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Status and trends of reef fish and benthic assemblages of the far northern Great Barrier Reef

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Cover photo:

The 'RV Solander' leaves Cooktown at the start of the GBRF funded monitoring trip to the far northern GBR.
Image: G. Gioffre

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1 EXECUTIVE SUMMARY

This report summarises the outcomes of a field-based project conducted in January 2019 to provide for selected locations in the far northern Great Barrier Reef information on:

- coral cover, based on standard manta tow surveys, before a forecasted coral bleaching event;
- baseline coral community composition and juvenile coral density, as an indicator for reef recovery and resilience, using standard transect based fixed site survey methods;
- baseline information about fish communities, using two complementary standard methods, underwater visual census (UVC) on fixed site surveys and baited remote underwater video stations (BRUVS);
- information to assist the operationalising of the RIMReP design recommendations from exploring the suitability of selected reefs, the logistics to combine a suite of survey methods and the scope for data integration with historical data for selected sites.

Broad-scale surveys of 18 reefs and detailed surveys of seven reefs in the far northern region indicate that reef condition was variable. Reefs severely impacted by the mass coral bleaching events in 2015/16 and 2016/17 were still in poor condition, while others had intact coral populations with moderate to high coral cover. This project has provided evidence that reefs that were less impacted by the bleaching events had moderate to high coral cover. The surveys recorded many juvenile corals at densities that are expected to promote future recovery.

There was little evidence of corallivorous crown-of-thorns starfish (*Acanthaster* c.f. *solaris* - CoTS) activity and very little coral disease. However, there was evidence of continued pressure on these reefs, e.g. storm impacts, and low-level coral bleaching generally restricted to scattered individual colonies. For full recovery, we predict that severely impacted reefs will require decades without recurrent disturbances.

Fish and shark populations were healthy and despite high variability between survey reefs, their abundance and diversity were slightly higher than in other areas of the GBR to the south. Several groups of fishes, including the commercially important coral trout, were more abundant on reefs closed to fishing compared to reefs that were open to fishing. This indicates that management zones such as marine reserves are effective in remote localities such as the far northern GBR. However, this difference was only detected from data collected by fixed site surveys of fishes using underwater visual census, and not from Baited Remote Underwater Video Stations (BRUVS) sampling. This highlights the complementary value of these two standard methods.

The project also served as a proof of concept for the integration of GBR monitoring programs. The extensive field campaign showed that collecting multiple data streams at the same time is logistically feasible if properly planned and resourced, for example by using a sufficiently large vessel.

Combining datasets from various methods and ecosystem components allows for a better description of the overall condition. Taken together, the benthic and fish surveys presented here show that the strong environmental gradients across the continental shelf which have been demonstrated to be a strong driver of community structure in more southern regions of the GBR also prevail in the far north.

We did not find reef degradation from the 2015/16 and 2016/17 bleaching events to be as widespread as previously reported. However, inferences about coral reef condition in the wider far northern GBR must be carefully contextualised. Safety concerns meant that inshore reefs, where bleaching mortality was severe following the 2016 bleaching (Hughes et al. 2018a, b), were not represented in the 2019 fixed-site surveys. The moderate to high levels of coral cover recorded on the surveyed mid- and outer-shelf reefs where bleaching effects were less severe suggests that these reefs had either been exposed to less heat stress, or that they had survived and recovered from these events.

2 INTRODUCTION

The far northern Great Barrier Reef (GBR) has long been considered pristine, owing to its remote locality and small human population (Fabricius et al. 2008, De'ath 2012). However, it is not immune to pressures which reduce the condition of coral and fish assemblages, highlighted by the first ever back-to-back coral bleaching events in 2015/16 and 2016/17. Aside from the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program (LTMP) broad scale manta tow surveys, which have collected categorical data of coarse taxonomic resolution (i.e. hard coral cover) intermittently since 1985, opportunistic sampling by Reef Life Surveys (Stuart-Smith et al. 2018) and some one-off studies (Castro-Sanguino et al. 2017, Gonzalez Rivero et al. 2017a, Johnson et al. 2019, Global FinPrint Project), there is little information about the effects of management zoning and particularly, the status of coral and fish assemblages after the 2016/17 coral bleaching event in this remote area of the GBR. The 2015/16 coral bleaching event caused widespread coral mortality across much of the far northern GBR (GBRMPA 2017, Hughes et al. 2018a) and a shift in community structure of coral assemblages (Hughes et al. 2018b). On reefs of the far northern GBR above 14°S, coral loss was most severe close to the coast with 75-100% mortality on inshore reefs north of Princess Charlotte Bay, but lower mortality between 25-50% on most offshore reefs (GBRMPA 2017, Hughes et al. 2018b). Mortality was unequal among coral families and reproductive modes, producing a shift in community structure after the bleaching, with assemblages containing more brooding rather than broadcast spawning corals post-bleaching (Hughes et al. 2018b). Similarly, a recent study reported that changes in hard coral cover was found to be variable and patchy in the far northern GBR with some reefs declining while others increased following the recent coral bleaching events (Stuart-Smith et al. 2018). Another study examining coral recruitment in 2017 found an 89% reduction in coral recruitment compared to previous decades prior to the 2015/16 bleaching, and that for the first time, the brooding Pocilloporid recruits replaced spawning Acroporid corals as the dominant taxon that recruited to recruitment tiles (Hughes et al. 2019). However, to place these results into context of the current project, several details need to be considered. Hughes' studies were all conducted in shallow water coral assemblages on the reef crests and were of short duration (Hughes et al. 2018a, b, 2019). Thus, it is unknown how these bleaching events affected coral assemblages in other types of reef habitats (e.g. reef slopes, back reefs) and what the current status of these reefs is in comparison to historical records.

There has been much less focus on fish assemblages in the far northern GBR, with few studies quantifying their diversity and abundance. A recent study found declines in coral feeding fishes following the 2015/16 coral bleaching, with few changes in other fishes that could be attributed to coral mortality (Stuart-Smith et al. 2018). Other work has highlighted that the effectiveness of marine reserves was variable, with higher abundance and biomass of fishery targeted species on far northern reefs around Cape Grenville, but negligible effects further south around Princess Charlotte Bay (Castro-Sanguino et al. 2017).

Similarly, reef associated parrotfishes were shown to have higher abundance and biomass on reefs closed to fishing in the far northern GBR, but there were also strong cross shelf gradients in their assemblage structure that distinguished sheltered inshore and mid-shelf assemblages from those of the more exposed outer-shelf (Johnson et al. 2019). The Global FinPrint Project aimed to quantify shark populations around the globe, and surveyed shark and fish assemblages on reefs of the far northern GBR in 2015 and 2016 to explore any post-bleaching community changes (www.globalfinprint.org). Data from the 2015 and 2016 surveys are currently being analysed for publication in conjunction with the 2019 data. While these studies provide snapshots of the spatial patterns in reef fish assemblages in the far northern GBR, there is currently no long-term data on indicators of reef fishes for this region.

Long-term data on indicators of coral reef condition are essential to understand the context of short-term changes as coral reefs go through cycles of disturbance and recovery. The 30+ year record of coral cover data from the LTMP has revealed the cumulative impact of multiple disturbances[1]. In this long-term context, the impacts of the 2015/16 and 2016/17 mass bleaching events are considered severe, especially in the far northern regions.

In October 2018, the Bureau of Meteorology issued an El Niño Alert[2], which typically means unusually warm sea surface temperatures along the GBR in late summer, increasing the likelihood of thermal conditions conducive to coral bleaching. By late October 2018, NOAA's Outlook of Coral Bleaching Heat Stress predicted a 90% probability that "bleaching was possible" on the GBR[3]. These forecasts highlighted a need to establish the status of reefs of the far northern GBR prior to events predicted to unfold later in the austral summer of 2018/19.

The extent of coral loss attributable to the latest coral bleaching in the summer of 2016/17, other disturbances, or any delayed stress-related mortality such as coral disease was not known for the northern GBR, as reefs in the northern reporting region of the GBR were last surveyed by the LTMP between August and December 2016 (2017 report year) and by the Bleaching Task Force in November 2016 (Hughes et al. 2018a, b). The most recent manta tow surveys AIMS conducted in December 2016 had found severe bleaching mortality on the most northern reefs in Cape Grenville (5 of 11 reefs had lower coral cover compared to previous surveys) and patchy, less severe mortality on reefs in Princess Charlotte Bay. In late 2016, a number of LTMP survey reefs still had high coral cover and the status of those reefs in 2019 was of particular interest given the overall declines in brood stock (Hughes et al. 2019). Overall, there had been a paucity of information about potential signs of recovery, e.g. presence of juvenile corals, on these far northern reefs.

The Reef 2050 Integrated Monitoring and Reporting Program (RIMReP) design recommendations for monitoring of coral reefs (Schaffelke et al. 2018) included an evaluation of limitations of existing programs (Cheal & Emslie 2018). One limitation that was addressed by the current project was inadequate monitoring, both in terms of spatio-temporal extent but also the number of indicators of reef condition recorded, and less than adequate survey frequency in the far northern GBR. The present

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[1] Annual update to May 2018: https://www.aims.gov.au/reef-monitoring/gbr-condition-summary-2017-2018

[2] http://www.bom.gov.au/climate/enso/outlook/

[3] https://coralreefwatch.noaa.gov/satellite/bleachingoutlook_cfs/outlook_cfs.php

study aimed to fill this knowledge gap and in doing so pave the way for regular monitoring of this remote region.

This report focuses on the status and trends of fish and benthic assemblages on reefs in the far northern GBR in 2019, determined from broad-scale manta tow surveys, intensive fixed site surveys and the use of Baited Remote Underwater Video Stations (BRUVS).

These data provide an updated status of reefs in this area following the 2015/16 and 2016/17 coral bleaching events, and a benchmark against which to gauge future changes in coral reef assemblages.

3 METHODS

In-water surveys on selected reefs (Figure 1) in the far northern GBR were carried out in January 2019. Pre-trip site selection criteria for the monitoring activity included: previous data history (LTMP, XL Catlin Seaview Survey, Global Finprint Project), management zoning (paired reefs open and closed to fishing) and representation of reef bioregions. Data were collected using an array of survey techniques, including:

1. Broad-scale manta tow (Miller et al. 2009), which estimates hard coral cover and provides counts of CoTS on 17 reefs.
2. Detailed underwater surveys of benthic reef communities from fixed site surveys on seven reefs using digital imagery (Jonker et al. 2008). Surveys were conducted on permanently marked transects to facilitate repeat surveys in the future. These surveys provide detailed information on benthic community composition and provide estimates of coral cover by genus, counts of agents of mortality (e.g. CoTS, *Drupella*, coral diseases, bleaching), counts of juvenile corals (<50mm) and estimates of reef rugosity measured from 3-dimensional modelling of video.
3. Underwater visual census of 244 species of reef fishes from fixed site surveys (Emslie et al. 2018) on seven reefs.
4. Surveys of reef fishes using Baited Remote Underwater Video Stations (BRUVS) of seven reefs.

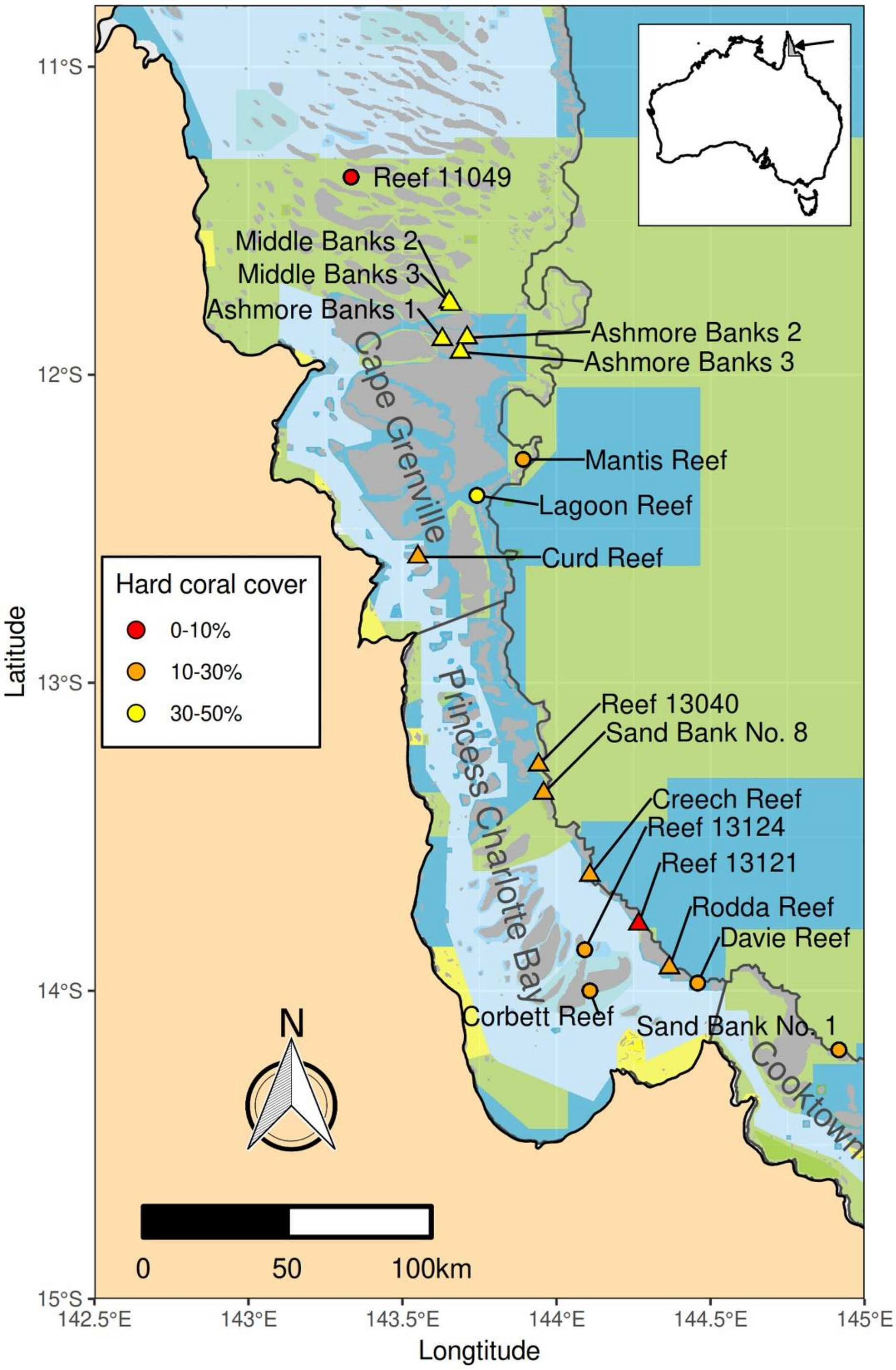

Figure 1: Map of the eighteen reefs surveyed in January 2019. Reefs are coded by survey technique such that triangles are reefs where only broad-scale manta tow surveys were conducted, while circles denote reefs where full surveys were undertaken using manta tow, fixed site surveys and BRUVS deployments. Reefs are coloured by the reef-wide median hard coral cover determined during manta tow surveys. Management zones are overlaid green = closed to fishing, dark and light blue and yellow = open to fishing. Solid grey lines denote the Cape Grenville and Princess Charlotte Bay latitudinal sectors.

3.1 Survey techniques - Manta tow

During manta tow surveys an observer is towed behind a small 5m inflatable boat in a series of two-minute tows around the entire perimeter of a reef (Figure 2). The number of tows required to complete an individual survey depends on the size of the reef. After each two minute tow, the observer records estimates of hard coral cover on a categorical scale (0 = 0%, 1 = >0 to 10%, 2 = 10.1 to 30%, 3 = 30.1 to 50%, 4 = 50.1 to 75%, 5 = 75.1 to 100%), as well as estimates of soft coral cover and the number of CoTS, coral trout and sharks observed for that tow. Two boats are used to complete the surveys. Both boats start at the same point on the reef and proceed in opposite directions until they meet up and the other end of the reef (Figure 2).

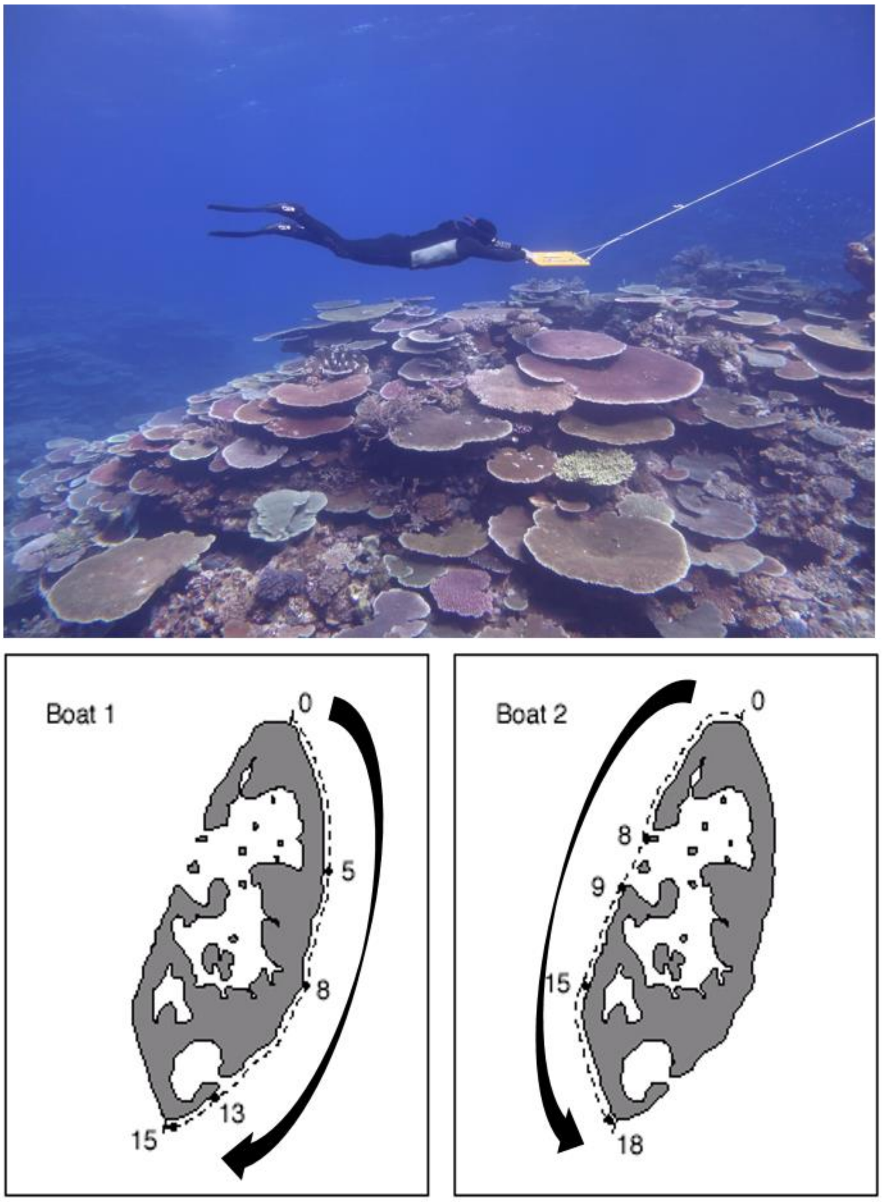

Figure 2: The manta tow technique is used to estimate reef-wide hard coral cover. An observer is towed behind a small inflatable boat in a series of two-minute tows (Top panel). At the end of each two-minute tow the observer records a categorical estimate of percent hard coral cover. Two boats are used to complete surveys at each reef, one boat proceeds clockwise around the reef until it meets the other boat, which has proceeded anti-clockwise around the reef (Bottom panels).

3.2 Survey techniques - Underwater fixed site surveys

3.2.1 Surveys of fish and benthic assemblages

Historically, the LTMP has surveyed forty-seven distinct reefs annually between 1995 and 2005, and biennially thereafter. Survey reefs were spread across six latitudinal sectors (CL = Cooktown/Lizard Island, CA = Cairns, TO = Townsville, WH = Whitsunday, SW = Swains, CB = Capricorn-Bunker) and within each sector, replicate reefs were surveyed in each of three positions across the continental shelf (inshore, mid-shelf, outer-shelf) where available. On each survey reef, benthic and reef fish assemblages were surveyed at three sites in a standard reef slope habitat on the northeast flank. The northeast flanks of GBR reefs are oblique to the prevailing south-easterly weather, ensuring consistency in relative exposure among different reef assemblages and so enabling valid spatial comparisons.

In addition, the LTMP has conducted biennial surveys in alternate years to the LTMP from 2006 to the present, to monitor the effectiveness of the 2004 rezoning of the GBRMP under the Representative Areas Program (RAP). This project utilised the same within-reef methodology on reefs spread across six latitudinal sectors (CA = Cairns, IN = Innisfail, TO = Townsville, PO = Pompey, SW = Swains, CB = Capricorn-Bunker; see Emslie et al. 2015 for further details). One difference was that in order to account for the effect of zoning (open or closed to fishing), reefs were paired by management zone such that one reef was open to fishing while the other was closed to fishing. As the current GBRF project was intended to act as a pilot study for future coral reef monitoring under RIMReP, the sampling design incorporated elements of both the historical LTMP and the RAP rezoning monitoring programs. Surveys undertaken for the current project followed the same methodology as described above for the LTMP, with the exception that no inshore reefs could be surveyed due to safety concerns. In each sector, reefs were paired by management zone (open or closed to fishing) and two reef pairs were selected for surveys.

During January 2019, benthic and fish surveys were conducted concurrently along five permanent 50m belt transects set at a depth between 6–9m in each of three sites (Figure 3) on each of seven reefs (Figure 1, n = 15 transects reef^{-1}). Visual surveys of 168 species of large mobile fishes (Table S1) occurred before benthic sampling to avoid issues with diver disturbance (Emslie et al. 2018). During each survey a 50m fibreglass tape was run out along the transect line after the first observer had recorded the abundance of large mobile fishes in a 5m wide belt. Digital images were taken at 1m intervals along each transect and surveys of agents of coral mortality were conducted along the same transects on a 1m wide belt, and included counts of CoTS, incidence of coral bleaching and coral diseases and numbers of the corallivorous snail *Drupella* spp. Additionally, juvenile corals (<50mm diameter) were counted along a five-metre section of each transect in a 34cm wide belt. Juveniles were identified to genus. Finally, another diver made the return swim counting 77 small site-attached species of damselfishes (family Pomacentridae) on one metre wide belts, while their dive buddy retrieved the transect tapes. See Jonker et al. (2008) and Emslie and Cheal (2018) for detailed methods.

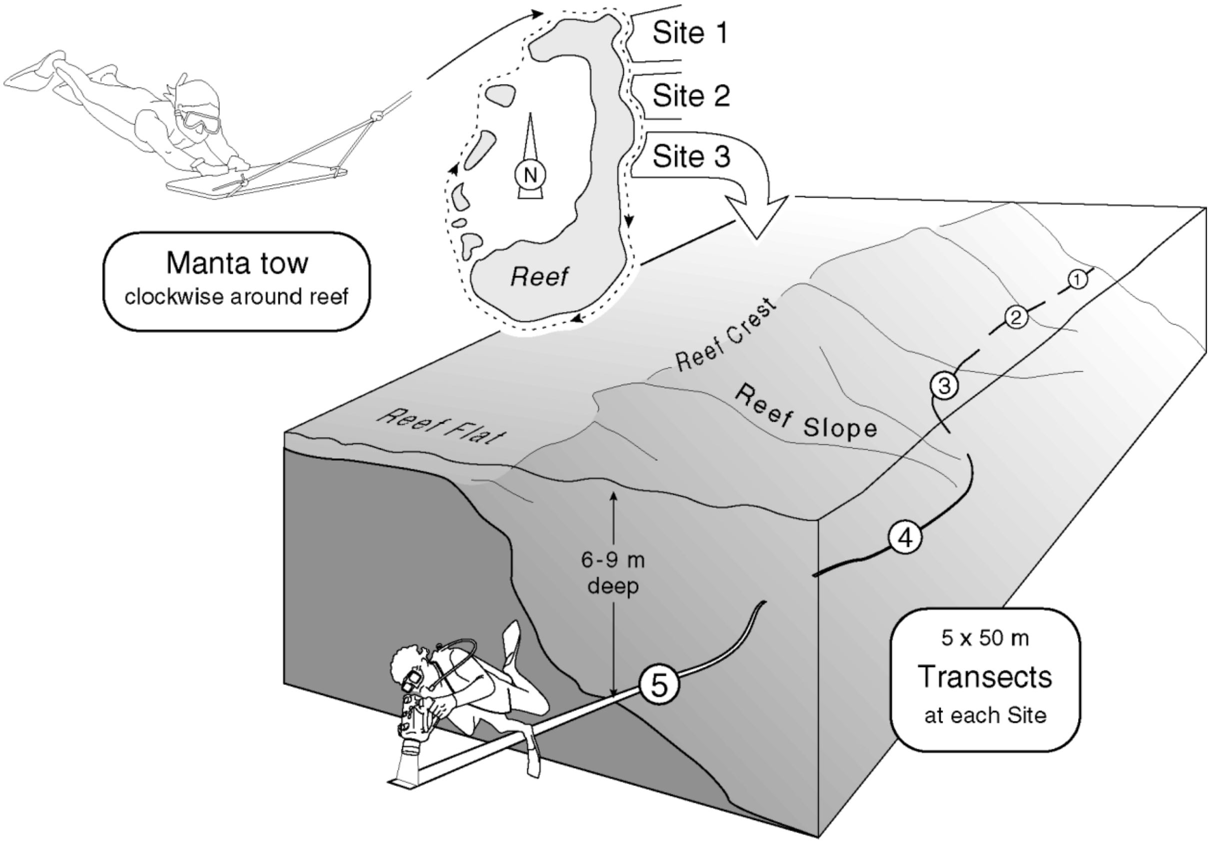

Figure 3: Within-reef sampling design used by the LTMP for fixed site surveys.

