

## Article

# Structure of Reef Fish Families (Butterflyfishes and Angelfishes) at Isolated Oceanic Reefs in the Indian Ocean: Christmas Island and the Cocos (Keeling) Islands

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**Abstract:** There has been substantial research on the factors that structure reef fish assemblages, but this has mostly focused on nearshore or continental reefs. This study examines patterns of abundance and species composition for two iconic groups of coral reef fishes, angelfishes (family Pomacanthidae) and butterflyfishes (family Chaetodontidae) at two isolated, oceanic reefs in the Indian Ocean: Christmas Island and the Cocos (Keeling) Islands. Six explanatory variables were investigated to determine whether large-scale physical factors are more important than fine-scale biotic factors in structuring reef fish communities on oceanic islands. For angelfishes, depth was the factor that most explained patterns in abundance (explaining 46.5% of the variation), species richness (44.8%) and composition (15.3%), with both abundance and species richness being greater at 20 m than at 5 m. Differences in species composition were greater between depths than between islands. For butterflyfishes, variation in abundance and species richness was best explained by the difference in aspect or exposure among sites, though abundance and composition also differed significantly between Christmas Island and the Cocos (Keeling) Islands. Large-scale variation in the structure of these reef fish assemblages could not be explained based on differences in habitat diversity, or coral and algal cover. This study indicates that large-scale physical factors (island location, exposure, depth) are more important than fine-scale biotic factors in structuring reef fish assemblages on oceanic islands.

**Keywords:** Chaetodontidae; Pomacanthidae; depth gradients; isolation; microhabitat; regression trees; wave exposure



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## 1. Introduction

Coral reef fishes are the most diverse vertebrate assemblages, and there has been much research to understand the specific drivers of their abundance, diversity and species composition [1]. A variety of physical and habitat related factors have been shown to influence the structure of reef fish communities, including reef size and location [2], wave exposure [3,4], depth [5], habitat complexity [6,7] and microhabitat availability [8,9]. Biological processes such as predation [10,11], competition [12–15] and larval supply [16,17] are also known to play important roles in structuring reef fish communities, and can interact with physical and habitat-related factors. Historical factors such as plate tectonics, reef development, and vicariance events can also influence species occurrence and composition [18–20]. Numerous studies have investigated the relative roles of physical and biological factors in determining the structure of reef fish communities on coastal reefs or continental islands, and highlight the importance of the fine-scale biological characteristics of the habitat [6–9]. However, relatively few studies [21–29] have explicitly considered isolated, oceanic systems. Thus, it is not clear whether the fine-scale characteristics important to structuring reef fishes on continental islands are also important to structuring communities on oceanic islands.

The physical and biological environments at isolated, oceanic reefs are different from those at continental reefs or islands, with concomitant effects on fish assemblages [21,22,28,29]. Most notably, wave energy is greater on oceanic islands and likely to have a strong influence on the structure of reef habitats and associated fauna, especially at sites that are directly exposed to prevailing waves. High wave energy can affect fish assemblages directly [3,4,21], or indirectly by reducing habitat complexity [21,24,30] and affecting the quality and availability of food resources [3,31,32]. Depth distributions of fishes may also differ between oceanic and continental reefs due to the greater wave energy, steeper aspect and greater depth range of reefs at oceanic islands [22,28].

The specific geological and ecological history of oceanic reefs and islands, their location, and the population connectivity of species, can have a major influence on species occurrence and composition [22,33,34]. Shallow marine habitats associated with isolated, oceanic islands and reefs are often surrounded by vast expanses of deep water, which may greatly constrain colonisation [35]. The physical characteristics of isolated systems (e.g., size and location) and the dispersal capabilities of species are both important determinants of local assemblages [36], though species persistence and local adaptation in such systems are also important [34,35]. Thus, long distance dispersal capabilities are critical to colonising oceanic locations, while local adaptation leads to the *in situ* evolution of endemic species—a group that dominates isolated, oceanic communities [27,33–36]. Given that the formation of communities on oceanic islands is dependent on colonisation from distant locations, large-scale physical factors that determine whether larvae can arrive, and settle, are likely to be strong determinants of community structure.

Changes in environmental conditions can have a major effect on the distribution and abundance of reef fishes. Coral cover has been decreasing on reefs around the world [37,38] due to a variety of anthropogenic impacts [39,40]. Coral cover at a given location is determined by the disturbance history [41,42], but also the recovery capacity of coral assemblages [43,44], where the latter may be constrained by isolation [44–46]. Reef fishes that rely on live coral for food and/or shelter are particularly susceptible to coral loss and the associated degradation of reef habitats [46–50]. Such changes in habitat have caused local extinctions at oceanic islands and recovery is slow due to the isolation, the limited amounts of larvae arriving from other locations, and the loss of juvenile habitat [46]. Determining the relative importance of factors structuring reef fish communities on oceanic reefs is fundamental in understanding their vulnerability to widespread and escalating changes in environmental and habitat conditions.

This study tests the hypothesis that large and meso-scale factors are more important than fine-scale factors in structuring reef fish communities on oceanic islands. To achieve this, six factors were investigated, including a large-scale factor (island location), two meso-scale factors (wave exposure and depth) and three fine-scale, habitat-related factors (microhabitat diversity, live coral cover and algal cover). This study examines how these factors influence the abundance, diversity and species composition of angelfishes (Pomacanthidae) and butterflyfishes (Chaetodontidae) at two oceanic reefs in the Indian Ocean: Christmas Island and the Cocos (Keeling) Islands.

Angelfishes and butterflyfishes were chosen as study groups for several reasons. Their life history characteristics are typical of most reef fishes. They are broadcast spawners with a pelagic larval duration of about 25–50 days [51–53] and are relatively sedentary as adults. Angelfishes and butterflyfishes are found on coral reefs around the world, and their evolution and phylogeographic patterns are linked to the historical development of coral reefs [54–57]. These two families are appropriate focal groups for this study because they are conspicuous and can be accurately surveyed using visual census, and their total abundance and species richness are relatively high at both study locations. Moreover, butterflyfishes and angelfishes have different diets (coral vs. algae, respectively) [58–60], and may exhibit contrasting patterns in abundance that are linked to the amount of coral on a reef.

