REEF LIFE SURVEY

Assessment of Coral Reef Biodiversity in the North Commonwealth

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Report to Parks Australia, the Department of the Environment

Citation

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EXECUTIVE SUMMARY

- Surveys of reef communities across northern Australian indicated a biota generally similar to that present across the Indo-Pacific (the tropical waters of the Indian Ocean, the western and central Pacific Ocean, and the Indonesian seas connecting the two).
- Variation in species composition from east to west was evident, but not as large as a strong biogeographic division between inshore and offshore reef community types. Offshore reefs were typified by a rich biota with wide Indo-Pacific affinities, while inshore reefs possessed communities with high cover of algal turf, high fish biomass, a high proportion of species endemic to Australia, but lower species richness.
- The analyses in this report provide new insight into an additional, strong faunal break in the area, which is not based on dispersal barriers between east and west, but likely on environmental factors and habitats between inshore and offshore. This highlights how the inshore-offshore faunal break reflects more striking compositional differences than the long-known Indian Ocean-Pacific Ocean biogeographic barrier.
- Most reefs across the North CMR Network had relatively high coral cover, between 15% and 40%.
- Reef communities within Commonwealth Marine Reserve (CMR) boundaries were generally typical of those of the region, with similar faunal composition, fish biomass and substrate types. Nevertheless, exceptions included:
    - relatively high densities of seasnakes in the Gulf of Carpentaria CMR;
    - a distinctive fish fauna in the Oceanic Shoals CMR;
    - high abundance and biomass of reef fishes, high abundance of cryptic fishes and invertebrates, and high species richness of invertebrates on some reefs of the Arnhem Coast-Gulf of Carpentaria ecoregion;
    - high biomass of piscivores in the Gulf of Carpentaria CMR; and
    - high species richness of reef fishes on a non-CMR reef of the Torres Strait to Northern GBR ecoregion.
- The only species listed under the EPBC Act recorded during northern Australian surveys were the green turtle *Chelonia mydas* (Vulnerable), the turtle-headed seasnake *Emydocephalus annulatus*, and the olive seasnake *Aipysurus laevis* (Protected Marine Species).
- Distance offshore and depth were the variables with the strongest relationships with fish community structure.
- The primary threats across the North CMR Network include illegal fishing from international fishers, commercial fishing, marine pests, marine debris, activities associated with oil and gas exploration and extraction, shipping and climate change. Changing the zoning of CMRs to no-take may restore fish stocks, prevent damage from oil mining and enhance resilience of the CMRs.
- Changing the zoning of some CMRs to accommodate more than one reef system protected within a no-take zone within the Northern CMR network (presently only Carpentaria Shoal in

West Cape York CMR) should assist restoration of marine species affected by fishing, reduce risks associated with oil mining, and enhance resilience of the CMR network.

- We recommend that:
    - ongoing monitoring of North CMR reefs takes place as often as is feasible, using the methods presented here;
    - baseline data presented here should guide efforts to select sites;
    - research priorities should include development of indicators that track changes in reef condition and biodiversity;
    - investigate factors limiting seasnake, turtle and elasmobranch distribution;
    - carry out detailed habitat mapping and categorisation of reef types, exposure and aspect;
    - carry out detailed mapping of distribution and impact of natural disturbances; and
    - analyse in more detail the value of the North CMR shoals as refugia for coral reef organisms from disturbances and stressors in shallow water.

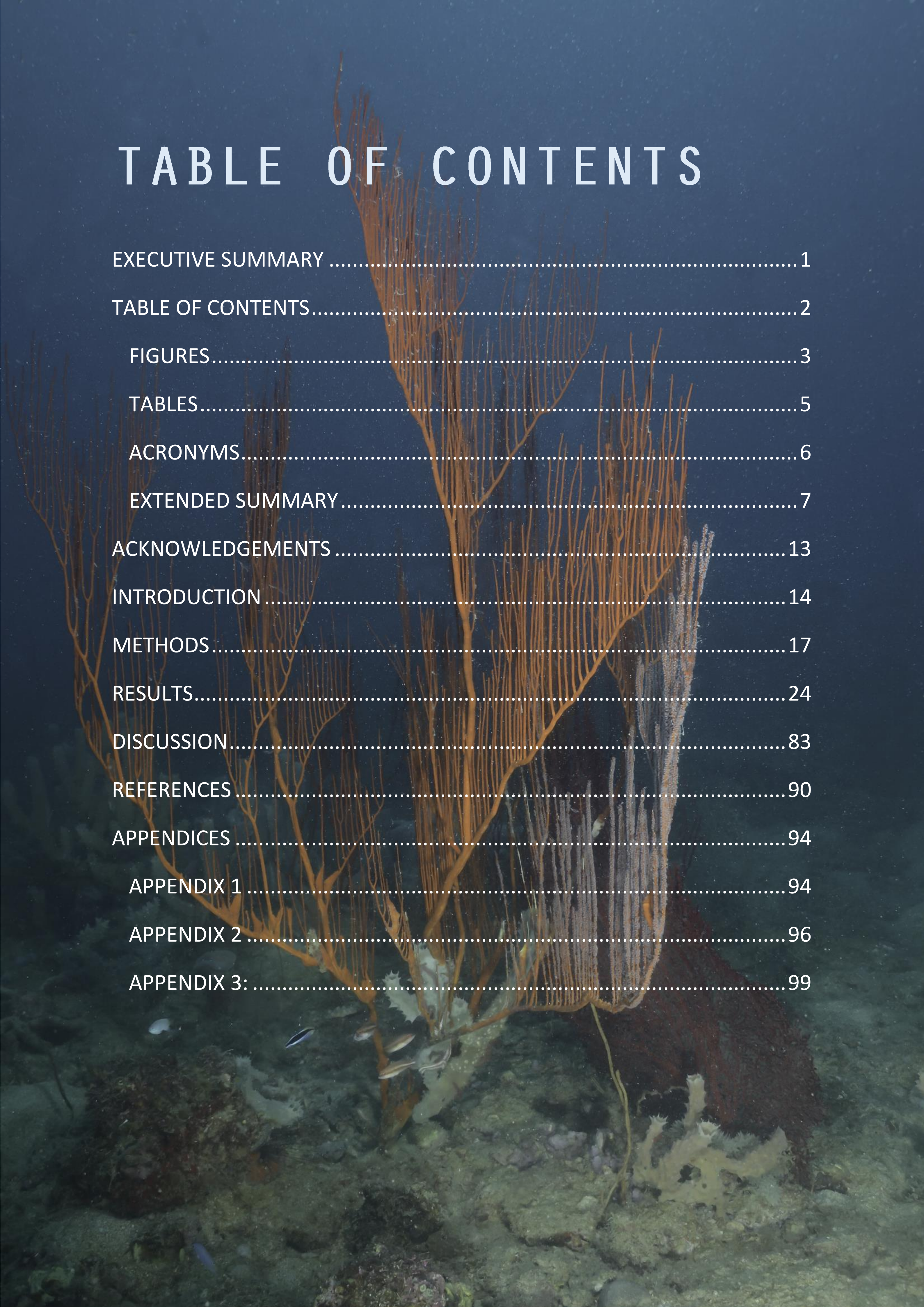

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Photo: Joe Shields

ACRONYMS

ACRONYM	EXPANDED
RLS	Reef Life Survey
IMAS	Institute of Marine and Antarctic Studies
CMR	Commonwealth Marine Reserve
IUCN	International Union for Conservation of Nature
GBR	Great Barrier Reef
GPS	Global Positioning System
EEZ	Exclusive Economic Zone
KEF	Key Ecological Features
UVC	Underwater Visual Census

Photo: Joe Shields

EXTENDED SUMMARY

The North CMR Network stretches across a large area of northern Australia, from the Joseph Bonaparte and Oceanic Shoals CMRs in the west to the West Cape York CMR in the east. The area contains some shallow coral reefs and numerous offshore seamounts reaching near to the sea surface, some of which have only recently been discovered. Very little is known of the biodiversity found on the vast majority of reef habitats across the whole network. In 2015, Reef Life Survey (RLS) dive teams surveyed 84 reef sites in the North CMR Network to provide baseline data on the ecological condition of these reefs. Every rise in the seabed marked on nautical charts to within 15-20 m of the surface in any of the CMRs was surveyed, other than the extensive offshore reef systems of Oceanic Shoals CMR. Fifty-five sites surveyed were within existing boundaries of six of the eight CMRs in the network.

RLS involves recreational divers trained to a scientific level of data-gathering to allow ecological surveys to be conducted across broad geographic areas in a cost-effective manner. This report and associated surveys were undertaken to greatly increase information on the distribution of marine biodiversity across the North. Specifically, the goals of this project were to:

- Provide a baseline for the development of future monitoring and assessment of biodiversity trends on shallow coral reefs in the North CMR Network;
- Assess the biogeographic affinities of reefs in the North CMR Network with those in the broader region, including the Coral Sea, northern GBR and Indonesia;
- Document substratum cover, macroinvertebrate and fish fauna associated with reefs in the North CMR Network, inside and outside CMR boundaries;
- Compare locations inside and outside CMRs to assess whether the North CMR Network encompasses most of the Top End offshore biodiversity values for shallow-water reefs (identified across the full range of sites surveyed);
- Provide information on the distribution and abundance of threatened and protected species in the North CMR Network;
- Describe geographic distribution patterns of coral reef organisms to determine key potential drivers of coral reef biodiversity (e.g. latitude, longitude, depth, distance offshore and live coral cover); and
- Discuss potential threats to biodiversity in the region.

LARGE-SCALE BIOGEOGRAPHIC PATTERNS – PUTTING REEFS IN THE NORTH CMR NETWORK INTO CONTEXT

The availability of directly comparable data from RLS surveys previously undertaken outside of the North CMR Network allowed an extensive biogeographic study, putting the North CMR Network reefs into a broader regional context with respect to biodiversity. Data from 328 sites surveyed by RLS divers were used to assess similarities in composition and abundance of reef fishes, mobile invertebrates and in the cover of major substrate categories.

The North CMR Network hosts abundant and diverse coral reef communities with characteristics that span a bridge between east and west, inshore and offshore, with assemblages typical of the tropical Indo-Pacific. Reefs in the North CMR Network had similar cover of live hard corals to the adjacent regions assessed, but also generally had a greater cover of turf and non-living substrate categories (such as bare coral rock). Massive and encrusting coral morphologies dominated the coral assemblage in the North CMR Network; branching *Acropora* spp were abundant only on non-CMR reefs of the Torres Strait to northern GBR ecoregion and foliose corals were abundant in the Arnhem, Wessel and West Cape York CMRs.

A very clear division is evident in the reef fishes and mobile invertebrates between relatively turbid inshore reefs, which possessed a relatively high proportion of endemic Australian species, and “blue-water” offshore reefs, which possessed an Indo-Pacific biota. Such differences were much greater than previously identified differences in the fauna between the eastern and western seaboards of Australia. Most reefs of the North CMR Network were characterised by the inshore reef community type, which corresponds with the general geomorphology of the region (dominated by a relatively shallow and turbid continental shelf). The high cover of turf on inshore reefs across the North suggests high primary productivity and habitat for invertebrate grazers. However, the high cover of turf did not correlate with higher densities of grazing fishes despite the usual link between the biomass and turnover of turf and grazing fishes.

The inshore-offshore distinction is especially strong in the reef fish communities. The inshore community type is characterised by reef-dwelling predators (e.g. Serranids), large wrasses and butterflyfishes, and was observed at most sites in the three ecoregions across the North CMR Network (Torres Strait and GBR, Arnhem Coast to Gulf of Carpentaria, and Bonaparte Coast). The offshore fish community, found in the Indonesian ecoregions, Cocos-Keeling / Christmas Island, the Coral Sea, the Gulf of Papua, and many sites in the Exmouth to Broome ecoregion further west of the North CMR Network, is characterised by medium-bodied wrasses, small surgeonfishes and planktivorous damselfishes. North CMR Network reefs tended to have lower abundance and species richness of reef fishes, but higher biomass than reefs in adjacent regions. The reef fish biomass across the north is not only high by Australian, but also by global standards, and the region thus has substantial commercial and conservation value, appearing to have benefited from reduced commercial and recreational fishing pressures as a result of geographic isolation.

Fish assemblages were more similar among inshore sites than offshore sites. This may be due to a combination of currents and the higher availability of dispersal stepping-stones closer the the coast, as some of the offshore locations is this study are highly isolated. Species richness on the Northern reefs was probably influenced by a combination of two primary factors: the proximity to the global centre of biodiversity (the Coral Triangle, comprising the waters of Indonesia, Malaysia, the Philippines, Papua New Guinea, Timor Leste and the Solomon Islands), which would promote high species richness, and the low complexity and diversity of habitats, which reduces species richness.

Inshore macroinvertebrate communities, characteristic of much of the North CMR Network, appeared richer and more diverse than those found offshore, which were dominated by a few species of tridacnid clams and sea urchins. Inshore communities had higher densities of nudibranchs, some bivalves, flatworms and sea urchins. The inshore-offshore effect on species richness and abundance varies for different mobile invertebrate taxa.

THE NORTH CMR NETWORK

Benthic communities across the North CMR Network reefs tended to be dominated by algal turf and live corals. The Bonaparte Coast (western part of the North CMR Network, including the Oceanic Shoals CMR) had lower coral cover than North CMR Network reefs elsewhere, but no significant differences between individual CMRs were detected. CMRs across the large Arnhem Coast to Gulf of Carpentaria ecoregion (from Darwin to near Cape York) had the most variable coral cover, ranging from 15% in the Arnhem CMR to 37% in the Wessel CMR. Some CMRs had particular characteristics, such as realtively higher sponge cover (e.g. the Arafura CMR) or more soft corals (e.g. the Wessel CMR). Corals also seemed to play less of a role in structuring the fish community, apart from presence of corallivorous fishes such as butteflyfishes, which are strongly dependent on the live coral tissue.

Fish species richness and biomass were higher inside CMRs that at non-CMR sites in each ecoregion, on average. In terms of individual CMRs representing the fish fauna of the ecoregion they sit within, the following patterns apply:

- Sites investigated in the Oceanic Shoals CMR have a distinct fish fauna from the non-CMR Bonaparte Coast ecoregion, which itself is split between inshore and offshore fish faunas.
- The Arnhem Coast-Gulf of Carpentaria ecoregion covers a number of CMRs, with the fish fauna of the Arnhem and Wessel CMRs characteristic of the ecoregion, but also with some Gulf of Carpentaria and Arafura CMR sites having distinct fish faunas. CMR sites in this ecoregion had the highest abundance and biomass of reef fishes of all North CMR Network sites (Cape Beatrice SW, Carpentaria Reef), as well as the highest abundance of cryptic fishes and invertebrates (Manowar Island), the highest species richness of cryptic fishes (Glasseye Reef), and species richness of invertebrates (Bremer Islet Anchorage). Carpentaria Reef (CMR) and Grouper Shoal (non-CMR) had the highest biomass of piscivores; Burston Bay (also non-CMR) had the highest biomass of grazers.
- The fish fauna of Torres Strait to Northern GBR ecoregion is represented in the West Cape York CMR. A non-CMR site in this ecoregion had the highest species richness of reef fishes of all North CMR Network sites (Mer Outer Reef).

Macroinvertebrate assemblages differed in the Bonapare Coast non-CMR reefs compared to all other CMRs, suggesting a community type not well covered in the North CMR Network CMR boundaries. These Bonaparte coast reefs were characterised by crinoids and an assortment of echinoderms and molluscs. The cryptic fish assemblage of the Bonaparte Coast ecoregion differed from all other CMRs; CMR reefs had higher species richness of cryptic fishes than non-CMR reefs. Macroinvertebrate and cryptic fish communities showed much greater variability in abundance between different CMRs than fish communities, suggesting different environmental and/or biological influences, or greater patchiness. The Arafura, Gulf of Carpentaria and Wessel CMRs had very high invertebrate abundance and species richness. The latter two CMRs had inshore macroinvertebrate communities, but the Arafura CMR had elements of both the inshore and the offshore assemblages.

DRIVERS AND THREATS

Latitude and depth were found to exert the strongest influences amongst potential drivers for North CMR Network reef communities. Latitudinal gradients reflect distance from the centre of reef diversity near the equator in the Coral Triangle. Marine habitats close to the equator are characterised by greater predictability than those at higher latitude, promoting a higher degree of specialisations and tolerance to environmental factors different from those found at higher latitudes. Depth is an important driver of fish community structure because of its effect on primary production, light, and wave energy attenuation. Variation in biological factors such as predation and competiton at different depths can also play a role. Longitude reflects the distance from the centre of diversity, much like latitude. In this case, due to the North CMR Network's proximity to the Indo-Pacific biogeographic barrier, longitude-driven differences may also reflect the distance from this barrier. Live coral cover can be an importance driver for some species, especially those that feed on live coral tissue or shelter in coral colonies. The effect of live coral cover on species that are not directly dependent on it is somewhat more ambiguous; in the North CMR Network its influence did not extend beyond corallivorous fishes.

The primary threats across the North CMR Network include illegal fishing from international fishers, marine pests, marine debris, activities associated with oil and gas exploration and extraction and climate change.

RECOMMENDATIONS

Ongoing monitoring of North CMR Network reefs is recommended as often as is feasible. This should include assessment of ecological changes associated with zoning - in particular if degradation within CMRs is similar to that experienced outside CMRs that could warrant changed zoning arrangements. It should also include tracking any changing biophysical conditions, outbreaks of crown-of-thorns seastars, and broad scale regional ecological shifts associated with changing climate.

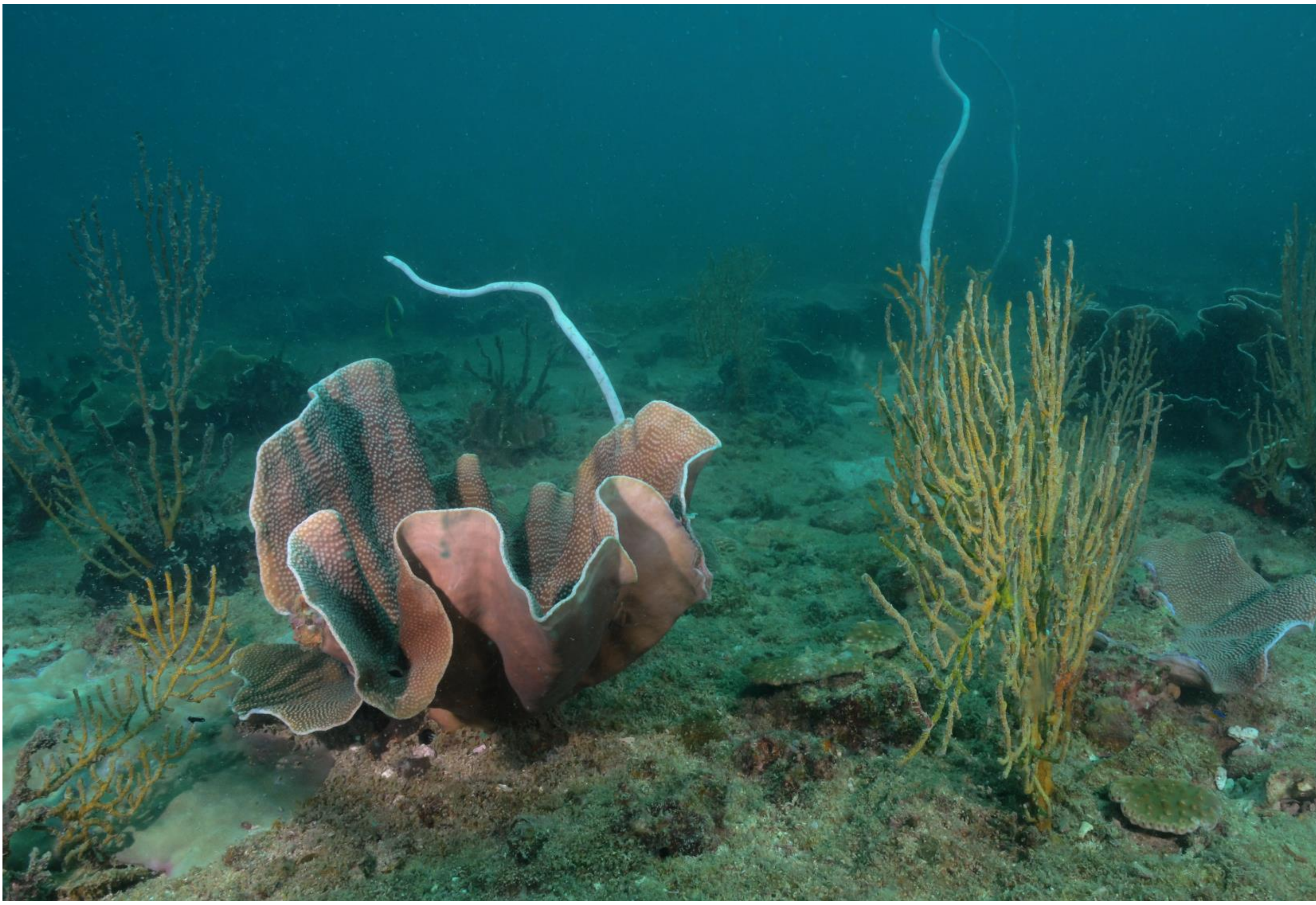
If available resources allow only a reduced set of sites to be monitored through the future, these should include all CMR sites surveyed here. Baseline data presented here should guide efforts to select appropriate non-CMR reference sites with similar ecological and environmental characteristics. Reference sites should span the longitudinal and latitudinal extent of the North CMR Network.

Future monitoring using the same methods would provide complete comparability and the most powerful means to detect change.

Research priorities associated with monitoring and evaluation should include development and selection of a suite of indicators that track changes in reef condition and aspects of biodiversity that are of most relevance to CMR management goals, as well as changes associated with ocean warming and storms.

Further research questions of relevance to managers when determining the condition of biodiversity in the North CMR Network, identifying key threats, and understanding management options include:

- Investigation of factors limiting seasnake, turtle and elasmobranch distribution, including assessment of ecological data for associations among species and functional groups, as well as with environmental data. This may require collection of additional habitat or environmental data.
- Detailed habitat mapping and categorisation of reef types, exposure and aspect.
- Detailed mapping of distribution and impact of natural disturbances, including cyclones. This should ideally include comparison with coral reef systems to the east and west, to allow the North CMR reefs to be considered in the broader regional geographic context.
- A more detailed analysis of the value of the North CMR shoals as refugia for coral reef organisms from disturbances and stressors in shallow water.



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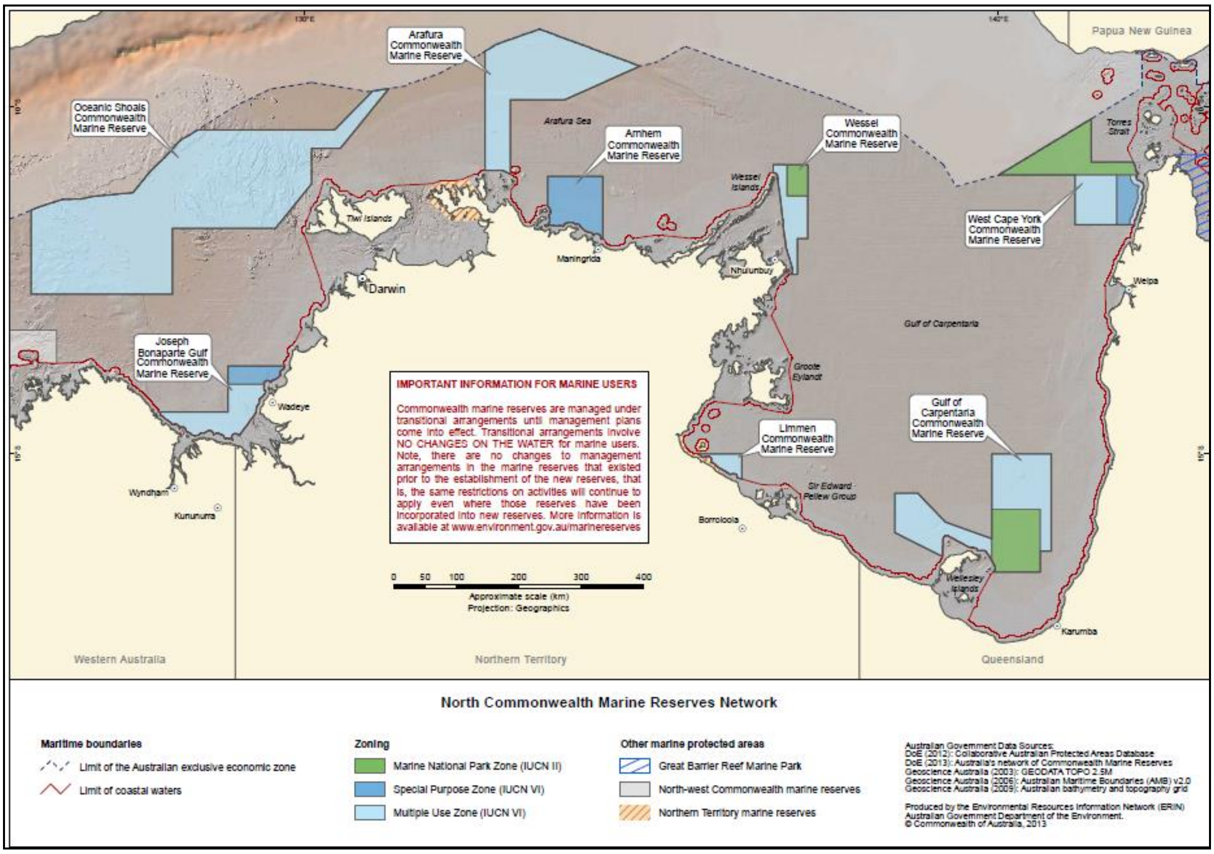
INTRODUCTION

The North Commonwealth Marine Reserve Network (North CMR Network) spans the extent of the North Marine Region as defined during the Commonwealth Government's Marine Bioregional Planning Program (FIGURE 1). It encompasses the Timor Sea, the Arafura Sea, the Gulf of Carpentaria and the Torres Strait, and includes eight Commonwealth Marine Reserves (CMRs). The main currents influencing climate and hydrodynamics in the region are the Indonesian Throughflow (Tomczak and Godfrey 1994), the Arnhem Current (Condie 2011) and strong tidal currents (Bulman and Fulton 2015).



IMPORTANT INFORMATION FOR MARINE USERS

Commonwealth marine reserves are managed under transitional arrangements until management plans come into effect. Transitional arrangements involve NO CHANGES ON THE WATER for marine users. Note, there are no changes to management arrangements in the marine reserves that existed prior to the establishment of the new reserves, that is, the same restrictions on activities will continue to apply even where those reserves have been incorporated into new reserves. More information is available at www.environment.gov.au/marinereserves

Australian Government Data Sources:
DoE (2012): Collaborative Australian Protected Areas Database
DoE (2013): Australia's network of Commonwealth Marine Reserves
Geoscience Australia (2003): GEODATA TOPO 2.5M
Geoscience Australia (2006): Australian Maritime Boundaries (AMB) v2.0
Geoscience Australia (2009): Australian bathymetry and topography grid

Produced by the Environmental Resources Information Network (ERIN)
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FIGURE 1. North Commonwealth Marine Reserves Network, as of 2013.

The North Marine Region is largely shallow, with a seabed made up primarily of soft sediment (Bulman and Fulton 2015). In this region, coral reefs have formed in the Gulf of Carpentaria, on carbonate banks and terraces of the Van Diemen Rise, on terraces and pinnacles of the Bonaparte basin, and as fringing reefs around the coastline (Heap and Harris 2008, Bulman and Fulton 2015). Many are submerged some 20 to 30 m below present day sea level (Harris et al. 2004, Commonwealth of Australia 2007). Coral reefs in the eastern Torres Strait form part of the northern Great Barrier Reef and well-developed fringing reefs occur around islands in Torres Strait and off Arnhem Land (National Oceans Office 2003). In the Gulf of Carpentaria, reefs are generally ovalshaped with steep spur-and-groove fore-reef slopes and talus accumulations on their leeward margins (Commonwealth of Australia 2007). Some coral-rich areas in the Gulf of Carpentaria are referred to as “coral carpets” (National Oceans Office 2004). Nearshore coral communities have developed on terrigenous substrates and in turbid water, and comprise a subset of Torres Strait species (Collins 1994, Veron 2004).

Very few surveys of coral reefs in have been conducted in the region; indeed, some reefs were only discovered relatively recenty (Harris et al. 2004, Harris et al. 2008). Most studies have focused on nearshore reefs (Wolstenholme et al. 1997, Veron 2004, Commonwealth of Australia 2007, Russell and Gomelyuk 2008). Some coral monitoring has occurred around Groote Eylandt (Wilson and Paling 2004), and a number of areas within the Oceanic Shoals CMR were recently subject to a comprehensive biodiversity survey, but reef habitats formed a minor component of the study (Nichol et al. 2013). Benthic diversity is highest in shallower, less turbid environments (Wilson and Paling 2004, Nichol et al. 2013).

Coral reef communities are biogeographically linked to the east and west, with influence from the Papua New Guinea / Torres Strait / northern GBR region to the east, and Indonesia and the northern Indian Ocean to the west (Veron 2004). Whilst less diverse than the Great Barrier Reef (Wolstenholme et al. 1997), coral reefs in the region are still considered to have high biodiversity in terms of species richness and endemism, especially around the Wessel Islands (Commonwealth of Australia 2008).

Marine fish communities are even less well-known than the benthic communities, and research has been driven by commercially important species (e.g. mackerel and snapper species) and species of conservation significance (e.g. sawfish) (Peverell and Pillans 2004). Some endemic taxa may still be undescribed; for instance, the coral trout that inhabit the Gulf reefs are generally smaller than those found on the Great Barrier Reef and may be a new subspecies (Commonwealth of Australia 2007). Feeding aggregations of demersal fishes are known to occur around pinnacles in the Bonaparte Basin (DEWHA 2009).

Coral reefs in the region are considered vulnerable to cyclones (National Oceans Office 2003), high turbidity levels, crown of thorns sea stars (COTS) and bleaching (Commonwealth of Australia 2007). Water temperatures across much of this shallow region are already considered to be towards the upper limit of tolerance for corals; ocean warming is a growing threat to coral communities (Gomelyuk 2007).

Documenting the flora, fauna, ecological communities in an area and their patterns and associations is an important first step towards the identification of their ecological and conservation value, which can then inform their conservation and management. The knowledge gaps across the North Marine Region are extensive; while there is an understanding that there may be important habitats, species and communities, their distribution and abundance remain to be described. In establishing marine reserves, it is important that they be at least representative of the ecological values present in the region, if not encompassing species, communities and habitats of particular vulnerability or value (Green et al. 2013). Coral reefs are the most biodiverse habitats in the world’s oceans. As such, they represent an appropriate starting point for investigation of the distribution of marine communities.

The aims of the present study were to:

PART A

- Assess the biogeographic affinities of North CMR Network reefs with those in the Coral Sea, northern GBR and Indonesia;

PART B

- Document substratum cover, macroinvertebrate and fish fauna across the region's reefs, inside and outside the North CMR Network CMRs;
- Compare species assemblages between reserves and with external sites to assess whether the CMR network encompasses most of the range in Top End offshore biodiversity (across the full range of sites surveyed); and
- Provide information on the distribution and abundance of threatened and protected species;

PART C

- Describe geographic distribution patterns of coral reef organisms to determine key potential associations between coral reef biodiversity and environmental and geographic variables (e.g. latitude, longitude, depth, distance offshore and live coral cover);
- Provide a baseline for the development of future monitoring;
- Assess biodiversity trends of shallow coral reefs in the North CMR Network; and
- Discuss potential threats to biodiversity in the region.

Mornington Island
Photo: Rick Stuart-Smith

METHODS

Reef Life Survey (RLS) dive teams surveyed 328 sites on reefs across the northern part of the Australian continent and in nearby ecoregions between 2008 and 2015 (Figure 2). Of these, 55 sites located in Commonwealth Marine Reserves in the North CMR Network, plus additional associated reference sites, were surveyed in 2015 to provide baseline data on shallow reef habitats. All sites in the North CMR Network were offshore with similar exposure to wind and waves. Every rise in the seabed marked on nautical charts to within 15-20 m of the surface in any of the CMRs was surveyed, other than the extensive offshore reef systems of Oceanic Shoals CMR. The North CMR Network zoning was not under active management when the surveys were undertaken.

Site locations of reference sites in the Elcho Island and Gove regions were selected with advice and field assistance from Gumurr Marthakal Rangers and Dhimurru Rangers, respectively.

Plate 1 Gumurr Marthakal Rangers assisting with surveys, Galiwinku Elcho Island

Plate 2 Collaborative surveys with Dhimurru Rangers

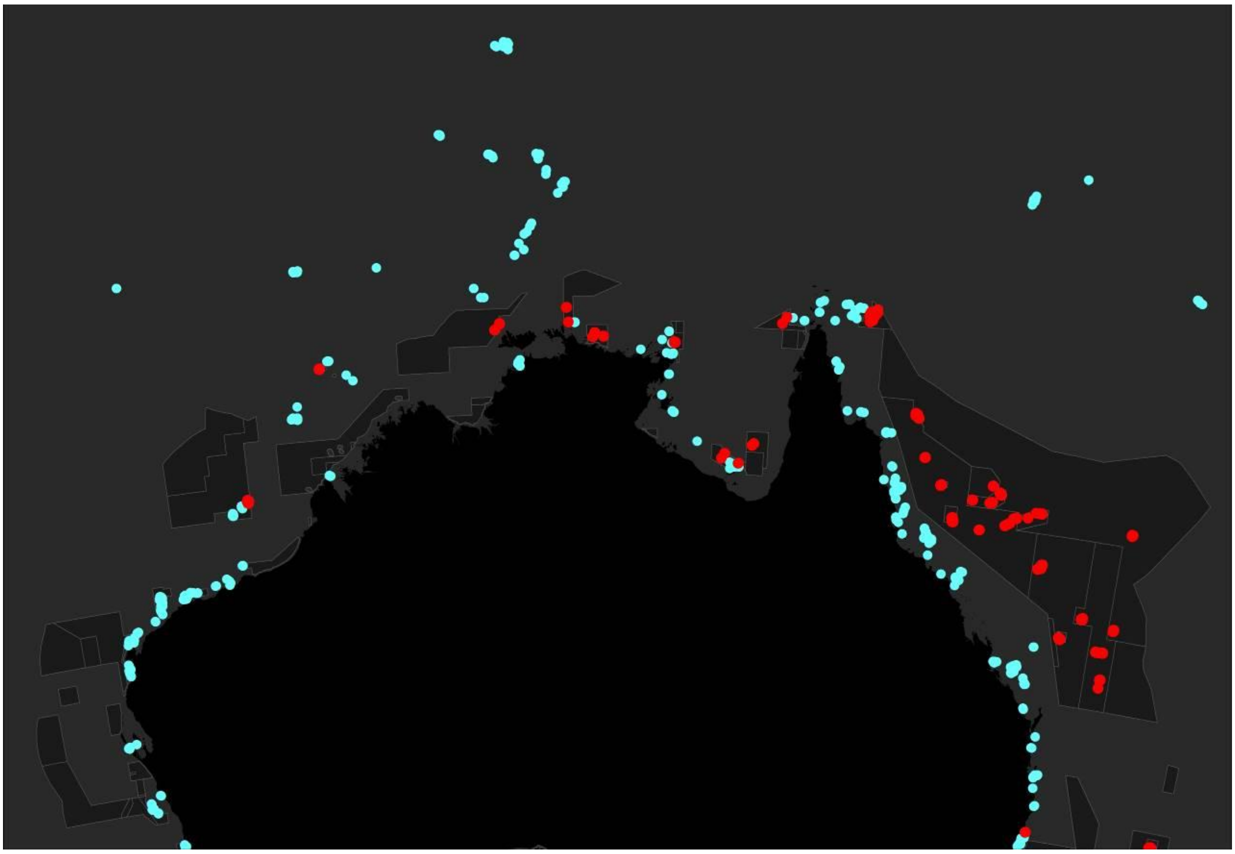


Figure 2. Australian locations of reefs where surveys were undertaken by RLS teams across northern Australia.

All surveys were conducted using the standardised underwater visual census methods applied globally by Reef Life Survey. 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.

A summary of these methods is provided here. Full details can be downloaded at: http://reeflifesurvey.com/files/2008/09/NEW-Methods-Manual_15042013.pdf.

Each RLS survey involves three distinct searches undertaken along a 50 m transect line: for fishes, invertebrates and cryptic fishes, and sessile organisms such as corals and macroalgae (described individually below). Two transects were usually surveyed at each site for this study, on predominantly coral reef habitat, and generally parallel at different depths. Depth contours were restricted by depth variations in individual reefs, but where possible were selected to encompass a wide depth range (e.g. 2 – 20 m), but constraints associated with diving bottom time and air consumption generally limited depths to above 22 m. Underwater visibility and depth were recorded at the time of each survey, with visibility measured as the furthest distance at which large objects could be seen along the transect line, and depth as the depth (m) contour followed by the diver when setting the transect line. For most sites, more detailed exposure categories were assigned (Table 1).

FISH SURVEYS (METHOD 1)

All fish species sighted within 5 m x 50 m blocks either side of the transect line were recorded on waterproof paper as divers swam slowly along the line. The number and estimated size-category of each species was also recorded. Size categories used were 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 400, 500, 625 mm, and above, which represent total fish length (from snout to tip of tail). All species sighted within the blocks were recorded, even for those with unknown identity. Photographs were used to later confirm identities with appropriate taxonomic experts, as necessary. In occasional circumstances when no photograph was available, taxa were recorded to the highest taxonomic resolution for which there was confidence (e.g. genus or family, if not species). Other large pelagic animals such as mammals, reptiles and cephalopods were also recorded during the Method 1 fish survey, but were excluded for analyses focusing on fishes. Species observed outside the boundaries of the survey blocks or after the fish survey had been completed were recorded as ‘Method 0’. Such records are a presence record for the time and location but were not used in quantitative analyses at the site level. ‘Method 0’ sightings were also made of invertebrates and any other notable taxonomic groups.

