Reef biodiversity surveys of Australia's Commonwealth Marine Reserve Network: An overview

REEF LIFE SURVEY

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Report to Parks Australia, Department of the Environment

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Important disclaimer

Images

Rick Stuart-Smith

Contents

Figures

Tables

List of acronyms

ACRONYM	EXPANDED
AMP/CMR	Australian Marine Park/ Commonwealth Marine Reserve
RLSF	The Reef Life Survey Foundation
MPA	Marine Protected Area
IUCN	International Union for Conservation of Nature
RLS	Reef Life Survey
EEZ	Exclusive Economic Zone
CTI	Community Temperature Index

Executive summary

In Australia's Commonwealth Waters, the broad areas used for marine planning include the South-east, Temperate East, Coral Sea, North, North-west and South-west regions. Each region is recognised as hosting areas or features of conservation significance, and the Australian Commonwealth Marine Reserve (CMR) Network recognises the value of marine reserves in the protection of biodiversity, habitats, ecological processes and resources. Shallow reefs occur in all the CMR Networks except the South-east, from coral reefs in the northern regions to a combination of rocky and limestone reefs in the temperate south.

Reef Life Survey (RLS) involves recreational divers trained to a scientific level of data-gathering to make it possible to conduct ecological surveys across broad geographic areas in a cost-effective manner. Over the last decade, this has allowed coverage of a large geographic area, including reefs worldwide, and enabled, for the first time, comparisons of shallow reefs across all Commonwealth Waters. The goal of this report is to compare ecological metrics from reefs in five CMR Network regions. Data analysed and presented include the major macroscopic groups of species – fishes, mobile macroinvertebrates, and sessile benthic organisms. Comparisons were made between the CMR Network (both proposed and actively managed), existing State marine protected areas (MPAs) and areas outside any CMR boundaries (referred to here as "Open"); comparisons were also made between areas assigned to different IUCN categories within CMR networks, where applicable.

Fish species assemblages surveyed by RLS divers subdivide into three distinct groups: temperate fish species, fishes of the northern coastline, and tropical eastern and western offshore species. Fish abundance, biomass and species richness (especially sharks and large fishes) were higher in CMRs across all ecoregions than either State MPAs or Open areas; biomass and species richness were higher in State MPAs than in Open areas. CMRs had almost double the biomass of large fishes than State MPAs and Open areas, and shark biomass was between four and five times higher. Macroinvertebrate communities were more similar to each other across offshore coral reefs than across northern Australian or temperate ecoregions. In many cases, CMRs appeared more unique than Open areas or State MPAs, especially in the coral reef provinces.

Across levels of protection (existing and proposed), macroinvertebrates were most abundant and diverse in State MPAs and Open areas, as well as Multiple Use areas (IUCN VI). The cover of different benthic groups varied greatly between temperate sites, with less dissimilarity between tropical areas. Southern and southwestern ecoregions were distinguished by a higher cover of macroalgae, and temperate eastern ecoregions had a greater diversity of sessile biota. Tropical regions were distinguished by either a high cover of soft corals and turf, or hard corals and abiotic substrata. Total live cover of sessile biota was slightly higher in CMRs than in State MPAs or Open areas.

The similarity between CMR and Open reefs varied between the different ecoregions. One goal of establishing the CMR Networks was to ensure representation of the range of Australia's marine flora and fauna in protected areas; this report provides insights into the extent that this has been achieved by the existing and proposed placement of CMRs for tropical, subtropical and temperate reefs. A number of key patterns emerged:

- The former Coral Sea CMR had no Open sites, but the comparison between highly protected (I and II) and less protected (IV) zones showed that these all had similar community structure.
- The Bassian, Great Australian Bight, Houtman, Shark Bay, South Australian Gulfs, Ningaloo, Cape Howe and central/southern GBR ecoregions lacked shallow reef in CMRs; State MPA sites were similar to Open sites, but with lower macroalgal cover in the State MPAs of the Bassian ecoregion and more distinctive invertebrate and benthic assemblages in the State MPAs of the Houtman ecoregion.
- Within the Exmouth to Broome ecoregion, CMRs capture most of the biodiversity and community structure present on Open reefs. Most of the North Network's reefs within CMR boundaries were also similar to the Open reefs; the largest difference was between Open reefs of the Torres Strait to northern GBR ecoregion and the West Cape York CMR. Together, however, the Northern CMR sites differed substantially from northwest and northeast tropical sites, with distinctive biota. However, no northern CMR is proposed to be IUCN I or II, hence none of these distinctive ecosystems will be fully protected from exploitation under the planned zoning arrangements.
- In the Manning-Hawkesbury ecoregion, the Cod Grounds CMR possesses a fish and benthic community different from State MPAs or Open sites, while the invertebrate assemblage is similar between the three levels of protection. This is most probably due to the unique geomorphic structure of the Cod Grounds. Similarly, the Solitary Islands CMR (Pimpernel Rock captures a unique pinnacle rising steeply from the seabed, a feature lacking in Open areas and State MPAs of the Tweed-Moreton ecoregion.
- Norfolk and Lord Howe CMRs were unique. These sites formed a distinct group rather than overlapping with other temperate sites. The Lord Howe CMRs and State MPAs together capture the biodiversity present within this group of islands and reefs. Norfolk Island, though somewhat similar to Lord Howe, has a distinctive flora and fauna again; a need exists to represent this unique environment through stronger protection, as the entire area of shallow reef is designated as a Multiple Use zone under planned zoning arrangements.
- In the Leeuwin ecoregion, the Geographe CMR had higher diversity of reef organisms than reference sites.

Observed ecological differences between CMR and Open reefs corresponded with expectations of the general objectives of marine protected areas, which is the protection of biodiversity and populations of exploited species. In this study, the differences were especially recognisable in the biomass of sharks and large fishes, suggesting that the proposed CMR network encompasses a combination of areas that are presently successfully managed, and those which still support healthy populations of sharks and large fishes, possibly due to offshore and remote location.

RECOMMENDATIONS

We recommend that:

- ongoing ecological monitoring of Australian tropical, subtropical and temperate reefs is scheduled on a regular basis (3 years or less), using the methods and sites described here;
- data presented in recent RLS surveys be combined with previous surveys to guide efforts to select sites for long-term monitoring;
- additional sites are added to the monitoring design, including additional reference sites outside CMRs in comparable habitats and depths where possible;
- research priorities include development of indicators that track changes in reef condition and biodiversity;
- data are collected on fishing effort on the different reefs to assess differences in extractive pressures;
- compliance metrics are developed;
- detailed habitat mapping and categorisation of reef types, exposure and aspect is undertaken for inclusion in analyses of ecological patterns;
- through the longer term, increased protection (through the allocation of more highly protected IUCN categories to proposed CMRs) for large predatory fishes and species vulnerable to being caught as bycatch from illegal, unreported, unregulated (IUU) and commercial fishing for North CMR Network reefs and Norfolk Island should be considered, to safeguard biodiversity values in these unique areas;
- detailed spatial and temporal mapping of the distribution and impact of natural disturbances such as cyclones is carried out; and
- further collaboration between agencies collecting data on reefs in State and Commonwealth waters should be actively encouraged.

1 Introduction

Australia’s Commonwealth Waters begin 3 nautical miles offshore (the limit of State Waters) and extend to the edge of the Exclusive Economic Zone (EEZ), 200 nautical miles offshore. Commonwealth Waters also surround Australia’s external territories, such as Christmas Island and Cocos-Keeling, Norfolk Island, and Heard and MacDonald Islands. Commonwealth Waters cover a vast area, from tropical waters bordering the global centre of marine biodiversity (the Coral Triangle) in Indonesia, Papua New Guinea and the Solomon Islands, to cold temperate environments south of Tasmania, and to subantarctic Heard Island. The broad bioregions used for marine planning include the South-east, Temperate East, Coral Sea, North, North-west and South-west. Each region is recognised as hosting areas or features of conservation significance, such ecological features comprising major elements within a network of marine reserves that is under development throughout Australian Commonwealth Waters.

The Australian Commonwealth Marine Reserve (CMR) Network, established through the National Representative System of Marine Protected Areas (NRSMPA), recognises the value of marine reserves in the protection of biodiversity, habitats, ecological processes and resources. MPAs have already been applied extensively in Australian State waters and around the world (McCook et al. 2010; Graham et al. 2011; Edgar et al. 2014; Emslie et al. 2015). The goals of establishing MPAs vary, and can include fisheries management or protection of exploited populations (Russ et al. 2008), conservation of species and genetic diversity through the protection of habitat structure (Fernandes et al. 2005), and the protection of specific threatened species and communities (Embling et al. 2010). The most effective protection method involves establishment of networked reserves that can buffer disturbance and allow connectivity between habitat patches (Jones et al. 2007; Emslie et al. 2015).

Each CMR Network in Australian Waters has a series of unique and valuable features that are afforded different degrees of protection from human extraction under a Multiple Use Zoning Plan, with each zone assigned an IUCN category that ranges from allowing exploitation of resources to strict protection. Some important features are listed as Key Ecological Features (KEFs), and are considered of regional importance due to their contribution to either a region's biodiversity or its ecosystem function and integrity. KEFs tend to be geological features such as seamounts or reefs, hydrodynamic features such as currents, or elements of a region’s flora or fauna. Due to the offshore nature of marine habitats within the CMR Networks, reefs and other geological structures occur isolated within otherwise relatively featureless areas, creating islands of life that attract aggregations of diverse flora and fauna. Therefore, numerous KEFs are reefs, either coral reefs in lower latitudes or rocky or limestone reefs in subtropical and temperate regions.

Reefs occur in all the CMR Networks; their underlying structure ranges from calcium carbonate produced by living corals, usually at the top of raised features of the seabed such as pinnacles or seamounts, to raised rock pinnacles, to limestone reefs. The North, North-west and Coral Sea Networks tend to have coral reefs; the Temperate East Network has a combination of coral (e.g. Elizabeth and Middleton Reefs) and rocky reefs (e.g. the Cod Grounds CMR), and the South-west and South-east Networks have a combination of rocky and limestone reefs. They often occupy a very small percentage of the available substratum in any given Network; despite this, they tend to host the bulk of the known species richness in each region. This reflects the role of reefs everywhere in attracting a high abundance of marine life. Despite occupying less than 1% of the ocean's surface, reefs across the globe host approximately 25% of marine biodiversity (Plaisance et al. 2011).

