Cocos Islands, Allen & Smith-Vaniz (1994), Allen *et al.* (2007), Hobbs *et al.* (2007, 2010); all other locations, Randall (1998 and references therein).

size of the area of habitat) this would indicate that some additional factors (e.g. isolation) are contributing to the low species richness. The proportions of species endemic to either Christmas Island or the Cocos Islands were calculated and compared with levels of endemism at other coral reef locations (Allen, 2008). For the purposes of this study we also considered populations of two species (*Centropyge flavissima* and *Stegastes insularis*) to be endemic species. These are the only populations in the Indian Ocean and are isolated by more than 3000 km from Pacific Ocean populations. They also exhibit differences in physical appearance, indicating that the populations may represent separate species (Allen *et al.*, 1998).

Does the composition of reef fish communities on isolated islands differ from that of neighbouring mainland communities by having an overrepresentation of species with greater dispersal abilities?

To determine if fish communities on the islands are a random subset of the closest species-rich mainland communities, we compared the shallow (0–60 m) reef fish communities (Allen & Smith-Vaniz, 1994; Allen *et al.*, 2007; Hobbs *et al.*, 2007, 2010) with the overall community composition of Indonesia (Allen & Adrim, 2003; G. Allen, unpublished data). The Indonesian region represents the global centre of reef fish diversity (Bellwood & Hughes, 2001; Allen & Adrim, 2003; Allen, 2008) and is the closest ‘mainland’ source community to the islands. To test for non-randomness of community composition, we constructed a null model in which species were sampled at random from the Indonesian species pool to populate the islands. We also used this null model approach to compare the mean pelagic larval duration (PLD) of reef fish species at the islands with the mean PLDs produced by the corresponding null model simulations. For more detailed information on the relationship between community composition and dispersal ability we used a null model test to determine which families were over- and underrepresented (defined as families whose richness levels are above or below, respectively, the 95% confidence limits of the corresponding null model predictions) and whether overrepresented families have longer PLDs than underrepresented families. The null model algorithm and the specific tests are described in Appendix S1 in the Supporting Information.

Are the composition and relative abundance of reef fishes on the Indo-Pacific biogeographical border influenced by the position of the island(s) relative to different biogeographical source regions?

Christmas Island is located closer to the Pacific Ocean and should contain a greater proportion of Pacific Ocean fishes compared to the Cocos Islands, and vice versa for Indian Ocean species. To test this, the proportions of shallow reef fishes (0–60 m depth) from different geographic distributions (Indian Ocean, Pacific Ocean, Indo-Pacific) were compared between the two locations using a chi-square test. This test was repeated using just Indian Ocean and Pacific Ocean species (with Yates’ correction for continuity: Zar, 1999). Approximately 7.3% and 4.9% of species at Christmas Island and the Cocos Islands, respectively, had geographic distributions that could not be classified into one of these three geographic distributions and were grouped as ‘other’.

In addition to species composition, the relative abundance of species at the biogeographical border may be linked to their biogeographical origins. That is, Pacific Ocean species should be more abundant at Christmas Island (compared with the Cocos Islands), and vice versa for Indian Ocean species. To test this, we conducted underwater visual censuses

(Appendix S1) of shallow reef fishes on the outer reefs at 14 sites at Christmas Island and at 12 sites at the Cocos Islands. Censuses were conducted in November and December 2002 and focused on six common reef fish families: Acanthuridae (surgeonfish and unicornfish), Balistidae (triggerfish), Chaetodontidae (butterflyfish), Labridae (wrasse), Pomacanthidae (angelfish) and Pomacentridae (damselfish). A Wilcoxon paired-sample test was used to examine differences in median rank abundance (combined for all six study families) of Indian Ocean and Pacific Ocean species common to both locations.

Do reef fish populations on isolated islands attain higher densities than mainland populations?

To determine if island populations attain greater densities than mainland populations owing to the lower number of competing species (density compensation, *sensu* MacArthur *et al.*, 1972) we compared the mean density of benthic feeding butterflyfishes (genera *Chaetodon* and *Forcipiger*) at the islands with that of the Indonesian region (see Appendix S1). Butterflyfish were selected for this analysis because this was the only group with sufficient density estimates for mainland populations in the Indonesian region.

Are reef fishes at the edge of their range less abundant than species that are at the centre of their range?

