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Cross-shelf Heterogeneity of Coral Assemblages in Northwest Australia

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Abstract: Understanding the spatial and temporal distribution of coral assemblages and the processes structuring those patterns is fundamental to managing reef assemblages. Cross-shelf marine systems exhibit pronounced and persistent gradients in environmental conditions; however, these gradients are not always reliable predictors of coral distribution or the degree of stress that corals are experiencing. This study used information from government, industry and scientific datasets spanning 1980–2017, to explore temporal trends in coral cover in the geographically complex system of the Dampier Archipelago, northwest Australia. Coral composition at 15 sites surveyed in 2017 was also modelled against environmental and spatial variables (including turbidity, degree heat weeks, wave exposure, and distance to land/mainland/isobath) to assess their relative importance in structuring coral assemblages. High spatial and temporal heterogeneity was observed in coral cover and recovery trajectories, with reefs located an intermediate distance from the shore maintaining high cover over the past 20 years. The abundance of some prominent genera in 2017 (*Acropora*, *Porites*, and *Turbinaria* spp.) decreased with the distance from the mainland, suggesting that inshore processes play an important role in dictating the distribution of these genera. The atypical distributions of these key reef-building corals and spatial heterogeneity of historical recovery trajectories highlight the risks in making assumptions regarding cross-shelf patterns in geographically complex systems.

Keywords: reserve design; environmental drivers; resilience; spatial patterns; coral bleaching

1. Introduction

Scleractinian corals are foundation species, underpinning biodiverse and productive coral reef ecosystems and supporting a multitude of environmental processes (e.g., wave mediation and sediment retention) [1,2]. Corals exhibit a diverse range of life-history strategies and resultant morphologies which play different functional roles and have variable levels of structural integrity, tolerance to stress and resilience to disturbance [3]. The structurally complex biological substrate provided by the diverse morphology of live corals provides food, habitats, and specific niches for reef-dwelling organisms, creating marine oases in often nutrient-poor tropical waters [1,4–7]. Coral cover, diversity and assemblage composition vary both spatially and temporally as a result of large-scale biogeographic processes, regional environmental conditions and disturbance events [8,9]. Assemblage composition is largely determined by individual species tolerance to persistent ambient environmental conditions and resilience to stochastic disturbance events (e.g., tropical storms, predator and disease outbreaks and anomalous heating events) [10–14].

Different coral assemblages provide contrasting physical structure and variation in fine and coarse-scale structural complexity, which facilitates disparate biological communities and has direct implications for the maintenance of ecosystem processes and resilience [3,15–18]. Coral assemblages are under threat from a suite of cumulative stressors from both natural and anthropogenic sources, including pollution, sedimentation, overfishing, climate change-induced marine heatwaves, and tropical storms [19]. Some evidence suggests that these stressors and disturbances threaten not only coral abundance and diversity, but also the heterogeneity of coral assemblages [3,20]. Differential vulnerability of individual coral taxa and variation in resilience may ultimately lead to homogenised coral communities, dominated by hardy, stress-tolerant taxa or fast growing opportunists [8,21]. Shifts in habitat-forming taxa such as the loss of ecological heterogeneity has consequences for biodiversity, resilience and ecosystem services [18,22–24]. In the face of a rapidly changing climate and range of additive stressors, management should therefore endeavor to protect adequate amounts of different coral assemblages, a concept typically referred to as CAR (comprehensive, adequate, representative) reserve design [25]. By designing marine reserve networks according to CAR principles, managers endeavor to preserve ecological viability and maintain the integrity of populations, species and communities [25]. Accordingly, marine reserves should span all major bioregions and be configured to adequately protect the full range of coral communities [25]. This concept of reserve design requires a strong understanding of how coral assemblages change across space and persist through time. Areas identified as potential sites for marine reserves, therefore, require current and accurate spatial descriptions of coral distributions and a solid understanding of key local environmental drivers. In many systems, coral reefs occur across the continental shelf, and as such, are exposed to a wide range of environmental conditions.

Cross-shelf systems present dramatic, persistent gradients in environmental conditions, with turbidity, sedimentation, nutrient loading, and temperature typically declining offshore and wave exposure often increasing [10,26]. The cumulative effects of these stressors give rise to spatially and temporally variable inshore benthic communities, usually with low cover and diversity of scleractinian corals, with assemblages dominated by robust, heat, predator, and sediment-resistant taxa, such as *Pavona*, encrusting *Porites* and *Turbinaria* spp. [27–33]. Conversely, offshore sites tend to have higher coral cover, greater diversity and are characterised by taxa that are more sensitive to heat stress, light limitation and sedimentation such as *Acropora* and *Pocillopora* [6,10,34]. Some studies have reported peaks in coral diversity on mid-shelf reefs, attributed to intermediate exposure to wave energy and gradients in disturbance frequency and intensity (i.e. tropical storms) [9,11,26]. Cross-shelf gradients in coral health, including partial mortality and bleaching of corals, have also been observed [35]. Spatial heterogeneity in coral assemblages has been attributed to gradients in nutrient loading [10,22], suspended sediment and sedimentation [10,29,30,35,36], freshwater input [30], depth [36], wave energy [9], recruit dispersal [27] and water temperature elevation and variability [32]. These environmental gradients may also affect coral health, causing partial mortality and bleaching of corals [35], contributing further to cross-shelf patterns of coral assemblages. However, these patterns are not universal. Despite the inshore reefs of the Florida Keys, USA, being subjected to higher turbidity, nutrients, light attenuation and dissolved organic matter, coral cover and growth rates were higher and partial mortality lower than on the corresponding offshore reefs [37]. A more recent study found no significant difference in long-term inshore and offshore growth rates for two key reef-building species [38]. These somewhat incongruous observations are attributed to the ability of inshore corals to shift their trophic mode in response to high levels of particulate organic matter on inshore reefs, outweighing the negative effects of suspended sediment and sedimentation [37,39]. The varied cross-shelf patterns of coral abundance, diversity, assemblage composition and growth rates, and the variation in environmental parameters posited to explain them, suggest gradients in environmental conditions are not always consistent predictors of coral cover or assemblage composition. Indeed, healthy and diverse coral communities have been recorded in several marginal environments ([40] and references therein). As such, the proximity of coral communities to potential stressors may be a poor predictor of potential risks to coral reefs (e.g., proximity to coast does not necessarily mean that corals will be detrimentally impacted by light limitation or elevated nutrients) [37,40]. The lack of consistency in the literature highlights the need for location-specific descriptions of spatial patterns and assessment of the relative importance of environmental drivers for appropriate management strategies to be developed.