3.2.2 Three-dimensional modelling of structural complexity

High-definition videos (4K) were collected concurrently to benthic photo transects to recreate the three-dimensional terrain of the reef substrate by photogrammetry and to estimate structural complexity. For this purpose, two GoPro Hero 6 cameras were arranged in stereo, fastened to a metal bar and separated by 40cm (Figure 4). Due to the sufficient ambient light, no additional light sources were used. Videos were collected along each survey transect, from an approximate distance of 50cm from the reef substrate, in line with the benthic surveys. Three pairs of Ground Control Points (GCP) were laid evenly across the transect (Figure 4). A Ground Control Point (GCP) is a feature that can be identified in the footage for which there is known ground coordinates. GCPs were deployed in pairs, separated by a fixed distance of 15cm. This known distance was used to scale the 3D reconstruction.

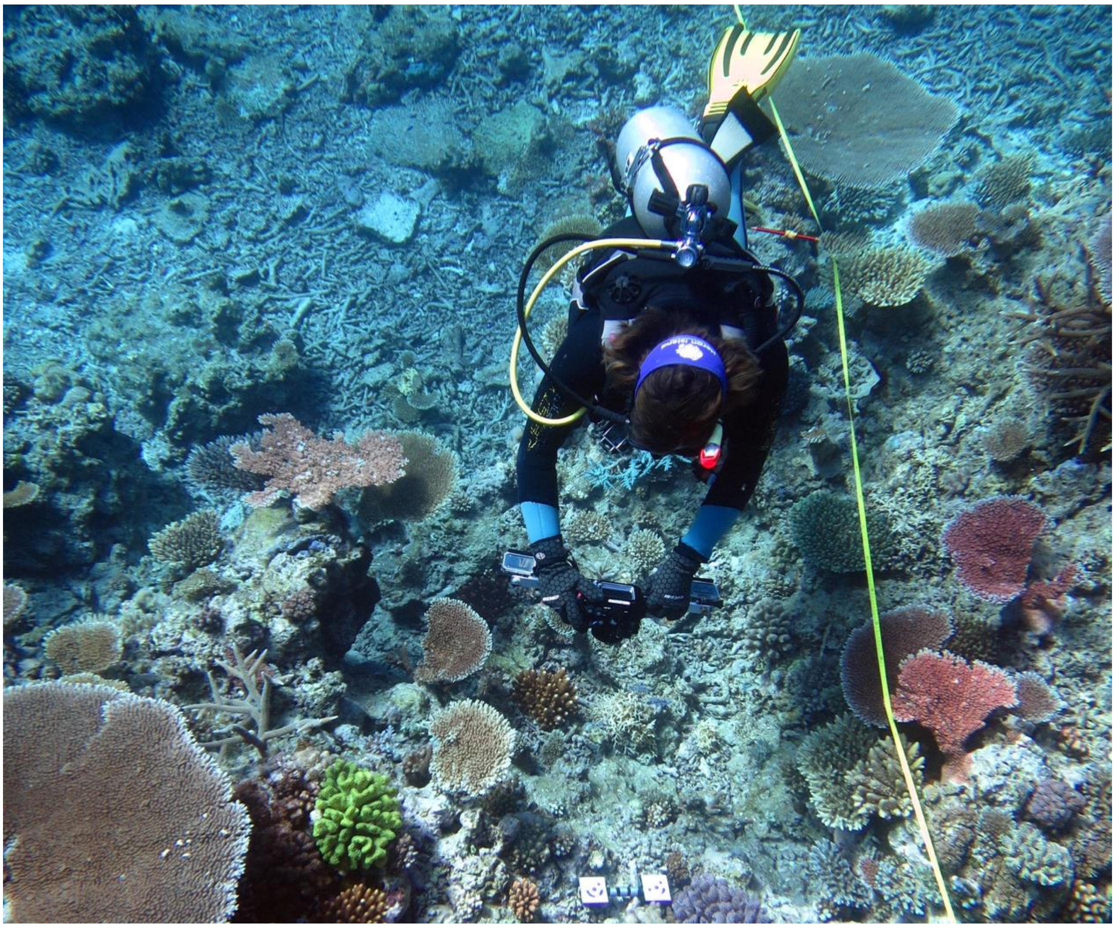

Figure 4: Diver collecting imagery along a transect for 3D reconstructions using a paired-arrangement of Go-Pro cameras set apart by 40cm. The picture also shows the Ground Control Markers (GCP) laid on the reef as a ground reference to scale the 3D reconstruction.

Three-dimensional bathymetric models of the reef topography were produced from two-dimensional and overlapping images extracted from survey videos using Structure from Motion (SfM) algorithms. SfM is a photogrammetric technique that finds correspondence between images and tracks common features (edges, shapes, etc) from one image to the next.

The feature trajectories are then used to reconstruct their location in the 3D space and create a high-resolution (millimetre scale) tridimensional representation of the reef topography. All computations were performed in Agisoft Metashape Professional (Autodesk, Inc. Version 1.5.2).

Videos were converted to frames (8 Megapixels) using the open software FFmpeg (www.ffmpeg.org) and at a rate of six frames per second of video. Still frames were first filtered by measuring the image quality, using a built-in function in Metashape that calculates the percentage area of the image that is in focus. Frames below a threshold of 50% were discarded from the analyses. Cameras were calibrated to estimate their optical parameters (e.g. focal length, lens curvature parameter, focal centre, etc.) and therefore ensure high accuracy from the 3D reconstructions (see Remondino and Fraser 2006 for details). To recreate the 3D models (Figure 5), the algorithm searches for common points (at pixel scale) in overlapping frames, matches them, and determines the position of the camera for each frame. The next step builds a dense point cloud based on the estimated camera positions and pictures. Finally, the produced point cloud (XYZ coordinates) was exported as a text file in relative coordinates.

Previous evaluations of the accuracy of 3D reconstructions using this methodology suggests that the technique can replicate the 3D structure of coral reefs within millimetres of error (Figueira et al. 2015). To evaluate this error, we used control scale-bars defined by a fixed distance between GCPs to estimate the difference in distance estimations between model representations and the actual distance.

Figure 5: Sample 3D reconstruction from a transect section. This reconstruction is comprised of hundreds of thousands of points in the 3D space (i.e. point cloud), which are then exported to estimate rugosity as a metric of structural complexity.

3.2.2.1 Estimation of structural complexity

Rugosity was the metric used to estimate structural complexity from each 3D reconstruction, using the approach described in Gonzalez-Rivero et al. (2017b). The rugosity index is a measure of the deformation of a surface relative to its planar projection, and it is a common metric used to characterize the architecture of reef habitats (Graham and Nash 2013), where a value of 1 depicts a perfectly flat surface and the index increases with the complexity of surface convolutions.

While rugosity is typically measured using the chain-and-tape method (Risk 1972, Graham and Nash 2013), it can be calculated with precision from 3D reconstructions of the seafloor (Friedman et al. 2012, Burns et al. 2015, Figueira et al. 2015, Ferrari et al. 2016). Here, rugosity (R) was calculated as the ratio of the surface area of the convoluted terrain (Ar) to its projected geometric surface area (Ag, Equation 1). See Friedman et al. (2012) for further details.

For this calculation, the 3D point cloud was converted to a surface area (mesh). To calculate rugosity, points were evenly sampled from the 3D surface area at intervals of approximately 30 cm, resulting in about 1000 points per transect. These points identified the centroid location of each reference area (Ag, 25cm^2) to estimate rugosity (Figure 6).

$$fr = Ar / Ag \qquad \text{(eq 1)}$$

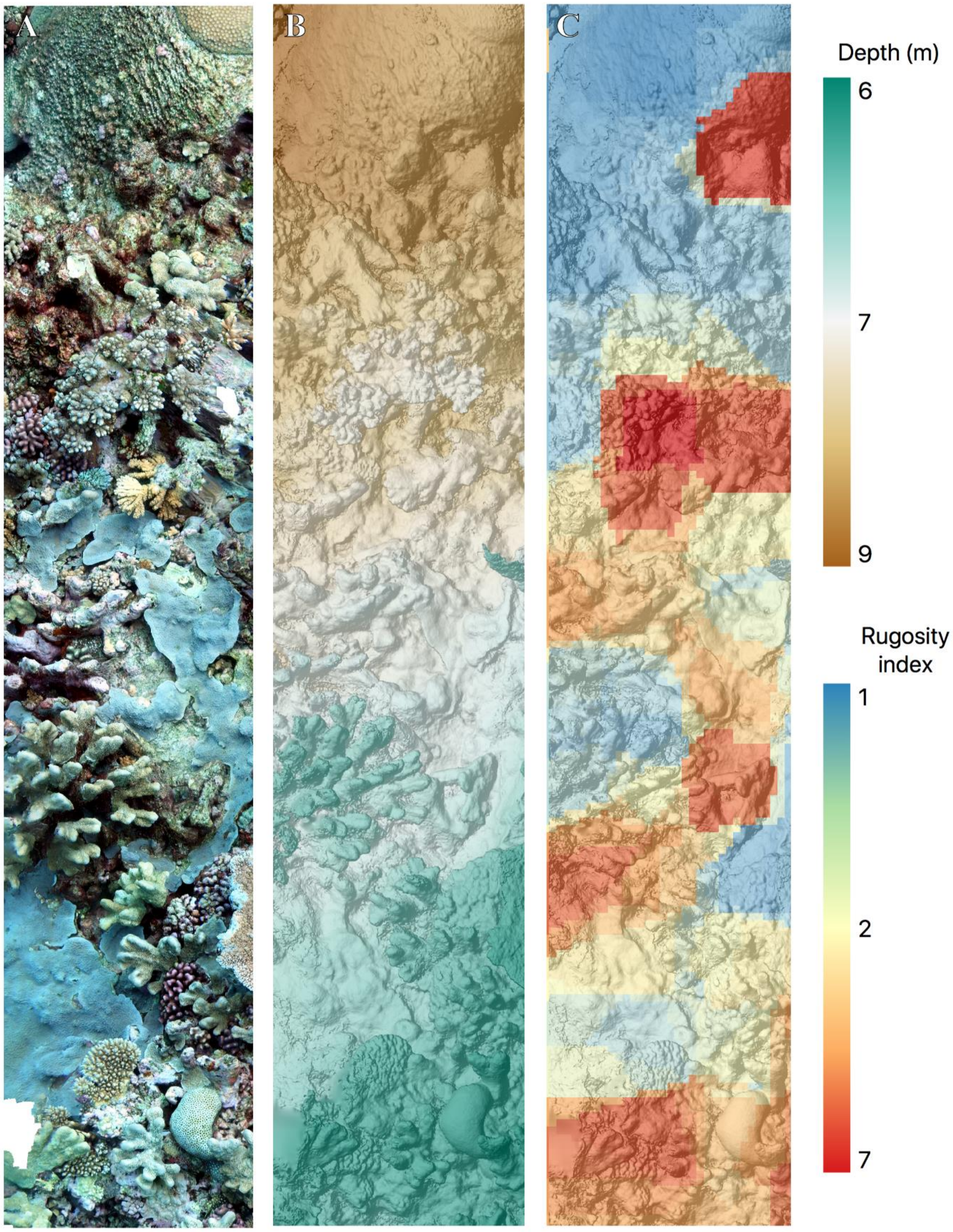

Figure 6: Visual representation of the outputs produced from the methodology to estimate structural complexity of coral reefs using photogrammetry and 3D data analysis: (A) Top view of a 3D reconstruction from a transect section, (B) Bathymetry generated from the 3D reconstruction and (C) Interpolated rugosity index estimated at specific point locations across the 3D reconstruction.

To determine the importance of habitat complexity for reef biota, we examined the relationships between structural complexity and damselfishes, and complexity and juvenile corals. Damselfishes are known to be strongly tied to the benthos for shelter and food, with structural complexity providing refuges from predation (Klumpp and Polunin 1989, Chabanet et al. 1997, González-Rivero et al. 2017b).

Similarly, early-stage hard corals (juveniles), rely on complex substrates to provide shelter from UV radiation, predation, competition and other sources of mortality (Gleason et al. 2006, Doropoulos et al. 2016, Gallagher and Doropoulos 2017).

3.3 Survey techniques - Baited Remote Underwater Video Stations (BRUVS)

3.3.1 Field surveys

The BRUVS consisted of a steel frame onto which one or two camera housings and an arm bearing a bait canister, ballast weights, ropes and floats were attached. Each housing contained a GoPro video camera (Hero 4 Silver, Figure 7), which recorded footage at 30 frames per second, at 1920x1080 pixel resolution, with a medium field of view. A bait arm held a steel mesh bait bag containing 1 kg of crushed pilchards (*Sardinops sagax*) at approximately 1.5m in front of the camera lens. BRUVS frames were ballasted according to the prevailing sea-state and current conditions to ensure stability on the seabed. An 8mm diameter polypropylene rope with surface floats attached enabled the BRUVS to be deployed by small tender vessels for 60 minutes duration on the seabed before retrieval (Figure 7).

The allocation of deployment positions across each reef was done using a regular-random design to within the bounds of the 30m depth contour, and where possible, integrated previously sampled sites where coral cover was recorded and legacy data exists (Corbett, 13-124, Lagoon and Mantis Reefs). A minimum distance of 350m between each BRUVS unit avoided overlap of bait plumes and reduced the likelihood of fish moving between deployments within the sampling period (Cappo et al. 2004). Once the positions were derived, the sequence of deployments, in sets of 6 replicate units, was determined for each of the two tenders by proximity and prevailing sea conditions on the day. Depth of each deployment was randomised between shallow (<10 m) and deep (11-30 m). Site locations on the seven reefs are shown in Figure 1.

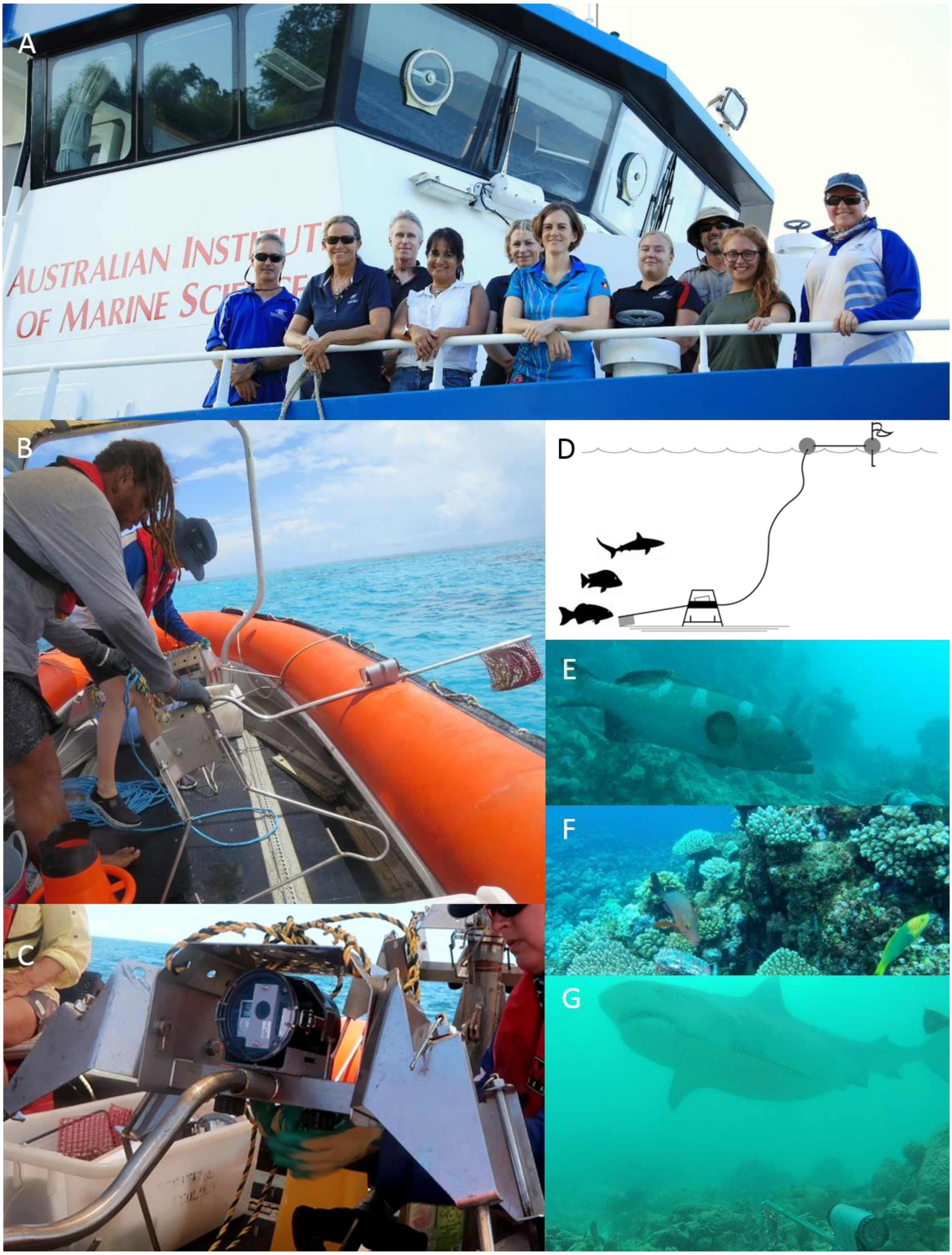

Figure 7: Launch of far northern GBR expedition (A), BRUVS units ready for deployment with bait arm attached (B, C), typical deployment with bait canister touching the seabed (D), and action on the seabed (E: blue-spot trout *Plectropomus laevis*; F: paddletail *Lutjanus gibbus*; and G: likely pregnant tiger shark *Galeocerdo cuvier*).

3.3.2 Video analysis

BRUVS videos were interrogated using custom software designed by AIMS ("BRUVS3.03".mdb) to capture and store the timing of events, reference images and counts of fish in the field of view. The maximum number of each species seen together in progression of the whole video (MaxN) were recorded. The use of MaxN has been reviewed by Schobernd et al. (2014) and Willis et al. (2000). It is the most common metric of relative abundance used in baited video studies.

Species identifications were made according to the Australian CAAB Codes national standard (Yearsley et al. 1997). For taxa indistinguishable on video footage, genera *Macolor*, *Ctenochaetus* and *Acanthurus*, these were pooled under one name. The term 'fish' hitherto refers to any marine vertebrate seen in the field of view, including sharks, rays and sea snakes.

A standardised classification scheme for the seabed in the BRUVS field of view was developed for shoals and reefs of the GBRMP by AIMS for previous studies of submerged coral reefs (Cappo et al. 2012). This scheme was applied by reviewing all images of the seafloor collected from all BRUVS videos from the far northern GBR in 2019.

Images were assigned to one of eight qualitative categories of "bedform" (flat sand or gravel or silt, sand ripples, sand dunes, rubble field, *Halimeda* bank, low reef/outcrop, high reef/outcrop, boulder field). The classification scheme identified percentage cover in the images (to the nearest 10%) of 6 categories of substratum within these bedforms (mud, sand, gravel, rubble, bedrock and boulder, calcareous reef) that summed to 100%.

In terms of epibenthic "cover" (or lack of it), the images were also assigned to one of 6 "habitat categories" (open sandy seabed, seagrass bed, macroalgal bed, low-relief rubble field, coral reef, gorgonian and seawhip gardens). The classification scheme identified percentage cover in the images (to the nearest 10%) of 12 categories of epibenthos (gorgonian fans, sponges, sea whips, soft corals, hard corals, macroalgae, seagrass, *Halimeda*, bryozoans and encrusting animals, zoanthids, hydroids and "Bare"). These classifications also summed to 100%.

Each of the "%cover" variables were measured on the same scale, so no data transformations were needed in subsequent analyses. Some of the categories of substratum or epibenthos were absent, or poorly represented, in the dataset. These were pooled with other, larger categories to derive the shorter list of covariates in Table 1.

Table 1: Definition of the 19 explanatory covariates used in univariate and multivariate models to examine the relative effect of "habitat" for the fish sighted on BRUVS on seven reefs in the far northern GBR

Covariate abbreviation	covariate type	Covariate Definition
location	spatial	reef name
depth	spatial	Depth (m) measured under the hull when the BRUVS were deployed
zone	spatial	2004 RAP management zoning plan for GBRMP: closed or open to fishing
BRUVS field-of-view (FOV)		
% composition of seafloor by 5 pooled categories of substratum		
bdrck	substratum	% substratum classified as "bedrock", or "boulder"
calc.rf	substratum	% substratum classified as "calcareous reef"
grvl	substratum	% substratum classified as "gravel"
rbbl	substratum	% substratum classified as "rubble"
snd	substratum	% substratum classified as "sand", or "mud/fine silt"
% coverage of 7 pooled categories of epibenthos		
bare	epibenthos	% coverage of seafloor with no epibenthos
encr	epibenthos	% coverage of the seafloor by "encrusting organisms"
fltrs	epibenthos	% coverage of the seafloor by "gorgonian fans", "sponges", "sea whips", or "zoanthids"
plant	epibenthos	% coverage of the seafloor by "*Halimeda*" or seagrasses
alg	epibenthos	% coverage of the seafloor by "turf algae" or "coralline algae" or filamentous algal films
crl	epibenthos	% coverage of seafloor by "live hard corals"
sft.crl	epibenthos	% coverage of seafloor by "soft corals"
Qualitative estimates of video quality and habitat condition		
fov	FOV	Scale 1-4 of quality of field of view; aspect, angle, ability to see seabed/water column interface
visibility	FOV	Metres depth of field beyond bait canister
topo	FOV	Index of topographic complexity (1-4) *sensu* Espinosa et al. (2014)
dead	FOV	Qualitative scale (0-4) of proportion of standing coral that were considered to be dead

3.4 Statistical analyses

Unless stated, all analyses were conducted in R 3.5.1 (R Core Development Team 2019) and all plots were produced using the package *ggplot2* (Wickham 2009). When discussing levels of percent hard coral cover, we define low as 0 to 10%, moderate as 10 to 30%, high as 30 to 50%, very high as 50 to 75% and extremely high as 75 to 100%.

3.4.1 Manta tow

Variation in hard coral cover on reefs in the Princess Charlotte Bay and Cape Grenville sectors were examined using Bayesian hierarchical linear models which were conducted via the *INLA* package. Reefs in these two sectors have been surveyed using manta tow surveys haphazardly since 1985 as part of the LTMP, enabling the results from 2019 to be placed into a temporal context. Categorical coral cover scores per manta tow were converted to percentage cover per tow using the mid-points of each category. Temporal patterns in coral cover were explored using logistic models in a Bayesian framework that incorporated varying intercept and slope effects of Reef.

Year was modelled as a fixed categorical effect with weakly informative Gaussian priors. Varying intercepts and slopes are assumed to be drawn from a multivariate Gaussian distribution with zero mean and covariance. For ease of prior specification, covariance matrices for each reef were decomposed into respective correlation matrices with LKJ prior (regularization=1; jointly uniform over all such correlation matrices) and variances (concentration=1; jointly uniform over variances) and gamma hyperprior (scale of 1 and shape of 1).

3.4.2 Benthic assemblages

The percent cover of benthic organisms was estimated to the finest taxonomic level possible by identifying the organisms beneath five points projected onto each of 40 randomly selected images of the 50 taken at each transect, equating to 3,000 points per reef (Jonker et al. 2008). Estimates of percent total hard coral cover were then calculated, along with the percent cover of four families of scleractinian corals (Acroporidae, Faviidae, Pocilloporidae, Poritidae) which account for >90% of coral assemblages on the GBR (Jonker et al. 2019). Similarly, percent cover estimates were calculated for the remaining families of scleractinian corals lumped together as ‘other corals’ (including Agariciidae, Dendrophylliidae, Euphyllidae, Fungiidae, Merulinidae, Mussidae, Oculinidae, Pectiniidae, Siderastreidae), and other categories such as soft corals, coralline algae, turf algae, macroalgae, sand and other (benthic organisms of very low abundance e.g. bryozoans, ascidians).

