Diversity on the edge: non-linear patterns of coral community structure at an isolated oceanic island

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ABSTRACT: Coral communities are expected to display predictable patterns of diversity and structure across depth and exposure gradients, yet these predictions have rarely been tested at oceanic locations. Here we tested 5 common ecological predictions about coral community structure at the remote Christmas Island in the eastern Indian Ocean. Our results suggest that not all of the predictions hold true at this oceanic location, primarily because the community is structured in non-linear ways. Each surveyed depth zone (5, 12, 20 m) supported a distinctive community, yet species diversity and coral abundance did not show the expected linear increase with depth. Habitat complexity was also shown to respond non-linearly with depth, with the highest habitat complexity occurring in the intermediate 12 m zone. We discuss the ‘cliff-edge effect’ as a possible explanation for the high diversity and abundance of corals at 20 m, while physical stress and competitive exclusion may explain the low diversity at 12 m. The cliff-edge habitat provides a narrow zone in between the wave-swept shallows and the low light/high shade environment of the steep outer reef walls, and this zone of heterogeneous environmental conditions supports a wide diversity of corals. If future storm events, bleaching, disease or predator outbreaks were to impact the corals living in the cliff-edge habitat, this may have a disproportionate impact on the coral reef community as a whole. Monitoring the status of corals on the cliff edge is important for understanding and predicting how oceanic reef systems will be affected by climate change.

KEY WORDS: Abundance · Christmas Island · Cliff-edge effect · Community ecology · Diversity · Habitat complexity · Indian Ocean

INTRODUCTION

The relative inaccessibility of oceanic coral reef ecosystems has limited our understanding of whether coral communities in these systems are structured in the same way as continental reefs. If they are, then a number of relatively predictable biotic and hydrodynamic factors are likely to influence coral zonation patterns. For example, physical disturbance from wave energy and light availability are important selective pressures that lead to characteristic and directional patterns of diversity and structure across depth and exposure gradients (Connell 1978, Huston 1985).

Generally, in shallow habitats (<5 m), coral species diversity is low and increases with depths to 15–30 m before decreasing again (Done 1983, Karlson 1999). Diversity is lowest near the ocean surface due to wave-induced stress. Corals are particularly vulnerable to physical breakage and thus diversity and morphological variation is limited in areas that receive constant swell (e.g. exposed reef flats) (Madin & Connolly 2006). Storms or cyclones can also cause various types of damage to corals through mechanical destruction, scouring and abrasion to changes in sedimentation and increases in turbidity (Harmelin-Vivien 1994). However, the responses of coral communities to phys-
ical disturbances can differ because a range of diversity–disturbance relationships are possible depending on the frequency and intensity of disturbances and angle and profile of the reef (Woodley et al. 1981, Done 1982, Huston 1985, Hall et al. 2012).

High wave energy also influences colony morphology whereby coral communities on shallow, exposed reefs are dominated by robust wave-tolerant species which exhibit simple encrusting, digitate and massive morphologies (Adjeroud et al. 2009, Williams et al. 2013, Madin et al. 2014). In contrast, on deeper or sheltered reefs, a reduction in wave exposure allows corals to grow into large and/or complex ‘canopy-forming’ morphologies (Goatley & Bellwood 2011). In addition, light becomes increasingly limited with depth, which enables shade-tolerant species to dominate on deeper reefs and grow as large flat horizontal plates (Wallace 1999, Veron 2000). Spatial gradients in wave energy and light also affect habitat complexity, which is defined by the morphology of individual corals and the complexity of the underlying topographic reef structure (Wilson et al. 2007, Alvare-Filip et al. 2009). Consequently, there is a close association between some morphologies (e.g. branching coral) and habitat complexity (Bergman et al. 2000, Graham & Nash 2013).