MACROINVERTEBRATE AND CRYPTIC FISH SURVEYS (METHOD 2)

Large macroinvertebrates (echinoderms, and molluscs and crustaceans > 2.5 cm) and cryptic fishes were surveyed along the same transect lines set for fish surveys. Divers swam near the seabed, up each side of the transect line, recording all mobile macroinvertebrates and cryptic fishes on the reef surface within 1 m of the line. This required searching along crevices and undercuts, but without moving rocks or disturbing corals. Cryptic fishes include those from particular, pre-defined families that are inconspicuous and closely associated with the seabed (and are thus disproportionately overlooked during general Method 1 fish surveys). The global list of families defined as cryptic for the purpose of RLS surveys can be found in the online methods manual. As data from Method 2 were collected in blocks of a different width to that used for Method 1 and were analysed separately from those data, individuals of cryptic fishes known to already be recorded on Method 1 were still recorded as part of Method 2. Sizes were estimated for cryptic fishes using the same size classes as for Method 1.

PHOTO-QUADRATS OF BENTHIC COVER (METHOD 3)

Information on the percentage cover of sessile animals and macroalgae along the transect lines set for fish and invertebrate surveys were recorded using photo-quadrats taken every 2.5 m along the 50 m transect. Digital photo-quadrats were taken vertically-downward from a height sufficient to encompass an area of approximately 0.3 m x 0.3 m. In total, images were available and processed for 252 of the 314 transects investigated for fishes and benthic invertebrates.

The percentage cover of different macroalgal, coral, sponge and other attached invertebrate species was obtained from photo-quadrats by recording the functional group observed under each of five points overlaid on each image, such that 100points were usually counted for each transect (thus percentage cover was calculated as the number of points each group was scored under).

Functional groups for photo-quadrat processing comprised the standard 50 categories applied in broad-scale analysis of RLS data (Appendix 1), which are aligned with the CATAMI classification system (Althaus et al. 2015). With greater time investment by a specialist operator than was achievable for this report, higher taxonomic resolution analyses are possible using the photo-quadrat set for groups such as corals and algae. Images have been archived and are available for processing at any resolution through the future.

Mean and maximum rugosity values were also estimated for each transect from photo-quadrats, on a scale of 1 to 4, as follows: 1) flat smoothly-curved seabed, occasional projecting rocks when present, not rising more than 5 cm; 2) smoothly-curved seabed with cracks and ridges (with rounded edges) rising vertically 5-20 cm but not undercut; 3) dissected reef surface with cracks and ridges (with some angular edges) rising vertically 20-50 cm and with small undercuts; and 4) highly-dissected reef with extensive (>0.5 m) undercuts.

STATISTICAL ANALYSES

Collection of detailed data on fishes, including species-level identities, length classes and abundance information, allow the calculation of species-specific biomass estimates. The RLS database includes coefficients for length–weight relationships obtained for each species from Fishbase (www.fishbase.org) (in cases of missing length-weight coefficients, these are taken from similar-shaped species). When length–weight relationships were described in Fishbase in terms of standard length or fork length rather than total length, additional length-length relationships provided in Fishbase allowed conversion to total length, as estimated by divers. For improved accuracy in biomass estimates, the bias in divers' perception of fish size underwater was additionally corrected using the mean relationship provided in Edgar et al. (2004), where a consistent bias was found amongst divers that led to underestimation of small fish sizes and overestimation of large fish sizes. Note that estimates of fish abundance 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.

UNIVARIATE ANALYSES

A range of univariate metrics were calculated from survey data: total fish abundance, fish species richness, abundance of fish functional groups, total fish biomass, abundance and biomass of large fishes (> 25cm), and percent cover of corals and other key benthic organisms. All metrics represent mean values per 500 m^2 transect area for Method 1 fishes, 100m^2 transect area for Method 2 fishes and invertebrates, and percent cover of benthic organisms from photo-quadrats. Analysis of Variance (ANOVA) with appropriate transformations was conducted on the above metrics, with Reef as a fixed factor. While Reef would normally be considered a random factor in biogeographical studies with a subset of reefs sampled, we considered it fixed for this application because we surveyed almost the full set of shallow reefs present in the North CMRs, and each reef is of specific interest in its own right.

MULTIVARIATE ANALYSES

Relationships between North CMR sites in percent cover of sessile biota, reef fish and invertebrate communities were initially analysed using non-metric Multi-Dimensional Scaling (MDS). These were run using the PRIMER+PERMANOVA program (Anderson et al. 2008). This analysis reduces multidimensional patterns (e.g. with multiple species or functional groups) to two dimensions, showing patterns of similarity between sites. MDS was used to investigate differences in community structure between reefs.

Data were converted to a Bray-Curtis distance matrix relating each pair of sites after square root transformation of raw data. The transformation was applied to downweight the relative importance of the dominant species at a site, and so allow less abundant species to also contribute to the plots. MDS was followed up with ANOSIM (to test the significance of differences between reefs) and Multivariate ANOVA (MANOVA) to test the significance of difference between fish and benthic functional groups.

To test the influence of reef area (data obtained from UNEP-WCMC, WorldFish Centre, WRI, TNC (2010)), depth and wave exposure on benthic and fish community structure, a linear mixed effects model (LME) was used to determine the best explanatory variables for key benthic components and fish functional groups, using the statistical package *R*. Distance offshore, Latitude, Longitude, Depth and Live hard coral cover (for fish only) were treated as fixed factors, with Site as a random factor. Model selection for LMEs was based on minimisation of Akaike Information Criterion. The top model based on AIC values is presented.

BIOGEOGRAPHIC ANALYSES

For initial analyses of biogeographic relationships among sites in the North CMR Network, eastern and western Australian and adjacent locations, sites were allocated to ecoregions, as defined in the Marine Ecoregions of the World (MEOW) (Spalding et al. 2007). This was necessary because regions recognised in the Australian Integrated Marine and Coastal Regionalisation of Australia (https://www.environment.gov.au/node/18075) do not cover adjacent bioregions in Indonesia, Papua New Guinea. Previous analyses with the RLS dataset have also used MEOW ecoregions, and these were readily available to partition sites in a broader biogeographic context. All MEOW ecoregions around Australia and neighboring waters that are referred to in biogeographic analyses are shown in Figure 3. The MEOW ecoregions covered by the North CMR Network and referred to in CMR specific analyses are the Bonaparte Coast, Arnhem Coast to Gulf of Carpentaria, and Torres Strait to Northern Great Barrier Reef.

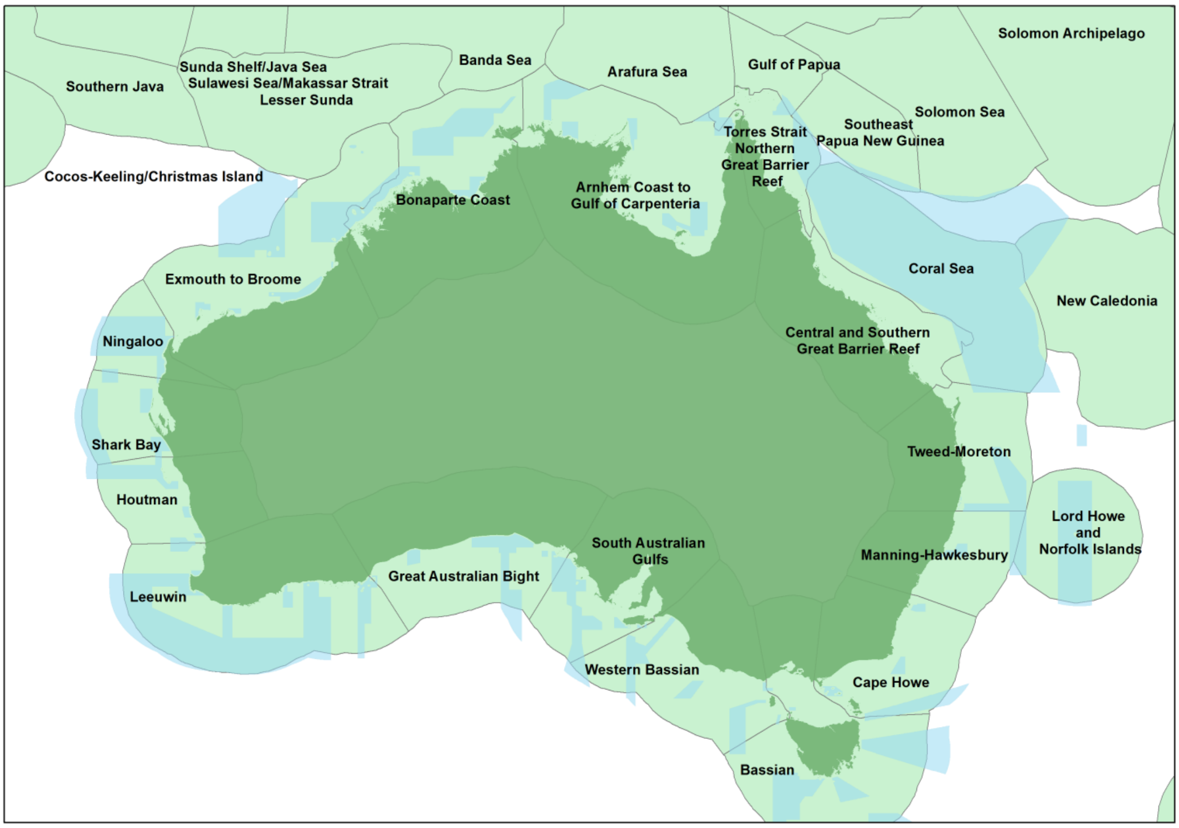


Figure 3. Ecoregions used for bioregional comparisons and analyses.

RESULTS

PART A: BIOGEOGRAPHIC PATTERNS

Benthic communities

Benthic composition varied between ecoregions (Figure 4; ANOSIM Global R = 0.225, p = 0.001), but with considerable overlap between some of the western and northern regions. The Exmouth to Broome region was similar in benthic composition to most other ecoregions, with the exception of the central and western GBR, the Coral Sea and the Bonaparte Coast. Coral Sea sites were characterised by a dominance of calcified and crustose coralline algae, whilst the Indonesian and Torres Strait / northern GBR sites had higher proportions of abiotic substrata and dead corals. Live hard coral was characteristic of Cococ-Keeling / Christmas Island sites, and individual sites of other ecoregions (Figure 4). There was a distinction between inshore and offshore sites (ANOSIM Global R = 0.229, p = 0.001), where inshore sites were grouped for MDS plots based on distance offshore and aspect (to account for nearshore sites exposed to clear, rather than turbid, conditions). Inshore sites were dominated by algae, abiotic substrata and dead corals, whilst offshore sites had a higher cover of corals and calcified and crustose coralline algae (Figure 5).

Across all regions, live hard coral, abiotic substrata and turf represented the dominant benthic cover, with significant variability between regions (Figure 6). Turf cover was highest on reefs across the North CMR Network than in all other regions (Table 1). Crustose coralline algae and calcified algae were especially dominant on Coral Sea reefs, and WA had particularly high cover of dead coral and macroalgae. Live coral cover was highest in the Indian Ocean, where it was almost double the cover of the other regions. Sites in the North CMR Network are characterised by comparable coral cover (28%) to surveyed reefs in other nearby ecoregions (except the Indian Ocean areas such as Cocos-Keeling and Christmas Island and Western Sumatra, which had the highest coral cover), and higher turf cover than sites surveyed in any of the neighbouring ecoregions.

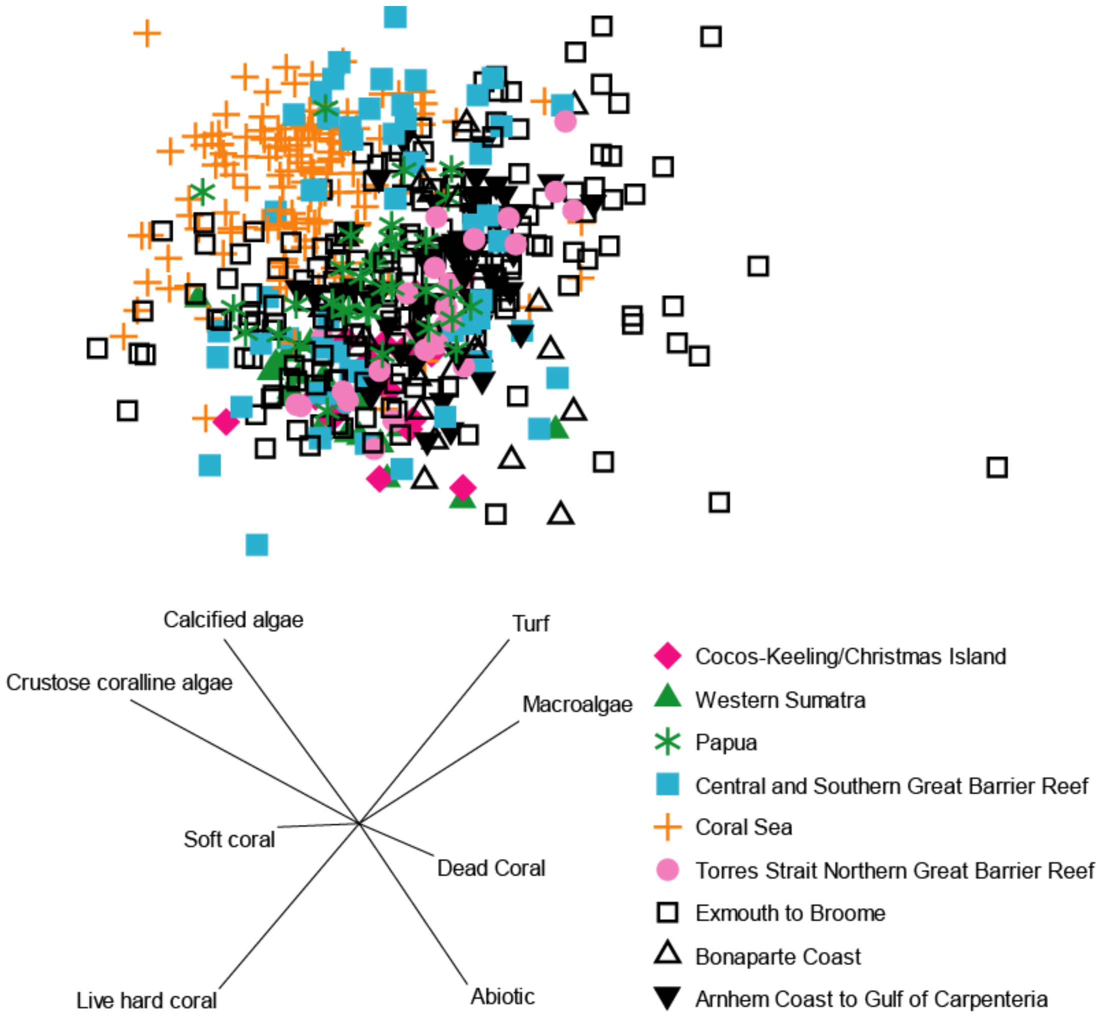


Figure 4. MDS ordination of key benthic components partitioned by ecoregions. Sites in the North CMR Network are identified by black symbols.

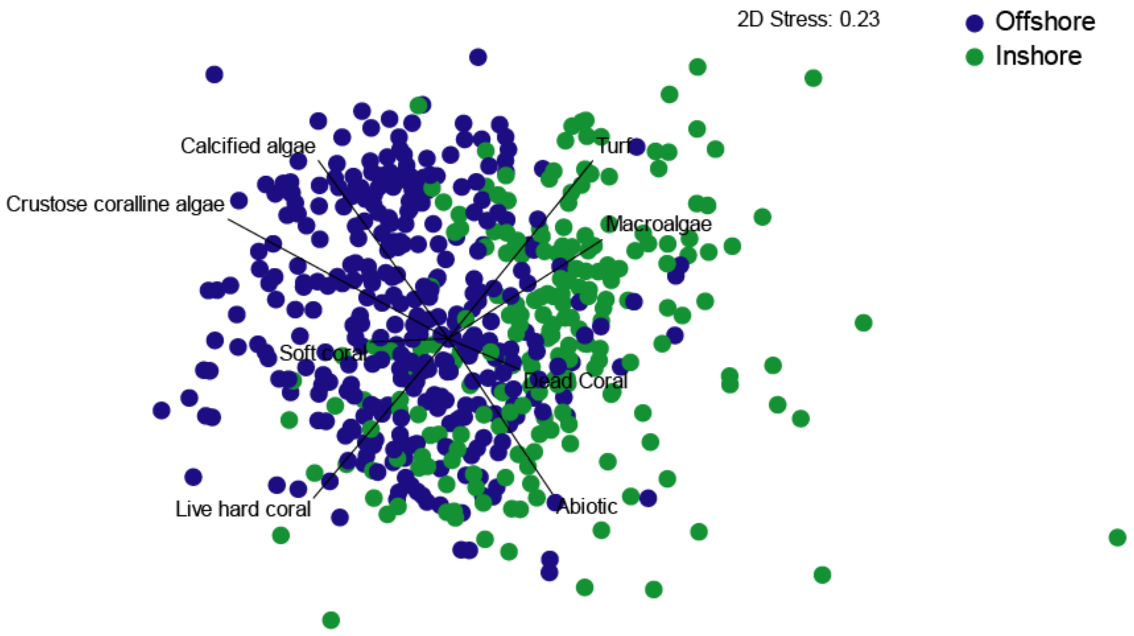


Figure 5. MDS ordination of key benthic components across all ecoregions, partitioned by shelf position.

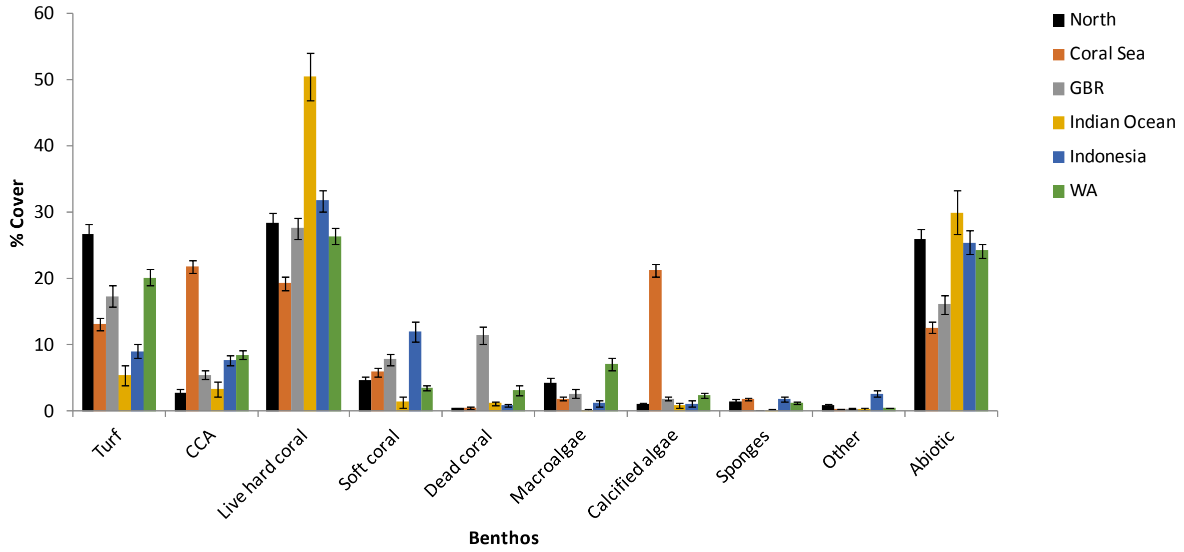


Figure 6. % cover of key benthic components across major regions, with the North CMR Network highlighted in black. Error bars ± 1 S.E.

Table 1. ANOVA results of regional differences in percentage cover of major benthic categories. Data were square-root transformed. Tukey HSD results are shown for differences between the Northern reefs and other regions; d.f. = 5, 968.

Benthic category	F	p	Tukey HSD – North CMR Network differences
Turf	18.74	<0.001	all
Crustose coralline algae	75.6	<0.001	Coral Sea, WA
Live hard coral	14.44	<0.001	Coral Sea, Indian Ocean
Soft coral	15.29	<0.001	Indonesia
Dead coral	29.96	<0.001	GBR, WA
Macroalgae	9.07	<0.001	
Calcified algae	179.0	<0.001	Coral Sea
Sponges	6.85	<0.001	GBR
Other sessile invertebrates	22.37	<0.001	Indonesia
Abiotic	21.48	<0.001	Coral Sea, GBR

REEF FISHES

Sites across the whole group of ecoregions were clearly divided into two groups on the basis of reef fish community structure (ANOSIM Global R = 0.538, P = 0.01) (Figure 7), which separated inshore from offshore reefs (ANOSIM Global R = 0.67, P = 0.01)(Figure 8). Species which characterised the offshore group, including medium-bodied wrasses (*Thalassoma lutescens*, *Halichoeres hortulanus*), small acanthurids (*Acanthurus nigrofuscus*, *Ctenochaetus striatus*) and planktivorous damselfishes (*Chromis margaritifer*), also distinguished certain ecoregions (the Indonesian ecoregions, Cocos-Keeling / Christmas Island, the Coral Sea, the Gulf of Papua, and approximately half of the Exmouth to Broome, Torres Strait and GBR sites). The second, inshore group, comprised typical inshore predators (*Plectropomus maculatus*, *Lutjanus carponotatus*), large wrasses (*Choerodon* spp.) and butterflyfishes (*Chaetodon aureofasciatus*, *Chelmon marginalis*), found at sites in Torres Strait and GBR, the Arnhem Coast to Gulf of Carpentaria and Bonaparte Coast ecoregions, as well as remaing sites in the Exmouth to Broome ecoregion. These species typically had much more restricted geographic ranges than fishes at offshore sites, and included some endemic Australian species.

Significant regional differences in the abundance, species richness and biomass of reef fishes were evident in Method 1 surveys (Table 2). Reefs in the North CMR Network generally had lower abundance and species richness than other regions, except for the Coral Sea, which had lower reef fish abundance than the North CMR Network (Figure 9). Biomass, however, was similar across all regions, and significantly higher only in Indonesia.

At the family level, only the abundance of Carangidae was even across all regions, all other families had significant regional differences in their abundance and species richness (Table 2). Besides a tendency for lower abundance and species richness in the Coral Sea and higher values in Indonesia, regional differences were less consistent than for cryptic fish families (Figure 9). Most families were towards to lower end of the abundance and species richness spectrum, often with higher abundance than the Coral Sea but roughly equivalent species richness. Haemulidae, Monacanthidae, Mullidae and Tetraodontidae had especially low abundance, whilst Siganidae were present in higher abundance on North CMR Network reefs than elsewhere. Labridae, Monacanthidae, Mullidae, Scaridae and Tetraodontidae were lower in species richness on North CMR Network reefs, whilst Lutjanidae were relatively species-rich (Table 2). Fish community patterns were generally consistent across ecoregions, albeit with slightly lower richness of fish species in the North CMR Network compared to other ecoregions. The North CMR Network had relatively high biomass of groupers, snappers and wrasses than other ecoregions.

Benthic carnivores, planktivores and grazers dominated fish communities across the regions, with a very high biomass of planktivores on Indonesian reefs. North CMR Network reefs were intermediate in their density and biomass of most functional groups, but were notable in terms of having the lowest biomass of cropping and farming herbivores than reefs in any other ecoregion, and second lowest biomass of excavating herbivores (Figure 10). The main difference between the North CMR Network and other regions was with the Coral Sea, where there were less benthic carnivores and omnivores but more grazers.

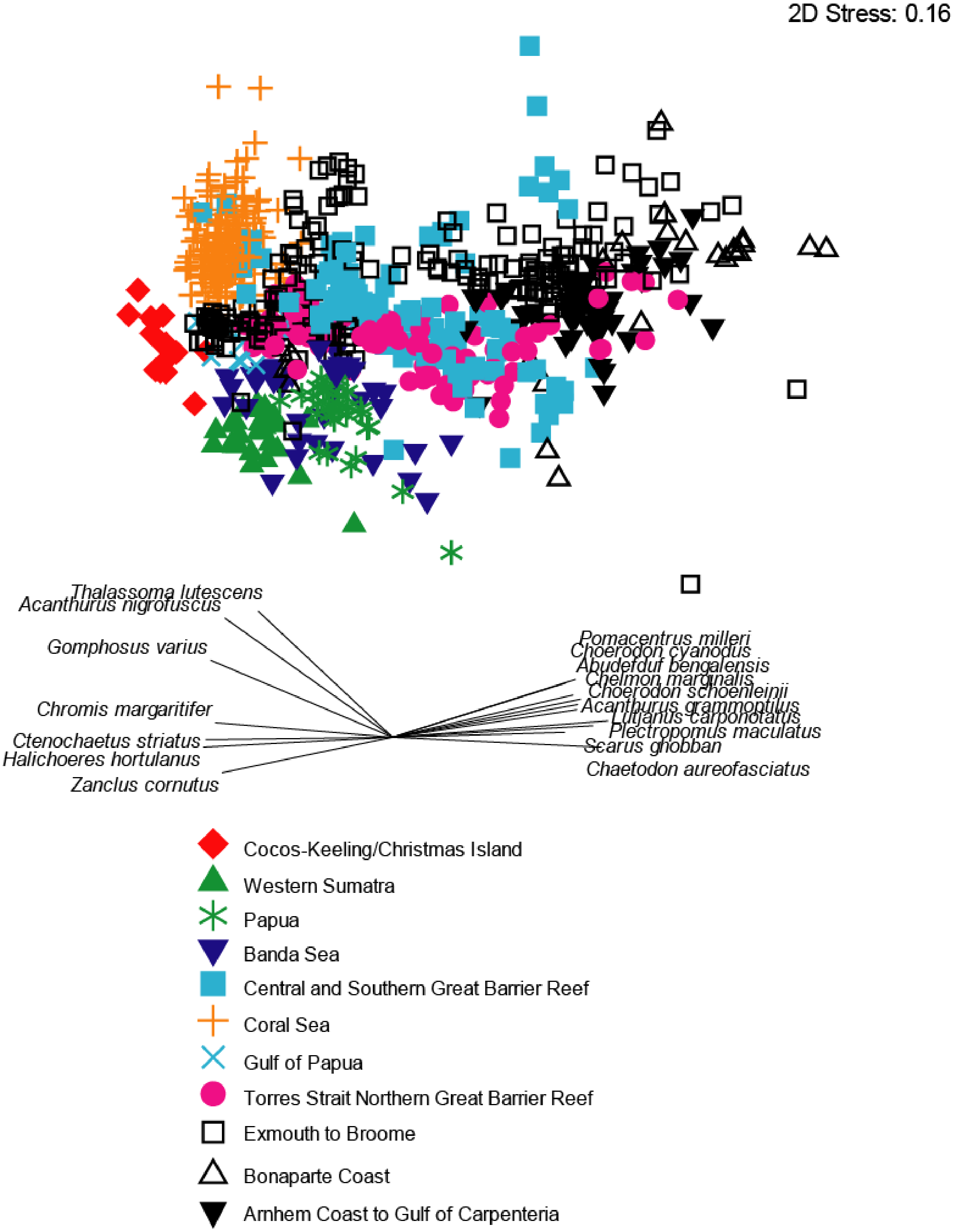


Figure 7. MDS ordination of key reef fish species composition partitioned by ecoregions. Vectors were included if they had a correlation of at least 0.6. Sites in the North CMR Network are identified by black symbols.

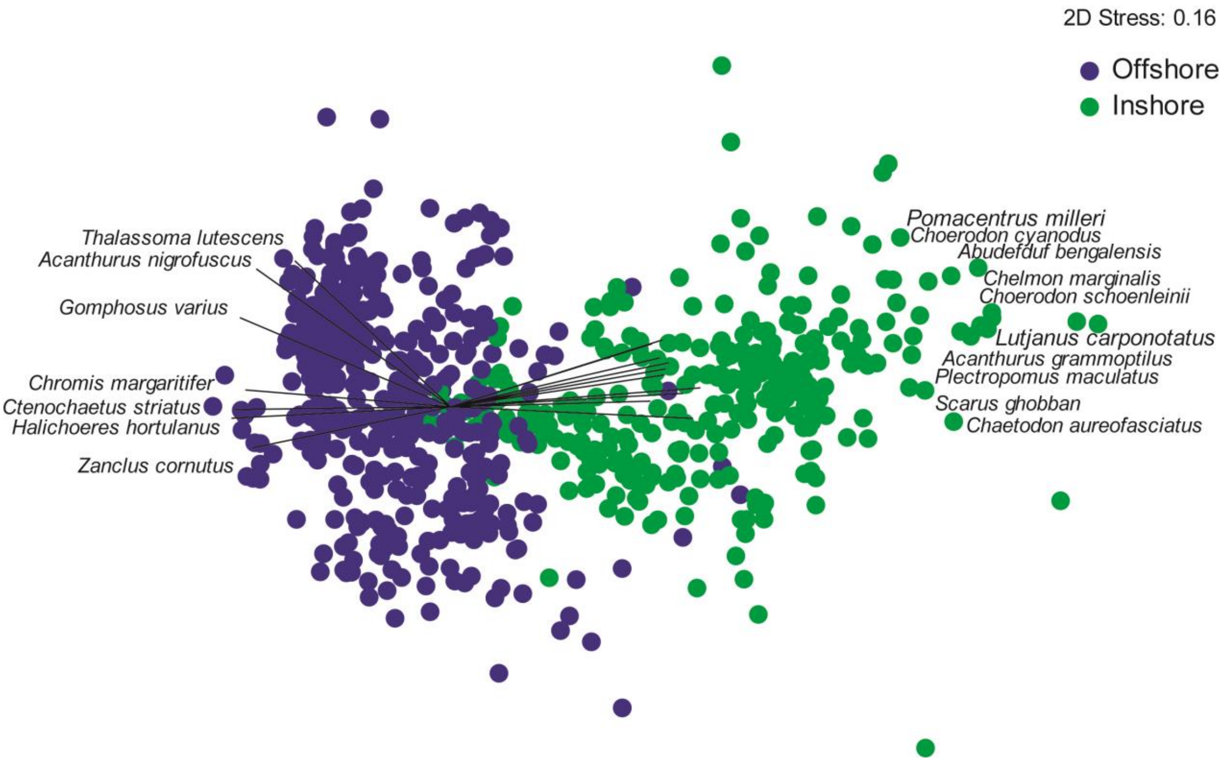


Figure 8. MDS ordination of key reef fish species composition across all ecoregions, partitioned by shelf position. Vectors were included if they had a correlation of at least 0.6.

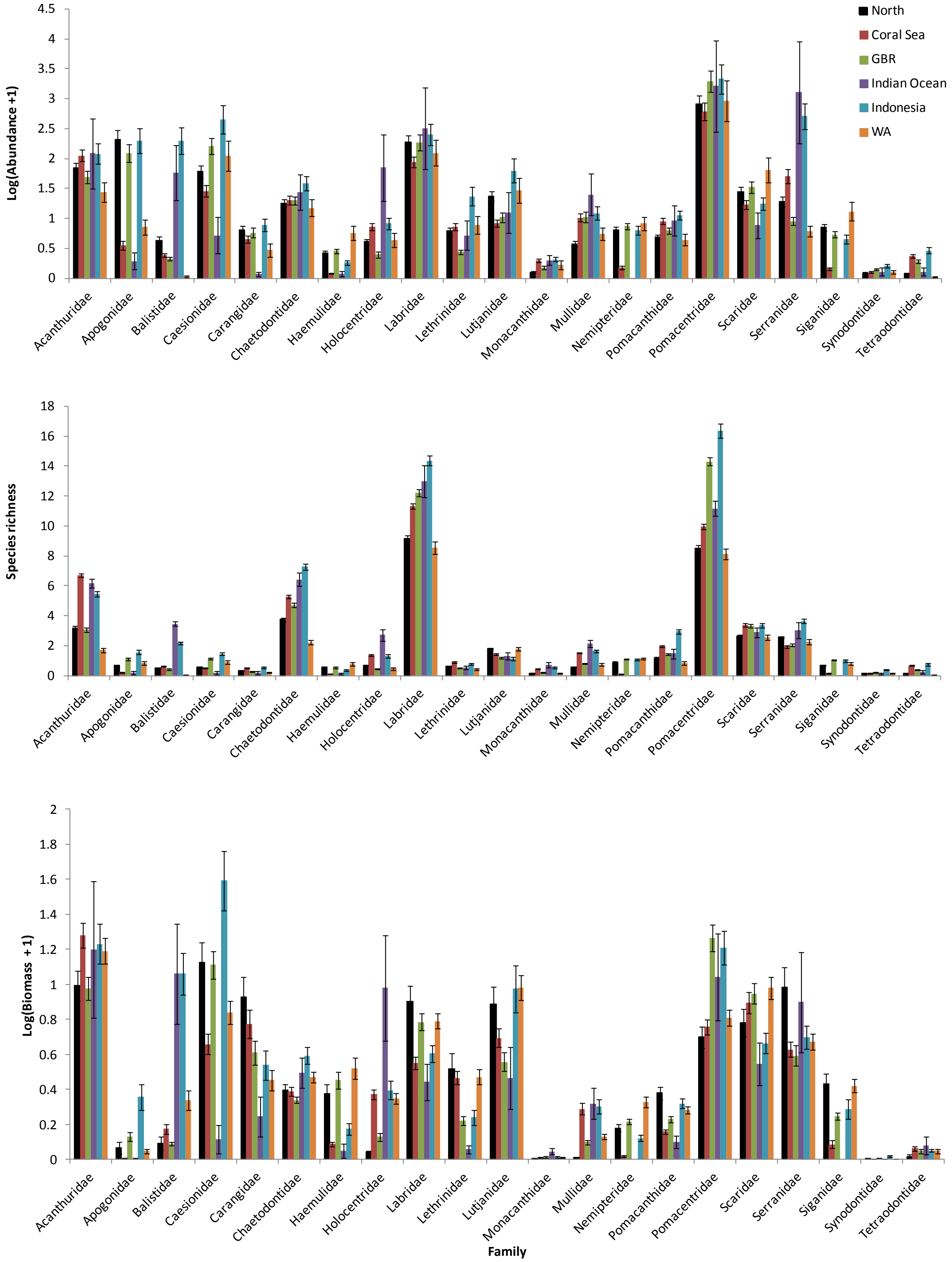


Figure 9. Total abundance, species richness and biomass (kg) of major reef fish families across regions. Abundance and biomass were converted to log(x+1). Error bars ± 1 S.E.

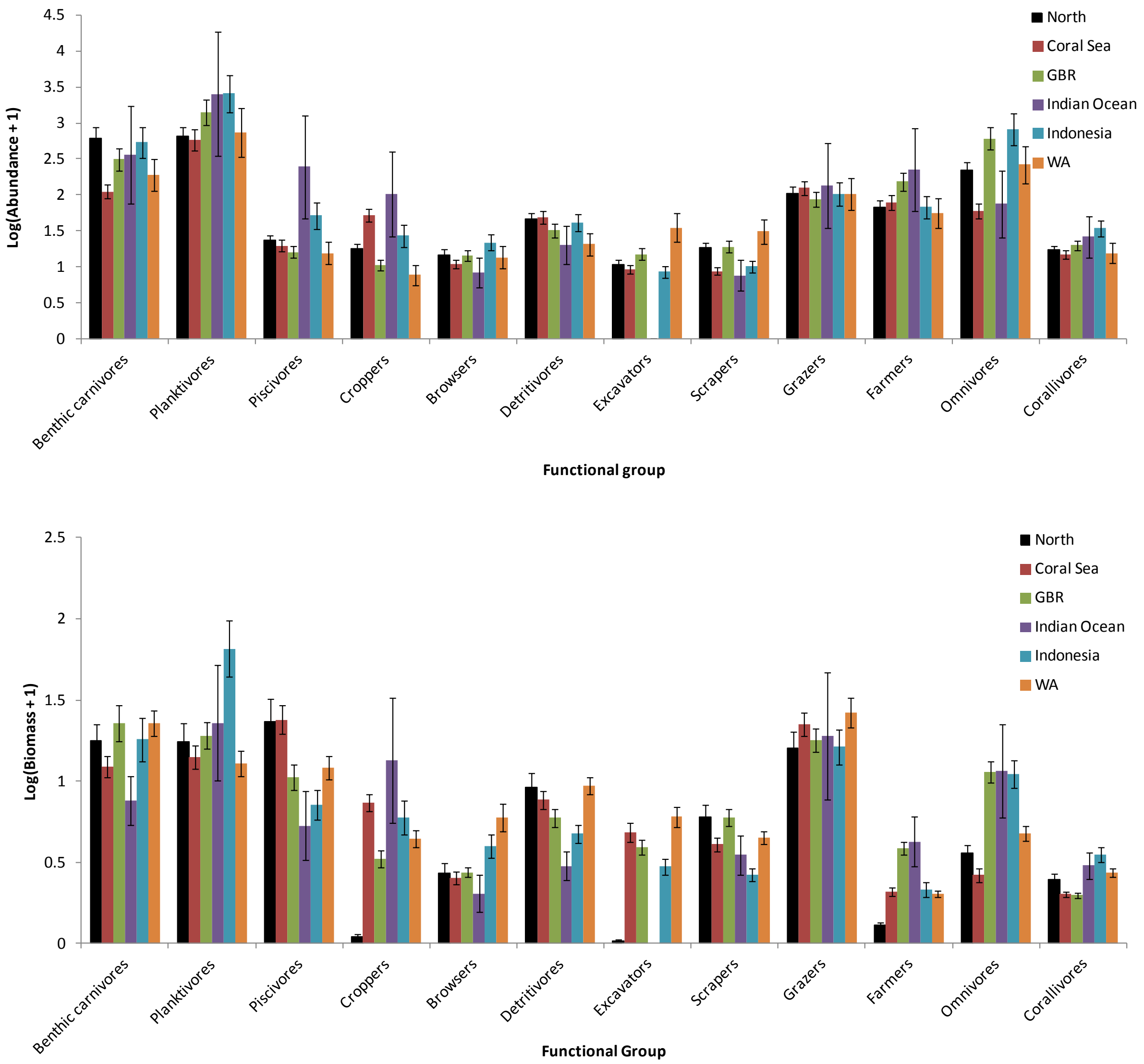


Figure 10. Abundance and biomass of functional groups – log(x+1 transformed) of reef fishes across regions. Error bars ± 1 S.E.

Table 2. ANOVA results of regional differences in abundance, species richness and biomass of pooled reef fishes and major reef fish families. Data were square-root transformed, df = 5, 1530. Tukey HSD results are shown for differences between the North CMR Network reefs and other regions.

