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Article

Regional Conservation Status of Scleractinian Coral Biodiversity in the Republic of the Marshall Islands

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Abstract: Preventing the loss of biodiversity is a major challenge in mega-diverse ecosystems such as coral reefs where there is a critical shortage of baseline demographic data. Threatened species assessments play a valuable role in guiding conservation action to manage and mitigate biodiversity loss, but they must be undertaken with precise information at an appropriate spatial scale to provide accurate classifications. Here we explore the regional conservation status of scleractinian corals on isolated Pacific Ocean atolls in the Republic of the Marshall Islands. We compile an integrated regional species list based upon new and historical records, and compare how well the regional threat classifications reflect species level priorities at a global scale. A similar proportion of the 240 species of hard coral recorded in the current survey are classified as *Vulnerable* at the regional scale as the global scale using the International Union for the Conservation of Nature (IUCN) Red List criteria (23% and 20% respectively), however there are distinct differences in the composition of species. When local abundance data is taken into account, a far greater proportion of the regional diversity (up to 80%) may face an elevated risk of local extinction. These results suggest coral communities on isolated Pacific coral reefs, which are often predicted to be at low risk, are still vulnerable due to the small and fragmented nature of their populations. This reinforces that to adequately protect biodiversity, ongoing threatened species monitoring and the documentation of species-level changes in abundance and distribution is imperative.

Keywords: atoll; conservation; coral reefs; hard coral; local abundance and occupancy patterns; Pacific Ocean; red list of threatened species; scleractinian

1. Introduction

In ecosystems with high biodiversity, such as coral reefs, there is often a lack of detailed biodiversity data and this presents a major challenge for the protection of that biodiversity [1]. Threatened species assessments play a crucial role in guiding biodiversity conservation action [2], however these assessments are highly dependent on the quality of data upon which they are based. The recent International Union for the Conservation of Nature (IUCN) assessment of the threatened status of shallow water reef-building corals suggests that on a global scale, one third of coral species face an elevated risk of extinction this century [3]. This global database of extinction risk highlights which regions contain the highest proportion of threatened species, improves the capacity to prioritize species in conservation initiatives, provides management targets and helps to stimulate biodiversity monitoring and research.

For reef building corals, many of which have extensive Indo-Pacific ranges [4], there is insufficient long-term species-specific baseline or long-term monitoring information to calculate population trends at a global scale. Thus, when the threatened status of shallow-water hermatypic corals was assessed by the IUCN [3], 99% of species were assessed under Criterion AF [5] whereby population reductions were estimated from a surrogate measure, the extent of habitat loss. The extent of habitat loss was quantified as the extent of coral cover loss in 17 regions defined in the 2004 Global Status of Coral Reefs report [6]. Thus, the rates of population decline for each species had their basis in the rate of coral cover loss within its range, adjusted by an assessment of the species-specific response to habitat loss (*i.e.*, more-resilient species have slower rates of decline), assuming the generation time of corals is 10 years [3].

The results of the global assessment suggested that extinction risk is not evenly spread across the globe [3]. Certain locations such as the Caribbean and the Indo-Malay-Philippine Archipelago (Coral Triangle) contain a disproportionately large number of species in elevated categories of threat. Conversely, oceanic islands of the Pacific generally have the lowest proportion of threatened species. This is because oceanic islands and atolls of the Pacific are exposed to lower anthropogenic threats due to their remoteness and relatively stable ocean climates [7,8]. As a result, threatened species conservation initiatives inspired by the global threat assessment are more likely to focus on work in the Caribbean and coral triangle rather than the Pacific Ocean.

This approach may jeopardize the future of coral biodiversity in the Pacific however because there are a number of reasons why the global estimates could misrepresent regional needs. Firstly, the global threat assessments were based on the assumption that coral generation times are 10 years, in fact they can be far longer (>78 years, [9]), hence the level of threat experienced by long-lived corals is likely to be higher than reported. Secondly, while often representing best available data, the assumption of a standard level of reef loss across each region is unrealistic and oversimplifies the spatial variability in disturbance and recovery dynamics [10]. The rate and extent of community recovery is complex, being influenced by many factors including initial community structure, the nature, duration, intensity and spatial characteristics of the disturbance [11], disturbance history [12,13] and population connectivity [14]. Hence, some coral communities are resilient to and/or recover rapidly after disturbance events [15], while complete non-recovery is reported from other communities [16].

Lastly, the relationship between habitat loss (*i.e.*, coral cover loss) and species population reduction is non-linear; because coral species respond differently to disturbance on spatial and temporal scales [17]. Some species are highly susceptible to disturbance events such as bleaching or disease, and others have inherent resistance or the ability to re-colonize rapidly [18,19]. Furthermore, the relationship between coral species richness and live coral cover is not a simple positive linear function as coral diversity has been shown to peak at intermediate levels of coral cover [20]. In addition, the impacts of habitat loss for individual species are likely to be more severe for locally rare or restricted species compared to locally abundant species.