The Dampier Archipelago, in northwestern Australia, is one of the most diverse regions for hard corals in Western Australia and has been identified as an area of high conservation value and a potential site for a future marine reserve [41–44]. The region is subject to strong cross-shelf gradients in turbidity, wave exposure and ocean temperature over a small spatial scale [41,45,46]. Regular cyclones, anomalous turbidity spikes and periods of anomalous seawater temperature also have a strong influence on benthic communities [41,47]. The archipelago is a geographically complex environment with little to no nutrient runoff due to limited agriculture in the region and minimal local riverine inputs. This eliminates nutrient enrichment as a confounding factor in analyses. The presence of a peninsula that protrudes across the shelf and a plethora of islands allows for both the terrestrial and oceanic influences to be assessed. Despite the region being home to extensive and diverse coral communities, the role that environmental gradients play in shaping marine communities has been limited [14,46]. The Dampier Archipelago therefore presents a unique opportunity to investigate cross-shelf patterns in coral cover, assemblage composition and resilience, and the relationship between these metrics with various environmental drivers.

While the region has limited terrestrial inputs, it is subjected to significant anthropogenic pressure through the development of a large port and associated dredging of the shipping channel, as well as some recreational usage [48–50]. Thus far, coral mortality associated with the port and shipping channels has been limited to within 1.3 km of dredging activity and was attributed to smothering caused by heavy sedimentation [28,51]. As a result of the development of extensive port facilities for salt, iron ore and LNG (liquified natural gas) processing and export, numerous surveys and monitoring programs have been conducted in the region by industry, consulting firms and government bodies over the past few decades. This body of 'grey literature' provides insights into temporal trajectories of coral cover throughout the region, allowing some inferences to be made about the relative importance of stochastic events in structuring present day coral assemblages.

This study aims to assess the drivers of coral cover, diversity and assemblage composition throughout the Dampier Archipelago by (i) investigating patterns in historical coral cover; (ii) describing present-day spatial patterns in coral cover, diversity, and assemblage composition; and (iii) modelling the effect a suite of environmental and geographical factors has on coral assemblages.

2. Materials and Methods

2.1. Study Location

The study area extends from Cape Preston to Delambre Island and will henceforth be referred to as the Dampier Archipelago (Figure 1). The Dampier Archipelago is situated adjacent to Karratha, 1650 km north of Perth in the Pilbara Nearshore Marine Bioregion (Figure 1) [52]. The region experiences a tidal range of up to 5 m and ocean temperatures between 18–32 °C [53]. A highly variable cross-shelf turbidity gradient is present in the region, with anomalous spikes caused by natural (cyclones and heavy rainfall) and anthropogenic (dredging) disturbance events [17]. Cyclones are frequent throughout the region, bringing destructive waves, freshwater runoff, extreme turbidity and sedimentation [45,46].

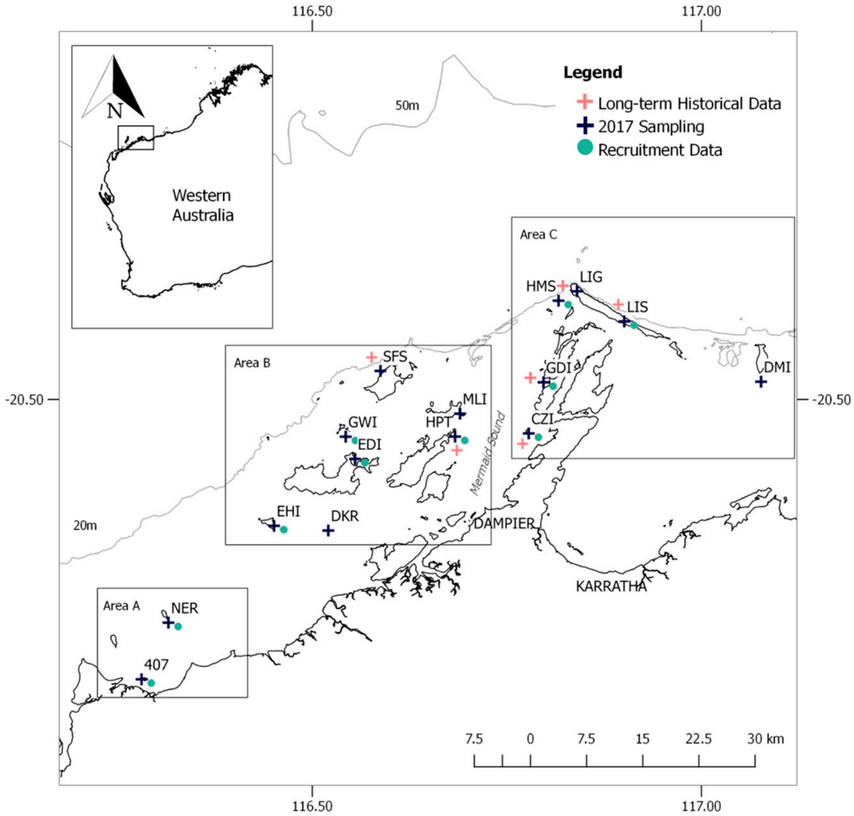

Figure 1. Location of the 15 study sites throughout the Dampier Archipelago, Western Australia, surveyed in 2017. Site abbreviations: 407 = Unnamed 407, NER = North East Regnard, EHI = Eaglehawk Island, DKR = Dockrell Reef, EDI = Enderby Island, GWI=Goodwin Island, HPT = High Point, SFS = Sailfish, MLI = Malus Island, CZI = Conzinc Island, GDI = Gidley Island, HMS = Hammersley Shoal, LIG = Legendre Island Gen, LIS = Legendre Island SZ, DMI = Delambre Island. Areas A, B and C are used to subdivide the study area.