Metric	Taxa	F	p	Tukey HSD results (North CMR Network differences)
Abundance	Total	65.6	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia
	Acanthuridae	58.19	< 0.001	Coral Sea, Indonesia, WA, GBR
	Apogonidae	10.85	< 0.001	Coral Sea
	Balistidae	41.65	< 0.001	Indian Ocean, Indonesia
	Caesionidae	38.21	< 0.001	Coral Sea, GBR, Indonesia
	Carangidae	2.301	0.0428	
	Chaetodontidae	31.97	< 0.001	Indonesia, WA
	Haemulidae	24.02	< 0.001	Coral Sea, Indonesia, WA
	Holocentridae	45.48	< 0.001	Coral Sea, Indian Ocean, Indonesia, GBR
	Labridae	22.56	< 0.001	Coral Sea, Indonesia
	Lethrinidae	10.43	< 0.001	Coral Sea, Indonesia, GBR
	Lutjanidae	11.55	< 0.001	Coral Sea, GBR, Indonesia
	Monacanthidae	14.98	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Mullidae	31.55	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Nemipteridae	85.50	< 0.001	Coral Sea, Indian Ocean, WA
	Pomacanthidae	35.57	< 0.001	Coral Sea, Indonesia, WA
	Pomacentridae	59.82	< 0.001	Coral Sea, GBR, Indonesia
	Scaridae	18.11	< 0.001	Coral Sea, Indonesia, WA
	Serranidae	100.9	< 0.001	Indian Ocean, Indonesia
	Siganidae	50.06	< 0.001	Coral Sea, Indian Ocean, Indonesia, WA
	Synodontidae	9.726	< 0.001	Indonesia
	Tetraodontidae	48.01	< 0.001	Coral Sea, GBR, Indonesia
	Benthic carnivores	19.08	< 0.001	Coral Sea
	Planktivores	58.48	< 0.001	GBR, Indian Ocean, Indonesia
	Piscivores	9.331	< 0.001	Indian Ocean
	Croppers	111.7	< 0.001	Coral Sea, Indian Ocean
	Browsers	10.12	< 0.001	Indonesia
	Detritivores	19.43	< 0.001	GBR, WA
	Excavators	5.873	< 0.001	WA
	Scrapers	19.54	< 0.001	Coral Sea, Indonesia, WA
	Grazers	14.3	< 0.001	Coral Sea
	Farmers	31.79	< 0.001	GBR, Indian Ocean
	Omnivores	105.6	< 0.001	Coral Sea, GBR, Indonesia
	Corallivores	34.37	< 0.001	Indonesia
Species richness	Total	99.53	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia
	Acanthuridae	130.3	< 0.001	Coral Sea, Indian Ocean, Indonesia, WA
	Apogonidae	40.17	< 0.001	Coral Sea, Indonesia
	Balistidae	129.5	< 0.001	Coral Sea, Indian Ocean, Indonesia, WA
	Caesionidae	40.1	< 0.001	Coral Sea, GBR, Indonesia
	Carangidae	11.48	< 0.001	Coral Sea

Metric	Taxa	F	p	Tukey HSD results (North CMR Network differences)
	Chaetodontidae	69.58	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia, WA
	Haemulidae	23.0	< 0.001	Coral Sea, Indonesia
	Holocentridae	52.33	< 0.001	Coral Sea, Indian Ocean, Indonesia, GBR
	Labridae	52.79	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia
	Lethrinidae	15.79	< 0.001	Coral Sea, GBR
	Lutjanidae	18.75	< 0.001	Coral Sea, GBR, Indonesia
	Monacanthidae	18.04	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Mullidae	68.64	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Nemipteridae	154.2	< 0.001	Coral Sea, Indian Ocean, Indonesia, WA
	Pomacanthidae	48.11	< 0.001	Coral Sea, Indonesia, WA
	Pomacentridae	111.0	< 0.001	GBR, Indonesia
	Scaridae	9.355	< 0.001	Coral Sea, GBR, Indonesia
	Serranidae	28.91	< 0.001	Coral Sea, GBR, Indonesia
	Siganidae	73.79	< 0.001	Coral Sea, Indian Ocean, GBR
	Synodontidae	12.11	< 0.001	Indonesia
	Tetraodontidae	55.99	< 0.001	Coral Sea, GBR, Indonesia
Biomass	Total	2.252	0.047	Indonesia
	Acanthuridae	24.52	< 0.001	Coral Sea, GBR
	Apogonidae	15.36	< 0.001	Indonesia
	Balistidae	51.18	< 0.001	Indonesia
	Caesionidae	22.40	< 0.001	Indonesia
	Carangidae	5.436	< 0.001	GBR, WA
	Chaetodontidae	22.95	< 0.001	GBR, Indonesia
	Haemulidae	15.05	< 0.001	Coral Sea
	Holocentridae	43.37	< 0.001	GBR, Indian Ocean
	Labridae	32.07	< 0.001	Coral Sea, Indonesia
	Lethrinidae	12.29	< 0.001	Coral Sea, Indonesia
	Lutjanidae	14.83	< 0.001	GBR, Indonesia
	Monacanthidae	6.477	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Mullidae	37.55	< 0.001	Coral Sea, Indonesia
	Nemipteridae	64.45	< 0.001	Coral Sea, GBR, Indonesia
	Pomacanthidae	16.89	< 0.001	Coral Sea, GBR
	Pomacentridae	64.2	< 0.001	GBR, Indonesia
	Scaridae	11.5	0.004	Indonesia
	Serranidae	10.18	< 0.001	Coral Sea, GBR
	Siganidae	35.02	< 0.001	Coral Sea, GBR
	Synodontidae	14.08	< 0.001	Indonesia
	Tetraodontidae	10.34	< 0.001	Coral Sea, GBR, Indonesia
	Benthic carnivores	9.259	< 0.001	Coral Sea
	Planktivores	28.48	< 0.001	Indonesia
	Piscivores	14.22	< 0.001	GBR, Indonesia
	Croppers	63.63	< 0.001	all

Metric	Taxa	F	p	Tukey HSD results (North CMR Network differences)
	Browsers	9.246	< 0.001	Indonesia, WA
	Detritivores	14.29	< 0.001	GBR, Indonesia
	Excavators	32.01	< 0.001	Coral Sea, GBR, Indonesia, WA
	Scrapers	9.978	< 0.001	Indonesia
	Grazers	12.01	< 0.001	Coral Sea, WA
	Farmers	44.56	< 0.001	all
	Omnivores	81.61	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia
	Corallivores	28.23	< 0.001	Coral Sea, GBR, Indian Ocean

MACROINVERTEBRATES

Similar assemblages of macroinvertebrates were recorded across GBR, Torres Strait and Exmouth to Broome sites (Figure 11). Sites in some ecoregions stood out as separate groups (ANOSIM Global R = 0.341, p = 0.001). Coral Sea sites were characterised by a dominance of *Tridacna maxima*, the sea urchins *Echinostrephus* spp. and *Echinometra mathaei,* and the nudibranch *Phyllidia elegans*. In contrast, the North CMR Network coastal sites (Arnhem, Gulf of Carpentaria, Bonaparte) were characterised by *Diadema setosum, Linckia laevigata* and *Holothuria edulis*. The difference between inshore and offshore macroinvertebrate communities was not as distinct as for the fish communities (ANOSIM Global R = 0.178, p = 0.001; see below). The offshore group was dominated by the two giant clams (*Tridacna crocea* and *T. maxima*) and a host of sea urchin species, whilst the inshore group was much more varied (Figure 12).

Significant regional differences were evident in the abundance and species richness of macroinvertebrates (Table 3). Reefs in the North CMR Network had significantly higher macroinvertebrate abundance than the GBR, and significantly lower abundance than Indonesian reefs. Species richness on North CMR Network reefs was lower than most other regions (Figure 13). When examining individual classes, all except the Cephalopoda displayed significant regional differences (Table 3). Reefs in the North CMR Network had higher abundance and species richness than the Coral Sea and GBR for most invertebrate classes, except Asteroidea (lower than the GBR) and Echinoidea (equal to or lower than the Coral Sea). Few differences were found between North CMR Network reefs and WA and the Indian Ocean reefs (Table 3).

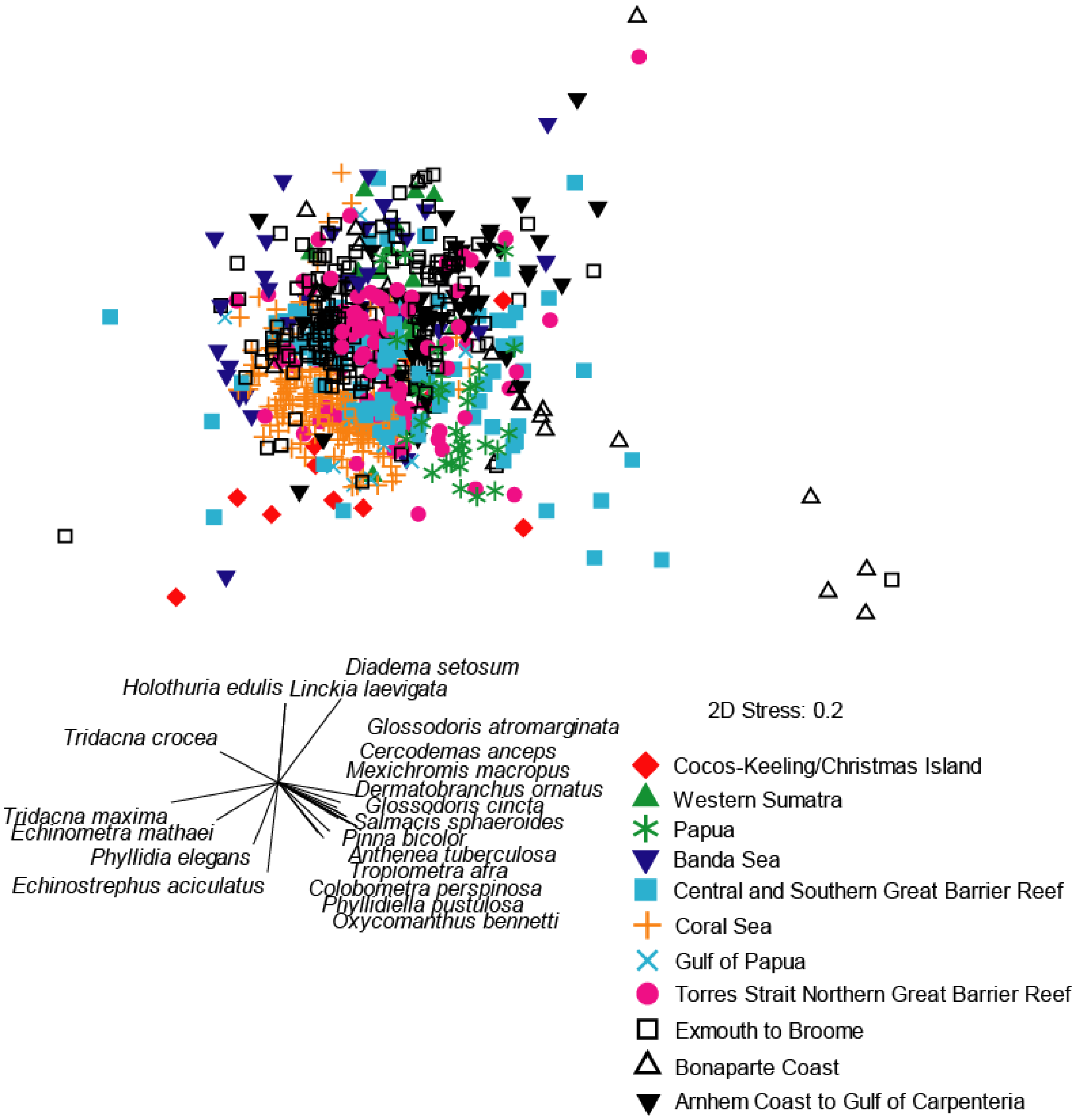


Figure 11. MDS ordination of key macroinvertebrate species composition partitioned by ecoregions. Vectors were included if they had a correlation of at least 0.2. Sites in the North CMR Network are identified by black symbols.

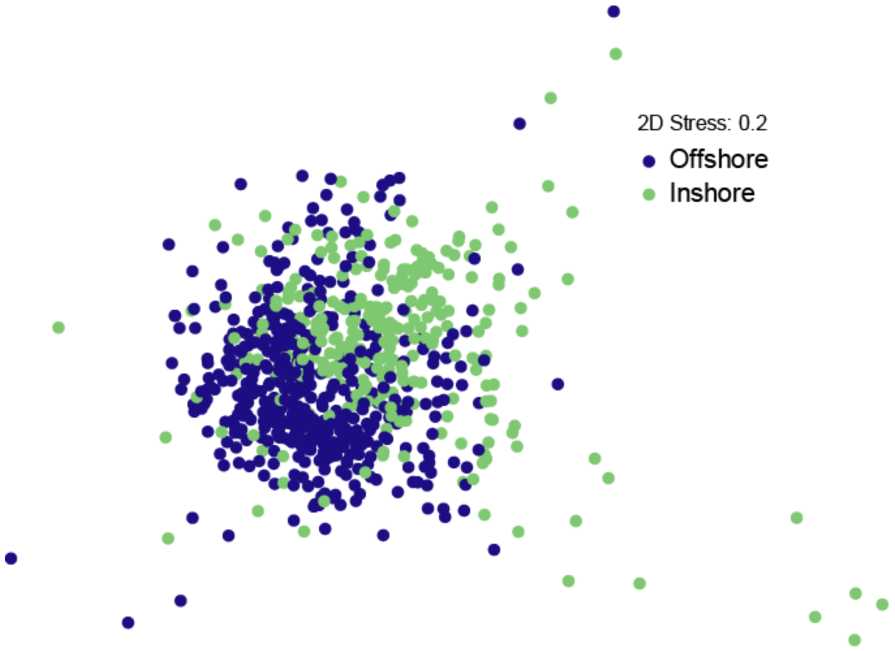


Figure 12. MDS ordination of key macroinvertebrate species composition across all ecoregions, partitioned by shelf position. See Figure 11 for vectors.

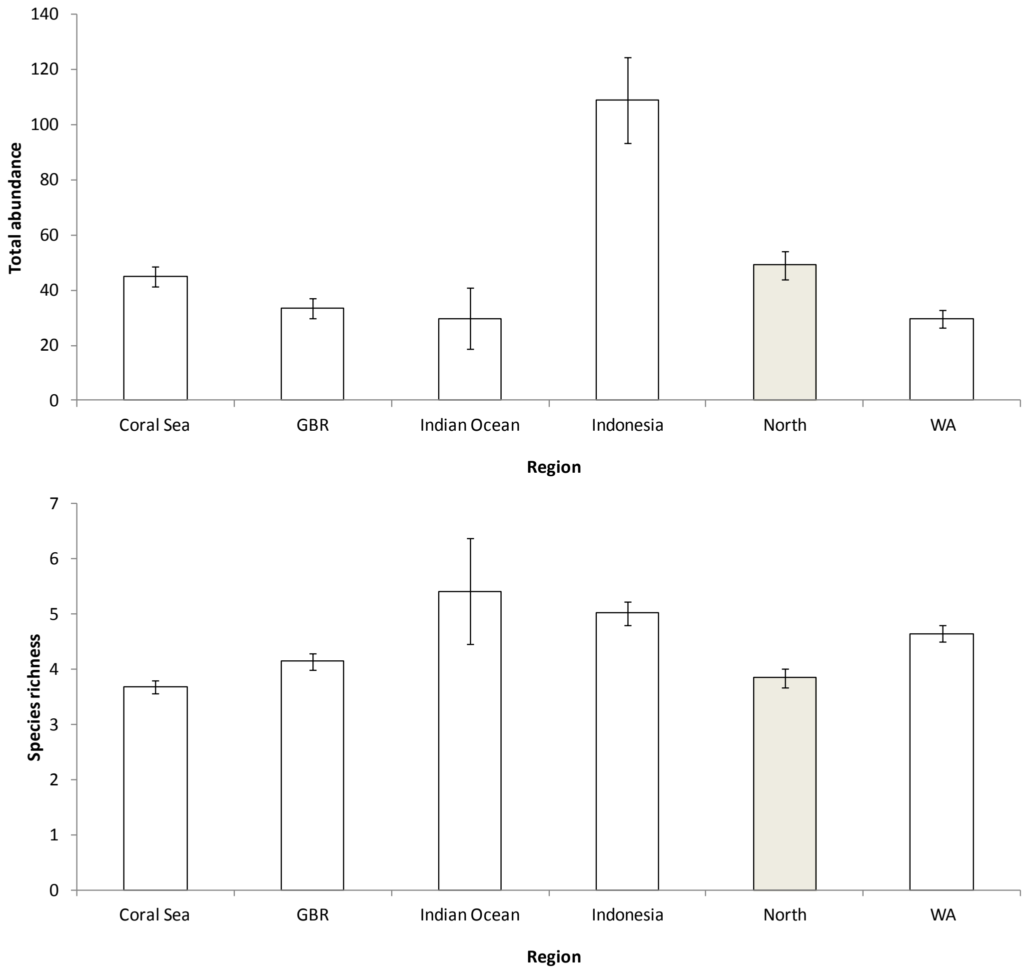
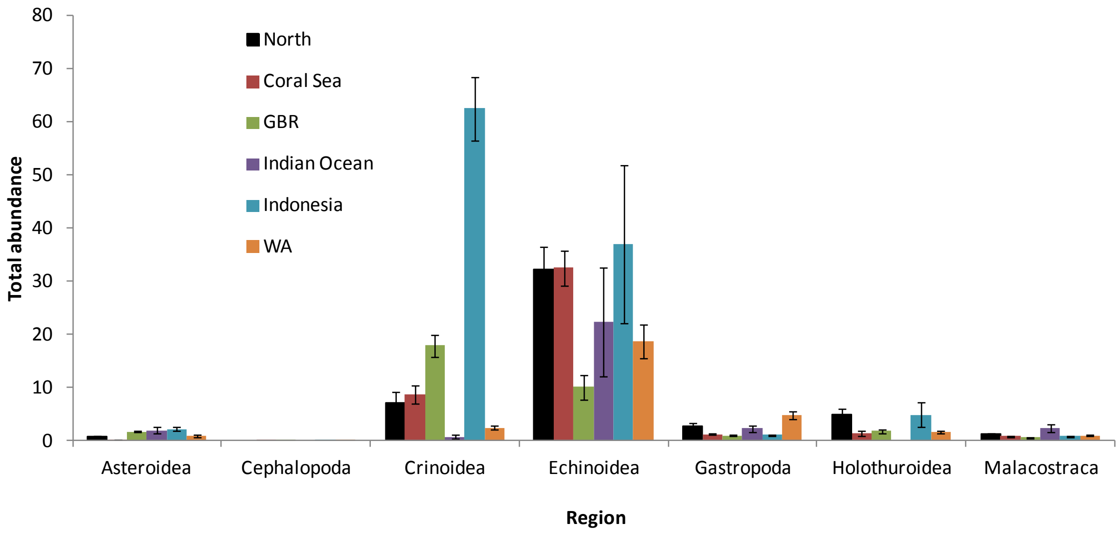


Figure 13. Total abundance and species richness of macroinvertebrates across major regions, with the North CMR Network highlighted. Error bars ± 1 S.E.



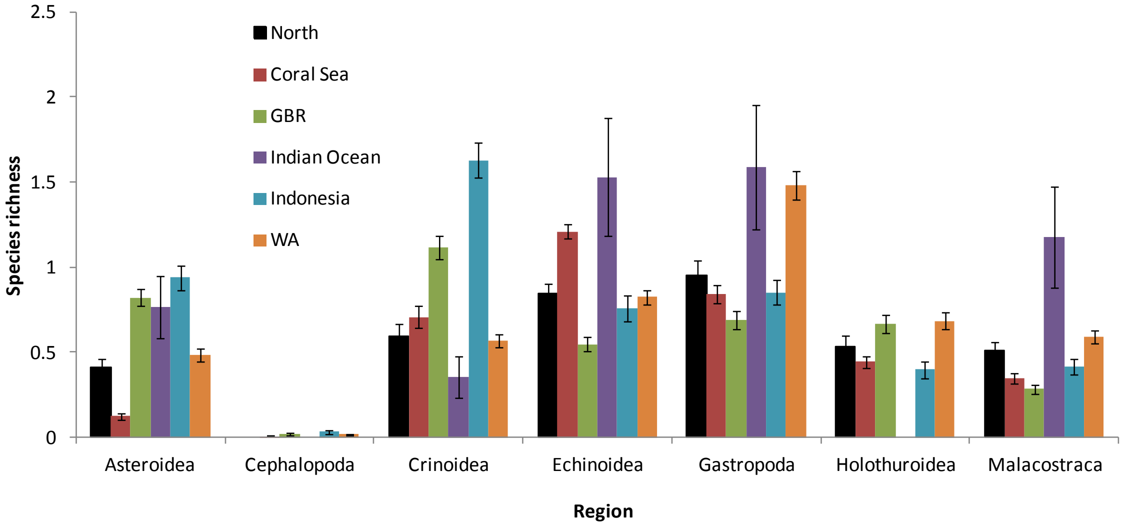


Figure 14. Total abundance and species richness of major macroinvertebrate classes across major regions. Error bars ± 1 S.E.

Table 3. ANOVA results of regional differences in abundance and species richness of pooled macroinvertebrates and major macroinvertebrate classes. Data were square-root transformed. DF = 5/1523. Where Tukey HSD test shows significant differences between the North CMR network and another region, that region is specified.

Metric	Taxa	F	p	Tukey HSD – North CMR Network differences
Abundance	Total	30.78	< 0.001	GBR, Indonesia
	Asteroidea	50.37	< 0.001	Coral Sea, GBR, Indonesia
	Cephalopoda	2.154	0.0567	
	Crinoidea	109.9	< 0.001	Indonesia
	Echinoidea	17.81	< 0.001	Coral Sea, WA, GBR
	Gastropoda	23.23	< 0.001	Coral Sea, GBR, Indonesia
	Holothuroidea	4.437	0.0005	Coral Sea
	Malacostraca	7.554	< 0.001	Indian Ocean
Species richness	Total	7.189	< 0.001	Coral Sea
	Asteroidea	52.36	< 0.001	Coral Sea, GBR, Indonesia
	Cephalopoda	2.023	0.0715	
	Crinoidea	36.46	< 0.001	Indonesia
	Echinoidea	29.66	< 0.001	Coral Sea, GBR
	Gastropoda	13.97	< 0.001	GBR
	Holothuroidea	6.363	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Malacostraca	11.97	< 0.001	Coral Sea, GBR, Indian Ocean

CRYPTIC FISHES

Similar assemblages of cryptic fishes were recorded across GBR, Torres Strait and Papua sites, and these two groups overlapped to a large extent with the Exmouth to Broome and Banda Sea groups (Figure 15). Some ecoregions stood out as separate groups (ANOSIM Global R = 0.242, p = 0.001). Western Sumatra, Cocos-Keeling / Christmas Island and most Coral Sea sites were characterised by a group of species dominated by the small ambush predators *Paracirrhites forsteri* and *P. arcatus* and regional endemic blennies in the genera *Ecsenius* and *Cirripectes*. A larger species group containing some blennies, gobies, cardinalfishes and small predators (serranids and synodontids) characterised the Bonaparte Coast and Arnhem Coast to Gulf of Carpentaria ecoregions. ANOSIM results showed that the greatest overlaps were between the Coral Sea and Cocos-Keeling / Christmas Island and the Coral Sea and the Gulf of Papua. Weak results for the R statistic (< 0.2) were also found for comparisons between Indonesian sites and the Coral Sea; the Banda Sea and the Torrest Strait / Northern GBR ecoregion, Exmouth to Broome ecoregions and the different GBR sections; the Coral Sea and Torres Strait and GBR sections; and Exmouth to Broome compared with the other North CMR Network ecoregions and with Papua (Figure 15). Much clearer distinctions were revealed when the assemblage was partitioned by shelf position (ANOSIM Global R = 0.205, p = 0.001); the first group of dominant cryptic fish species characterised offshore reefs and the second was typical of inshore reefs (Figure 16).

There were significant regional differences in the abundance and species richness of cryptic fishes recorded with Method 2 (Table 4). Reefs in the North CMR Network had significantly higher abundance and species richness than the Coral Sea, but lower species richness than Indonesia (Figure 17). All families displayed significant differences between North Netowrk reefs and other regions (Table 4). Abundance and species richness of most families was generally higher than the Coral Sea and GBR, but lower than Indonesia (Figure 18). Where differences existed between North CMR Network reefs and the Indian Ocean and WA, North CMR Network reefs usually had a lower abundance and species richness of families of cryptic fishes. A notable exception was lower abundance and species richness of Scorpaenidae on North CMR Network reefs than other regions. Cirrhitidae was in higher abundance on North CMR Network reefs than most other regions, but lower species richness (Table 4).

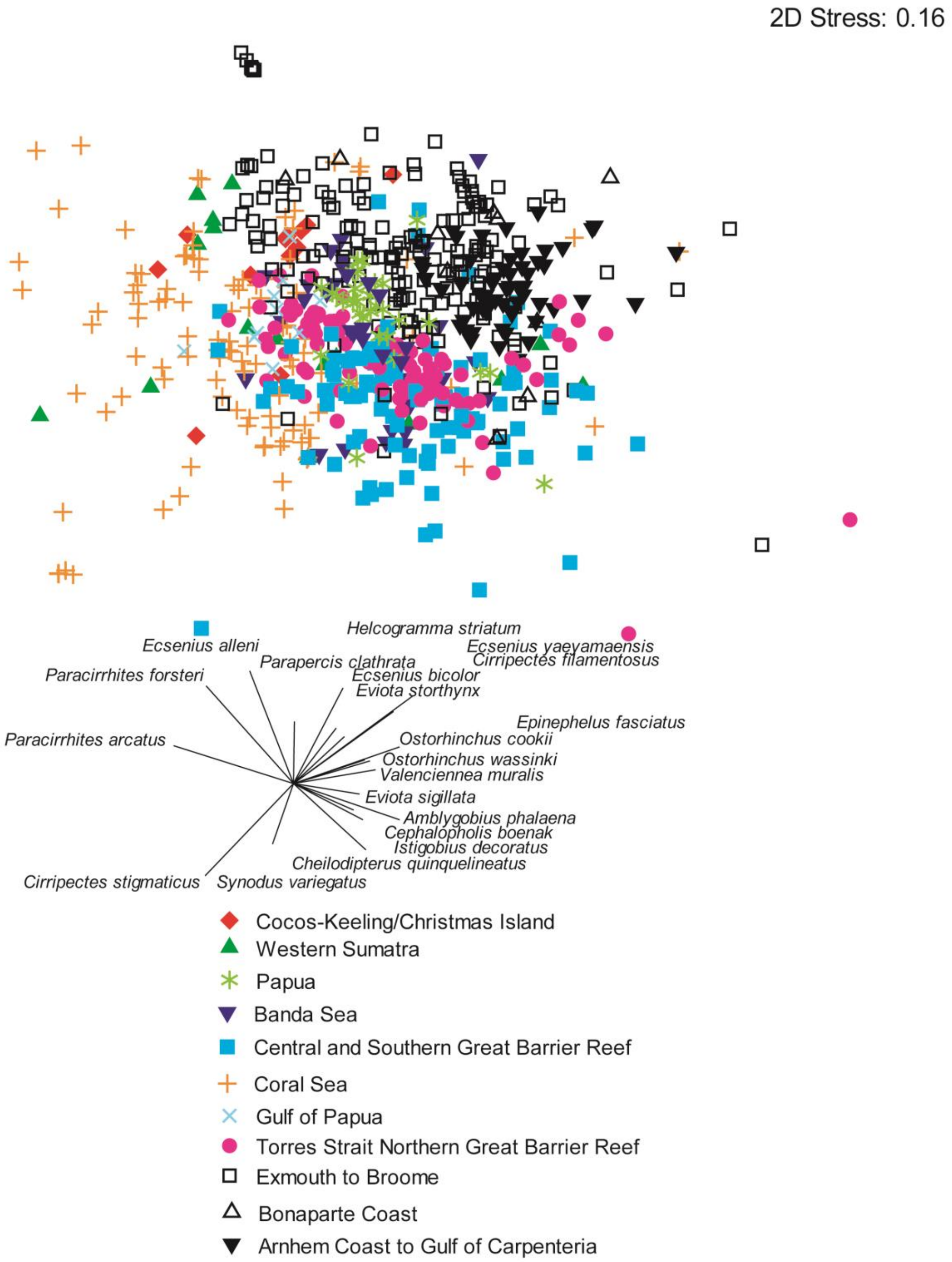


Figure 15. MDS ordination of key cryptic fish species composition partitioned by ecoregions. Vectors were included if they had a correlation of at least 0.2. Sites in the North CMR Network are identified by black symbols.

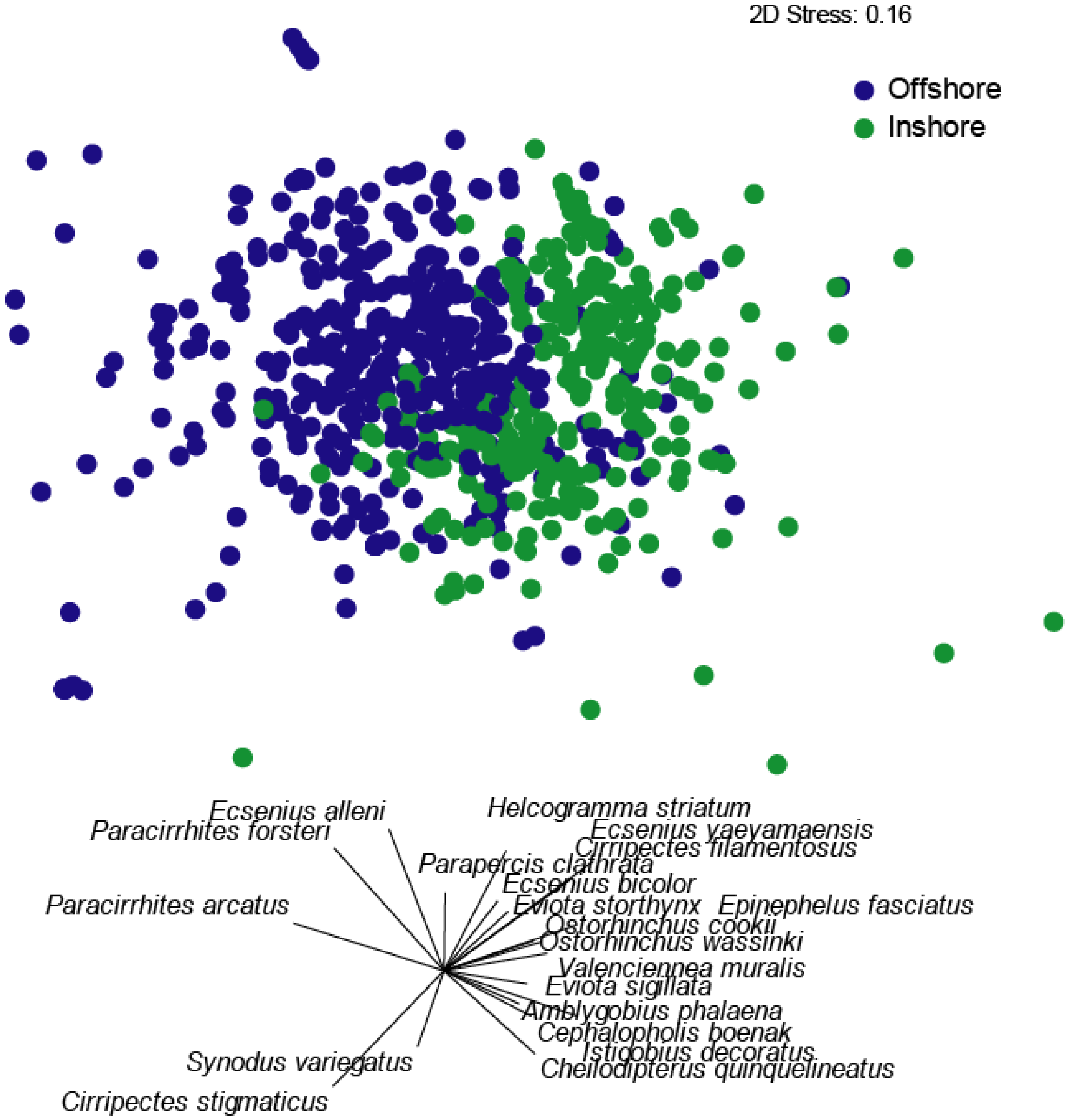


Figure 16. MDS ordination of key cryptic fish species composition across all ecoregions, partitioned by shelf position. Vectors were included if they had a correlation of at least 0.2.

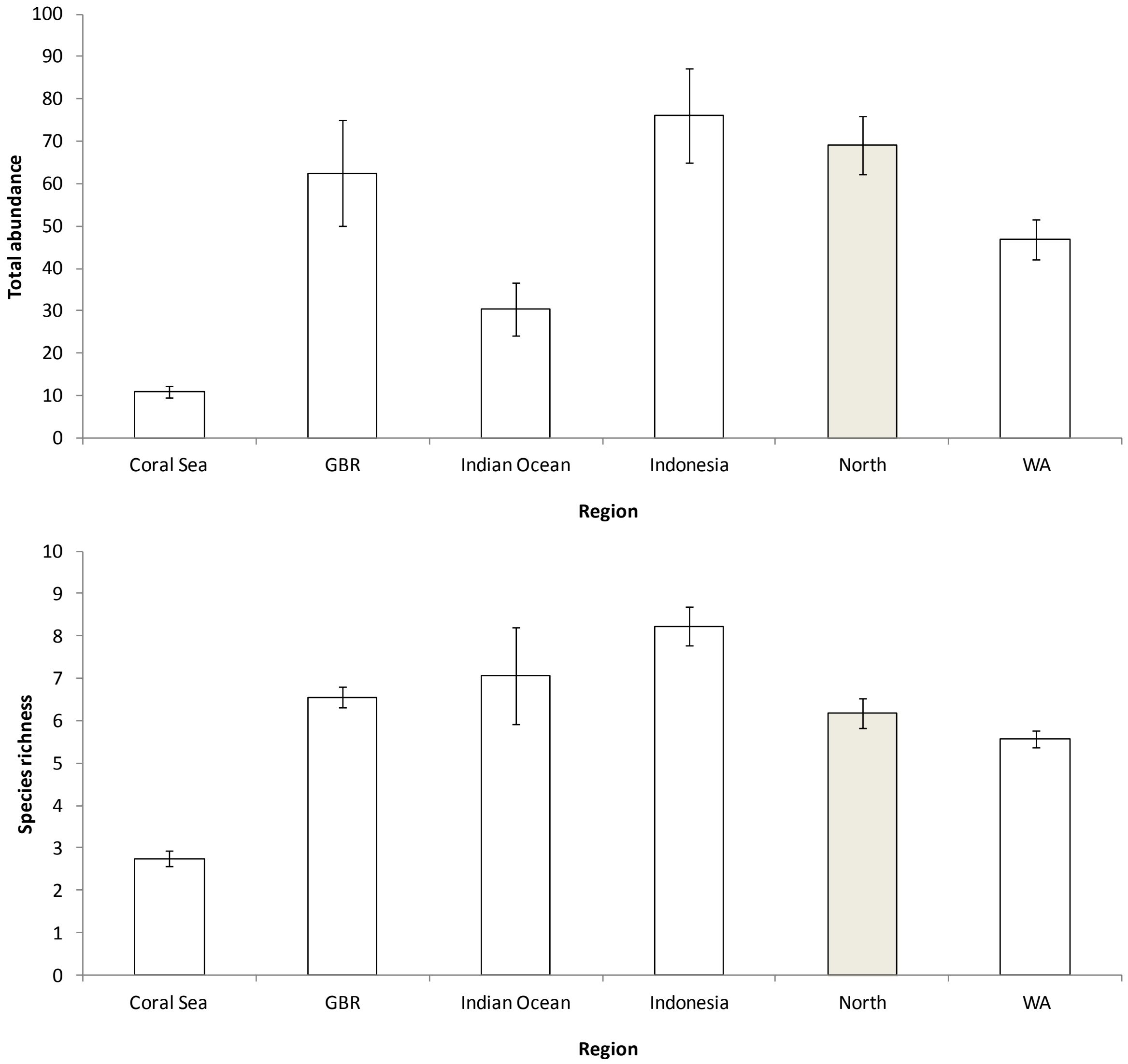


Figure 17. Total abundance and species richness of cryptic fishes recorded with Method 2 across major regions, with the North CMR Network highlighted. Error bars ± 1 S.E.