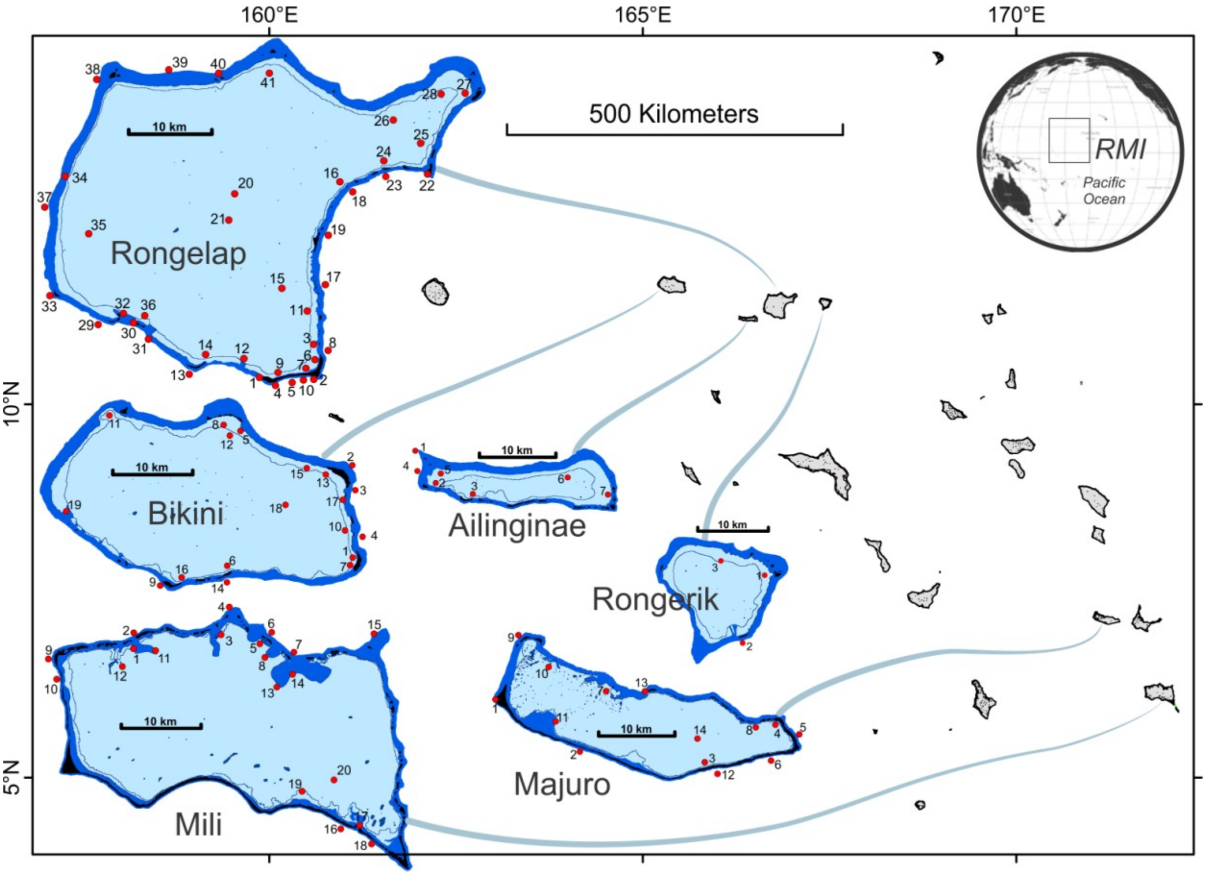
If surrogate measures (such as the extent of coral cover) are not strongly linked with species richness and prevalence, it is doubtful that global threatened species assessments that are founded in a surrogate approach can capture species conservation needs well [2]. Therefore, the Species Survival Commission advocates that regional threatened species assessments should be undertaken to complement global threatened species assessments [5]. Here we down-scale the global threatened coral species assessment to evaluate regional conservation needs in the Republic of the Marshall Islands (RMI) in the Central Pacific. Using empirical abundance data of complete suites of scleractinian coral species, an updated regional species list based upon new and historical data, we explore spatial patterns of coral biodiversity in the RMI, and examine the relationship between species occupancy and abundance.

2. Methods

2.1. Study Site

The study focussed on coral reefs in the Republic of the Marshall Islands (RMI) that are among the most isolated in the western Pacific which is one of the regions considered to contain the lowest proportion of coral species facing elevated global extinction risk [3]. The low-lying coral atolls are scattered over two main chains, Ratak (Sunrise) in the east and Ralik (Sunset) in the west; both run north-south and together spread out across 750,000 square miles (Figure 1). In a twist of fate, the isolated coral communities in the north (e.g., Bikini, Rongelap, Rongerik, Ailinginae) have been relatively untouched by human impacts over the last 50 years because of their nuclear history [21]. The northern atolls are occasionally exposed to cyclones, but there are few records of coral mortality resulting from bleaching, predator or disease outbreaks [22]. On the contrary, in the south of the country, Majuro Atoll (the capital of the RMI) is a major urban centre, and here corals are threatened by growing anthropogenic impacts including pollution, land reclamation, unsustainable fishing practices and aquarium collecting [23]. Majuro’s neighbouring atoll, Mili is readily accessed by boat and for that reason is also exposed to elevated levels of fishing and aquarium collecting. In the last decade, increasing incidents of coral bleaching, coral disease and crown-of-thorns outbreaks have been recorded at these two southern atolls [22].

Figure 1. Map of the Marshall Islands with insets of atolls showing survey sites. Site numbers correspond to those provided in Table S2, which contains coordinates. Base map from Millennium Coral Reef Mapping project [24].



2.2. Threatened Status Assessments

Due to the lack of comprehensive species-level data, the global IUCN assessment of threatened status tested the population decline for each species on the rate of coral cover loss within its range, adjusted by the species-specific response to habitat loss based on the criterion of "estimated, inferred or suspected population size reduction" [3,5]. Here we use records of the local distribution of scleractinian corals from 104 sites across the RMI (41 at Rongelap Atoll, 20 at Mili Atoll, 19 at Bikini Atoll, 7 at Ailinginae Atoll, 14 at Majuro Atoll and 3 at Rongerik Atoll) to determine the regional threatened status following assessment criterion VU D2: "population very restricted in the number of locations (typically five or fewer) such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future" [5].