## 2. Materials and Methods

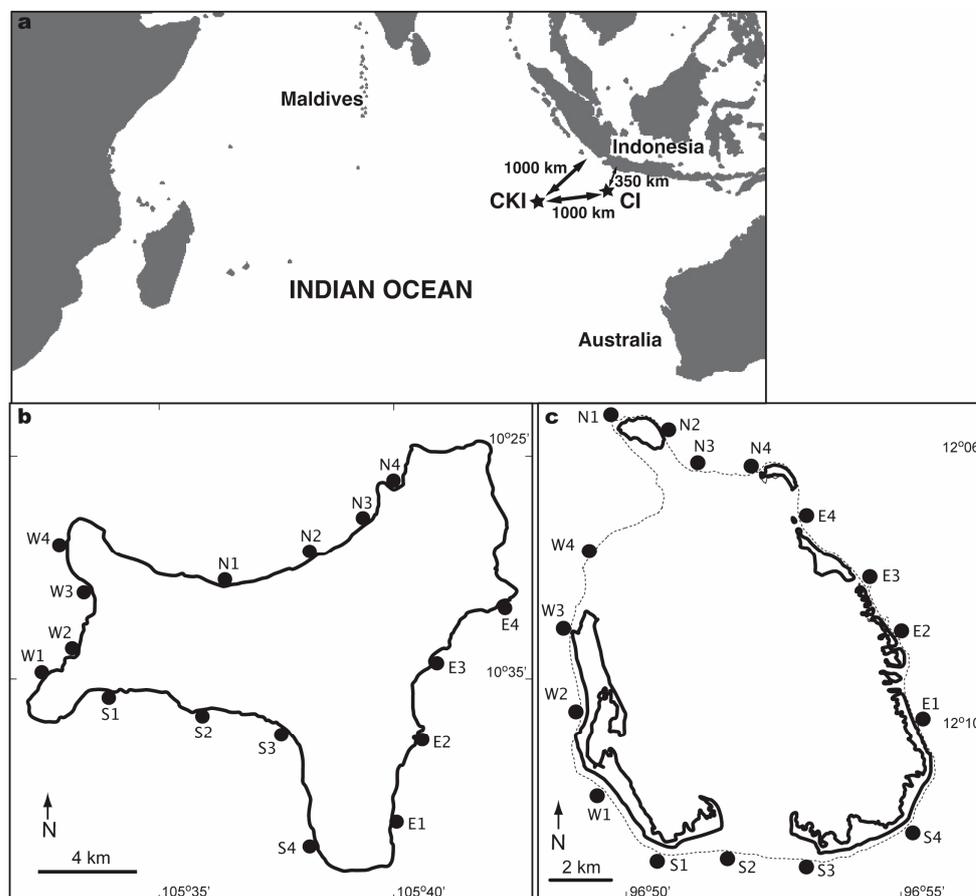
This study was conducted at Christmas Island and the Cocos (Keeling) Islands (Australia's Indian Ocean Territories), located in the eastern Indian Ocean approximately 350 km and 1000 km southwest of Indonesia, respectively. The Indonesian islands of Java and Sumatra are the closest landmasses to the study islands and there are no other reef systems in between. The study islands are considered to be isolated because they are of oceanic origin and are more than 300 km from any other reefs. Thus, the reef fish communities on these islands have formed via colonisation events (i.e., individuals dispersing from other locations, e.g., Indonesia), or *in situ* evolution of endemic species. The Indonesian Archipelago lies within the 'Coral Triangle' region, which harbours the greatest diversity of coral reef fishes [2], with species richness declining with increasing distance from this region. Christmas Island is closer to the Coral Triangle than the Cocos Islands. Christmas Island and the Cocos Islands are volcanic seamounts that rise steeply from 4000 to 5000 m of water. Christmas Island is a single high island that rises to 361 m above sea level. The island is surrounded by a narrow (0–100 m wide) fringing reef, which drops steeply to the abyssal plain. The Cocos Islands lie approximately 1000 km west of Christmas Island and consist of 26 low-lying sandy islands distributed around the perimeter of a central lagoon. The lagoon is about 15 km long, 10 km wide and the maximum depth is about 30 m. The coral reef on the outside of the atoll drops off steeply to the ocean floor. At both locations, trade winds blow from the southeast for most of the year and consequently, the southern coastline at each location receives relatively constant oceanic swells almost all year [61]. The eastern and western coastlines are moderately exposed, while the northern coastline is relatively sheltered most of the time [61].

Underwater visual surveys were conducted from February to May in 2008 to estimate the densities, species richness and spatial distributions of angelfishes and butterflyfishes at both locations. At each island location, surveys were conducted at sixteen sites, with four sites each on the north, south, east and west coasts (Figure 1). At each site, surveys were conducted using three 50 × 5 m transects at each of two depths, 5 m ('shallow') and 20 m ('deep'). That is, a total of six replicate transects per site. All surveys were conducted on the outer reef slope, which is similar in area and structure at both locations [41]. The densities of all angelfish and butterflyfish species were recorded by one diver whilst swimming slowly and simultaneously laying out a 50 m tape. To ensure similar sampling effort, fish surveys were carried out whilst swimming at the same speed, with stoppages to record individuals when encountered.

To estimate microhabitat availability, two 2 m<sup>2</sup> quadrats were randomly placed within each of the fish transects (after the fish were counted) and the percent cover of benthic substrata within the quadrat was visually estimated. Quadrats are a commonly used approach for quantifying marine benthos [62], and because data can be collected relatively quickly, they were ideal for this study given the time constraints associated with SCUBA diving at depth. Benthic substrata were divided into 14 categories: 7 live scleractinian coral morphologies (corymbose, branching, foliose, massive, submassive, plate and encrusting), soft corals, calcareous coralline algae, turf algae, sand, rubble, dead hard coral and "other" (rare benthic organisms with a combined cover of about 1%, e.g., fungid corals, sponges, anemones, zooanthids, gorgonians, seagrasses and macroalgae). Microhabitat diversity was calculated for each replicate using the Shannon–Weiner diversity index,  $H' = -\sum p_j \log p_j$  (where  $p$  is the proportion of each substrate category). This index was used because most quadrats contained multiple substrata, and the index accounts for both the number and evenness of substrate types.

Regression tree analysis was used to examine the relative importance of six explanatory variables (island location, exposure, depth, microhabitat diversity, live coral cover and algal cover) in determining spatial patterns in the structure of angelfish and butterflyfish communities. Regression tree analysis, as opposed to ordination analysis, was chosen because it is an effective, visually intuitive tool for describing meaningful patterns in large, complex ecological datasets and quantifying the relative importance of different

explanatory factors [28,63]. Also, both continuous and categorical explanatory variables can be included in the same analysis [63]. The variation in one or more response variables is split according to the explanatory variables in a series of binary splits [63]. Given the limitations with the data, greater emphasis is placed on the higher-level splits.



**Figure 1.** (a) Location of Christmas Island (CI) and the Cocos (Keeling) Islands (CKI) in the eastern Indian Ocean. The survey sites on the outer reef slopes are shown for (b) Christmas Island and (c) the Cocos Islands. Sites are denoted by N, S, E and W to indicate the side of the island(s). The dotted line on the Cocos Islands map represents the approximate position of the outer reef slope.

Separate univariate regression trees were used to examine the relative importance of each of the six factors in explaining (i) species richness and (ii) total density (all species pooled) of each of the two fish families. Total density was pooled across transects for each depth at each site due to there being very low numbers on some transects and data were  $\log_{10}(x + 1)$ -transformed to reduce the effect of patchiness. The explanatory variable ‘live coral cover’ included all scleractinian coral morphologies, and ‘algal cover’ included turf algae and macroalgae but not crustose coralline algae. As the values of both variables are percentages, the data were arcsine-transformed prior to the analyses.