Differences in total hard coral, soft coral and algal cover among reefs and between management zones were investigated using Bayesian hierarchical models, with reef and zone (open and closed to fishing) as fixed factors. Site and transect were fitted as random factors to account for spatial autocorrelation. Data were modelled against a binomial error distribution in the *brms* package.

Differences in the assemblage structure of broad taxonomic groupings (Acroporidae, Faviidae, Pocilloporidae, Poritidae, other corals, soft corals, coralline algae, turf algae, macroalgae, sand and other), among reefs were tested using a permutational multivariate analysis of variance using distance matrices utilising the ‘adonis’ function in the *vegan* package (Anderson 2001).

A graphical examination of benthic assemblage structure was conducted by using a temporally stable grouping of corals that combines finer scale taxonomy (genus and family) with functionally important growth forms (e.g. branching, massive, table, digitate). Such groupings allowed a more nuanced investigation of differences in benthic assemblage structure among reefs in the far northern GBR. The percent cover of these groups was square root transformed prior to analysis and converted to a Bray-Curtis dissimilarity matrix and modelled using Multidimensional Scaling (MDS) in the *vegan* package.

Counts of juvenile corals were converted to density per area of substrate suitable for coral settlement (percent cover of turf and coralline algae). Juvenile density was calculated by dividing the total abundance of juvenile corals by the surveyed area multiplied by the proportion of substrate occupied by algae, which was estimated from photo transects described above. Differences in juvenile densities among reefs and management zones of the far northern GBR were investigated using Bayesian hierarchical linear models, with reef and zone (open and closed to fishing) as fixed factors and site and transect treated as random factors to account for spatial autocorrelation. Data were modelled against a binomial error distribution in the *brms* package.

Finally, the status of far northern GBR reefs was compared to data from the latest surveys of seven more southerly latitudinal sectors. Evaluations of hard coral, soft coral and algal cover and juvenile densities were undertaken using Bayesian hierarchical linear models with the fixed factor of sector, and random effects of reef, site and transect modelled against a binomial error distribution in the *brms* package.

3.4.3 Fish assemblages

Patterns in the total abundance and number of fish species (species richness), as well as the abundance of eight families (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Pomacentridae, Serranidae, Siganidae) and the scarine parrotfishes (formerly family Scaridae but now classified as the tribe Scarinae within the Labridae), were examined using Bayesian hierarchical linear models both among reefs in the far northern GBR, and among latitudinal sectors using the same model structure as for hard coral cover described above. Data were modelled against a negative binomial error distribution, except for those fishes of very low abundance (e.g. Lethrinidae, Lutjanidae and Serranidae), which necessitated the use of zero-inflated negative binomial error distributions. All models were conducted using the *brms* package.

A comparison of the structure of reef fish assemblages among far northern GBR reefs was explored graphically via MDS in the *vegan* package. The abundances of 224 fish species were transformed prior to analyses using the Hellinger metric to reduce the influence of highly abundant species (Legendre and Gallagher 2001) and converted to a Bray-Curtis dissimilarity matrix. Differences in assemblage composition were then analysed using a permutational MANOVA with a fixed effect of Reef using the ‘adonis’ function in the *vegan* package.

3.4.4 Structural complexity

Average rugosity was compared among reefs within the study area and across latitudinal sectors, where structural complexity has been assessed using the same methodology. No statistical analysis was performed for this comparison, acknowledging that there are a wide range of spatial drivers of structural complexity across the GBR. However, this comparison was intended to add a GBR-wide perspective to the assessment of structural complexity for reefs of the far northern GBR.

Given the recent patterns of disturbance that have occurred in the study region, survey sites were aggregated based on those recently affected by the 2015/16 and 2016/17 coral bleaching events (hereafter “bleaching”), Tropical Cyclones (hereafter “cyclones”; i.e. TC Penny, 2019) as well as those reefs where no evidence of disturbance was recorded (hereafter “No evidence of impact”). Reefs impacted by the bleaching were identified by previous aerial surveys during the peak of the events (Hughes et al. 2018a). Reef sites affected by cyclones were identified from evidence of substrate disturbance observed from the 3-D reconstructions and field observations (i.e. rubble beds) as well as their position in relation to the cyclone (i.e. TC Penny) track. The remaining of the reef sites were classified as “No evidence of impact”.

A strong relationship between damselfishes and juvenile hard coral abundance with structural complexity (i.e. rugosity) has been previously documented. For example damselfish are highly dependent on complex habitats for shelter, refuges from predation and food resources (Klumpp and

Polunin 1989, Chabanet et al. 1997, González-Rivero et al. 2017b), while juvenile corals are often located in complex habitats, which provides shelter from UV radiation, predation and competition (Gleason et al. 2006, Doropoulos et al. 2016, Gallagher and Doropoulos 2017).

We examined the relationship between the abundance of damselfishes and the density of juvenile corals with rugosity, using generalised mixed-effects models (glmm), to confirm whether the observed levels of structural complexity maintain the expected structuring properties of communities known to exhibit a strong association to the reef substrate. Reef position across the continental shelf was used as a random effect to account for expected spatial variability across reefs. A Poisson link function parameterised the over-dispersion of model residuals given the nature of the count data, using an Automatic Differentiation (AD) model building framework from the *glmmadmb* package. The natural logarithm of coral cover and algae cover were considered in the regression models as offsets for juvenile corals and damselfish, respectively. Rugosity was used as the main explanatory co-variate, interacting with a categorical classification of reefs based on recent disturbance events. The explanatory power of the three metrics of structural complexity in explaining the spatial distribution of fish and juvenile corals was evaluated by the pseudo coefficient of determination (r2), as described in Nakagawa and Schielzeth (2013).

3.4.5 BRUVS

3.4.5.1 Univariate statistics - aggregated boosted regression trees

The techniques used here were identical to those applied for the same types of exploration of the Great Barrier Reef Marine Park (Cappo et al. 2007, 2012), James Price Point in north-western Australia (Cappo et al. 2011), and the remote shoals off the north-west shelf (Moore et al. 2017).

Boosted regression methods were introduced to the ecological literature by De'ath (2002; 2007). This approach derives from both classification and regression trees starting with a data model (De'ath & Fabricius 2000) and from 'machine learning' where no data model is specified, and algorithms are used to learn the relationship between a predictor and its response (Breiman 2001). Boosted regression trees are therefore an 'ensemble' method, whereby models are improved by first fitting many simple models and then combining them for prediction, using an algorithm from classification and a 'boosting' algorithm (Elith et al. 2008).

Boosted regression trees are complex but can be summarised in ways that give powerful ecological insight by representing complex information in a visual way that is easily interpretable. They are robust and flexible, because explanatory (predictor) variables can be numeric, categorical, binary, or of any other type, and model outcomes are unaffected by transformations and different scales of measurement of the predictors. They are not sensitive to outliers and handle missing data in predictors by applying best surrogates with little loss of information. Trees are hierarchical structures, and input variables at the tree leaves are dependent on input variables at higher nodes. This allows simple modelling of complex, non-linear interactions that simply cannot be handled by other approaches (see examples in De'ath 2007).

A mixture of 19 explanatory covariates (see Table 1) were used to predict two univariate responses using aggregated boosted regression trees via the abt package (De'ath 2007, Ridgeway 2007):

1. Species richness (total number of species on all BRUVS deployments; square root transformed)
2. Total fish abundance (∑*MaxN* ; 4th root transformed)

The models were run for interaction depths of 1, 2 and 3, and the results show the relative influence of all covariates explaining and predicting the response.

Partial dependency plots show the effect of one particular covariate with the effects of all others held constant, and interactions can be viewed with partial interaction plots.

3.4.5.2 Multivariate statistics

Relative fish abundance data (MaxN) was 4th root transformed to down-weight the influence of rarely occurring but abundant fish, such as schooling fusiliers (Caesionidae) and trevallies (Carangidae), and raise the influence of common species that occur in low numbers.

3.4.5.2.1 Distance-based redundancy analysis

Data from BRUVS deployed on tropical shoals and reefs are characterised by having more species than replicates. The presence of many zeros in such data matrices, caused by rarer species being only occasionally present, will violate the normality assumption for multivariate tests of the effect of management zone.

To allow tests of the effect of reef management zone on a multivariate response we used distance-based redundancy analysis (db-RDA). It begins with the calculation of dissimilarities (distances) among samples, followed by principal coordinate analysis (PCoA), followed by RDA, where the X matrix (independent variables; zone and habitat variables) contains dummy variables in an ANOVA model and the Y matrix (response variables; abundances of genera) consists of the principal coordinates. It uses non-parametric permutation methods which do not rely on assumptions of multivariate normality (Legendre & Anderson 1999).

Four of the 129 BRUVS lacked information on the full suite of covariates defining the seafloor habitats in the field of view and were excluded from analyses. The dissimilarity (distance) matrix comprised of 115 fish genera at 125 BRUVS sites (xdiss) was used as the response in the models:

xdiss ~ zone + calc.rf + snd + crl + bare + topo + visibility + depth (1)

xdiss ~ zone + Condition (calc.rf + snd + crl + bare + topo + visibility + depth) (2)

xdiss ~ 1 (3)

These covariates were chosen because of their powerful surrogacy for other environmental variables in the field of view (FOV), and for their predictive power in other, similar studies (e.g. Moore et al. 2017, Cappo et al. 2007). High percentages of sand ("snd") in the FOV indicates low coverage by complex topography. High percentages of "bare" seafloor implies a lack of epibenthos of any type. The presence of live hard coral ("crl") as epibenthos and high percentages of coral reef matrix, as the substratum ("calc.rf") are also known to provide better habitat for site-attached reef fishes.

Depth is a surrogate for unmeasured (e.g. light penetration at the seabed), or unknown, drivers of fish abundance and diversity. The use of the "Condition ()" term allows the individual effect of management zone of the BRUVS sites to be quantified in redundancy analysis. Models were compared with a null model (3) unconstrained by any predictors.

We avoided rare species and singletons by aggregating fish counts at the level of 115 fish genera occurring on at least 3 BRUVS (~2.5% of samples). The transformed abundance (4th root *MaxN*) data for the genera was converted to a matrix of dissimilarities using site-standardised extended dissimilarity (xdiss()) in library *mvpart* to calculate dissimilarity matrices (De'ath 1999). Function 'capscale' in library *vegan* was used to accomplish the remainder of the db-RDA process. 'Capscale' is an ordination method similar to RDA, but it allows non-Euclidean dissimilarity indices yet remains strictly linear and metric.

The function 'envfit' in the *vegan* package was used to find the direction of abundance vectors for fish genera (in the k-dimensional ordination space) that had maximal correlation with predicting management zone of reef. A threshold correlation of $p<0.001$ was set to select significant fish vectors for biplots. The site scores were plotted to reveal trends by management zone, and the longest fish vectors were also plotted to show high correlations between principal coordinates and the abundance of genera.

3.4.5.2.2 Multivariate prediction and regression trees

To explain and predict the fish community composition at BRUVS sites in relation to the 19 covariates (see Table 1), multivariate prediction and regression trees were used to model the transformed abundance of 290 species that occurred on at least 3 individual BRUVS (~2.5% of samples), using the package mvpart (see De'ath 2002).

Multivariate response ~ depth + reef.name + zone + (topo + fov + dead + visibility) +

(fltrs + encr + crl + bare + sft.crl + plant + alg) + (bdrck + calc.rf + grvl + rbbl + snd) (4)

By repeatedly splitting the data based on covariates defining each split, multivariate prediction and regression trees minimise the dissimilarity of sites within clusters, forming clusters of sites (De'ath 2002). Each terminal node of the tree (leaf) can be defined by the multivariate mean of its sites, the predictors that define it, the number of sites that were grouped there, and by Dufrêne-Legendre species indicators (DLI). Nodes represent fish assemblages.

Indicator values (DLI; Dufrêne and Legendre 1997) were calculated for each species for each upper (branch) and terminal (leaf) node of the tree. For a given species and a given group of sites, the DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups (specificity), times the proportion of sites within the group where the species occurs (fidelity), multiplied by 100. Each species can be associated with the tree node (assemblage) where its maximum DLI value occurred. The index distinguishes between ubiquitous species that dominate many groups in absolute abundance, and species that occur consistently within single groups but have low abundance (Dufrêne and Legendre 1997). The DLI for species at the root node are simply the prevalence of those species in the entire dataset. Species with high DLI were used as characteristic representatives of each fish assemblage.

The use of common and scientific names follows those reported in Allen & Swainston (1988).

4 RESULTS

4.1 Condition and long-term trends in hard coral cover and CoTS abundance

4.1.1 Manta tow surveys – Cape Grenville sector

Nine reefs were surveyed in this sector, six reefs could not be surveyed due to weather. Historically, sector-wide hard coral cover had been variable through time with periods of declines and recovery following Incipient Outbreaks of CoTS, particularly in the decade from 2003 to 2013. There was a substantial decline in hard coral cover from 2015 to 2017, which was the lowest level recorded since surveys began, largely in response to the 2015/16 bleaching event, although Incipient Outbreaks of CoTS also occurred. In 2019, sector-wide hard coral cover had increased from the lowest levels recorded in 2017 (Figure 8). In 2019, few CoTS were observed (Figure 8) and there were low levels of coral bleaching throughout the sector that were restricted to scattered individual colonies.

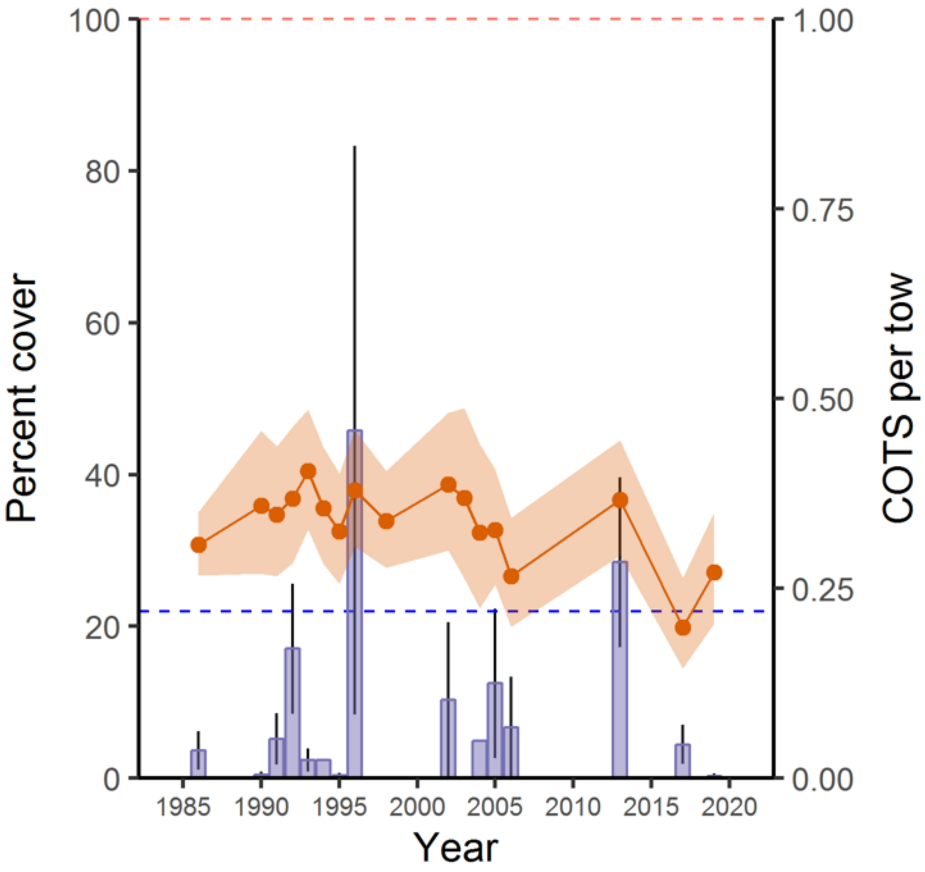

Figure 8: Sector-wide trends in hard coral cover and numbers of CoTS from broad-scale manta tow surveys for the Cape Grenville sector. Orange points are average hard coral cover, while shaded band is the 95% C.I. Blue bars are the mean number of CoTS per 2-minute tow ± 1 S.E. The dashed blue line is the level of Incipient Outbreak of CoTS while the orange dashed line is the level of Active Outbreaks.

Of the nine reefs surveyed in 2019, six were previously surveyed in 2017 after the major coral bleaching event in 2015/16. Between 2017 and 2019, hard coral cover declined on five of those reefs and was unchanged on one (Table 2). Three previously unsurveyed reefs had low, moderate and high coral cover (Table 2) and their inclusion contributed to the 7% increase in sector-wide hard coral cover between 2017 and 2019 (Figure 8).

One CoTS was recorded at Reef 11049. Coral bleaching was found on all nine reefs, but at very low levels restricted to scattered, individual colonies. Manta tow surveys also revealed recent storm damage (extensive rubble beds, smashed and overturned coral colonies) on some reefs, which was likely due to Tropical Cyclone Penny in early January 2019.

Table 2: Summary of manta tow surveys of reefs in the Cape Grenville sector. Arrows indicate the trend in live coral cover and CoTS since last survey; ▲ = increase, ▼ = decrease, no arrow = no change. CoTS outbreak Status: RE recovering, NO= no CoTS outbreak, IO = Incipient CoTS Outbreak (>0.22 CoTS per tow), AO = Active CoTS Outbreak (>1 CoTS per tow).

Reef	Shelf position	Number of Manta tows	Previous survey year	Median live coral cover	CoTS	CoTS per tow	CoTS outbreak status
Curd	Inner	34	2017	10-20%	0 ▼	0	NO
Reef 11049	Mid	37	N/A	0-5%	1	0.03	NO
Ashmore Banks (1)	Mid	11	2017	40-50% ▼	0	0	NO
Ashmore Banks (2)	Mid	15	2017	40-50% ▼	0	0	NO
Ashmore Banks (3)	Mid	11	2017	30-40% ▼	0	0	NO
Middle Banks (2)	Mid	10	2017	30-40% ▼	0	0	NO
Middle Banks (3)	Mid	13	2017	40-50% ▼	0	0	NO
Lagoon	Outer	55	2006	30-40% ▲	0	0	NO
Mantis	Outer	60	N/A	10-20%	0	0	NO

4.1.2 Manta tow surveys – Princess Charlotte Bay

Nine reefs were surveyed in this sector, with six inshore reefs not surveyed due to the presence of crocodiles. Historically, sector-wide hard coral cover has been relatively stable with no clear multi-decadal trend (1985 to 2006), although there were some periods of decline and recovery associated with CoTS outbreaks (Figure 9). An outbreak of CoTS in 2004 drove sector-wide coral cover to the lowest levels yet recorded by the LTMP in 2006, however by 2015, hard coral cover had recovered to levels equivalent to the highest observed (Figure 9). The 2015/16 bleaching event drove hard coral cover below 20% by 2017 and in 2019, there had been a small increase in sector-wide coral cover (Figure 9). Overall, there were low numbers of CoTS (Figure 9) and few incidents of severe bleaching in this sector.

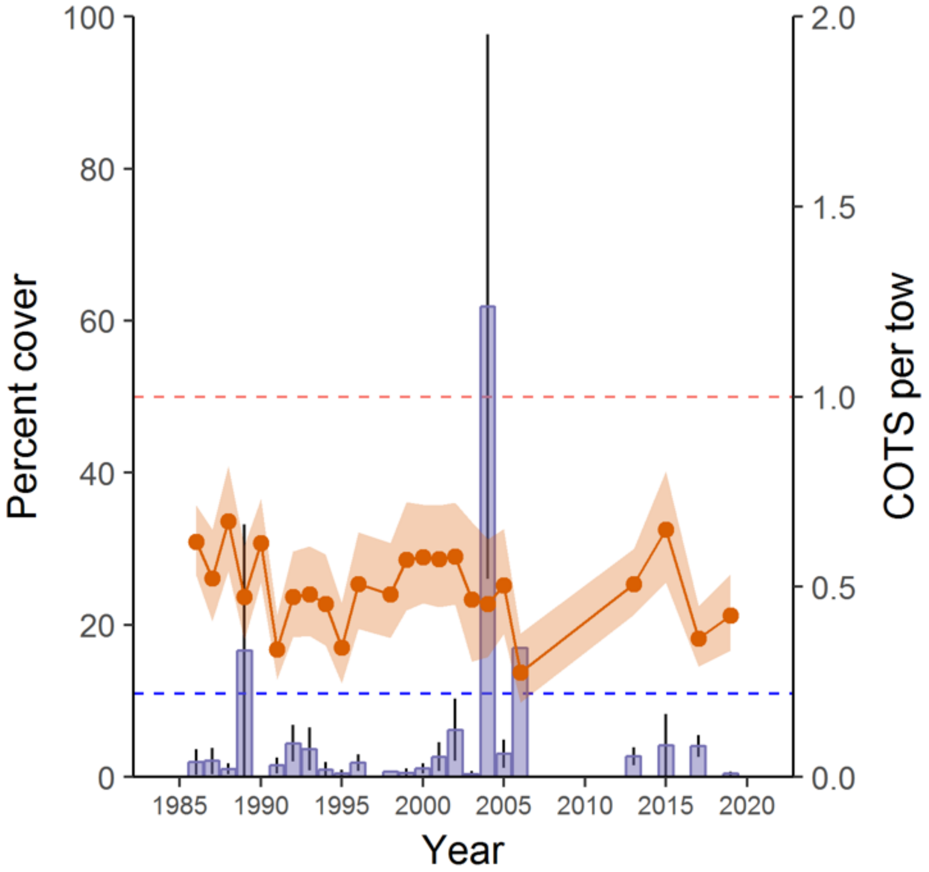

Figure 9: Sector-wide trends in hard coral cover and numbers of CoTS from broad-scale manta tow surveys for the Princess Charlotte Bay sector. Orange points are average hard coral cover, while shaded band is the 95% credible intervals. Blue bars are the mean number of CoTS per 2-minute tow ± 1 S.E. The dashed blue line is the level of Incipient Outbreak of CoTS while the orange dashed line is the level of Active Outbreaks.

Of the nine reefs surveyed in 2019, five were previously surveyed in 2017, after the major bleaching event in 2015/16. Between 2017 and 2019, hard coral cover declined on three and was unchanged on three reefs (Table 3). Four reefs were not surveyed in 2017 but were previously surveyed at varying intervals ranging from six to twenty years (Table 3). Of these, hard coral cover had declined on two reefs, increased on one, and remained unchanged on the other (Table 3).

Very low numbers of CoTS were recorded on two reefs, but these numbers were well below outbreak levels (Table 3). Coral bleaching was observed on six reefs at very low levels (scattered, individual colonies), however significant coral bleaching (up to 50% of hard coral) was observed on localised parts of the reef flat of Rodda Reef and the reef slope on one side of Reef 13124. Recent storm damage was observed on three outer-shelf reefs and was likely due to Cyclone Penny in January 2019.

Table 3: Summary of manta tow surveys of reefs in the Princess Charlotte Bay sector. Arrows indicate the trend in live coral cover and CoTS since last survey; ▲ = increase, ▼ = decrease, no arrow = no change. CoTS outbreak Status: RE recovering, NO= no CoTS outbreak, IO = Incipient CoTS Outbreak (>0.22 CoTS per tow), AO = Active CoTS Outbreak (>1 CoTS per tow).

Reef	Shelf position	Number of Manta tows	Previous survey year	Median live coral cover	CoTS	CoTS per tow	CoTS outbreak status
Reef 13124	Mid	68	2017	10-20% ▼	0 ▼	0	NO
Corbett	Mid	100	2013	10-20%	0 ▼	0	RE
Reef 13040	Outer	39	2006	20-30% ▲	0	0	NO
Reef 13121	Outer	39	2017	5-10%	0	0	NO
Creech (A)	Outer	44	2017	20-30% ▼	2 ▲	0.05	NO
Davie	Outer	51	2017	20-30%	1 ▲	0.02	NO
Rodda	Outer	40	2017	20-30%	0	0	NO
Sandbank No. 8	Outer	26	1999	10-20% ▼	0	0	NO
Sandbank No. 1	Outer	42	2005	10-20% ▼	0	0	NO

4.1.3 Condition of benthic assemblages from fixed site surveys

4.1.3.1 Spatial comparisons among far northern reefs

Fixed survey sites were established on seven reefs on the mid- and outer-shelf of the far northern GBR (Figure 1). In 2019, the mean percent cover of hard corals varied among reefs from 14.5 - 51% (Figure 10). Soft coral cover ranged from 1-15% and algae cover ranged from 41-63%.