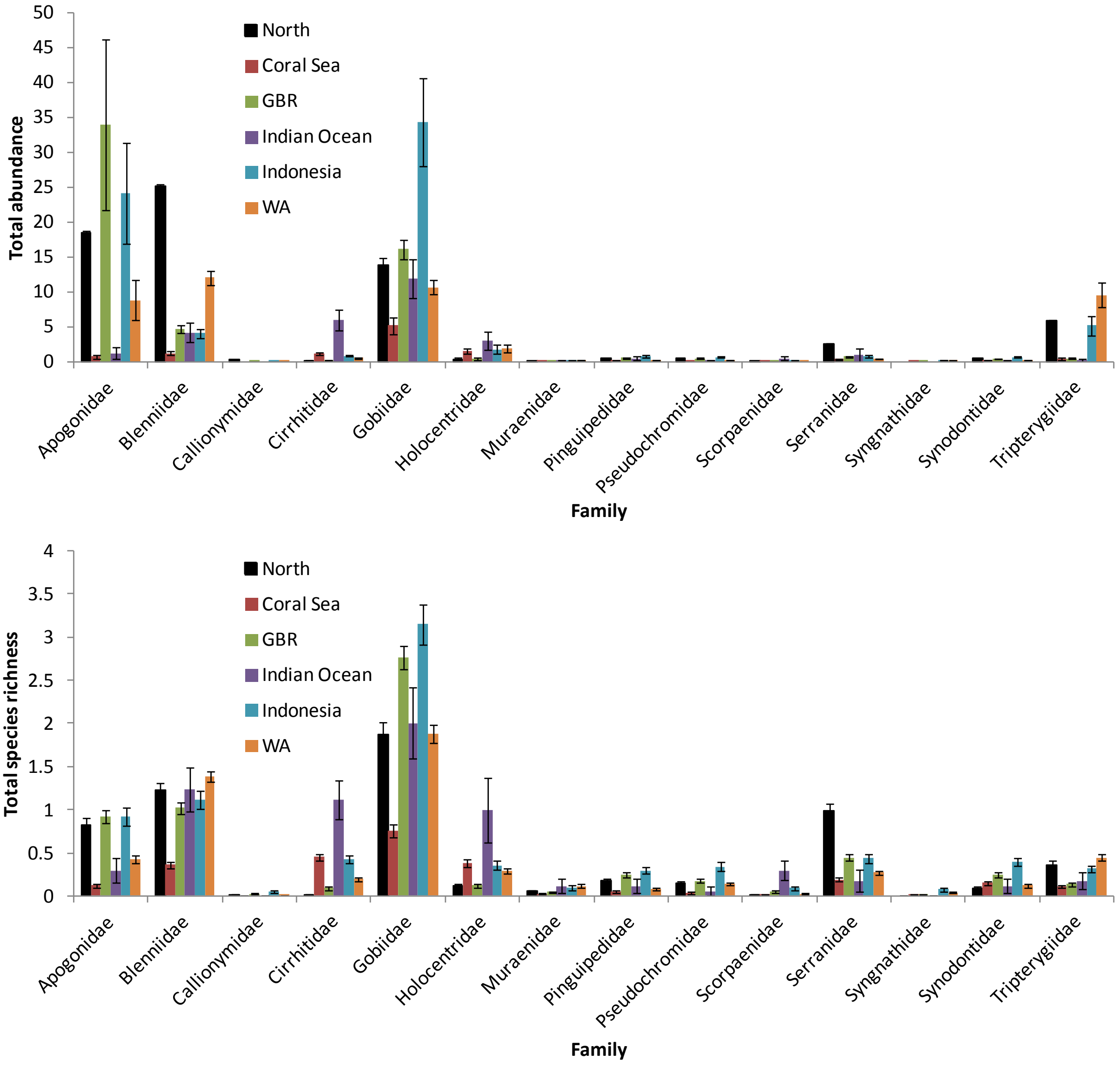


Figure 18. Total abundance and species richness of major cryptic fish families across major regions. Error bars ± 1 S.E.

Table 4. ANOVA results of regional differences in abundance and species richness of pooled cryptic fishes and major cryptic fish families. Data were square-root transformed. DF = 5/1523. Where Tukey HSD test shows significant differences between the North CMR network and another region, that region is specified.

Metric	Taxa	F	p	Tukey HSD – North CMR Network differences
Abundance	Total	42.93	< 0.001	Coral Sea
	Apogonidae	18.53	< 0.001	Coral Sea
	Blenniidae	67.65	< 0.001	Coral Sea, GBR, Indonesia, WA
	Callionymidae	3.789	0.002	
	Cirrhitidae	45.28	< 0.001	Coral Sea, GBR, Indian Ocean, Indonesia
	Gobiidae	39.46	< 0.001	Coral Sea, Indonesia
	Holocentridae	8.137	< 0.001	GBR
	Muraenidae	6.393	< 0.001	Coral Sea, WA
	Pinguipedidae	12.69	< 0.001	Coral Sea, Indonesia
	Pseudochromidae	10.81	< 0.001	Coral Sea, Indonesia
	Scorpaenidae	13.02	< 0.001	GBR, Indian Ocean, Indonesia, WA
	Serranidae	44.79	< 0.001	Coral Sea, GBR, WA
	Syngnathidae	6.143	< 0.001	Indonesia
	Synodontidae	11.23	< 0.001	Indonesia
	Tripterygiidae	28.41	< 0.001	Coral Sea, GBR, WA
Species richness	Total	68.66	< 0.001	Coral Sea, Indonesia
	Apogonidae	38.73	< 0.001	Coral Sea
	Blenniidae	50.27	< 0.001	Coral Sea, GBR, Indonesia, WA
	Callionymidae	6.012	< 0.001	Indonesia
	Cirrhitidae	39.3	< 0.001	Coral Sea, Indian Ocean, Indonesia
	Gobiidae	59.65	< 0.001	Coral Sea, Indonesia
	Holocentridae	10.47	< 0.001	GBR, Indian Ocean
	Muraenidae	5.974	< 0.001	Coral Sea, WA
	Pinguipedidae	16.62	< 0.001	Coral Sea, GBR, Indonesia
	Pseudochromidae	11.83	< 0.001	Coral Sea, Indonesia
	Scorpaenidae	11.13	< 0.001	GBR, Indian Ocean, Indonesia, WA
	Serranidae	34.49	< 0.001	Coral Sea, GBR, WA
	Syngnathidae	6.805	< 0.001	Indonesia
	Synodontidae	15.1	< 0.001	Indonesia
	Tripterygiidae	27.24	< 0.001	Coral Sea, GBR, WA

PART B: NORTH CMR NETWORK PATTERNS

BENTHOS

Benthic communities were similar across the North CMR Network's reefs, with few distinctions among the CMRs and corresponding non-CMR areas (ANOSIM Global R = -0.102; p = 0.07). Nevertheless, some distinctions did occur; non-CMR reefs in the Bonaparte Coast ecoregion were different from those of the Arnhem Coast to Gulf of Carpenteria ecoregions, and within the latter ecoregion, the Arnhem, Gulf of Carpenteria and Wessel CMRs were different from each other. Sites tended to have a dominance of either live corals and algae, or calcified algae and abiotic substrata (Figure 19). The Bonaparte Coast had lower coral cover than the other ecoregions in the North CMR Network ($F_{2,145}$ = 7.607, p < 0.001), but there were no significant differences between individual CMRs ($F_{6,145}$ = 1.531, p = 0.172). The Arnhem Coast to Gulf of Carpentaria ecoregion, which is the largest, had the most variable coral cover, ranging from 15% in the Arnhem CMR to 37% in the Wessel CMR (Figure 20).

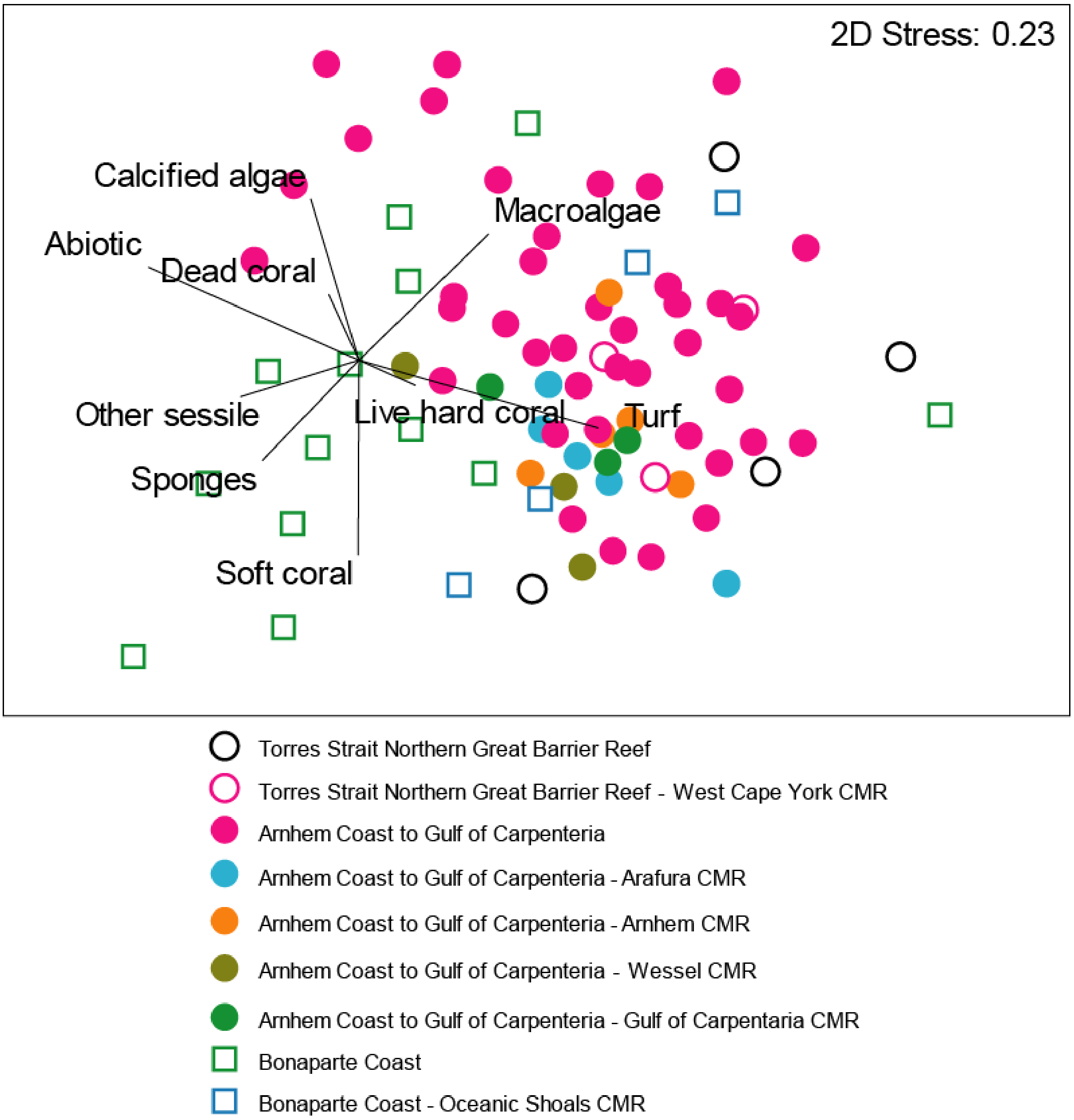


Figure 19. MDS ordination of key benthic components across reefs of the North CMR Network, partitioned by ecoregion and CMR status.

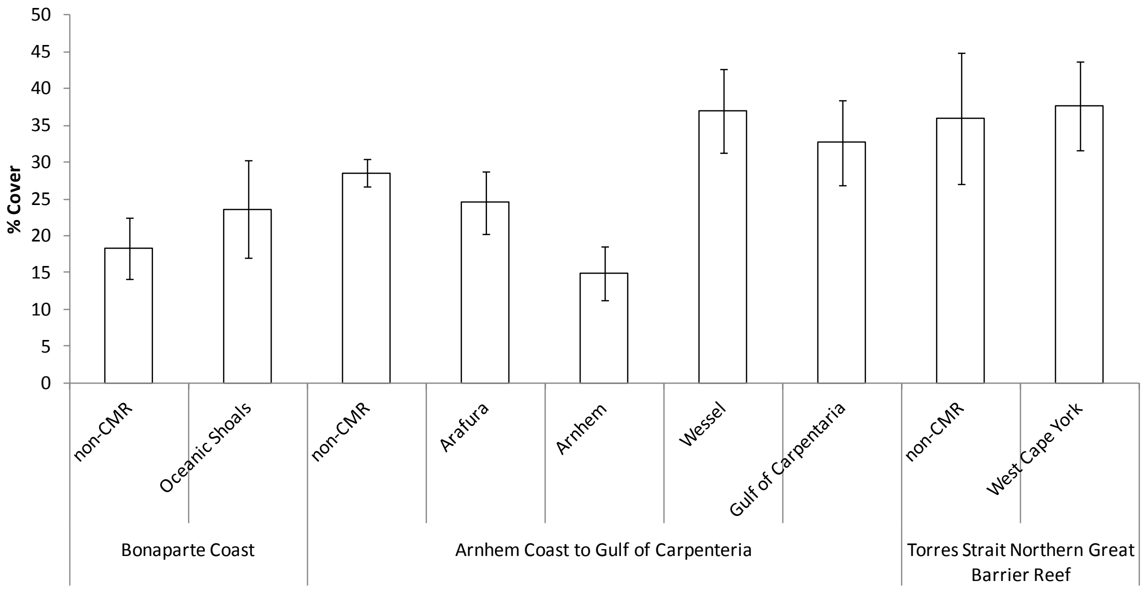


Figure 20. Percentage cover of live hard coral across reefs in the North CMR Network, inside at CMR and non-CMR sites in each area. Error bars ± 1 SE.

REEF FISHES

At a community level, reefs fishes recorded with Method 1 were split into a number of ecoregion – CMR groups, but the clearest separation was again between inshore and offshore assemblages (Figure 21, Figure 22). Two distinct species groups emerged; the first, typical of "clear-water" offshore coral reefs, was dominated by small wrasses (*Halichoeres biocellatus*, *Gomphosus varius*), planktivorous damselfishes (*Chromis* spp., *Dascyllus* spp., *Pomacentrus vaiuli*) and small acanthurids (*Acanthurus pyroferus*, *Ctenochaetus striatus*). The second, containing a smaller number of species, included typical inshore predators (e.g. *Lutjanus carponotatus*), damselfishes (e.g. *Pomacentrus milleri*) and butterflyfishes (e.g. *Chelmon marginalis*). A third group of fishes included small ambush predators (*Cephalopholis boenak*, *Epinephelus fasciatus*) and some planktivorous damselfishes (*Neopomacentrus cyanomos*). The first group of species characterised around half of the non-CMR Bonaparte Coast ecoregion, the Oceanic Shoals CMR and the Arafura CMR (Figure 21). Most other sites were characterised by the second group of fishes, with the third group being characteristic of the Gulf of Carpenteria CMR. Ecoregions had significantly different reef fish assemblages (ANOSIM Global R = 0.549, p = 0.001), with slightly weaker, but still significant, differences between CMRs within ecoregions (ANOSIM Global R = 0.486, p = 0.024). Partitioning the sites by their distance offshore showed a clear distinction between inshore and offshore sites (ANOSIM Global R = 0.616, p = 0.001) (Figure 22).

The abundance and species richness of reef fishes recorded with Method 1 were not significantly different between CMR and non-CMR reefs, but fish biomass was signficiantly higher inside CMRs in general ($F_{1,169}$ = 8.16, p=0.005) (Figure 23). Reef fish abundance did not vary significantly across ecoregions and CMRs, but species richness and biomass did (Figure 24). The highest species richness was recorded at the Mer Outer Reef site (Torres Strait to northern GBR ecoregion, non-CMR), and the highest biomass occurred at Carpentaria Reef (Gulf of Carpentaria CMR).

Dominant fish families in terms of abundance and species richness were the Pomacentridae and Labridae; the highest biomass was recorded for Caesionidae inside CMRs (Figure 25). Key differences in the abundance of fishes between CMR and non-CMR reefs were higher abundance of Chaetodontidae and Scaridae outside CMRs, and higher abundances of Labridae, Lethrinidae and Pomacentridae inside. These patterns were slightly different for species richness and biomass; there was higher species richness of Lethrinidae, Nemipteridae and Serranidae inside CMRs and higher species richness of Pomacentridae outside. Biomass was higher inside CMRs for Caesionidae, Chaetodontidae, Holocentridae, Lutjanidae, Mullidae and Pomacanthidae, but higher outside CMRs for Scaridae (Figure 25Figure 9).

CMR and non-CMR reefs across the North CMR Network could be distinguished by their relative dominance of individual functional groups of reef fishes; some CMRs had an overwhelming dominance of either benthic carnivores and/or planktivores, and others had a more even representation of functional groups (Figure 26). In the Arnhem Coast to Gulf of Carpentaria Ecoregion, benthic carnivores dominated non-CMR reefs, followed by planktivores and grazers; the Gulf of Carpentaria CMR reflected this pattern. The Arafura and Wessel CMRs showed the opposite trend, with more planktivores than benthic carnivores, and the Arnhem CMR had more even, albeit very low, abundance of all functional groups. The Oceanic Shoals CMR was similar to the non-CMR reefs of the Bonaparte Coast ecoregion, except for an order of magnitude more planktivores inside the CMR. Piscivores were most abundant in the Gulf of Carpentaria and Wessel CMRs. Biomass was generally more evenly spread across functional groups in most ecoregions and CMRs, except for a very high biomass (133 kg 500m^{-2}) of piscivores in the Gulf of Carpenteria CMR. Non-CMR reefs of the Bonaparte Coast and Torres Strait to Northern GBR ecoregions had low biomass of all functional groups (Figure 26).

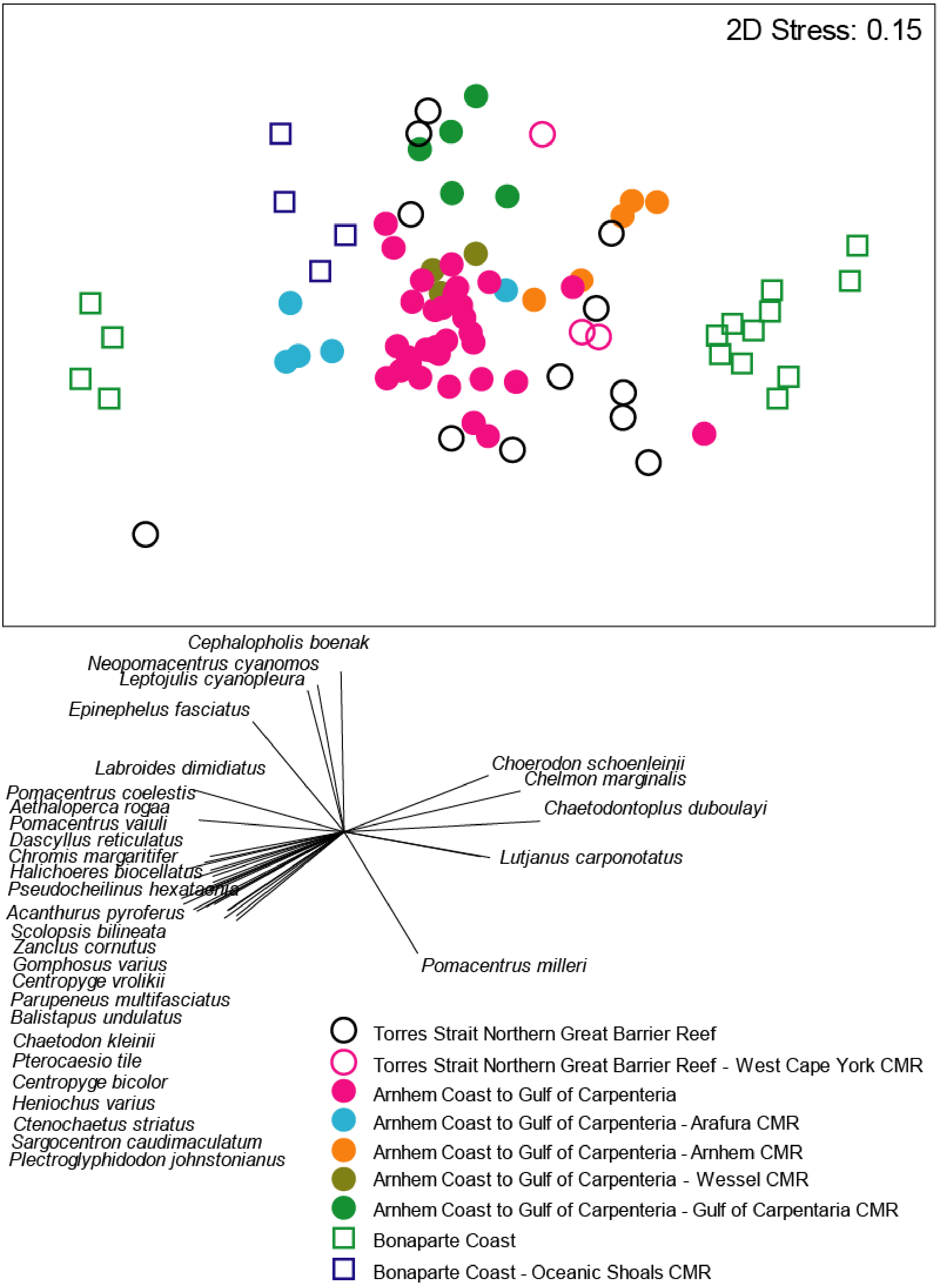


Figure 21. MDS ordination of key reef fish species composition across reefs in the North CMR Network, partitioned by ecoregion and CMR. Vectors were included if they had a correlation of at least 0.5.

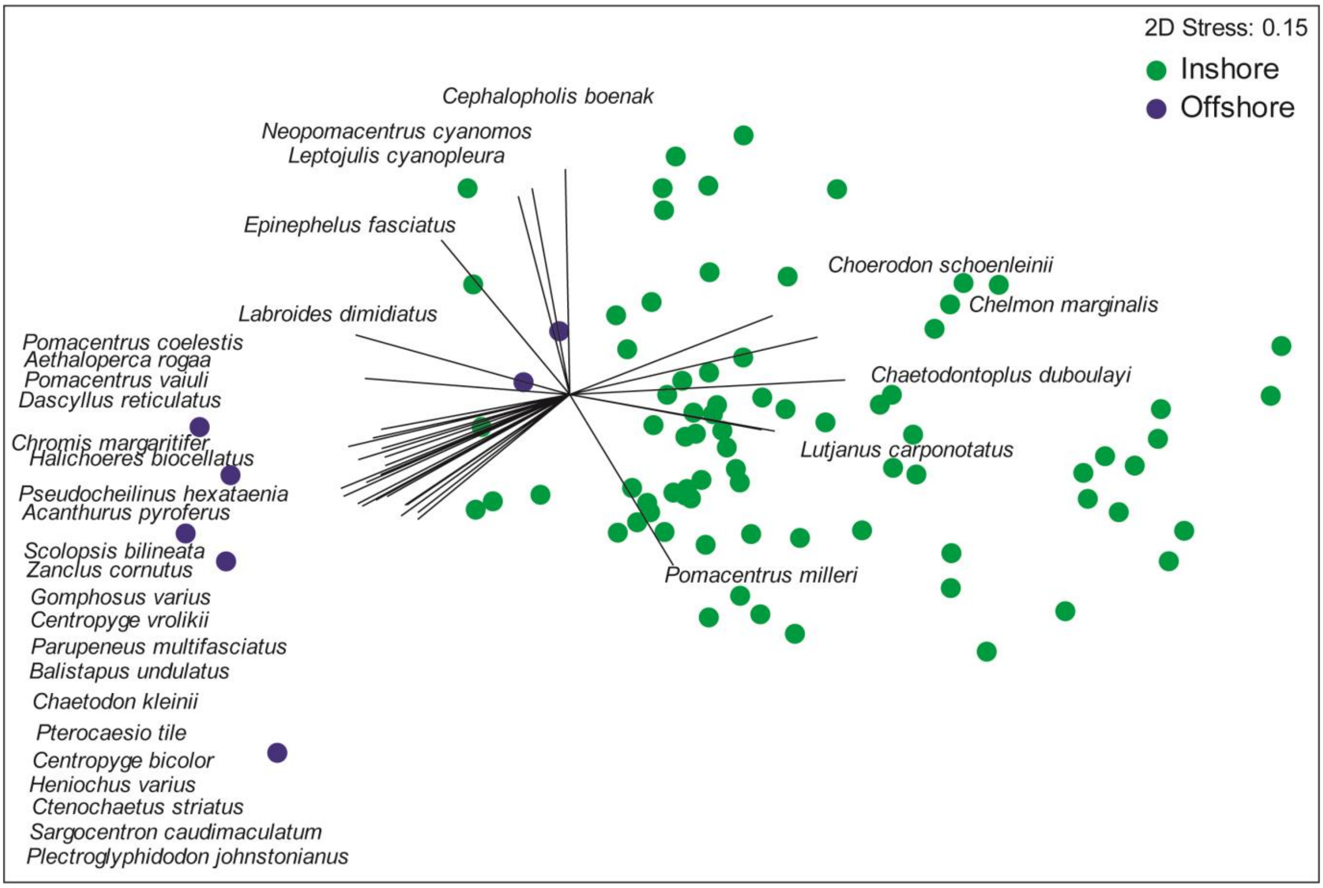


Figure 22. MDS ordination of key reef fish species composition across reefs of the North CMR Network, partitioned by shelf position. Vectors were included if they had a correlation of at least 0.5.

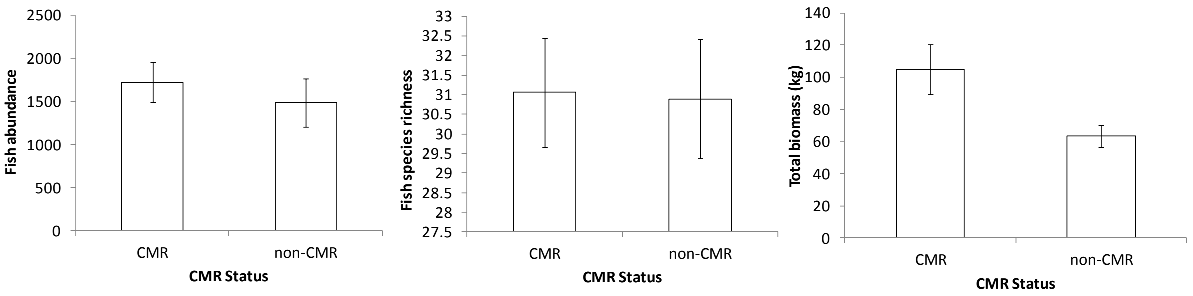


Figure 23. Abundance, species richness and biomass of reef fishes across reefs of the North CMR Network, on CMR and non-CMR reefs. Error bars ± 1 SE.

Table 5. Results of 2-way ANOVA testing differences between ecoregions and CMRs within ecoregions. Contrasts show significant differences between individual Ecoregions or CMRs; BC: Bonaparte Coast; Arn_GoC: Arnhem Coast to Gulf of Carpenteria; TS-GBR: Torres Strait to Northern Great Barrier Reef.

		F	**df**	**p**	**Contrasts**
Abundance	Ecoregion	1.862	2,157	0.159	
	CMR	1.489	6,157	0.185	
Species richness	Ecoregion	6.702	2,157	0.002	BC - Arn_GoC BC - TS-GBR
	CMR	2.277	6,157	0.039	
Biomass	Ecoregion	4.821	2,162	0.009	BC - Arn_GoC
	CMR	6.293	6,162	<0.001	Arafura- non-CMR Arnhem- non-CMR GoC- non-CMR

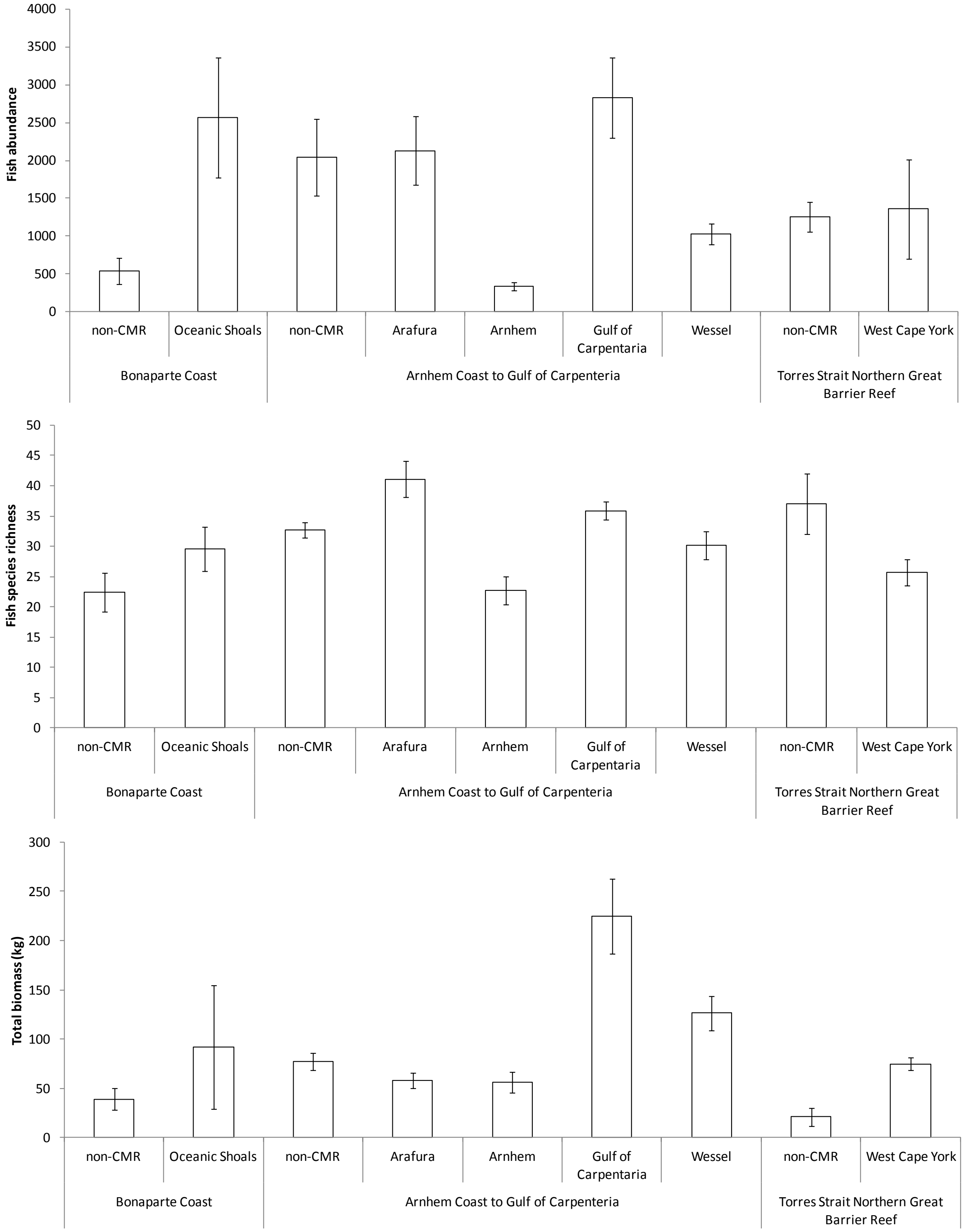


Figure 24. Abundance, species richness and biomass of reef fishes across reefs of the North CMR Network, at CMR and non-CMR sites in each area. Error bars ± 1 SE.

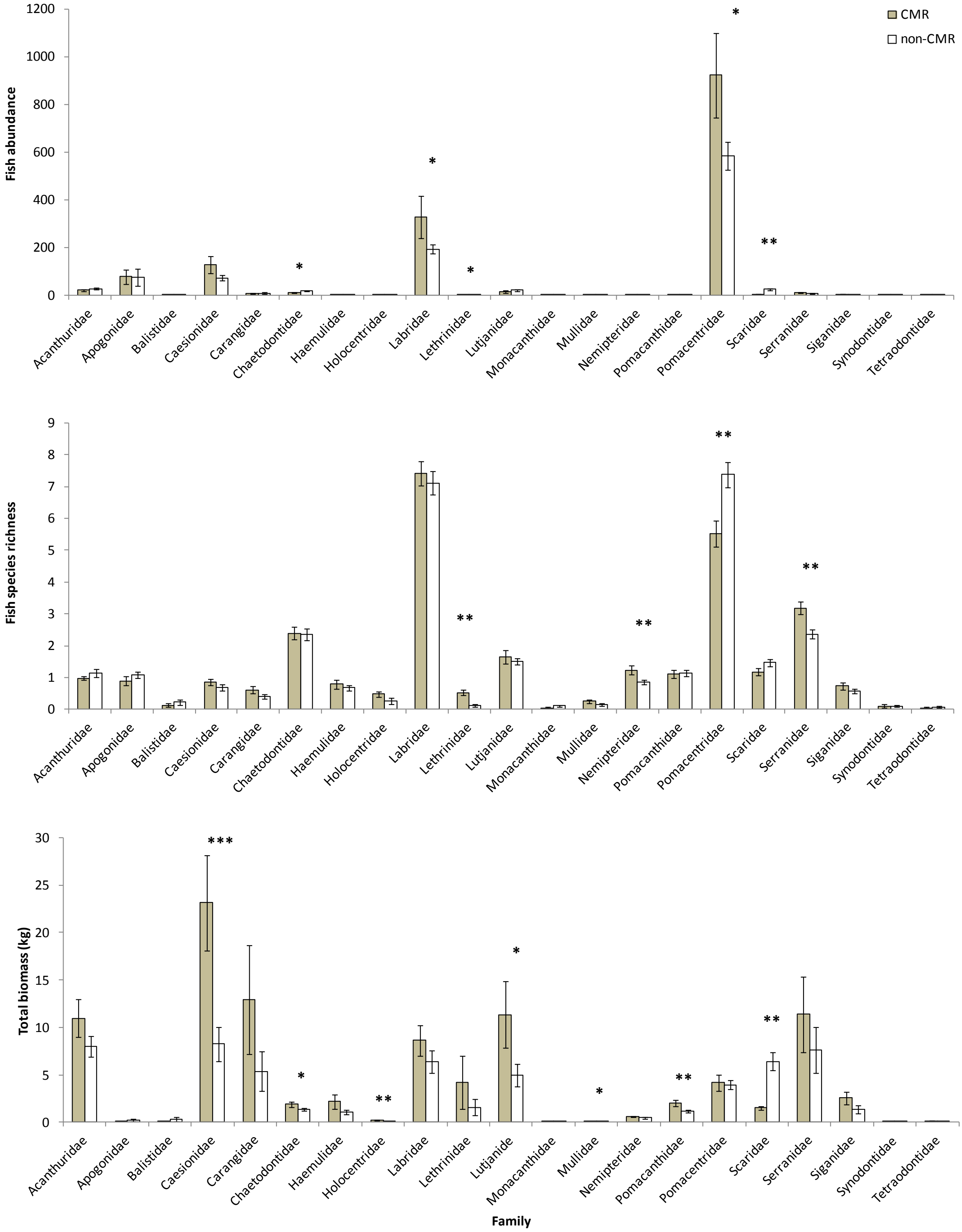


Figure 25. Abundance, species richness and biomass of reef fish families on CMR and non-CMR reefs in the North CMR Network. Symbols for ANOVA significance: * p < 0.05; ** p < 0.01; *** p < 0.001.

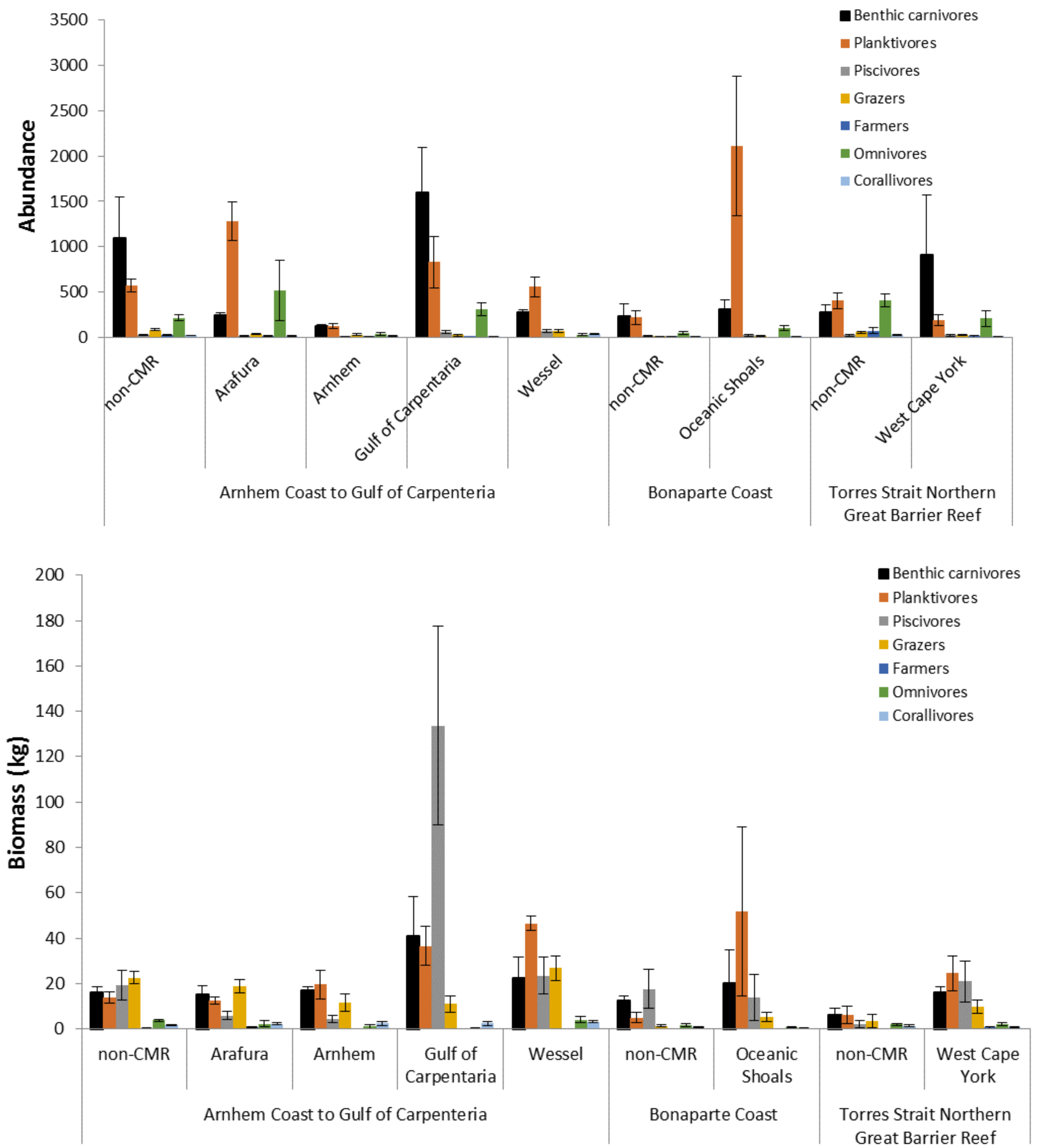


Figure 26. Abundance and biomass of reef fish functional groups on CMR and non-CMR reefs in the North CMR Network.

MACROINVERTEBRATES

Macroinvertebrate assemblages were distinct across CMRs in the North CMR Network. The main distinction was between the Bonapare Coast non-CMR reefs and all CMRs (ANOSIM Global R = 0.393, p = 0.001). Bonaparte coast reefs were characterised by crinoids and an assortment of echinoderms and molluscs (Figure 27). The Arafura and Arnhem CMRs had a high proportion of *Echinaster luzonicus*, *Linckia multifora*, *Fromia indica* and *Phyllidia coelestis*, whilst the Wessel, Gulf of Carpentaria and West Cape York CMRs were characterised by *Culcita novaeguineae* and *Diadema setosum*.