Many reefs in the CMR Networks lie at shallow depths accessible on SCUBA; this makes the reefs the best-studied habitats within Commonwealth Waters around Australia. For example, in the Coral Sea CMR, coral reefs have attracted ~30% of all the research (Ceccarelli et al. 2013). Due to their recognised value as critical habitat for many species in these otherwise open-ocean regions, many of these reefs have a history of protection. Lihou Reef and the Coringa-Herald group of reefs, Ashmore Reef (WA), Mermaid Reef, Middleton Reef, the Cod Grounds, are a few of the reefs that have been under some form of protection in the past, either because of their near pristine state or to protect one or more species for which these areas provide key habitat (Commonwealth of Australia 2001; Gilmour et al. 2007). Surveys of all these areas have been sporadic, conducted by different groups of scientists with different methods, making comparisons difficult (Ceccarelli 2010).

Reef Life Survey (RLS) involves recreational divers trained to a scientific level of data-gathering to make it possible to conduct ecological surveys across broad geographic areas in a cost-effective manner. RLS divers partner with management agencies and university researchers to undertake detailed assessment of biodiversity on coral and rocky reefs, but all divers and boat crew do so in a voluntary capacity. Over the last decade, this has allowed coverage of a large geographic area, including reefs worldwide, and enabled, for the first time, comparisons of reefs across all Commonwealth Waters. Comparisons can also be made with relevant EEZs outside Australia.

The goal of this report is to compare ecological reef metrics from five CMR Networks, and to relate these metrics to those of reefs further afield. RLS data are used to evaluate characteristics that distinguish different locations from each other, as well as commonalities between locations. Data analysed and presented include the major macroscopic groups of species – fishes, mobile macroinvertebrates, and sessile benthic organisms.

2 Methods

Field surveys were conducted from 2008 to 2016 by a team of skilled divers from the Reef Life Survey program (www.reeflifesurvey.com) and the University of Tasmania. Geographical coordinates of sites (in WGS84) were recorded using handheld Garmin GPS units. Ecological surveys were undertaken at varying depths along 6304 transect blocks at 1666 sites in total. Data collected from each site consisted of abundance and size of fishes, abundance of mobile macroinvertebrates and cryptic fishes, and percentage cover of corals and other sessile biota. These are described separately below. Sites were selected to encompass the range of reef types and depth both inside and outside the CMRs in each Network, but with the depth range limited by dive safety considerations and bottom time restrictions. Within multi-zoned CMRs, sites in different zones of protection were analysed separately. IUCN categories have been assigned to different CMR zones, but these are currently under transitional arrangements and may change when Management Plans for the expanded CMR Network are finalised. Comparisons were made between the CMR network (both proposed and actively managed), existing State marine protected areas (MPAs) and areas outside the CMR network (referred to here as "Open"); comparisons were also made between areas assigned to different IUCN categories (APPENDIX 1).

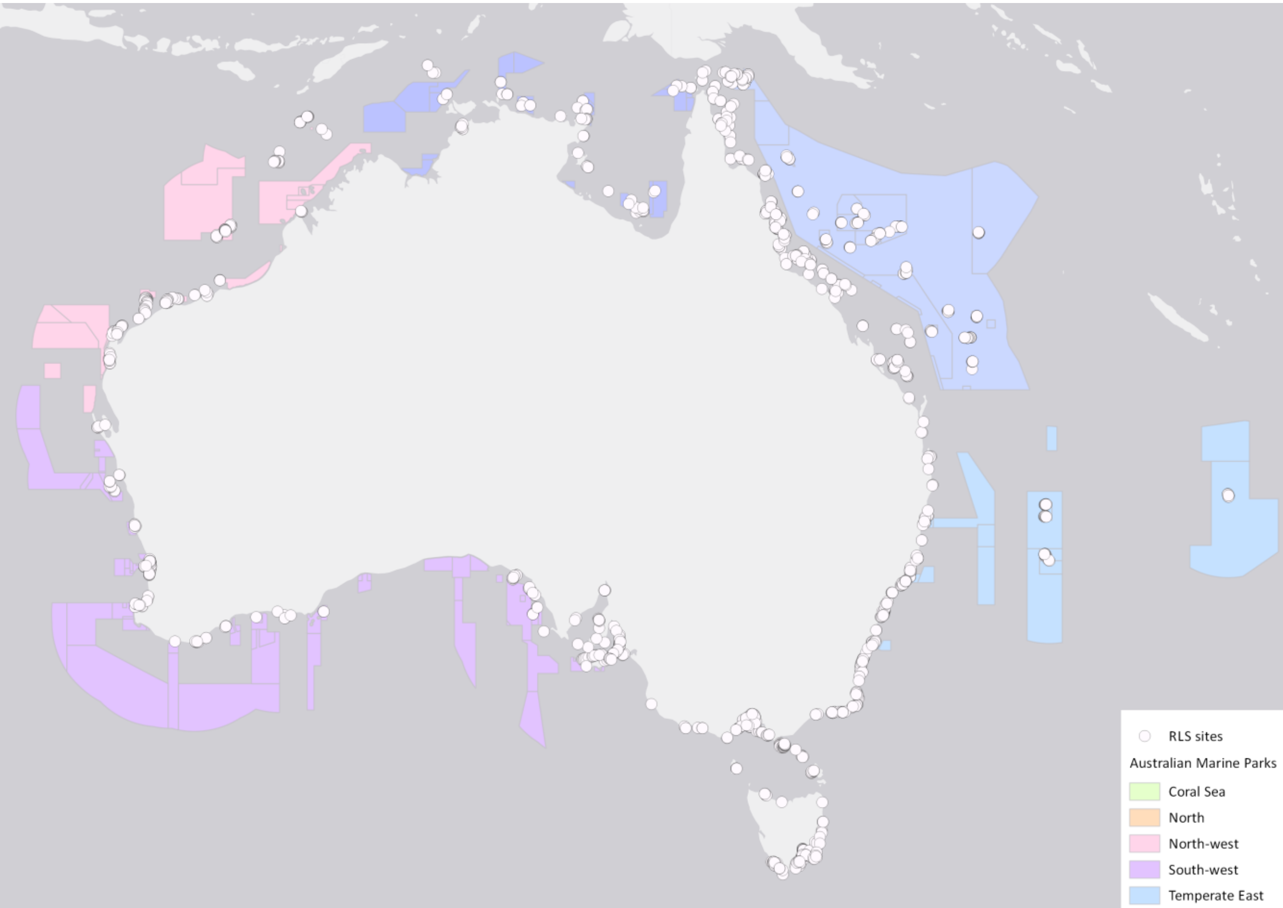

Figure 1. Map of National Reserve sites surveyed between 2009 - 2016.

FISH SURVEYS (METHOD 1)

Fish census protocols involved a diver laying out a 50 m transect line along a depth contour on reef. The number and estimated size-category of all fishes sighted within 5 m blocks either side of the transect line were recorded on waterproof paper as the diver swam slowly up and down each side. Size-classes of total fish length (from snout to tip of tail) used were 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 400, 500, 625 mm, and above. Lengths of fish larger than 500 mm were estimated to the nearest 12.5 cm and individually recorded.

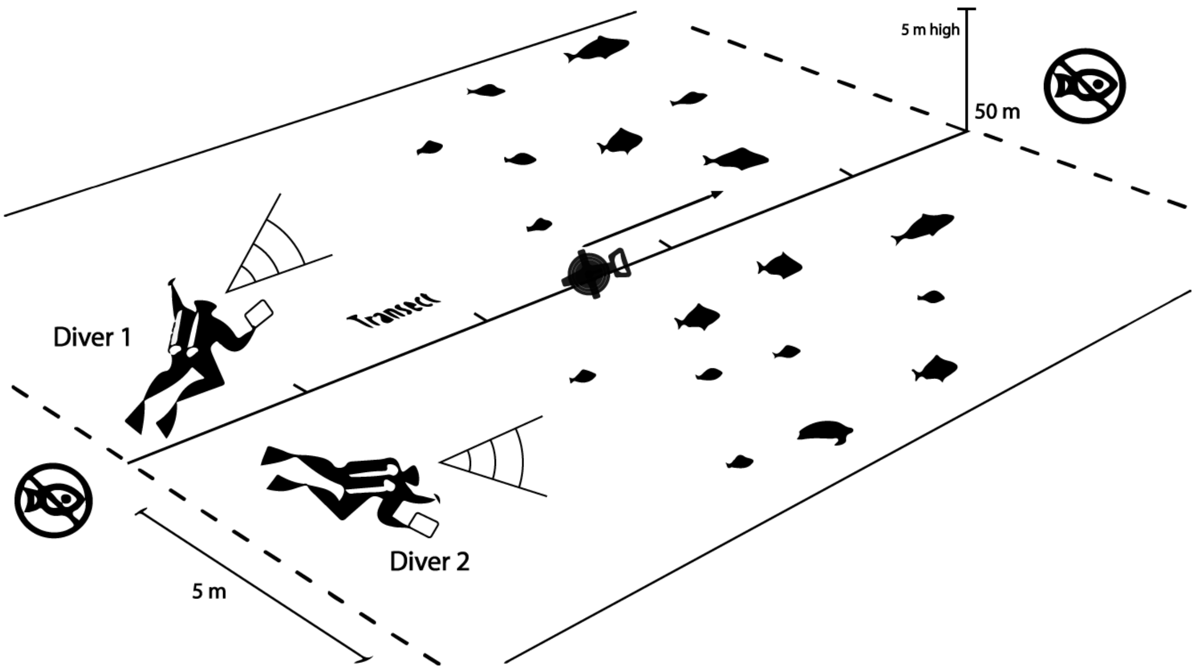

Figure 2. Stylised representation of method 1 survey technique

MACROINVERTEBRATE AND CRYPTIC FISH SURVEYS (METHOD 2)

Large macro-invertebrates (molluscs, echinoderms and crustaceans > 2.5 cm) and cryptic fishes (i.e. inconspicuous fish species closely associated with the seabed that were likely to be overlooked during general fish surveys) were censused along the same transect lines set for fish surveys. Divers swam along the bottom, up then down each side of the transect line, recording all mobile macroinvertebrates and cryptic fishes on exposed surfaces of the reef within 1 m of the line.