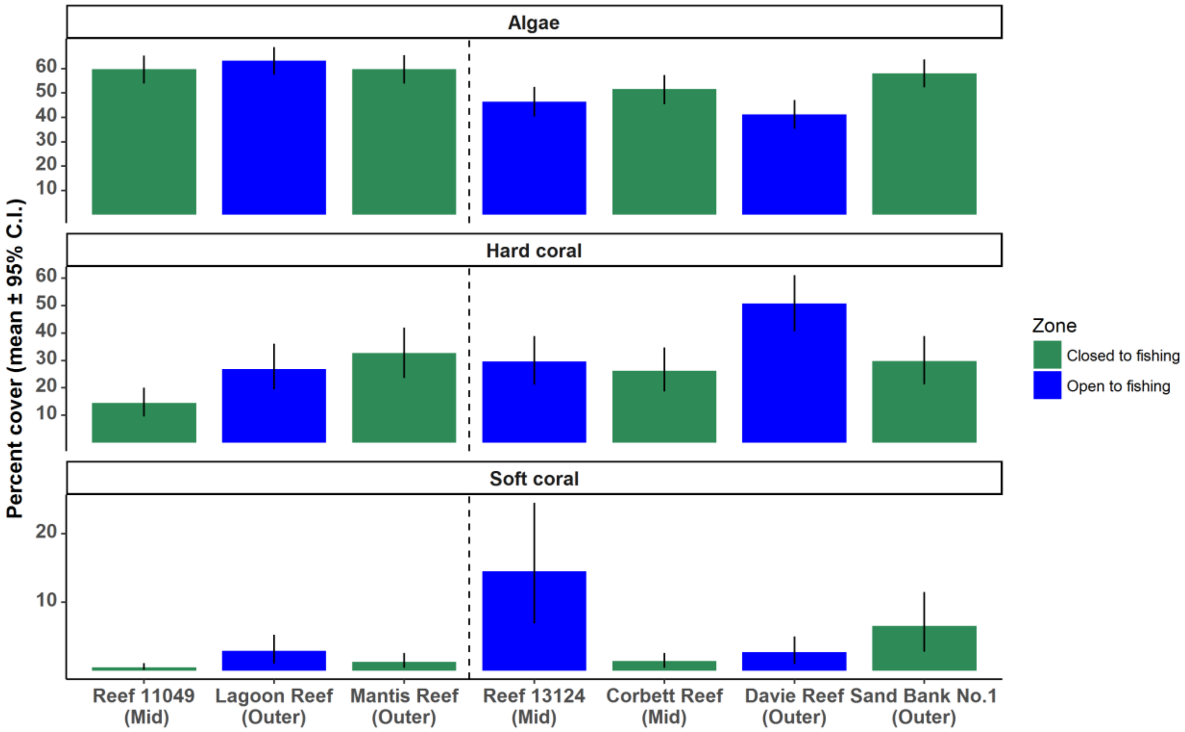

Figure 10: Percent cover of algae, hard corals and soft corals on reefs of the far northern GBR. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). The reefs are arranged north to south from left to right, with the vertical dotted line delineating the Cape Grenville sector (left hand side) from the Princess Charlotte Bay sector (right hand side).

The composition of benthic assemblages varied among reefs in the far northern GBR (ADONIS F = 27.248, d.f. = 6, p=0.001). Hard coral assemblages were dominated by the families Acroporidae, Poritidae, Pocilloporidae and Faviidae, with the abundance of each family varying among reefs (Figure 11). Acroporidae and Poritidae were the only families that had absolute abundance greater than 10% at any reef. Acroporidae was the most abundant coral family at five reefs, where it accounted for 10-32% of benthic cover. Poritidae was the most abundant coral family at two mid-shelf reefs, reaching 15% cover at Reef 13124 and 12% at Reef 11049 (Figure 11). Maximum abundance for Pocilloporidae and Faviidae was 10% and 5% respectively. Proportionally, these families accounted for no more than 23% (Pocilloporidae) and 16% (Faviidae) of hard corals. All other hard coral families occurred in very low abundance, rarely with cover greater than 5% (Figure 11).

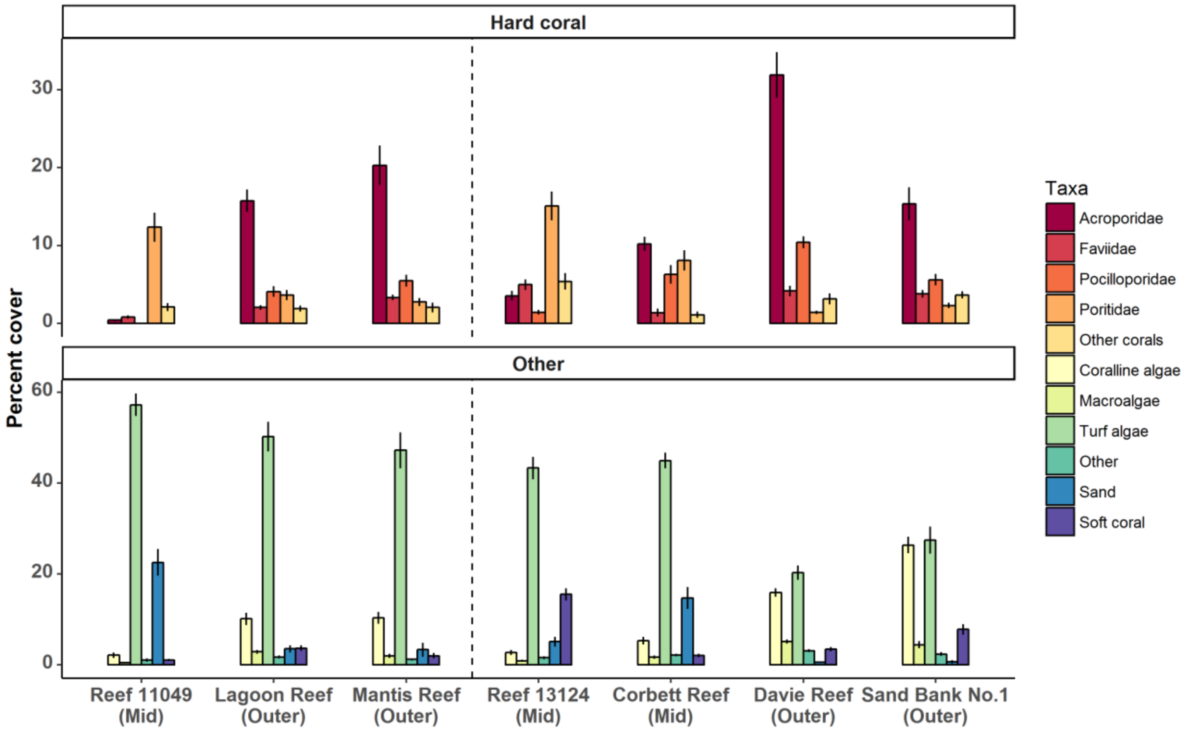

Figure 11: Percent cover of benthic assemblages from fixed site surveys on reefs in the far northern GBR. Data are raw means ± 1 S.E. The reefs are arranged north to south from left to right, with the vertical dotted line delineating the Cape Grenville sector (left hand side) from the Princess Charlotte Bay sector (right hand side).

Reef 11049 on the mid-shelf of the Cape Grenville sector was unique among reefs surveyed during this study, as its hard coral assemblage was dominated by corals from the family Poritidae, with very low abundance of Acroporidae (less than 1%) and no corals from Pocilloporidae recorded on the fixed survey sites (Figure 11).

The percent cover of soft corals was generally low except on Reef 13124 and Sand Bank No. 1, which had moderate cover (Figure 11). Turf algae was by far the dominant component of the benthic assemblages on most reefs, with cover ranging from 20 - 57% (Figure 11). Coralline algae was also an important component, particularly on outer reefs, while fleshy macroalgae was not common on any reef (Figure 11).

Analyses of finer taxonomic resolution of hard coral assemblages revealed that outer-shelf reefs were dominated by various growth forms of *Acropora* spp. and *Montipora* spp. (Figure 12). Coral assemblages on the mid-shelf reefs were more variable due to a more diverse range of habitat structure available on these reefs, and exposure to a broader spectrum of impacts from the bleaching events in the summers of 2015/16 and 2016/17, compared to the steep-sided outer-shelf reefs. Specifically, Corbett Reef on the mid-shelf had coral assemblage characteristics in common with outer-shelf reefs (particularly the presence and abundance of branching *Acropora* spp.), while the assemblage at the neighbouring mid-shelf reef (Reef 13124) was characterised by corals common in relatively turbid habitats, including *Porites* spp., *Goniopora*/*Alveopora* spp., Fungiidae, Pectiniidae, and *Echinopora* spp. (Figure 12).

The coral assemblage at Reef 11049 was quite distinct from all other reefs due to low coral abundance, high abundance of dead standing coral skeletons and a remnant coral community dominated by *Porites* spp. (Figure 12).

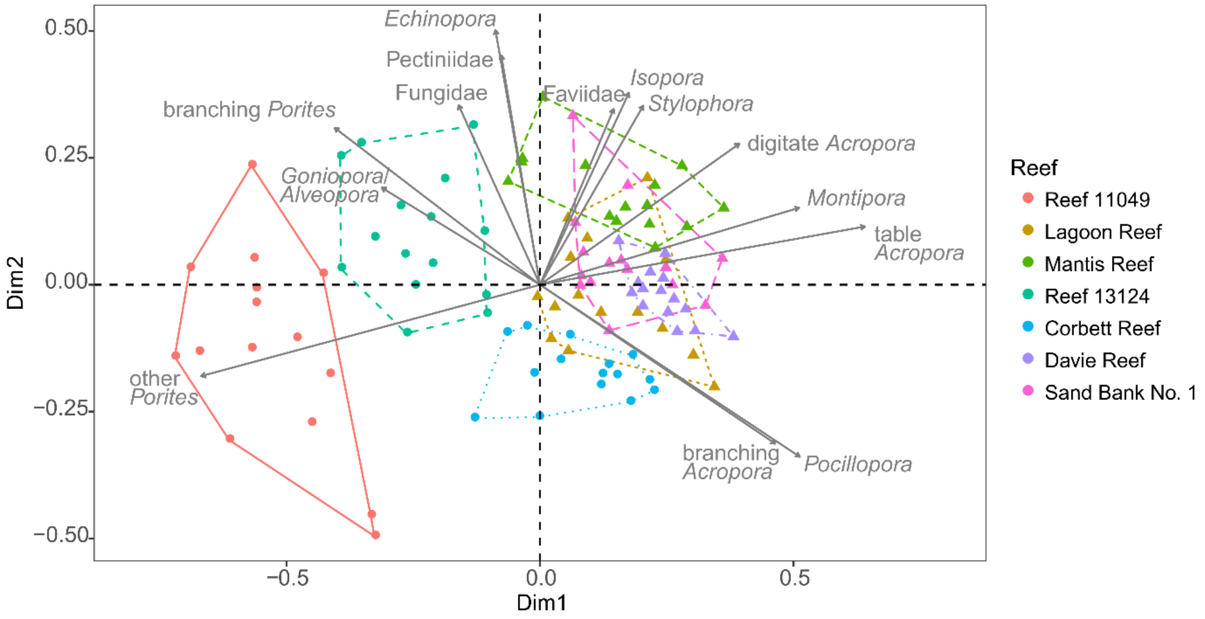

Figure 12: Ordination plot based on a Multidimensional Scaling (MDS) analysis of fine scale taxonomic resolution of benthic assemblages, recorded on fixed site surveys of reefs in the far northern GBR. Data are coded by shelf position: circles = mid-shelf, triangles = outer-shelf. Convex hulls encapsulate the fifteen transects surveyed at each reef.

4.1.3.2 Zoning comparisons among far northern reefs

Fixed survey sites were established on paired reefs that were open and closed to fishing in the Princess Charlotte Bay and Cape Grenville sectors, with one reef pair located on the mid-shelf and one on the outer-shelf in each sector (Figure 1). In 2019, Reef 11049, a reef closed to fishing, did not have a paired reef open to fishing, as bad weather prevented surveys.

There were small differences in benthic cover between reefs open and closed to fishing. Hard and soft corals were less abundant on reefs closed to fishing compared to those open to fishing, although the difference was less than 2% (Figure 13). In contrast, there was a higher abundance of algae on reefs closed to fishing compared to those open to fishing (Figure 13).

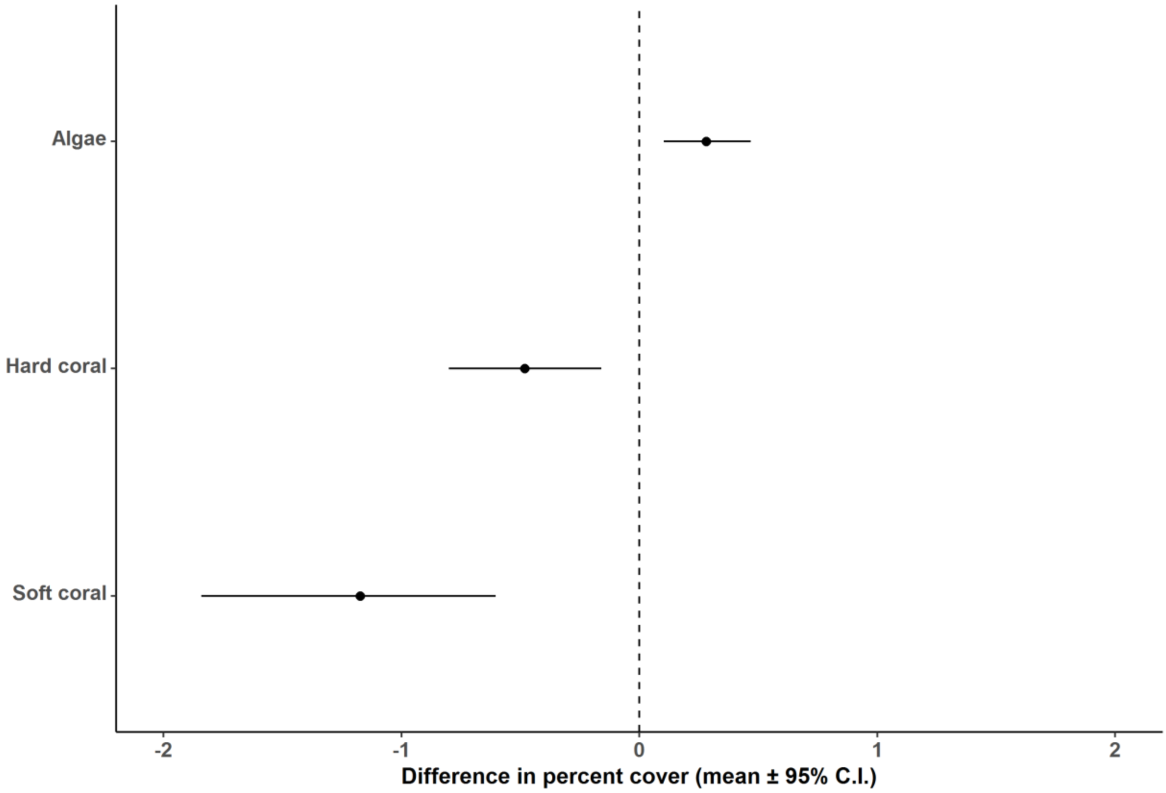

Figure 13: Differences in the percent cover of algae, hard corals and soft corals recorded on fixed site surveys between reefs of the far northern GBR that were open and closed to fishing. Contrasts are estimated from Bayesian hierarchical models with associated 95% credible intervals (C.I.). Negative contrasts indicate higher cover on reefs open to fishing, while positive contrasts indicate higher cover on reefs closed to fishing. Statistical significance can be inferred where 95% credible intervals do not intersect zero.

4.1.3.3 Comparisons of far northern coral assemblages to the wider GBR

In a GBR-wide context, hard coral cover recorded on fixed site surveys in the Princess Charlotte Bay and Cape Grenville sectors was slightly higher than most other sectors, although there was high variability (Figure 14). Only one other sector (Capricorn Bunker) had comparable hard coral cover (Figure 14). The high within-sector variability in hard coral cover recorded in the PCB and CG sectors (16-51%) suggests that disturbance impacts (such as from recent coral bleaching events) were more patchy in the far north, compared to the widespread cumulative impacts evident in the Cooktown-Lizard Island and Cairns sectors to the south. Only one reef surveyed in the far north (Reef 11049) had evidently suffered severe mortality from the recent bleaching events. Conversely, some reefs, such as Davie Reef, were in relatively good condition. Whether hard corals at these reefs were not subjected to temperature stress or recovered from sub-lethal impacts is difficult to discern.

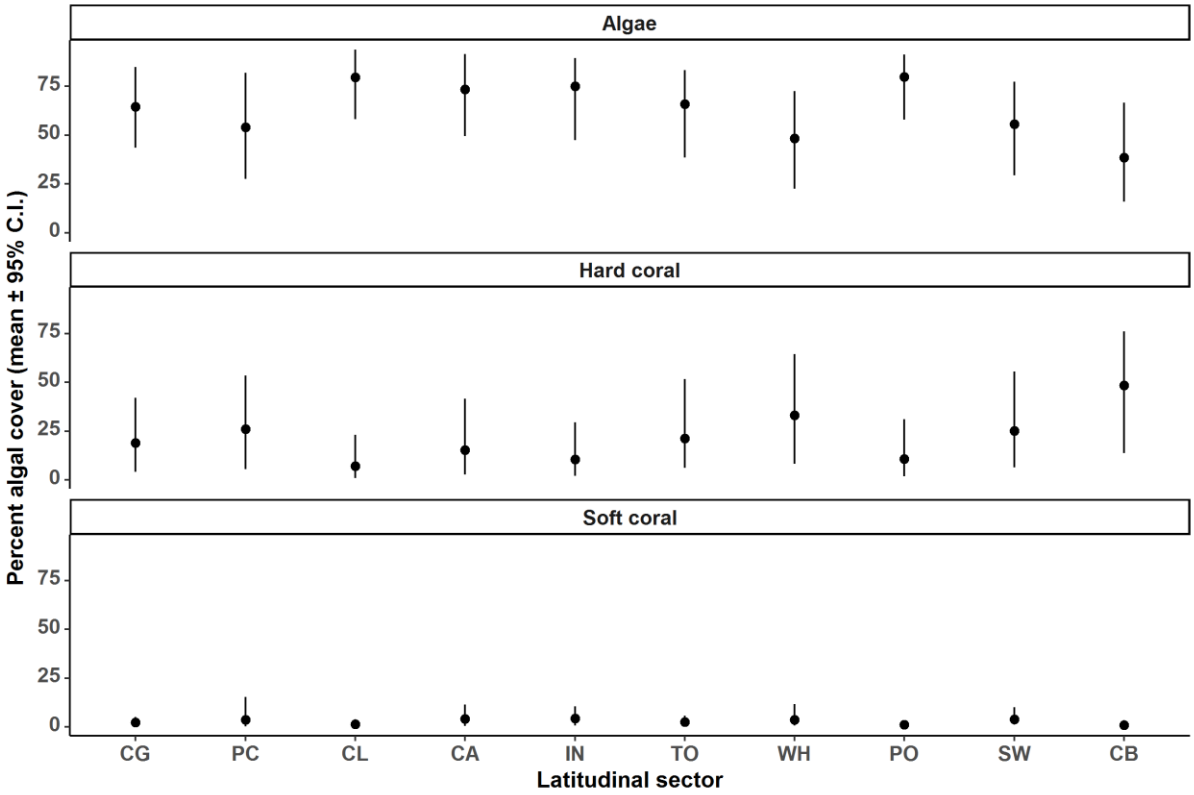

Figure 14: Percent cover of algae, hard coral and soft coral recorded during fixed site surveys in latitudinal sectors of the GBR. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.), and were taken from the latest year available (see years in parentheses following). Sectors are arranged north to south from left to right such that CG = Cape Grenville (2019), PC = Princess Charlotte Bay (2019), CL = Cooktown Lizard (2017), CA = Cairns (2018), IN = Innisfail (2018), TO = Townsville (2018), WH = Whitsunday (2017), PO = Pompeys (2018), SW = Swains (2018), CB = Capricorn-Bunker (2019).

Broadly, the composition of hard coral communities in the far northern sectors was similar to that in most other GBR sectors, with Acroporidae the dominant group (Figure 15). The exceptions were the sectors that have had high disturbance frequency in recent years and had the lowest hard coral cover (Cooktown-Lizard, Cairns, Innisfail and Pompeys).

Particularly, cover of Acroporidae in these sectors was relatively low (Figure 15). Historically, Acroporidae corals have been shown to be sensitive to most disturbances including CoTS outbreaks, coral bleaching, coral disease and storms. Poritidae had relatively high coral cover in the far northern sectors compared with most other sectors (Figure 15). This may reflect the difference in zonation around the reefs observed for far northern reefs. That is, the survey sites more closely resembled habitats sheltered from prevailing winds and with high tidal flows, which often support a relatively high abundance of Poritidae. The composition of the algal community in the far northern sectors resembled most other sectors, with turf algae clearly dominant, moderate levels of coralline algae and very low cover of macroalgae (Figure 15).

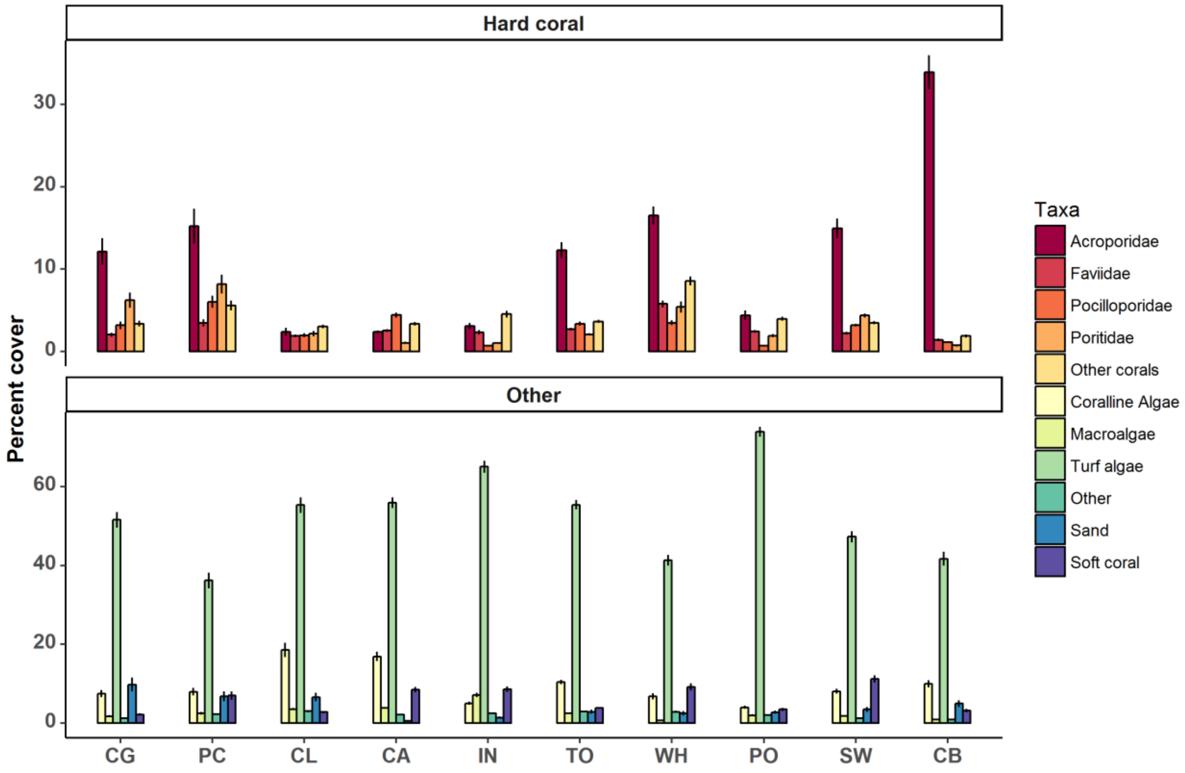

Figure 15: Percent cover of benthic assemblages recorded during fixed site surveys in latitudinal sectors of the GBR. Data are raw means ± 1 S.E. All conventions as for Figure 14.

4.1.4 Juvenile corals

Mean juvenile coral density on far northern reefs ranged from 6.3 m^{-2} on the outer-shelf Lagoon Reef to 26.9 m^{-2} on another outer-shelf reef, Mantis Reef (Figure 16). There was a tendency for there to be higher coral juvenile densities on outer-shelf reefs compared to mid-shelf reefs (Bayesian contrast mean = 1.41 m^{-2}, lower 95% credible interval = 1.02, upper 95% credible interval = 1.91) and overall, there was a higher density of juvenile corals on reefs closed to fishing, although the differences were small (Bayesian contrast mean = 1.26 m^{-2}, lower 95% credible interval = 0.91, upper 95% credible interval = 1.72).