Coral colony abundance (i.e. the total abundance of all species) follows a similar pattern to diversity whereby it increases with depth (peaking at ~30 m) and decreases with exposure. This pattern is largely caused by wave action that decimates large or fragile coral colonies in shallow and exposed habitats (Madin 2005, Madin et al. 2014). However, colony abundance is also influenced by biological interactions that are not strictly depth-dependent, such as predation, herbivory and disease (Connell et al. 1997, Rudolf & Antonovics 2005). For example, the feeding preferences of corallivorous predators, such as the crown-of-thorns starfish Acanthaster planci, are not greatly influenced by depth (De’ath & Moran 1998). Grazing by herbivorous fishes influences competitive interactions between corals and macroalgae (Lirman 2001), and the removal of herbivores can lead to phase shifts that are not depth restricted (Russ 2003, Fox & Bellwood 2007). Further, coral disease is influenced by demographic and environmental factors, but depth does not seem to be the most important factor (Bruno et al. 2007, Hobbs & Frisch 2010).

Due to climate change, the frequency and intensity of disturbance events is predicted to increase (Emanuel 2005). Consequently, Madin et al. (2008) have predicted that future reefs will be dominated by small, morphologically simple and robust coral species with low abundance. Branching coral species such as Acropora are particularly susceptible to disturbance because they often have limited attachment to the substrate (Marshall & Baird 2000, Carpenter et al. 2008). As a result, Acropora-dominated communities, particularly those growing in sheltered habitats, can be severely damaged when exposed to rare storm events (Jackson 1979, Madin & Connolly 2006, Fabricius et al. 2008). Furthermore, on contemporary reefs, the range and velocity of disturbances occurring at depth is increasing (e.g. coral bleaching, Hoegh-Guldberg & Salvat 1995, Penin et al. 2007; cyclones, Bongaerts et al. 2013; and corallivore predation, Kayal et al. 2012); hence, those species that have previously found refuge at depth may also be more vulnerable in the future.

Detecting change in coral communities is crucial, but documenting patterns in coral community composition has been limited by difficulties in identifying corals to species level. Valuable insights have been gained from species level studies conducted on continental reefs (e.g. Great Barrier Reef, Connell et al. 1997, De Vantier et al. 2006, Wakeford et al. 2008). While some studies have examined spatial patterns in the benthic composition of oceanic Pacific islands at various levels of resolution (Williams et al. 2008, Gove et al. 2015), the species level responses of coral communities have rarely been examined in oceanic Indian Ocean communities (see the seminal studies of Spencer-Davies et al. 1971, Sheppard 1980, Bou- chon 1981). Given the increasing scale, frequency and intensity of disturbances on coral reefs over the last 2 decades, it is timely to re-evaluate the spatial distribution and abundance of coral communities at remote Indian Ocean locations to better predict how these disturbances will impact the coral communities (Kenyon et al. 2006, Adjeroud et al. 2010) and associated taxa.

Christmas Island is an isolated oceanic island situated on the Indo-Pacific biogeographic border, and as a result, the coral reef ecosystem there includes a unique mix of Indian and Pacific Ocean species and numerous endemics (Allen 2008, Brewer et al. 2009, Hobbs et al. 2012). Preliminary benthic surveys conducted at Christmas Island between 2005 and 2012 documented relatively high cover of live coral (41 to 58%, Gilligan et al. 2008, Speed et al. 2013). Taxonomic surveys conducted by the Western Australian Museum in 1987 identified 88 species of scleractinian corals across 38 genera at Christmas Island (Done & Marsh 2000). More recently, Richards & Hobbs (2014) documented 145 species of scleractinian coral from 51 genera, bringing the total number of sclerac-
tinian corals known from the island to 169. However, these benthic and taxonomic surveys did not assess the spatial variation in coral community composition or structure around the island.

While Christmas Island is relatively pristine, impacts from disease outbreaks and coral bleaching have been documented (Hobbs & Frisch 2010, Hobbs 2014, Hobbs et al. 2015) and increases in the frequency and intensity of storm activity and bleaching events are predicted for the coming decades (Sheppard et al. 2002, Hyder Consulting 2008, AECOM Australia 2010, NOAA Coral Reef Watch 2015). Such burgeoning threats highlight the need to study how natural processes structure coral communities before their influence becomes intermixed with anthropogenic disturbances. Examining the way coral communities are structured will help predict which taxa and habitats will be most affected by increasing impacts. Moreover, understanding the response of the local community to disturbances is particularly important at remote locations because isolated coral communities are expected to have limited resilience due to the reliance on self-recruitment, rather than long-distance dispersal, for recovery (Ayre & Hughes 2000, Gilmour et al. 2013).