Because the islands represent the eastern or western edge of the geographic distributions of a number of species, the abundances of these edge species are predicted to be low. For widespread (Indo-Pacific) species, the islands are located in the middle of their range and, therefore, might be expected to have higher abundances than edge species. To test this hypothesis, we used density estimates from our underwater visual censuses to compare the mean densities of edge (Pacific and Indian Ocean edge species combined) and mid-range (Indo-Pacific species) species for angelfishes, butterflyfishes and damselfishes using *t*-tests (or the Mann–Whitney *U*-test if assumptions were not met). For surgeonfishes and wrasses, only rank abundance data were collected, and medians were compared using Mann–Whitney *U*-tests. Tests were conducted separately for each family and at each of the two locations. The triggerfish assemblages at both locations and the angelfish assemblage at the Cocos Islands were not included in the analysis owing to insufficient numbers of edge species.

The underwater visual censuses may have missed some of the rare species, and this group of species may contain a high proportion of edge species. To determine whether rare species as a group had a greater proportion of edge species, we examined qualitative abundance estimates published for fishes at Christmas Island (Allen *et al.*, 2007), supplemented with underwater observations for new records identified in 2002, 2004, 2005 and 2008 (Hobbs *et al.*, 2007, 2010) (see Appendix S1). The proportions of species whose range was classed as

Pacific Ocean, Indian Ocean, Indo-Pacific or ‘other’ (described above) were compared across the three abundance categories (common, uncommon and rare) using a chi-square contingency test.

Are endemic reef fishes less abundant than species with broad geographic ranges?

Underwater visual censuses were used to determine whether reef fishes at the islands conform to the terrestrial pattern of endemics having a lower abundance than widespread species (Gaston, 1994). Study species included the endemic *Centropyge jocularis* and endemic populations of *C. flavissima* and *S. insularis* (Allen *et al.*, 1998, 2007).

RESULTS

Are isolated reef fish communities depauperate with a high level of endemism?

The species richnesses of shallow reef fishes at Christmas Island (618 species) and the Cocos Islands (550) were the lowest across a range of Indian Ocean locations (Fig. 1a). The two island locations conform to the species–area relationship for the Indian Ocean region, indicating that the low species richness is explained by the relatively small area of reef habitat at these islands (Fig. 1b). The number of shallow reef fishes at the islands was generally less than half that of neighbouring mainland fish communities of the Indonesian region.

There were seven endemic species or populations at Christmas Island and two at the Cocos Islands, and, overall,

these accounted for only a small proportion of the reef fish communities (1.1% and 0.4% of species richness, respectively).

Does the composition of reef fish communities on isolated islands differ from that of neighbouring mainland communities by having an overrepresentation of species with greater dispersal abilities?

The taxonomic composition of the island reef fish communities was significantly different from that of neighbouring Indonesia ($P < 0.0001$ in each case; Fig. 2, and Fig. S1 in Appendix S2). Species constituting the island communities tended to have greater dispersal potential than those in the mainland communities, as evidenced by the overall mean PLDs of species across the island communities being significantly greater than null model predictions (Christmas: $P = 0.0002$; Cocos: $P < 0.0001$) (Fig. S2 in Appendix S2). Specifically, for both island locations, Muraenidae, Acanthuridae, Chaetodontidae, Scaridae, Holocentridae, Labridae and Balistidae were overrepresented, and Syngnathidae, Pseudochromidae, Nemipteridae, Opistognathidae and Gobiidae were underrepresented (Table S1 in Appendix S2). Examination of the PLDs of the under- and overrepresented families revealed that overrepresented families had a longer PLD (mean PLD = 45.4 days \pm 3.6 SE) than taxa that were underrepresented (mean PLD = 28.7 days \pm 6.1 SE) ($t = 2.55$, d.f. = 26, $P = 0.02$). In addition, 63% of the underrepresented families brood or lay demersal eggs (which potentially limits dispersal: Munday & Jones, 1998), whereas only one (9%) of the overrepresented families lays demersal eggs and the rest are broadcast spawners.