The marine and coastal environment of the Dampier Archipelago comprises a northwards extending peninsula, 42 offshore islands, intertidal and subtidal reefs, mangroves, seagrass and macroalgal communities and coral reefs. The peninsula extends approximately 20 km from the coast, or halfway to the 20 m depth isobath, whilst the islands are distributed all the way to the 20 m isobath (the area henceforth referred to as 'cross-shelf') (Figure 1). The distribution of landmasses over the cross-shelf area allowed an exploration of the relative effects of proximity to land and/or oceanic influences on the distribution of corals (Table S1). Coral reef covers approximately 18,300 ha and consists of 229 scleractinian coral species from 57 genera [43].

The region has been exposed to significant commercial development, including the construction of the world's second largest bulk export port facility, capital and regular maintenance dredging within Mermaid Sound, and ongoing commercial vessel traffic for the export of iron ore, salt, LNG and cargo [54,55]. Additional industrial works in the archipelago include salt production, pearling, aquaculture and commercial fishing, along with moderate levels of recreational boat usage and diving and fishing effort [54].

2.2. Historical Data Collection

The presence of environmental data in the Dampier Archipelago was solicited from commercial and research organisations known to have worked in the marine environment within the region. Once potential datasets were identified, requests were sent to proponents to access the data, including metrics used, collection methods (including replication) and spatial and temporal extent. This search yielded 871 datasets dating back to the early 1970s, 175 of which pertained to coral communities, generally describing coral cover, from 1980 to 2010 [56]. Of the 175 coral datasets, 90% were provided by industry sources, while the remainder came predominantly from government agencies. This data was then collated and mapped using the QGIS geographical information system (version 2.18.16) [57]. To investigate changes in coral cover through time, datasets in close spatial proximity to the long-term monitoring sites sampled in 2017 were identified and extracted. The metadata, reports and associated documentation were then examined to ensure that all datasets used comparable sampling methods (photo/video transects and line-intercept), covered similar reef position (lower slope/base) and were collected at subtidal reefs at depths between 2–8 m, with any datasets not meeting these criteria subsequently excluded. Six sites contained comparable data spanning 15 years or more. To assess temporal trends in coral cover, generalised additive models (GAM) were fitted to better illustrate temporal trends in coral cover using the gam package (version 1.16) and R language for statistical computing [58,59]. The best model was selected based on the lowest Akaike Information Criterion (corrected for small sample sizes; AICc) [60].

2.3. Benthic Data Collection

Spatial variation in coral cover and assemblage composition was investigated in more detail at 15 sites, surveyed in May 2017. Sites were selected based on historical data, spatial spread and preliminary surveys in 2015, and encompassed a range of combinations of environmental conditions. Corals were surveyed using photo quadrats taken every meter along three replicate subtidal (3–7 m depth) 50 m transects aligned end to end along the depth contour and separated by >5m at each site. Digital images were taken 1 m above the substrate capturing an area of ~0.85 sq. m (e.g., Reference [61]). Images were analysed using the EcoPAAS software package using a ‘point’ count method [62]. Six random points were overlaid over each image, the benthic category under each point was identified to the genera level, and then data was pooled to transect level for analysis [61,63].

2.4. Coral Recruitment Data Collection

To determine whether recruit availability was linked to present day coral cover and assemblage composition, coral recruitment data, where available, was included in the suite of predictor variables for coral cover. As part of a separate study, coral recruitment data was collected at nine of the 15 sites between 2015–2017 [64]. At each location, 15 (11cm × 11cm × 1cm) unglazed recruitment tiles were mounted on stainless steel plates haphazardly affixed to the reef within a 10 m^2 area [65]. Tiles were deployed 4 weeks prior to the predicted autumn spawning period and retrieved 8–10 weeks after deployment. Post-retrieval, all organic material was removed from the tiles using chlorine bleach and the tiles were subsequently dried and examined under a stereomicroscope to determine the abundance of coral recruits [66]. Recruit density varied significantly between sites (0.1–72 recruits per tile) and years (3.9–17.6 annual mean recruits per tile); however, the rank order of sites remained similar between years [64]. As this study aimed to model spatial patterns in coral cover, recruit data for each site was therefore averaged over the 3 years.

2.5. Environmental Variables

Environmental and geographical variables were collected at each site using a combination of techniques. Depth was recorded by divers at each site and the GPS coordinates of each site were used to calculate the shortest distance to the mainland and nearest landmass using Google Earth [67]. Distance to the 50 m isobath was generated using bathymetry data from NOAA and the marmap package (version 10.0.2) and R language for statistical computing [59,68]. KD490 (diffuse attenuation coefficient at 490 nm [KD2 algorithm]; turbidity proxy) and degree heating weeks (DHW) were retrieved from NOAA’s ERDDAP data server (Dataset ID: nesdisVHNSQkd490Daily and NOAA_DHW, respectively; see Table 1 for details). Wave exposure for each site was calculated using the wave fetch cartographic methods based on three-hourly wind speed and direction from 2009–2014 from the closest Bureau of

Meteorology weather monitoring station (Legendre Island), as per Reference [69–71]. The rationale for the inclusion of each of the selected environmental variables is presented in Table 1.

Table 1. Environmental variables included in the analysis of coral assemblage in the Dampier Archipelago, Western Australia.