Here we tested the following 5 hypotheses about the coral community structure at Christmas Island, where coral communities grow along steep depth and wave-exposure gradients: (1) coral diversity decreases with exposure and increases with depth; (2) colony abundance decreases with exposure and increases with depth; (3) morphological complexity decreases with exposure and increases with depth; (4) habitat complexity decreases with exposure and increases with depth; and (5) coral community structure is predictable across depth and exposure gradients as a linear trend.

MATERIALS AND METHODS

Study site

Located in the eastern Indian Ocean, 1400 km north-west of Western Australia (Berry & Wells 2000), Christmas Island (10°30’S, 105°39’E) is the summit of a submarine mountain that rises to a central plateau of approximately 361 m above sea level. Its jagged limestone coastline is fringed by a coral reef that extends 0 to 200 m seaward before a rapid drop in depth from 12−20 m to several thousand metres. With no lagoons there is a restricted subset of habitat types. The typical tidal range is approximately 1 m (Mean Lower Low Water [MLLW] to Mean Higher High Water [MHHW]).

Survey methodology

Eight sites and 3 depths (5, 12 and 20 m) were surveyed around Christmas Island between 25 April and 7 May 2013. The survey sites spanned the east, west and north coast of the island and represented different levels of wave exposure (Fig. 1); the southern coast was inaccessible due to constant large swell.

To test for depth-related changes in coral community composition, 3 depth zones were surveyed: the reef flat (5 m), reef crest/upper reef slope (12 m) and reef slope/wall (20 m). Three replicate 15 × 2 m wide belt transects (total 90 m²) were surveyed within each depth zone. Every colony
within the belt transect was counted and identified to species; however, juvenile corals (<5 cm diameter) were not included in the assessment due to the difficulty of identifying them accurately to species level (Richards 2013). In the case of large thickets of branching coral where the beginning and end of colonies could not be determined, 2 colonies were recorded for every 1 m² of thicket. Habitat complexity was assessed every 5 m on each transect using a 5 point scale (Richards 2013) as follows: 1 is extremely low habitat complexity (e.g. sand and rubble); 2 is scattered coral outcrops among rubble; 3 is numerous low profile coral outcrops; 4 is defined as well developed reef structure with overhangs; and 5 is the highest possible complexity defined as a large complex reef structure with well developed crevices and caves.

**Wave energy**

Following Williams et al. (2013), wave power per unit length of wave crest was calculated for Christmas Island using the archived NOAA Wavewatch III global, 30 min arc dataset (ftp://polar.ncep.noaa.gov/pub/history/waves/). The hindcasts at 3 h intervals from January 2010 to July 2015 of significant wave height and peak wave period were used to calculate wave power at each timestamp. The average direction of the wave peak period was used to bin the resultant dataset into 16 segments of 22.5° each. The average wave power and proportional occurrence for each segment were then calculated.

**Statistical analysis**

The mean and standard error of the number of species (species density), the number of individuals and the habitat complexity scores were calculated for each depth zone at each site. The experimental design consisted of 2 factors: ‘exposure’ (2 levels, fixed and crossed) and ‘depth’ (3 depths, fixed and crossed) with 3 replicates at each site by depth combination. In order to determine sampling adequacy, rarefaction was calculated from raw data (Gotelli & Colwell 2011) using sample-based abundance methods (Colwell et al. 2012). The species density results were then plotted against sampling unit (transects). To determine if coral species diversity and colony abundance varied between exposures and depths, a 2-way permutational multivariate analysis of variance (PERMANOVA) (Anderson & Millar 2004) was undertaken with PRIMER-E version 6 with the PERMANOVA+ add-on (Anderson et al. 2008). We chose this approach due to the predominance of zeros in the datasets, the highly skewed relative abundances of corals and the variability between samples (Anderson 2001).