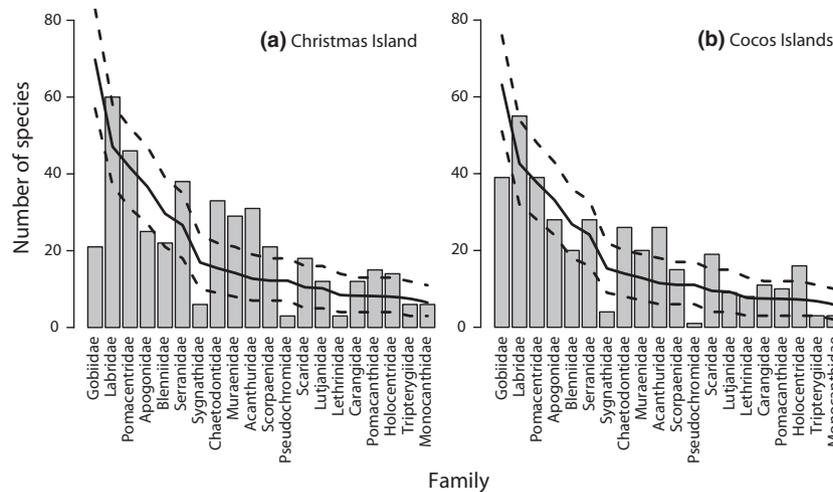


Figure 2 Comparison of observed and expected taxonomic composition of reef fish communities at (a) Christmas Island (550 species) and (b) the Cocos Islands (497). Bars show the observed taxonomic composition. The expected distribution (shown as solid lines, with 95% confidence limits indicated by dotted lines) is based on a null model in which species were sampled at random from the Indonesian species pool (2169 species). Although the analysis was conducted on all families, the plot shows only the 20 most species-rich families, shown in descending order of species richness (based on the Indonesian species pool) from left to right. See Appendix S1 for further details on the methods.

Are the composition and relative abundance of reef fishes on the Indo-Pacific biogeographical border influenced by the position of the island(s) relative to different biogeographical source regions?

The reef fish assemblages at both Christmas Island and the Cocos Islands typically contained 72% Indo-Pacific species, 17% Pacific Ocean species and 5% Indian Ocean species. There was no significant difference in the proportions of species from different geographic distributions between the two locations ($\chi^2 = 5.485$, d.f. = 3, $P = 0.14$). The large number of Indo-Pacific species could potentially mask differences in the proportions of Pacific and Indian Ocean species between the two locations. However, restricting the analysis to comparing just the proportions of Pacific and Indian Ocean species still resulted in no significant difference between the two locations (χ^2 with Yates' correction = 1.97, d.f. = 1, $P = 0.16$).

Not only were the proportions of Indian and Pacific Ocean species similar between the two locations, but the relative abundances of those species were similar too. There were no significant differences between the two locations in the rank abundances of Pacific Ocean species ($Z = -1.065$, $P = 0.287$, $n = 11$) or Indian Ocean species ($Z = -1.461$, $P = 0.144$, $n = 4$) for the study families.

Do reef fish populations on isolated islands attain higher densities than mainland populations?

Although the islands have relatively depauperate shallow reef fish communities, there was no evidence of density compensation. Both locations have approximately half the number of butterflyfish species of the neighbouring Indonesian region. However, there was no significant difference in the mean density of butterflyfishes at the islands (0.54 per 300 m² ± 0.12 SE) compared with the mean density recorded from locations in the Indonesian region (0.37 per 300 m² ± 0.08 SE; Findley & Findley, 2001) ($t = 1.02$, d.f. = 8, $P = 0.34$) (Table S2 in Appendix S2).

Are reef fishes at the edge of their range less abundant than species that are at the centre of their range?

Species at the edge of their range did not have significantly lower mean densities or lower median rank abundance compared with closely related mid-range species. There were no significant differences in edge and mid-range species densities for eight of the nine families ($P > 0.05$, Table 1), and in the remaining family (Cocos Islands butterflyfishes) edge species exhibited a greater mean density than mid-range species ($t = 0.266$, d.f. = 19, $P = 0.015$). Similarly, there was no significant difference in the proportions of Indian Ocean, Pacific Ocean and Indo-Pacific species that made up the common, uncommon and rare species groups at Christmas Island ($\chi^2 = 9.82$, d.f. = 6, $P = 0.13$). That is, the rare species group did not contain a significantly higher proportion of species at the edge of their range.

Table 1 Comparisons of abundance between edge and mid-range species of reef fishes at Christmas Island and the Cocos Islands. Mean densities were compared using t -tests for chaetodontids, pomacanthids and pomacentrids, and Mann–Whitney U -tests were used to compare median rank abundance for acanthurids and labrids.