These densities are considered moderate to high (Thompson et al. 2016) and are comparable to juvenile densities of 11.8 m^{-2} and 11.2 m^{-2} reported for other GBR mid-shelf and outer-shelf reefs respectively (Jonker et al. 2019).

In the context of the wider GBR, juvenile density on the far northern reefs was lower than the densities observed on southern GBR reefs, although there was substantial variation within each sector (Figure 17). Juvenile densities in the far northern Cape Grenville and Princess Charlotte Bay sectors were similar to other northern sectors such as Cairns and Cooktown-Lizard Island at between 9 to 10 juveniles m^{-2}. Juvenile coral densities on central and southern GBR reefs tended to be up to two times higher than northern and far northern reefs, particularly in the Whitsunday and Swains sectors where densities reached 20 to 23 juveniles m^{-2} (Figure 17).

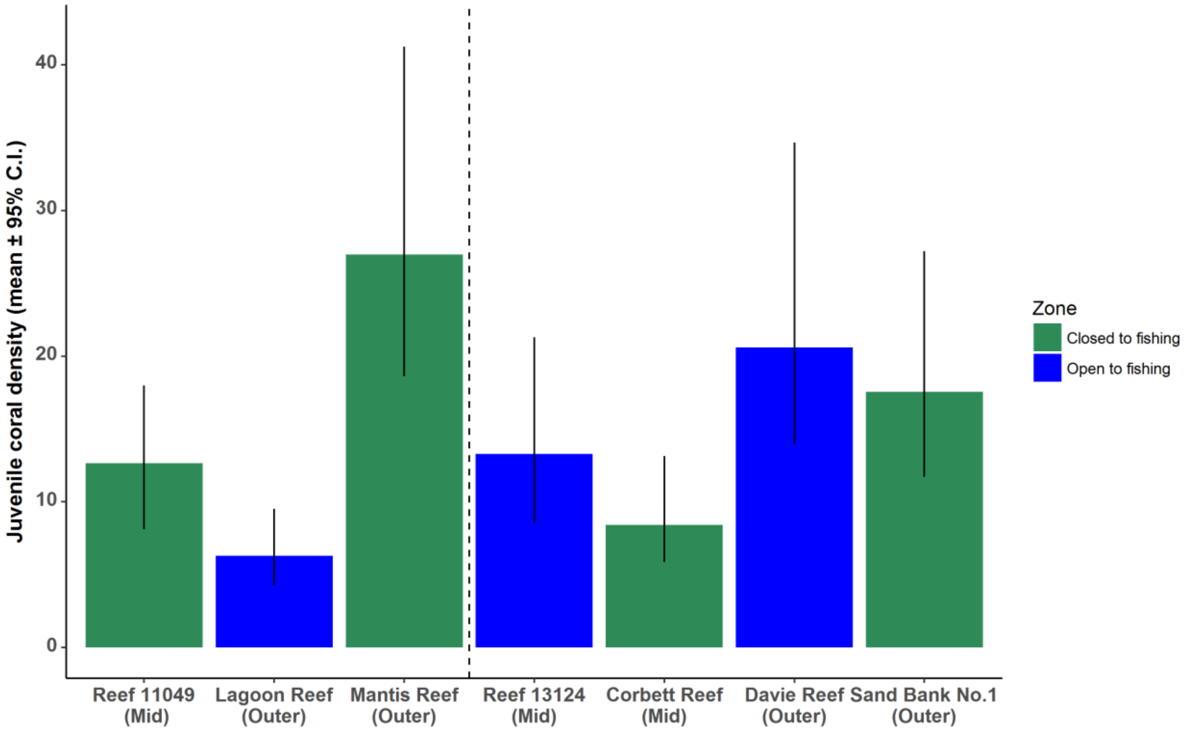

Figure 16: Density of juvenile corals (<50mm diameter) per m^2 from fixed site surveys on reefs in the far northern GBR. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). The reefs are arranged north to south from left to right, with the vertical dotted line delineating the Cape Grenville sector (left hand side) from the Princess Charlotte Bay sector (right hand side).

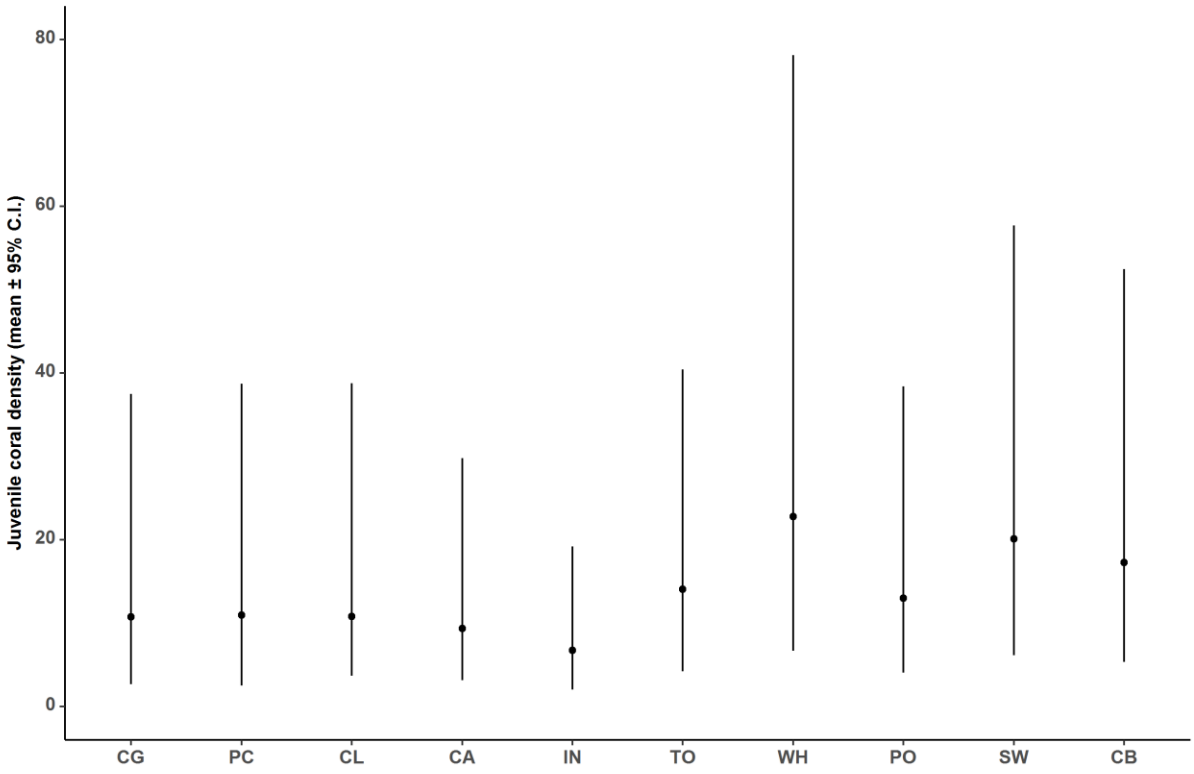

Figure 17: Juvenile coral densities per m^2 from the most recent fixed site surveys in each latitudinal sector of the GBR. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). All conventions as for Figure 14.

4.1.5 Agents of coral mortality

Surveys of agents of coral mortality on far northern reefs revealed low numbers of CoTS at survey sites. Five large individuals were observed in total across the seven reefs (Table 4). The occurrence of coral diseases including white syndrome, skeletal eroding band disease, brown band disease and black band disease was low at all reefs (Table 4). Bleaching was recorded along transects at all reefs, but at very low levels with only scattered, individual colonies (<1%) affected (Table 4). The hard coral genus *Acropora* was most affected (42 bleached colonies across seven reefs), followed by *Porites* (16), *Seriatopora* (16) and *Pocillopora* (10). The highest densities of the corallivorous snail *Drupella* spp. were recorded at Davie Reef (693ha^{-1}) and Corbett Reef (533ha^{-1}). The level of Coral White Band Syndrome (CWBS – Miller et al. 2013) was relatively high at Sand Bank No. 1 and rare at all other reefs (Table 4). Physical damage caused by Tropical Cyclone Penny, which passed by these far northern reefs in early January 2019, was clearly evident at Lagoon Reef, with coral colonies uprooted from the reef matrix and broken at the reef base. With several disturbances having recent impacts in the region, there were numerous colony scars to which a cause could not be attributed (Table 4).

Table 4: Summary of agents of coral mortality recorded during fixed site surveys at seven far northern GBR reefs. Values are total occurrences per reef unless otherwise specified (n = 15 transects). Adult CoTS are individuals >25cm in diameter. The bleaching category "0+" represents individual colonies that account for <1% of hard coral cover. WS = White Syndrome; BrBD = Brown Band Disease, BBD = Black Band Disease, Scar = unknown scars, CWBS = Coralline White Band Syndrome, CLOD = Coralline Lethal Orange Disease, Phys = Physical damage, Drup= *Drupella* spp per hectare, Bleach = number of transects with bleaching, with the maximum category recorded for any transect in parentheses.

Reef	WS	SEB	BrBD	BBD	Unknown Scar	Adult CoTS	CoTS scars	CBWS	CLOD	Phys	*Drup*	Bleach
Reef 11049	1	0	0	1	4	2	4	0	0	1	7	7 (0+)
Lagoon Reef	6	0	1	0	23	1	0	0	7	252	47	6 (0+)
Mantis Reef	16	0	0	0	7	0	0	5	13	24	33	8 (0+)
Reef 13124	3	4	2	1	11	2	7	0	0	2	247	9 (0+)
Corbett Reef	6	6	1	0	39	0	0	0	1	26	533	9 (0+)
Davie Reef	17	6	5	0	23	0	0	5	0	25	693	4 (0+)
Sand Bank No. 1	6	0	1	0	13	0	0	54	10	11	87	7 (0+)

4.1.6 3-D rugosity estimates

3D reconstructions of the reef substrate using Structure from Motion algorithms provide a viable technique for assessing and monitoring patterns of structural complexity in coral reefs (Fukunaga et al. 2019). Our models successfully captured the complexity in reef structure with an average error of 13 mm (± 4 mm, 95% confidence interval), similar to those previously reported using the same approach (Figueira et al. 2015, Ferrari et al. 2016). Overall, coral reefs in the far northern GBR showed an average rugosity of 1.9 (± 0.7, 95% Confidence Interval, Figure 18), within the range of previously reported values (Klumpp and McKinnon 1992) and comparable to other regions across the GBR, although lower on outer-shelf reefs (Figure 19). While recent disturbances, such as coral bleaching events and cyclones can drive significant losses of habitat structure (Madin and Connolly 2006, Magel et al. 2019), our results showed no evidence of differences between reefs affected or not by disturbances (Figure 20). Given that this survey only captured one point in time, it is impossible to determine the cause of the differences observed in rugosity across sectors, reefs and recent disturbance patterns. However, the observed values suggest that the structural complexity of coral reefs in this region maintain values expected across the GBR (Figure 20).

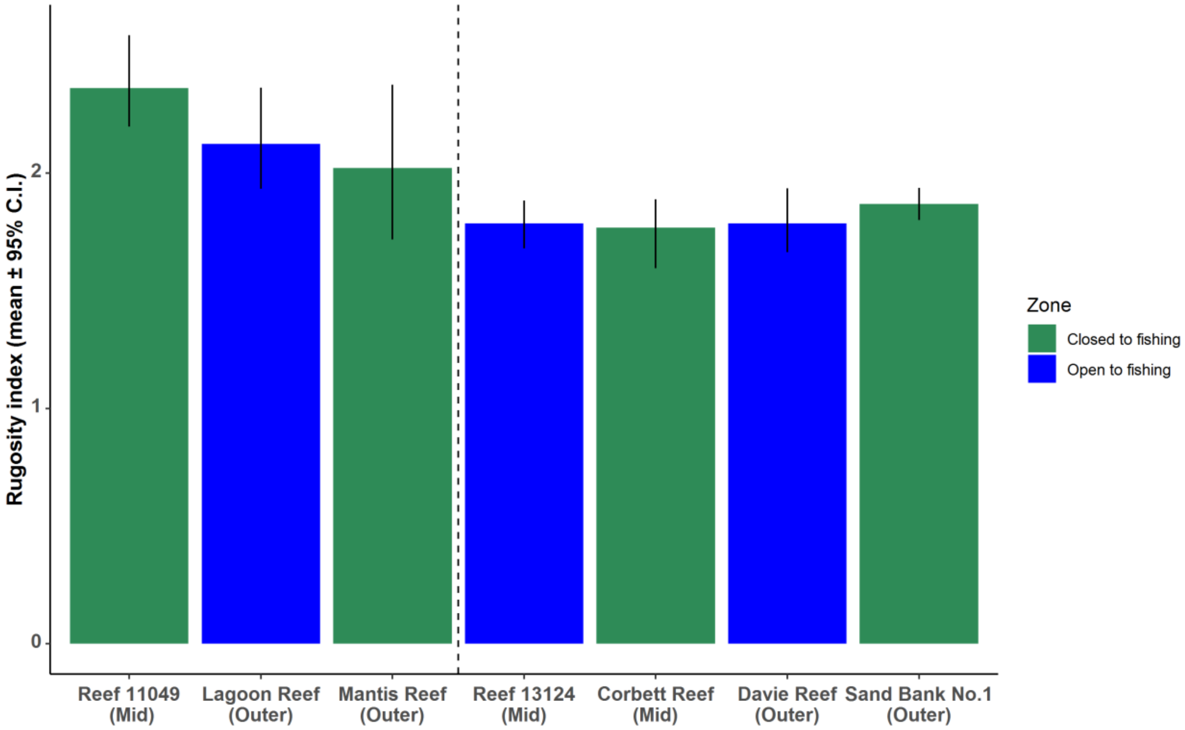

Figure 18: Mean rugosity estimated from fixed site surveys across surveyed reefs. Error bars denote the 95% Confidence Intervals (CI 95%). The reefs are arranged north to south from left to right, with the vertical dotted line delineating the Cape Grenville sector (left hand side) from the Princess Charlotte Bay sector (right hand side).

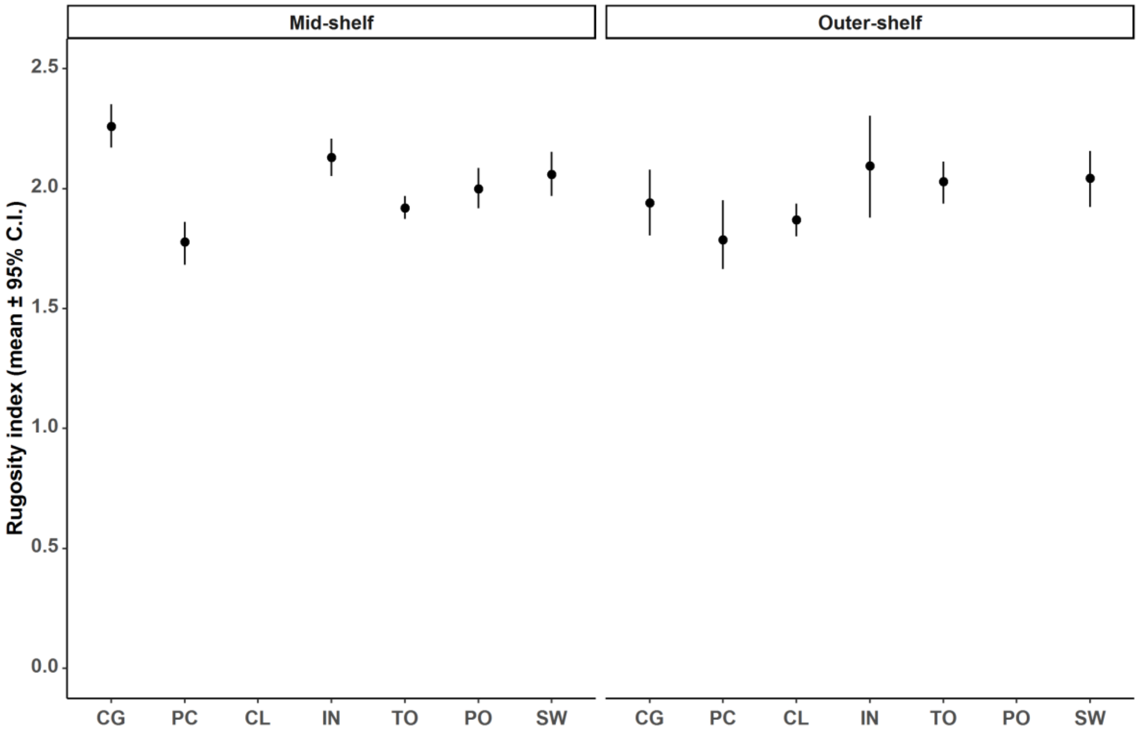

Figure 19: Comparison of rugosity from fixed site surveys estimated across the wider GBR, grouped by latitudinal sectors and shelf position where data is available. Error bars denote the 95% Confidence Intervals (C.I.).

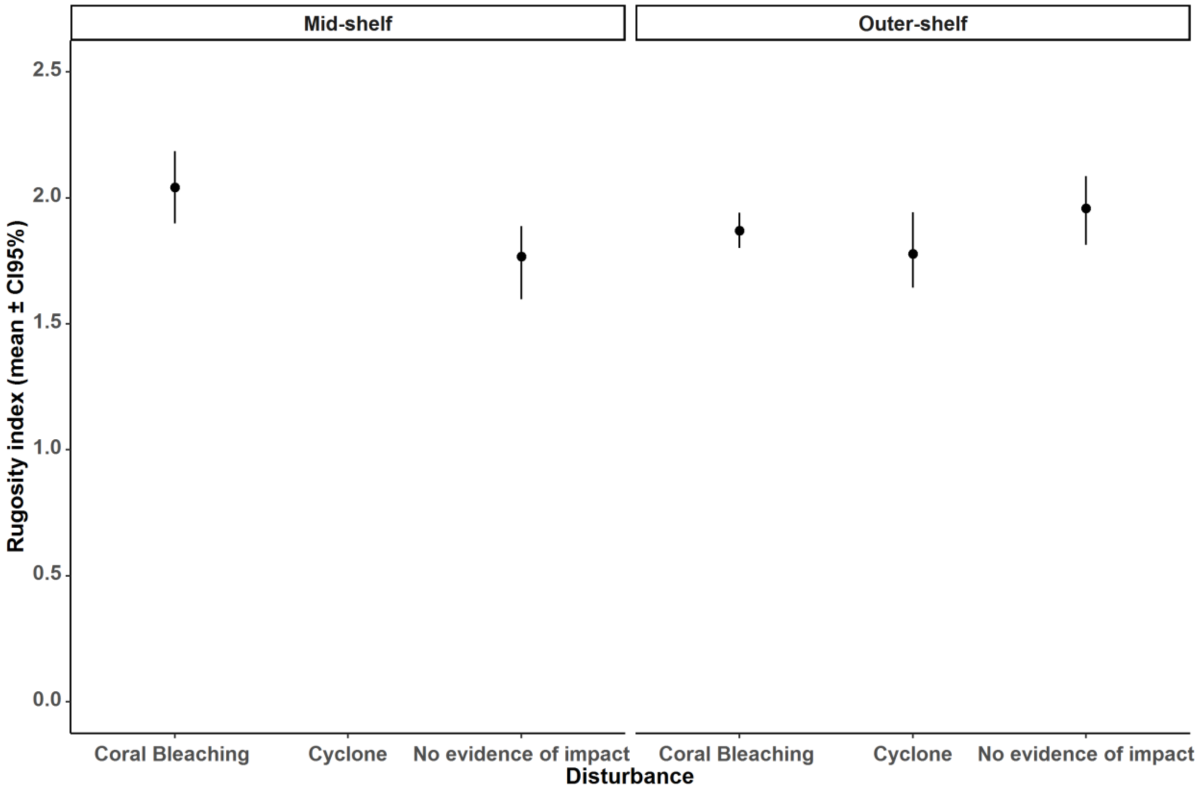

Figure 20: Average rugosity from fixed site surveys of northern GBR reefs, aggregated by reef sites exposed to different disturbances, and shelf position across the GBR. Error bars denote the 95% Confidence Intervals (C. I.).

In general, increasing levels of structural complexity (i.e. rugosity) strongly correlated with an increase in the abundance of both hard coral juveniles and damselfish. There was a significant relationship between the complexity of the reef structure and the abundance of coral juveniles ($r^2 = 0.69$). However, the strength and direction of this relationship varied across disturbances and abundance of hard coral (Figures 21). These results suggest that structural complexity estimated in this study performs a function in structuring the distribution of biota known to be strongly associated to the reef structure. However, further analysis reveal that this relationship is affected by other factors. The density of hard coral juveniles was influenced by the abundance of adult hard corals (i.e., coral cover), where low coral cover translates in a lower abundance of juveniles across the reef, and vice versa. On reef sites where there was no evidence of impacts from disturbance, the abundance of juvenile corals was strongly positively correlated to increases in structural complexity (Figure 21). However, the strength and direction of the correlation between juvenile corals and structural complexity significantly varied depending on the nature of recent disturbance events. There was no significant relationship between the abundance of juveniles and rugosity on reefs affected by bleaching events, while there was a negative relationship between juvenile abundance and rugosity on cyclone-impacted reefs (Figure 21). In addition, the abundance of damselfishes correlated to increasing levels of structural complexity ($p = 0.0035$, $r^2 = 0.85$), although we detected no significant effect of disturbances altering the relationship (Figure 22).

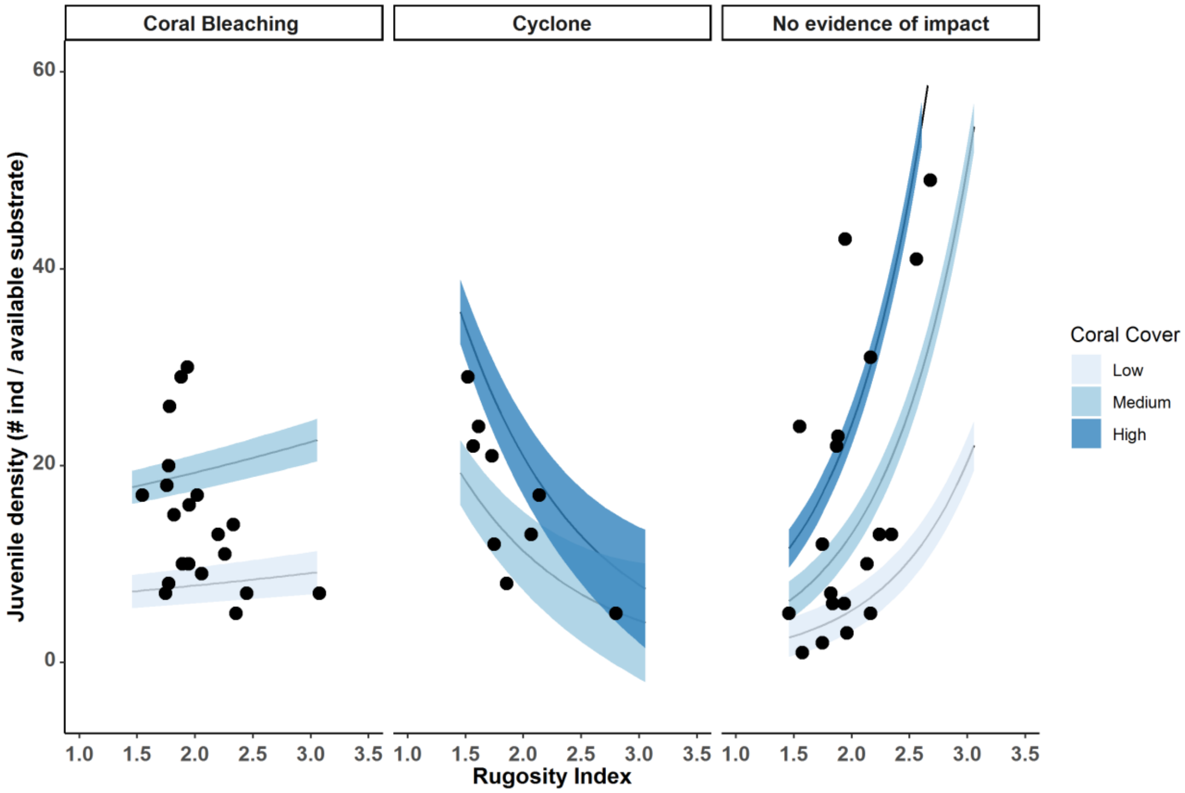

Figure 21: Relationship between structural complexity (i.e. rugosity) and the density of juvenile corals recorded from fixed site surveys of northern GBR reefs impacted by coral bleaching (non-significant, p-value = 0.45), cyclones (negative, p-value = 0.001) and reefs with no evidence of disturbance impact (positive, p-

value < 0.0001). Relationships were assessed for transects with low (0-11%), medium (12-30%) and high (>30%) hard coral cover. Data are estimates from individual transects, however due to long processing times, 3-D rugosity estimates are not available for analysis from all transects.