2.3. Field Surveys

The distribution and abundance of corals were documented by rapid visual assessment whereby all species of scleractinian coral observed on a 60 minute timed swim (covering an area of approximately 2,500 m^2) at 104 sites. To maximize the detection of rare species, all habitat zones to a maximum depth of 30 m were carefully searched within each site. Sites were randomly stratified within 2 general exposures (exposed and protected). Multiple habitat zones were surveyed within exposed sites including reef flat, reef crest and reef slope, and protected sites encompassed sandy inter-reefal areas and submerged bommies featuring deep vertical and shallow reef top habitats.

All target species encountered were identified and species abundance was roughly tallied underwater. Post dive, all abundance tallies were converted to a 5-point DAFOR scale: 1 = rare (1–2 colonies); 2 = infrequent (3–5 colonies); 3 = frequent (6–20 colonies); 4 = common (21–50 colonies); 5 = dominant (51 + colonies) [25]. These categories (1–5) differ in relative magnitude, such that a mean difference of "1" corresponds approximately to a log difference in abundance. Where *in situ* species identification was not possible, skeletal material was collected to facilitate further identification in the laboratory. Skeletal voucher specimens were identified by ZR with input from Dr. Carden Wallace, Dr. Doug Fenner, Mr. Emre Turak and Dr. Michel Pichon. Four hundred and twenty-three skeletal samples were collected and registered into the Museum of Tropical Queensland, Townsville, Australia.

Three major scleractinian coral taxonomic studies have been conducted in the RMI prior to the current survey. Firstly, Wells studied material collected from Bikini Atoll, Rongelap Atoll, Rongerik Atoll, Enewetak Atoll, Jaluit Atoll, Nugol Atoll, Kwajalein Atoll, Arno Atoll, Wotke Atoll, Namorik Atoll, Ailuk Atoll, Pokak Atoll, Ebon Atoll, and Likiep Atoll via snorkel and trawl/dredge grabs that were conducted between 1931 and 1950 [26]. A group of taxonomists including Michel Pichon, Carden Wallace, John Wells, James Maragos, Maya Best and JEN Veron surveyed Enewetak Atoll in 1976 and this work was published in 1987 [27]. James Maragos surveyed Bikar Atoll, Bok-ak Atoll, Tōke Atoll, Jemo Island, Wōtto Atoll, Rongerik Atoll and Adkup Atoll in 1988 and this work was published in 1994 [28]. Veron [4] includes the Marshall Islands in the known range of many species documented in "*Corals of the World*" however the data upon which these records are based is not known. In this study, we integrate our new data with the historical data of [4,26–29]. Assimilating these data involved resolving many taxonomic discrepancies and synonymy's.

2.4. Analysis

Species accumulation curves were calculated for each location using the "vegan" library in R using the function "specaccum" with jack-knifed standard errors [30,31]. This provided a graphical check of whether sampling was sufficient to detect rare members of the assemblage in the RMI and within each location. To control for sampling bias, we calculated the expected number of species per sample for Bikini, Rongelap, Mili and Majuro ($n \geq 14$ surveys) based on species-abundance relationships using the programme CatchAll [32]. The expected number of species was used to compute the ratio of listed species per atoll to assess if species in elevated categories of threat are clustered at particular atolls or evenly spread across the RMI.

The number of sites occupied by each species within three IUCN categories (*Vulnerable*, *Near Threatened*, *Least Concern*) at the global scale was calculated. At the regional scale, a species was classified as *Vulnerable* if it occurred at 5 or less sites, *Near Threatened* if it occurred between 6–10 sites and *Least Concern* if it occurred at 11 or more sites. To further explore the regional conservation status of corals, local abundance patterns were explored in the context of the 5-point scale which delineates species from rare to dominant and the frequency of occurrence of the five abundance categories was calculated.

To closer examine the relationship between species abundance and site occupancy, an estimate of the absolute abundance of each species (per 2,500 m^2) was calculated using the minimum absolute abundance of each abundance category (*i.e.*, abundance category 1 = 1; abundance category 2 = 3; abundance category 3 = 6; abundance category 4 = 21; abundance category 5 = 51) using (Equation 1) [33–35].

Equation 1, formula for calculating mean local abundance from categorical data.

$$mean\ local\ abundance = \frac{minimum\ absolute\ abundance\ (from\ DAFOR\ categories)}{(number\ of\ sites\ occupied)}.$$

When average abundance was measured across all sites, zero values were not included to avoid a biased estimate of population size. Further, to explore if species abundance was consistent across sites, the modal category of abundance for each species was plotted (± minimum and maximum abundance categories).

To explore if species abundance increased as a function of the number of sites occupied, we further examined the relationship between local distribution and abundance via linear regression. In order to examine if coral communities at the six different RMI locations were structured similarly, or whether exposed and protected communities are significantly different, Multivariate Analysis of Variance tests (MANOVA) were conducted and a visual representation of the results was performed via a non-metric multidimensional scaling (nm-MDS) analysis in R [30] using the Bray-Curtis distance measure [36,37].