Variable	Description	Justification	References
Distance to Mainland	Distance to the mainland (km) Range 3.14–24.57 km	Nearshore marine communities are subjected to higher turbidity due to terrigenous runoff and river plumes containing sediment, nutrients and pesticides. Coral reefs closer to shore also experience higher levels of recreational fishing pressure.	[72,73]
Distance to Land	Distance to the nearest land mass (km) Range 0.04–4.35 km	Distance to the nearest land mass influences how exposed a site is to wind and wave energy. Additionally, sites closer to land have increased terrestrial runoff.	[70,73]
Distance to 50 m Isobath	Distance to the 50 m depth isobath (km) Range 30.5–69.79 km	Sites closer to the 50 m isobath are influenced more by oceanic waters and generally have lower levels of turbidity.	[74]
Wave exposure	Exposure of the site based on average wave fetch and wind energy for across 32 angular sectors. Range 1005288–83322391 wave exposure index	Wave and wind energy act as a mechanical stress on corals and indirectly affect corals by influencing temperature, sediment flux, nutrient intake and productivity.	[69,75,76]
Turbidity (Mean KD490)	MODIS diffuse attenuation coefficient at 490 nm (KD2 algorithm). Higher KD490 value reflects a smaller attenuation depth, and lower clarity of ocean water. Range 0.074–0.259 KD490 index	Water turbidity influences the amount of available light for photosynthesis of coral symbionts whilst settling sediments can smother or abrade corals.	[27,77,78]
Depth	Depth of site (m) Range 3–7 m	Increasing depth reduces light availability, decreasing the autotrophic capacity of coral endosymbionts. Corals at shallower depths are also exposed to greater incidental light and subsequently increase the likelihood of bleaching.	[79,80]
Heat stress 2011 (Max DHW 11)	Maximum degree heating weeks between 01/12/2010–31/05/2011 (°C-weeks) Range 0–2.52 °C-weeks	Degree Heating Weeks represents accumulated thermal stress over the past 12 weeks. Coral bleaching is likely when DHW reaches 4°C-weeks. Severe bleaching was recorded in northwestern Australia in the summer of 2010–2011.	[47,81]
Heat stress 2013 (Max DHW 13)	Maximum degree heating weeks between 01/12/2012–31/05/2013 (°C-weeks) Range 8.4–12.56 °C-weeks	Severe bleaching was recorded in northwestern Australia in the summer of 2012–2013.	[81,82]
Mean Coral Recruits	Average density of coral recruits (2015–2017) for the 9 sites where data were available (recruits cm^{-2}) Range 0.215–13.652 recruits cm^{-2}	Successful coral recruitment is essential for the maintenance of coral communities and recovery of reefs after disturbance events.	[64,83,84]

2.6. Data Analysis

Differences in coral cover and number of coral genera among the 15 sites surveyed in 2017 were assessed using analysis of variance tests (ANOVA; site as a fixed factor) with a robust standard error (due to non-normal distribution of data) and Tukey's post-hoc tests using the AER and multcomp packages (versions 1.2-5 and 1.4-8, respectively) and R language for statistical computing [59,85,86]. Spatial variation in genera-level coral assemblage data was analysed using permutational multivariate analysis of variance (PERMANOVA; site as a fixed factor) and pairwise tests using the vegan and pairwiseAdonis packages (versions 2.4-6 and 0.0.1, respectively) and R language for statistical computing [59,87,88]. Data was log(x+1) transformed for normality and converted into a Bray–Curtis dissimilarity matrix prior to analysis.

Generalised additive mixed models (GAMMs) were used to assess the influence of environmental variables (Table 1) on total coral cover, number of coral genera present and the five most abundant coral genera [89]. Site was included as a random effect to increase the inferential power of the model [90]. A second set of GAMMs were used to assess the influence of recruitment (in conjunction with all other environmental and spatial variables) on total coral cover using the subset of sites where coral recruitment had been recorded. Data was not transformed as selecting an appropriate error distribution (in this case a negative binomial distribution) accounted for non-normal data distribution. A full subsets approach was used to fit all possible combinations of variables, limiting models to three explanatory variables to avoid difficulty in interpreting results [91]. Models containing variables with correlations exceeding 0.28 were excluded to avoid issues with collinearity among predictor variables, which can cause overfitting (Table S1) [91,92]. The model with the lowest AICc was selected as the best model; models were considered to have similar explanatory power if they were within two AIC units of the model with the lowest AIC value, corrected for small sample size (AICc). Of these, the model(s) with the lowest edf (estimated degrees of freedom) and highest AICc weight were presented. R^2 values were used to provide an indication of the predictive power of the model, and variable importance, determined by summing the weight for all models containing each variable, was used to assess the relative importance of predictor variables [93]. All statistical analyses were conducted using the R language for statistical computing and the gamm4 (version 0.2–5) and mgcv (version 1.8–22) packages [59,89,94].

3. Results

3.1. Historical Coral Cover and Composition in the Dampier Archipelago

Coral data collection in the Dampier Archipelago was limited in the 1980's but increased in the late 1990s and 2000s due to an increase in environmental assessments related to industrial development. At the coarse resolution (combined data for all sites), coral cover throughout the archipelago was highly variable within a single year, appearing to peak in 2004 (Figure 2A). When the data is presented by site, it is apparent that there are distinctly different trajectories through time. Gidley Island experienced a sharp decline in coral cover in the mid-2000s (~10%) and a subsequent rapid recovery (50–60%), and High Point and Conzinc Island have maintained variable but stable levels of cover since the early 1990s (~40–60%; Figure 2B–D). Conversely, Offshore sites (Hammersley Shoal and Legendre Island SZ) have exhibited declines in coral cover since the 1980s (~40% and ~60%, respectively) and now have <10% cover (Figure 2E,F). Coral cover at Sailfish Reef, located on the northwestern seaward edge of the archipelago, has remained below 5% since 1987 (Figure 2G).