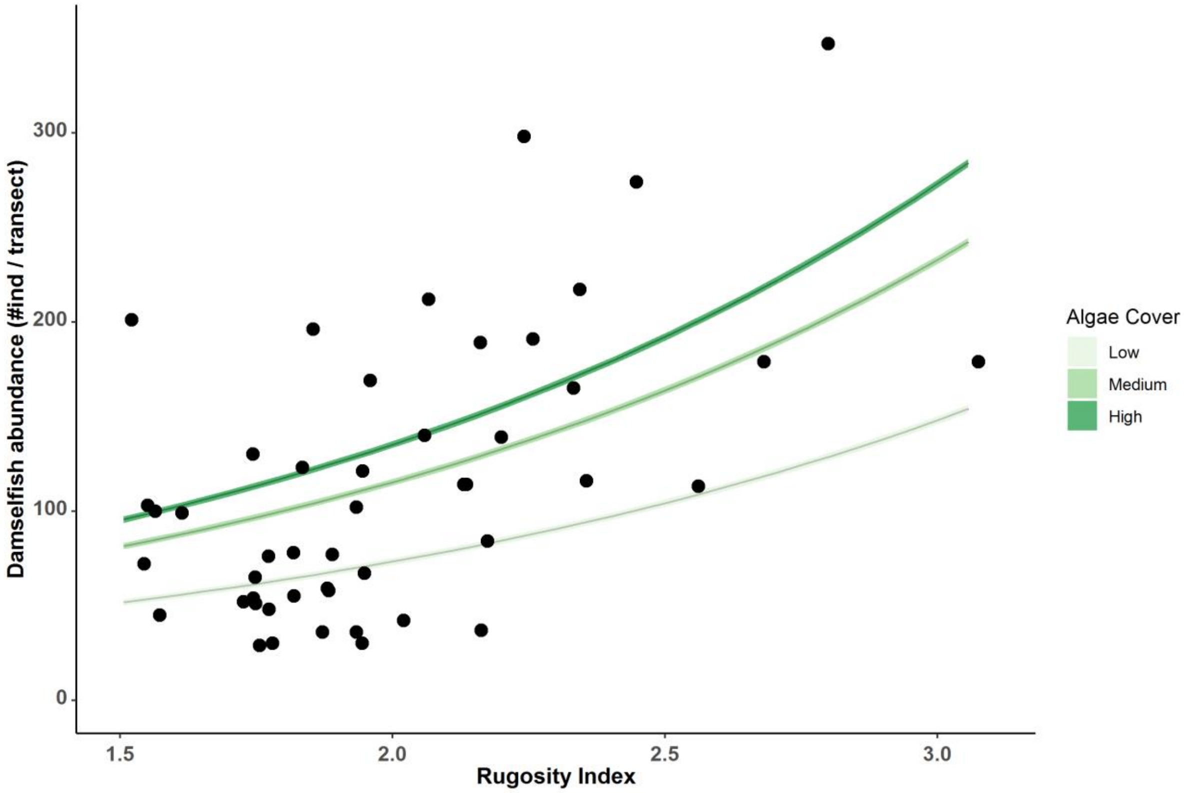

Figure 22: Abundance of damselfish (Pomacentridae) in relation to the structural complexity (i.e. rugosity) from fixed site surveys. Relationships were assessed for transects with low (0-11%), medium (12-30%) and high (>30%) hard coral cover.

4.1.7 Condition of reef fish assemblages from fixed site surveys

There was a total of 18,314 individual reef fishes from 173 species recorded across 105 transects on seven reefs during this study. Damselfishes (Pomacentridae) were the most numerous family, but snappers (Lutjanidae), parrotfishes (Scarinae) and surgeonfishes (Acanthuridae) were also abundant. There were three species that were new records for the LTMP, including the butterflyfishes *Chelmon marginatus* and *Chaetodon oxycephalus,* as well as the damselfish *Pomacentrus simsiang*.

4.1.7.1 Spatial patterns in fish species richness and abundance

Total species richness obtained from fixed site surveys was similar among the seven reefs, with the mean number of fish species per reef ranging from 26 to 35 (Figure 23). This range in species richness was similar for areas open and closed to fishing. Total fish abundance varied considerably among the seven reefs surveyed, increasing from south to north, from a mean total abundance of 80 individuals per 250m^2 at the southernmost reef, Sand Bank No. 1, to 250 per 250m^2 at the northernmost reef, Reef 11049 (Figure 23). This trend was evident regardless of management zones. The trend was driven by the damselfishes (Pomacentridae), the most abundant family, which had a 3-fold increase in abundance from the southernmost reef, Sand Bank No. 1, to the northernmost reef, Reef 11049 (Figure 23).

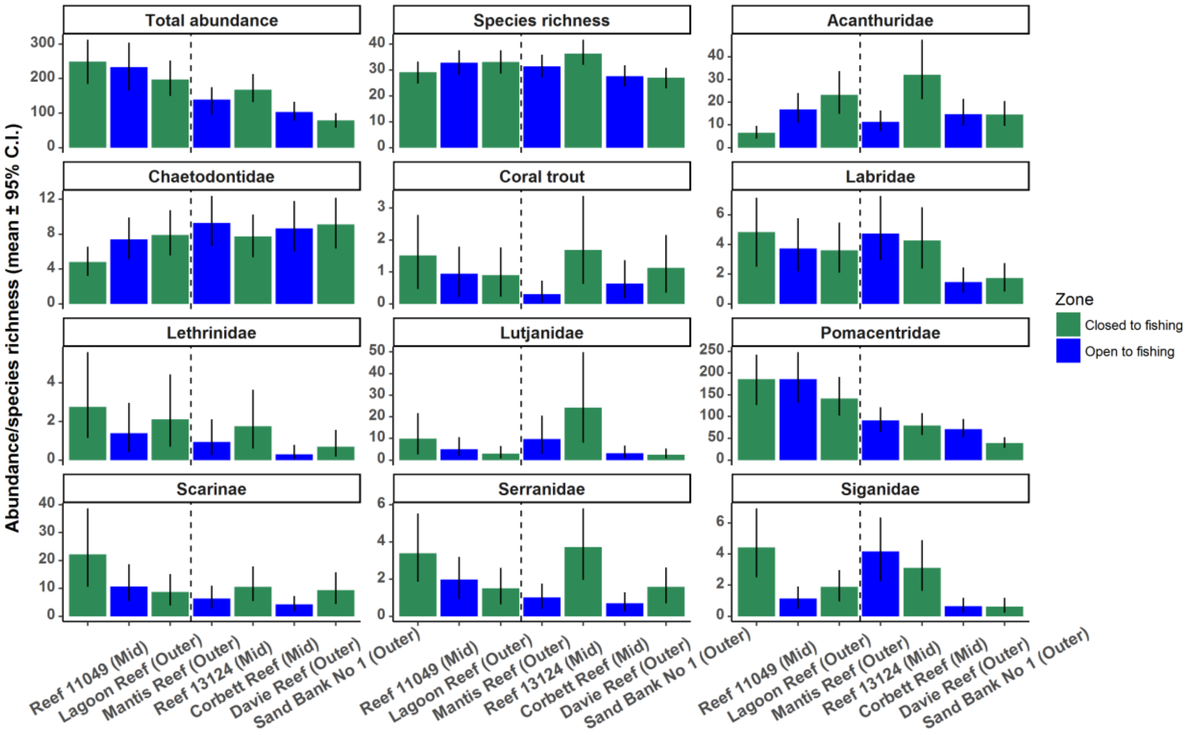

Figure 23: Abundance and species richness of reef fishes from fixed site surveys on the seven far northern GBR reefs. Reefs are coloured by management zone and labelled by shelf position (Mid & Outer). Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). The reefs are arranged north to south from left to right, with the vertical dotted line delineating the Cape Grenville sector (left hand side) from the Princess Charlotte Bay sector (right hand side).

There were no similar latitudinal trends in abundance for the other fish families, however there were differences among reefs for various families. Notably, Corbett Reef and Reef 11049, both mid-shelf reefs that are closed to fishing, had the highest abundances of groupers and coral trout (Serranidae). When the primary target of the Reef Line Fishery, coral trout (*Plectropomus* and *Variola* spp.), were analysed separately from the rest of the serranids, the same pattern was evident (Figure 23). Corbett Reef also had the greatest abundances of surgeonfishes (Acanthuridae) and snappers (Lutjanidae), while Reef 11049 had the greatest abundance of the parrotfishes (Scarinae) and emperors (Lethrinidae) (Figure 23). The abundance of the emperors was highest at three of the four reefs closed to fishing. Abundances of the wrasses (Labridae) were similar among the five northernmost reefs, but lower on the two southernmost outer-shelf reefs. Butterflyfishes (Chaetodontidae) had the lowest abundance at the northernmost reef with similar abundance among the remaining reefs (Figure 23).

Total fish abundance and species richness were similar between reefs open and closed to fishing (Figure 24). Groupers and coral trout (Serranidae), parrotfishes (Scarinae), and emperors (Lethrinidae) all had higher abundances on reefs closed to fishing compared to reefs where fishing was allowed (Figure 24). When analysed separately from the rest of the serranids, the important fishery species coral trout (*Plectropomus* spp.) also had higher abundances on reefs that were closed to fishing (Figure 24). For the damselfishes (Pomacentridae) and butterflyfishes (Chaetodontidae) there is a high probability that the opposite is true, i.e. that abundances were lower on reefs closed to fishing compared to those open to fishing, however the error bars overlapped the zero line (Figure 24). For the remaining families, there is a high probability that abundances were higher in reefs closed to fishing than those where fishing was allowed, however the error bars overlapped the zero line (Figure 24).

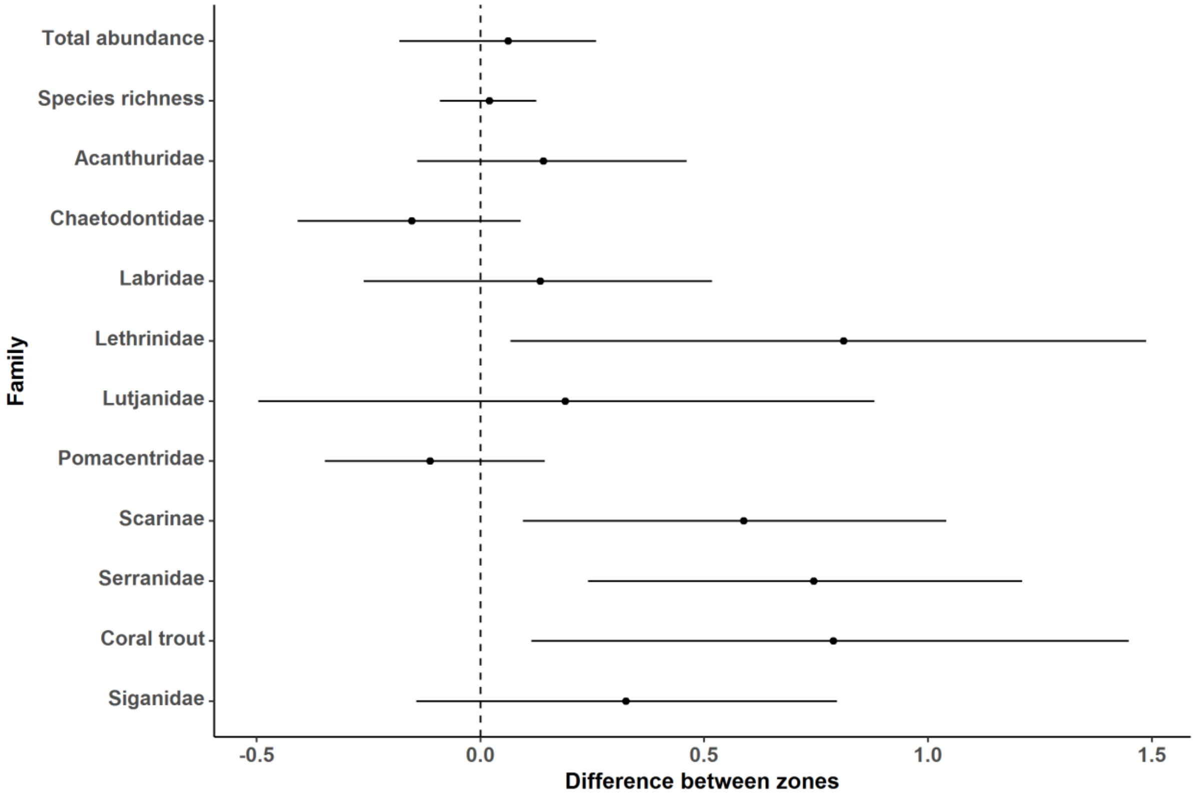

Figure 24: Differences between management zones in the abundance of reef fishes from fixed site surveys. Negative contrasts indicate higher abundance on reefs open to fishing, while positive contrasts indicate higher abundance on reefs closed to fishing. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). Statistical significance can be inferred where 95% credible intervals do not intersect zero.

4.1.7.2 Spatial patterns in community structure

MDS analysis revealed a predominantly cross-shelf pattern in fish assemblage structure. Replicates within each of the seven reefs were clustered together, but differences in assemblage structure were apparent between the mid-shelf and outer-shelf reefs. The four outer-shelf reefs (Davie, Sandbank No 1, Lagoon, Mantis) had overlapping community structure regardless of zoning, and the three mid-shelf reefs had distinct community structures regardless of zoning (Figure 25). Two mid-shelf reefs, Reef 13124 in the Princess Charlotte Bay region and Reef 11049 north of Cape Grenville, formed distinct assemblages from all other reefs characterised by the snapper *Lutjanus carponotatus* and *Pomacentrus moluccensis,* a small damselfish. The other mid-shelf reef, Corbett Reef had an assemblage more similar to the outer-shelf reefs than the two other mid-shelf reefs, while all four outer-shelf reefs had very similar fish assemblages (Figure 25). The differences among sites were largely driven by damselfish (Pomacentridae), however there were a number of species of parrotfishes (Scarinae), surgeonfishes (Acanthuridae), rabbitfishes (Siganidae), snapper (Lutjanidae), cods (Serranidae), wrasses (Labirdae) and butterflyfishes (Chaetodontidae) that influenced the spatial patterns in assemblage structure.

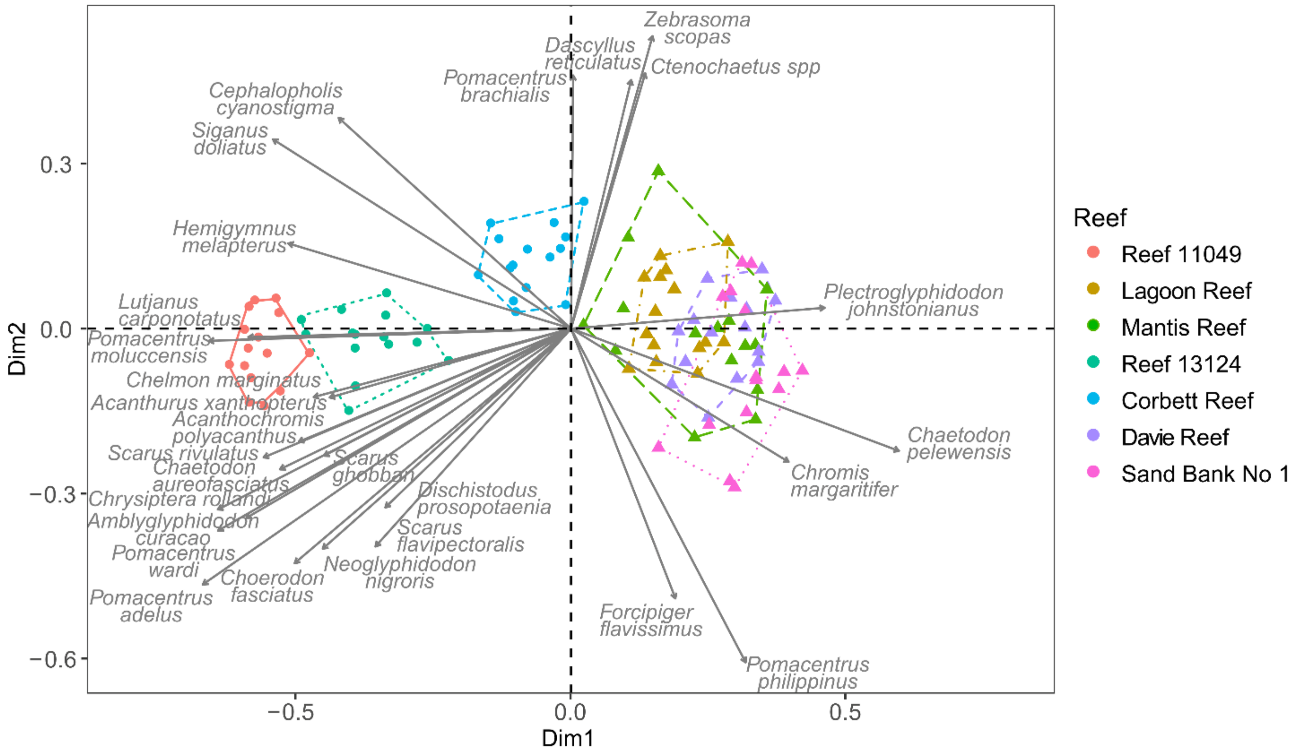

Figure 25: Ordination plot based on a Multidimensional Scaling (MDS) analysis of fish assemblages recorded on fixed site surveys of reefs in the far northern GBR. Data are coded by shelf position: circles = mid-shelf, triangles = outer-shelf. Convex hulls encapsulate the fifteen transects surveyed at each reef.

4.1.7.3 Comparisons to the wider GBR

There were no consistent differences in the abundances of reef fish families surveyed between far northern GBR regions and other regions to the south (Figure 26). The variability among reefs within a latitudinal sector was very high for some families, but it was particularly high in the two far northern GBR sectors compared to other regions for the surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), emperors (Lethrinidae), snappers (Lutjanidae), and rabbitfishes (Siganidae). Despite the high variation, there was a tendency for the abundance of some families of reef fishes to be higher in the far northern GBR (Figure 26).

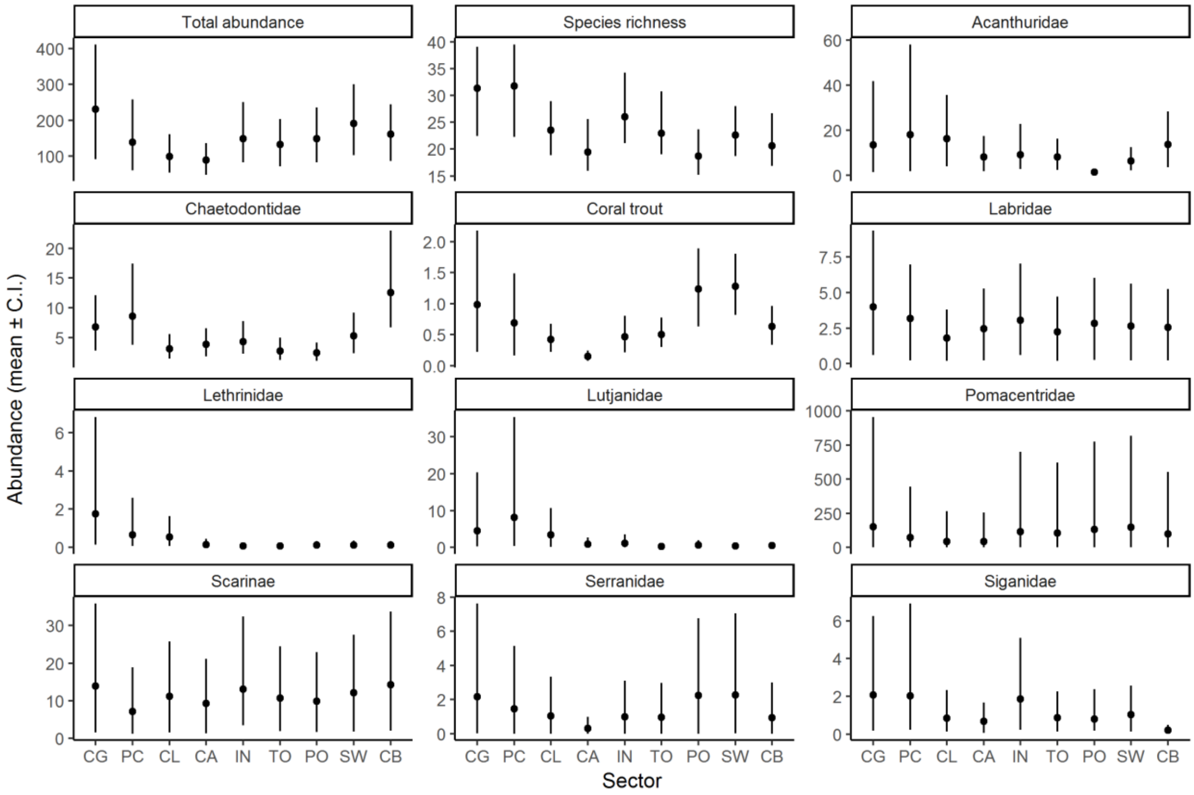

Figure 26: Abundance and species richness of reef fishes recorded during fixed site surveys in latitudinal sectors of the GBR. Data are means estimated from Bayesian hierarchical linear models with associated 95% credible intervals (C.I.). Sectors are arranged north to south from left to right such that CG = Cape Grenville, PC = Princess Charlotte Bay, CL = Cooktown Lizard, CA = Cairns, IN = Innisfail, TO = Townsville, PO = Pompeys, SW = Swain, CB = Capricorn-Bunker.

4.2 BRUVS

4.2.1 General patterns of diversity and abundance

A total of 11,495 fish from 413 species were recorded in videos from 129 BRUVS deployments on seven reefs: Reef 11049 (11); Reef 13124 (20); Corbett Reef (22); Davie Reef (20); Lagoon Reef (22); Mantis Reef (16); and Sand Bank No1 Reef (18). These included a diverse range of demersal and semi-pelagic fishes, sharks, and rays (see Table S2). The bony fishes were most numerous (11333 individuals) followed by the sharks and rays (162). Sea snakes were notably absent, and turtles were excluded from analysis.

Comparisons of species richness and abundance of the seven far northern GBR reefs with BRUVS data from other regions of the GBR showed no consistent effect of zoning but did suggest the far northern GBR had higher median diversity and fish abundance, with the exception of Corbett Reef (Figure 27). This was expected, given other BRUVS samples were generally from deeper waters on reef bases or submerged banks and shoals (e.g. Cappo et al. 2007, 2012). Greater density of BRUVS sampling would be required to more fully capture diversity.

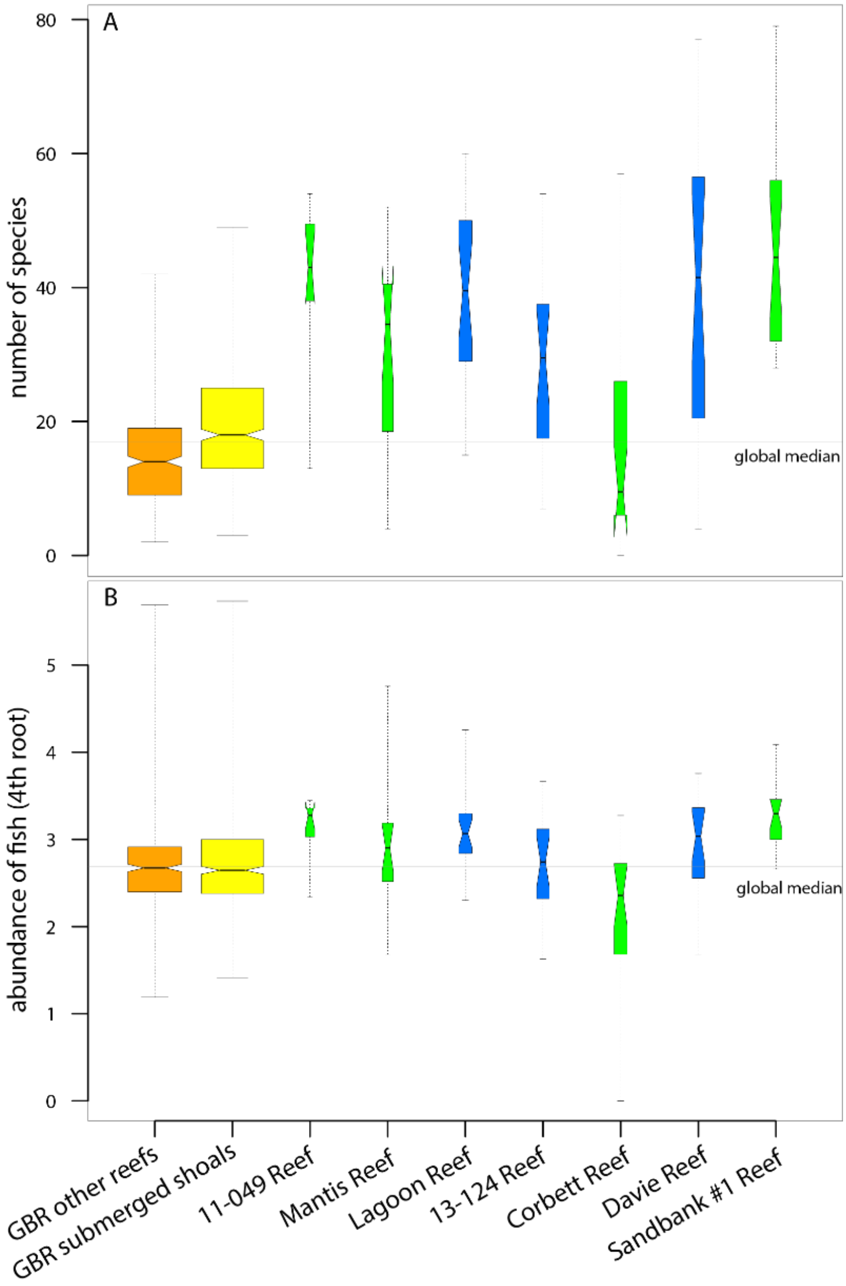

Figure 27: Comparisons of species richness (number of species) and transformed abundance (4th root) of fishes, sharks, rays and sea snakes pooled among baited videos (BRUVS) set in different GBR regions sampled by AIMS. Samples from GBR reefs and banks were selected to have similar habitats as the BRUVS imagery analysed from the reefs sampled in the far northern GBR. Box and whisker plots show ranges, medians, and interquartile ranges. Box widths are proportional to the square root of the sample size (number of BRUVS deployments). Horizontal lines show the global medians in richness and transformed abundance. Far northern reefs are coloured by zoning (open to fishing: blue; closed to fishing: green).