The Euclidean distance matrix (Anderson & Millar 2004) based on raw data units was used to analyse the total number of species, the total number of individuals and average habitat complexity. The Bray-Curtis dissimilarity measure was used on the transformed coral species assemblage and morphology assemblage data because it provides a robust measure of ecological distance in terms of community structure and can manage joint absences (double zeros) (Anderson & Robinson 2003). A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was performed on all datasets prior to testing the data with PERMANOVA. The coral species assemblage data and habitat complexity data yielded a significant result, so the data were transformed using a fourth-root and a square-root transformation, respectively. The species density data also showed a significant result after the PERMDISP test; however, the data were left untransformed as subsequent transformations retained a significant result. Due to the relatively small sample size (n = 72), the test was done using unrestricted permutations of the raw data (Anderson 2001) with 9999 permutations of each term in the analysis to obtain p-values (Anderson & Millar 2004). Significant terms were further investigated with pair-wise comparisons. In analyses where possible permutations were less than 100, Monte Carlo p-values were used (Anderson & Robinson 2003).

To visualise patterns in the coral species assemblages and morphologies, a 2-dimensional, non-metric multidimensional scaling (MDS) plot was constructed and key taxa and morphologies contributing to differences between depths and exposures were recognised using a similarity of percentages analysis (SIMPER) in PRIMER-E version 6. To further visualise which components are contributing to the dissimilarities, we conducted a constrained canonical analysis of principal coordinates (CAP) (Anderson & Robinson 2003, Anderson & Willis 2003, Anderson & Millar 2004). These CAP analyses were conducted using the original replicate observations (n = 72). The leave-one-out allocation success provides a statistical estimate of error (proportion of incorrect allocations) for this classification method and gives a reasonable measure of how distinct groups are in multivariate space (Anderson & Willis 2003, Anderson & Robinson 2004).
The appropriate number of axes \((m)\) to use for the canonical analysis was chosen based on minimising misclassification error and keeping \(m\) small relative to \(n\) (Anderson & Robinson 2003, Anderson & Willis 2003). The null hypothesis of no difference in the coral assemblages from different exposures and depths was tested by calculating the trace statistic and obtaining a \(p\)-value by permutation (Anderson & Robinson 2003, Anderson & Willis 2003). Individual species likely to be responsible for any observed differences were determined by examining Pearson correlations of untransformed species counts with canonical axes. Spearman rank correlation values greater than \(r_S = 0.36\) or less than \(r_S = -0.36\), and greater than \(r_S = 0.51\) or less than \(r_S = -0.51\) were used as an arbitrary cut-off for the colony morphology and community structure correlation vectors, respectively. A BEST test was undertaken to determine whether depth or exposure were most important in determining the patterns in the species assemblage matrix, along with a DistLM test to examine how much of the variation was explained by each variable.

RESULTS

Wave energy

Christmas Island experiences south-easterly trade winds throughout the dry season (April to November). The prevailing wave energy (63.55%) propagates from the south-west (202.5° to 225°) with an average power of 44 kW m\(^{-1}\) (Fig. 2). Overall, 94.67% of waves propagate from the south-west, south and south-east (157.5° to 248°) with an average power of 40 kW m\(^{-1}\). These data indicate that the southern coastline is constantly exposed to large wave swell. Waves propagating from the north-east are rare (0.03%) but can have high energy (61 kW m\(^{-1}\)). Hence, rare north-east swell events can be extremely damaging for the east coast of the island. Waves from the north-west are also relatively rare (3.2%) and normally associated with wet season tropical cyclones which occasionally pass close to the island (Department of Transport 2009). These waves can also have high energy, ranging from 41 to 51 kW m\(^{-1}\) and impact the north-west of the island.