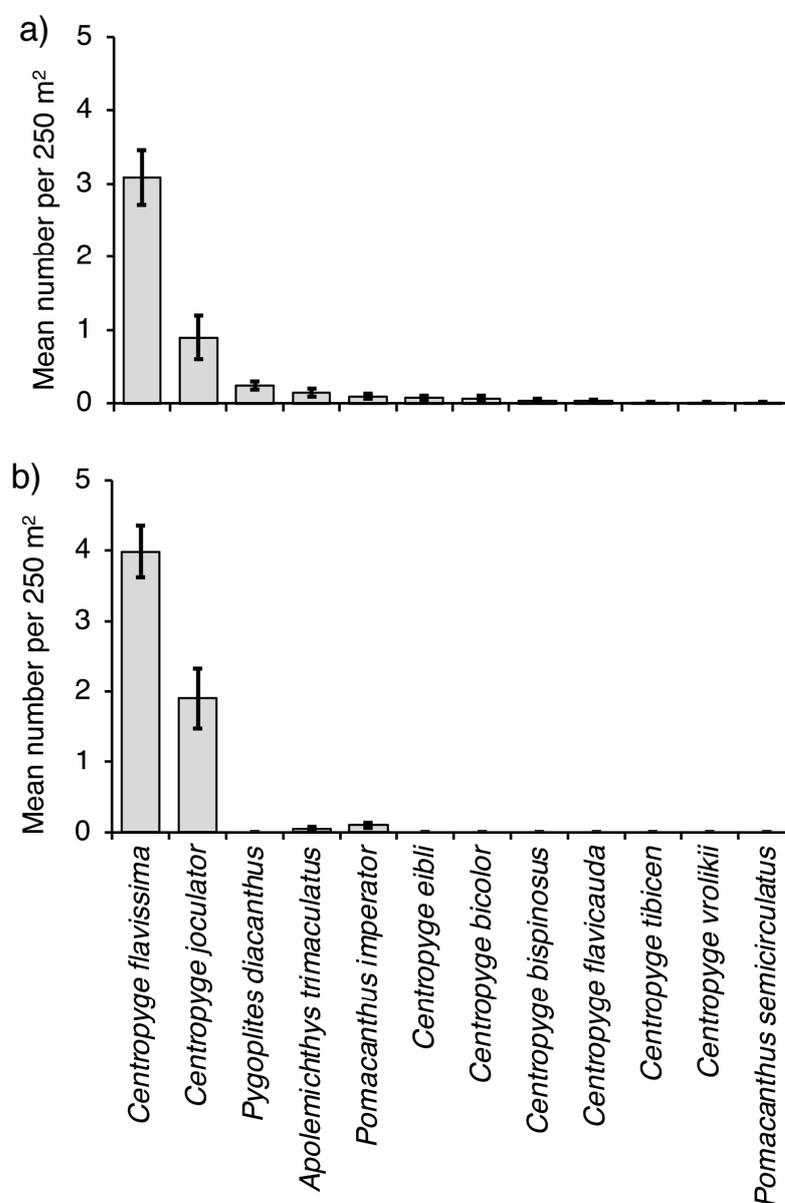
Multivariate regression trees were used to examine the relative importance of each of the six factors on the species composition of the angelfish and butterflyfish assemblages. Of the 12 angelfish species surveyed, 2 species (*Centropyge flavissima* and *C. jocularis*) were extremely abundant and dominated preliminary analyses (even after transformations); therefore, the multivariate regression tree for the angelfish community was based on presence–absence data at the transect level. This reduced the influence of the two most common species whilst still preserving some information on relative abundance. For example, species with high abundance had a high frequency of occurrence (i.e., were present in many transects). As multivariate regression trees tend to be dominated by

the most abundant species, two separate multivariate regression trees were used for the butterflyfishes, one with the twelve most abundant species (with mean densities  $> 0.3$  per  $250 \text{ m}^2$ ), and one with sixteen less abundant species. For both regression trees, densities were pooled across transects at each depth and  $\log_{10}(x + 1)$ -transformed.

### 3. Results

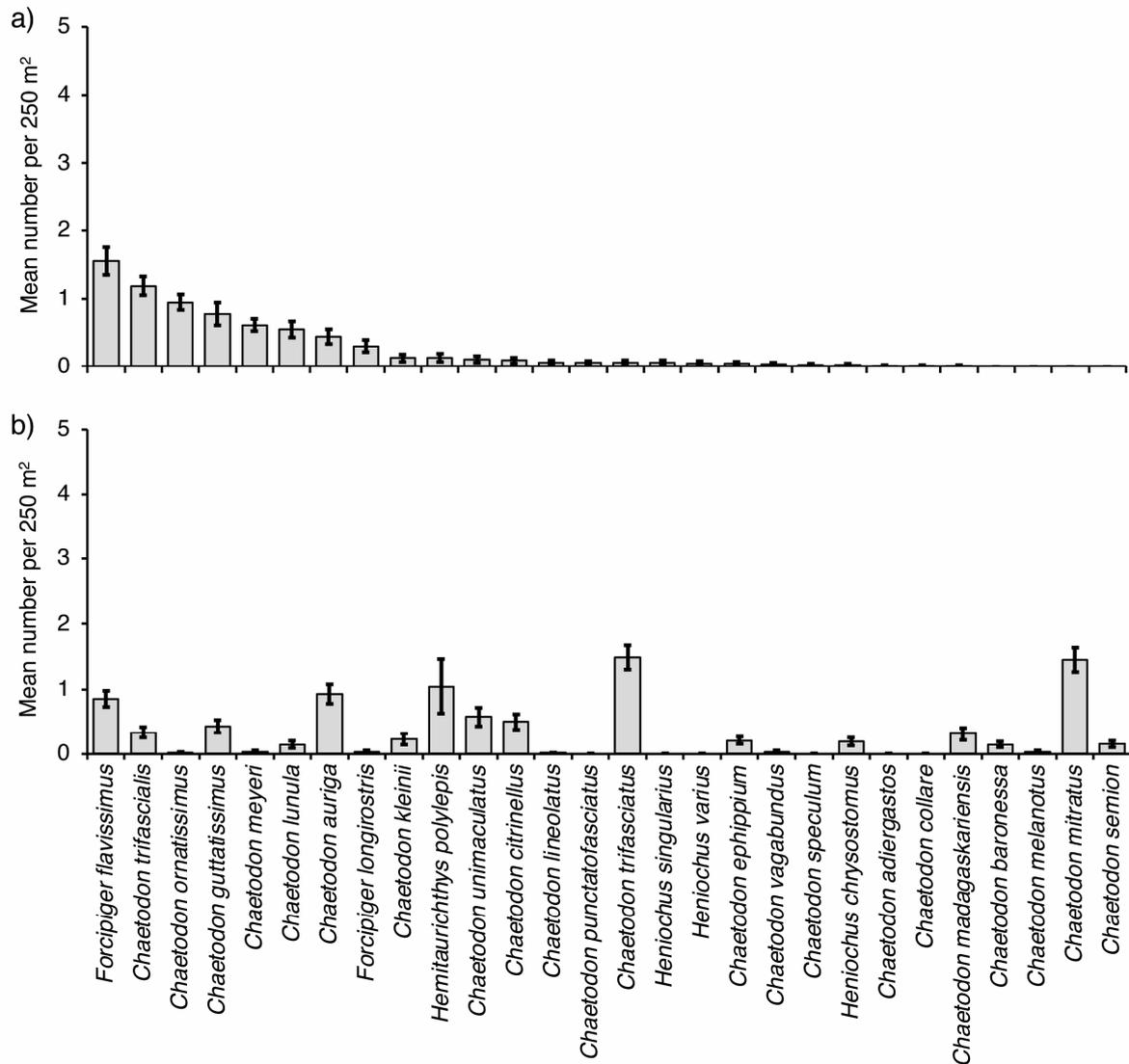
#### 3.1. Relative Abundances of Angelfishes and Butterflyfishes

A total of 12 species of angelfishes were recorded across both locations, with all species (451 individuals) observed at Christmas Island but only 4 species (580 individuals) seen at the Cocos (Keeling) Islands. The most abundant species at both locations was *Centropyge flavissima*, with mean densities (pooled across all sites and depths) of  $3.08 (\pm 0.37 \text{ SE})$  and  $3.98 (\pm 0.36 \text{ SE})$  per  $250 \text{ m}^2$  at Christmas Island and the Cocos Islands, respectively (Figure 2). *Centropyge joculator* was also abundant, with densities of  $0.89 (\pm 0.30 \text{ SE})$  and  $1.91 (\pm 0.42 \text{ SE})$  per  $250 \text{ m}^2$  at Christmas Island and the Cocos (Keeling) Islands, respectively (Figure 2). Other angelfish species occurred at much lower densities ( $< 0.24$  per  $250 \text{ m}^2$ ; Figure 2).