3. Results

3.1. Coral Biodiversity

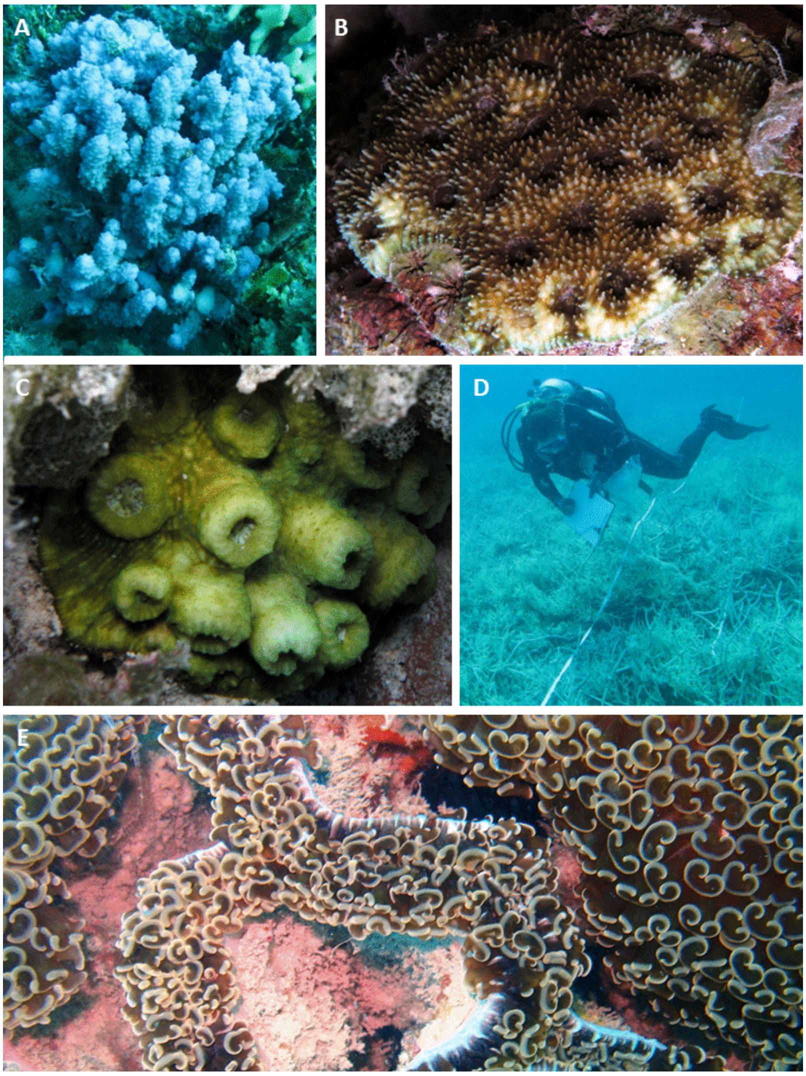
In this survey the local abundance and distribution of 240 species of reef-building coral in the RMI was recorded as follows: 196 species at Rongelap Atoll (n = 41); 168 species from Bikini Atoll (n = 19); 156 species from Mili Atoll (n = 20); 129 species from Majuro Atoll (n = 14); 112 species from Ailinginae Atoll (n = 7) and 89 species from Rongerik Atoll (n = 3) (corals in Table S1, site details in Table S2). This dataset provides a robust representation of the region-wide diversity because the regional species accumulation curve approaches an asymptote. Nevertheless, atoll-specific species accumulation curves suggest species richness is underestimated at all locations except Rongelap Atoll (Figure S1). Models of the expected species richness *ES* (for Rongelap, Mili, Bikini and Majuro) indicate Bikini Atoll contains the greatest proportional subset of the regional diversity and that the Majuro Atoll coral community is comparatively depauperate (Table S4).

Our integrated species list, combining the new and historical scleractinian coral species records provides a comprehensive summary of all the species recorded from the Marshall Islands to date. After clarifying taxonomic discrepancies (where possible), a total of 308 species of scleractinian coral have been recorded from the RMI. Further, the current survey has extended the known distribution of 19 species of scleractinian coral from 11 genera to the RMI (Table 1, Figure 2). Of these 19 new specimen/photo-based records, 10 species were present at Rongelap Atoll, 6 species were present at each of Bikini and Mili Atolls, 4 at Ailinginae Atoll, and 3 species were present at Rongerik and Majuro Atolls.

Table 1. Nineteen new scleractinian coral records from the Marshall Islands based on skeletal voucher specimens (and photos) collected from 2002–2010. Known distribution records based upon [4,26–29].

New Species Records	Previous knowledge	Atolls	Accession Numbers
Acanthastrea brevis	No Marshall Is. records–Known from Indian Ocean, Red Sea, SE Asia, North Pacific Ocean	Bikini, Rongelap, Ailinginae, Mili	G56252
Acanthastrea hemprichii	No Central Pacific records–known from SE Asia, Australia, W. Indian Ocean	Bikini, Rongelap, Mili, Majuro	G56253-54
Acropora awi	No Pacific records–Known from SE Asia	Mili	G57241
Acropora bushyensis	No Northern Hemisphere records–known from East and West coasts of Australia and South Pacific	Bikini	G56198
Acropora kimbeensis	No Central Pacific records–Known from SE Asia, PNG and East Coast of Australia	Rongelap, Bikini, Mili, Rongerik, Majuro	G56194, G56212, G57262, G57263-64
Acropora loisetteae	No Central Pacific records–Known from SE Asia & East Indian Ocean	Bikini, Rongelap, Ailinginae	G57232, G56217, G57125-38
Acropora gomezi	No Central Pacific records–Known from SE Asia	Rongelap	G57236-38
Anacropora reticulata	No Central Pacific records–known from Indo-West Pacific	Rongerik	See Figure 2A
Cantharellus jebbi	No Central Pacific records–known from PNG, Australia and dubious records from the Red Sea.	Rongelap	G57292
Coscinarea monile	No Pacific records–known from Indian Ocean, Red Sea and SE Asia	Rongelap	G56302
Cyphastrea agassizi	No Marshall Island records–known from Indo-West Pacific and Hawaii	Bikini	G56272
Echinophyllia patula	No Central Pacific records–known from SE Asia, Japan, India.	Bikini, Rongelap, Ailinginae	G56322
Echinophyllia orpheensis	No Micronesian records–Known from Indian Ocean, SE Asia, South Pacific and Australia	Rongelap, Ailinginae, Mili	G57303-05
Euphyllia ancora	No Central Pacific records–Known from Indo West Pacific and Eastern Indian Ocean.	Mili	See Figure 2E
Montastrea salebrosa	No Micronesian records–Known from SE Asia, ONG, South Pacific, Eastern Australia	Bikini, Rongelap, Ailinginae, Rongerik	G57340
Montipora cocosensis	No Central Pacific records–Known from SE Asia and South Pacific	Bikini	G56285
Pectinia africanus	No S.E. Asia or Pacific records–Known only from the Indian Ocean	Rongelap, Mili	G57186
Seriatopora aculeata	No Marshall Island records–known from Micronesia, PNG, Solomon Is., Timor Sea	Rongelap, Mili, Majuro	G57188
Seriatopora dentritica	No Central Pacific records–known from SE Asia	Rongelap, Mili, Majuro	G56315, G57189