Location	Family	Test statistic	P
Christmas Island	Labridae	$U = 152.0$	0.39
Christmas Island	Acanthuridae	$U = 63.0$	0.26
Christmas Island	Pomacanthidae	$t = 0.67$	0.52
Christmas Island	Pomacentridae	$U = 36.5$	0.65
Christmas Island	Chaetodontidae	$t = 0.65$	0.52
Cocos Islands	Labridae	$U = 88.0$	0.78
Cocos Islands	Acanthuridae	$U = 33.0$	0.60
Cocos Islands	Pomacentridae	$t = 0.24$	0.82
Cocos Islands	Chaetodontidae	$t = 2.66$	0.02

Are endemic reef fishes less abundant than species with broad geographic ranges?

Endemics had high abundances compared with their widespread relatives. The mean densities of endemic angelfishes (*C. jocularis* and *C. flavissima*) at both locations were more than 45 times greater than the overall mean densities for widespread angelfishes (Fig. 3a). The mean density of the

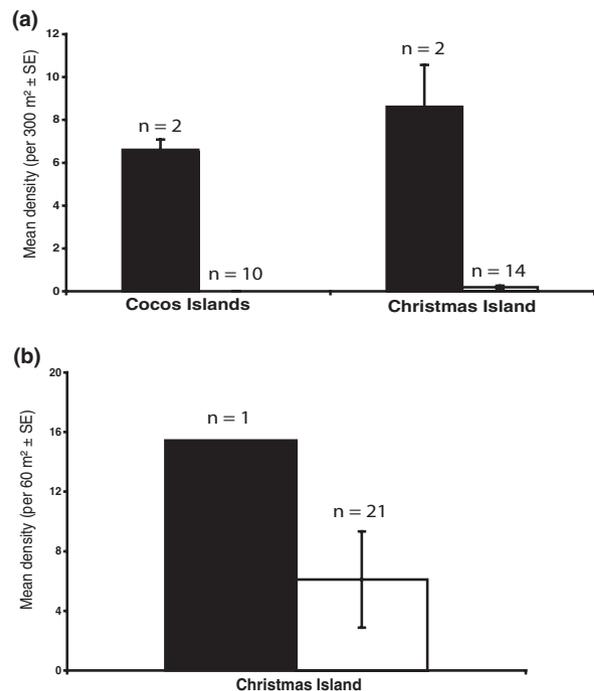


Figure 3 (a) The mean density (per 300 m² ± SE) of endemic (black bars) and widespread (white bars) angelfishes (Pomacanthidae) from surveys at 20 m depth at Christmas Island and the Cocos Islands. Mean density is pooled across species, n = number of species. (b) The mean density (per 60 m² ± SE) of endemic (black bars) and widespread (white bars) damselfishes (Pomacentridae) from surveys at 5 m depth at Christmas Island. Mean density is pooled across species, n = number of species.

endemic population of *S. insularis* at Christmas Island (15.4 per 60 m²) was more than double the overall mean density of widely distributed damselfishes (6.1 per 60 m²) (Fig. 3b).

DISCUSSION

As for terrestrial island communities, area was an important determinant of species richness of reef fishes at Christmas Island and the Cocos Islands, while isolation influenced species composition. However, the abundance of reef fishes on these isolated islands did not conform to expectations based on terrestrially derived biogeography theory.

Are isolated reef fish communities depauperate with a high level of endemism?

According to island biogeography theory, small islands far from population sources should be the most depauperate in species (MacArthur & Wilson, 1967). However, the low species richness of reef fishes on isolated islands was explained very well by a simple species–area relationship. This is consistent with previous work suggesting that area is more important than isolation in determining species richness of reef fishes (Bellwood & Hughes, 2001). The species–area regression provided only tentative evidence for a small additional effect of isolation, because the more remote Indian Ocean islands (Mauritius, Seychelles, Chagos and Maldives) tended to fall below the regression line (indicating lower than expected species richness for a given island area) (Fig. 1b).

Species richness is believed to be low on small islands because of associations with low habitat diversity, higher extinction rates and lower rates of colonization and speciation (Williams, 1964; MacArthur & Wilson, 1967; Gilpin & Diamond, 1976; Rosenzweig, 1995, 1999). Although rates of speciation, colonization and extinction have not been determined for the study locations, the effect of low habitat diversity is evident. For example, Christmas Island lacks estuaries, bays, mangrove coasts, seagrass meadows and lagoons, and consequently many reef fishes that use these shallow sheltered habitats as juveniles or adults are absent (Allen *et al.*, 2007; Hobbs *et al.*, 2010).