**Figure 2.** Mean number (across all sites and depths) per  $250 \text{ m}^2$  ( $\pm \text{SE}$ ) of pomacanthids (angelfishes) at (a) Christmas Island and the (b) Cocos Islands.

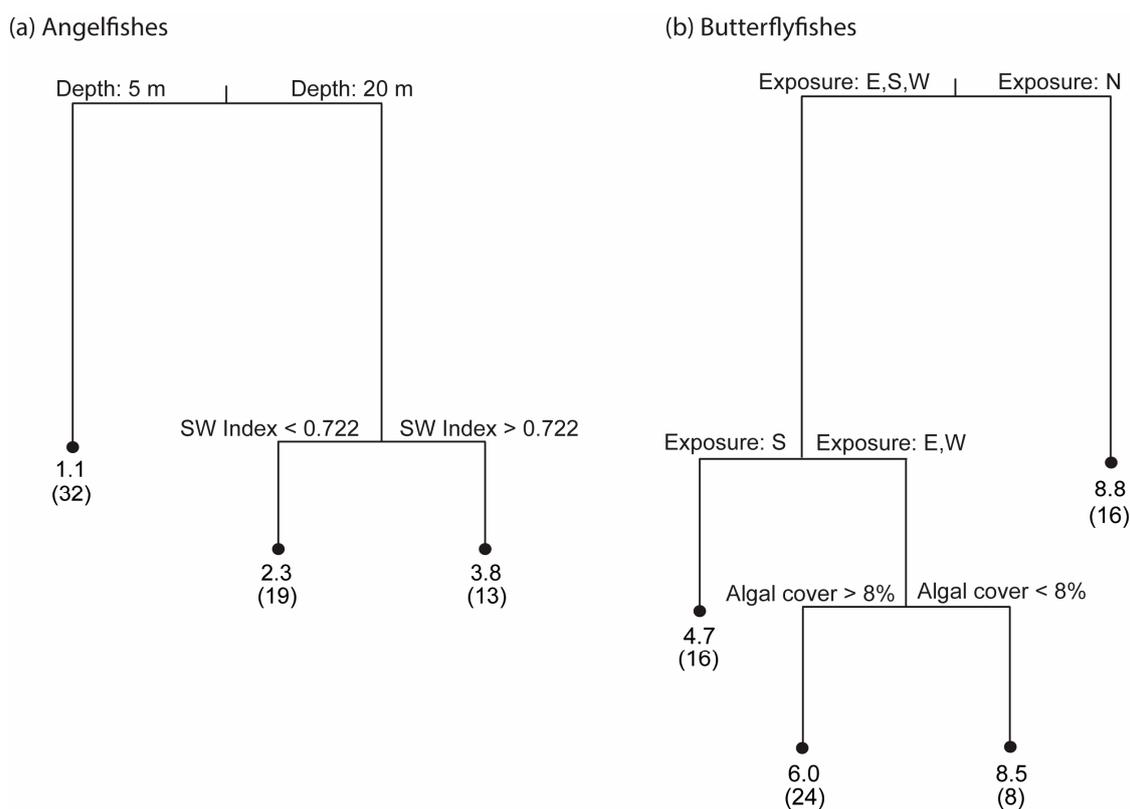
A total of 28 species of butterflyfishes were recorded in surveys across both locations, with 24 species (877 individuals) at Christmas Island and 22 species (697 individuals) at the Cocos (Keeling) Islands (Figure 3). Eighteen species were found at both locations. Relative abundances differed between the two locations. The most abundant butterflyfish species at Christmas Island was *Forcipiger flavissimus*, with a mean density (pooled across all sites and depths) of 1.55 per 250 m<sup>2</sup> ( $\pm 0.2$  SE) and the most abundant species at the Cocos (Keeling) Islands was *Chaetodon trifasciatus*, with a mean density of 1.49 per 250 m<sup>2</sup> ( $\pm 0.19$  SE).



**Figure 3.** The mean number (across all sites and depths) per 250 m<sup>2</sup> ( $\pm$ SE) of chaetodontids (butterflyfishes) at (a) Christmas Island and the (b) Cocos Islands.

### 3.2. Spatial Patterns of Species Richness

Univariate regression tree analysis of spatial patterns in species richness of angelfishes resulted in a three-leaf tree (i.e., two splits) explaining 61.4% of the variation (Figure 4a). The first split, explaining 46.5% of the variation, was determined by depth, with greater numbers of species at 20 m than at 5 m. The second split, which explained 14.9% of the variation, separated the 20 m data according to microhabitat diversity, with higher species richness at the sites where microhabitat diversity was high.

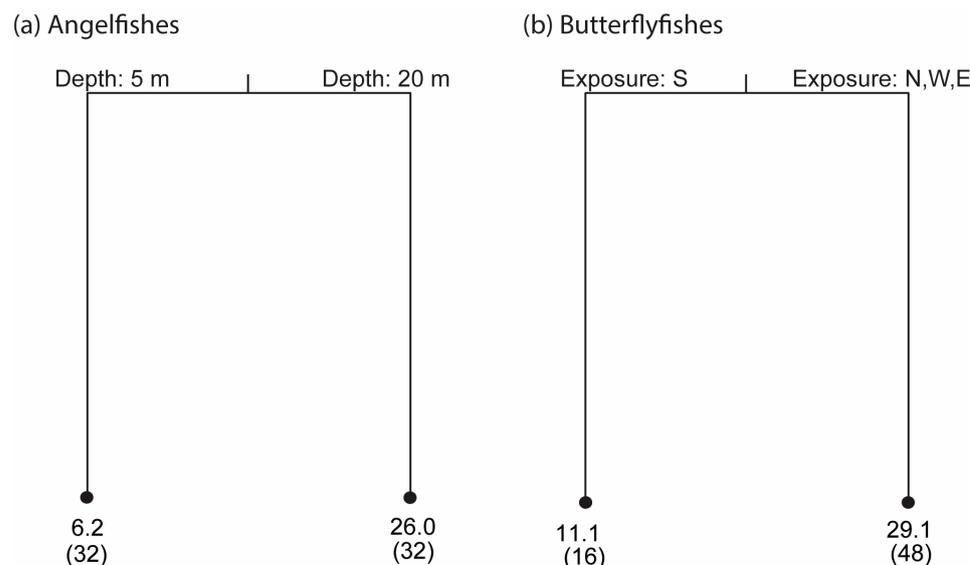


**Figure 4.** Univariate regression trees for species richness of (a) pomacanthids (angelfishes) and (b) chaetodontids (butterflyfishes). SW Index = microhabitat diversity represented by the Shannon–Weiner index. The value below each node represents the mean species richness per replicate (site/depth combinations in this case) and the value in brackets is the number of replicates.