Diversity

Rarefaction analyses indicated that the local species diversity was adequately sampled in our surveys (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m546p061_supp.pdf). Approximately 75% of the recorded species were detected during the first 18 (25%) of the 72 transects, suggesting that additional sampling would not substantially increase...
the number of species recorded. Coral diversity (species density) did not decrease linearly with depth as predicted, but was greater at sheltered sites. Hence, the results only partially confirm the hypothesis that diversity increases with depth up to 20 m, because species density was lowest at the 12 m depth zone, intermediate at the 5 m depth zone, and highest at the 20 m depth zone (Table 2, Fig. 3a). Mean species density peaked at 20 m depth at the sheltered site Thundercliff (TC) (37.6 ± 0.6) and was lowest at 5 m depth at the exposed site Ethel Beach (EB) (9.6 ± 4.1) (see Fig. S2 in the Supplement). The diversity of corals was significantly higher at sheltered sites (mean species density = 26.917 ± 3.538 per 30 m²) than at exposed sites (22.75 ± 3.668 per 30 m²) (p < 0.005, Table 1, Fig. 3a). Overall, there was no significant interaction between depth and exposure for species density (see Table S1a in the Supplement).

**Abundance**

A total of 9265 coral colonies from 125 coral species and 43 genera were recorded across the 72 belt transects. On average, 128 (±7.97 SE) coral colonies were recorded per transect. As expected, colony abundance was highest at the 20 m depth zone (178.917 ± 8.533), but contrary to expectations, colony abundance was significantly higher at the 5 m depth (152.542 ± 11.739) than at 12 m (54.583 ± 2.190) depth zone. Overall, colony abundance was highest at sheltered sites (138.667 ± 10.615 colonies per 30 m²); and there was considerable variability in colony abundance among exposed sites (118.694 ± 33.984) (Table 1). The number of colonies recorded were significantly different between the 5 and 12 m and the 12 and 20 m depth zones (all p < 0.001) (Table 2). There was no significant difference in the abundance of colonies between 5 and 20 m and there was no significant interaction between exposure and depth (see Table S1a in the Supplement).

**Colony morphology**

The complexity of coral morphologies conformed to the expectations of being highest at the 20 m depth zone and decreasing with exposure. The morphological types that were present differed significantly between depth and exposures (p < 0.001, Tables 1 & 2), and a greater variety of morphological types was...
recorded at the 20 m depth zone compared to the shallower zones (see Fig. S3 in the Supplement). However, there was no significant interaction between depth and exposure (see Table S1b). Differences in exposure and depth are illustrated in the CAP plot (Fig. 4) and in the MDS (see Fig. S4). These plots and the SIMPER analysis (see Tables S2 & S3), identify encrusting colonies as contributing to the distinctness of the 20 m depth zone and columnar and massive colonies as characteristic of the 5 m zone. The columnar species *Isopora palifera* was one of the 5 most abundant species at all sheltered sites in the 5 m depth zone and contributed to the characterizing of these sites (see Tables S3, S4 & S5), and the encrusting species *Pavona varians* was one of the 5 most abundant species at 20 m depth across the majority of sites (see Tables S2, S3 & S4).

**Habitat complexity**

Spatial patterns in habitat complexity at Christmas Island conformed to the hypothesis of decreasing complexity with exposure (p < 0.001, Table 1, Fig. 3b). However, contrary to our hypothesis that habitat complexity would increase with depth, the highest level of complexity was recorded at 12 m, the lowest at 5 m and intermediate levels at 20 m (Fig. 3b). There were also significant differences across the 3 depth zones examined (Table 2), but no significant interaction between exposure and depth (see Table S1a in the Supplement).

**Community structure**

Contrary to our hypothesis, the structure of coral communities was not consistent or predictable across depth gradients. There was a significant interaction between exposure and depth (p < 0.05, see Table S1b in the Supplement), which is illustrated in the CAP plot (Fig. 5) and in the MDS (see Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m546p061_supp.pdf). The BEST analysis also indicated that both depth and exposure were correlated with patterns in the community composition (R² = 0.294); however, depth explained most of the correlation (R² = 0.275) because there was little improvement in the correlation when exposure was added (R² = 0.107) (see Table S5). This result was corroborated by the DistLM test, which showed significant correlations between community structure and each of these variables (all p < 0.001); however, the correlation was not very high (R² = 0.205) (see Table S6). The sequential test also showed that depth contributed the most to the correlation.