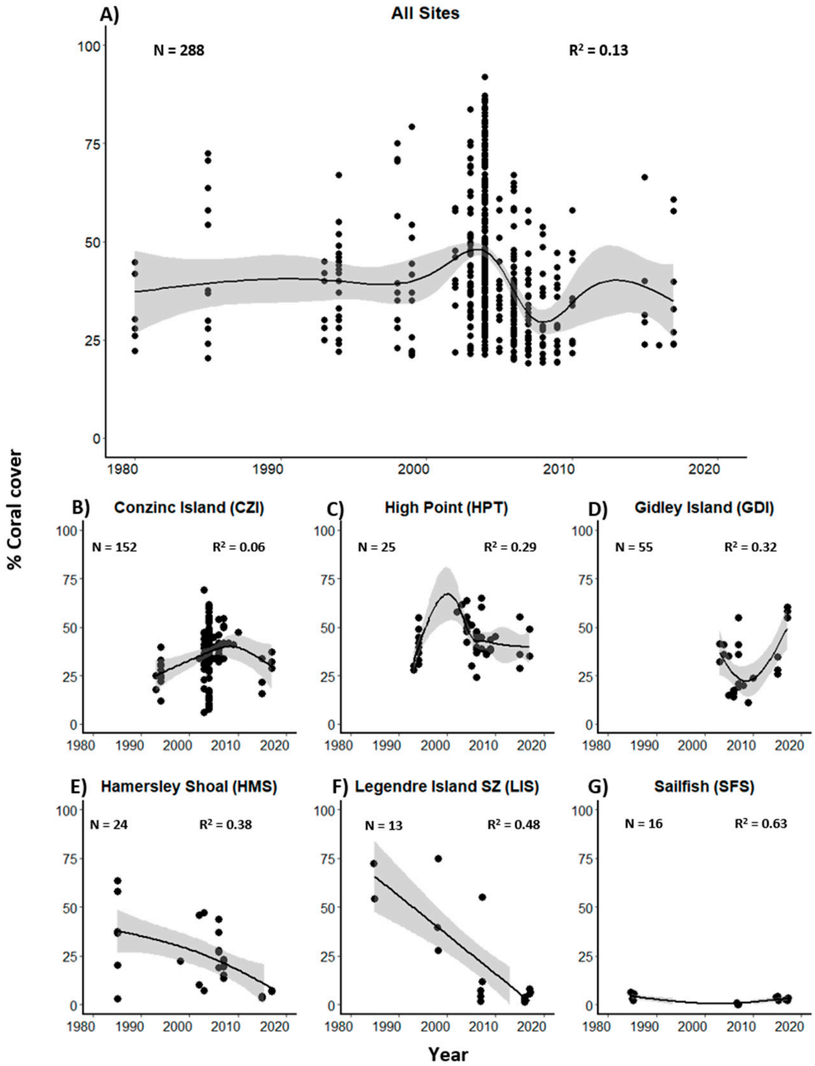

Figure 2. Percent live coral cover over time throughout the entire Dampier Archipelago, Western Australia, and at six study sites. The black line is the best generalised additive model (GAM) ± standard error (grey shading).

3.2. Present Day Coral Cover and Assemblage Composition in the Dampier Archipelago

Percentage coral cover differed significantly among the 15 sites surveyed in 2017 and was highest at those located an intermediate distance from the mainland on either side of Mermaid Sound (Malus Island, High Point, Gidley Island and Conzinc Island; Figure 3), whilst sites on the northern margin of the archipelago tended to have the lowest coral cover ($F_{14,30}$ = 237.7, $p < 0.001$). Coral diversity also differed significantly among sites, with the highest number of coral genera per transect recorded at North East Regnard (19), Malus Island (15) and Conzinc Island (15), whist Unnamed 407 (4), Eaglehawk (4) and Sailfish (3) had the lowest number of genera present ($F_{14,30}$ = 38.964, $p < 0.001$, Figure 3). Coral assemblage composition also differed significantly between sites, with the coral composition at Malus Island and Goodwin Island being dominated by *Porites* spp., whilst Gidley Island was characterised by an *Acropora*-dominated assemblage, and High Point and Conzinc Island communities having a relatively even distribution of genera ($F_{14,30}$ = 7.1, p = 0.001; Figure 3).

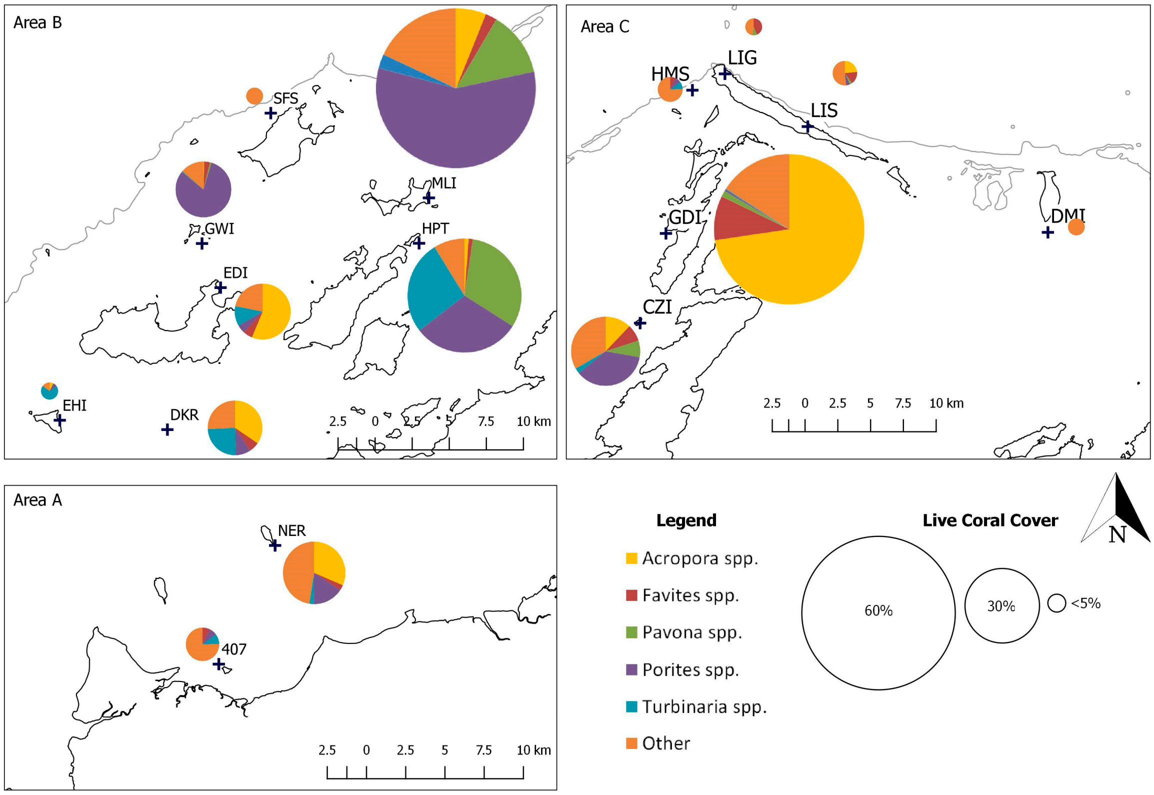

Figure 3. Percent cover of coral and breakdown of most abundant coral genera at 15 sites throughout the Dampier Archipelago, Western Australia in 2017. Site abbreviations: 407 = Unnamed 407, NER = North East Regnard, EHI = Eaglehawk Island, DKR = Dockrell Reef, EDI = Enderby Island, GWI = Goodwin Island, HPT = High Point, SFS=Sailfish, MLI = Malus Island, CZI = Conzinc Island, GDI = Gidley Island, HMS = Hammersley Shoal, LIG = Legendre Island Gen, LIS = Legendre Island SZ, DMI = Delambre Island. Areas A, B and C refer to subsets of the entire study area (see Figure 1).