A four-leaf tree explained 42.4% of the variation in butterflyfish species richness (Figure 4b). The greatest percentage of spatial variation in butterflyfish species richness was explained by wave exposure (33.2%), which determined the first two splits. The first split explained 23.5% of the variation in species richness and separated the sites on the north coasts of both locations, which were the least exposed and had the highest species richness, from the other sites. The second split, explaining 9.7% of the variation, separated the sites on the south coasts of both locations, which were the most exposed and had the lowest species richness, from sites on the east and west coasts. The third split, explaining 9.2% of the variation, divided the sites on the east and west coasts according to algal cover, with higher species richness at sites with lower algal cover.

### 3.3. Spatial Patterns in Abundance

Univariate regression tree analysis of spatial patterns in the total density of angelfishes resulted in a two-leaf tree with a single split determined by depth, which explained 44.8% of the variation (Figure 5a). The total density of angelfishes was greater at 20 m than at 5 m. Spatial variation in the total densities of butterflyfishes was also best explained by a two-leaf tree (accounting for 37.6% of the variation), with exposure determining the split (Figure 5b). The total density of butterflyfishes at both island locations was lower at sites on the exposed south coasts than at sites on the other coasts.



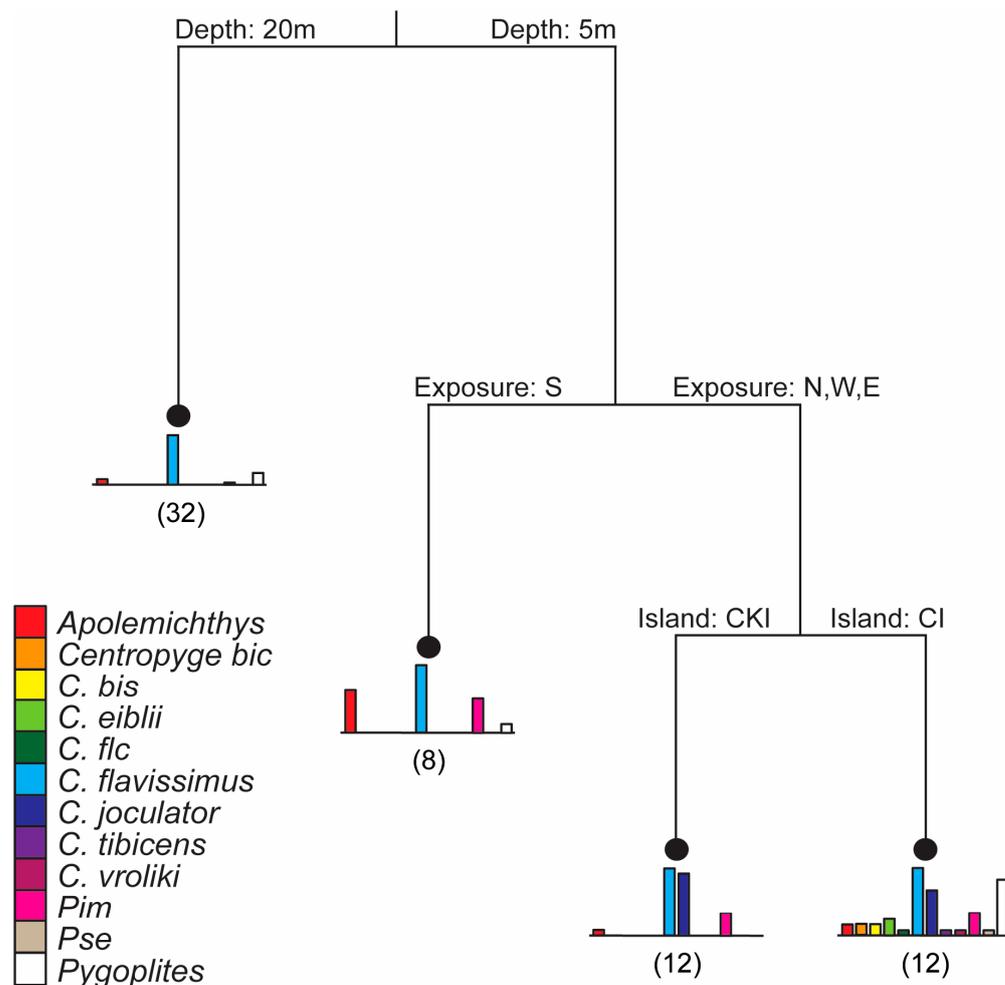
**Figure 5.** Univariate regression trees for total density of (a) pomacanthids (angelfishes) and (b) chaetodontids (butterflyfishes) from Christmas Island and the Cocos Islands. The value below each node represents the mean total density (untransformed) per replicate (i.e., transect) and the value in brackets is the number of replicates.

### 3.4. Spatial Patterns in Species Composition

Multivariate regression tree analysis of spatial patterns in the species composition of angelfishes resulted in a three-leaf tree, which explained 33.8% of the variation (Figure 6). The first split explained 15.3% of the variation and was determined by depth. This split was influenced most by *C. jocularis* and *Pomacanthus imperator*, which were both common at 20 m but seldom encountered at 5 m (Figure 6, Table 1). The second split explained 9.8% of the variation and divided the 20 m data between sites on the exposed south coasts of both locations from sites on the other coasts. This split was mostly determined by *C. jocularis*, which was absent on the south coast at both locations, and *Apolemichthys trimaculatus*, which occurred more frequently on the south coasts (Table 1). The north, east and west coast sites were further divided by island location in the third split, which explained 8.7% of the variation. This split was mostly influenced by *Pygoplites diacanthus* (Table 1), which was the third most abundant species at Christmas Island but was not recorded at the Cocos Islands (Figure 2).

**Table 1.** Summary of the splits in the multivariate regression tree for pomacanthids (angelfishes), showing the contribution of each species to the percentage of variation explained by each split. The species contributing the most to each split are presented in bold.

Nature of Split	Island	Exposure	Depth	Total
<i>Apolemichthys trimaculatus</i>	0.07	<b>2.38</b>	0.62	3.07
<i>Centropyge bicolor</i>	0.26	0.07	0.10	0.43
<i>C. bispinosa</i>	0.26	0.07	0.10	0.43
<i>C. eibli</i>	0.60	0.15	0.22	0.97
<i>C. flavicauda</i>	0.07	0.02	0.02	0.11
<i>C. flavissima</i>	0.00	0.00	1.59	1.59
<i>C. jocularis</i>	0.60	<b>5.97</b>	<b>8.96</b>	15.52
<i>C. tibicen</i>	0.07	0.02	0.02	0.11
<i>C. vrolikii</i>	0.07	0.02	0.02	0.11
<i>Pomacanthus imperator</i>	0.00	0.26	<b>3.00</b>	3.27
<i>P. semicirculatus</i>	0.07	0.02	0.02	0.11
<i>Pygoplites diacanthus</i>	<b>6.62</b>	0.81	0.62	8.05
Split total	8.67	9.77	15.31	33.75