Figure 2. New scleractinian coral records from the Marshall Islands. (**A**) A single colony of *Anacropora reticulata* was located in the lagoon at Rongerik Atoll. (**B**) *Acanthastrea brevis* was documented at almost half of the sites surveyed. (**C**) *Echinophyllia orpheensis* is frequently encountered in overhangs and crevices. (**D**) *Acropora loisetteae* forming an extensive thicket in the eastern part of Rongelap Lagoon. (**E**) Only a single colony of *Euphyllia ancora* was observed at a single site at Mili Atoll.



Four additional species that were identified *in-situ* (*Echinophyllia taylorae*, *Coscinaraea crassa*, *Lobophyllia dentatus* and *Montipora angulata*) may also represent new records for the RMI; unfortunately however neither skeletal specimens nor photos were taken to enable their identity to be confirmed. Furthermore, skeletal specimens were collected of another 11 species presumed by Veron 2000 to occur in the RMI, but there is no published record of these species having previously been collected from the RMI (*Pavona duerdeni*; *Acropora microclados*, *Acropora divaricata*; *Acropora chesterfieldensis*; *Acropora solitaryensis*; *Goniopora minor*; *Alveopora fenestrata*; *Porites vaughani*; *Cycloseris tenuis*; *Montipora incrassata* and *Montiora efflorescens*). Accessioned specimens housed at the Museum of Tropical Queensland now validate the existence of these species in the RMI.

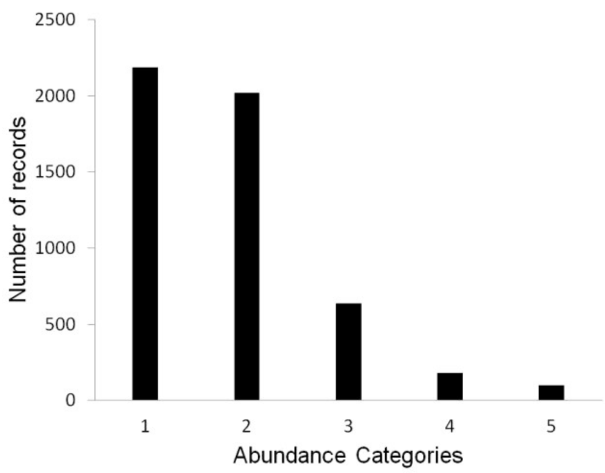
3.2. Local Abundance and Distribution Patterns

Overall, 17 species occur at 50% or more of the sites surveyed and 56 species occur at 5% or less of sites. Nineteen species were recorded at a single site only, and for eleven of these species, only a single colony was located (e.g., *Anacropora reticulata* and *Euphyllia ancora* (Figure 2A,E, Table S3)). The species occupying the largest number of the sites surveyed in the RMI were (in decreasing order) *Acropora nasuta*, *Pocillopora verrucosa*, *Astreopora myriophthalma*, *Porites lutea*, *Pavona varians*, *Pocillopora eydouxi*, *Herpolitha limax* and *Porites cylindrica*.

Of our total of 5,118 observations of relative abundance, the "rare" category (category 1, 1–2 colonies per 2,500 m^2) was the most prevalent, accounting for 43% of relative abundance observations (n = 2,187) (Figure 3). The "infrequent" category (category 2, 3–5 colonies per 2,500 m^2) was also prevalent with 39% of relative abundance observations (n = 2018). The observations of 'frequent, common and dominant' species were markedly more sparse, accounting for a total of 17% of the records (n = 913) (Figure 2).

Overall 81% of species (n = 194) had an average local abundance (Equation 1) of less than 2 colonies per 2,500 m^2 (Table S2). The modal abundance category and range of abundance categories occupied by each species reinforces that the majority of species are rare or infrequent, but also that there is a great deal of variation in the local abundance of each species across the region (Figure S3). Eighteen percent of species (n = 42) had an average local abundance of over 5 colonies per site and *Isopora palifera* was over twice as abundant as all other species. Of the species that reach high abundance, only 12 species were ever recorded to dominate a community (Category 5, 51 + individuals per 2,500 m^2) (*Acropora cytherea*, *Acropora digitifera*, *Acropora loripes*, *Acropora muricata*, *Acropora nasuta*, *Goniastrea pectinata*, *Isopora palifera*, *Pocillopora damicornis*, *Porites cylindrica*, *Porites lutea*, *Seriatopora hystrix*, *Pocillopora verrucosa*). Nevertheless, none of these species were dominant at every site surveyed, and all were either absent or rare at some sites.

Figure 3. Local abundance patterns in Republic of the Marshall Islands (RMI) coral communities. Histogram of the frequency of occurrence of the five abundance categories (per 2,500 m^2) where: Category 1 = 1–2 colonies *i.e.*, rare; Category 2 = 3–5 colonies *i.e.*, infrequent; Category 3 = 6–20 colonies *i.e.*, frequent; Category 4 = 21–50 colonies *i.e.*, common; Category 6 = 51 + colonies *i.e.*, dominant.