3.3. Predictors of Total and Genera Cover 2017 Data

None of the variables or interactions between variables considered in the analyses were good predictors of variation in coral cover or diversity among sites within the Dampier Archipelago (Table 2, Table S2). The subset of sites modelled with both environmental variables and recruitment data were also not adequately modelled with this suite of predictors (i.e., recruitment was not a good predictor of coral cover). Of the five numerically dominant coral genera in the archipelago, the cover of *Acropora* and *Turbinaria* spp. were best described by the distance of sites from the mainland with cover of these corals decreasing when sites were greater than 15 km from the coast (Table 2, Figure 4). There were two competing top models for *Porites*, one of which reflected the same relationship (higher cover closer to the mainland); however, the slope of this decline was less steep for *Porites* than *Acropora* or *Turbinaria*. The competing model for *Porites* indicated a moderate decline with decreasing exposure to heat stress in 2013 (max DHW13); however, it should be noted that several predictor variables had similar variable importance to those included in the top models (Figures 4 and 5). Higher cover of *Favites* was observed at sites with intermediate wave exposure than very sheltered or highly exposed sites (Figure 4). Finally, a model that included distance to the 50 m isobath, turbidity and depth was the best predictor of *Pavona* cover (Figures 4 and 5). *Pavona* cover was highest at shallow turbid sites that were close to the 50 m isobath; however, this relationship was weak (R^2 = 0.12) with multiple outlying data points (Figure 4).

Table 2. Best generalised additive mixed models (GAMMs) for predicting coral cover, diversity and most abundant coral genera in the Dampier Archipelago, Western Australia. edf = estimated degrees of freedom. All models within two units of the lowest AICc value are reported in Table S2.

Response Variable	Model	ΔAICc	AICc Weight	R^2	edf
Coral cover	null	1.61	0.03	0.55	14.38
Coral cover (including recruitment data)	null	0.00	0.50	0.00	2.00
No. coral genera	null	0.41	0.06	0.83	13.17
Acropora spp.	Distance to mainland	0.11	0.13	0.36	12.84
Favites spp.	Wave exposure	0.00	0.19	0.49	11.56
Pavona spp.	Depth + Mean KD490 + Distance to 50 m isobath	0.00	0.57	0.13	5.92
Porites spp.	Distance to mainland	0.00	0.10	0.38	13.19
	Max DHW13	1.01	0.06	0.43	13.29
Turbinaria spp.	Distance to mainland	1.39	0.14	0.36	12.04