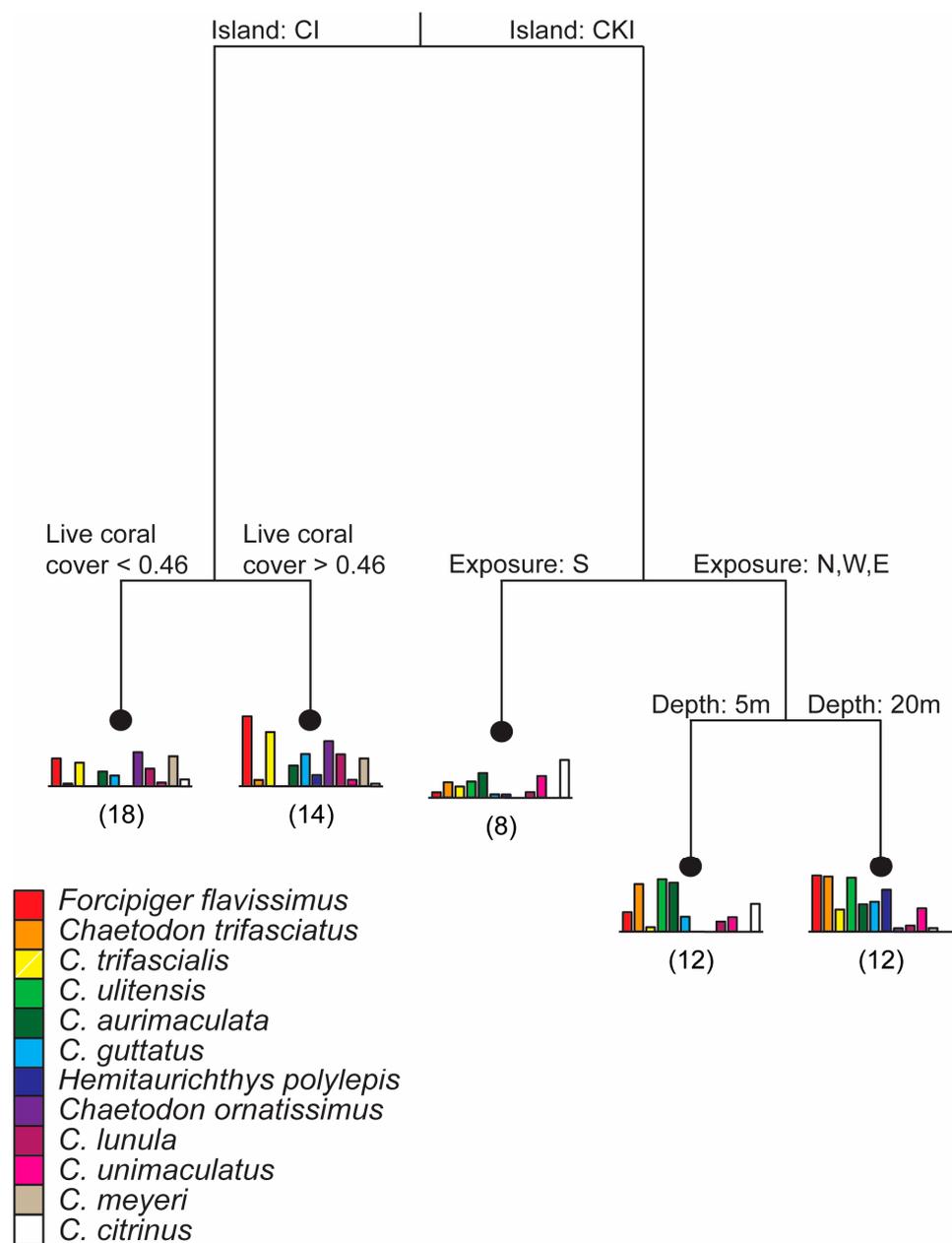


**Figure 6.** Multivariate regression tree for pomacanthids (angelfishes). The bar plots show the presence/absence patterns of each species. The height of each bar represents the number of sites a species was present at. The number of depth  $\times$  site replicates that comprise each node is provided in brackets.

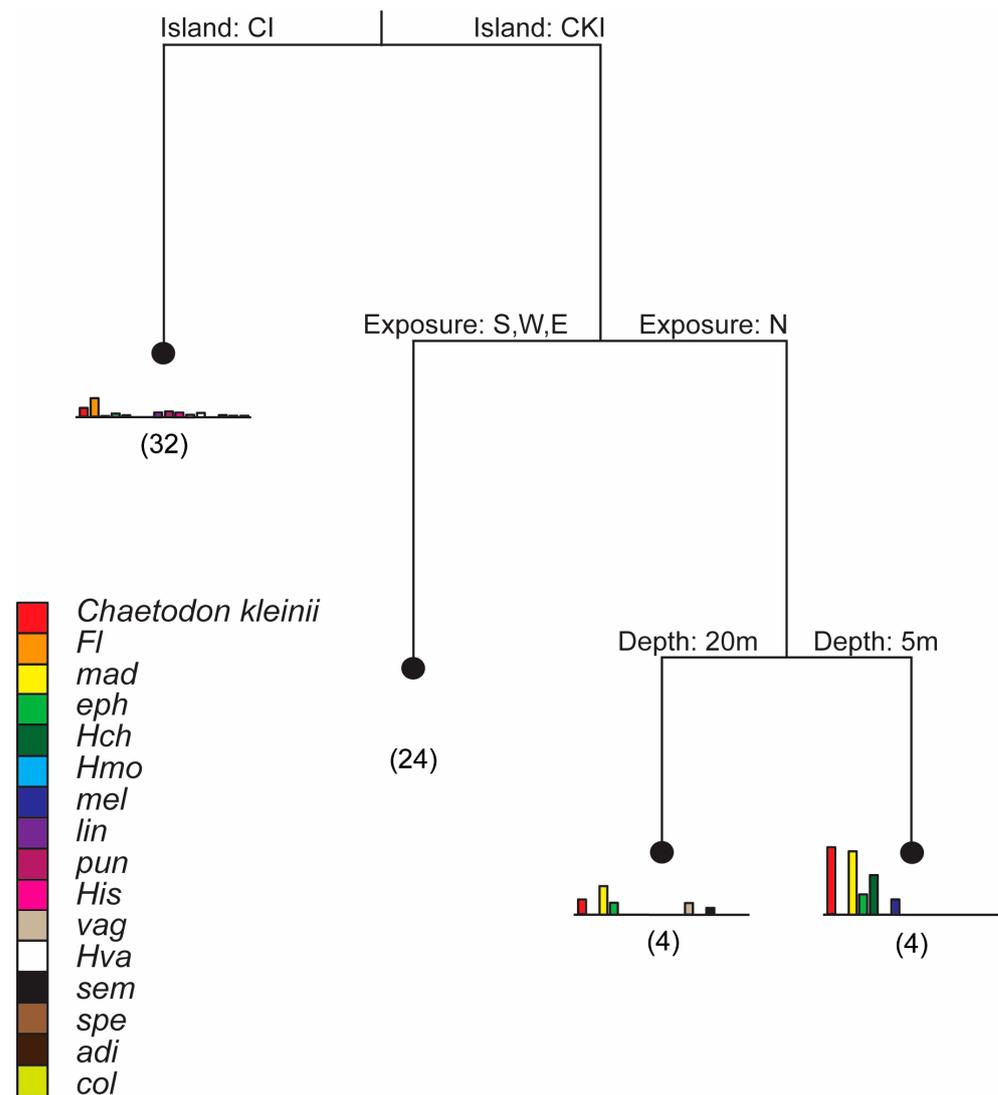
Multivariate regression tree analysis of spatial variation in species composition and relative abundance of the 12 most abundant butterflyfishes resulted in a 5-leaf tree, which accounted for 42.4% of the variation (Figure 7). The first split, explaining 24.2% of the variation, was determined by island location and influenced most by three species: *Chaetodon ulietensis*, *C. trifasciatus* and *C. ornatissimus* (Table 2). *C. ulietensis* and *C. trifasciatus* were the two most abundant butterflyfish species at the Cocos Islands but both species had very low densities at Christmas Island (Figure 2). *C. ornatissimus* was the third most abundant species at Christmas Island but had very low densities at the Cocos Islands (Figure 2). The second split explained 6.3% of the variation and separated the south coast sites at Cocos Island from sites on the other coasts, and was largely influenced by the low abundance of *C. ulietensis* and *C. trifasciatus* on the south coast. The third split explained 6.1% of the variation and split the north, west and east coast sites at the Cocos Islands by depth, and was largely due to the relatively high abundance of *H. polylepis* and *F. flavissimus* at 20 m (Table 2). The fourth split explained 5.8% of the variation in butterflyfish community structure and separated sites at Christmas Island based on live coral cover (Table 2, Figure 7). This split was mostly due to *F. flavissimus* and *C. trifasciatus* having greater relative abundance at sites where live coral cover was greater than 44%.