There was a significant positive linear relationship between the average abundance of each species and its site occupancy ($p < 0.0001$) (Figure 4). Nevertheless species occupancy provided a weak explanatory variable for the average abundance of species because only 14% of the variation was explained as a positive linear function ($r^2 = 0.137$, df = 237, F = 39.42, Figure 4). This result most likely reflects patterns where species with restricted prevalence (*i.e.*, occurring at less 10% of sites) had relatively high abundance where they occur (e.g., *Heliopora coerulea*, *Acropora loisetteae*), whilst others occurred at a large proportion of sites in low abundances (e.g., *Oulophyllia crispa*, *Scapophyllia cylindrica*).

Figure 4. Regression of the site occupancy against the average abundance of scleractinian corals for each species recorded in the Marshall Islands (n = 240). A significant relationship exists between these two variables (Regression analysis, $r^2 = 0.14$, df = 237, F = 39.4, $p < 0.0001$).

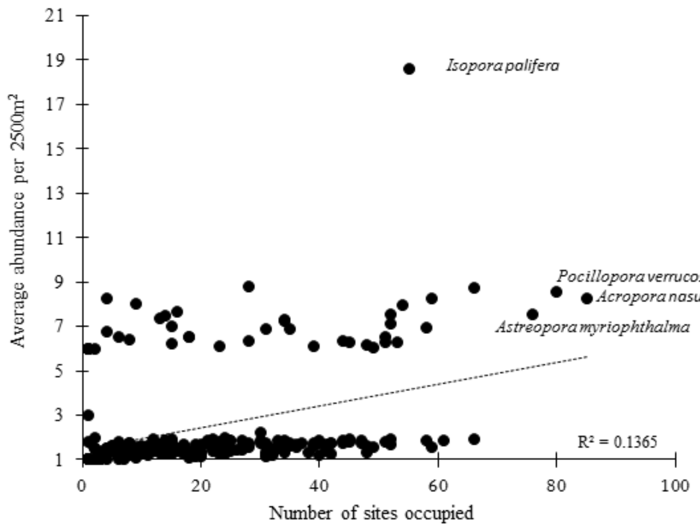


Figure 5. Two-dimensional nMDS of coral assemblages in the Marshall Islands using the Bray-Curtis distance measure. Square symbols represent exposed sites; circular symbols represent protected sites.

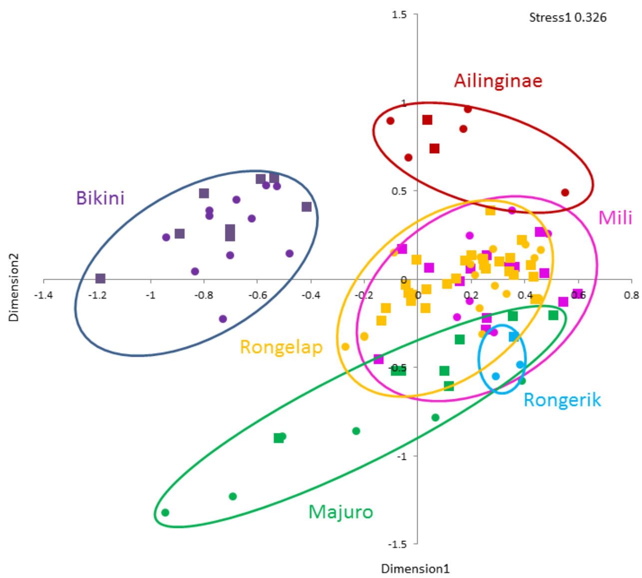


Table 2. Multivariate Analysis of Variance of the first 15 dimensions between locations and between sheltered and exposed sites (Stress1 0.326) from nm-MDS of the Bray-Curtis distance measure.

	Pillai's Trace	F	d.f.	Significance
Atoll	3.7469	17.7270	70,415	$<2.2 \times 10^{-16}$ ***
Exposure	0.4545	4.7014	14,79	3.732×10^{-6} ***
Atoll:Exposure	1.0677	1.6098	70,415	2.611×10^{-6} **

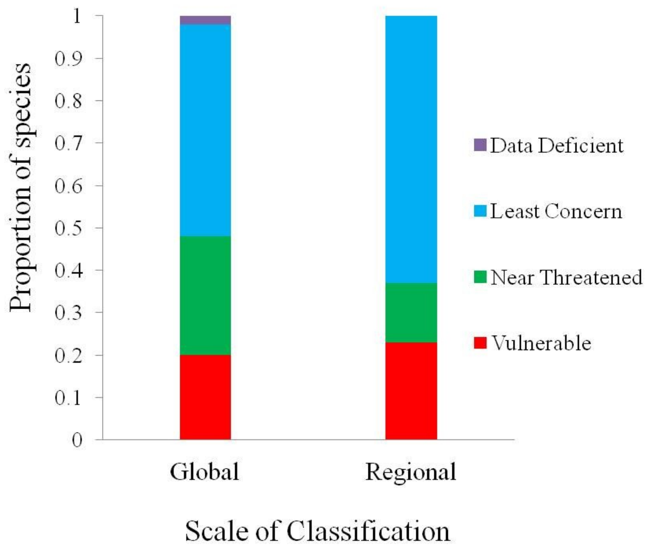
Sig. codes: 0.000 "***" 0.005 "**".

A MANOVA confirmed a significant difference in the composition and abundance of hard coral communities in the RMI ($p < 0.0001$) between atolls, and between sheltered and exposed habitats (Table 2). There was also a significant interaction effect, however the dimensionality of the data was very high with 15 dimensions required to obtain a Stress value of < 0.05. In 2D, the Bikini Atoll and Majuro Atoll communities were clearly distinct from the tightly clustered Rongelap Atoll and Mili Atoll communities (Figure 5).