4.2.2 The effect of zoning on the fish assemblage

Distance based redundancy analysis (db-RDA) of 115 genera of fishes explained 39% of the distance variation, of which management zone comprised only 1.05%. The centroid for reefs open to fishing, was correlated with deeper, sandy sites bare of any epibenthos with lower species richness (Figure 28A), and genera of fish known to prefer sandy habitats such as emperors (Lethrinidae) and trevallies (Carangidae). In contrast, there were many significant vectors for reef-associated genera correlated with the centroid for reefs open to fishing, such as butterflyfishes (Chaetodontidae) and parrotfishes (Scarinae). The major target of the reef line fishery on the GBR (coral trout *Plectropomus* spp.) was significantly correlated with the higher coral cover, higher reefal substrata, clearer waters and higher topography characteristic of the "blue" zone sites (Figure 28B).

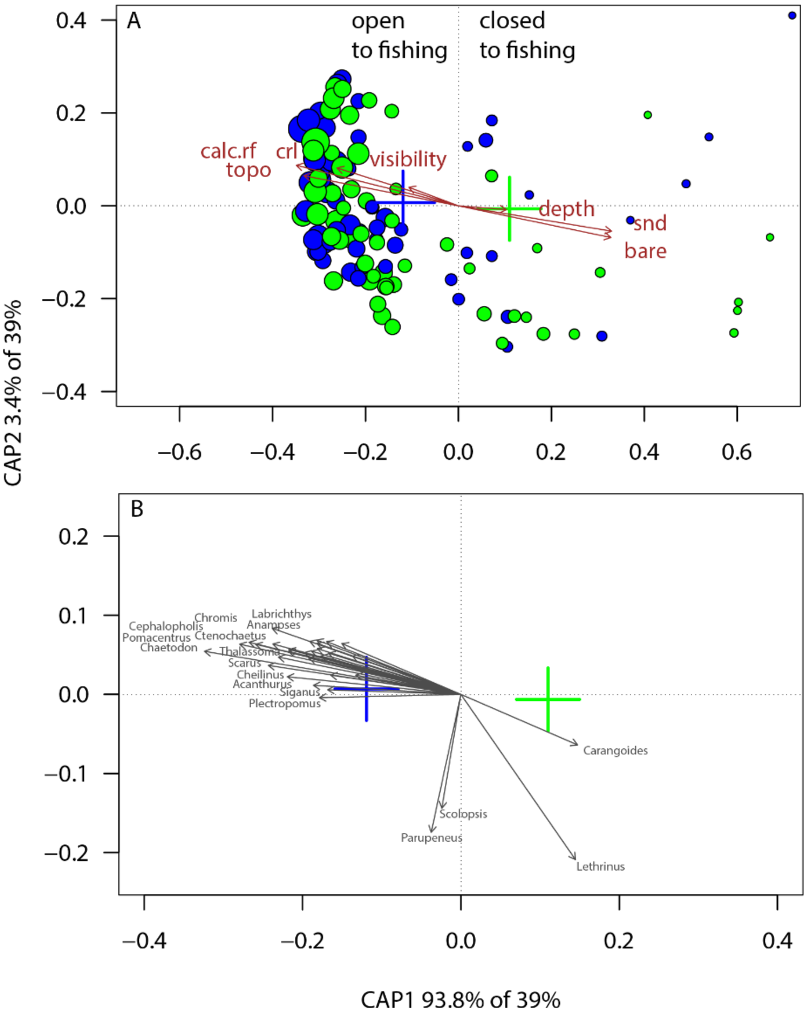

Figure 28: Distance based redundancy analysis (db-RDA) of 115 genera of fish occurring on at least 2.5% of BRUVS at seven reefs pooled (A). Weighted averages of site scores are scaled by site richness and coloured by the management zoning of each BRUVS site such that green = closed to fishing and blue = open to fishing. Significant fish vectors (p<0.005) correlated with linear constraints are shown (B).

The marginal effects of each covariate were estimated for Model (1) when each term was eliminated from the model containing all other terms. The marginal effect of management zone was not significant in explaining the variation in the dissimilarity matrix when all other environmental covariates were accounted for (Table 5).

Table 5: Permutation tests of the effects of management zoning and habitat covariates on a dissimilarity matrix of 115 fish genera (Model 1). If the modelled relationship is stronger than the randomly permuted relationships (at alpha = 0.05, beta = 0.01), then the relationship is significant.

Covariates	d.f.	Var	Pseudo-F	Number of permutations	Pr(>F)
Management zone	1	0.2380	2.0169	199	0.1350
Calcareous reef	1	0.1897	1.6076	99	0.1600
Sand	1	0.5283	4.4766	199	0.0150
Live hard coral	1	0.2633	2.2312	399	0.0925
Bare substrate	1	0.0432	0.3658	99	0.7700
Topographic complexity	1	0.6187	5.2418	199	0.0100
Visibility	1	0.3122	2.6448	5399	0.0581
Depth	1	0.1620	1.3727	99	0.2400
Residual	116	13.6908			

4.2.3 Models of richness and abundance as a function of habitat

Composition of the seabed was a major influence on species richness, with sites containing more than about 30% calcareous substrata, and less than about 10% sand, having above average species richness. Substrata where epibenthos was lacking, with greater than 60% bare substrate had lower than average species richness (Figure S1). The r^2 statistic for this model (1-rel.pred.err) was 64.4%, and the influence of the top three variables, calcareous reef (31.4%), sand (23.8%) and bare substrate (12.4%), together accounted for 67.8% of the variation explained by the model (Figure S1). Interestingly, there was little effect of management zoning once the other covariates were accounted for.

The influences on transformed abundance were similar, with 62.5% of the variation accounted for by the same three predictors of calcareous reef, sand and bare substrate, however the r^2 statistic was much lower at 48.5% (Figure S2). Higher variation is expected with abundance data, especially when schooling species such as fusiliers (Caesionidae) are included in the analyses, as was the case here. Fish abundance was above average at sites containing more than ~30% calcareous substrata, and less than ~40% sand. Conversely, sites with amounts of bare substrata above ~80%, tended to have lower than average abundance (Figure S2).

4.2.4 Community assemblage structure as a function of habitat

Multivariate regression trees explained 20.9% of the variation in fish assemblages, with an average success of only 6.3% in predicting the total fish fauna of a BRUVS site based on the 19 covariates. This is not unexpected, given the extremely large number of species in the response, and their wide variation in numbers. Schooling species including plankton feeding fusiliers (Caesionidae), small predatory cardinalfishes (Apogonidae), detritus and algal feeding surgeonfishes (Acanthuridae), the omnivorous damselfishes and wrasses (*Chromis* and *Cirrhilabrus* genera) were all included in the response, and these have extreme variation in numbers compared to coral trout and triggerfishes (genera *Plectropomus* and *Balistapus*).

The first split in the tree distinguished sites on mid-shelf reefs from those on the outer-shelf. The mid-shelf reefs split to separate the northern-most reef from the pair of open/closed reefs in Princess Charlotte Bay (Figure 29). The final split on this side of the tree occurred based on the percentage cover of live hard coral (~15%), not the zoning of the sites. On the other side of the tree, splits occurred first on the nature of the substrata, not the epibenthos, and then by water depth. Two outer-shelf assemblages were characterised by mixed, non-reefal substrata (leaf #6) or mixed substrata (leaf #14). Node 15 had almost complete reefal substrata (calcareous reef ≥95%), and then split by depth at 11.5 metres, into deep and shallow leaves (Figure 29).

The histograms on each leaf show the individual (transformed) abundances of the 290 species. It is notable that the Princess Charlotte Bay mid-shelf sites with low coral cover had consistently low abundances for a reduced species pool, whereas the outer-shelf sites had consistently higher diversity and abundance. The Cape Grenville mid-shelf reef (Reef 11049; leaf #5) had lower diversity than the outer-shelf leaves, but a relatively large number of species with high abundances (Figure 29).

Surrogates for each split can also be examined in the *mvpart* output to identify correlated and competing covariates in the model. Most importantly, management zone did not appear in any node or leaf of the tree as a surrogate splitting term, meaning the influence of management zoning is vastly outweighed by the nature of the habitat in the field of view (FOV) of the BRUVS in this study.

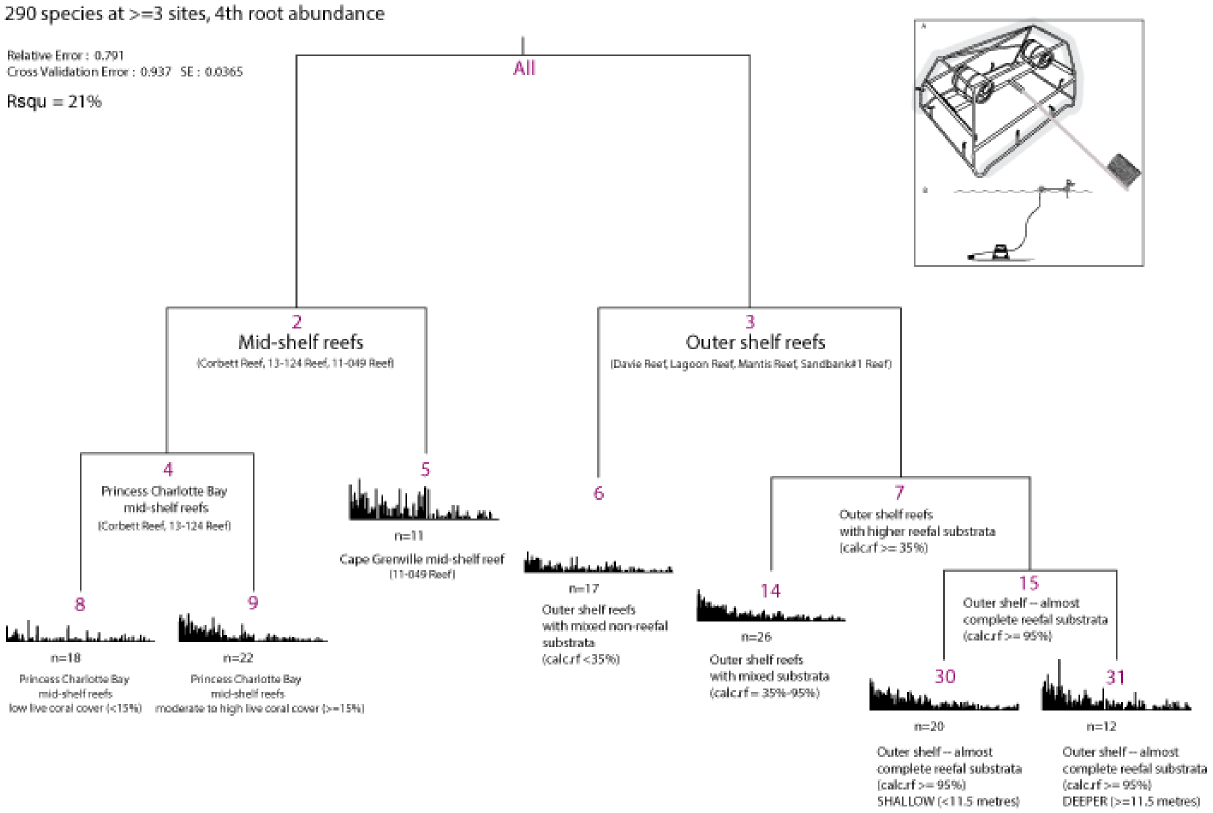

Figure 29: The best tree structure from a multivariate analysis of the transformed abundance (4th root MaxN) of 290 species (present on at least 3 BRUVS, ~2.5% of samples) predicted by the biotic and abiotic explanatory covariates. Histograms on the "leaves" show abundance of each species, and the number of sites (*n*) are given with node names and node numbers.

Inspection of the Dufrene-Legendre Indices (DLI) species values shows species with high DLI at the tree stump (e.g. coral trout *Plectropomus leopardus,* bristletooth surgeonfish *Ctenochaetus striatus* and moon wrasse *Thalassoma lunare*) were ubiquitous, but others with very high DLI on a leaf were largely confined to the sites in those leaves (Figure S3). The most notable of those high DLI were found at Reef 11049 (leaf #5). These were the tuskfishes *Choerodon cyanodus* and *Choerodon schoenleinii*, and the grassy sweetlip *Lethrinus laticaudis* (Figure S3).

The tree leaves characterised by high coral cover on the mid-shelf, or high reefal substrata offshore, had high DLI amongst species known to be site-attached in coral reef habitats (e.g. *Chelmon rostratus*, *Cephalopholis argus*, *Chrysiptera talboti* Figure S3). In contrast, the mid-shelf reef sites with low coral cover (leaf #8) had high DLI amongst species known to be associated more with soft-sediments (threadfin breams *Nemipterus furcosus, and* goatfish *Parupeneus indicus*) or gravel reef bases (drab emperor *Lethrinus ravus*).

Habitats with mixed substrata would be expected to have a wide variety of trophic groups. The outer-shelf assemblage characterised by mixed, non-reefal substrata (higher sand, rubble, gravel; leaf #14) were most notable for their larger body size and were mainly benthic macro-carnivores (e.g. spangled emperor *Lethrinus nebulosus*) or mobile piscivores from the genera *Aprion* (snappers) and *Caranx* (trevallies), with the notable exceptions of the large roving herbivores *Hipposcarus longiceps* (longnose parrotfish) and *Acanthurus dussumieri* (pencil surgeonfish), which often occurred in schools (Figure S3).

The outer-shelf assemblage which was characterised by mixed, reefal substrata had DLI species with small body sizes and a variety of feeding modes, from sediment sifting feeders, such as the goatfish *Parupeneus* spp. to small planktivores, small omnivores, facultative corallivores and blennies known to eat mucus and scales from larger species. Species from those reported by Cole et al. (2008) to be facultative or obligate corallivores, had highest DLI values on the outer-shelf side of the tree, in assemblages where calcareous reefal substrate comprised more than 35% of the FOV.

There were a number of genera with different species having highest DLI in different assemblages (Figure S3). For example, the passionfruit trout *Plectropomus areolatus* characterised shallow, outer-shelf sites with almost complete coverage of reefal substrata (leaf #30), whereas the common coral trout *P. leopardus* had highest DLI at the tree base, and the bar-cheeked trout *P. maculatus* had highest DLI on the mid-shelf reefs of Princess Charlotte Bay with low live coral cover (leaf #8). The blue-spot trout *P. laevis* was also seen commonly but was not in the top 10 DLI in any node or leaf. It had a maximum DLI value of 49%, in the node #3 of sites on outer-shelf reefs (Table S3).

The lowest diversity, abundance and number of DLI species occurred in sites from the open/closed pair of reefs on the mid-shelf of Princess Charlotte Bay where coral cover was less than 15%. The single reef (Reef 11049) in the Cape Grenville sector (mid-shelf node #5), had the highest number of DLI species, high average diversity and high average abundance on BRUVS despite having only 11 samples. The outer-shelf assemblages had consistently high measures of DLI numbers, richness and abundance irrespective of substrata in the FOV (Table 6).

Table 6: Summaries of the overall abundance and species richness in the seven fish assemblages identified in the multivariate tree (Figure 29). Each BRUVS site was assigned to an assemblage. The range in species richness (*S*) and abundance (∑*MaxN*) for each of the *n* BRUVS sites within an assemblage was then tallied as *S* and ∑∑*MaxN.* The node number and assemblage name, from Figure 29, is accompanied by the total number of DLI species (*n*DLI) from Table S2.

nodes	***n* sites**	**Node name**	**Richness *S***	**∑∑ *MaxN***	***n* DLI**	***S* range**	***S* mean**	**∑*MaxN* range**	**∑*MaxN* mean**
8	18	Princess Charlotte Bay mid-shelf reefs low live coral cover (<15%)	96	533	8	(0 - 26)	(11 ± 8.4)	(0 - 115)	(29.6 ± 29.5)
9	22	Princess Charlotte Bay mid-shelf reefs moderate to high live coral cover (>=15%)	178	1575	15	(6 - 57)	(33 ± 12.7)	(8 - 181)	(71.6 ± 40.1)
5	11	Cape Grenville mid-shelf	145	1131	53	(13 - 54)	(41.8 ± 11.3)	(30 - 141)	(102.8 ± 32.7)
6	17	Outer-shelf - reefs with mixed non-reefal substrata	139	821	17	(4 - 40)	(19.6 ± 11.7)	(8 - 143)	(48.3 ± 40.9)
14	26	Outer-shelf reefs with mixed substrata	241	2907	21	(19 - 67)	(41.3 ± 12.5)	(28 - 512)	(111.8 ± 90.5)
30	20	Shallow outer-shelf - - almost complete reefal substrata	233	2296	24	(26 - 79)	(48.4 ± 13.7)	(43 - 261)	(114.8 ± 60.2)
31	12	Deeper outer-shelf - - almost complete reefal substrata	182	2128	24	(29 - 60)	(46.1 ± 9.5)	(75 - 328)	(177.3 ± 87)

5 DISCUSSION

5.1 Broad-scale assessment of coral reef condition and trends

While many reefs in this region experienced severe bleaching in 2015/16 and 2016/17, and subsequent mortality (Hughes et al. 2017), there are still reef communities that retain intact coral populations. Sixteen out of eighteen reefs surveyed in 2019 had moderate to high coral cover, which suggests they escaped the worst of the bleaching-related mortality. Seven reefs were not surveyed in 2017, hence no assessment of change in coral cover immediately after the bleaching events could be made. Most of the survey reefs were located on the outer-shelf, and recent hydrodynamic modelling suggests that upwellings of deep water cooled sea surface temperatures along the edge of the continental shelf during the worst of the 2015/16 bleaching event (Benthuysen et al. 2018). This could mean that the outer-shelf reefs were less exposed to heat stress.

Inshore and mid-shelf reefs in the far northern GBR were severely impacted during the 2015/16 bleaching (Hughes et al. 2018a, b). Inshore reefs are under-represented in the present surveys. Four inshore and seven mid-shelf reefs that had low coral cover when previously visited in 2017, were unable to be re-surveyed in 2019 due to safety concerns. Reefs with low coral cover in 2017 that could be re-surveyed in 2019 were mostly unchanged and still had low hard coral cover. This is likely the result of the 2015/16 and 2016/17 bleaching events that caused widespread declines in hard coral cover in both sectors (Hughes et al. 2018b). Small increases in sector-wide hard coral cover in the present surveys compared to 2017 no doubt reflect a partially different suite of reefs being surveyed in 2019. It is likely that if all reefs that had been planned to be visited were surveyed, the small increase in sector-wide hard coral cover would have been negated. The inclusion of a number of outer-shelf reefs that escaped the worst of the 2015/16 bleaching probably accounts for the small sector-wide increases observed in hard coral cover during the present surveys.

A key objective for conducting the present surveys was that in late 2018, there were early indications that another bleaching event was possible in late summer of 2019. In October and November 2018, sea surface temperatures were above the long-term average by up to one degree[4] and by late October 2018, NOAA's Outlook of Coral Bleaching Heat Stress predicted a 90% probability that "bleaching was possible" on the GBR[5] . The present surveys recorded low level bleaching on most reefs, and two incidences of localised moderate and severe bleaching on two reefs in the Princess Charlotte Bay sector. This suggests that water temperatures had already reached levels where bleaching was initiated, however the formation of a very active monsoon trough from December 2018 to January 2019 cooled sea surface temperatures such that this region avoided a repeat of the heat stress, bleaching levels and mortality recorded in 2015/16 and 2016/17.

While widespread severe bleaching did not occur in early 2019, our surveys indicated there were low numbers of CoTS and evidence of recent storm damage that had reduced coral cover. This highlights that the far northern GBR reefs remain vulnerable to ongoing disturbances.

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[4] AIMS Coral Watch http://138.7.2.11/CoralWatch/index.html

[5] NOAA Bleach watch https://coralreefwatch.noaa.gov/satellite/bleachingoutlook_cfs/outlook_cfs.php

Storm damage was recorded at substantial parts of four reefs and is most likely the result of gale force winds associated with the formation of a monsoon trough in late December 2018, and the passage of Tropical Cyclone Penny in early January 2019. Wind speeds of 60kts were encountered by the AIMS Research Vessel 'Solander' during its transit down Cape York to meet the scientific crew at Cooktown in the first days of 2019. Winds of this speed are capable of causing widespread damage to shallow water coral communities (Puotinen et al. 2016).

5.2 Detailed coral assemblage condition assessments

Compared to broad-scale manta tow surveys, fixed site surveys provide more detailed and nuanced information about the condition and composition of coral assemblages. However, the intensive nature of the work also means that fewer reefs can be surveyed in a limited time period. The results from these surveys support the findings of manta tow surveys that reef condition was variable among the surveyed reefs. However, inferences about coral reef condition in the wider far northern GBR must be carefully contextualised.

Like for the broad-scale assessments, safety concerns meant that inshore reefs, where bleaching mortality was severe, particularly following the 2015/16 bleaching (Hughes et al. 2018a, b), were not represented in the 2019 fixed site surveys. The moderate to high levels of coral cover recorded on all seven reefs with fixed site surveys likely reflects the over-representation of mid- and outer-shelf reefs where bleaching effects were not as severe (Hughes et al. 2018b). For example, Reef 11049, a mid-shelf reef, had hard coral cover of 14.5% and was likely in a degraded condition as a result of the 2015/16 and 2016/17 bleaching. However, the remaining six reefs surveyed had moderate to high hard coral cover that ranged from 26% to 51%. This suggests that they had either been exposed to less heat stress, or that they had survived and recovered from these events. Additionally, our surveys were from deeper reef slopes (7-9m depth) than those of Hughes et al. (2018a, b), who surveyed the reef crests. It is possible that there was an attenuation of heat stress and mortality with depth, especially on reef slopes exposed to currents and swell, as shallow reef crests are warmer than deeper areas and are most exposed to solar radiation which can be an additive factor in bleaching response (Courtial et al. 2017). Water movement and upwelling can help drop ambient temperature and resuspended particulates can protect corals from bleaching (Benthuysen et al. 2018). Reefs in the Cape Grenville sector also sit in an area of high water movement due to tidal flushing (www.portal.ereefs.info). Despite having high degree heating weeks during the summers of 2016 and 2017, water movement may have been a factor in bleaching resistance or recovery.

The structure of coral assemblages was variable among reefs. The greatest difference was due to shelf position, a result consistent with all other GBR reef regions (Mellin et al. 2019). Shelf position captures a complex array of environmental drivers including water quality, exposure to ocean swells and connectivity related to water movement at a variety of scales (Wolanski 1994, Steinberg 2007). In the classification of GBR reefs that was the basis of the 2004 rezoning (Fernandes et al. 2009) there are 31 reef bioregions of which seven occur north of Princess Charlotte Bay. Our survey reefs were in two bioregions; RA2 Outer Barrier Reefs and RC2 Far Northern Protected Mid Shelf Reefs and Shoals. The bio-regionalisation demonstrates that, while the cross-shelf gradients are strong, there are important latitudinal differences reflected in reef communities.