For the 16 less abundant species of butterflyfish, spatial variation in species composition was best described by a 4-leaf multivariate regression tree, explaining 22.2% of the

variation (Figure 8). The first split was determined by island location, which explained 8.2% of the variation. This was mostly influenced by *C. madagascariensis* having a much higher relative abundance at the Cocos Islands than Christmas Island, and by *Forcipiger longirostris* being more abundant at Christmas Island (Table 3). The second split was determined by exposure (explaining 8.8% variation) and separated the assemblages on the most sheltered coast (north) of the Cocos Islands from those on the more exposed coasts (east, south, west). This split was influenced by the relatively high abundance of *C. kleinii* and *C. madagascariensis* on the sheltered north coast sites at the Cocos Islands (Table 3). The third split, explaining 5.1% of the variation, was determined by depth, and was mostly due to *C. kleinii* and *Heniochus chrysostomus* having greater relative abundances at 20 m at the Cocos Islands (Table 3).



**Figure 7.** Multivariate regression tree for the 12 most abundant chaetodontids (butterflyfishes) at Christmas Island (CI) and the Cocos Islands (CKI). The bar plots show the relative abundance of each species. The number of depth × site replicates that comprise each node is provided in brackets.



**Figure 8.** Multivariate regression tree for the 16 less abundant chaetodontids (butterflyfishes) at Christmas Island (CI) and the Cocos Islands (CKI). The bar plots show the relative abundance of each species. The number of depth × site replicates that comprise each node is provided in brackets.

**Table 2.** Summary of the splits in the multivariate regression tree for the 12 most abundant chaetodontids (butterflyfishes), showing the contribution of each species to the variation explained by each split. The species contributing the most to each split are presented in bold.

Nature of Split	Island	Exposure	Depth	Coral Cover	Total
<i>Forcipiger flavissimus</i>	<b>1.63</b>	1.25	0.86	<b>2.74</b>	10.31
<i>Chaetodon trifasciatus</i>	0.07	<b>1.56</b>	<b>4.85</b>	0.05	11.96
<i>C. trifascialis</i>	0.38	0.01	1.82	<b>1.46</b>	10.82
<i>C. ulietensis</i>	0	<b>1.7</b>	<b>6.2</b>	0	11.18
<i>C. auriga</i>	0.57	0.24	0.97	0.05	8
<i>C. guttatissimus</i>	0.27	0.48	0.01	0.71	9.75
<i>Hemitaurichthys polylepis</i>	<b>2.1</b>	0.39	0.42	0.2	8.7
<i>C. ornatissimus</i>	0.02	0	<b>4.46</b>	0.21	7.02
<i>C. lunula</i>	0.02	0.01	0.83	0.33	5.19
<i>C. unimaculatus</i>	0.1	0.01	0.72	0.02	6.62
<i>C. meyeri</i>	0	0.01	2.29	0.01	4.91
<i>C. citrinellus</i>	0.94	0.68	0.75	0.04	5.53
Split total	6.1	6.33	24.2	5.81	42.44

**Table 3.** Summary of the splits in the multivariate regression tree for the 16 rarer chaetodontids (butterflyfishes), showing the contribution of each species to the variation explained by each split. The species contributing the most to each split are presented in bold.

Nature of Split	Island	Exposure	Depth	Total
<i>Chaetodon kleinii</i>	<b>2.23</b>	<b>4.22</b>	0.03	6.48
<i>Forcipiger longirostris</i>	0	0.03	<b>1.8</b>	1.83
<i>C. madagascariensis</i>	1	<b>3.71</b>	<b>1.96</b>	6.67
<i>C. ephippium</i>	0.06	0	1.12	1.18
<i>Heniochus chrysostomus</i>	<b>1.38</b>	0.21	0.93	2.53
<i>H. monoceros</i>	0	0.5	0.74	1.24
<i>C. melannotus</i>	0.23	0.06	0.96	1.25
<i>C. lineolatus</i>	0	0	0.1	0.11
<i>C. punctatofasciatus</i>	0	0	0.22	0.22
<i>H. singularius</i>	0	0	0.16	0.16
<i>C. vagabundus</i>	0.14	0.07	0	0.21
<i>H. varius</i>	0	0	0.12	0.12
<i>C. semeion</i>	0.12	0.01	0.05	0.12
<i>C. speculum</i>	0.02	0	0.02	0.02
<i>C. adiergastos</i>	0.01	0	0.01	0.01
<i>C. collare</i>	0.01	0	0.01	0.01
Split total	5.1	8.81	8.24	22.15

To summarise, across all the angelfish analyses, depth accounted for the greatest percentage of the spatial variation in species richness, total abundance, and species composition/relative abundance (Table 4). For the butterflyfishes, exposure accounted for the greatest percentage of the spatial variation in species richness and total abundance, while island location accounted for the greatest percentage of the spatial variation in species composition/relative abundance (Table 4).

**Table 4.** Summary of the relative importance of each of the six factors in explaining variation in species richness, total abundance, and the species composition/relative abundance of pomacanthid (angelfish) and chaetodontid (butterflyfish) species at Christmas Island and the Cocos Islands. The following categories were used to classify the percentage of variation explained by each variable, calculated using regression tree analyses: High > 20%, Medium = 10–20%, Low = 5–10%, Negligible = 0–5% (indicated by -).

Nature of Split	Island	Exposure	Depth	Microhabitat Diversity	Coral Cover	Algal Cover
<b>Angelfishes</b>						
Species richness	-	-	High	Medium	-	-
Total abundance	-	-	High	-	-	-
Species composition and relative abundance	Low	Low	Medium	-	-	-
<b>Butterflyfishes</b>						
Species richness	-	High	-	-	-	Low
Total abundance	-	High	-	-	-	-
Species composition and relative abundance (12 common species)	High	Low	Low	-	Low	-
Species composition and relative abundance (16 rarer species)	Low	Low	Low	-	-	-

#### 4. Discussion

This study shows that large-scale factors (island location, wave exposure and depth) appear to have the greatest influence on the structure of butterflyfishes and angelfishes on isolated, oceanic reefs, rather than finer-scale biological components of the habitat (live

coral cover, algal cover and microhabitat diversity). This is consistent with other studies that have reported the importance of physical factors in structuring reef fish assemblages at other oceanic locations [21,23,64], especially depth [22,28]. However, these results contrast with studies conducted at continental reefs where habitat characteristics and other biotic factors have a strong influence on the composition and abundance of reef fish communities [9,47,65–68].