Macroinvertebrate abundance and species richness were not significantly different between CMR and non-CMR reefs overall (Figure 28). Macroinvertebrates were most abundant in the Arnhem Coast to Gulf of Carpentaria ecoregion, with the highest abundances in the Arafura and Wessel CMRs; the Arnhem CMR had the lowest abundances of macroinvertebrates (Figure 29, Table 6). Species richness of macroinvertebrates also varied across the region's reefs. The highest species richness was found in the Arafura CMR and from non-CMR reefs, and the lowest species richness values were recorded from two CMRs (Oceanic Shoals and Arnhem, Figure 29). Crinoids and echinoids were the most abundant macroinvertebrate classes on the North CMR Network's reefs, but gastropods were the most species-rich (Figure 30). The classes Asteroidea and Crinoidea were more abundant and species-rich inside CMRs, but the classes Holothuroidea and Malacostraca were more species-rich on non-CMR reefs. Thus, although the CMRs included equivalent densities of holothurians (sea cucumbers), the local richness of holothurian species was lower inside the CMRs than reefs outside these.

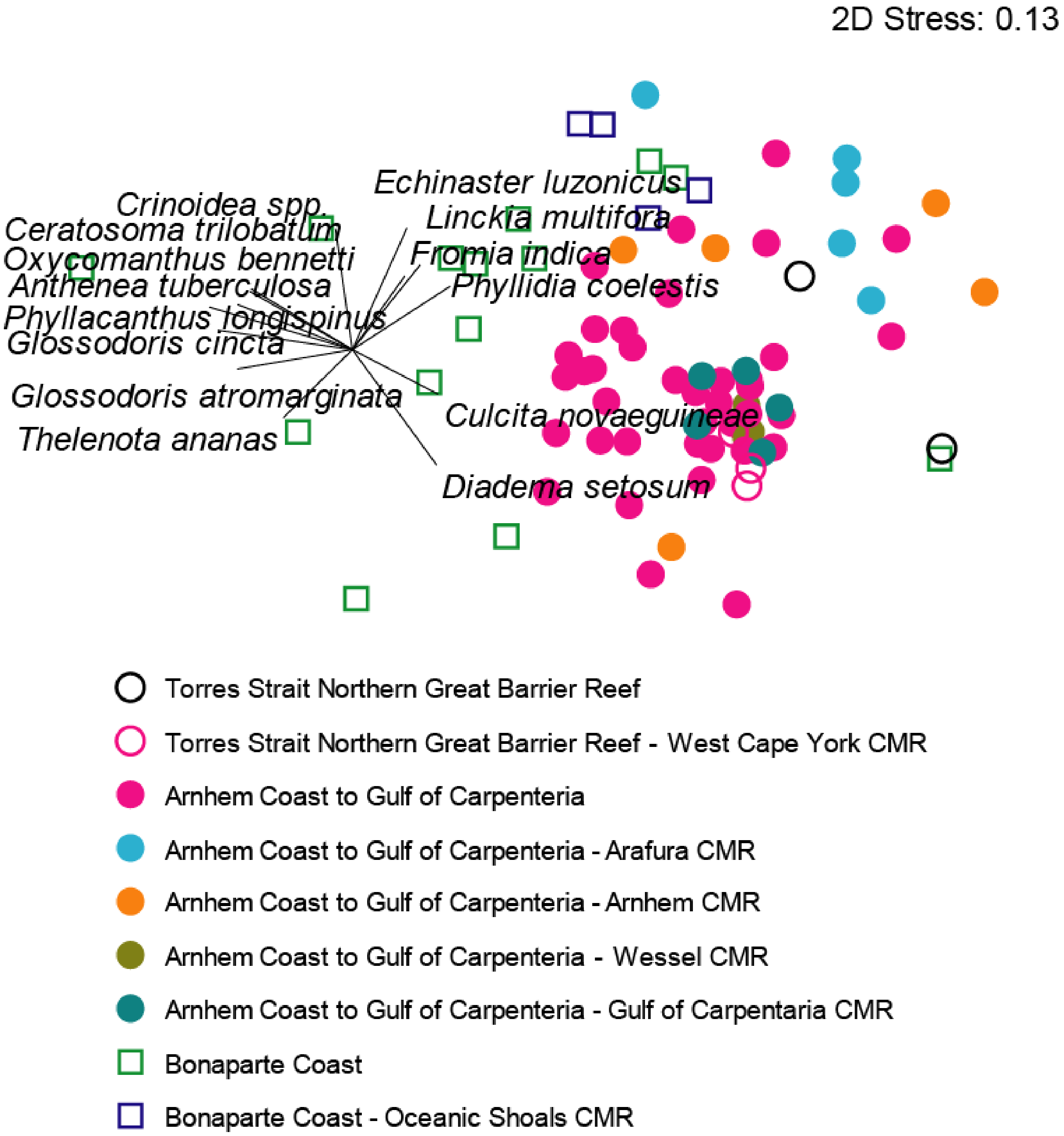


Figure 27. MDS ordination of key macroinvertebrate species composition across reefs of the North CMR Network, partitioned by ecoregion and MPA name. Vectors were included if they had a correlation of at least 0.3.

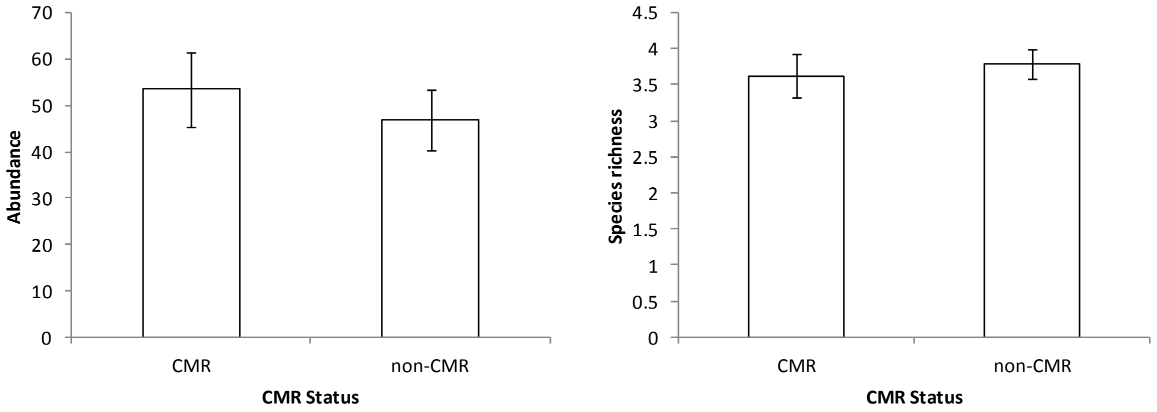


Figure 28. Abundance and species richness of macroinvertebrates across reefs of the North CMR Network, on CMR and non-CMR reefs. Error bars ± 1 SE.

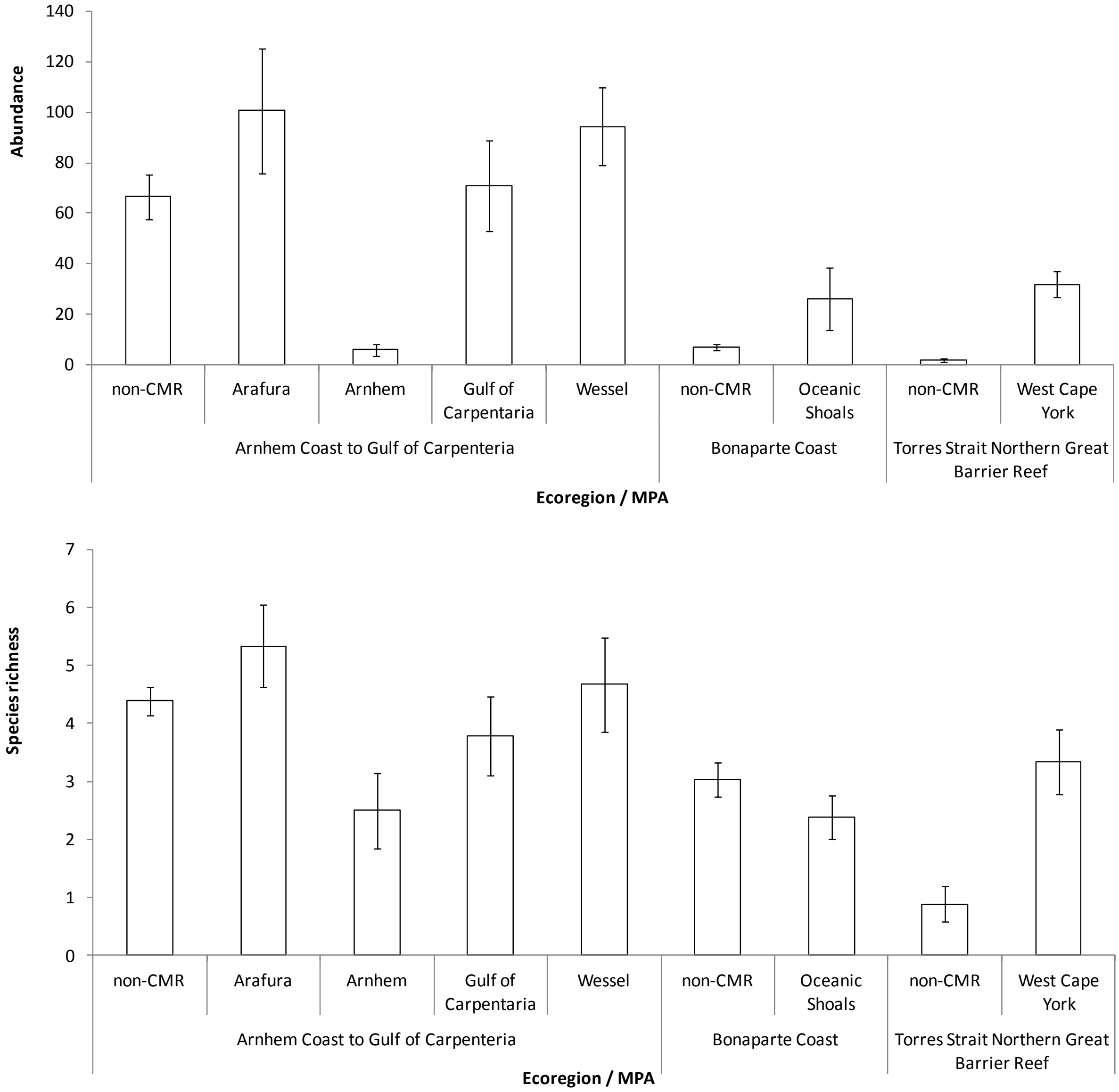


Figure 29. Abundance and species richness of macroinvertebrates across reefs of the North CMR Network, on CMR and non-CMR sites in each area. Error bars ± 1 SE.

Table 6. Results of 2-way ANOVA testing differences between ecoregions and CMRs within ecoregions. Contrasts show significant differences between individual Ecoregions or CMRs; BC: Bonaparte Coast; Arn_GoC: Arnhem Coast to Gulf of Carpenteria; TS-GBR: Torres Strait to Northern Great Barrier Reef.

		F	df	p	Contrasts
Abundance	Ecoregion	14.183	2,162	<0.001	BC-Arn_GoC
					TS-GBR – Arn_GoC
	CMR	2.515	6,162	0.0236	Arhem-Arafura
Species richness	Ecoregion	14.244	2,162	<0.001	BC - Arn_GoC
					TS-GBR – Arn_GoC
	CMR	2.952	6,162	0.00923	Arhem-Arafura
					W Cape York - Arnhem

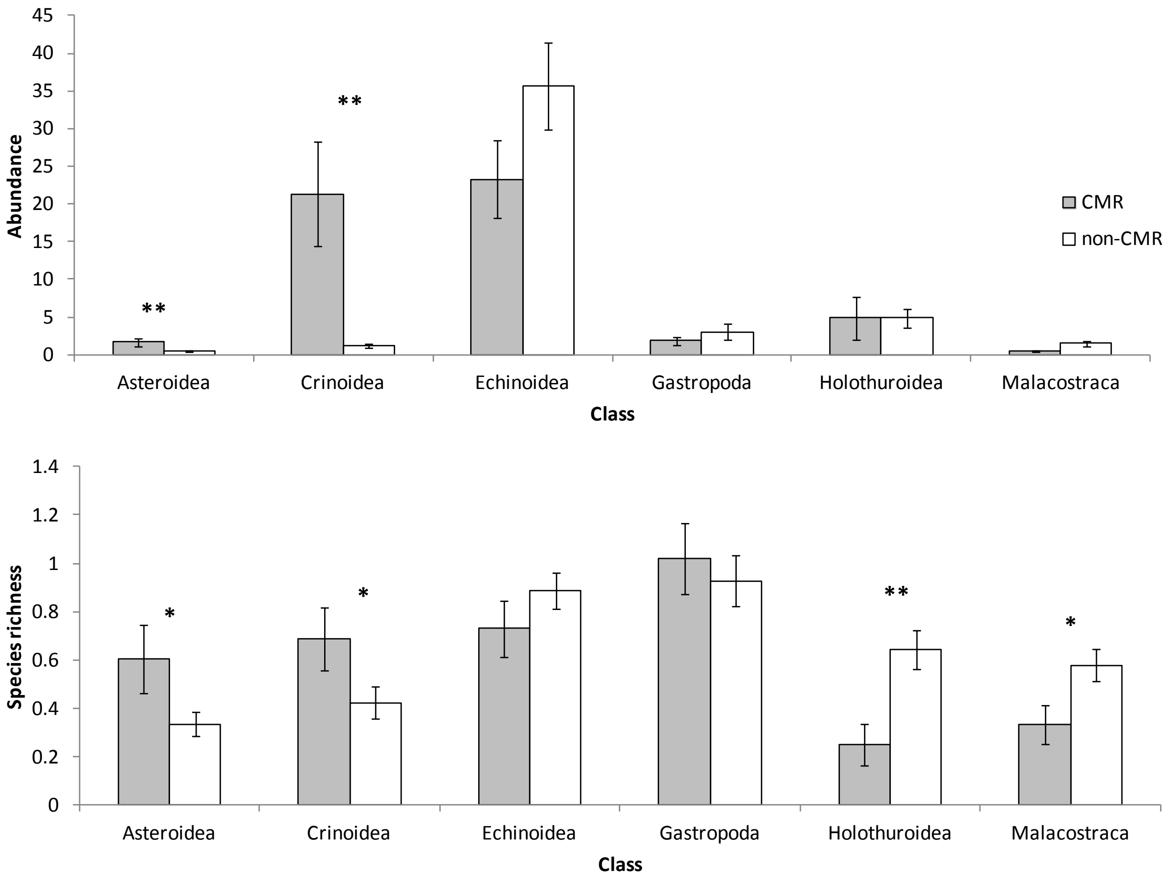


Figure 30. Abundance and species richness of macroinvertebrate classes on CMR and non-CMR reefs in the North CMR Network. Symbols for ANOVA significance: * p < 0.05; ** p < 0.01; *** p < 0.001.

CRYPTIC FISHES

At a community level, cryptic fishes recorded with Method 2 effectively separated the Bonaparte Coast's assemblages from all other CMRs, as well as driving some smaller groupings (ANOSIM Global R = 0.482, p = 0.001). The Bonaparte Coast, especially non-CMR reefs, were characterised by high proportion of *Istigobius* spp., small ambush predators and *Amblyeleotris wheeleri*. The West Cape York CMR was dominated by *Cephalopoholis boenak*, and the Arnhem and Gulf of Carpentaria CMRs had high abundances of *Istigobius rigilius* and *Cheilodipterus quinquelineatus* (Figure 31).

Overall, CMR and non-CMR reefs had similar abundance, but CMRs had higher species richness of cryptic fishes recorded using Method 2 ($F_{1,168}$ = 4.783, p = 0.03, Figure 32). Abundance and species richness were highest in the Arnhem Coast to Gulf of Carpentaria ecoregion, and particularly high in the Gulf of Carpentaria CMR, where species richness was significantly higher than elsewhere (Figure 33, Table 7). In the Bonapart Coast and Torres Strait to northern GBR ecoregions, abundance and species richness of cryptic fishes tended to be higher inside CMRs than outside. Dominant fish families in terms of both abundance and species richness were the Apogonidae, Blenniidae and Gobiidae (Figure 34). Key differences between CMR and non-CMR reefs were higher abundances and species richness of Holocentridae, Pinguipedidae, Serranidae and Synodontidae inside CMRs.

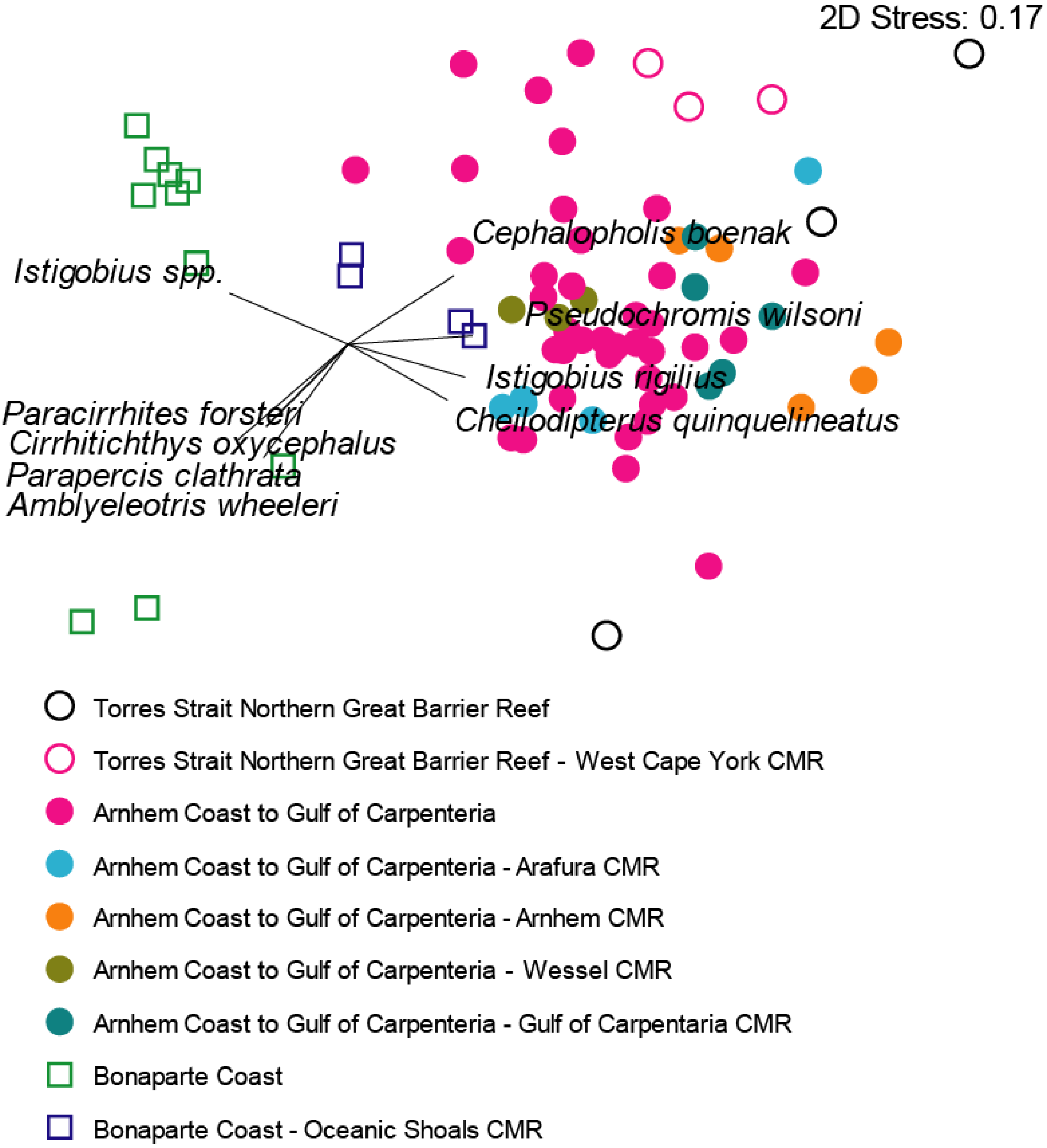


Figure 31. MDS ordination of key cryptic fish species composition across reefs of the North CMR Network, partitioned by ecoregion and CMR. Vectors were included if they had a correlation of at least 0.4.

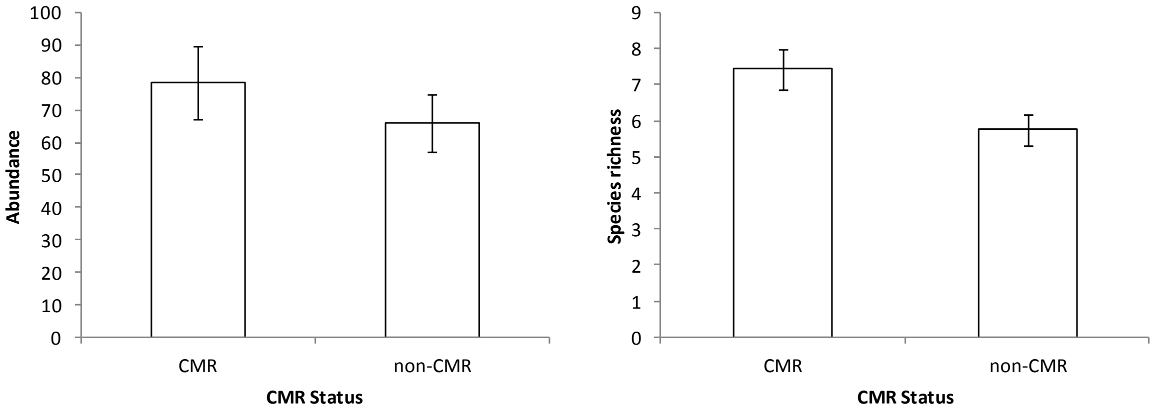


Figure 32. Abundance and species richness of cryptic fishes across reefs of the North CMR Network, on CMR and non-CMR reefs. Error bars ± 1 SE.

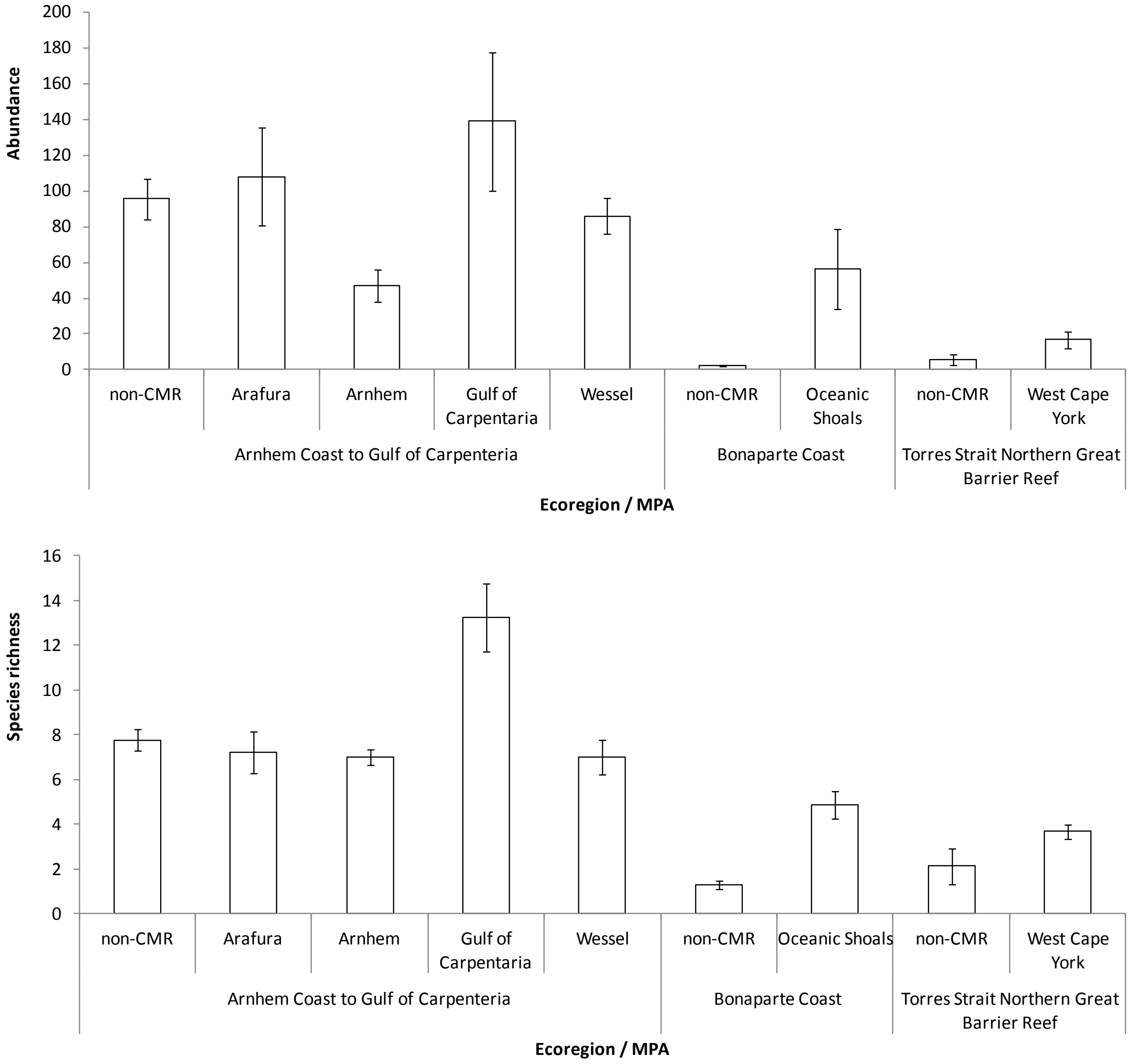
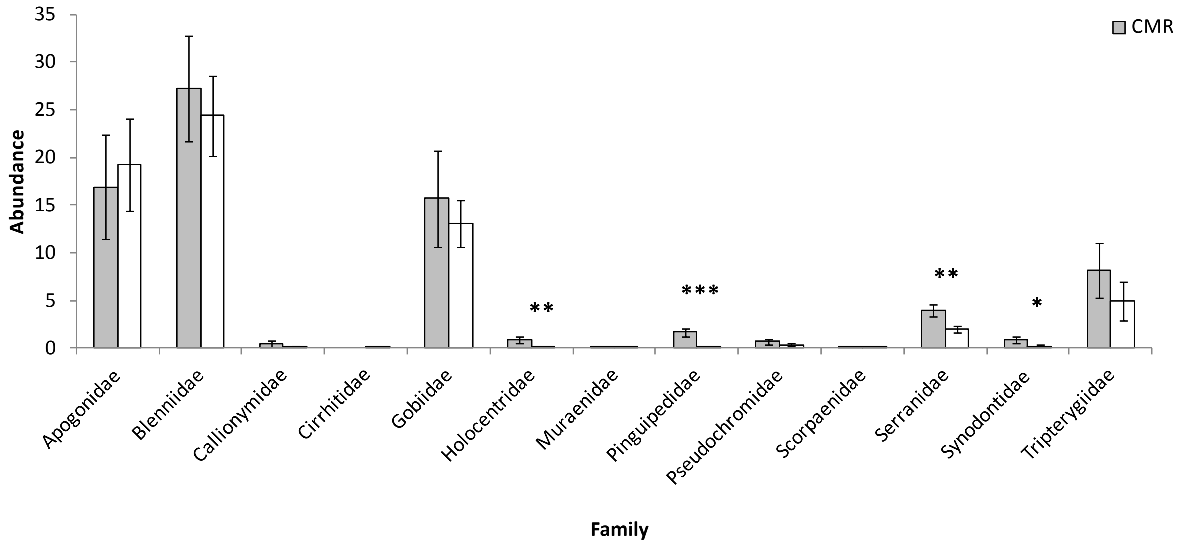


Figure 33. Abundance and species richness of cryptic fishes across reefs of the North CMR Network, CMR and non-CMR sites in each area. Error bars ± 1 SE.

Table 7. Results of 2-way ANOVA testing differences between ecoregions and CMRs within ecoregions. Contrasts show significant differences between individual Ecoregions or CMRs; BC: Bonaparte Coast; Arn_GoC: Arnhem Coast to Gulf of Carpenteria; TS-GBR: Torres Strait to Northern Great Barrier Reef.

		F	df	p	Contrasts
Abundance	Ecoregion	18.492	2,161	<0.001	BC-Arn_GoC TS-GBR – Arn_GoC
	CMR	1.518	6,161	0.175	
Species richness	Ecoregion	51.85	2,161	<0.001	BC - Arn_GoC TS-GBR – Arn_GoC
	CMR	5.03	6,161	<0.001	GoC – Arafura GoC – Arnhem GoC - Wessel GoC - non-CMR



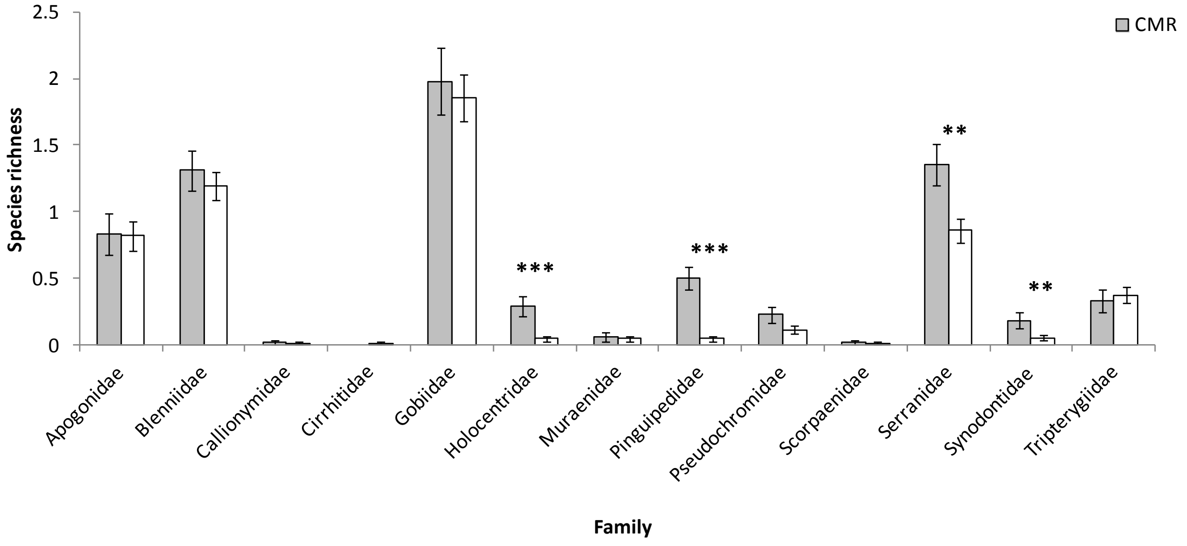


Figure 34. Abundance and species richness of cryptic fish families on CMR and non-CMR reefs in the North CMR Network.

NORTH CMR SNAPSHOTS

BONAPARTE COAST

OCEANIC SHOALS CMR

Substrate cover was similar in the Oceanic Shoals CMR to sites outside the CMR in the same ecoregion (Appendix 2; Figure 38). Reefs in the Oceanic Shoals CMR had similar cover of live corals and macroalgae as those outside, but higher cover of calcified and turf algae. In contrast, non-CMR reefs had higher cover of abiotic substrata (Figure 35).

Fish and invertebrate communities were also highly similar between the Oceanic Shoals CMR and non-CMR sites (Figure 38). The species richness of invertebrates was lower inside the CMR and the species richness of reef fishes slightly higher. The fish community was very different in composition between inshore and offshore reefs in the area, but reefs surveyed in the Oceanic Shoals CMR seem to have a mix of fish species; still more characteristic of the offshore sites, but not as strongly as found on the offshore non-CMR reefs. There was very high biomass of planktivorous fishes on reefs surveyed inside the CMR, overwhelming other differences in feeding groups (Figure 36). The biomass of large predators (piscivores) was similar inside and outside the Oceanic Shoals CMR, but biomass of grazing herbivorous fishes was higher inside the CMR.

Species of conservation interest were found in low abundance, and mostly on non-CMR reefs. No turtles were observed on any of the surveyed reefs, and sharks were only present in low abundance on the Oceanic Shoals CMR reefs (Figure 37).

Values of key biodiversity indicators were also similar, with high variability masking significant differences. COTs were only found inside the CMR, and there were no IUCN listed threatened species inside the CMR.

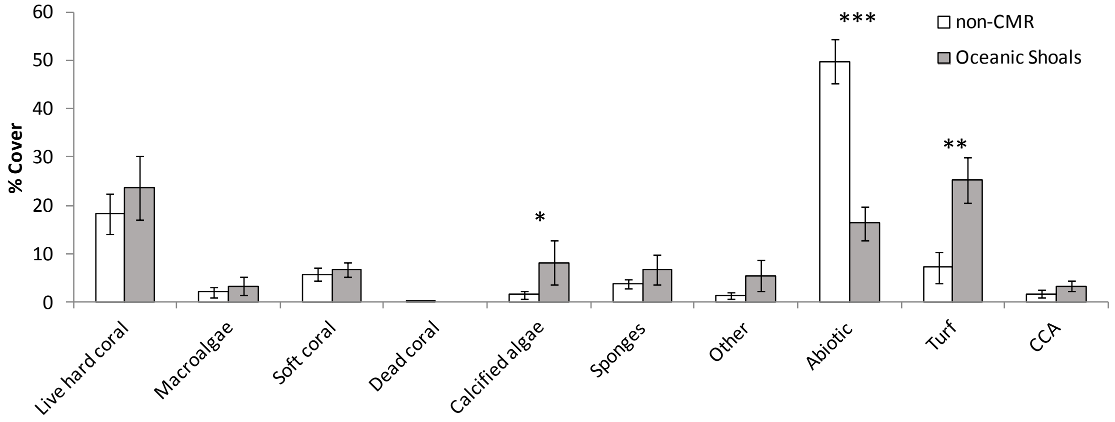


Figure 35. Percentage cover of benthic categories on non-CMR reefs of the Bonaparte Coast ecoregion, and in the Oceanic Shoals CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

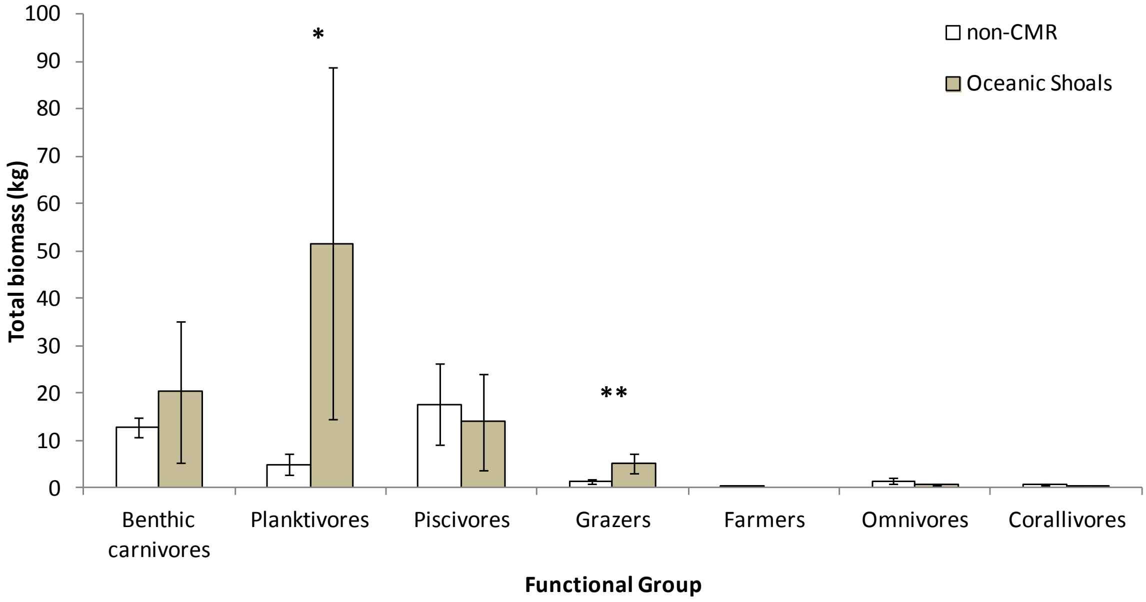


Figure 36. Biomass of functional groups of reef fishes on non-CMR reefs of the Bonaparte Coast ecoregion, and in the Oceanic Shoals CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

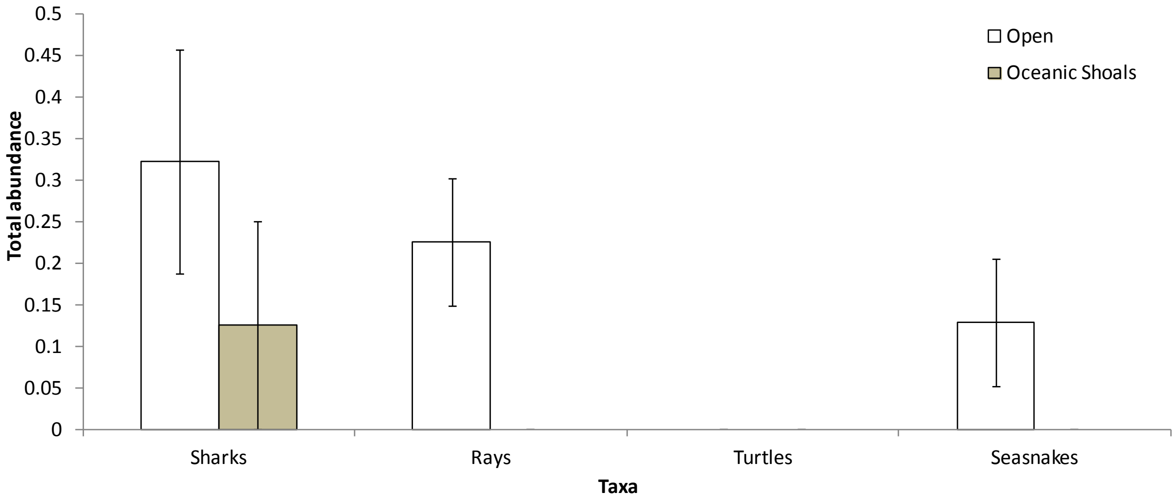


Figure 37. Abundance of species of conservation interest inside and outside the Oceanic Shoals CMR, +/- 1 SE.