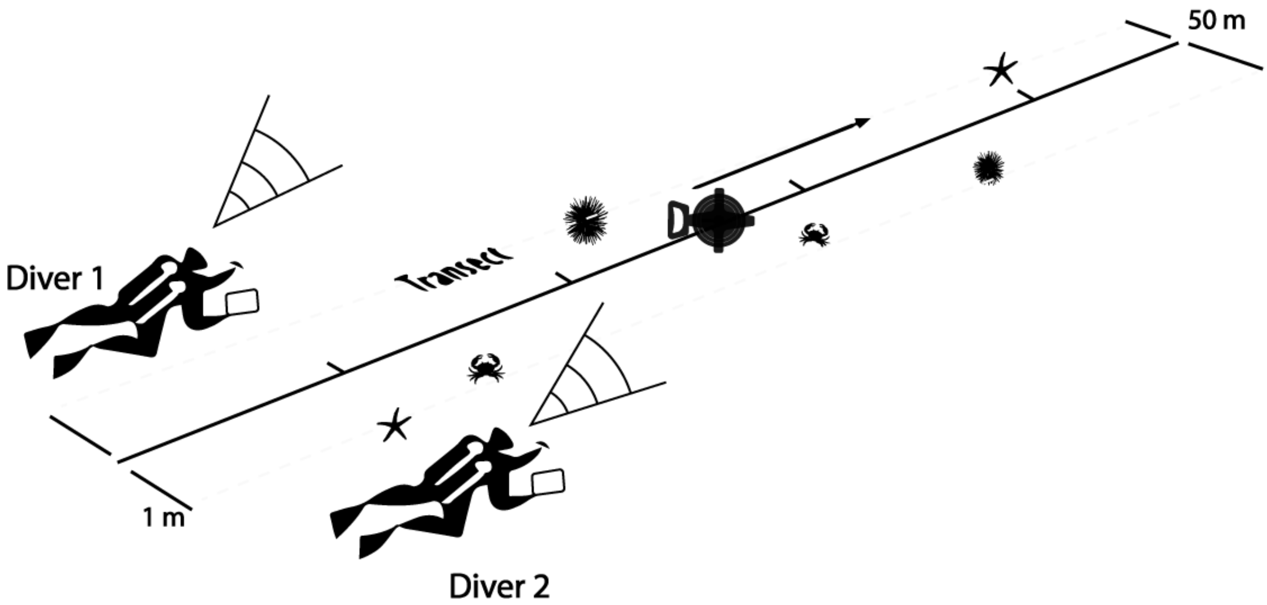

Figure 3. Stylised representation of method 2 survey technique

MACROALGAL AND SESSILE INVERTEBRATE SURVEYS

Information on the cover of coral and other sessile animals and seaweeds along the transect lines set for fish and invertebrate censuses were recorded using photo-quadrats taken sequentially each 2.5 m (or 5 m, see below) along the 50 m transect. Digital photo-quadrats were taken vertically-downward from a height sufficient to encompass an area of at least 0.3 m x 0.3 m. When a wide-angle lens was used during early surveys, and the photo-quadrats encompassed at least 0.5 m x 0.5 m, only 10 images were taken (one every 5 m).

The percentage cover of different macroalgal, coral, sponge and other attached invertebrate species in photo-quadrats was digitally quantified in the laboratory by scoring the substratum category under each of 100 points in total on images taken along the transect line (usually 5 points per image). Substratum categories were those used for previous RLS reports, which can be mapped directly to the CATAMI system (Althaus et al. 2015).

STATISTICAL ANALYSES

At most sites, multiple transects were surveyed at different depths. Each transect was regarded as an independent sample in analyses, and the unit of replication was the summed value for the two blocks in each transect (i.e. per 500 m^2 for fishes and per 100 m^2 for mobile macroinvertebrates). Exceptions to this rule were sessile biota percent cover data, which were expressed as % per transect.

Separate univariate analyses and data exploration techniques were used for fish, mobile macroinvertebrate communities, and sessile communities, and then these major taxonomic groups were combined to examine multivariate patterns in overall community structure in the reef communities surveyed. Univariate metrics that described important community characteristics were calculated for each transect and compared between transects surveyed at different locations, CMR Networks, CMRs and reference (or Open) sites, or ecoregions. Metrics examined for fishes were: relative abundance, estimated total biomass (see below for biomass estimation), biomass of fishes > 20 cm TL, biomass of different functional groups, and number of species. Mobile invertebrate metrics were: total relative abundance of mobile invertebrates, abundance of major taxonomic groups, and number of species. Sessile community/benthic cover metrics were: total live cover, number of benthic categories, and % cover of various key benthic organisms (e.g. live hard corals, turf, abiotic substrata, macroalgae, crustose coralline algae). All dependent variables were log(x+1) transformed, to comply with the assumptions of statistical tests.

Biomass estimates were made for each species on each transect using fish abundance counts, size estimates, and the length-weight relationships presented for each species (in some cases genus and family) in Fishbase (Froese and Pauly 2016). In cases where length-weight relationships were described in Fishbase in terms of standard length or fork length rather than total length (TL), length-length relationships provided in Fishbase allowed conversion to total length, as estimated by divers. For improved accuracy in biomass assessments, the bias in divers' perception of fish size underwater was additionally corrected using relationships presented in Edgar et al. (2004). Note that estimates of fish abundance and size made by divers can be greatly affected by fish behaviour for many species (Edgar et al. 2004); consequently biomass determinations, like abundance estimates, can reliably be compared only in a relative sense (i.e. for comparisons with data collected using the same methods) rather than providing an accurate absolute estimate of fish biomass for a patch of reef.

Community characteristics and relationships between transects were explored using Multidimensional Scaling (MDS) and associated plots of principal axes based on Bray-Curtis similarity matrices. Firstly, data for fish, mobile macroinvertebrate and sessile communities were considered separately, with a log(x+1) transformation applied to all data. Vector diagrams were added to all MDS plots to show the most important species/taxa in driving overall differences in the community type present.

3 Results

FISH SURVEYS

Fish communities across Australian reefs were more variable between temperate reefs than tropical coral reefs (Figure 4). Some CMRs appeared different from the Open sites within the same ecoregion (e.g. Geographe CMR, Cod Grounds CMR and Solitary Islands CMR), whilst others had fish communities similar to Open sites (Lord Howe CMR, CMRs of the North CMR Network). Fish species subdivided into three distinct groups: temperate fish species, fishes of the northern coast, and tropical eastern and western offshore species. The northern CMRs form a highly distinct group, but all the reefs represented by this major biogeographic grouping of fishes are recommended as IUCN IV and VI; there is no reef with full protection proposed for this group.

Fish abundance, biomass and species richness were higher in CMRs across all ecoregions than either State MPAs or Open areas (Figure 5). Biomass and species richness were also higher in State MPAs than in Open areas. The biomass of large fishes and sharks showed this pattern most clearly. CMRs had almost double the biomass of large fishes than State MPAs and Open areas, and shark biomass was between four and five times higher (Figure 6, Table 1). Generally, CMR locations appear to have naturally higher fish abundance, biomass and species richness than Open sites.

Fish metrics across different CMR zones, State MPAs and Open areas showed high variability (Figure 7, Table 1). Abundance was highest in Zone VI, but was only significantly higher than in State MPAs and Open areas. Biomass was significantly higher in Zone II than in State MPAs or Open areas. Species richness was significantly higher in the zones of highest protection than in Multiple Use (VI) Zones, State MPAs or Open areas. The biomass of large fishes and sharks were also significantly higher in CMRs than in State MPAs and Open areas. This was especially evident for sharks, which had their highest biomass in Zone II (Figure 8).

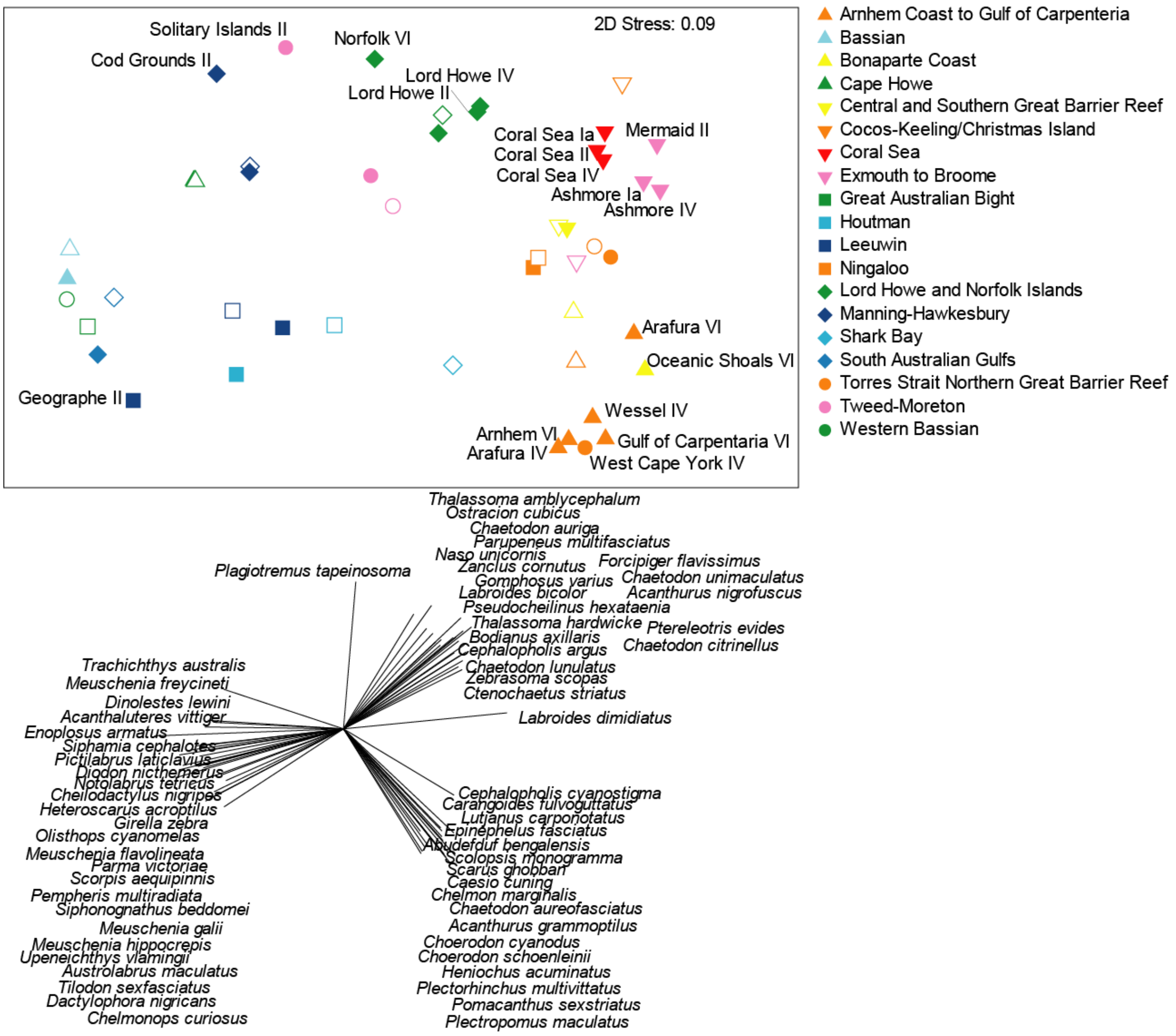

Figure 4. Multidimensional Scaling (MDS) plot of reef fish communities throughout Australian ecoregions, using Bray-Curtis similarity matrix of square-root-transformed average biomass data for each Commonwealth Marine Reserve (CMR), State MPA and Open area for each ecoregion. Vectors are shown if they have correlation values of at least 0.5. Tropical ecoregions are shown with "warm" colours, temperate ecoregions are shown with "cool" colours. Closed symbols are CMRs/State MPAs, open symbols are Open sites. Individual CMRs are labelled in the plot. IUCN categories associated with each CMR are as recommended by Buxton and Cochrane (2015).