3.3. Global and Regional Conservation Status

At a global scale, 51% of the species in the RMI are classified as *Least Concern* according to IUCN categories and criteria (n = 122). 19.6% are classified as *Vulnerable* (n = 47); 28.8% are *Near Threatened* (n = 69), and 0.8% are *Data Deficient* (n = 2) (Figure 6, Table S3). At the regional scale, the majority of species (63%, n = 151) are classified as *Least Concern* according to their distribution patterns. 23% of species are *Vulnerable* (n = 56), and 14% *Near Threatened* (n = 33). Thus, at both global and regional scales, the vast majority of coral species in the RMI are classified as *Least Concern*. Seventeen species are classified as *Vulnerable* at both the global and regional scales and of imminent conservation concern (Figure 6, Table S3).

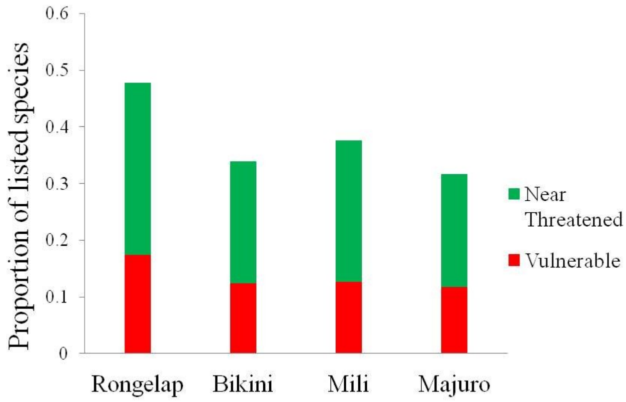
Figure 6. Proportion of species listed in each category of threat according to the International Union for the Conservation of Nature (IUCN) categories and criteria at global and regional scales.



While the proportion of species classified as *Vulnerable* at global and regional scales (20% and 23% respectively) is similar, there are important scale-dependant differences in the species falling into the *Vulnerable* category. For example 21 species that are classified as *Least Concern* at the global scale are classified as *Vulnerable* at the regional scale. Conversely, 23 species that are classified as *Vulnerable* at the global scale are classified here as *Least Concern* at the regional scale.

Based on the model of expected species richness, Rongelap Atoll contains the highest proportion of globally threatened species, followed by Bikini and Mili Atolls. Majuro has the fewest species that are classified as globally threatened (Figure 7).

Figure 7. Proportion of *Near Threatened* and *Vulnerable* coral species per atoll (global scale) based on estimated total species number (n = 14 sites). Ailinginae and Rongerik were omitted due to the low number of surveyed sites.



4. Discussion

The success of conservation action is heavily impingent upon the data on which decisions are based. Here we have consolidated all existing knowledge about the coral biodiversity in the RMI in an effort to inform managers and conservation scientists and quantify the level of threat facing corals in this isolated region. Our results suggest that 17 species are of immediate conservation concern because they are *Vulnerable* on both global and regional scales (Table S3). There are also 21 species that are classified of *Least Concern* globally but appear to be *Vulnerable* within the region (e.g., *Acropora clathrata*, *Leptoseris explanulata*, *Echinophyllia patula*, *Cantharellus jebbi*, *Caulastrea furcata*). Conversely, there are 23 species that are classified as *Vulnerable* at the global scale but are of *Least Concern* within the region (e.g., *Acropora echinata*, *Acropora striata*, *Acropora vaughani*, *Leptoseris yabei*, *Pavona cactus*). This may be a reflection of the relatively pristine status of reefs in RMI, hence whilst species are still relatively abundant in this region, they are in sharp decline in other parts of their ranges.

While the proportion of species categorized as *Vulnerable* is similar across scales (20% global and 23% regional), the species concerned are not consistent. There was a larger proportion of species considered as *Least Concern* at the regional scale than global (51% global and 63% regional), and more species *Near Threatened* at the global scale than regional (29% global, 14% regional). Again there were notable scale-dependent differences in the level of threat facing each species (see Table S3).

At a genus-level there were hints of phylogenetic signatures in the level of vulnerability. Even though *Vulnerable* species were found right throughout the coral phylogeny, with almost every coral genera having at least one species in an elevated category of threat at one or more scales, certain genera (e.g., *Psammocora*, *Stylocoeniella*, *Goniastrea*) contained disproportionately large numbers of *Least Concern* species. At the coarser family level, certain families, such as *Acroporidae* and *Agariciidae*, appear to contain a disproportionately large number of threatened species (Table S3).

The is no clear clustering of threatened species at any one particular atoll, however it is apparent Rongelap and Bikini Atolls may act as regional refuges for species that are threatened in other parts of their range (Figure 7). Whilst Bikini experienced chronic disturbance from nuclear testing about 50 years ago [21], both atolls have been largely inhabited by humans since the testing, and therefore have not been relatively unimpacted by fishing or urban pollution for five decades. The lower prevalence of globally *Vulnerable* species at those atolls with the highest degree of existing human impacts (Majuro, Mili) could indicate that threatened species may already have been lost from these communities. Moreover, the potential for the largely uninhabited northern atolls to act as refuges for threatened coral biodiversity highlights the need for threat mitigation and special protection measures at these locations to ensure the persistence of regionally threatened species.