For angelfishes, depth explained the greatest variation in total abundance, species richness, and species composition at Christmas Island and the Cocos Islands. Species richness and the total abundance of angelfishes was higher at 20 m than at 5 m. Greater density and species richness of angelfishes has been recorded in deeper waters (>15 m) at other oceanic locations [69–72]. In contrast, species richness and abundance of angelfishes is greatest in shallow waters (1–5 m) at non-oceanic locations, such as the Great Barrier Reef (GBR) and Papua New Guinea (PNG) [73,74]. The same species (i.e., *Centropyge bicolor*, *Centropyge bispinosa*, *Centropyge vrolikii* and *Pygoplites diacanthus*) that are most common in the shallows (1–5 m) on the GBR and in PNG, are most abundant in deeper waters (20 m) at Christmas Island and the Cocos Islands. While angelfishes can inhabit a wide range of depths [58,75], they appear to inhabit greater depths on oceanic islands.

Greater depths may provide a refuge for species that are incapable of inhabiting shallow areas exposed to high wave energy [3,4]. Bridge et al. [75] found that in contrast to many other reef fishes, the fin aspect ratio in angelfishes (*Centropyge* sp.) is low, which limits their ability to swim in high wave energy environments. In our analyses, wave exposure (side of the island) did not explain spatial structure in angelfishes, possibly because wave exposure in shallow waters is too great for angelfishes even on the most sheltered sides of Christmas and Cocos Islands.

In addition to declining wave energy, coral and algal communities change with depth [61,76,77], and these provide shelter and food (respectively) for *Centropyge* angelfishes [58,60,78]. However, coral and algal cover were included in the analyses and neither were important in explaining the spatial variation in angelfish communities. Similarly, Eagle et al. [73] found that the abundance of three *Centropyge* species was not correlated with the abundance of their algal food source.

It is possible that the depth-related patterns observed in angelfishes are due to variables that were not measured in this study. For example, habitat complexity is linked to higher densities and species richness of reef fishes, including angelfishes [46,66,79–83], and appears to be particularly important on oceanic reefs [23,24]. *Centropyge* angelfishes shelter in small holes and are absent on reefs that lack suitable habitat complexity [83]. Habitat complexity is lower in areas of high wave energy [30] and is therefore expected to increase with depth, particularly at oceanic islands where wave energy is typically high [23]. Habitat complexity and shelter hole availability were not measured in this study; however, other studies at Christmas Island found that habitat complexity is greater at 20 m than 5 m [61] and therefore deeper reefs may support more angelfishes. In contrast, wave energy is lower around continental islands, and shallow waters tend to have higher habitat complexity and a higher abundance and richness of angelfishes [73,74].

The abundance, species richness, and species composition of butterflyfishes on continental reefs is largely influenced by the availability and diversity of suitable resources, especially hard coral [65,82,84–86]. However, in this study, fine-scale habitat factors (live coral cover, algal cover and microhabitat diversity) had little influence on the spatial structure of butterflyfish communities relative to the larger-scale factors (island location and wave exposure). Wave exposure has a strong influence on the spatial structure of reef fish communities at oceanic islands. For example, in the Hawaiian Islands, areas that are sheltered from wave action tend to support greater abundance, species richness and diversity of reef fishes than more exposed areas [21,24]. The lower total abundances and species richness of butterflyfish species on the exposed sides of Christmas Island and the Cocos Islands is possibly because they lack the locomotory abilities required to persist in high wave energy environments. Butterflyfishes use a pectoral–caudal swimming mode,

which has relatively low efficiency and manoeuvrability in high wave energy environments, making it difficult for these species to seek shelter, or maintain position and obtain food from the substrate [4].

Previous studies have shown that abundance and species richness of butterflyfishes are positively correlated with habitat complexity [82,83,87]. Habitat complexity is lower in areas of high wave energy [30] and this may contribute to lower abundance and species richness of butterflyfishes [24]. Low habitat complexity along the most wave-exposed coastlines of Christmas and Cocos Islands probably explains (at least partly) why species richness and abundance of butterflyfishes was lower at exposed sites and higher at sheltered sites. In addition, coral community structure is strongly influenced by wave energy [30], which influences the distribution and abundance of some butterflyfishes, particularly those with very specialised diets [87,88].

Differences in species composition between island locations included four butterflyfish species (*Chaetodon melannotus*, *C. semion*, *C. ulietensis*, and *Heniochus monoceros*) that were recorded in transects at the Cocos Islands but not at Christmas Island. These four species are known to occur at Christmas Island, but are rare [89,90]. Six butterflyfishes (*Chaetodon adiergastos*, *C. collare*, *C. punctatofasciatus*, *C. speculum*, *Heniochus singularius* and *H. varius*) recorded at Christmas Island were not observed in surveys at the Cocos Islands. Other than *C. punctatofasciatus*, these species have never been recorded at the Cocos Islands [91,92]. Both study locations are likely to be colonised by larvae arriving from the nearest source populations (Indonesia). Christmas Island is 350 km from Indonesia, whereas the Cocos Islands are 1000 km from Indonesia (and 1000 km from Christmas Island). Species capable of dispersing to Christmas Island may not be able to disperse to the Cocos Islands due to the extra distance. Indeed, the reef fish communities at Christmas Island and the Cocos Islands contain higher proportions of species with long pelagic larval durations (which infers greater dispersal capabilities), compared to communities on continental reefs [27].

There were also differences between the two island locations in the relative abundances of butterflyfishes. Three of the four most abundant species at the Cocos Islands (*C. trifasciatus*, *C. ulietensis* and *C. auriga*) use lagoonal or sheltered environments at some stage of their life [58,93]. The presence of an extensive lagoon at the Cocos Islands, but not at Christmas Island, probably explains the greater relative abundance of these species at the Cocos Islands [94]. Many of the other butterflyfish species also use the lagoon at the Cocos Islands and this may explain the differences in relative abundance between the two islands locations. Data on other reef fish families (e.g., lethrinids and serranids) that require lagoonal recruitment habitat also show clear differences in abundance between Christmas and Cocos Islands [90,92]), whereas groups (e.g., angelfishes) that do not use the lagoon at the Cocos Islands show little difference in relative abundance between island locations. The abundance of recruits was not measured in this study; however, it is likely that patterns in the abundance of some adult populations could be explained by recruitment patterns and the availability of recruitment habitat. The importance of a lagoon on the structure of outer reef fish communities is likely to vary depending on the taxonomic group and its reliance on the lagoon environment.

## 5. Conclusions

The establishment of reef fish communities on oceanic reefs is largely dependent on colonisation from distant locations, and thus is influenced by reef location, size, and the degree of isolation. On continental reefs, connectivity is much higher, and different factors influence community structure [84,85]. Once a species colonises an oceanic reef, this study shows that three additional physical variables (exposure, depth, reef structure) determine its distribution and abundance [21,23,64,71]. Compared to continental reefs, oceanic reefs receive greater wave energy, which likely results in steeper gradients in habitat complexity among sites and depths.

Overall, this study demonstrates that large-scale factors associated with island location (e.g., exposure and depth), had greater importance than fine-scale microhabitat factors in de-

termining spatial patterns in species richness, total density and composition of angelfishes and butterflyfishes. Given the importance of large-scale factors, reef fish communities on oceanic reefs are probably more vulnerable than continental communities to the predicted increase in destructive weather events [95,96]. The recovery of remote communities is also likely to be slower than continental communities due to the isolation from source populations [46]. Understanding which factors are most important to structuring reef fish communities, and how these factors vary between locations, is important to predicting how fish communities will be affected by, and recover from, different impacts.

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