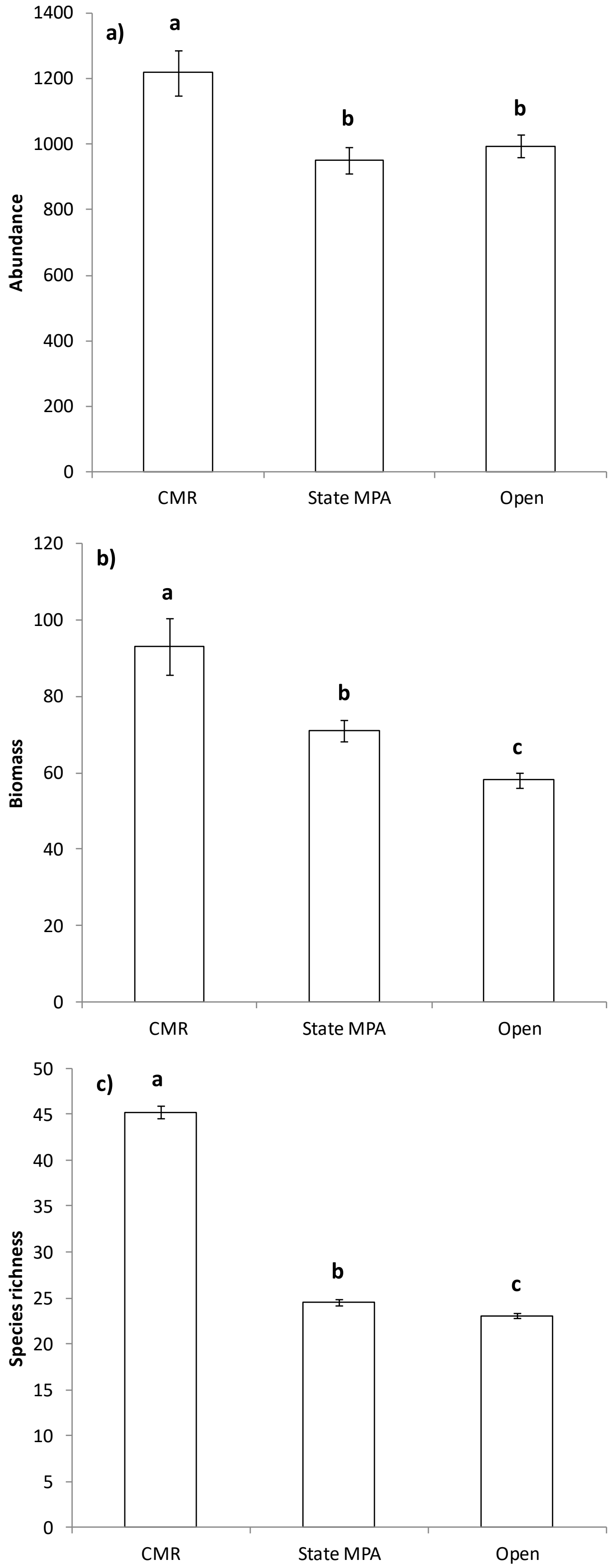

Figure 5. Fish metrics across combined CMRs, State MPAs and Open areas of Australian reefs. a) Abundance per 500m^2, b) Biomass in kg per 500 m^2, c) Number of species. Letters show which areas are significantly different. Error Bars = 1SE.

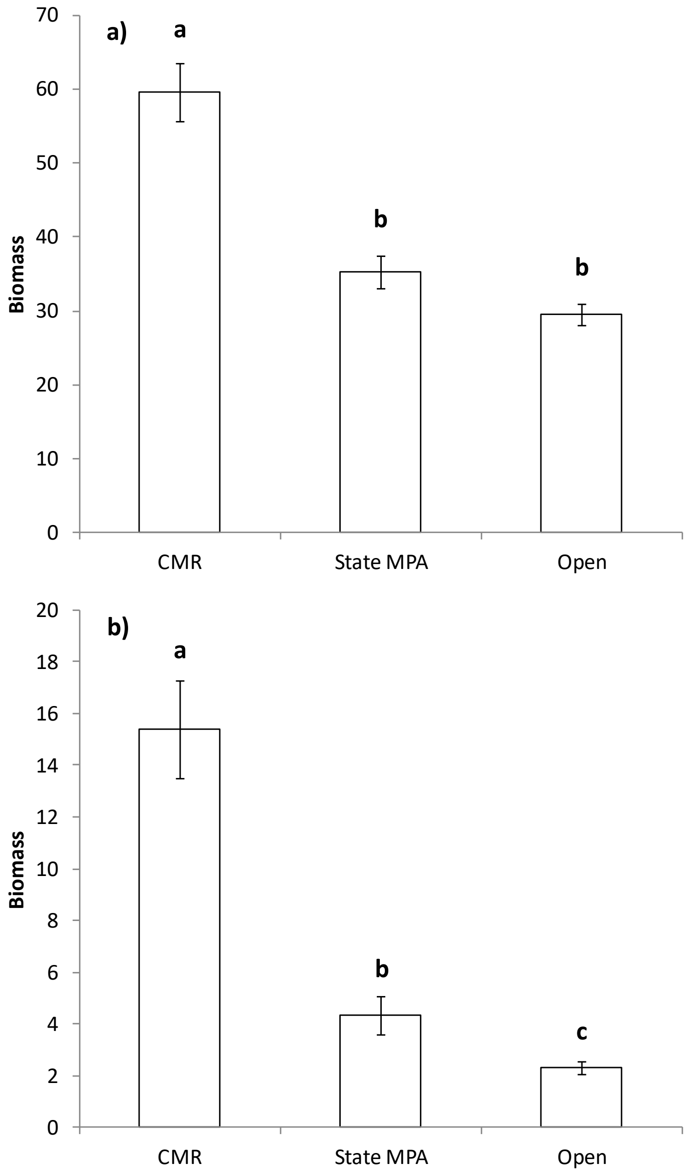

Figure 6. Biomass (kg) of a) large fishes (>20cm TL) and b) all sharks combined across all CMRs, State MPAs and Open areas of Australian reefs. Letters show which areas are significantly different. Error Bars = 1SE.

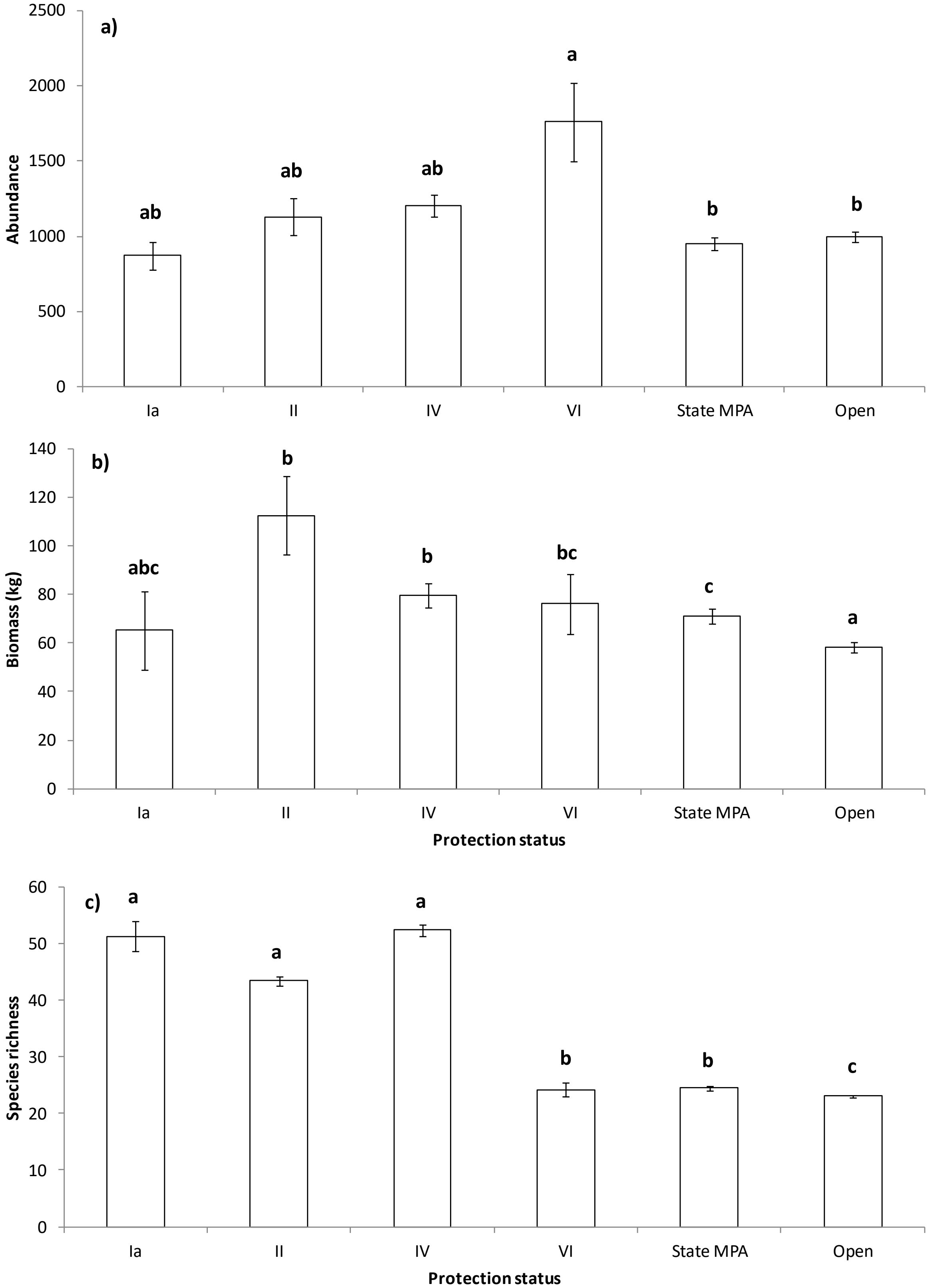

Figure 7. Reef fish metrics across CMR IUCN Zones (as recommended by Buxton and Cochrane, 2015), State MPAs and Open areas of Australian reefs. a) Abundance per 500 m^2, b) Biomass (kg per 500m^2), c) Species richness per 500 m^2. Letters group statistically similar areas. Error Bars = 1SE.