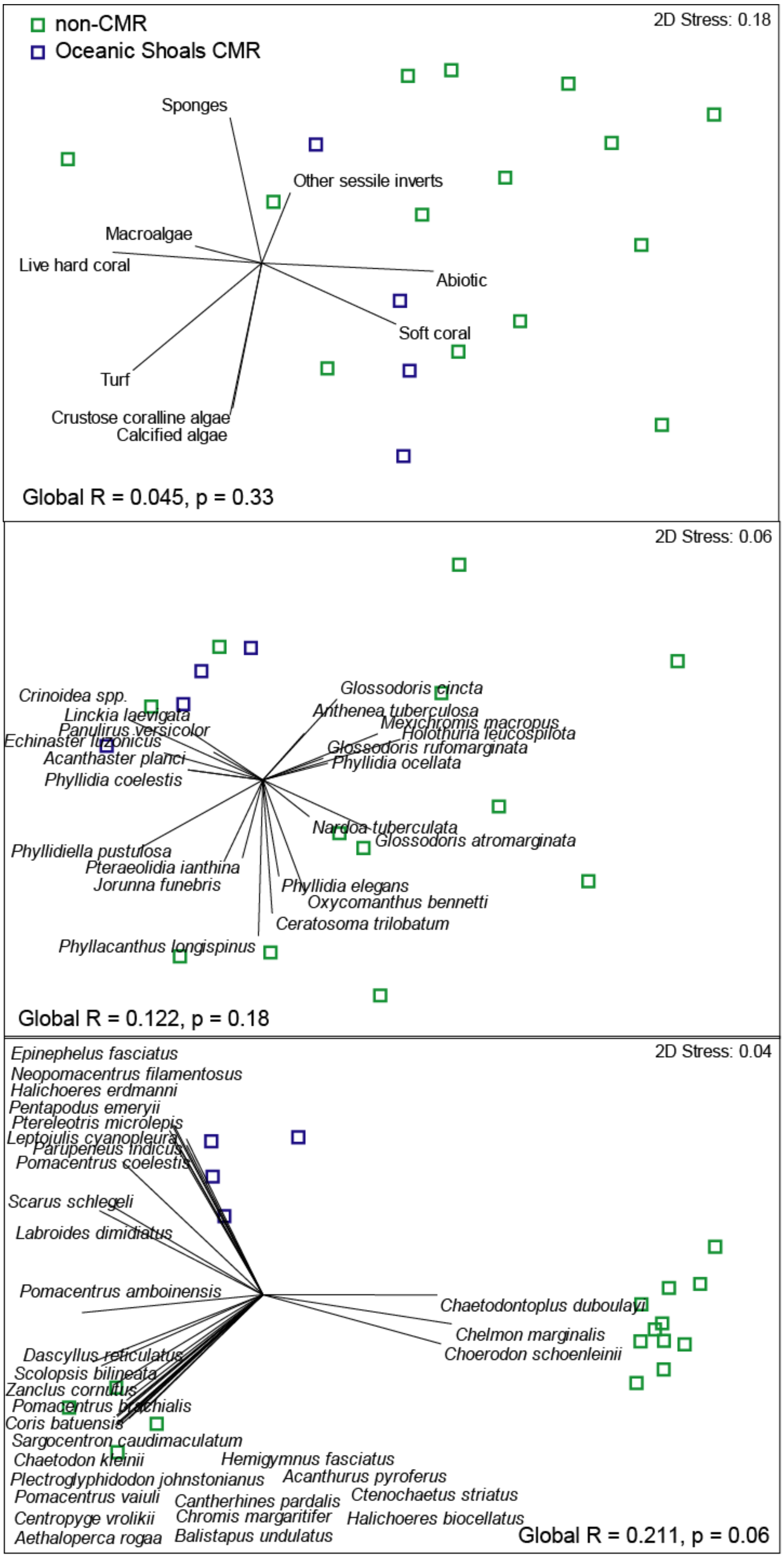


Figure 38. MDS plots of the Bonaparte Coast ecoregion (non-CMR reefs, Oceanic Shoals CMR), analysing the benthic community (top, vectors for variables with a correlation of at least 0.2), macroinvertebrates (middle, vectors for variables with a correlation of at least 0.2), and reef fishes (bottom, vectors for variables with a correlation of at least 0.8). Data were transformed to comply with assumptions. Results of ANISIM are given for each: Global R.

ARNHEM COAST TO GULF OF CARPENTARIA

ARAFURA CMR

The Arafura CMR and corresponding non-CMR reefs were characterised by turf-covered substrate, but similar and relatively high cover of live coral (Figure 39).

Fish and invertebrate communities differed more between CMRs and non-CMR reefs (Figure 51), with more echinoderms a characteristic that separated the Arafura CMR sites from all other sites in the broader ecoregion. CMR reefs also had higher species richness of invertebrates and fishes. Key differences in fishes included in small wrasses, planktivorous damselfishes and the parrotfish *Scarus rivulatus*. Biomass of fish functional groups was similar inside and outside the CMR, but with lower biomass of large predatory fishes and grazing herbivorous fishes inside the CMR (Figure 40).

Species of particular conservation interest were scarce outside the CMR and not recorded at sites within the CMR (Figure 47).

Values of key biodiversity indicators were slightly lower for the CMR, except for the absence of crown-of-thorns seastars inside the CMR, which can be considered a positive result.

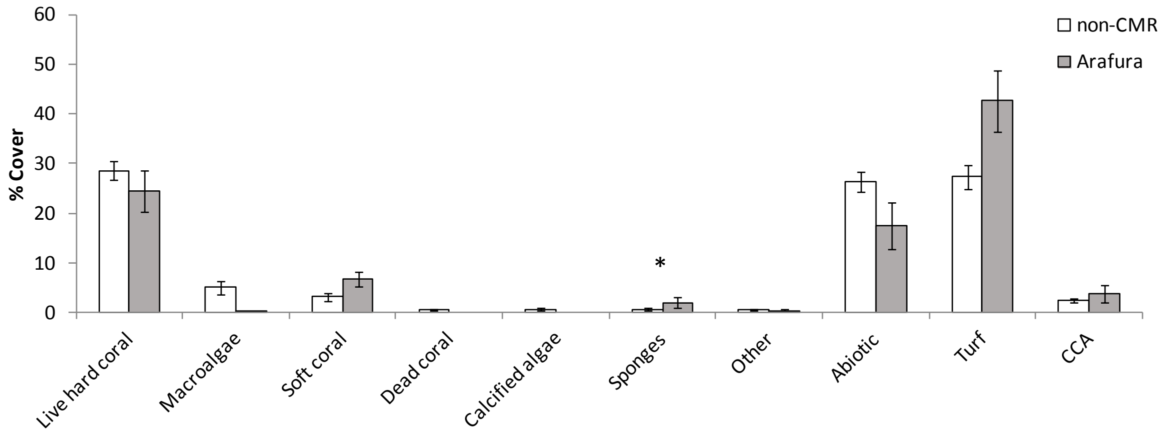


Figure 39. Percentage cover of benthic categories on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Arafura CMR. Significant differences are highlighted with stars (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

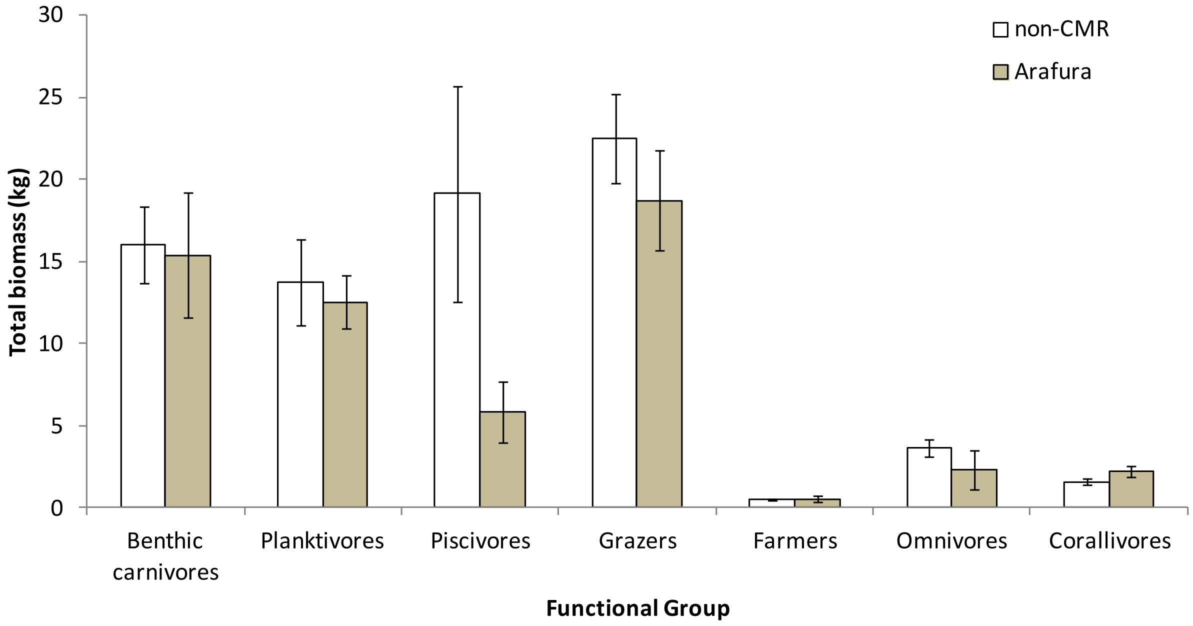


Figure 40. Biomass of functional groups of reef fishes on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Arafura CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

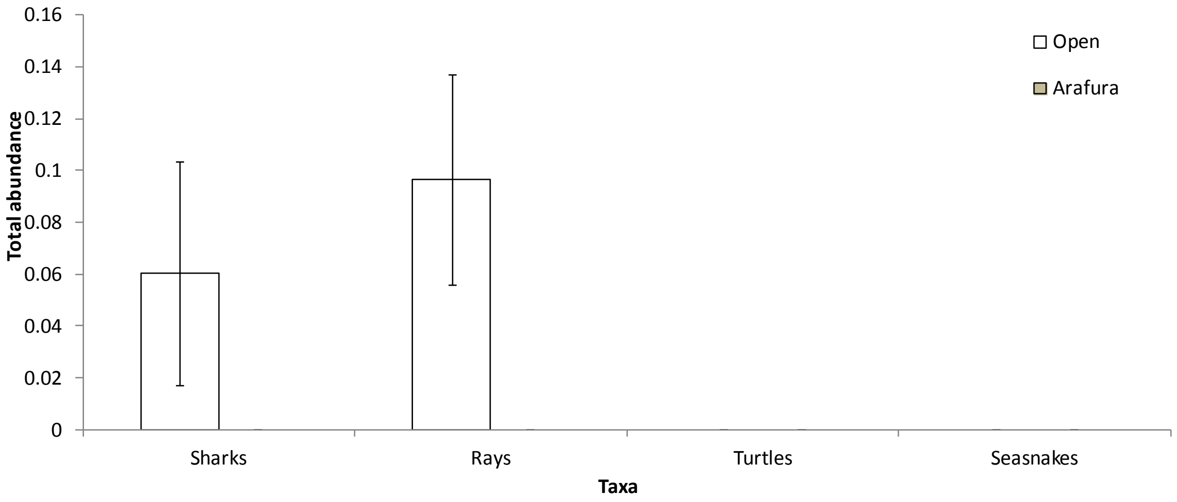


Figure 41. Abundance of species of conservation interest inside and outside the Arafura CMR, +/- 1 SE.

ARNHEM CMR

Arnhem CMR and non-CMR reefs differed in important elements of substrate cover, with lower cover of live corals and higher cover of turf on CMR reefs (Figure 42).

Fish and invertebrate communities were quite variable inside and outside the CMR. The richness of reef fish species was similar between non-CMR and CMR reefs, but richness was lower for mobile invertebrates inside the CMR, where *Drupella cornus* and some of the sea urchins dominated.

Non-CMR reefs tended to have higher biomass of predatory and grazing herbivorous fishes (Figure 46).

Among species of conservation significance, sharks were only recorded outside the CMR, and a similar number of rays recorded inside and outside (Figure 47).

Values of key biodiversity indicators were slightly lower for the CMR sites, except for the absence of COTs inside the CMR. The fish community temperature index (CTI) indicated that reef fishes inside the CMR are generally suited to slightly warmer waters than those species recorded on other reefs in the ecoregion (which include the 'cooler' fish community of the lower Gulf of Carpentaria – see next CMR). But all reefs in the ecoregion have cooler affinities than the local waters, and the implications of CTI values are that warming may lead to substantial change in the fish community, independently of habitat change (e.g. through coral bleaching).

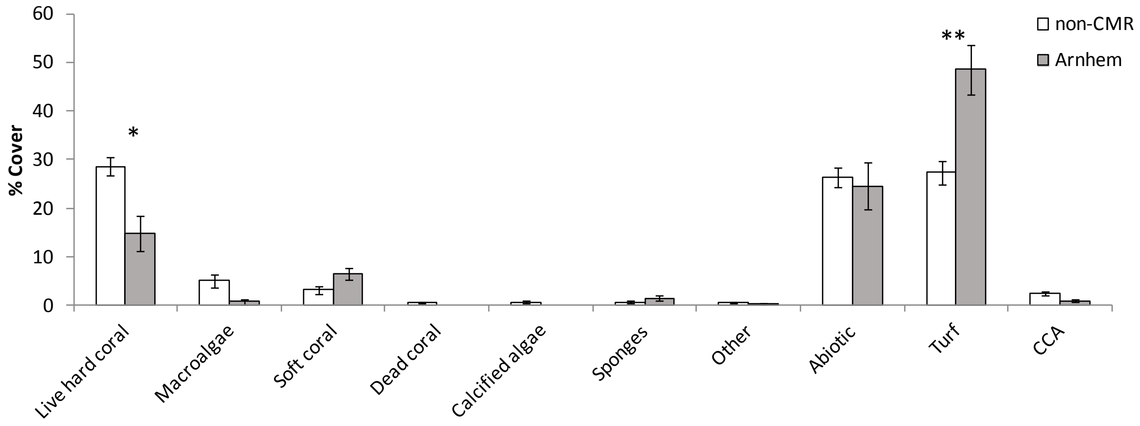


Figure 42. Percentage cover of benthic categories on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Arnhem CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

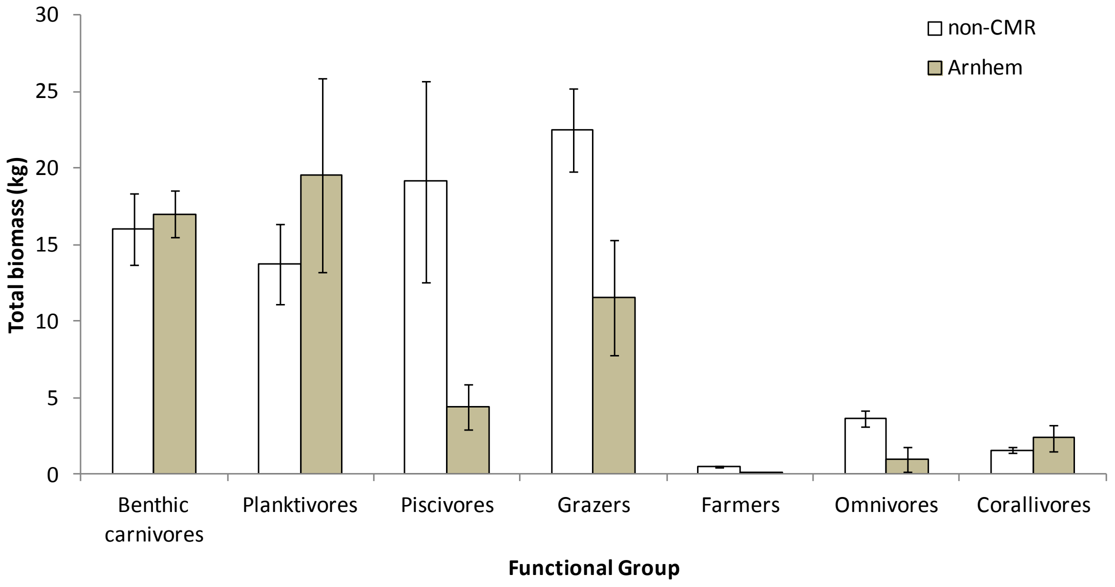


Figure 43. Biomass of functional groups of reef fishes on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Arnhem CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

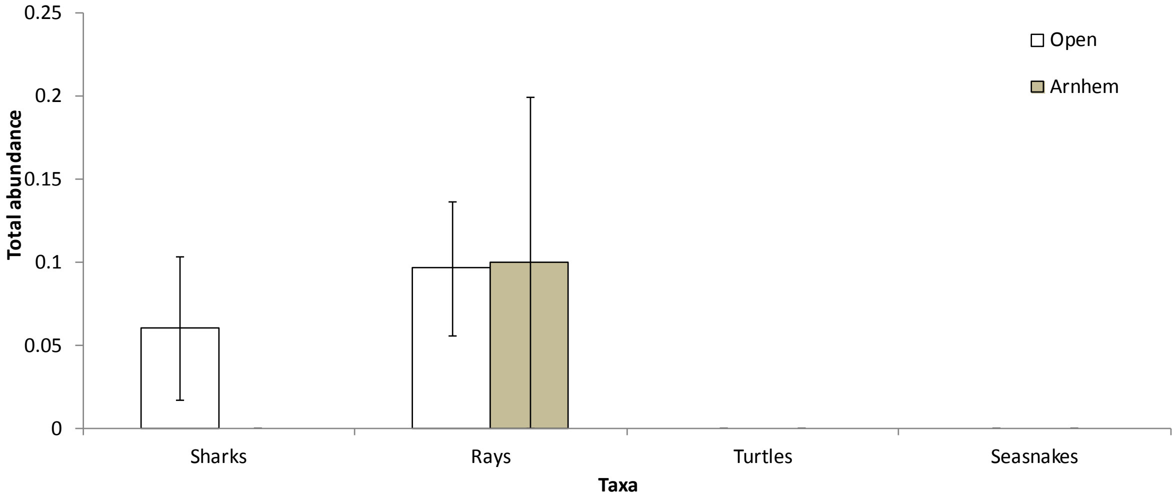


Figure 44. Abundance of species of conservation interest inside and outside the Arnhem CMR, +/- 1 SE.

GULF OF CARPENTARIA CMR

This CMR also had relatively similar substrate cover to sites outside the CMR in the broader ecoregion, with a reasonable coverage of live hard coral (ca. 30%)(Figure 45).

Mobile invertebrate and fish communities differed considerably inside this CMR from those at non-CMR reefs in the ecoregion, despite being similar in richness. The fish community in the CMR was characterised by very high biomass, comprised mostly of more predatory species, but also more planktivores than other reefs in the ecoregion. Grazing herbivorous fishes were less well-represented (in biomass), however (Figure 46).

Species of conservation significance were scarce, with low numbers of sharks and rays on non-CMR reefs, but a high abundance of seasnakes inside the CMR. This was the highest abundance of seasnakes in any location across the North CMR Network (Figure 47).

Values of key biodiversity indicators were higher for the CMR, except for the presence of COTs inside the CMR, and the CTI revealed the fish community inside the CMR to reflect a general affinity of species for cooler waters than sites outside the CMR in the ecoregion (which include locations mostly further north). This implies a higher sensitivity to change in the fish community in this CMR (and likely the lower portion of the Gulf) due to long-term warming. CTI values are so low that any substantial warming may lead to some local extinctions through the future (loss of local populations, not global extinction).

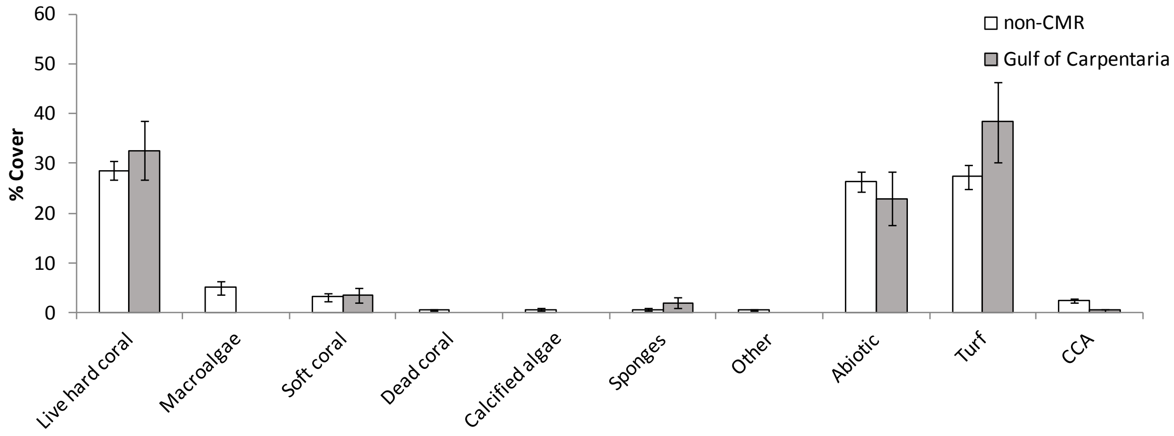


Figure 45. Percentage cover of benthic categories on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Gulf of Carpentaria CMR. Significant differences are highlighted with stars (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

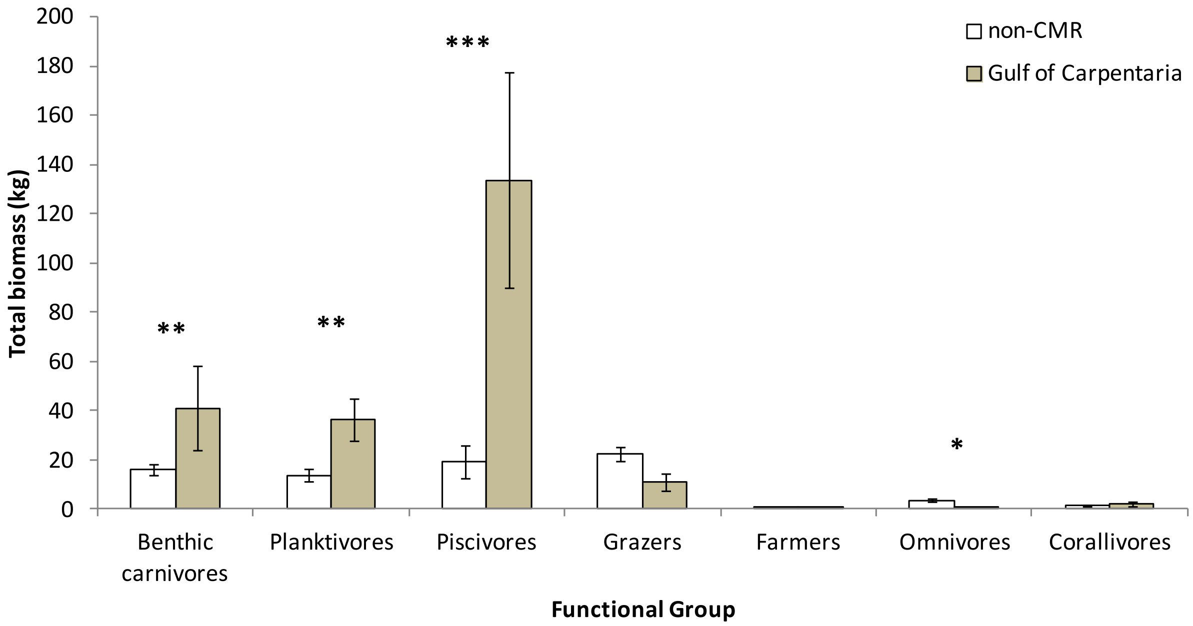


Figure 46. Biomass of functional groups of reef fishes on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Gulf of Carpentaria CMR. Significant differences are highlighted with stars (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

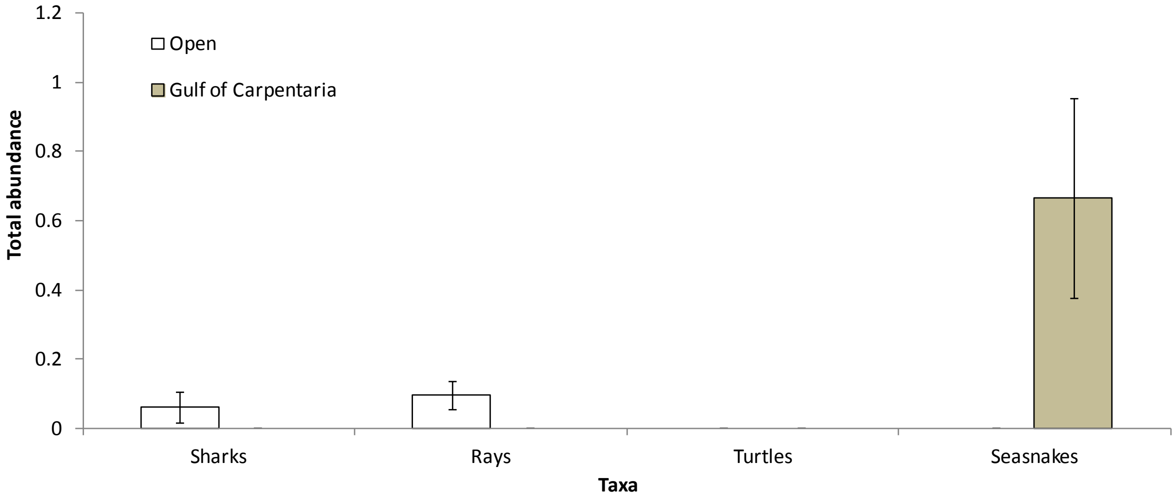


Figure 47. Abundance of species of conservation interest inside and outside the Gulf of Carpentaria CMR, +/- 1 SE.

WESSEL CMR

The Wessel CMR was characterised by higher cover of soft corals and crustose coralline algae, and lower turf cover than found at non-CMR reefs across this ecoregion (Figure 48).

A relatively consistent fish species composition between sites was observed, although sampling more sites could lead to a wider spread of site values (Figure 51). This was similar to that in the Gulf of Carpentaria CMR, but with different groups dominating by biomass. Plantkivores dominated by biomass inside this CMR, and there were also more corallivorous fishes than at non-CMR sites in the ecoregion (Figure 49). The species richness of invertebrates and fishes was similar between CMR and non-CMR reefs.

Very few species of conservation interest were observed, other than a low abundance of sharks and rays on non-CMR reefs (Figure 50).

Values of key biodiversity indicators were higher for the CMR than at non-CMR sites, except for the presence of COTs inside the CMR, and a slightly lower predicted sensitivity to change in the fish community due to long-term warming.

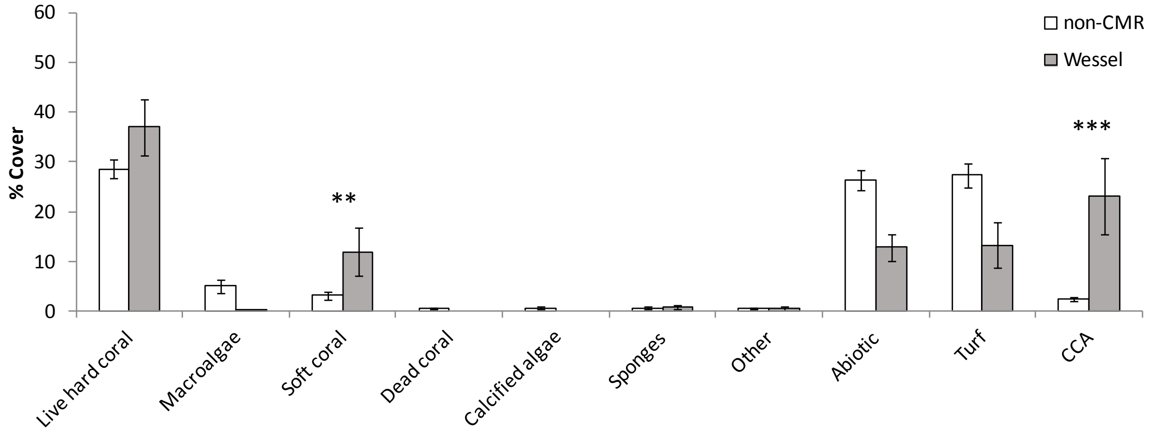


Figure 48. Percentage cover of benthic categories on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Wessel CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

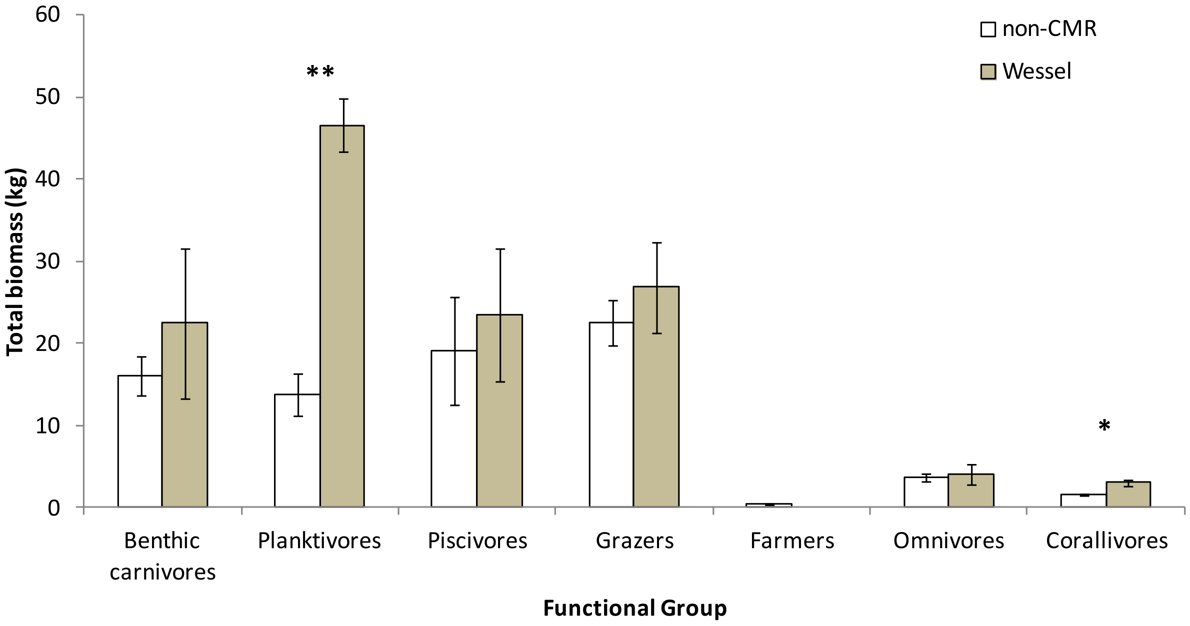


Figure 49. Biomass of functional groups of reef fishes on non-CMR reefs of the Arnhem Coast to Gulf of Carpentaria ecoregion, and in the Wessel CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

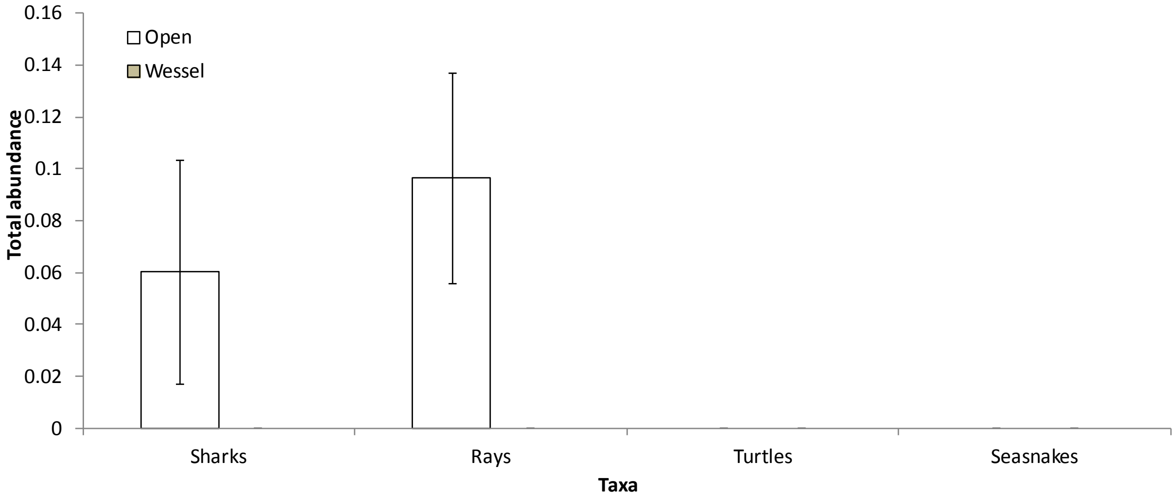


Figure 50. Abundance of species of conservation interest inside and outside the Wessel CMR, +/- 1 SE.

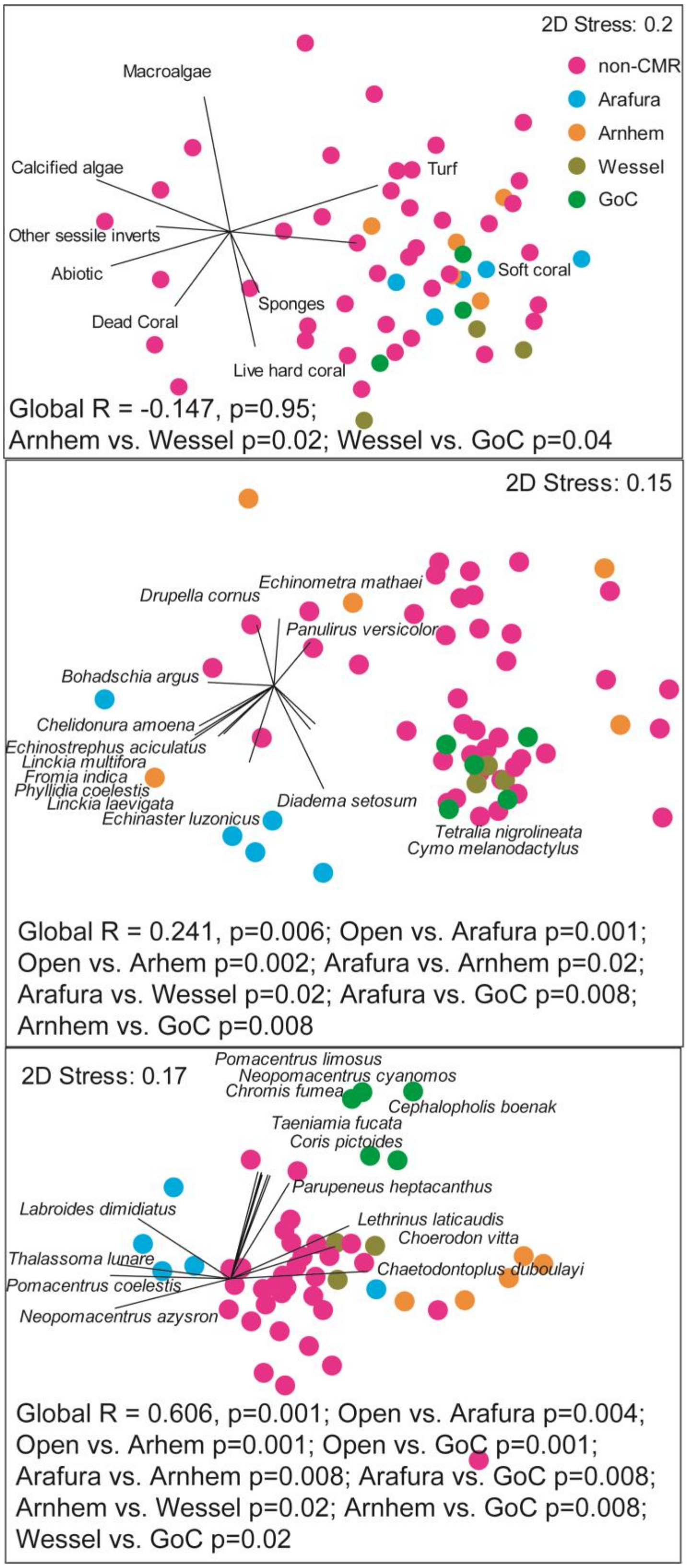


Figure 51. MDS plots of the Arnhem Coast to Gulf of Carpenteria (GoC) ecoregion (non-CMR reefs, Arafura, Arnhem, GoC and Wessel CMRs), analysing the benthic community (top, vectors for variables with a correlation of at least 0.2), macroinvertebrates (middle, vectors for variables with a correlation of at least 0.2), and reef fishes (bottom, vectors for variables with a correlation of at least 0.6). Data were transformed to comply with statistical assumptions. Results of ANOSIM are given for each: Global R, and any significant differences between CMRs.

TORRES STRAIT TO NORTHERN GREAT BARRIER REEF

WEST CAPE YORK CMR

Substrate cover on reefs in the West Cape York CMR was generally representative of the surveyed reefs in the ecoregion (Figure 55), with little difference in cover of corals or algae inside and outside the CMR (Figure 52).

The invertebrate community was dominated by *Diadema setosum* and *Holothuria atra*, and the species richness of invertebrates was higher on non-CMR reefs. The fish community inside the CMR was very different from sites outside, with much higher biomass of large fishes in each of the major feeding groups that contain large fishes (Figure 53).

Low abundances of shark and seasnakes were recorded from CMR reefs; no species of conservation interest were recorded on non-CMR reefs (Figure 54).

Values of key biodiversity indicators were similar, except for the presence of crown-of-thorns seastars on non-CMR reefs. Suprisingly given their close proximity and similar habitat conditions, reefs inside the CMR had fish communities with a cooler affinity, and thus are predicted to be more sensitive to negative change with long-term warming than nearby non-CMR sites.