Isolated island communities typically contain a high proportion of endemic species (Whittaker, 1998). However, endemism in reef fish communities at Christmas Island (1.1%) and the Cocos Islands (0.4%) is well below the values of the world's top 10 locations for percentage reef fish endemism (3.8–23%: Allen, 2008). The young age of the Cocos Islands (the current landmass is less than 4000 years old) and environmental instability may have limited the evolution of endemics at this location (Woodroffe & Berry, 1994). However, the low level of reef fish endemism at Christmas Island is more surprising, given its age (37 million years: Whittaker, 1998) and its much higher levels of terrestrial endemism (*c.* 7%: James, 2007). Although Christmas Island may be sufficiently remote to inhibit the dispersal of terrestrial taxa, it may not be isolated enough to counteract the broad-scale

dispersal capabilities of reef fishes. Indeed, genetic studies of widespread reef fishes reveal that both locations receive enough gene flow from other populations to prevent isolation and speciation, despite being 400 and 1000 km from the nearest source population (Horne *et al.*, 2008; Gaither *et al.*, 2010). The world's most remote coral reef locations occur in the Pacific Ocean, and it is only these locations that appear to pose a challenge to reef fish dispersal (Mora *et al.*, 2003; Lester & Ruttenberg, 2005), restricting gene flow and allowing endemics to form. It is these locations (Easter Island, Hawaiian Islands, Galapagos Islands, Marquesas Islands) that have the world's highest levels of reef fish endemism (Allen, 2008).

Does the composition of reef fish communities on isolated islands differ from that of neighbouring mainland communities by having an overrepresentation of species with greater dispersal abilities?

Christmas Island and the Cocos Islands may not be isolated enough to allow a high proportion of endemics to evolve, but they are sufficiently isolated to influence community composition. The reef fish communities had longer PLDs, on average, than the Indonesian species pool. In addition, families that were overrepresented on the islands had greater dispersal potential (longer PLDs and broadcast spawning), compared with underrepresented families. Longer PLDs also appear to be important in colonizing remote Pacific Ocean locations (Mora *et al.*, 2003; Lester & Ruttenberg, 2005; Paulay & Meyer, 2006). Therefore, as has been observed for many terrestrial communities (Diamond *et al.*, 1976; Whittaker, 1998), species with the greatest dispersal potential are more likely to colonize isolated islands and thus become overrepresented in the community.

Are the composition and relative abundance of reef fishes on the Indo-Pacific biogeographical border influenced by the position of the island(s) relative to different biogeographical source regions?

The geographic location of the study islands on the Indo-Pacific biogeographical border did not affect the composition or abundance of fishes from different biogeographical regions. This may be because oceanic currents in the region generally flow east to west (the Southern Equatorial Current), which would mean that, even though the Cocos Islands are closer to the Indian Ocean bioregion, the Islands mainly receive immigrants from the east (i.e. from Christmas Island and Indonesia). We observed higher proportions of Pacific Ocean species (17%) than Indian Ocean species (5%) at both locations, supporting the role of oceanographic currents. A similar scenario has been reported for reef fish communities across the East Pacific Barrier, where prevailing currents influence the direction of larval dispersal and the biogeographical composition of island communities (Robertson *et al.*, 2004). It appears that the effect of prevailing currents on larval dispersal means that biogeographical edges are not as

well defined as those in the terrestrial environment (Cox & Moore, 2010).

Do reef fish populations on isolated islands attain higher densities than mainland populations?

There was no evidence of density compensation in butterflyfishes, suggesting that competitive interactions are not a major factor in regulating the abundances of butterflyfishes at these two isolated islands. Given that numerous studies have demonstrated the importance of competition in reef fishes at local scales (Robertson, 1996; Schmitt & Holbrook, 1999; Munday *et al.*, 2001; Forrester *et al.*, 2006), this finding is surprising. However, it adds to a growing body of evidence indicating that competitive interactions play a relatively minor role in determining biogeographical patterns in the structure of local reef fish communities (Bellwood & Hughes, 2001; Sandin *et al.*, 2008).

Are reef fishes at the edge of their range less abundant than species that are at the centre of their range?

The pattern of low abundance at species range edges (Brown, 1984; Gaston *et al.*, 1997) was not observed for the fish assemblages we examined. Similarly, reef fishes studied in other locations do not necessarily have low abundances at their range edges (Jones *et al.*, 2002; Tuya *et al.*, 2008). The biological and ecological traits of most reef fishes (and of marine species in general: Carr *et al.*, 2003) typically result in high recruitment variability (Doherty & Williams, 1988; Doherty, 1991; Ripley & Caswell, 2006), and, given that isolation and variable recruitment increase the likelihood of extinction (Diamond, 1984), it would be difficult for small populations of a marine species to persist at isolated locations on the edge of their range. Therefore, high abundance at the edge of the range may well be required for population persistence of marine species, and this can be achieved through local adaptation and increased self-recruitment (discussed below).