The uniqueness of the coral community structure at the 5 m depth zone is likely due to the high abundances of *Goniastrea retiformis*, *Montipora informis* (Fig. 5) and *I. palifera* (see Tables S7 & S8). The community composition at 20 m depth was distinct due to the high abundances of *P. varians* and *Cyphastrea serailia* (Fig. 5, see Table S8). There was also a high

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**Fig. 4.** Canonical analysis of principal coordinates (CAP) of colony morphology for depth and exposure explained 94.62% of the total variation in the first 8 principal coordinates (squared canonical correlation = 0.895) with the smallest cross-validation error achieved when m = 3. (a) Biplot of species community structure correlations with the canonical axes and (b) Pearson’s Overlay r > 0.36.
level of variation in the dominant species between sites, which was most evident at Ethel Beach where a single species (*Galaxea astreata*) was almost 7 times more abundant than any other species at the 5 m depth zone (see Table S2). Furthermore, the most dominant species in the 12 m depth zone tended to have 2 to 3 times lower abundance than that recorded in the 5 and 20 m depth zones.

**DISCUSSION**

Maintaining healthy coral communities is imperative for securing the wider biodiversity and socioeconomic benefits of coral reefs. Over the last few decades corals have proven extremely susceptible to climatic change. Being able to forecast, detect and mitigate departures from ‘natural’ is crucial and represents a great challenge for ecologists, conservation scientists and managers. Theory of coral reef ecology is generally based on studies undertaken in relatively sheltered and shallow continental reefs that have often been exposed to an undisclosed level of anthropogenic disturbance. Here, we tested ecological theory in an oceanic location characterised by steep gradients in physical factors (e.g. depth and exposure) and minimal anthropogenic impacts. By testing 5 traditional hypotheses of coral community structure at the relatively pristine Christmas Island we find that not all of the expectations of traditional ecological theory are supported. Understanding how and why coral communities are structured differently on oceanic versus continental reefs is important for predicting how increasing anthropogenic disturbances will impact different types of reefs.

**Diversity and abundance**

The results of this study only partially met expectations of the traditional hypotheses of coral diversity and abundance. We found abundance and diversity were highest at the 20 m depth zone across all sites, which concurs with earlier seminal studies (Loya 1972, Glynn 1976, Sheppard 1980, Ross & Hodgson 1982) that found these variables were highest between 15 and 30 m depth. Our finding of highest coral diversity at the edge of the steepest habitat zone (almost vertical walls) is consistent with the ‘cliff-edge’ effect. In a study of patterns of coral species diversity on the San Blas Islands in Panama, Porter (1972) proposed that the peak in species richness that was consistently observed at 25 m was due to abrupt changes in light and turbulence (i.e. water circulation which delivers nutrients). Similarly, in a study of reef community structure in north Jamaica, the highest diversity of corals was recorded at 22 m depth.
and this was attributed to an edge effect (Liddell & Ohlhorst 1987).

At Christmas Island, the upper section of the cliff occurs between 15 and 20 m and this depth also represents the zone where physical impacts are less pronounced. This zone is deep enough to escape the effect of waves but has much more light available than on the steep walls beyond 20 m. The zone represents a sharp change in the angle of the reef where water from on top of the reef mixes with oceanic water washing against the outer reef walls. Consequently, this zone experiences abrupt changes in temperature from thermoclines and other variables associated with different water bodies. It is therefore likely that this narrow zone represents an ecotone where there is a very sharp transition in environmental conditions resulting in a heterogeneous environment that contains a range of ecological niches suited to a wider diversity of corals.

Edge effects have been shown to increase diversity in seagrass systems (Tanner 2005, Macreadie et al. 2010) and are also well known in terrestrial ecosystems (Harris 1988, Laurance & Yensen 1991). Given that oceanic islands are exposed to considerable swell and have steep drop-offs, it is likely that edge effects are a common feature of oceanic coral reefs, with diversity peaking in the narrow zone where physical impacts from waves are less pronounced and where light remains at suitable levels for optimal growth. At Christmas Island, we detected the signal of edge effects at 20 m, beyond which depth the steep wall becomes shaded and the conditions become suboptimal for photosynthetic organisms like corals. However, the precise depth range of the edge zone will vary between oceanic islands and will be dependent on the amount of wave energy received and the depth of the outer reef wall. Further investigation is required to test whether the cliff edge effect detected at Christmas Island and elsewhere (Porter 1972, Liddell & Ohlhorst 1987) is a general phenomenon of oceanic coral reefs.