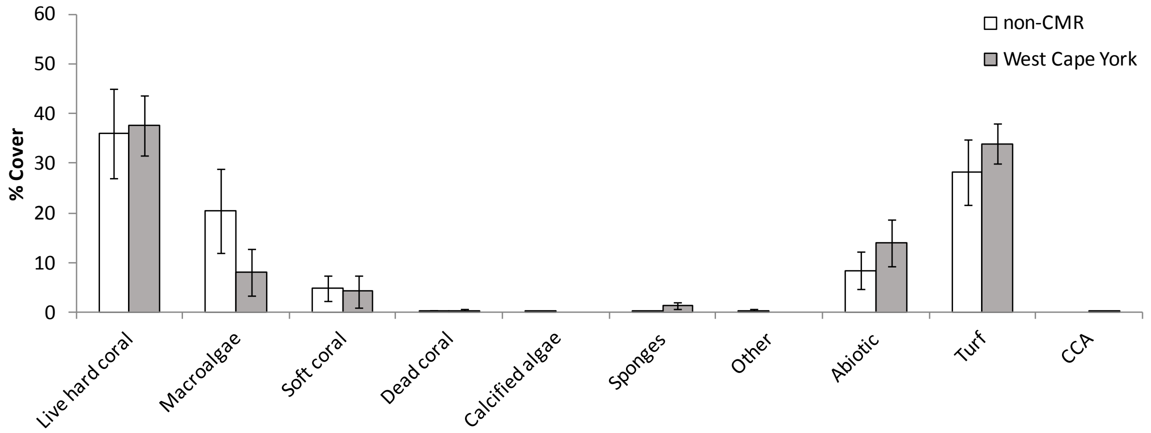


Figure 52. Percentage cover of benthic categories on non-CMR reefs of the Torres Strait to northern Great Barrier Reef ecoregion, and in the West Cape York CMR. Significant differences are highlighted with stars (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

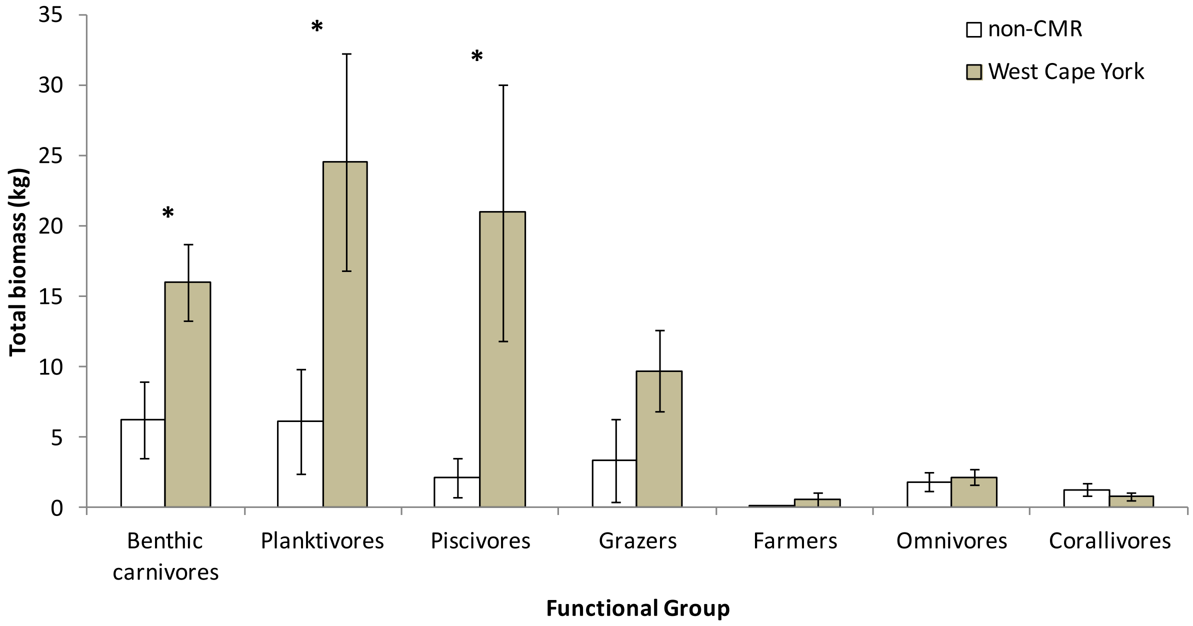


Figure 53. Biomass of functional groups of reef fishes on non-CMR reefs of the Torres Strait to northern Great Barrier Reef ecoregion, and in the West Cape York CMR. Significant differences are highlighted with stars (* p < 0.05; ** p < 0.01; *** p < 0.001).

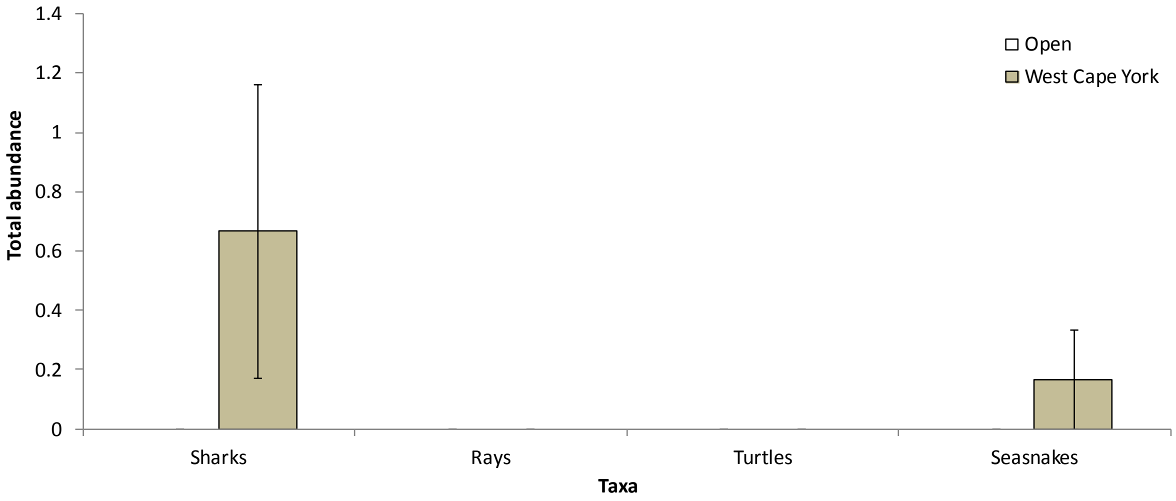


Figure 54. Abundance of species of conservation interest inside and outside the West Cape York CMR, +/- 1 SE.

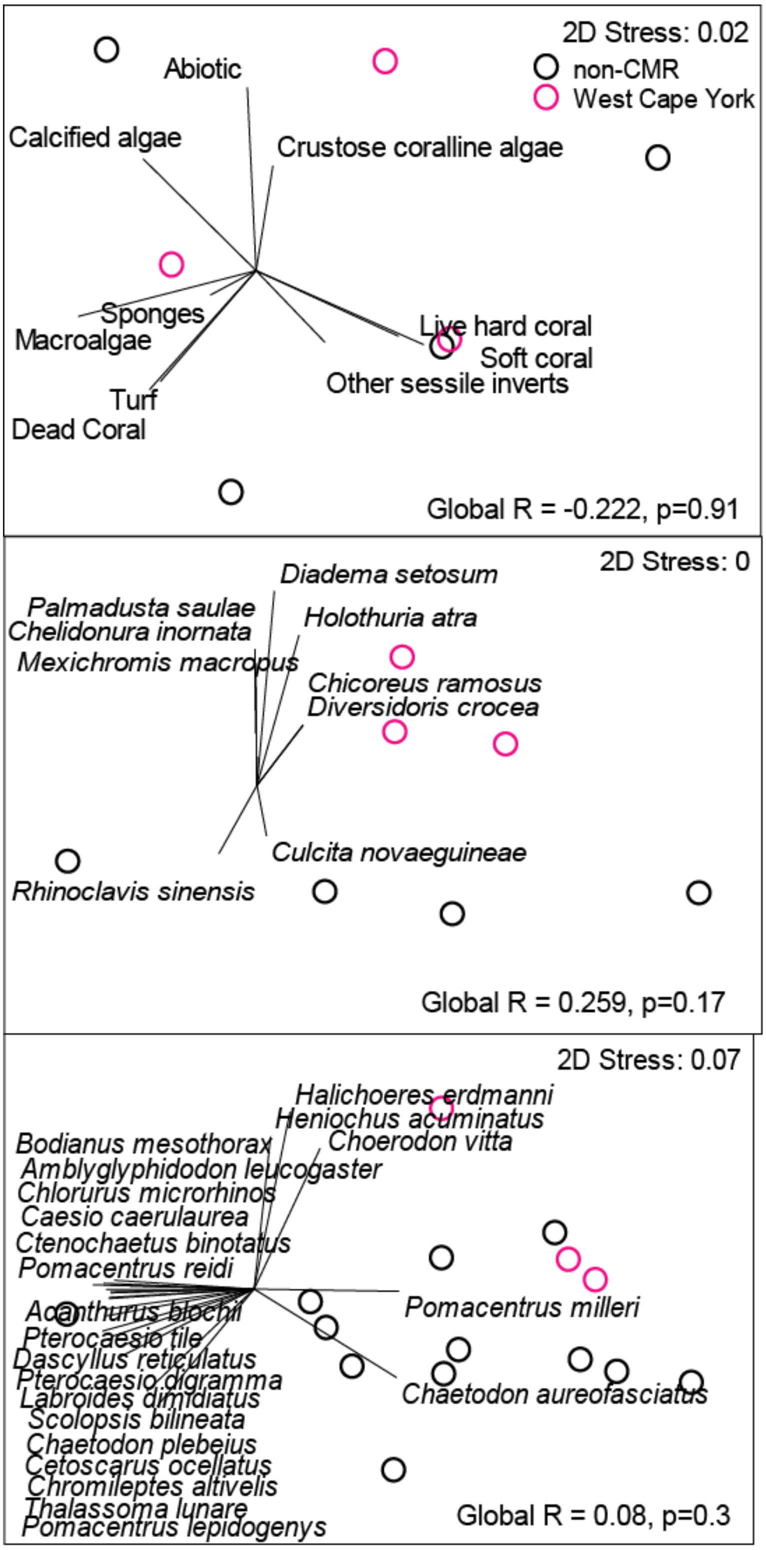


Figure 55. MDS plots of the Torres Strait to Northern Great Barrier Reef ecoregion (non-CMR reefs, West Cape York CMR), analysing the benthic community (top, vectors for variables with a correlation of at least 0.2), macroinvertebrates (middle, vectors for variables with a correlation of at least 0.3), and reef fishes (bottom, vectors for variables with a correlation of at least 0.7). Data were transformed to comply with statistical assumptions. Results of ANOSIM are given for each: Global R.

PART C: ECOLOGICAL ASSOCIATIONS AND DISCUSSION

There were few consistencies in the environmental factors that best described the variability in the benthic and fish community; even those variables that were considered for the most parsimonious model did not always have a significant relationship with the variable in question (Table 8). Live hard coral cover was best defined by a combination of distance offshore and latitude, whilst depth best described the variability in macroalgal cover. Neither of these were significant, however.

Among the potential correlates, distance offshore was only significantly related to calcified algae and the species richness of surgeonfishes, both of which increased with increasing distance offshore (Appendix 3). Some elements of the reef community increased with increasing latitude, while others declined. At higher latitudes, cover of soft corals was lower, as was species richness of butterflyfishes, angelfishes and damselfishes, and biomass of emperors (Appendix 3). Conversely, closer to the equator, there was higher abundance of emperors and piscivores, higher species richness of emperors, and higher biomass of reef fishes, especially emperors, groupers, piscivores, omnivores, wrasses and benthic carnivores. Longitude was a less important correlate of patterns than latitude, but the abundance of angelfishes and planktivores, and the species richness of butterflyfishes, declined significantly from west to east (Appendix 3). Depth was often a significant driver in combination with latitude, longitude or both (Table 8). Increasing depth was correlated with an increase in the abundance of planktivores and piscivores, total fish species richness, and the species richness of groupers; total fish biomass and the biomass of snappers, angelfishes, groupers, planktivores and piscivores (Appendix 3). Other groups of fishes declined with depth, including the abundance of grazers and farmers, and the biomass of parrotfishes, farmers and omnivores. Live hard coral cover was significantly positively related to total fish abundance, the abundance of butterflyfishes, benthic carnivores and corallivores, and the biomass of planktivores (Appendix 3).

Table 8. Linear Mixed Effects model (an extension of simple linear models to allow both fixed and random effects) outputs depicting the influence of distance offshore, longitude, latitude, depth and (for fishes only) live hard coral cover on benthic and fish metrics. Twenty-three candidate models were compared and model selection was based on the lowest Akaike Information Criterion (AIC). Only the most parsimonious model is presented, and where variables in the model had significant effects, these are also presented.

Metric	Variable	AIC	Model	Significant factor	df	F	p
% cover	Live hard coral	1286	Distance x Latitude				
	Macroalgae	1139	Depth				
	Turf	1313	Latitude x Longitude	Longitude	1,76	5.59	0.0207
	Crustose coralline algae	959	Latitude				
	Calcified algae	733	Distance	Distance	1,78	14.23	0.0003

Metric	Variable	AIC	Model	Significant factor	df	F	p
	Soft coral	989	Latitude	Latitude	1,78	5.92	0.0172
Abundance	Total	2815	Latitude x Longitude x Live hard coral	Live hard coral	1,70	11.96	0.0009
				Latitude x Live hard coral	1,70	18.32	0.0001
	Acanthuridae	1456	Latitude				
	Chaetodontidae	1236	Live hard coral	Live hard coral	1,73	14.90	<.0001
	Haemulidae	895	Latitude				
	Labridae	2210	Latitude x Longitude x Depth	Longitude x Depth	1,70	13.35	0.0005
	Lethrinidae	1013	Latitude	Latitude	1,78	9.059	0.0035
	Lutjanidae	1444	Latitude x Longitude	Longitude	1,76	8.32	0.0051
				Latitude x Longitude	1,76	7.14	0.0092
	Pomacanthidae	892	Longitude	Longitude	1,78	7.45	0.0078
	Pomacentridae	2410	Latitude x Longitude x Depth				
	Scaridae	1440	Depth	Depth	1,73	23.00	<.0001
	Serranidae	1069	Latitude x Depth	Latitude	1,78	26.16	<.0001
				Depth	1,72	17.12	0.0001
				Latitude x Depth	1,72	9.38	0.0031
	Siganidae	3881	Latitude x Depth	Latitude	1,241	30.92	<.0001
				Latitude x Depth	1,207	10.58	0.0013
	Benthic carnivores	2783	Latitude x Depth x Live hard coral	Latitude	1,78	6.29	0.0142
				Live hard coral	1,68	9.10	0.0036
				Latitude x Live hard coral	1,68	26.67	<.0001
				Latitude x Depth x Live hard coral	1,68	5.92	0.0176
	Planktivores	2381	Latitude x Longitude x Depth	Longitude	1,76	5.41	0.0227
				Depth	1,70	4.12	0.0461
	Piscivores	1577	Latitude x Depth	Latitude	1,78	7.74	0.0068
				Depth	1,72	12.48	0.0007
				Latitude x Depth x Live hard coral	1,72	4.61	0.0351

Metric	Variable	AIC	Model	Significant factor	df	F	p
	Grazers	1608	Latitude x Longitude x Depth	Depth	1,70	10.64	0.0017
	Farmers	1479	Latitude x Longitude x Depth	Depth	1,70	9.40	0.0031
				Latitude x Longitude	1,76	7.88	0.0064
	Omnivores	2139	Latitude x Longitude x Depth				
	Corallivores	1241	Live hard coral	Live hard coral	1,73	14	<.0001
Species richness	Total	1107	Latitude x Longitude x Depth		1,70	6.81	0.0111
				Latitude x Longitude	1,76	36.43	<.0001
	Acanthuridae	322	Distance	Distance	1,78	50.82	<.0001
	Chaetodontidae	514	Latitude x Longitude	Latitude	1,76	5.23	0.025
				Longitude	1,76	10.97	0.0014
				Latitude x Longitude	1,76	18.59	<.0001
	Haemulidae	406	Latitude				
	Labridae	717	Latitude x Longitude	Latitude	1,76	4.41	0.0391
				Latitude x Longitude	1,76	37.98	<.0001
	Lethrinidae	247	Latitude	Latitude	1,78	11.33	0.0012
	Lutjanidae	485	Latitude				
	Pomacanthidae	382	Latitude	Latitude	1,78	7.21	0.0088
	Pomacentridae	704	Latitude x Longitude	Latitude	1,76	8.86	0.0039
				Latitude x Longitude	1,76	17.91	0.0001
	Scaridae	384	Latitude				
	Serranidae	524	Depth	Depth	1,73	10.57	0.0017
	Siganidae	333	Live hard coral				
Biomass	Total	1757	Latitude x Depth	Latitude	1,78	11.11	0.0013
				Depth	1,72	34.84	<.0001
				Latitude x Depth	1,72	10.49	0.0018
	Acanthuridae	1209	Latitude				
	Chaetodontidae	591	Latitude				
	Haemulidae	845	Latitude	Latitude	1,78	6.01	0.0165

Metric	Variable	AIC	Model	Significant factor	df	F	p
	Labridae	1218	Latitude x Live hard coral	Latitude	1,78	12.00	0.0009
				Latitude x Live hard coral	1,72	12.34	0.0008
	Lethrinidae	1092	Depth	Depth	1,73	6.92	0.0104
	Lutjanidae	1209	Latitude x Depth	Latitude	1,78	13.74	<.0001
				Depth	1,72	52.70	<.0001
				Latitude x Depth	1,72	30.63	<.0001
	Pomacanthidae	641	Depth	Depth	1,73	5.39	0.0231
	Pomacentridae	945	Latitude				
	Scaridae	1086	Depth	Depth	1,73	14.58	<.0001
	Serranidae	1416	Latitude x Depth	Latitude	1,78	14.22	<.0001
				Depth	1,72	31.41	<.0001
				Latitude x Depth	1,72	26.67	<.0001
	Siganidae	922	Latitude	Latitude	1,78	4.02	0.0483
	Benthic carnivores	1360	Latitude	Latitude	1,78	8.01	0.0059
	Planktivores	1482	Depth x Live hard coral	Depth	1,71	9.49	0.0029
				Live hard coral	1,71	9.76	0.0026
	Piscivores	1609	Latitude x Depth x Live hard coral	Latitude	1,78	21.56	<.0001
				Depth	1,68	88.04	<.0001
				Latitude x Depth	1,68	53.32	<.0001
				Latitude x Live hard coral	1,68	5.34	0.0239
				Depth x Live hard coral	1,68	4.21	0.044
				Latitude x Depth x Live hard coral	1,68	15.60	0.0002
	Grazers	1344	Depth	Depth	1,73	5.42	0.0227
	Farmers	311	Depth	Depth	1,73	9.79	0.0025
	Omnivores	847	Latitude x Depth	Latitude	1,78	7.92	0.0062
				Depth	1,72	8.53	0.0047
				Latitude x Depth	1,72	9.88	0.0024
	Corallivores	591	Latitude				

THREATENED AND PROTECTED SPECIES

The only species species listed under the EPBC Act recorded in the North CMR Network included the green turtle *Chelonia mydas* (Burston Bay) (Vulnerable); the turtle-headed seasnake *Emydocephalus annulatus* (Blackwood Shoal), and the olive seasnake *Aipysurus laevis* (Merkara Shoal, West Cape York CMR; Carpentaria Reef and Chinamans Reef, Gulf of Carpentaria CMR; Flinders Shoal) (Protected Marine Species). Only *A. laevis* was recorded more than once; other records consisted of a single observation.

Species listed under international conservation legislation (CITES, Bonn Convention, IUCN Red List) that were recorded during the surveys included sea snakes (*Aipysurus laevis*, *Emydocephalus annulatus*) and several species of grouper, of which (*Epinephelus coioides*, *E. malabaricus, E. polyphekadion, E. lanceolatus, Plectropomus laevis,* and *P. leopardus*) are listed as 'Near Threatened' or 'Vulnerable' on the Red List. The few rays recorded included the ribbontailed stingray *Taeniura lymma* ('Near Threatened'). There were no records of the humpheaded Maori wrasse *Cheilinus undulatus* on reefs of the North CMR Network.

DISCUSSION

The North CMR Network hosts abundant and diverse coral reef communities with characteristics that span a bridge between assemblages on the eastern and western sides of the tropical Indo-Pacific. This is the first study to comprehensively survey coral reef communities in the North CMR Network, both for nearshore and offshore waters, in a manner comparable to other regions. Greater distinctions in coral reef organisms were evident between inshore and offshore reefs than between east and west, with clearly different assemblages associated with offshore "blue-water" reefs and more turbid inshore reefs. Most reefs of the North CMR Network overlapped more closely with inshore reef communities than those found offshore. This coincides with the general geomorphology of the Region, which is dominated by a relatively shallow and turbid continental shelf (Chivas et al. 2001, Heap and Harris 2008).

Regional patterns

Benthic communities across the North CMR Network were similar to those of the Great Barrier Reef in their coarse characteristics, although species-level analysis of benthic flora and fauna may yet detect endemics or rare species (Commonwealth of Australia 2008). In terms of reef condition, the Bonaparte Coast ecoregion showed signs of recent damage, with a greater proportion of recently dead corals and abiotic substrata than other ecoregions, pointing to the possibility of a recent disturbance. The Coral Sea was distinctive in its high cover of calcified and crustose coralline algae; this pattern is typical of oceanic reefs and was rare across the North CMR Network reefs, with significant cover of calcified and crustose algae only recorded in the Oceanic Shoals CMR.

Across the Great Barrier Reef shelf, crustose coralline algae declined from ~20% on offshore reefs to <1% inshore, presumably due to adverse effects of sedimentation, turbidity and low topographic complexity (Fabricius and De'ath 2001). These conditions are also likely to prevail across other reefs that are closer to the coast (Commonwealth of Australia 2007). Crustose coralline algae contribute significantly to reef calcification (Chisholm 2000) and provide a favourable substratum for the settlement of corals and other benthic biota; this may be one of the factors accounting for what has typically been observed to be low coral cover on turbid inshore reefs (Heyward and Negri 1999, Yadav et al. 2016). Interestingly, most reefs across the North CMR Network had relatively high coral cover between 15 and 40%, with high coral cover even on some inshore reefs. The coral community was dominated by massive and encrusting corals, and to a lesser degree also foliose corals, which is typical of inshore reefs where corals must be resistant to conditions of high turbidity (Anthony 2000, Sofonia and Anthony 2008).

Reefs in the North CMR Network have a higher apparent cover of turf than other regions. The expectation is generally that high cover of turf or macroalgae is a sign of degraded reefs (McCook 1999) and coral communities are more depauperate on turbid inshore reefs (Done 1982), but the North CMR Network reefs, as a group, had coral cover on a par with all other regions except the Indian Ocean reefs (which had exceptionally high coral cover at the time of the surveys).

Reef fish communities were clearly separated along the inshore-offshore gradient, much more so than the separation between east and west coast assemblages. Generally, the key biogeographic break in this region is between eastern (SW Pacific) and western (Indian Ocean) faunas, at the western Indonesian Islands. Indian Ocean species tend not to be found much further east than Christmas/Cocos-Keeling Islands and western Indonesia while many Pacific species continue to occur all along the northern and western coastlines of Australia (Randall 1998), implying an eastward dispersal limitation for Indian Ocean species. While this break appears to occur to the west of north-western Australia, a similar eastward dispersal limitation may restrict many western Australian species (Australian endemics, rather than the Indian Ocean species) from occurring east of Torres Strait. Currents through the Torres Strait are strongly tidal, and mainly controlled by seasonal winds, which switch from north-westerly monsoon winds in summer to south-easterly trades in winter (Saint-Cast and Condie 2006). Although this means there is not a uni-directional flow, there is still a tendency for westward flowing currents to dominate (Saint-Cast and Condie 2006) through Torres Strait, which may contribute to this additional break for Australian fauna.

The analyses in this report provide new insight into an additional, strong faunal break in the area, which is not based on dispersal barriers between east and west, but likely on environmental factors and habitats between inshore and offshore. The previously documented inshore-offshore gradient for the Great Barrier Reef appears to be a more widespread phenomenon that is very clearly observed in the North CMR Network. The magnitude of differences associated with the inshore-offshore break can be seen by the greater similarity of the Coral Sea fauna in multidimensional space to that of Cocos-Keeling / Christmas Island, than to a large portion of the Great Barrier Reef, despite the geographic proximity of the latter. This highlights how the inshore-offshore faunal break reflects more striking compositional differences than the long-known Indian Ocean-Pacific Ocean biogeographic barrier.

Conditions between inshore and offshore reefs can vary greatly (Fabricius and De'ath 2001), and reef fishes have different habitat preferences and tolerance to environmental factors such as turbidity (Johansen and Jones 2013). Proximity to the coast and associated water quality and geomorphological characteristics appear to have greater influence in driving fish community structure than geographic location and dispersal barriers. Species richness on the North CMR Network reefs also probably reflected a mix of influences from their proximity to the global centre of biodiversity (Randall 1998), and the low complexity and diversity of habitats formed by encrusting and massive corals, rather than branching morphologies, which probably reduced species richness.

The inshore-offshore gradient in assemblage structure was mirrored to a lesser degree in the cryptic fish and macroinvertebrate assemblages. Inshore macroinvertebrate communities appeared much more rich and diverse than those found offshore, which were dominated by a few species of tridacnid clams and sea urchins. Inshore communities had high proportions of nudibranchs, and some bivalves, flatworms and sea urchins. Nudibranchs are often associated with turbid reefs and high cover or algal turf and detritus (Cheney et al. 2014). Studies on sessile benthic organisms such as sponges indicate a more diverse fauna occurs offshore in the North CMR Network, compared with inshore (Przeslawski et al. 2014), suggesting that the inshore-offshore effect on species richness and abundance varies for different taxa.

A large amount of the information on inshore-offshore coral reef gradients come from cross-shelf studies conducted on the Great Barrier Reef (Done 1982, Williams 1982). Inshore reefs are characterised by higher algal biomass than offshore reefs (Russ and McCook 1999). Herbivorous fish assemblages are strongly partitioned across the GBR shelf, with different functional roles dominating inshore and offshore (Hoey and Bellwood 2008), and, apart from higher rabbitfish biomass (Hoey et al. 2013), generally depauperate herbivore populations inshore (Cheal et al. 2012). Molluscs also showed a strong cross-shelf pattern in subtropical eastern Australia, with a dominance of herbivores inshore (Harrison and Smith 2012).

Reef fish species can be widely distributed across the inshore-offshore gradient, but inshore and offshore “specialists” exist; the families Pomacentridae and Chaetodontidae appear to have more specialists with particular habitat preferences than the Acanthuridae, Labridae and Scaridae (Williams 1982). Inshore-offshore gradients have also been measured in processes such as bioerosion (Tribollet and Golubic 2005), productivity and grazing rates (Russ and McCook 1999, Hoey and Bellwood 2008). This type of research has yet to be done for other regions, and these patterns are only just being highlighted for the reefs of the North CMR Network.

North CMR Network

Benthic communities across the North CMR Network appeared typical of inshore reef communities elsewhere, although the cover of turf was higher than at other locations across the broader region. Some CMRs had particular characteristics such as higher sponge cover than non-CMR reefs (e.g. the Arafura CMR) or more soft corals (e.g. the Wessel CMR). None of the reefs were dominated by hard corals, and corals also seemed of low importance as a driver for the fish community, apart from corallivores such as butterflyfishes, which are strongly dependent on the live coral tissue (Pratchett 2005).

The inshore-offshore gradient is evident when examining fish assemblages across the North CMR Network, even more so than in the ecoregional analysis. Previous studies have also found an inshore-offshore gradient in the Timor Sea and Joseph Bonaparte Gulf, with habitat heterogeneity and epifaunal species richness increasing offshore and infaunal species richness increasing inshore (Przeslawski et al. 2011). All the Arnhem Coast-Gulf of Carpentaria sites and some Bonaparte sites had fish communities characteristic of inshore reefs. Within inshore reefs, a number of sites formed distinctive groups: non-CMR Bonaparte coast sites were set apart from the Oceanic Shoals CMR, even though the latter still grouped with the inshore sites. Among the Arnhem Coast-Gulf of Carpentaria CMRs, the Gulf of Carpentaria CMR, Wessel CMR, Arnhem CMR and Arafura CMRs all formed separate groups (Figure 21), while also overlapping to varying degrees with the non-CMR sites. These groupings suggest that, in terms of individual CMRs representing the fish fauna of the general ecoregion, the following patterns apply:

- Sites investigated in the Oceanic Shoals CMR have a distinct fish fauna from the non-CMR Bonaparte Coast ecoregion, which itself is split between inshore and offshore fish faunas.
- The fish fauna of the Arnhem Coast-Gulf of Carpentaria ecoregion is represented in the Arnhem and Wessel CMRs, but the Gulf of Carpentaria and Arafura CMRs have some sites with distinct fish faunas. Non-CMR sites in this ecoregion had the highest abundance and biomass of reef fishes of all sites in the North CMR Network (Cape Beatrice SW, Carpentaria Reef), as well as the highest abundance of cryptic fishes and invertebrates (Manowar Island), the highest species richness of cryptic fishes (Glasseye Reef), and species richness of invertebrates (Bremer Islet Anchorage). Carpentaria Reef

(Gulf of Carpentaria CMR) and Grouper Shoal (non-CMR) had the highest biomass of piscivores; Burston Bay (also non-CMR) had the highest biomass of grazers.

- The fish fauna of Torres Strait to Northern GBR ecoregion is represented in the West Cape York CMR. A non-CMR site in this ecoregion had the highest species richness of reef fishes of all sites in the North CMR Network (Mer Outer Reef).

None of the CMR sites stood out for having particularly fish abundance, biomass or species richness in any of the taxonomic groups recorded. Macroinvertebrate and cryptic fish communities showed much greater variability in abundance between different CMRs than fish communities, suggesting different environmental and/or biological influences. The Arnhem CMR was especially depauperate and its sites appeared scattered in multidimensional space, suggesting a high degree of variability in the dominant species at each site. This in part related to the offshore location of Money Shoal, with many more Indo-Pacific species present than for sites closer inshore. As with other inshore locations, the Arnhem CMR appeared taxonomically quite diverse. In contrast, the Arafura, Gulf of Carpentaria and Wessel CMRs had very high invertebrate abundance and species richness. The latter two CMRs had inshore macroinvertebrate communities, but the Arafura CMR had elements of both the inshore and the offshore assemblages. The cryptic fish community showed patterns similar to the reef fish community.

The fish species most closely associated with inshore communities included omnivorous pomacentrids, corallivores, large benthic carnivores and key coral reef piscivores, while offshore assemblages were dominated by smaller benthic carnivores and algal croppers, and planktivorous pomacentrids. It therefore appears that the dominant species within the fish community are influenced by resource availability. Light availability for algae for herbivores, structural complexity to provide cover for a diverse suite of small reef species, and local plankton availability, are all expected to be key drivers of the functional structure of the North CMR Network's reef communities. Previous studies linking biophysical habitat characteristics to fish assemblages have stressed the importance of substratum (consolidated or unconsolidated, with the latter further classified into sand and gravel habitats), cross-shelf position and depth (Malcolm et al. 2016).

A dominance of planktivores is common in areas of clear water, strong currents, and high structural complexity associated with high live coral cover, as many small planktivorus species use live branching coral as shelter (Wilson et al. 2006; Ceccarelli et al. 2016). Planktivorous fishes form the interface between pelagic primary production and the benthic detritivorous food chain, and often they are the primary prey source for piscivores (Johansen and Jones 2013). Among reefs of the North CMR Network, the Gulf of Carpentaria, Wessel, West Cape York and Oceanic Shoals CMRs stood out as having high planktivore density and biomass. The Gulf of Carpentaria is considered a relatively pristine coastal ecosystem, and nitrogen cycling and nutrient availability is driven in large part by nutrients generated by nitrogen-fixing cyanobacteria (Burford et al. 2009).

Piscivores are also associated with healthy reefs, as they are the primary target of many fisheries, and pristine systems are often characterised by high piscivore biomass (Friedlander et al. 2007). Many sites in the Gulf of Carpenteria and West Cape York CMRs had very high predator biomass and low grazer biomass compared to most other sites across the region. A clear difference in trophic structure existed compared to coral reefs on the east coast of Australia that suggested different processes may be more important here. Degraded reefs are often associated with higher numbers of farming damselfishes and benthic carnivores, as are turbid inshore reefs (Williams 1982; Sandin et al. 2008). Grazers, on the other hand, are often cast as indicators of resilient reefs, as their foraging reduces algal biomass in favour of coral dominance (Mumby et al. 2006). Advocates of reef resilience often highlight the importance of protecting herbivores on coral reefs (e.g., http://www.icriforum.org/caribbeanreport), especially after disturbances, when they perform the critical task of maintaining free space for coral settlement during periods of recovery (Mumby 2006).

Latitude and depth were found to be most strongly associated with aspects of the reef fish community of the environmental variables examined; these are well-known correlates of community composition in marine systems. Latitudinal gradients 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 tolerance to 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 live coral 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 (Jankwoski et al. 2015b).

Live coral cover can be an important driver for some species, especially those that feed on live coral tissue or shelter in coral colonies (Wilson et al. 2006). The effect of live coral cover on species that are not directly dependent on it is somewhat more ambiguous (Ceccarelli et al. 2016); in the North CMR Network its influence did not extend beyond corallivorous fishes.

Threats

All the CMRs in the North CMR Network are currently open to fishing, and therefore subject to the same threats and pressures as non-CMR areas. The primary threats across the North CMR Network include illegal fishing from international fishers, marine pests, marine debris (including derelict fishing gear) and activities associated with oil and gas exploration and extraction (Commonwealth of Australia 2008). There appear to be no invasive species of accumulation of debris on the surveyed reefs, but the paucity of large predatory fishes and sharks may be a result of illegal fishing activities. Changing the zoning of CMRs to no-take may restore fish stocks, but surveillance and enforcement must be in place to prevent poaching. Furthermore, changing the zoning may protect the reefs within CMRs from potential future impacts from oil and gas associated activities. A further more pervasive threat is from the changing ocean temperature and weather patterns associated with climate change. Whilst these threats will transcend CMR boundaries, recent evidence suggests greater stability, lower impact magnitude and faster recovery from disturbances inside no-take marine reserves than equivalent unprotected areas (Mellin et al. 2016).

CONCLUSIONS

Reefs across the North CMR Network are representative of the diverse ecological communities present on reefs across the region, with some distinctive assemblages and characteristics that set them apart from reefs to the east or west. Reefs within CMRs appear representative of the (relatively lightly) exploited reefs in each ecoregion, especially in their benthic structure. Coral cover ranged between 15 and 40%, with little evidence of macroalgal dominance, and a high cover of turf. On offshore reefs, high biomass of planktivores (Oceanic Shoals CMR) suggests high pelagic productivity. As with non-CMR reefs, some CMR reefs were particularly rich in species of invertebrates and fishes (e.g. Gulf of Carpentaria CMR), and others were more depauperate (Arnhem CMR).

Potentially, a more important factor affecting reef communities is their depth range. Coral bleaching might be expected to be less of a threat to the deeper coral reefs, which are also isolated in deeper water and are not subject to warming shallow lagoon waters such as many reefs on the GBR, for example. But the future of these reef communities under warming is still uncertain, with a balance of fish species that is unusually ‘cool’ for their location. CTI values across the whole North CMR Network suggest that thermal stress may become an issue for fishes that currently inhabit its reefs, particularly so in the lower Gulf of Carpentaria, where a greater proportion of the species surveyed are living closer to their warm limit than in any of the other parts of the north coast (due to differences in composition). This may not be an issue if future warming rates are not rapid in this area, but implies the greatest potential for negative changes in reef fish communities, such as reduced abundance and local extinction.

It is nevertheless also possible that a previous lack of records for many fish species across the north of the continent has led to underestimates of the warm limit for many Australian endemics. Future recalculation of species’ thermal distributions and CTI using the data collected through this project will indicate whether this is the case, and may reduce the magnitude of the negative ‘thermal bias’ obsvered in the lower Gulf of Carpentaria. Regardless, the potential depth refuge for coral bleaching and potential vulnerability of fish communities highlight the importance of continued efforts to document the region’s reef communities.

RECOMMENDATIONS

Comprehensive monitoring of reefs in the North CMR Network is recommended as often as is feasible. This should include assessment of ecological changes associated with zoning - in particular whether CMRs experience any degradation as experienced on reefs outside the CMRs, which could warrant changed zoning arrangements. Monitoring should also provide information that improves understanding of any change to biophysical conditions, any outbreaks of crown-of-thorns seastars, ecological changes associated with reduced effects of fishing in protected zones, and broad scale regional ecological shifts associated with changing climate.

If available resources allow only a reduced set of sites to be monitored on future occasions, these should include all CMR sites surveyed here. Baseline data described in this report should guide selection of appropriate non-CMR sites with similar ecological and environmental characteristics. Sites covered should ideally span the longitudinal and latitudinal extent of the North CMR Network.

Ideally, future monitoring should utilise the same methods as used here, to provide complete comparability, and the most powerful means to detect change. Research priorities to guide monitoring and evaluation should include development and selection of a suite of indicators that sensitively track changes in reef condition and aspects of biodiversity that are of most relevance to CMR management goals, as well as changes associated with ocean warming and storms.

Further research questions relevant to managers when determining the condition of biodiversity in the North CMR Network, identifying key threats, and understanding management options include:

- Investigation of factors limiting seasnake, turtle and elasmobranch distribution, including assessment of ecological data for associations among species and functional groups, as well as with environmental data. This may require collection of additional habitat or environmental data.
- Detailed habitat mapping and categorisation of reef types, exposure and aspect.
- Detailed mapping of distribution and impact of natural disturbances, including cyclones. This should ideally include comparison with coral reef systems to the east and west, to allow the North CMR reefs to be considered in the broader regional geographic context.
- A more detailed analysis of the value of the North CMR shoals as refugia for coral reef organisms from disturbances and stressors in shallow water.

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APPENDICES

APPENDIX 1

Reef Life Survey benthic functional groups.