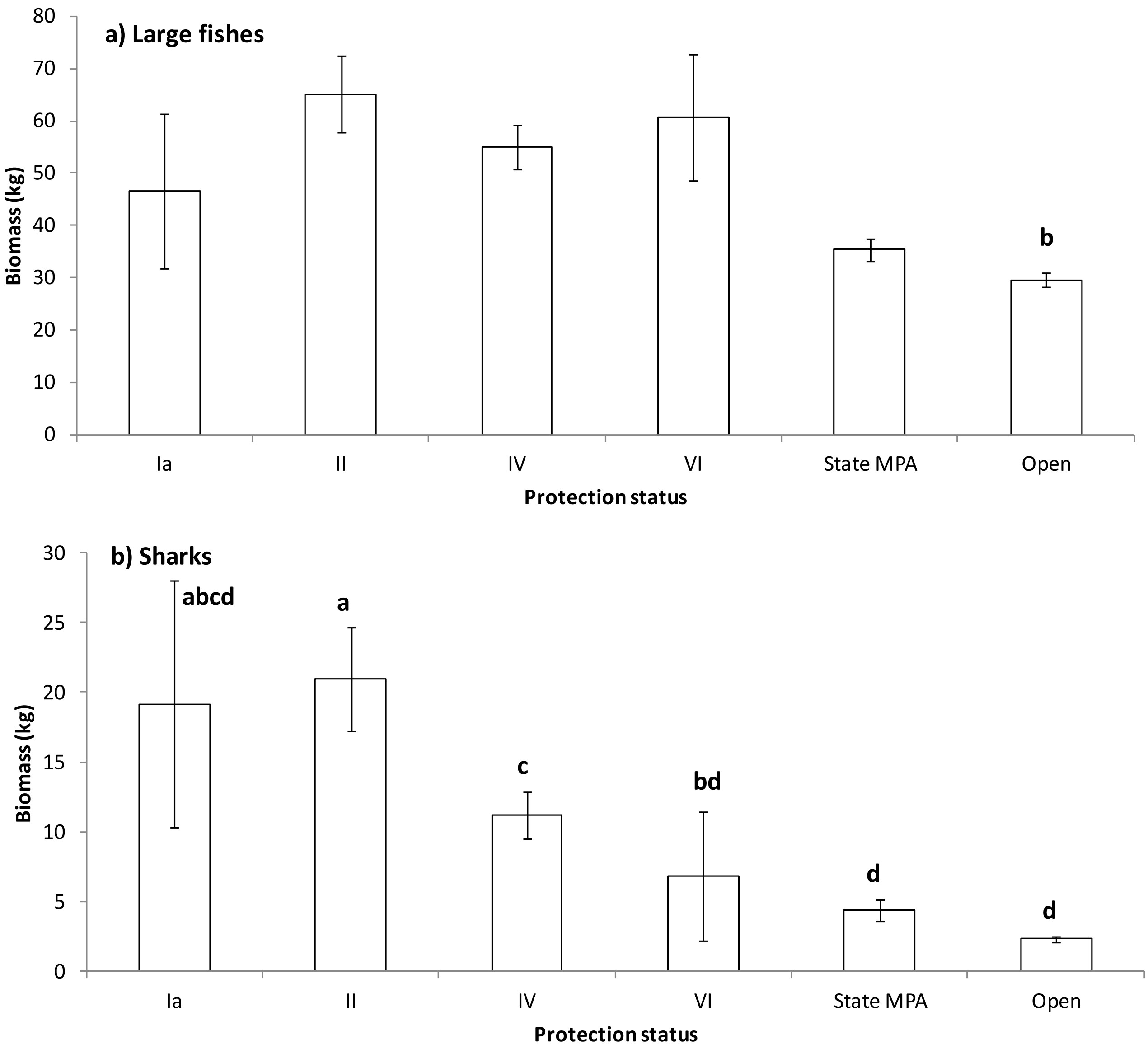

Figure 8. Biomass of large fishes (>20cm TL) and sharks per 500m^2 across CMR IUCN Zones (as recommended by Buxton and Cochrane, 2015), State MPAs and Open areas of Australian reefs. Letters group statistically similar areas. Error Bars = 1SE.

Table 1. Results of ANOVA on primary fish metrics by area (including CMRs, State MPAs and Open). Data were square root transformed.

Factor	Metric	MS	$F_{2,6301}$	p
CMR-State-Open	**Abundance**	17978439	4.7	0.009
	Biomass	386442	21.8	<0.001
	Species richness	144042	564.4	<0.001
	Large fish biomass (>20cm)	262047	32.8	<0.001
	Sharks	49288	74.0	<0.001
IUCN Zones	**Abundance**	16633173	4.6	<0.001
	Biomass	856	37.3	<0.001
	Species richness	627	331.6	<0.001
	Large fish biomass (>20cm)	804	54.7	<0.001
	Sharks	221	49.8	<0.001

MOBILE MACROINVERTEBRATE SURVEYS

Macroinvertebrate communities were more similar to each other across offshore coral reefs than across northern Australian or temperate ecoregions (Figure 9). In many cases, CMRs appeared more unique than Open areas or State MPAs, especially in the coral reef provinces. Corals reefs were distinguished by a much smaller group of species than temperate sites, which appeared to have much richer invertebrate assemblages. The blue sea star, *Linckia laevigata*, was characteristic of offshore reefs, whilst the lobster *Panulirus versicolor* and urchin *Diadema setosum* were more typical of northern Australian reefs. The barrens-forming grazing urchin, *Centrostephanus rodgersii*, was typical of the Solitary Islands, Cod Grounds and nearby coastal sites.

Across levels of protection, macroinvertebrates were most abundant and diverse in State MPAs and Open areas, as well as Multiple Use Zones (VI) (Figure 10, Table 2). Among the higher levels of active or proposed CMR protection, Marine National Parks (II) had the highest abundance. Holothurians were highly abundant in the Multiple Use zone, with the second highest numbers in the Marine National Park (II) zone (Figure 11).

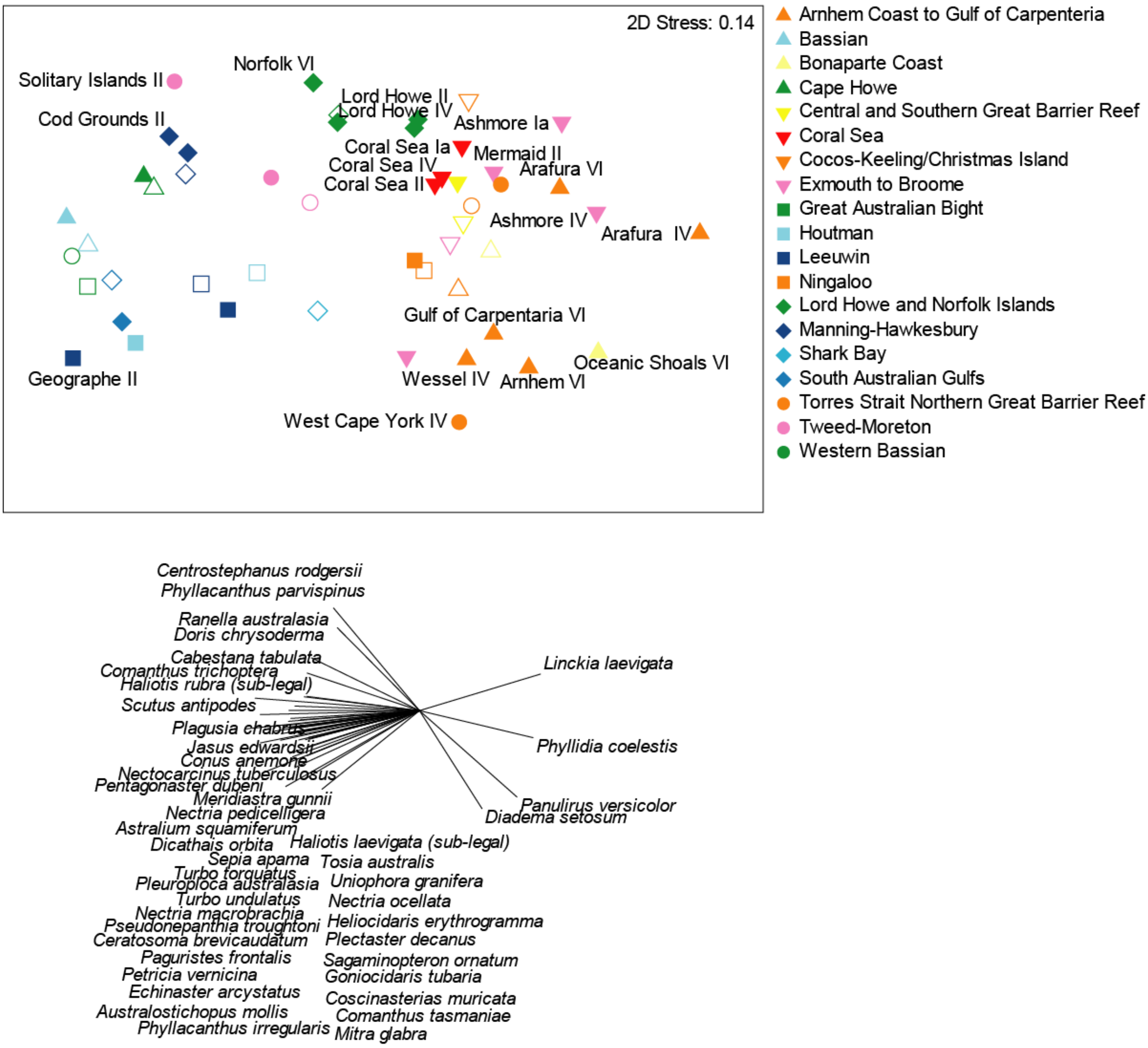

Figure 9. Multidimensional Scaling (MDS) plot of invertebrate communities throughout Australian ecoregions, using Bray-Curtis similarity matrix of square-root-transformed average abundance data for each Commonwealth Marine Reserve (CMR), State MPA and Open area for each ecoregion. Species were selected if there was a positive identification, and if they occurred with a frequency of at least 10 within the dataset. Vectors are shown if they have correlation values of at least 0.5. Tropical ecoregions are shown with “warm” colours, temperate ecoregions are shown with “cool” colours. Closed symbols are CMRs/State MPAs, open symbols are Open areas. Individual CMRs are labelled in the plot.