Coral abundance and diversity did not increase with depth in a linear trend, but rather they were lowest at the intermediate depth 12 m, suggesting a J-curve distribution may best describe the relationship between these variables and depth at this isolated oceanic location (Fig. 6c). The reason for the J-curve distribution may relate to 2 features that are typical of oceanic islands. Firstly, the heterogeneity of environmental conditions at the cliff edge may prevent species from dominating or establishing large colonies, hence enabling high diversity. Secondly, oceanic islands are exposed to persistent swell and the role of wave action creates sufficient disturbance to facilitate turnover on the reef flat (Madin et al. 2014). At 12 m depth near the reef crest, wave-tolerant massive species (such as massive *Porites*) grow into large colonies, and fast growing and competitive branching species (such as *Acropora abrotanoides*) tend to dominate and appear to competitively exclude other corals. While the size of corals was not specifically measured here, we anecdotaly observed coral colonies to be larger in the 12 m depth zone than the other 2 depth zones, particularly at sheltered sites. Hence, competitive exclusion is likely to be a factor limiting the diversity of corals at this depth (Connell 1978). Thus, the less physical but more environmentally variable conditions associated with the cliff-edge habitat (at 20 m) sustains a more heterogeneous community, whilst the wave-exposed habitats at 5 m experience a high turnover and a limited number of species dominate at 12 m.

**Colony morphology**

The relative dominance of branching, foliose, corymbose, columnar and massive morphologies at 5 m was exposure-dependent. In contrast to expectations, the more structurally complex branching and corymbose morphologies were most common at exposed sites. Generally, branching morphologies are typical in sheltered, shallow areas due to their structural fragility and vulnerability to breakage from wave energy (Madin & Connolly 2006). However, at Christmas Island, the main taxa contributing to this morphology were Pocilloporids and *A. abrotanoides*, which have robust and/or highly compact branches that are resistant to strong wave action (Dollar 1982, Veron 1993, Kaandorp 1999). However, the exposed site Ethel Beach was dominated by corals with massive morphology. This site experiences constant wave action and rare high energy wave events; hence, massive forms that are more resistant to dislodgement dominate (Connell 1978, Madin & Connolly 2006). At 20 m depth, tabulate and free-living colonies, which are vulnerable to dislodgement or being overturned (Madin & Connolly 2006), occurred in higher abundance, most likely because they are protected from wave energy at this depth.

**Habitat complexity**

As predicted by established hypothesis, habitat complexity was generally lower at exposed sites and
in the shallow waters (5 m). However, contrary to expectations (Fig. 6b), there was no linear pattern of increase in habitat complexity with depth, as habitat complexity was highest at the 12 m depth zone across all sites, suggesting a negative skew distribution may best describe the relationship between habitat complexity and depth at this isolated oceanic location (Fig. 6d). This unexpected result may be explained by the coral community at this depth. Although abundance and species diversity (density) was lowest at 12 m, the number of corals with complex colony morphologies was higher at this depth and this will have contributed to the higher habitat complexity score. The most abundant morphological types at the 12 m depth zone were the branching, columnar and massive morphologies (i.e. *A. abrotanoides, Isopora palifera* and *P. lobata*). These growth forms are considered to create complex habitats as they can form large 3-dimensional habitats with numerous intricate spaces (Veron 1993).