The regional threatened species assessment conducted here is based on distribution patterns; however it is important to note that when abundance patterns are considered, it is apparent that a much greater proportion of coral species in the RMI may be threatened. More specifically, our estimates of mean local abundance suggest as many as 80% of the hard coral species recorded in the RMI on the latest survey have an average abundance of 2 or less individuals per 2,500 m^2. Whilst it is possible that at some atolls more sampling would lead to more rare species records, our database suggests that most corals in the RMI occur in low abundance (*i.e.*, small, fragmented populations). Natural communities are typically characterized by a small number of abundant species and a much larger number of rare species [38–40]. Hence, the presence of rare species in the community is not unusual, but the fact that such a large proportion of the community has low populations sizes has important implications for biodiversity conservation. Not only does it mean that extensive searching across multiple habitats is required to accurately document, monitor, or detect changes in coral biodiversity in the RMI, but also that a substantial proportion of the regional species pool is at risk of local or ecological extinction.

Local extinction (the disappearance of a species from part of its range) and ecological extinction (when a species is reduced to such low abundance that, although still present, it no longer plays its typical ecological role) are precursors to global extinction. Generally, the permanence of a species is related to its local population size [39]. Thus, even if a species has a widespread global distribution, if it occurs sparsely across that distribution, it is vulnerable to population fragmentation [41,42]. The vulnerability of small populations to local extinction relates to the high level of stochasticity in natural communities [43,44] which naturally drives some subpopulations towards extinction [45]. Furthermore, genetic drift acts to force small populations to local extinction due to a loss of heterozygosity and eventual fixation of (sometimes deleterious) alleles [46,47].

In locations where coral communities exist in relatively continuous habitats (e.g., Great Barrier Reef, Australia), the finding of a large number of small populations may not be of primary conservation concern as these species may connected via a regional network of larval exchange [14,48]. However in the RMI, the coral atolls are isolated from each other by large expanses of deep water and this can limit connectivity for poor dispersers. Furthermore, in an atoll reef environment the availability of suitable habitat is severely limited, so competitive exclusion is likely to play an important role in preventing the colonization of new immigrants [49].

We find a relatively small number of species (n = 11) dominate the Marshall Island hard coral communities. This handful of species are of primary functional importance for reef-building in the low-lying Marshall Islands and whilst none of these species are classified in heightened categories of threat (*i.e.*, *Critically Endangered*; *Endangered* or *Vulnerable*) at the global scale, four of these species, *Acropora nasuta*, *Pocillopora eydouxi*, *Porites cylindrica* and *Isopora palifera* are *Near Threatened*. Thus, ensuring these populations persist is of critical regional importance because common species are disproportionately influential in shaping macro-ecological patterns [50]. *Isopora palifera* for example is over 2× as abundant as any other species of coral in the RMI. This species is relatively vulnerable to bleaching and sedimentation threats, and despite being a successful colonist of isolated reef systems [4], it has experienced severe declines throughout most of its range. If populations of common species with complex morphologies such as *Isopora palifera* are lost, cascading ecosystem effects such as habitat simplification, decline of reef accretion potential and the loss of associated species are likely [51].

The extraordinarily high abundance of *I. palifera* on RMI atolls may relate to its life history characteristics. The larvae of *I. palifera* are produced sexually through internal fertilization. Larvae are brooded within the polyp and then released into the water column at an advanced developmental stage; hence they are competent to settle almost immediately after release. Thus, the majority of brooded larvae settle close to their natal colony (*i.e.*, within 20 m, see [52]). Preponderance for local recruitment, accompanied by high survival rates in the oceanic conditions may explain the abundance of this species in the RMI coral communities, however; the molecular ecology of this species has not been examined to date. To safeguard the keystone functional role this species plays in the RMI coral reef ecosystem, further targeted research into all aspects of its conservation biology is recommended.

Overall, the RMI coral communities are heterogeneous; hence the composition and local abundance-occupancy patterns of one location do not necessarily reflect the community structure at another. In addition to this, there was a large amount of variability in the local abundance of individual species across the sites surveyed (Figure S3). For example, the Bikini and Majuro assemblages are significantly different from each other and from the other locations (Figure 5). The Bikini coral community is highly heterogeneous leading to a steep slope in the species accumulation curve (Figure S1). Conversely, Majuro's coral community is the most homogeneous of the atolls examined, possibly because many species that are rare or threatened elsewhere are already missing (Figure S1).

The finding of spatial heterogeneity in the RMI coral meta-community is consistent with another study that examined the occupancy-abundance patterns of *Acropora* corals [35], but it is inconsistent with other published literature that suggest coral communities are homogenous and highly predictable across spatial scales [53–59]. While this may be true to an extent at the genus-level, it does not hold up at the species-level. The discrepancy may relate to the survey methodology of this study whereby species abundance was documented across multiple habitat zones whilst former studies analysed either presence-absence data only [57–59]; sampled within a restricted subset of habitats [54–56]; or species were categorized into ecological groups rather than at a species level [53].

5. Conclusions

Our results illustrate those regions such as the RMI that are globally less at risk still have high conservation merit for two reasons. Firstly they contain a substantial number of regionally threatened species with small and fragmented populations, and secondly, it is possible that the RMI (Rongelap Atoll in particular) could play an important longer-term role as a refuge for species that are threatened in other parts of their range (especially those species with relatively long pelagic larval durations [60]). Thus, while coral reefs in the Western Pacific are today some of the most pristine in the world, threatening processes such as coral bleaching events, crown of thorns outbreaks and incidences of coral diseases have increased in the over the last decade [22,61]. To safeguard regionally threatened species in the RMI, and the possibility that RMI coral communities could provide internationally significant 'rescue' populations in the future, ecosystem managers must be informed at an appropriate scale. Furthermore, ongoing threatened species monitoring and the documentation of species-level changes in abundance and distribution is imperative. Moreover, we hope this dataset will lead to further updates of the coral threatened species assessment and listing process and lead the way for similar regional studies in other parts of the world.

Supplementary Materials

Supplementary materials can be accessed at: http://www.mdpi.com/1424-2818/5/3/522/s1.

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Conflict of Interest

The authors declare no conflict of interest.

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