Are endemic reef fishes less abundant than species with broad geographic ranges?

The positive relationship between range size and abundance is considered 'one of the most general and robust patterns in nature' (Gaston *et al.*, 1997). However, the three endemics examined in this study had considerably higher abundances than widespread relatives. Endemic reef fishes in other isolated locations also have high abundance (Randall, 1998; Jones *et al.*, 2002; DeMartini, 2004; DeMartini & Friedlander, 2004; Hobbs *et al.*, 2011), indicating that this is not an unusual occurrence. High abundance in endemic reef fishes may be achieved through local adaptation (Hourigan & Reese, 1987; Randall, 1998), and facilitated by effective self-recruitment mechanisms in island locations (Swearer *et al.*, 2002; Hobbs *et al.*, 2011).

For example, the very high abundance of endemic reef fishes in Hawaii (DeMartini & Friedlander, 2004) is associated with restricted dispersal (Eble *et al.*, 2009) and consistently high recruitment (DeMartini, 2004).

Island size, the likelihood of receiving colonists, and species dispersal ability are fundamental determinants of island biogeographical patterns in terrestrial systems. Our results suggest that similar processes determine species richness and community composition in reef fish communities on isolated islands. However, species abundances do not conform well to the proposed generalizations tested here: there is a lack of density compensation, endemics are highly abundant, and range-edge species do not have low abundances. These differences appear to be due to key life history traits shared by many marine organisms, such as a pelagic larval phase capable of dispersing great distances, and the very high recruitment variability that characterizes marine populations. By using isolated reef fish communities to highlight important similarities and differences between marine and terrestrial communities, we hope that this study will stimulate the development of a more unified theory for the processes structuring island communities in the oceans, as well as on land.

ACKNOWLEDGEMENTS

We are grateful for the logistical and financial support provided by Parks Australia North, Wet 'n' Dry Adventures and Envirofund Australia Natural Heritage Trust. We thank G. Christie, J. Clunies-Ross, J. Gilligan, A. Graham, T. Hamanaka, J. Hender, E. Johari, K. Munday, M. Orchard and A. Yon for assistance in the field; M. Hisano for assistance with statistical programming; and G. Allen for information on fishes of Indonesia. Thanks to C. Mora and an anonymous referee for providing constructive comments on the manuscript. Comments and suggestions from the editor, A. Crame, further improved the manuscript. This research was partially funded by a James Cook University Competitive Research Incentive Grant to G.P.J. and P.L.M. J-P.A.H. was supported by a Nancy Vernon Rankine Award.

REFERENCES

- Allen, G.R. (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 541–556.
- Allen, G.R. & Adrim, M. (2003) Coral reef fishes of Indonesia. *Zoological Studies*, **42**, 1–72.
- Allen, G.R. & Smith-Vaniz, W.F. (1994) Fishes of Cocos (Keeling) Islands. *Atoll Research Bulletin*, **412**, 1–21.
- Allen, G.R. & Swainston, R. (1988) *The marine fishes of north-western Australia: a field guide for anglers and divers*. Western Australian Museum, Perth.
- Allen, G.R., Steene, R. & Allen, M.A. (1998) *Guide to angelfishes and butterflyfishes*. Odyssey Publishing/Tropical Reef Research, Perth.