**Community structure**

The distinct coral community across depth and exposure highlights the importance of wave energy in structuring community composition at this oceanic location. Species that are tolerant of varied and harsh conditions, such as massive corals like *P. lutea* or encrusting species like *Montipora informis*, were characteristic of the 5 m depth zone at exposed sites. At exposed sites, the community at 12 m was similar in functionality to that at 5 m, albeit composed of different species (*P. lobata* and *M. grisea*). *Acropora* species often dominate shallow habitat zones at sheltered sites (Huston 1985, Toda et al. 2007, Williams et al. 2013), so we expected to find this pattern; however, *Acropora* were rarely the most dominant species at sheltered sites. Moreover, *Acropora* was more commonly recorded in abundance at the exposed sites where *A. nana*, *A. abrotanoides* and *A. papillare* were all recorded among the top 5 dominant taxa. A.
papillare is a primarily encrusting species that occurs in shallow marginal habitats (Wallace 1999), so its presence is not surprising. However, the presence of corymbose and branching Acropora in shallow zones at more exposed sites goes against predictions based on mechanical vulnerability (Madin 2005, Madin et al. 2014). Nevertheless, in this case, the branching coral A. abrotanoides is an exceptionally robust species with thick branching units approximately 10 cm in diameter (Wallace 1999) that is well suited to strong current and high wave energy conditions. The presence of A. nana in abundance at Jackson’s Point may be a result of a recent pulse recruitment event of this ‘weedy’ (opportunistic or early colonizing) species (Darling et al. 2013) and temporal data are needed to examine the longer term persistence of this species at this site (Kenyon et al. 2006, Smith et al. 2008).

The coral community growing at 20 m depth was characterised by encrusting species that make efficient use of light at lower saturations and can grow on vertical faces without risk of toppling, such as Cyphastrea serailia, Leptastrea pruinosa, Pavona varians and Porites lobata (Bouchon 1981, Wellington 1982, Titlyanov & Latypov 1991). Our results suggest that the 20 m depth zone appears to be a refuge for a wide range of species that are not found in shallower zones. We infer, therefore, that any disturbances that affect the reef at this depth (i.e. increasing frequency or intensity of storms, coral bleaching, coral disease, predator outbreaks) could have major and lasting ramifications for the diversity and abundance of the wider coral reef community (Graham et al. 2006).

Corals occurring across all depth zones in sheltered habitats along the north coast (i.e. Thundercliff, Million Dollar Bommie and Eidsvold), are also particularly vulnerable to changes in wave frequency or intensity. While the loss of corals from storm events may open up space for coralline and turf algae (see Fig. S6 in the Supplement for more detail about the current level of benthic cover of these taxa), it may also drive fishes into deeper water and change trophic relationships (Friedlander et al. 2003). Our surveys revealed that turf algae can reach approximately 60% cover in places and indicates that it has become well established and may be outcompeting corals at some sites. The reason for such high turf cover at this remote and relatively pristine location is unknown but it is not necessarily an indicator of degradation given that both natural and anthropogenic disturbances can provide opportunities for turf algae to dominate coral reef communities (Barott et al. 2012). Our results show that if the predicted increases in bleaching events at Christmas Island eventuate (Sheppard et al. 2002, NOAA Coral Reef Watch 2015), it will be particularly important to monitor the status of corals and coral–algal interactions at the 20 m depth zone.

CONCLUSIONS

This species-level study at an oceanic Indian Ocean location found that natural environmental factors such as exposure and depth strongly influence coral community structure. Contrary to expectations, however, there was no clear, consistent or linear increase in diversity, abundance or habitat complexity across the depth gradient examined. This finding of non-linear patterns in community structure at this isolated oceanic location concurs with patterns reported for coral communities in the northern Line Islands (Gove et al. 2015) and the Hawaiian Archipelago (Jouffray et al. 2015). We identify a cliff-edge effect where coral diversity is greatest in a narrow zone between the wave-dominated shallows and the light-limited outer reef wall. Further investigations of community structure at other oceanic locations are needed to determine the generality of the edge effect. The need to understand natural processes structuring oceanic coral communities is reinforced when human impacts are considered, because these impacts have been found to decouple natural biophysical relationships on coral reefs (Williams et al. 2015). Species currently finding refuge in the cliff-edge zone may be impacted by changing climatic conditions (e.g. increasing frequency and intensity of storm and bleaching events). In order to make accurate predictions about the future of isolated oceanic coral reefs there is a need to re-evaluate and update our understanding of how these coral communities are structured. In addition, species diversity and abundance in cliff-edge habitats (beyond the reef flat and crest) must be monitored in order to predict or detect how increasing climate and local impacts may affect these unique coral reef ecosystems.

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