Broad group	RLS Functional group
Coral	Ahermatypic corals
Coral	Bleached coral
Coral	Branching *Acropora*
Coral	Encrusting corals
Coral	Hydrocoral
Coral	Large-polyp stony corals
Coral	Massive corals (Live)
Coral	Other branching/erect corals (Live)
Coral	*Pocillopora*
Coral	Soft corals and gorgonians
Coral	Tabular Coral (Live)
Other	Ascidians (stalked)
Other	Ascidians (unstalked)
Other	Bare Rock
Other	Barnacles
Other	Bryozoan (hard)
Other	Bryozoan (soft)
Other	Colonial Anemones, Zoanthids and Corallimorphs
Other	Dead Coral
Other	Hydroids
Other	Pebbles/unconsolidated rocky bottom/coral rubble
Other	Polychaete
Other	Sand
Other	Seagrass (*Halophila*)
Other	Seagrass (other)
Other	Sessile bivalves
Other	Sessile gastropods
Other	Solitary Anemones
Other	Sponges (encrusting)
Other	Sponges (erect)
Other	Sponges (hollow)
Other	Sponges (massive)
Algae	algal mat/slime
Algae	*Caulerpa*
Algae	Crustose coralline algae
Algae	cyanobacterial mat/slime
Algae	*Desmarestia* and *Himantothallus*
Algae	*Durvillaea*
Algae	Encrusting leathery algae
Algae	Filamentous epiphytic algae

Broad group	**RLS Functional group**
Algae	Filamentous rock-attached algae
Algae	Foliose red algae
Algae	Geniculate coralline algae
Algae	Green calcified algae
Algae	Large brown laminarian kelps
Algae	Other foliose green algae
Algae	Other fucoids
Algae	*Phyllospora*
Algae	Small to medium foliose brown algae
Algae	Turfing algae (<2 cm high algal/sediment mat on rock)

APPENDIX 2

Northern sites used in the comparative analyses

Ecoregion	CMR	Site code	Site name
Arnhem Coast to Gulf of Carpenteria	**non-CMR**	NT100	Truant Island NE
		NT101	Truant Island SW
		NT102	Burston Bay
		NT103	Norruum Islet
		NT25	New Year Island anchorage
		NT26	New Year Island East
		NT27	New Year Island Boulder
		NT28	New Year Island light
		NT29	New Year Island South West
		NT35	Warrnga Reef
		NT36	Guluwuru Island NE
		NT37	Truant Island SW
		NT38	Truant Island N
		NT39	Truant Island S
		NT43	Buccaneer Shoal
		NT44	East Bremer Islet bay
		NT45	Porlsche Rock
		NT46	East Bremer Islet SW
		NT47	Bremer Islet anchorage
		NT48	Bremer Island East
		NT49	Bonner Rocks NE
		NT50	Bonner Rocks NW
		NT51	Bremer Island west
		NT52	Dudley Island SE
		NT53	Dudley Island
		NT54	Dudley Rock
		NT55	Brady Rock
		NT56	Cape Beatrice SW
		NT57	Cape Beatrice South
		NT58	Turtle Cave
		NT59	Cape Beatrice Islet West
		NT60	Groper Shoal
	Arafura	NT20	Money Shoal NW
		NT21	Money Shoal S
		NT22	Money Shoal E
		NT23	Money Shoal SE
		NT24	Bramble Rocks

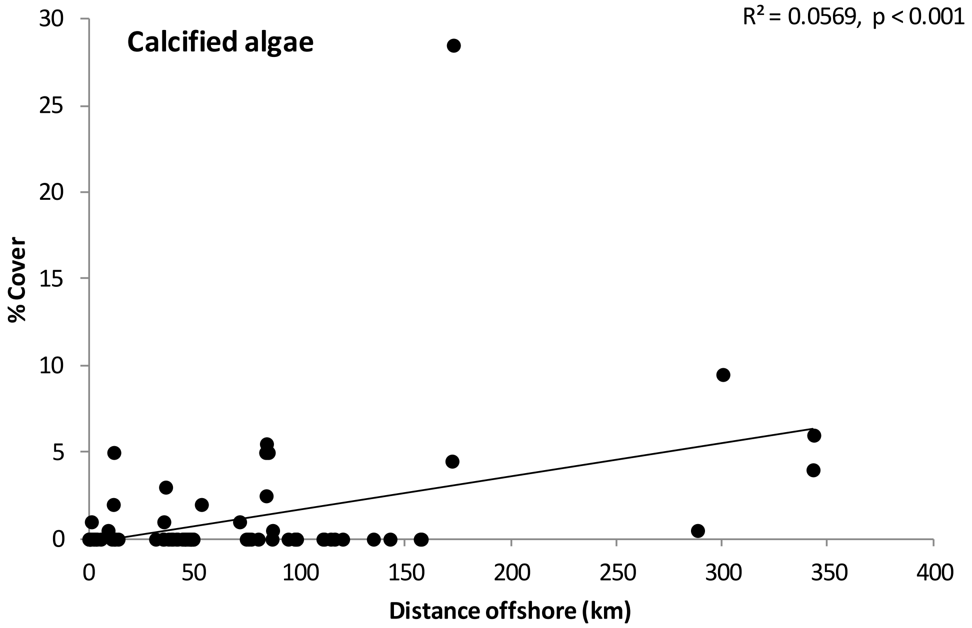
Ecoregion	CMR	Site code	Site name
	Arnhem	NT30	Arnhem CMR Gadgets Reef North West
		NT31	Arnhem CMR Gadgets Reef West
		NT32	Arnham Shoal
		NT33	Paxie Shoal North West
		NT34	Paxie Shoal West
	Gulf of Carpentaria	QLD81	Chinamans Reef
		QLD82	Foggy Bottom
		QLD83	Glasseye Reef
		QLD84	Carpentaria Reef SW
		QLD85	Carpentaria Reef
	Wessel	NT40	Truant Bank SW
		NT41	Truant Bank SE
		NT42	Pugh Shoal
Bonaparte Coast	**non-CMR**	NT10	Edge Town Hall Hole
		NT11	Old Man Rock
		NT12	The Grottos
		NT13	East Point North
		NT14	Anglers Reef
		NT2	Edge Town Hall Hole
		NT3	Weed Reef
		NT4	Stevens Rock
		NT5	Platter Rock
		NT8	Dudley Point Bommies
		NT9	East Point Coral Gardens
		OS1	Flinders Shoal East
		OS2	Flinders Shoal Central
		OS3	Evans Shoal
		OS4	Blackwood Shoal
	Oceanic Shoals	OS5	Moss Shoal Central
		OS6	Moss Shoal West
		OS7	Marie Shoal
		OS8	Marie Shoal South
Torres Strait Northern Great Barrier Reef	**non-CMR**	QLD86	Booby Island SW
		QLD87	Booby Island NW
		QLD88	Proudfoot Shoal
		QLD92	Nagir Islet W
		QLD93	Nagir Islet NW
		QLD94	Mourilyan Reef
		QLD95	Bourke Islet W
		QLD96	Bourke Islet NW
		QLD97	Hannah Banks SW

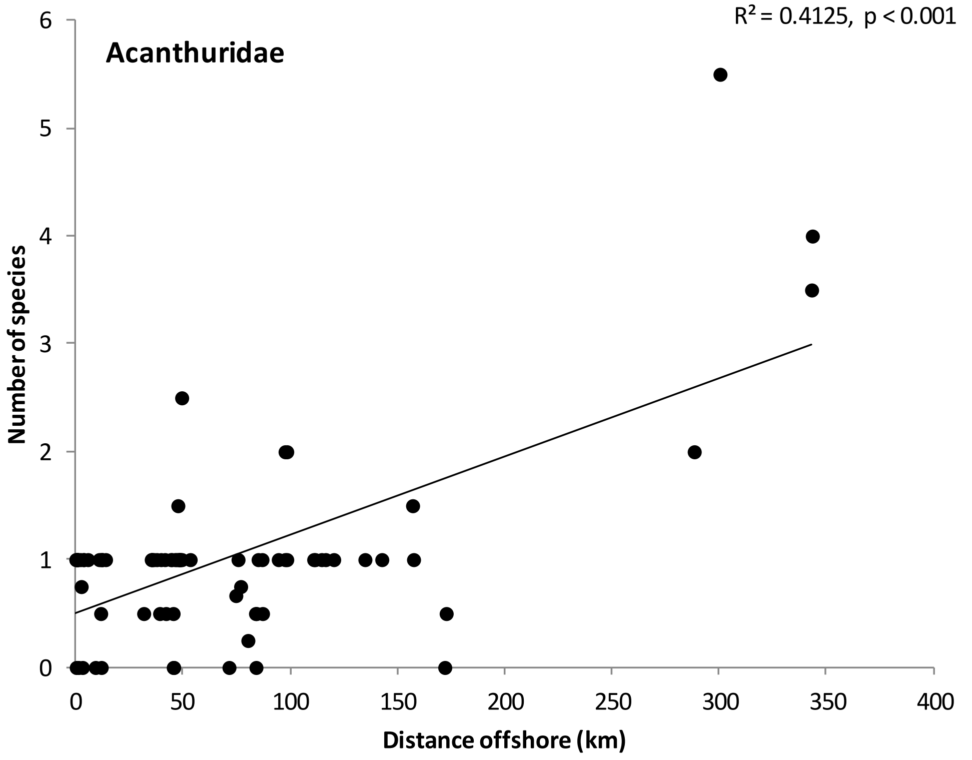
Ecoregion	CMR	Site code	Site name
		QLD98	Hannah Bank E
		QLD99	Mer Outer Reef
		TS1	Booby Island
	West Cape York	QLD89	Merkara Shoal N
		QLD90	Merkara Shoal SW
		QLD91	Carpentaria Shoal

APPENDIX 3:

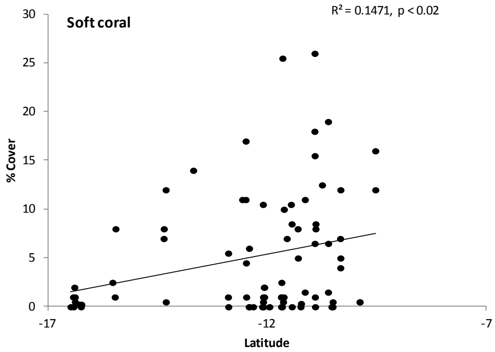
Significant relationships between benthic and fish community components and potential drivers

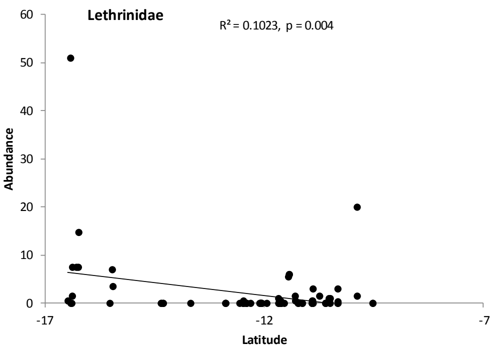
Relationship between distance offshore and the percent cover of calcified algae and the species richness of Acanthuridae.

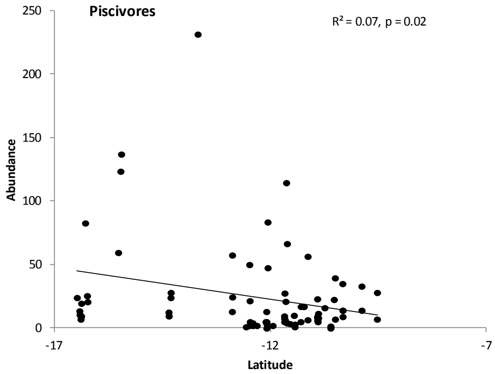


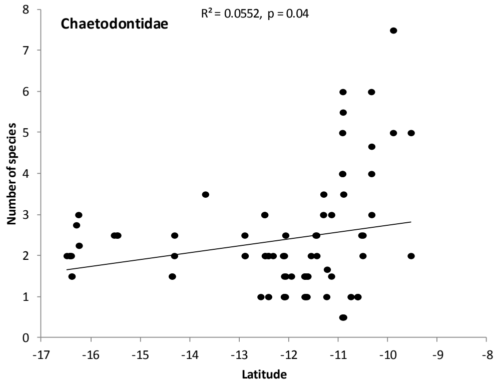


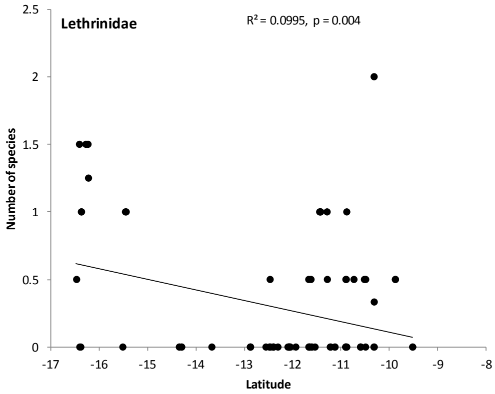
Relationship between latitude and and elements of the benthic and fish community.

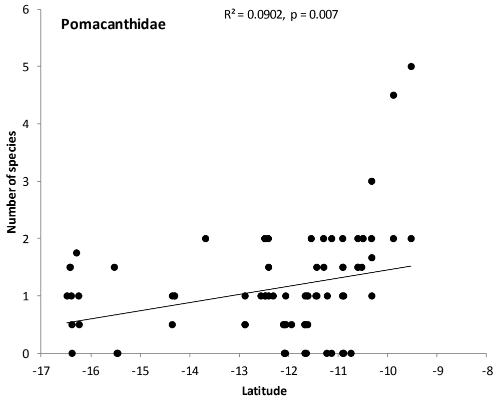


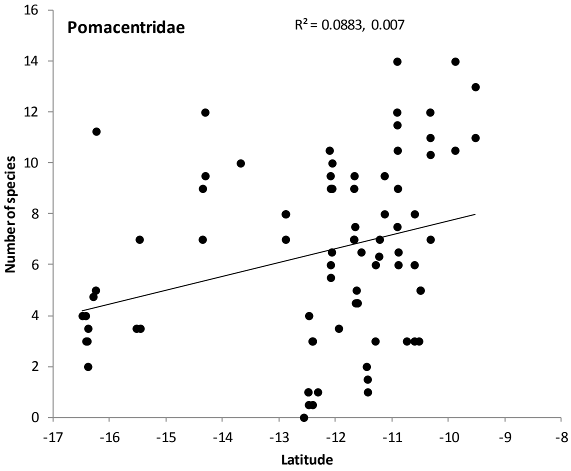


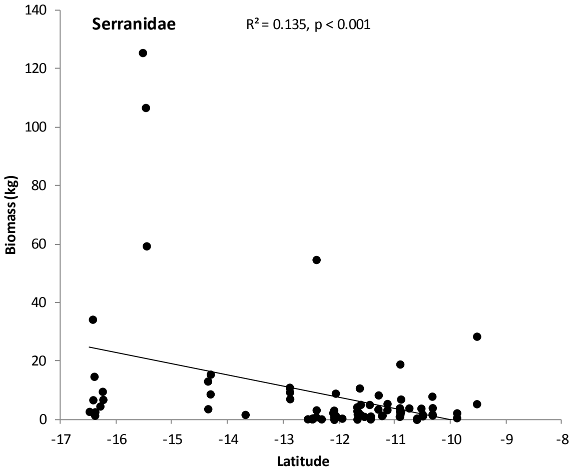


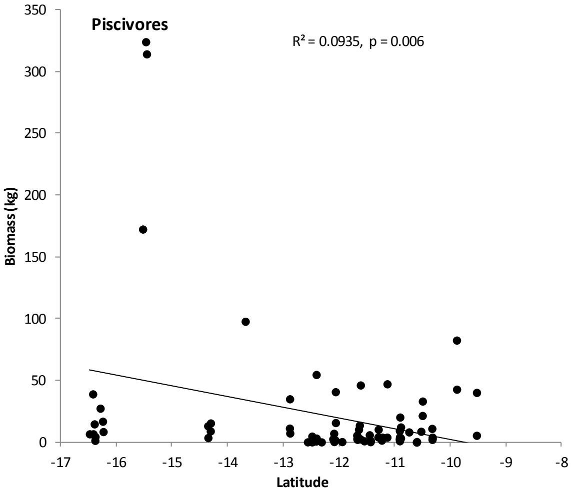


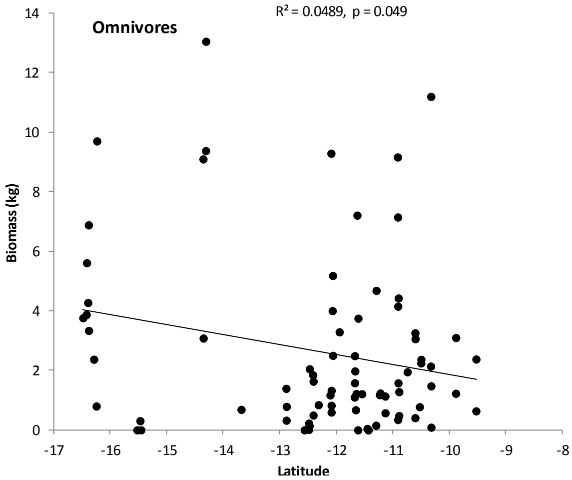


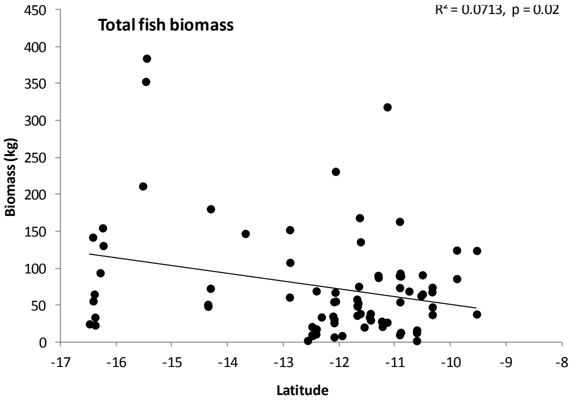


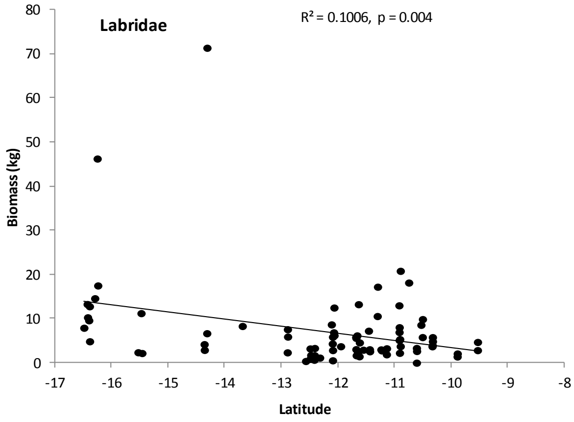

Pomacentridae
R² = 0.0883, 0.007
Number of species
0
2
4
6
8
10
12
14
16
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude


Serranidae
R² = 0.135, p < 0.001
Biomass (kg)
0
20
40
60
80
100
120
140
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude

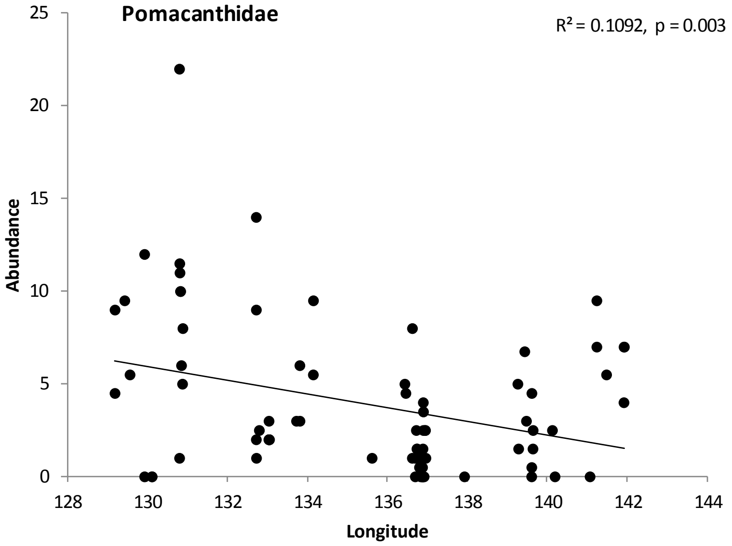

Piscivores
R² = 0.0935, p = 0.006
Biomass (kg)
0
50
100
150
200
250
300
350
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude

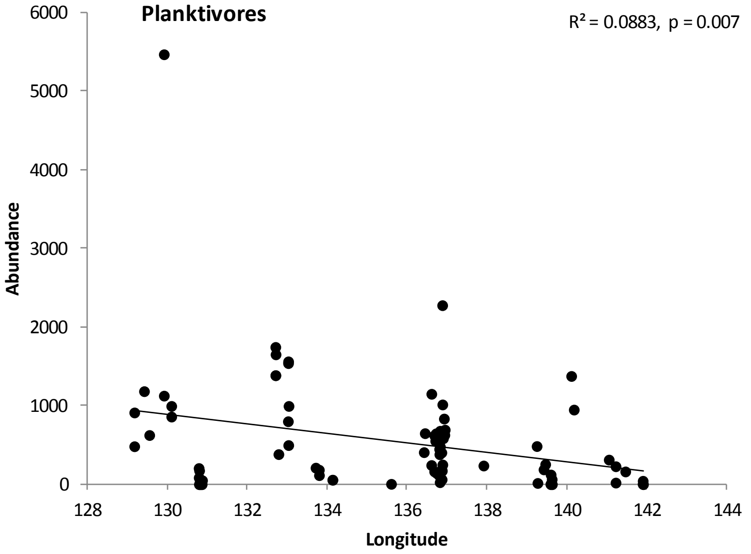

Omnivores
R² = 0.0489, p = 0.049
Biomass (kg)
0
2
4
6
8
10
12
14
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude

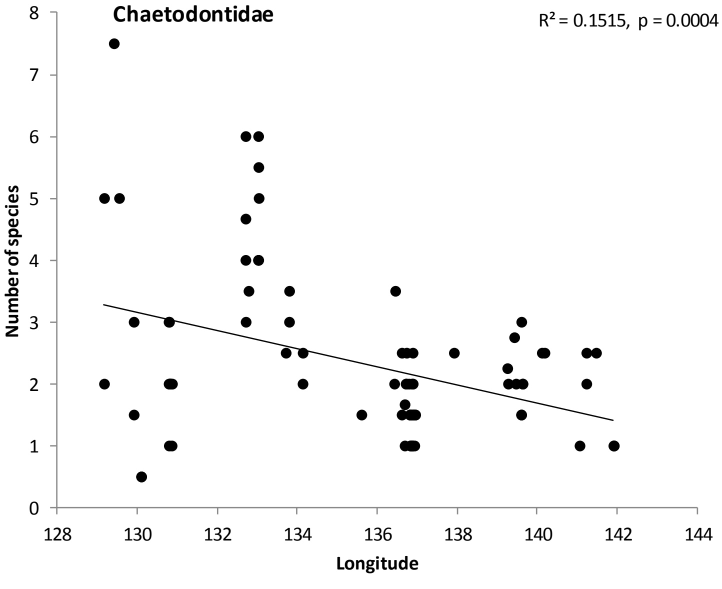

Total fish biomass
R² = 0.0713, p = 0.02
Biomass (kg)
0
50
100
150
200
250
300
350
400
450
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude


Labridae
R² = 0.1006, p = 0.004
Biomass (kg)
0
10
20
30
40
50
60
70
80
-17
-16
-15
-14
-13
-12
-11
-10
-9
-8
Latitude

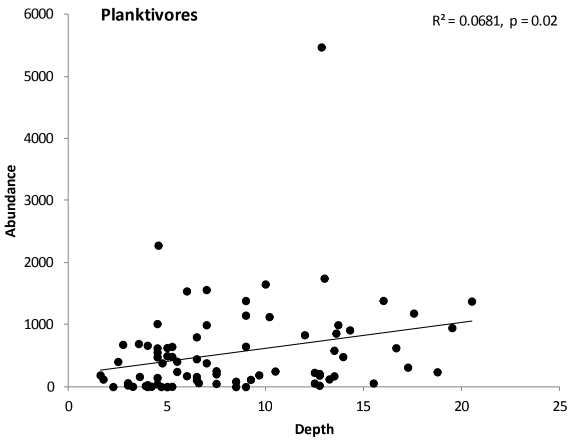
Relationship between longitude and the abundance of Pomacanthidae, planktivores and the species richness of Chaetodontidae.

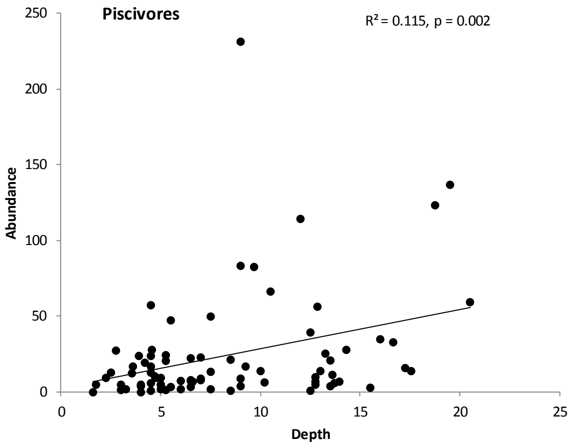


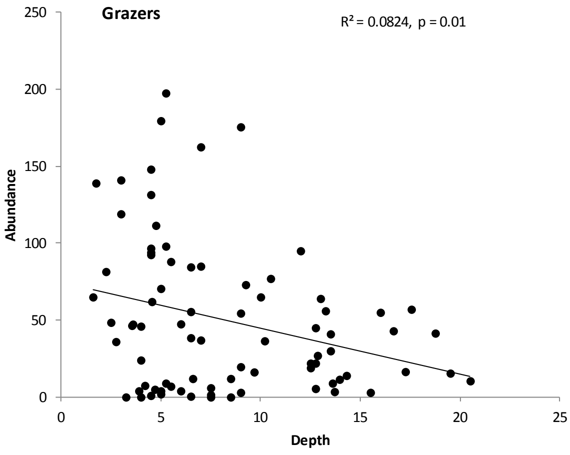


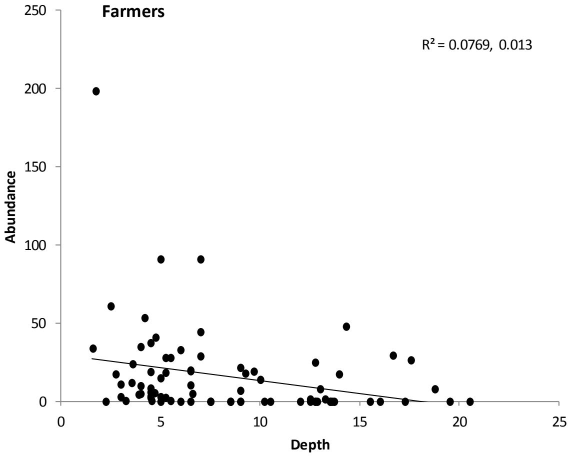


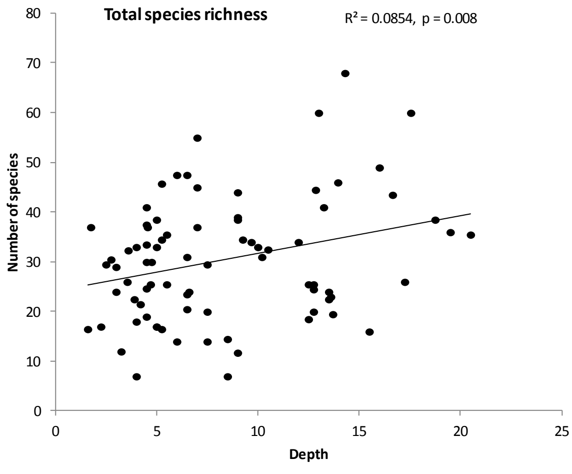
Relationship between depth and and elements of the benthic and fish community.

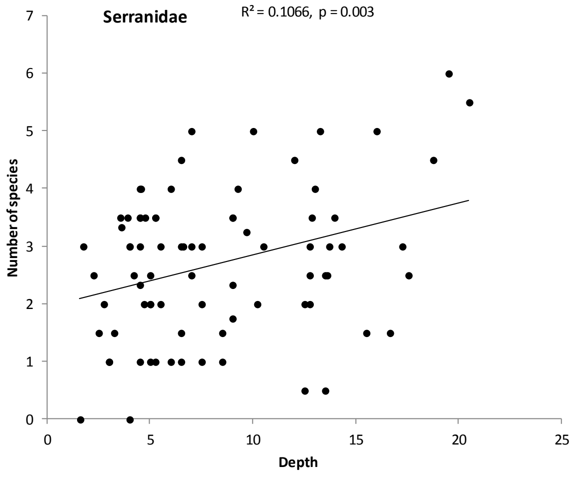


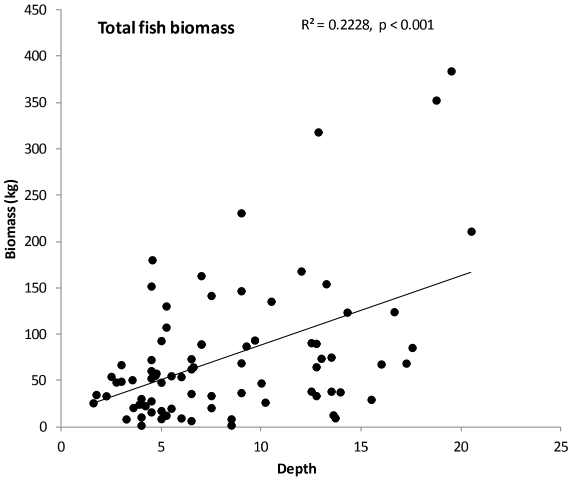


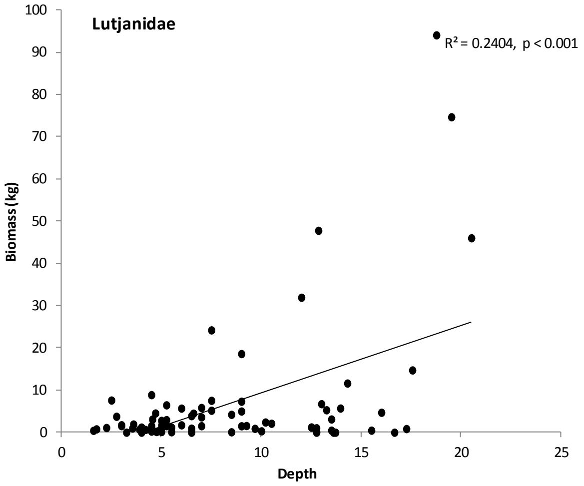


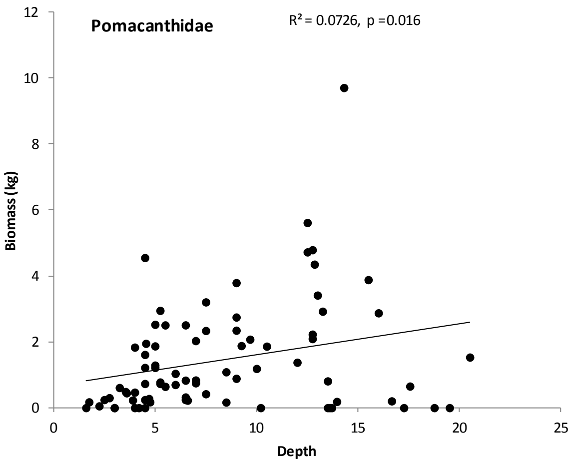


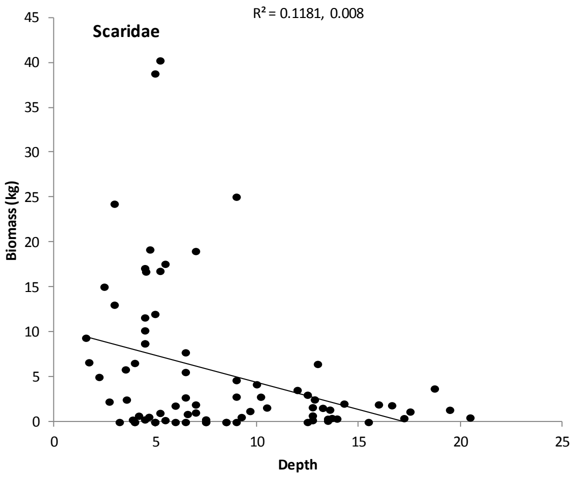


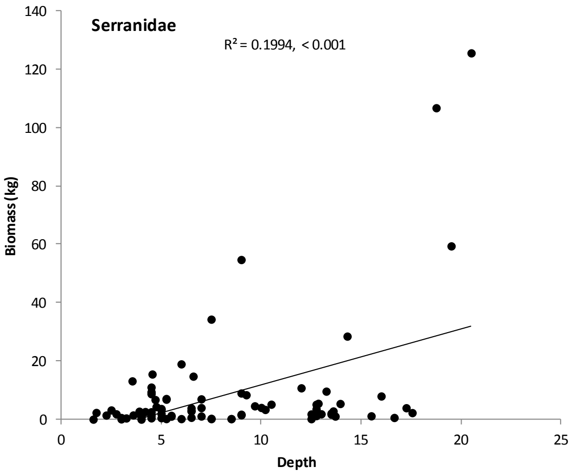


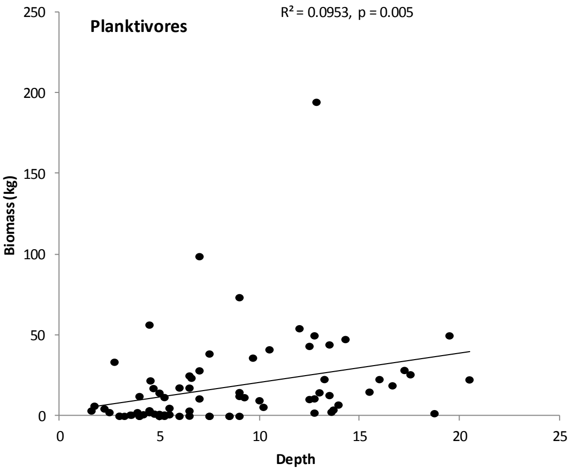

Total fish biomass
R² = 0.2228, p < 0.001
Biomass (kg)
Depth
0
50
100
150
200
250
300
350
400
450
0
5
10
15
20
25

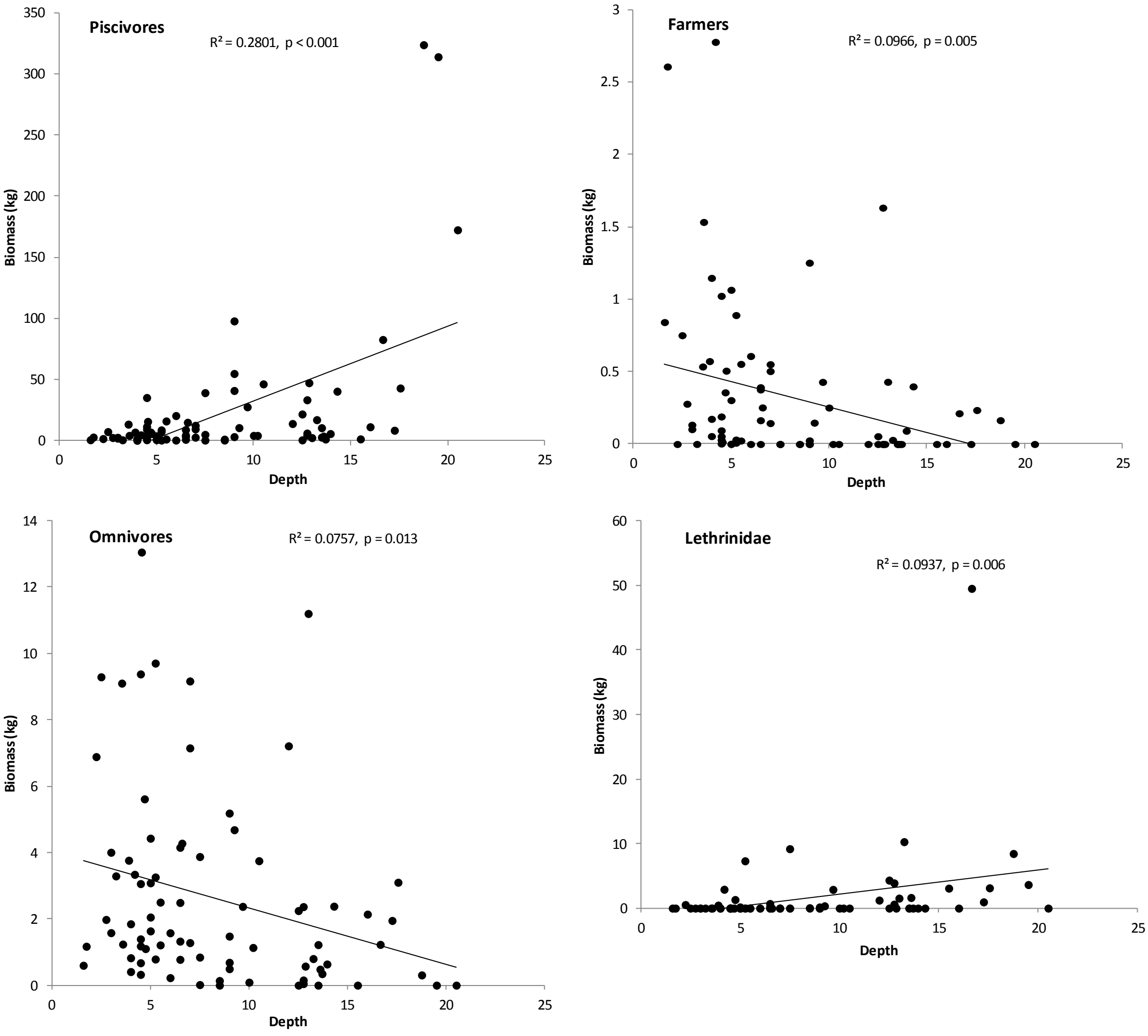

Lutjanidae
R² = 0.2404, p < 0.001
Biomass (kg)
Depth
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25


Pomacanthidae
R² = 0.0726, p =0.016
Biomass (kg)
Depth
0
2
4
6
8
10
12
0
5
10
15
20
25


Scaridae
R² = 0.1181, 0.008
Biomass (kg)
Depth
0
5
10
15
20
25
30
35
40
45
0
5
10
15
20
25


Serranidae
R² = 0.1994, < 0.001
Biomass (kg)
Depth
0
20
40
60
80
100
120
140
0
5
10
15
20
25


Planktivores
R² = 0.0953, p = 0.005
Biomass (kg)
Depth
0
50
100
150
200
250
0
5
10
15
20
25


Piscivores
R² = 0.2801, p < 0.001
Biomass (kg)
0
50
100
150
200
250
300
350
Depth
0
5
10
15
20
25
Farmers
R² = 0.0966, p = 0.005
Biomass (kg)
0
0.5
1
1.5
2
2.5
3
Depth
Omnivores
R² = 0.0757, p = 0.013
Biomass (kg)
0
2
4
6
8
10
12
14
Depth
Lethrinidae
R² = 0.0937, p = 0.006
Biomass (kg)
0
10
20
30
40
50
60
Depth

Relationship between live hard coral cover and reef fishes.