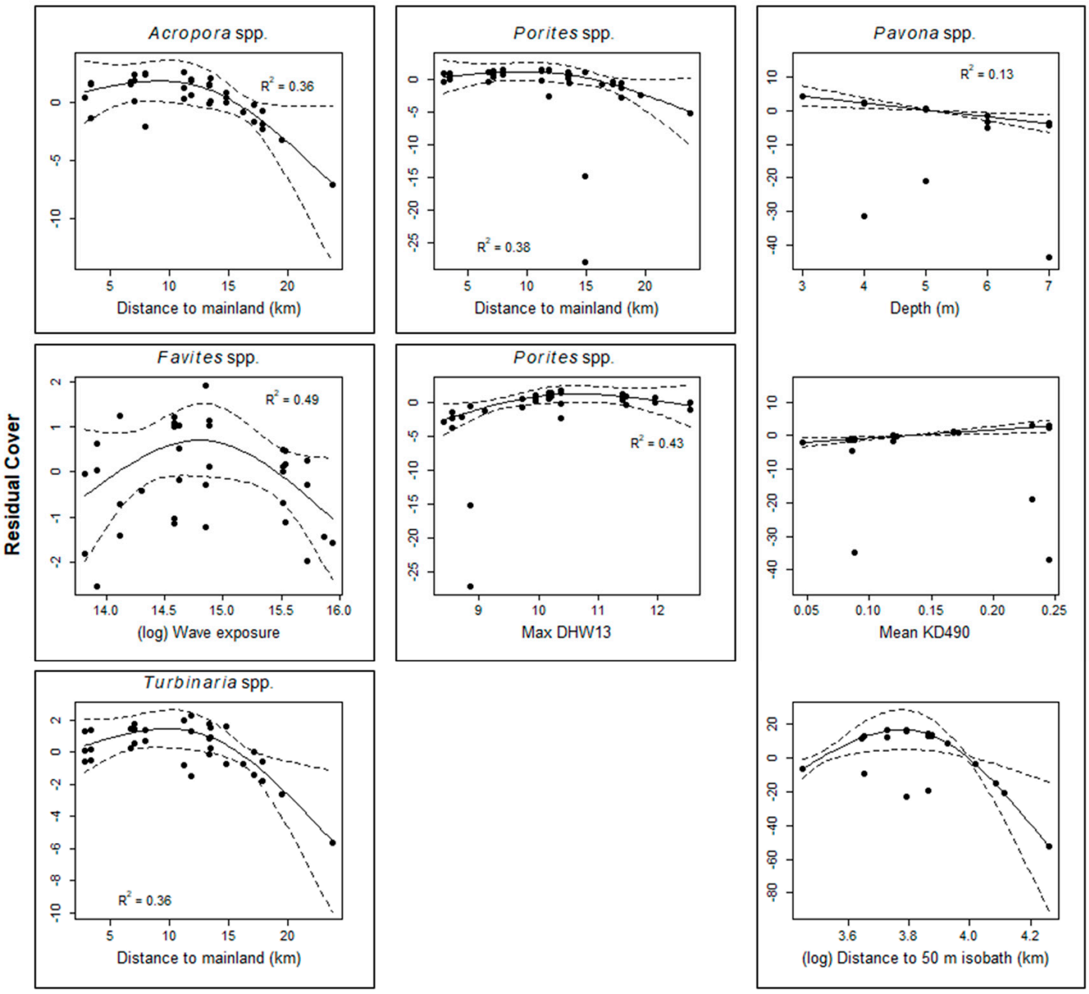

Figure 4. Best generalised additive mixed models (GAMMs) for the cover of *Acropora*, *Favites*, *Pavona*, *Porites* and *Turbinaria* spp. corals in the Dampier Archipelago, Western Australia (Table 2).

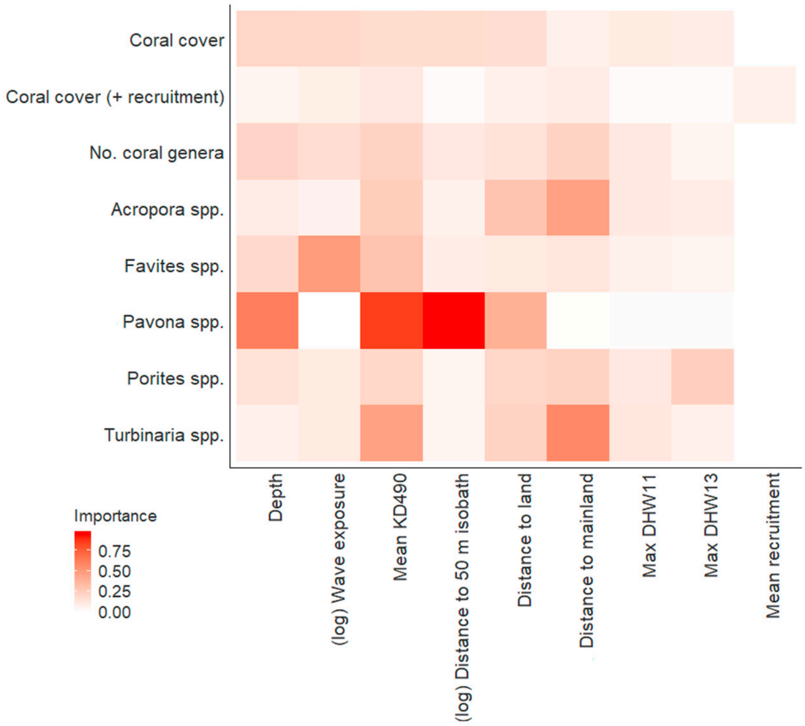

Figure 5. Variable importance plot for generalised additive mixed models for coral cover, diversity, and the cover of *Acropora, Favites, Pavona, Porites* and *Turbinaria* spp. corals in the Dampier Archipelago, Western Australia (Table 2).

4. Discussion

Coral cover and assemblage composition in the Dampier Archipelago exhibited significant spatial variation and did not display the typical cross-shelf patterns, with coral cover and diversity peaking at sites located an intermediate distance from the mainland, rather than the sites closest to the isobath. Abundant and diverse coral assemblages were observed in marginal environmental conditions (high heat stress, turbidity and proximity to potential anthropogenic stressors) at sites close to the mainland. Temporal trends in total coral cover exhibited similar spatial variability, with sites located an intermediate distance from the mainland peninsula within Mermaid Sound appearing to have greater intrinsic capacity to resist (High Point and Conzinc Island) or recover from (Gidley Island) acute and chronic stress. Conversely, sites located closer to the 50 m isobath have declined in coral cover, particularly in later years. Several key reef-building coral genera (*Acropora*, *Turbinaria*, and *Porites*) were also more abundant at sites closer to the mainland, despite varying tolerances to heat and sedimentation. The presence of an extended peninsula in the region appears to play a significant role in structuring coral communities in the region and may be responsible for the patterns in coral cover, assemblage composition and temporal trends observed in this study. Higher turbidity on reefs closer to the mainland may also afford some protection from irradiation and heat stress, reducing coral bleaching and mortality [95–97]. The naturally turbid reefs of the inner Dampier Archipelago may therefore have greater resilience to acute and chronic stress and may be of high conservation value in the face of climate change and continued anthropogenic development.

Coral assemblage composition varies significantly throughout the Dampier Archipelago, resulting in different levels of vulnerability to bleaching and other disturbances among reefs. Historically, reefs on the northern edge of the Archipelago, furthest from the mainland, were dominated by fast-growing *Acropora* species susceptible to bleaching, whilst reefs within Mermaid Sound closer to the mainland consisted of more diverse assemblages including both massive and branching taxa [41,43,98]. Bleaching-induced mortality caused by anomalously high water temperatures may have contributed to spatial heterogeneity in WA coral communities [47,82,99]. Cross-shelf gradients in temperature stress in Belize, for example, have been linked to low coral cover and assemblages dominated by stress-tolerant species on inshore reefs [32]. A strong temperature-stress gradient was present in the Dampier region, although current patterns in assemblage composition do not reflect those expected following heat exposure, with both vulnerable and hardy taxa peaking in abundance on reefs closest to the mainland and the highest coral cover and diversity observed on reefs at an intermediate distance from the coast. Although the region has experienced levels of heat stress typically associated with coral bleaching and mortality [47,82], these effects may have been mediated by local factors in the Dampier Archipelago, resulting in unexpected distribution patterns. Environmental factors not investigated in this study, including substrate type, nutrient influx and hydrodynamic patterns, may have influenced the distribution of species and resilience of coral reefs in the Dampier Archipelago [100,101].