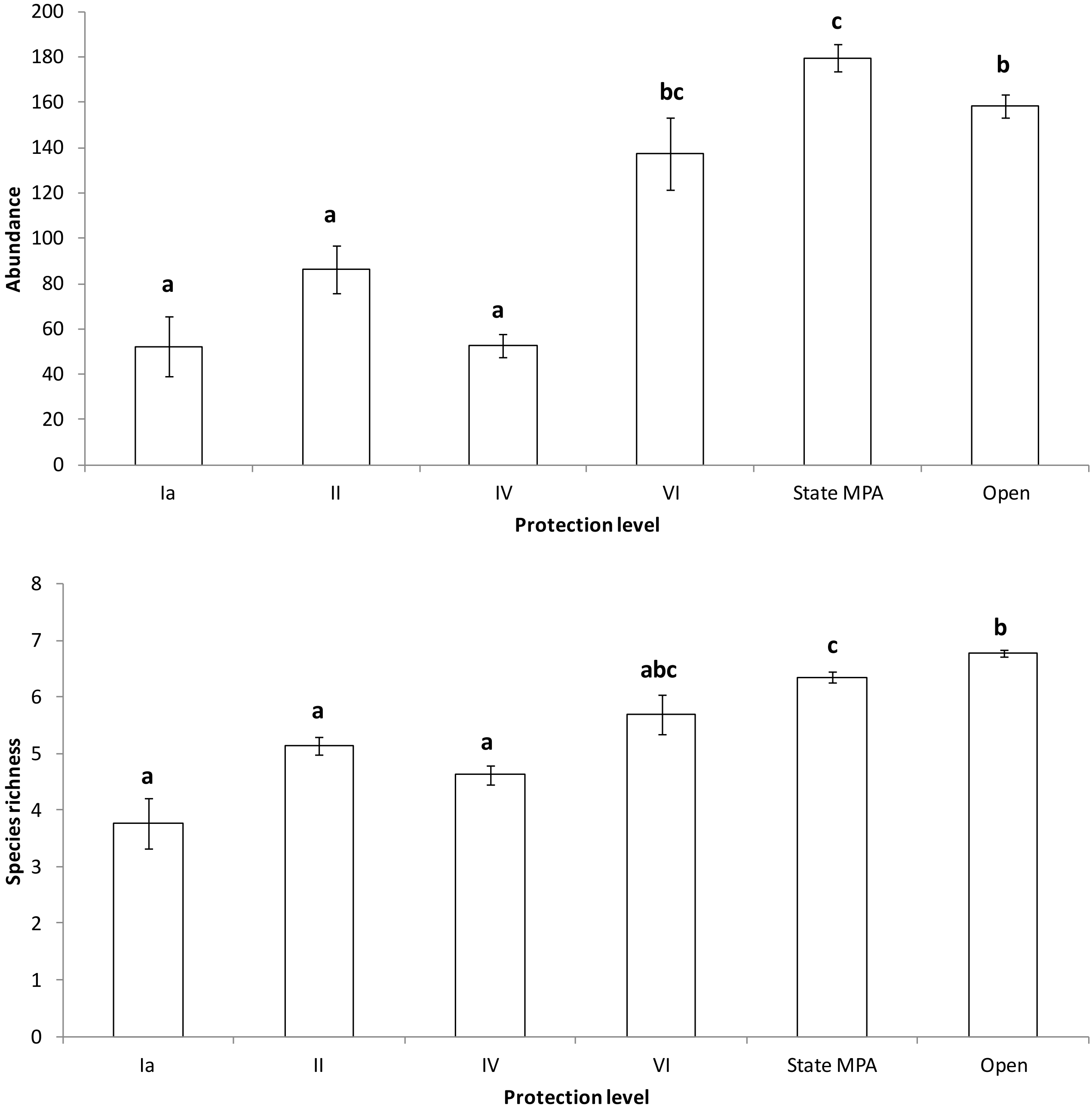

Figure 10. Macroinvertebrate metrics across IUCN Zones, State MPAs and Open areas of Australian reefs. a) Abundance per 100 m^2, b) Species richness per 100 m^2. Letters group statistically similar areas. Error Bars = 1SE.

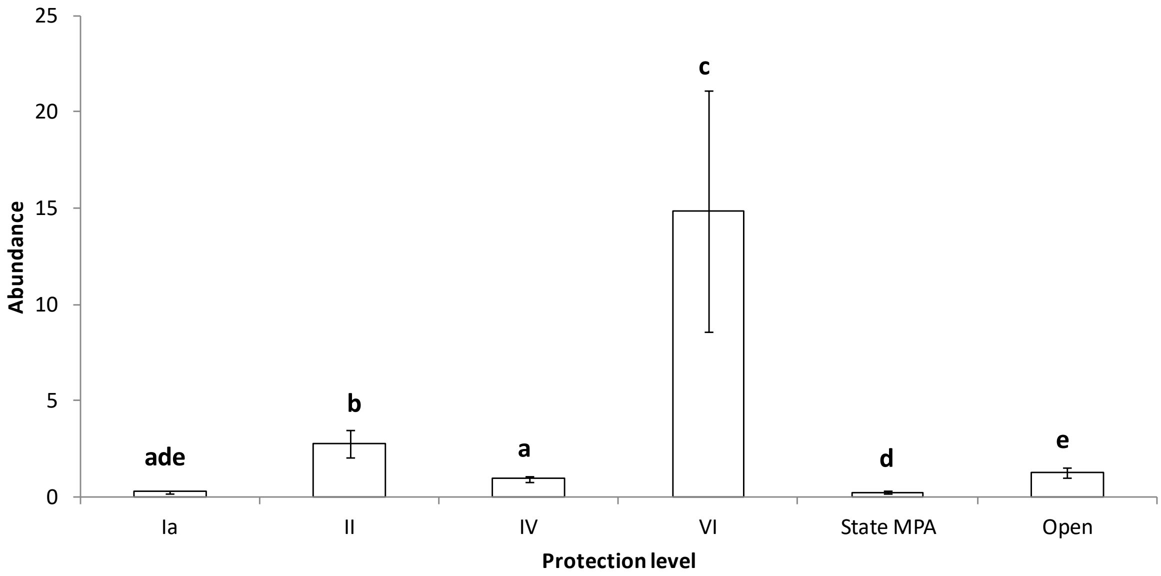

Figure 11. Abundance of holothurians across IUCN Zones, State MPAs and Open areas of Australian reefs. Letters group statistically similar areas. Error Bars = 1SE.

Table 2. Results of ANOVA on macroinvertebrate abundance, species richness and holothurians abundance by area (including CMRs, State MPAs and Open). Data were square root transformed.

Metric	MS	$F_{5,6267}$	p
Abundance	1892	34.4	<0.001
Species richness	16.9	30.7	<0.001
Holothurian abundance	58.0	54.3	<0.001

SESSILE BIOTA

The cover of different functional groups varied greatly between temperate sites, with less dissimilarity between tropical areas (Figure 12). Geographe CMR, Cod Grounds CMR, Solitary Islands CMR, Lord Howe CMR and Arafura CMR differed in benthic composition from the Open areas and State MPAs within the same ecoregion; the other Northern CMRs, Ashmore Reef CMR and Mermaid Reef CMR were similar to Open areas. The different categories of the Coral Sea CMR were similar to one another. Southern and southwestern ecoregions were distinguished by a higher cover of macroalgae, and temperate eastern ecoregions had a greater diversity of sessile biota. Tropical regions were distinguished by either a high cover of soft corals and turf, or hard corals and abiotic substrata.

Total live cover of sessile biota was slightly higher in CMRs than in State MPAs or Open areas, and abiotic cover was relatively even across categories, while individual benthic categories were variable (Figure 13, Table 3). Live hard coral cover was higher in CMRs with lower protection levels (IV and VI) than in highly protected zones, State MPAs or Open areas. CCA and soft coral were highest in highly protected CMRs, and Zone IV. Macroalgae, on the other hand, was most abundant in Open areas and State MPAs, and in CMR VI zones.

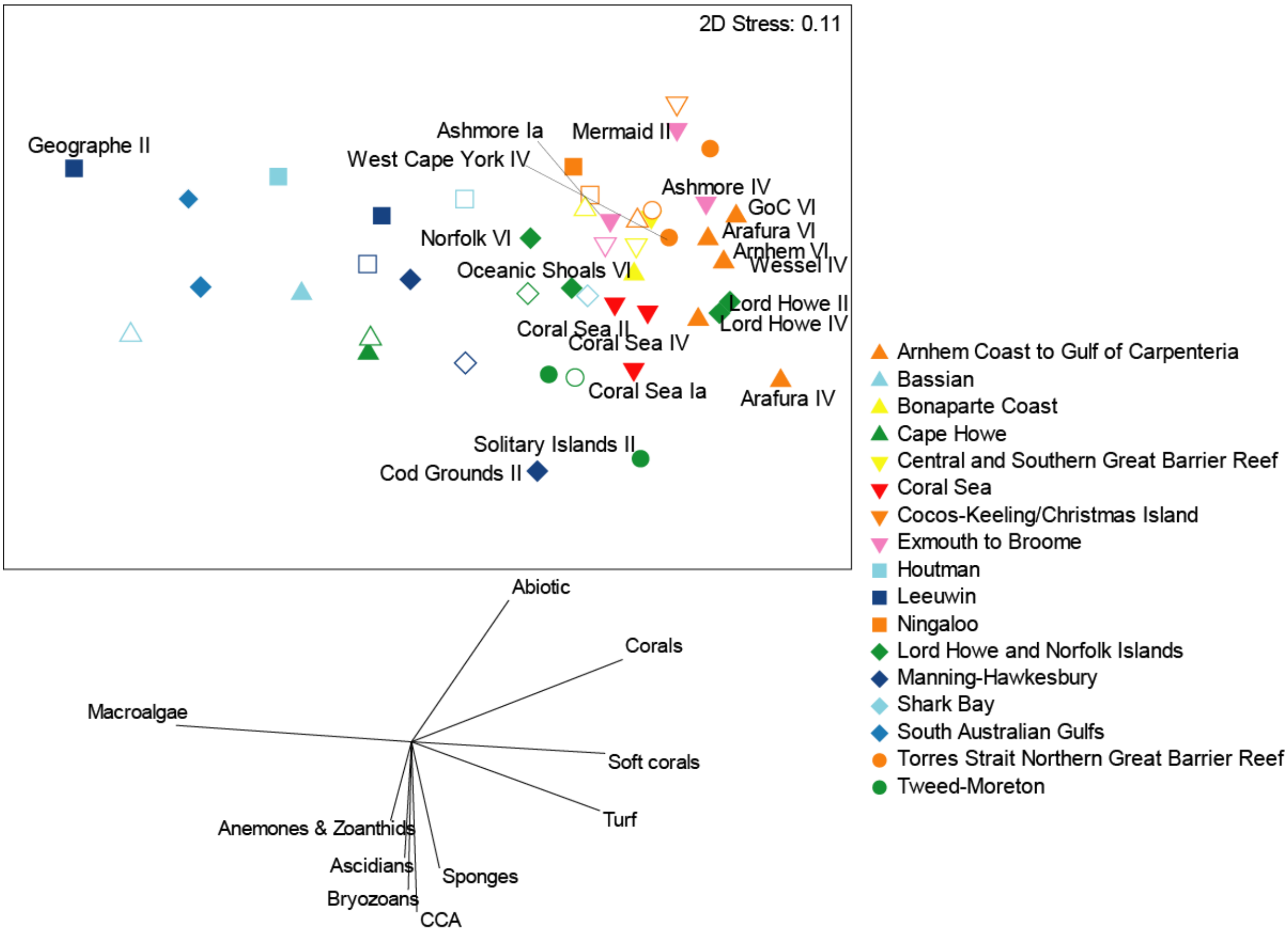

Figure 12. Multidimensional Scaling (MDS) plot of major benthic categories throughout Australian ecoregions, using Bray-Curtis similarity matrix of square-root-transformed average percentage cover data for each Commonwealth Marine Reserve (CMR), State MPA and Open area for each ecoregion. Vectors are shown if they have correlation values of at least 0.3. Tropical ecoregions are shown with “warm” colours, temperate ecoregions are shown with “cool” colours. Closed symbols are CMRs/State MPAs, open symbols are Open areas. Individual CMRs are labelled in the plot.