- Allen, G.R., Steene, R. & Orchard, M. (2007) *Fishes of Christmas Island*, 2nd edn. Christmas Island Natural History Association, Christmas Island.
- Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science*, **292**, 1532–1534.
- Blackburn, T.M., Gaston, K.J., Quinn, R.M., Arnold, H. & Gregory, R.D. (1997) Of mice and wrens: the relation between abundance and geographic range size in British mammals and birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **352**, 419–427.
- Briggs, J.C. (1974) *Marine zoogeography*. McGraw-Hill, New York.
- Briggs, J.C. (2004) A marine center of origin: reality and conservation. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 255–269. Sinauer Associates Inc., Sunderland, MA.
- Brown, J.H. (1984) On the relationship between abundance and distributions of species. *The American Naturalist*, **124**, 255–279.
- Carlquist, S. (1965) *Island life: a natural history of the islands of the world*. Natural History Press, New York.
- Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R. & Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications*, **13**(supplement), 90–107.
- Cox, C.B. & Moore, P.D. (2010) *Biogeography: an ecological and evolutionary approach*, 8th edn. John Wiley, Hoboken, NJ.
- DeMartini, E.E. (2004) Habitat and endemism of recruits to shallow reef fish populations: selection criteria for no-take MPAs in the NWHI Coral Reef Ecosystem Reserve. *Bulletin of Marine Science*, **14**, 185–205.
- DeMartini, E.E. & Friedlander, A.M. (2004) Spatial patterns of endemism in shallow-water reef fish populations of the Northwestern Hawaiian Islands. *Marine Ecology Progress Series*, **271**, 281–296.
- Diamond, J.M. (1984) “Normal” extinctions of isolated populations. *Extinctions* (ed. by M.H. Nitecki), pp. 191–246. University of Chicago Press, Chicago.
- Diamond, J.M., Gilpin, M.E. & Mayr, E. (1976) Species–distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. *Proceedings of the National Academy of Sciences USA*, **73**, 2160–2164.
- Doherty, P.J. (1991) Spatial and temporal patterns in recruitment. *The ecology of fishes on coral reefs* (ed. by P.F. Sale), pp. 261–293. Academic Press, San Diego.
- Doherty, P.J. & Williams, D.M. (1988) The replenishment of coral reef fish populations. *Oceanography and Marine Biology: an Annual Review*, **26**, 487–551.
- Eble, J.A., Toonen, R.J. & Bowen, B.W. (2009) Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. *Marine Biology*, **156**, 689–698.
- Findley, J.S. & Findley, M.T. (2001) Global, regional, and local patterns in species richness and abundance of butterflyfishes. *Ecological Monographs*, **71**, 69–91.
- Forrester, G.E., Evans, B., Steele, M.A. & Vance, R.R. (2006) Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia*, **148**, 632–640.
- Gaither, M.R., Toonen, R.J., Robertson, D.R., Planes, S. & Bowen, B.W. (2010) Genetic evaluation of marine biogeographical barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *Journal of Biogeography*, **37**, 133–147.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Inter-specific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.
- Gilpin, M.E. & Diamond, J.M. (1976) Calculations of immigration and extinction curves from the species–area–distance relation. *Proceedings of the National Academy of Sciences USA*, **73**, 4130–4134.
- Hendriks, I.E., Duarte, M.C. & Heip, C.H.R. (2006) Biodiversity research still grounded. *Science*, **312**, 1715.
- Hobbs, J.-P.A. & Salmond, J.K. (2008) Cohabitation of Indian and Pacific Ocean species at Christmas and Cocos (Keeling) Islands. *Coral Reefs*, **27**, 933.
- Hobbs, J.-P.A., Frisch, A.J., Hender, J. & Gilligan, J.J. (2007) New records of angelfishes (Pomacanthidae) and butterflyfishes (Chaetodontidae) from Christmas and Cocos (Keeling) Islands. *Journal of the Royal Society of Western Australia*, **90**, 107–109.
- Hobbs, J.-P.A., Frisch, A.J., Allen, G.R. & van Herwerden, L. (2009) Marine hybrid hotspot at Indo-Pacific biogeographic border. *Biology Letters*, **5**, 258–261.
- Hobbs, J.-P.A., Ayling, A.M., Choat, J.H., Gilligan, J.J., McDonald, C.A., Neilson, J. & Newman, S.J. (2010) New records of marine fishes illustrate the biogeographic importance of Christmas Island, Indian Ocean. *Zootaxa*, **2422**, 63–68.
- Hobbs, J.-P.A., Jones, G.P. & Munday, P.L. (2011) Extinction risk in endemic marine fishes. *Conservation Biology*, doi: 10.1111/j.1523-1739.2011.01698.x
- Horne, J.B., van Herwerden, L., Choat, J.H. & Robertson, D.R. (2008) High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution*, **49**, 629–638.
- Hourigan, T.F. & Reese, E.S. (1987) Midocean isolation and the evolution of Hawaiian reef fishes. *Trends in Ecology and Evolution*, **2**, 187–191.
- James, D.J. (2007) *Christmas Island biodiversity monitoring programme: summary report, December 2003 to April 2006*. Report to Department of Finance & Administration and Department of the Environment & Water Resources, Canberra.
- Jones, G.P., Caley, M.J. & Munday, P.L. (2002) Rarity in coral reef fish communities. *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 81–101. Academic Press, San Diego, CA.
- Lester, S.E. & Rutenber, B.I. (2005) The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 585–591.

- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H., Karr, J.R. & Diamond, J.M. (1972) Density compensation in island avifaunas. *Ecology*, **53**, 330–342.
- Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933–936.
- Munday, P.L. & Jones, G.P. (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: an Annual Review*, **36**, 373–411.
- Munday, P.L., Jones, G.P. & Caley, M.J. (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology*, **82**, 2177–2189.
- Paulay, G. & Meyer, C.P. (2006) Dispersal and divergence across the greatest ocean region: do larvae matter? *Integrative and Comparative Biology*, **46**, 269–281.
- Raffaelli, D., Solan, M. & Webb, T.J. (2005) Do marine and terrestrial ecologists do it differently? *Marine Ecology Progress Series*, **304**, 283–289.
- Randall, J.E. (1998) Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies*, **37**, 227–268.
- Richardson, A.J. & Poloczanska, E.S. (2008) Ocean science: under-resourced, under threat. *Science*, **320**, 1294–1295.
- Ripley, B.J. & Caswell, H. (2006) Recruitment variability and stochastic population growth of the soft-shell clam, *Mya arenaria*. *Ecological Modelling*, **193**, 517–530.
- Robertson, D.R. (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology*, **77**, 885–899.
- Robertson, D.R. (2001) Population maintenance among tropical reef fishes: inferences from small-island endemics. *Proceedings of the National Academy of Sciences USA*, **98**, 5667–5670.
- Robertson, D.R. & Allen, G.R. (1996) Zoogeography of the shorefish fauna of Clipperton Atoll. *Coral Reefs*, **15**, 121–131.
- Robertson, D.R., Grove, J.S. & McCosker, J.E. (2004) Tropical transpacific shore fishes. *Pacific Science*, **58**, 507–565.
- Rocha, L.A., Craig, M.T. & Bowen, B.W. (2007) Phylogeography and the conservation of coral reef fishes. *Coral Reefs*, **26**, 501–512.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L. (1999) Heeding the warning in biodiversity's basic law. *Science*, **284**, 276–277.
- Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Sandin, S.A., Vermeij, M.J.A. & Hurlbert, A.H. (2008) Island biogeography of Caribbean coral reef fish. *Global Ecology and Biogeography*, **17**, 770–777.
- Schmitt, R.J. & Holbrook, S.J. (1999) Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. *Oecologia*, **118**, 76–86.
- Spalding, M.D., Ravilious, C. & Green, E.P. (2001) *World atlas of coral reefs*. University California Press, Berkeley, CA.
- Steele, J.H. (1985) A comparison of terrestrial and marine ecological systems. *Nature*, **313**, 355–358.
- Swearer, S.E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D.R., Morgan, S.G., Selkoe, K.A., Ruiz, G.M. & Warner, R.R. (2002) Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science*, **70**, 251–271.
- Tuya, F., Wernberg, T. & Thomsen, M.S. (2008) Testing the 'abundant centre' hypothesis on endemic reef fishes in south-western Australia. *Marine Ecology Progress Series*, **372**, 225–230.
- Vermeij, G.J. (2004) Island life: a view from the sea. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 239–254. Sinauer Associates Inc., Sunderland, MA.
- Wallace, A.R. (1860) On the zoological geography of the Malay Archipelago. *Biological Journal of the Linnean Society*, **4**, 172–184.
- Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Williams, C.B. (1964) *Patterns in the balance of nature*. Academic Press, London.
- Woodroffe, C.D. & Berry, P.F. (1994) Scientific studies in the Cocos (Keeling) Islands: an introduction. *Atoll Research Bulletin*, **399**, 1–16.
- Zar, J.H. (1999) *Biostatistical analysis*. Prentice Hall, London.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods for estimating and analysing reef fish community composition and species abundances.

Appendix S2 Additional tables (Tables S1 and S2) and figures (Figs S1 and S2) of results.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

The authors have broad interests in the ecology and biodiversity of coral reef fishes. Their research group studies endemism, community structure and the roles of larval biology and population connectivity in determining recruitment dynamics and community composition (<http://www.coralcoe.org.au/research.html>).

Author contributions: all authors were involved in conceiving the ideas, collecting the data and the writing; J.-P.A.H. and S.R.C. analysed the data.

Editor: Alistair Crame