Despite obvious differences in physiology and tolerance to heat stress and sedimentation, the abundance of *Acropora*, *Porites* and *Turbinaria* spp. were best predicted by distance to the mainland, with all taxa being most abundant close to either the coast or the peninsula. This pattern is typical of corals from the genera *Turbinaria*, which are generally tolerant of high temperatures [102], sedimentation and freshwater inundation and often dominate inshore coral communities, declining in abundance further offshore [103–105]. Slow-growing *Porites* corals are also able to tolerate a wide range of environmental conditions and are typically present across the shelf [10,27]. Conversely, fragile *Acropora* species are sensitive to elevated temperatures [30,103] yet were still far more abundant at sites that experienced greater temperature stress close to the mainland. The anomalous cross-shelf distribution patterns of *Acropora* corals may relate to coral communities on turbid reefs being better able to cope with temperature stress [95–97]. Whilst this hypothesis was not tested in this study, the Dampier Archipelago presents an opportunity for further investigation, as there are a range of turbidity and temperature conditions present and a lack of significant nutrient or freshwater input in the region. At present, it is still unclear whether turbidity will provide protection during extreme heating events and at what point turbidity levels become detrimental to corals [106].

The supply of coral recruits and connectivity can also be important in determining the composition and resilience of coral assemblages. Recent work in northwestern Australia suggests that coral communities in the Dampier Archipelago may be largely self-recruiting [107]. The lack of substantial coral reefs to the north of the Dampier Archipelago limit opportunities for allocthonous recruitment from predominantly southerly transport during austral autumn when the majority of spawning occurs in the region [107–109] and anomalous pulses when storm events coincide with mass spawning [107,109]. Coral recruitment data shows that sites continue to receive a steady supply of recruits but models including coral recruitment do not explain spatial variation in present-day coral cover [64]. This suggests that recruit limitation is unlikely and that post-settlement mortality may be responsible for spatial variation in the region. Terrigenous nutrient enrichment is unlikely to have had a strong influence as local agriculture is limited, and nutrient levels are indicative of an oligotrophic system [53]. However, we were unable to include nutrient variables in our analyses and cannot definitively rule out the possibility that they influence distribution and abundance patterns of corals. Fishing is also an unlikely source of stress, as whilst the region boasts large numbers of recreational fishermen, herbivorous species that consume macroalgae—maintaining space for coral recruits to settle—are not typically targeted [49,110]. Capital and maintenance dredging are periodically conducted in Mermaid Sound, which may have influenced the survival of recruits and/or the cover and composition of communities at nearby sites [28,48]. Past impact assessments of dredging in the Dampier Port were not designed to assess the effects of dredging on reproductive output; however, significant adult coral mortality was limited to reefs within 1.3 km of the dredge site and dredging has historically occurred in proximity to sites with the highest coral cover observed in this study [28]. Identifying the complex post-settlement processes mediating coral cover and assemblage composition throughout the archipelago would be useful for future conservation planning in the region. This will require a long-term monitoring program that investigates coral assembles relative to the most pertinent drivers of change in a standardised manner.

Spatial heterogeneity in coral cover, assemblage composition, and resilience have significant implications for conservation planning. In the Dampier Archipelago, there are clear differences between sites with coral communities varying with distance from the mainland. A reserve network that aims to follow the CAR principles will therefore need to include reefs across the shelf. Our findings also highlight the influence that terrestrial processes can have on marine communities and that management of coastal land can have a positive effect on nearby coral reefs [111,112]. Reefs at sites an intermediate distance from the mainland have maintained consistent coral cover or recovered from temporary decreases over several decades, indicating high resilience in a region regularly subjected to acute and chronic stress. Spatial planning should consider the resilience of coral communities and indeed, those areas that are highly resilient are likely to acquire greater conservation value as reefs are increasingly exposed to climate-related disturbances [113].

Science-based environmental management relies on robust data and communication between scientists and managers [114]. The use of 'grey' literature in this study provides some insight into the composition and resilience of coral reefs in the Dampier Archipelago. Grey literature is generally unavailable or unknown to the public and broader scientific community; the inclusion of this data facilitated the creation of datasets that spanned a greater temporal and spatial scale, giving insight into the historical condition of Dampier reefs. As unpublished data often includes insignificant results, the inclusion of this literature can also help to limit bias against the null hypothesis that is present in the published literature [115,116]. However, the utility of this data is not always clear and it must be interpreted cautiously. When data collected for a variety of purposes is combined, results are often highly variable, making analyses and interpretations difficult. Comprehensive descriptions of study sites and sampling methodology are required to ensure that studies are comparable. Accordingly, a number of datasets were excluded from our analyses as methods were inappropriate or there was insufficient information available to assess data suitability. Our study has shown that whilst grey literature is useful for giving an indication of spatially-coarse trends, there was substantial variation in the temporal trajectory of coral cover between sites within the archipelago. Consistently surveyed long-term monitoring sites with standardised methodology are, therefore, required to robustly assess temporal trends in the condition of coral communities.

Corals are key foundation species that provide habitat and food to a plethora of other marine species providing a variety of ecosystem services [1,2]. Variation in coral assemblages facilitate disparate biological communities, play different functional roles and have varying capacity for resilience [3,18]. Detailed descriptions of spatial patterns in coral distribution and a solid understanding of the environmental drivers of these patterns are therefore central to comprehensively and adequately represent the diversity of coral ecosystems in marine reserves [25]. We found that the Dampier Archipelago is a region of high spatial heterogeneity in coral cover, diversity, assemblage composition, and resilience that does not follow typical cross-shelf patterns. The highest coral cover and diversity was observed on reefs located an intermediate distance from the mainland, and cover of key reef-building *Acropora* corals was highest on reefs closer to shore, despite higher heat stress and turbidity. The atypical distributions of key reef-building corals observed in this study show the danger of making assumptions regarding cross-shelf patterns in geographically complex systems. The high coral cover and diversity of mid-shelf reefs and relatively consistent long-term level of coral cover suggests that these reefs may be among the most resilient assemblages and, as such, should be a priority for protection. This study also provides further evidence of healthy and diverse reefs existing in marginal environmental conditions.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/2/15/s1, Table S1: Correlation between environmental variables in the Dampier Archipelago, Western Australia, Table S2: All generalised additive mixed models (GAMMs) within 2 delta AICc for predicting cover of coral cover, diversity and genera in the Dampier Archipelago, Western Australia.

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