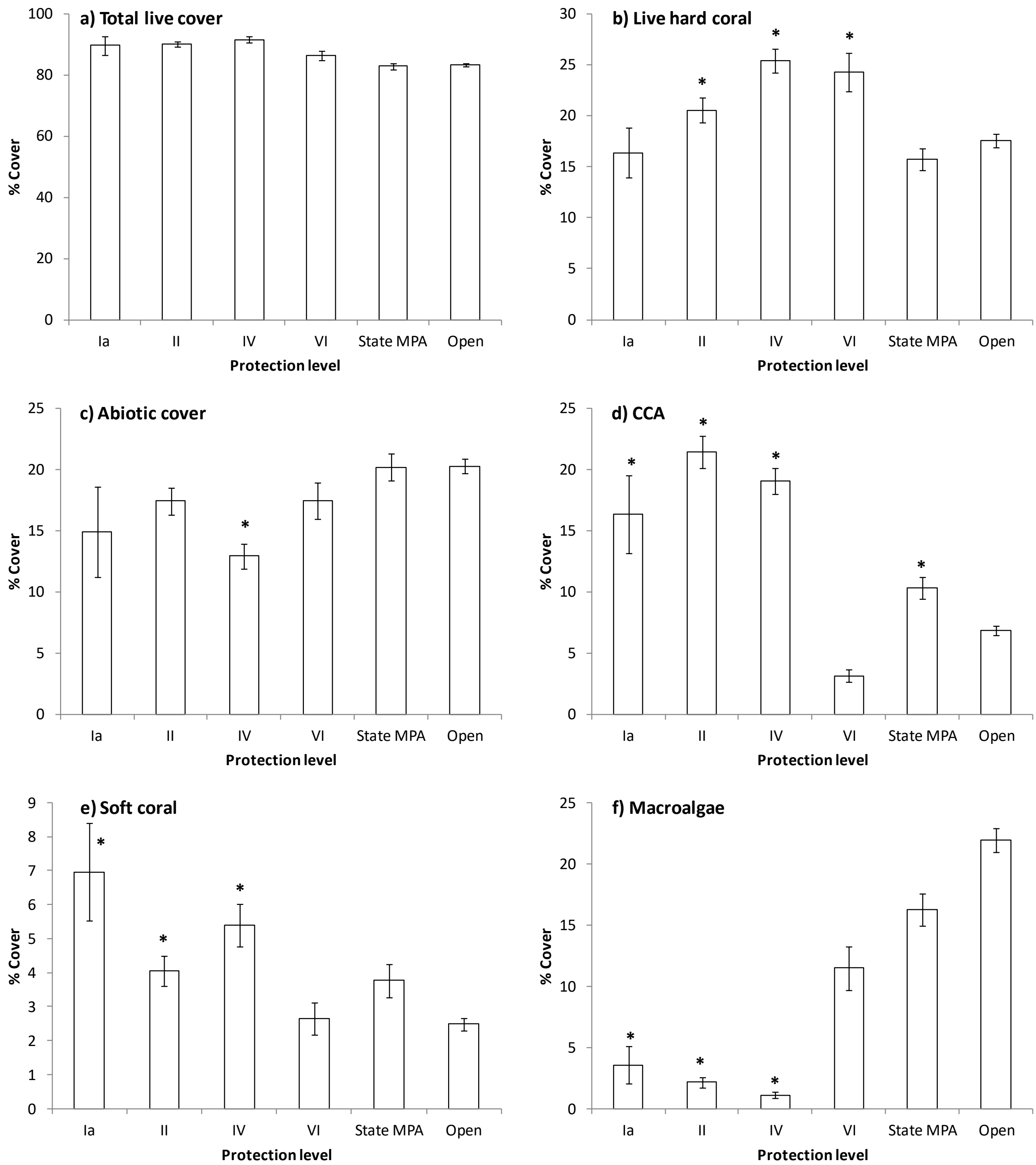

Figure 13. Percentage cover of major benthic categories across IUCN Zones, State MPAs and Open areas of Australian reefs. Asterisks mark zones that are significantly different from Open areas. Error Bars = 1SE.

Table 3. Results of ANOVA on key benthic categories by area (including CMRs, State MPAs and Open). Data were square root transformed.

Benthic category	MS	$F_{5,1800}$	p
Total live cover	13.9	12.5	<0.001
Live hard coral	132.7	20.5	<0.001
Abiotic cover	38. 8	7.7	<0.001
Crustose coralline algae	302.4	73.6	<0.001
Soft coral	37.8	17.5	<0.001
Macroalgae	460.5	57.3	<0.001

4 Discussion

Reef communities across Australian waters showed clear groupings that distinguished tropical and temperate reefs, and tropical reefs were split between offshore and coastal / continental shelf reefs. These patterns were evident for all surveyed reef organisms, but were especially pronounced in the fish community. Temperate reefs were very different from each other, much more so than tropical reefs. In terms of representing a wide range of reef types and communities, a broader coverage may be desirable for temperate reefs.

Latitudinal gradients, usually strong drivers of changes in reef community structure throughout Australian waters, reflect the distance from the centre of diversity near the equator in the Coral Triangle and gradients in sea surface temperature (Briggs 1999; Bellwood and Hughes 2001). Marine habitats close to the equator tend to have more stable environmental conditions than those at higher latitude, promoting a higher degree of specialisation and narrower tolerance to changing environmental factors different from those found at higher latitudes (Hughes et al. 2002). These patterns may be even stronger if measured at the species level; at higher taxonomic resolution other drivers, such as longitude, distance offshore and the type of substratum cover, may also become more important. Many fish and invertebrate species have depth preferences, but this is complicated by the structure and profile of the underlying habitat (Jankowski et al. 2015a). Depth is an important driver of fish community structure because of its effect on primary production, light and wave energy attenuation (Jankowski et al. 2015b).

Some of the separation between temperate sites could clearly be attributed to the major water masses influencing broad marine areas. South-western sites, influenced by the Leeuwin Current, had different assemblages from Bassian, South Australian Gulfs, Western Bassian reefs and Great Australian Bight sites, and different again from coastal sites of the Temperate East. The Leeuwin Current transports warmer water and tropical larvae into southwestern habitats (Commonwealth of Australia 2007), whilst the East Australian Current (EAC) plays the same role along the east coast. The EAC is the southern arm of the bifurcation of the westward-flowing Southern Equatorial Current, which enters the Coral Sea region from the Pacific Ocean. The EAC flows southwards in a series of eddies and areas of upwelling, drawing nutrient rich water from a depth of at least 200 m. The EAC, its upwellings, interactions with the structurally complex seabed, and transport of warmer waters and tropical larvae, promote a rich flora and fauna on both inshore and offshore reefs of the temperate east and southeast regions (Oke and Middleton 2001; Brewer et al. 2007). Species moving southwards along the west coast are more likely to have a tropical Indian Ocean influence, while those along the east coast have a more tropical Pacific character. These tropical and subtropical influences do not reach the Bassian, South Australian Gulfs, Western Bassian and Great Australian Bight sites, where a more distinctive temperate assemblage is evident.

Western reefs showed large differences between northern and southern ecoregions, and Shark Bay especially appeared to host different assemblages from the other WA reefs. In contrast, in the east there was a gradual change (especially in the fish community) from tropical to subtropical to temperate fish assemblages. It may be that reefs along the eastern coastline provide a more contiguous stretch of appropriate shallow habitats, or that the hydrodynamics provide greater connectivity. The larger extent of shallow inter-reef areas are likely to have influenced the general similarities between tropical northern and eastern coastal reefs. GBR sites grouped more closely with sites of the North CMR Network than with Coral Sea sites that were geographically closer. This further reflects the inshore-offshore gradient. Similarly, the Coral Sea reefs were more similar to the North-western offshore reefs such as Ashmore and Mermaid than to the nearby reefs of the GBR.

Reasons for the greater differences between temperate reefs may relate to the extent and position of available habitats and the strength and direction of connectivity patterns, both of which may be greater in the tropics. Geomorphologically, the south and southwest are less diverse than regions across the northern Australian margin (Heap and Harris 2008). Tropical reefs have connectivity to the vast and diverse Indo-Pacific network of reefs to the north, and many are situated on broad continental shelves where they are separated by relatively shallow waters (<200 m deep) (Heap and Harris 2008). Nevertheless, oceanic reefs in the tropics host different communities from those further inshore, likely driven by a combination of larval dispersal and biophysical variables; inshore-offshore gradients are common in marine assemblages that respond to coastal influences.

Inshore-offshore reef gradients have been widely studied in both tropical and temperate systems, and different patterns tend to characterise the different regions (Done 1982; Williams 1982; Malcolm et al. 2010). Inshore tropical reefs tend to have higher algal biomass and lower herbivore abundance than offshore reefs (Russ and McCook 1999; Cheal et al. 2012), with different reef fish functional groups dominating inshore and offshore (Hoey and Bellwood 2008). On temperate reefs, herbivory is more prevalent on inshore reefs (Harrison and Smith 2012). Previous studies linking biophysical habitat characteristics to fish assemblages have stressed the importance of substratum, cross-shelf position and depth (Malcolm et al. 2016), whilst others have found strong effects of turbidity (Fabricius and De'ath 2001; Johansen and Jones 2013).

The establishment of marine protected areas in Australian waters is guided by four main goals: 1) the representation of each provincial bioregion within reserves; 2) the representation of all depth ranges; 3) the inclusion of examples of benthic and demersal biota, including, for example, habitats, communities and important ecosystems; and 4) the inclusion of all 21 identified types of seafloor features. This report provides insights into the extent that adequate representation and inclusion of bioregional marine ecosystems and habitats has been achieved for tropical, subtropical and temperate reefs. The similarity between CMR and Open reefs varied between the different ecoregions.

In the Leeuwin ecoregion, the Geographe CMR had higher diversity of reef organisms than Open sites. The Coral Sea CMR had no Open sites, but the comparison between highly protected (I and II) and limited fishing (IV) zones showed that these all had similar community structure. The Bassian, Great Australian Bight, Houtman, Shark Bay, South Australian Gulfs, Ningaloo, Cape Howe and central / southern GBR ecoregions had no CMRs with shallow reefs surveyed; State MPA sites were similar to Open sites, but with lower macroalgal cover in the State MPAs of the Bassian ecoregion and more distinctive invertebrate and benthic assemblages in the State MPAs of the Houtman ecoregion.

Within the Exmouth to Broome ecoregion, the CMRs appear to capture the biodiversity and community structure present on Open reefs. Most of the North CMR Network's CMR reefs were also similar to the Open reefs; the largest difference was between Open reefs of the Torres Strait to northern GBR ecoregion and the West Cape York CMR. Together, however, the Northern CMR sites differed substantially from northwest and northeast tropical sites, with distinctive biota. However, no northern CMR with reef is recommended as IUCN I or II, hence none of these distinctive reef systems are expected to be fully protected from exploitation.

In the Manning-Hawkesbury ecoregion, the Cod Grounds CMR has a fish and benthic community different from State MPAs or Open sites, while the invertebrate assemblage is similar between the three types of areas. This is most probably due to the unique geomorphic structure of the Cod Grounds. Similarly, the Solitary Islands CMR (Pimpernel Rock) captures a unique pinnacle rising steeply from the seabed, making it different from the Open and State MPAs of the Tweed-Moreton ecoregion

Norfolk and Lord Howe CMRs were unique. These sites formed a distinct group, rather than overlapping with other temperate sites. The Lord Howe CMRs and State MPAs together capture the biodiversity present within this group of islands and reefs. Norfolk Island, though somewhat similar to Lord Howe, has a distinctive flora and fauna again; there is a need to represent this unique environment through stronger protection, as it is currently proposed as a Multiple Use zone.

CMRs overall had higher abundance, species richness, total biomass, large fish biomass and shark biomass than Open areas, and in most cases even State MPAs. To some extent these trends may be influenced by reserve management, for those sites in previously established no-take CMRs. However, given few CMRs are presently actively managed and/or include no-take protection, these trends suggest that the placement of CMRs covers reefs with higher predator and large fish abundance that reefs found closer to the coast, or offshore and outside CMR boundaries. Subdividing the CMRs by individual protection zones was, in most cases, less useful, due to particular idiosyncrasies of many of these zones (e.g. the Cod Grounds CMR), and the fact that active management is not yet in place. Furthermore, some highly protected reefs (Zones I and II) were depauperate, perhaps a consequence of a long history of heavy, and sometimes illegal, exploitation. Given these particularities, the overall results showing higher biodiversity values in CMRs indicates their substantial future value as a marine management tool, including conservation of some of the least impacted reefs around the continent.

Observed ecological differences between CMR and Open reefs corresponded with a key goal of marine protected areas—the representation of habitats and ecological communities. In other studies, well-enforced marine reserves have repeatedly been shown to greatly enhance total biomass and size of fished species within boundaries (Russ et al. 2008; Graham et al. 2011; Edgar et al. 2014). To be most effective in recovery of fish biomass, marine reserves need to possess large size, an extended period of protection, a no-take policy, good enforcement, and physical habitat barriers (Edgar et al. 2014). Given that Australian fisheries avoid destructive fishing practices that physically damage reefs, the effects of CMRs on benthic structure is expected to be variable (Emslie et al. 2015).

Marine reserves can promote recovery in benthic communities through “trophic cascades”, where the removal of top predators has flow-on effects through the food web to primary producers and habitat engineers (Mumby et al. 2006). Such effects are more easily detectable in temperate systems with lower species diversity than on tropical coral reefs, where each ecological function can be performed by a number of species and redundancy in function exists (Pinnegar et al. 2000). The 20-year period since fishing prohibitions were enacted in some of the CMRs studied was probably too short for trophic effects to clearly manifest through reef food webs. While recovery of top predators in reserves is likely to affect all levels of the food web through the long-term, such indirect effects typically require multi-decadal time periods to become apparent (Babcock et al. 2010; Selig and Bruno 2010). In the long-term, entire assemblages in protected zones that are well enforced are predicted to show signs of change, possibly including enhanced resilience to disturbance, through the recovery of higher tropic levels. Whether such changes lead to overall ecosystem stability depends in large part on tangible additional efforts to protect water quality and minimise climate change. For CMRs in areas where fishing has not substantially supressed target species biomass, no such trophic cascades should be expected, as protection should result in retention of existing values in the face of any degradation outside reserve boundaries, rather than a process of recovery.

5 Recommendations

We recommend that:

- ongoing ecological monitoring of Australian tropical, subtropical and temperate reefs is scheduled on a regular basis (3 years or less), using the methods and sites described here;
- data presented in recent RLS surveys be combined with previous surveys to guide efforts to select sites for long-term monitoring;
- additional sites are added to the monitoring design, including additional reference sites outside CMRs in comparable habitats and depths;
- research priorities include development of indicators that track changes in reef condition and biodiversity;
- data are collected on fishing effort on the different reefs to assess differences in extractive pressures;
- compliance metrics are developed;
- detailed habitat mapping and categorisation of reef types, exposure and aspect is undertaken for inclusion in analyses of ecological patterns;
- through the longer term, increased protection (through the allocation of more highly protected IUCN categories to proposed CMRs) for large predatory fishes and species vulnerable to being caught as bycatch from illegal, unreported, unregulated (IUU) and commercial fishing for North CMR Network reefs and Norfolk Island should be considered, to safeguard biodiversity values in these unique areas;
- detailed spatial and temporal mapping of distribution and impact of natural disturbances is carried out; and
- further collaboration between agencies collecting data on reefs in State and Commonwealth waters should be actively encouraged.

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8 Appendices

APPENDIX 1. REGIONS, ZONING, AND NUMBER OF SITES SURVEYED. CMR NETWORK NAMES ARE GIVEN FOR OFFSHORE WATERS; STATE WATERS ARE LABELLED "COASTAL". "OPEN" REFERS TO AREAS WHERE NO ZONING HAS BEEN IMPLEMENTED OR PROPOSED.

Ecoregion	CMR Network	Zoning	IUCN Zone	CMR Name	Number of sites
Arnhem Coast to Gulf of Carpenteria	North	CMR	Habitat Protection Zone (IUCN IV)	Arafura	1
				Wessel	3
			Multiple Use Zone (IUCN VI)	Arafura	4
			Special Purpose Zone (IUCN VI)	Arnhem	5
			Special Purpose Zone (B) (IUCN VI)	Gulf of Carpentaria	5
		Open	Open		40
Bassian	Coastal	Open	Open		210
		State MPA	State MPA		52
Bonaparte Coast	Coastal	Open	Open		5
	North	CMR	Multiple Use Zone (IUCN VI)	Oceanic Shoals	4
		Open	Open		15
Cape Howe	Coastal	Open	Open		132
		State MPA	State MPA		66

Ecoregion	CMR Network	Zoning	IUCN Zone	CMR Name	Number of sites
Central and Southern Great Barrier Reef	Coastal	Open	Open		79
		State MPA	State MPA		28
	Coral Sea	CMR	Habitat Protection Zone (Reefs) (IUCN IV)	Coral Sea	6
Cocos-Keeling/Christmas Island	Coastal	Open	Open		15
Coral Sea	Coral Sea	CMR	Sanctuary Zone (IUCN Ia)	Coral Sea	13
			Marine National Park Zone (IUCN II)	Coral Sea	87
			Habitat Protection Zone (IUCN IV)	Coral Sea	5
			Habitat Protection Zone (Reefs) (IUCN IV)	Coral Sea	66
Exmouth to Broome	Coastal	Open	Open		82
		State MPA	State MPA		3
	North-West	CMR	Sanctuary Zone (IUCN Ia)	Ashmore	6
			Marine National Park Zone (IUCN II)	Mermaid Reef	18
			Recreational Use Zone (IUCN IV)	Ashmore	6
		Open	Open		64
Great Australian Bight	Coastal	Open	Open		13
Gulf of Papua	Coral Sea	CMR	Habitat Protection Zone (IUCN IV)	Coral Sea	10
Houtman	Coastal	Open	Open		29
		State MPA	State MPA		3
Leeuwin	Coastal	Open	Open		64
		State MPA	State MPA		7
	South-West	CMR	Marine National Park Zone (IUCN II)	Geographe	1

Ecoregion	CMR Network	Zoning	IUCN Zone	CMR Name	Number of sites
		Open	Open		6
Lord Howe and Norfolk Islands	Coastal	Open	Open		24
		State MPA	State MPA		24
	Temperate East	CMR	Marine National Park Zone (IUCN II)	Lord Howe	17
			Recreational Use Zone (IUCN IV)	Lord Howe	16
			Multiple Use Zone (IUCN VI)	Norfolk	13
		Open	Open		3
		State MPA	State MPA	Lord Howe	1
Manning-Hawkesbury	Coastal	Open	Open		120
		State MPA	State MPA		13
	Temperate East	CMR	Marine National Park Zone (IUCN II)	Cod Grounds	7
		Open	Open		4
Ningaloo	Coastal	Open	Open		21
		State MPA	State MPA		14
Shark Bay	Coastal	Open	Open		6
South Australian Gulfs	Coastal	Open	Open		81
		State MPA	State MPA		3
Torres Strait Northern Great Barrier Reef	Coastal	Open	Open		52
		State MPA	State MPA		11
	Coral Sea	CMR	Habitat Protection Zone (IUCN IV)	Coral Sea	24
	North	CMR	Marine National Park Zone (IUCN II)	West Cape York	2

Ecoregion	CMR Network	Zoning	IUCN Zone	CMR Name	Number of sites
			Habitat Protection Zone (IUCN IV)	West Cape York	1
		Open	Open		1
Tweed-Moreton	Coastal	Open	Open		19
		State MPA	State MPA		15
	Temperate East	CMR	Marine National Park Zone (IUCN II)	Solitary Islands	1
		Open	Open		3
		State MPA	State MPA		2
Western Bassian	Coastal	Open	Open		15