Far northern reefs typically have fewer days exposed to swell but many are regularly exposed to high water movement from moderate to large scale tidal flows (www.portal.ereefs.info). On the outer-shelf reefs in the far northern GBR, steep slopes and vertical walls were common. Far northern mid-shelf reefs tended to be quite shallow, limiting the depth to which coral-dominated habitats could grow. Particularly, the proportion of hard substrate declined rapidly, and the substrate became sandy around 5m below datum.

Outer-shelf reefs had the strongest dominance of corals of the genus *Acropora,* compared to mid-shelf reefs where the cover of *Acropora* was 10% or less. Mid-shelf coral assemblages had higher abundance of Poritid corals. These differences may partly reflect differential mortality of the 2015/16 and 2016/17 bleaching events (Hughes et al. 2018b) but are also indicative of basic habitat differences. Poritids are indicators of turbid inshore assemblages (Mellin et al. 2019), and massive *Porites* bommies can be dominant in sheltered reef zones where sandy substrates dictate patchy reef development.

We recorded moderate (4.6 to 13 juveniles m^{-2}) to high (>13 juveniles m^{-2}) densities of juvenile corals on all seven reefs, at levels equivalent to those observed at mid- and outer-shelf reefs further south on the GBR (Jonker et al. 2019). The densities of juvenile corals recorded during these surveys are a promising sign for future recovery of coral populations in the far northern GBR. Previously, a density of 6.3 juveniles m^{-2} has been shown to be necessary for coral recovery on reefs in the Seychelles (Graham et al. 2015) and modelling has suggested that beyond a threshold of 4.6 juveniles per m^{-2}, coral cover would likely increase on GBR inshore reefs (Thompson et al. 2016). Juvenile densities recorded during the present study were higher than these thresholds on all reefs and suggest that in the absence of further disturbances, coral cover should increase on all of the far northern reefs surveyed. However, we were unable to discern exactly when the observed juvenile corals recruited. A recent study highlighted a large decrease in the amount of coral settlement onto experimental panels on the reef crest, which reflects the decline in adult *Acropora* brood stock in these areas (Hughes et al. 2019). The presence of multiple size classes in our surveys, including very small juveniles (pers. obs.), suggests that there has been coral recruitment in the years since the bleaching events and that some juveniles also survived the bleaching events. These survivors would be a valuable source of coral populations, potentially with some increased tolerance to heat stress (Kirk et al. 2018).

The positive relationship between complexity and juvenile corals documented in this study was expected, as structural complexity generally provides habitat refuge for the settlement and survival of early-stage corals from the effects of UV radiation (Gleason et al. 2006, Nordborg et al. 2018), predation from fish (Doropoulos et al. 2016) and sedimentation (Gilmour 1999, Babcock and Smith 2002). Similar results have been reported by previous studies suggesting that coral settlement and survival is promoted by abundance of adult corals, influencing settlement preferences, competition by increasing grazing pressure and self-recruitment (Williams et al. 2001, Ceccarelli et al. 2011, Figueiredo et al. 2013, Mumby et al. 2016).

The potential mechanisms explaining the observed relationships between rugosity and the abundance of coral juveniles also vary between disturbances. Coral bleaching can have a differential effect on the mortality of early-stage corals , and such destabilisation of the community structure can support two hypotheses: 1) a random organisation of juvenile communities (Snaydon 1987), or 2) a resulting community comprised of species less reliant on the resources provided by structural complexity (Gallagher and Doropoulos 2017).

These observations correlate with low abundance of juveniles in high-rugosity reefs recently affected by mass bleaching events (Dajka et al. 2019). In the case of survey reefs affected by a recent cyclone event, the observed interaction between juvenile abundance and rugosity was significant and negative (Figure 7). The putative mechanisms aforementioned can also be considered to explain the pattern observed in cyclone-affected reefs, perhaps with a more accentuated effect given the shorter time since the event (weeks, January 2019), compared to the bleaching events (2 years, 2017). In addition, cyclones also destabilise the reef substrate and produce a heterogenous distribution of rubble fragments across the reef (Highsmith et al. 1980, Harmelin-Vivien 1994). This rubble accumulation tends to show high structural complexity because of the intricate deposition of fragments from branching coral morphologies. Rubble fragments can decrease the abundance of early juvenile corals because rolling of rubble due to water movement can cause mortality via abrasion (Johns et al. 2018). In addition, rubble tends to accumulate in specific areas of the reef favoured by the local bathymetry and circulation patterns, smothering and covering settled corals (Harmelin-Vivien 1994).

5.3 Detailed assessments of reef fish assemblages

Sampling of reef fish assemblages during the 2019 expedition to the far northern GBR provided baseline information on species richness, abundance and community composition of fishes across a broad spatial extent. The selection of reefs, zoned open and closed to fishing at mid-shelf and outer-shelf positions along the far northern GBR, underpins future monitoring to identify changes (or stability) in fish diversity and abundance across reefs characterised by a variety of aspects. Cross-shelf position, nature of the substratum, cover of live hard coral, and depth were the most influential parameters influencing the richness, abundance, and community composition of fishes. Management zone influenced the abundance of some fishes on fixed site surveys; however, it had a lower influence on assemblages recorded from BRUVS. Given the prevailing knowledge of associations between reef fishes and their habitats in the GBR, it was not surprising that seven fish assemblages were distinguished on the basis of cross-shelf position, substratum type, hard coral cover and depth. The best model accounted for about 21% of the variation in the abundance of 290 species, which is similar to other regions using the same analyses (e.g. Cappo et al. 2011, Moore et al. 2017).

It has been well established that no-take marine protected areas can be an effective fisheries management tool, with higher abundance and biomass of exploited fish species in areas closed to fishing compared to nearby fished areas (Russ et al. 2008, Russ & Alcala 2011, Emslie et al. 2015) and evidence that juveniles produced in areas closed to fishing can replenish fished areas (Russ & Alcala 2011, Harrison et al. 2012). The comparisons from fixed site surveys between areas open and closed to fishing for the seven far northern reefs surveyed showed that the abundances of several fish families containing large-bodied species commonly targeted in both recreational and commercial fisheries, notably the groupers and coral trout (Serranidae) and the emperors (Lethrinidae), were higher at reefs closed to fishing than those that are open. This is consistent with a previous study on the far northern GBR which showed that there was greater biomass of target fish species in zones closed to fishing compared to fished reefs (Castro-Sanguino et al. 2017). Our survey results show that two families of smaller reef fishes, the damselfishes and the butterflyfishes, had slightly lower abundances on reefs closed to fishing than fished reefs, which may be due to top-down influences of the higher abundances of larger, predatory fish on reefs closed to fishing. It has been demonstrated on several inshore islands on the GBR that the abundances of coral trout prey species were lower on reefs closed to fishing compared to fished zones, due to the abundance of coral trout being 3-4 times higher on reefs closed to fishing (Graham et al. 2003).

In contrast to surveys of reef fishes on fixed sites, we found no significant effect of closure to fishing on overall richness and abundance, or the abundance of 115 genera of fish encountered on BRUVS. The effect of zone accounted for only about 1% of the variation explained by a constrained ordination of the abundance of these genera. This may be because the comparison was confounded by the fact that sites closed to fishing were correlated with deeper, sandier habitats bare of any epibenthos. In contrast, sites open to fishing were correlated with clearer waters, higher coral cover and higher topographic complexity. This favourable habitat axis was also correlated with higher abundances of the coral trout genus *Plectropomus* which is the major target of the GBR reef line fishery. Additionally, measures of relative abundance (MaxN) provided by BRUVS data are conservative and may not fully capture the true abundances of fishery targeted species. The differences in fish sampling methodology and results suggest further research is required and that these methods should be applied together to more fully understand the abundance and community structure of coral reef fishes across locations and depths.

While protection of reefs from fishing pressure can benefit abundance (Williamson et al. 2014, Emslie et al. 2015) and diversity (Mellin et al. 2016), fish communities are also shaped by reef position and habitat characteristics. Cross-shelf and along-shore position of reefs are well known to be an over-arching driver of fish community structure on the GBR (e.g. Williams and Hatcher 1983, Gust et al. 2001, Emslie et al. 2010, 2012, 2017, 2019, Cheal et al. 2012). Likewise, the location within a reefal landscape (e.g. top, crest, base, front, back, corner pressure-points, channels) is also a well-known governor of habitat structure and hence fish faunal composition. This was reflected in this study on the far northern GBR reefs. We found fish communities sampled with BRUVS reflected position on the continental shelf, with mid-shelf (Reef 13124 and Corbett Reef) and outer ribbon shelf-edge reefs (Sandbank#1 and Davie Reefs) in Princess Charlotte Bay, outer-shelf edge reefs in the Cape Grenville sector (Lagoon and Mantis Reefs), and the northernmost mid-shelf reef (Reef 11049) forming distinct assemblages that reflected their position. Results from the fixed site surveys yielded similar groupings. All outer-shelf fish communities were alike and clustered together, while mid-shelf reefs were distinct from the outer-shelf assemblages. There were small differences to the groupings observed in BRUVS analysis in that Corbett Reef was distinct from Reefs 11049 and 13124, which clustered together. Nonetheless, the overarching distinction between mid- and outer-shelf assemblages was evident in both datasets and highlights the importance of environmental gradients in physical conditions, and the availability of suitable habitat and niche space in shaping reef fish assemblages on the GBR.

Far northern GBR reefs contained abundant and diverse fish communities, however where there were differences in abundance and diversity, they reflected cross-shelf variation in environmental drivers (e.g. depth, exposure and water clarity). Despite differences in coral cover and benthic structure among the far northern reefs, species richness of reef fish was similar among reefs. However, when community structure was examined, differences among reefs were apparent, mainly between the outer-shelf reefs and the mid-shelf reefs, and among the three mid-shelf reefs. Such differences have been reported numerous times on the GBR (Williams and Hatcher 1983, Russ 1984, Gust et al. 2001, Hoey and Bellwood 2008, Cheal et al. 2012, Emslie et al. 2010, 2012, 2017, 2019) and generally reflect environmental gradients (e.g. wave action, turbidity, exposure) and differences in benthic/coral assemblages across the continental shelf, which provide different habitats and niche availability that are exploited by a different suite of species.

Small differences in distance from shore among the mid-shelf reefs could also strongly influence benthic and fish communities. The total abundance of fish increased from the southernmost reef to the northernmost reef, a trend that was driven by damselfish, as there were no north-south trends among sites in the abundances of other families. The abundance of butterflyfish, although similar among most of the reefs, was lowest at the northernmost reef, Reef 11049, compared to the other reefs. This is possibly due to this reef having the lowest coral cover among the seven reefs surveyed since the abundance and distribution of butterflyfishes is often reliant on the availability of live coral, particularly *Acropora* species (Cole et al. 2008).

The abundance and diversity of reef fishes in the far northern GBR recorded from fixed site surveys and BRUVS were similar to or slightly higher than other regions of the GBR. While there was substantial variability for some families (e.g. butterflyfishes, surgeonfishes, emperors and snappers) from fixed site surveys, there was a general tendency for total abundance and species richness to be higher in the north compared to the rest of the GBR. Such high variability in fish abundance and diversity may be partially explained by high variability in coral cover, resulting from inherent spatial patchiness in the abundance of corals. This is particularly true for groups like butterflyfishes (Chaetodontidae), which are heavily reliant on live coral for food. Other fishes which are not reliant on live coral for food, may be dependent on live coral for shelter and recruitment sites and may also co-vary with changing availability of live coral. While the patterns of abundance and diversity from both fixed site surveys and BRUVS were largely similar, one interesting difference to emerge was that BRUVS recorded the lowest abundance and diversity of fishes at Corbett Reef, which stands in contrast to the results from fixed site surveys for this reef. This disparity may reflect the high levels of non-reefal habitat recorded in BRUVS. Corbett Reef had a shallow reef slope with large tracts of sand at its base, which may have hindered the ability to place BRUVS in comparable coral dominated habitats thus resulting in lower fish abundance and diversity. This indicates that greater BRUVS sampling would be needed to refine estimates of diversity and abundance at this reef.

Univariate models of transformed richness and abundance from BRUVS data identified habitat as the strongest driver of fish assemblage structure. In particular, the percentage composition of calcareous reefal substrata (dead or alive), percentage composition of the substratum by sand, percentage cover of the field of view with no epibenthos, and reef identity were the most important determinates of fish abundance and diversity. As discussed above, the influence of management zoning was negligible when these covariates (and others) were accounted for. However, we identified “thresholds” in substratum composition and epibenthic cover above which richness and abundance increased or decreased above mean values. These relationships are not expected to be strictly linear because fish are known to be more diverse in patchy habitats offering edges, interstices, pressure-points for impinging currents, and sediment pockets. Such habitats will support a wide range of foraging modes and trophic groups from sand-sifting carnivores of micro- and macrobenthos, planktivores, herbivores and mobile predators.

In the case of damselfish, the abundance of algae generally correlated with an increase in the total number of damselfishes. The results agree with previous studies highlighting the importance of turf algae, and the associated epilithic microalgae, as a food resource for damselfish (Geoffrey et al. 2006, González-Rivero et al. 2017b).

The positive relationship between structural complexity and damselfish abundance supports a body of literature describing the importance of structural complexity for damselfish species (Harborne et al. 2012a, Harborne et al. 2012b, González-Rivero et al. 2017, Emslie et al. 2019), our results also differ from previous observations that show a significant change in behaviour and abundance of planktivorous damselfish species to loss in coral tissue from disturbance (Boström-Einarsson et al. 2018, Emslie et al. 2019). This difference may be explained by the aggregation of multiple species when measuring the relationship between damselfish abundance and rugosity in this study. It has been suggested that damselfish species exhibit differential social and ecological behaviours in relation to habitat complexity (González-Rivero et al. 2017, Emslie et al. 2019). Therefore, by grouping all damselfish species we may be masking the species-specific and versatile nature of the associations of damselfish to the habitat structure.

Analysis of indicator species for the assemblages defined by BRUVS surveys showed facultative and obligate corallivores were more numerous in the outer-shelf assemblages where higher calcareous substrata was observed, although corallivores were also important in a mid-shelf assemblage where coral cover was high. These results suggest that disturbances such as bleaching events have the capacity to affect the broader fish community through potential declines in corallivore abundance. However, a focus on corallivory (e.g. Cole et al. 2008) is not a true measure of the critical associations between some fish species and live coral cover. A large number of fishes from other trophic groups rely on live coral (Coker et al. 2014) for recruitment (e.g. carnivores including coral trout *Plectropomus* spp.; Wen et al. 2013), with several species of planktivorous damselfish (e.g. *Chromis* spp.) known to recruit successfully only into live coral thickets and colonies. Adults of these species can persist after a disturbance reduces live coral cover, but the population will decline through predation and natural mortality until coral regrowth allows successful replenishment of the population (Booth and Beretta, 2002). The variation in abundances of different coral trout species we observed, where *P. leopardus* and *P. laevis* were common to all locations while *P. maculatus* was most abundant on the mid-shelf, has previously been explained in the GBR by niche separation and depth use (Matley et al. 2016, 2017).

Charismatic megafauna in the form of reef sharks, Maori wrasse *Cheilinus undulatus* and sea turtles were encountered in BRUVS videos in relatively high numbers. This result matches preliminary data from the Global FinPrint shark surveys which indicate greater species richness and high abundance of sharks in the far northern GBR. Of particular note were the size and abundance of female grey reef sharks *Carcharhinus amblyrhynchos* at Mantis Reef**.** Some of these grey reef sharks, and a very large tiger shark *Galeocerdo cuvier*, appeared to be pregnant. The total absence of sea snakes from BRUVS footage despite the presence of favourable habitat was notable (see Udyawer et al. 2014 for models of abundance in the GBR).

5.4 Integrated monitoring

This study provided proof of concept that integrated, multidisciplinary monitoring of the GBR can be achieved using appropriate research platforms. Seven reefs were successfully surveyed using multiple methodologies (e.g. manta tow, fixed site surveys and BRUVS), although such extensive sampling means that the time taken to complete a given reef is longer than is needed for any one method in isolation. However, this should be weighed against the time and expense of going to the same sites repeatedly using separate methods. Using multiple methods allowed for some, albeit limited, inter-method comparisons.

For example, fish data collected using BRUVS did not detect any effect of management zoning on reef fish assemblage composition, including fishery targeted species like the coral trout (*Plectropomus* spp.). Conversely, higher abundance of several groups of fishes on reefs closed to fishing compared to those open to fishing was detected using the UVC method. Patterns revealed in BRUVS sampling were more related to habitat type than zoning and as such reflected the variable habitats sampled through BRUVS deployments which spanned a range of depths and habitat types. This difference in the habitats sampled, and specifically the inclusion of non-coral habitats that are not preferred by coral trout, could explain the differences in zoning results from the two methods. In contrast, BRUVS were better at capturing the presence of large predators such as sharks. Thus, each of these methods provides benefits and when combined can provide a greater understanding of the diversity of fish communities on GBR reefs. Additionally, while both techniques captured a similar number of species, they sampled different parts of the fish assemblage. Therefore, these two methods should be considered complementary and one should not be used as a replacement for the other. Future work should carefully consider the amount of sampling conducted at reefs and what will be required to fully capture dynamics in fish communities. For example, species accumulation curves from BRUVS indicated more sampling would be required to better describe communities within reefs. The current sampling was based on initial plans for an integrated GBR monitoring program (i.e., RIMReP) where 20 BRUVS deployments per reef have been recommended. Results indicate this is not enough sampling to capture the entire species richness in these high biodiversity reefs. With latent diversity evident in the data, rarer species might be observed one year and not the next but does not indicate absence. BRUVS data can, however still be used to investigate trends in species richness and abundance (stability across years, although turnover may occur at the species level), community analyses (to look at genera or species by year and with habitat), and by trophic groups (to detect changes over time and with habitat by function). Thus, future sampling should consider how to apply fish survey methods and how much sampling can realistically be achieved. However, data have not been integrated across methods to determine if the combination of transect and BRUVS data can produce a more reliable representation of the community.

While the present study has proven that collecting multiple data streams at the same time is logistically feasible, integrating data from disparate sources has its own challenges. For example, BRUVS data produce estimates of relative abundance that are likely conservative due to the possibility of re-counting fish swimming in and out of the field of view (Cappo 2003), while fixed site surveys indicate absolute abundance. Thus, comparisons of these two data streams require conversion to a common measure of relative abundance. Preliminary analyses directly comparing BRUVS and UVC techniques and data streams is currently underway from data collected on the central GBR (LTMP unpublished data). Another advantage of employing multiple methods simultaneously at a site is the capacity for integration of data streams. For example, data collected from BRUVS can be matched to information collected on benthic condition at the same time from fixed site surveys. Previously, matching BRUVS fish data to habitat variables has required the use of qualitative estimates of benthic condition obtained from the BRUVS field of view. This limits the context and scale of information to the field of view, while integration with transect and manta tow data provides a broader understanding of reef condition to provide context for fish data. By integrating multiple techniques, such information can be paired with quantitative estimates of benthic condition from fixed site surveys, enabling a more rigorous investigation of habitat drivers of fish assemblage structure.

Integration of other remote technologies, such as using underwater vehicles, will also be necessary in future if reefs close to the coast, which pose a high risk of crocodile encounters, are to be surveyed. The loss of these reefs from the sampling design may have resulted in an over-estimate in the region-wide status of coral reefs, as many of the inshore reefs were severely impacted by the 2015/16 and 2016/17 bleaching events. The validation and operationalisation of such technologies is advancing rapidly (see e.g. González-Rivero et al. 2018) and should be considered in future monitoring frameworks.

5.5 Engagement of Traditional Owners

AIMS is committed to forming relationships and building partnerships with Aboriginal and Torres Strait Islanders in the land and sea areas in which we work, as evidenced by our Indigenous Partnerships team and our inclusion of Traditional Owners in the *AIMS Strategy 2025* (EC3). Before the current project commenced, AIMS sought to involve Traditional Owners from the far northern GBR where possible and to inform all groups about the work that was planned. All communities were notified, and a poster was placed in the communities (Figure S4). With only a short lead time before the project commenced in January, and the timing of public holidays, we were only able to include Mr Trinity Georgetown on the field trip, who was a Lama Lama Traditional Owner and Ranger, nominated by the chairperson of the Yintjingga Aboriginal Corporation (YAC). Mr Georgetown was actively involved in the field trip, driving tenders, acting as dive attendant, learning new techniques for monitoring reefs and assisting with BRUVS deployment. Following on from the field work, AIMS scientists have met with community groups in Cooktown to discuss the results from the surveys in the far northern GBR. Many Traditional Owners from Cape York were concerned about the status of reefs in their sea country, and very much appreciated the information provided to them about how their country had fared, particularly following the coral bleaching of 2015/16 and 2016/17. There are additional events planned, such as information and discussion forums throughout the Cape York region.

Figure 30: Mr Trinity Georgetown, a Lama Lama Traditional Owner and Ranger working with AIMS staff to deploy BRUVS in the far northern GBR.

6 CONCLUSIONS

In conclusion, surveys conducted during January 2019 and funded by GBRF have revealed a mixed bill of health for the far northern GBR. Some reefs that were severely impacted by 2015/16 and 2016/17 bleaching had low hard coral cover and showed no signs of recovery. Other reefs were less affected by the mass bleaching event and retained relatively abundant coral populations, with coral cover between 10 and 50%. Most surveyed reefs also had moderate levels of coral juveniles (4.6 to 13 juveniles m^{-2}). The results presented here show that there are still intact adult coral populations on some reefs of the far north, however this knowledge should be tempered by reports of a reduction in coral reproduction across much of this region (Hughes et al. 2019). Whether reefs of the far northern GBR can recover back to levels of hard coral cover recorded prior to the 2016/17 bleaching event is contingent on a disturbance-free period of a decade or longer, and sufficient adult brood stock to produce enough coral larvae to re-seed depleted coral communities. However, it is likely that recovery will be impaired to some degree, given the reduction of brood stock and physiological constraints imposed by extended periods of heat stress on remnant coral populations, as energy is diverted away from reproduction to tissue repair (Anthony et al. 2009, Randall and Smantz 2009, Heyward and Negri 2010). The net effect of reduced brood stock and impaired physiology is reduced reproductive output which results in much slower recovery in the years following thermal stress (Osborne et al. 2017).

Physiological constraints notwithstanding, the probability of the far northern GBR undergoing a disturbance-free period long enough to ensure full recovery is unlikely, as recent analyses from the LTMP demonstrate that the frequency of severe disturbances such as coral bleaching and cyclones has increased substantially on the far northern GBR since the mid-1980s (Emslie et al. submitted). Indeed, there was evidence of ongoing disturbances recorded during this study, such as physical damage caused by Cyclone Penny. Reef fish assemblages were abundant and diverse, and there was some evidence to suggest that the levels of abundance and species richness were slightly above the GBR average. Large numbers of sharks and turtles were observed, particularly during BRUVS surveys, suggesting that these communities are intact and healthy. Additionally, higher abundance of fishery targeted fishes such as coral trout were detected on reefs closed to fishing compared to areas open to fishing, demonstrating that management zoning is effective even in the remote far north.

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8 REFERENCES

Allen GR, Swainston R. (1988) The marine fishes of north-western Australia. A field guide for anglers and divers. Western Australian Museum, Perth, Western Australia. 201 pp.

Anderson MJ. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.

Anthony KR, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R. (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Functional Ecology* 23: 539-550.

Babcock R, Smith L. (2002) Effects of sedimentation on coral settlement and survivorship. Pages 245-248 in *Proceedings of the Ninth International Coral Reef Symposium*. Bali, 23-27 October 2000. Citeseer.

Benthuysen JA, Oliver EC, Feng M, Marshall AG. (2018) Extreme marine warming across tropical Australia during austral summer 2015–2016. *J Geophysical Research: Oceans*, 123(2): 1301-1326.

Booth DJ, Beretta GA. (2002) Changes in a fish assemblage after a coral bleaching event. *Marine Ecology Progress Series* r 245:205-212.

Boström-Einarsson, L, Bonin MC, Munday PL, Jones GP. (2018) Loss of live coral compromises predator-avoidance behaviour in coral reef damselfish. *Scientific Reports* 8:7795.

Breiman L. (2001) Random Forests. *Machine Learning* 45: 5-32.

Burns JHR, Delparte D, Gates RD, Takabayashi M. (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ* 3:e1077.

Cappo M, Harvey E, Malcolm H, Speare P. (2003). Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas. Aquatic Protected Areas - what works best and how do we know? In World Congress on Aquatic Protected Areas proceedings (Beumer, J., Grant, A. & DC, S., eds.), pp. 455-464. Cairns, Australia, August 2002: Australian Society of Fish Biology.

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology* 302: 123-152.

Cappo M, De'ath G, Speare P. (2007) Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series* 350: 209-221.

Cappo M, Stowar M, Stieglitz T, Lawrey E, Johansson C, Macneil A. (2012) Measuring and communicating effects of MPAs on deep "shoal" fisheries. In: Proceedings of the 12th International Coral Reef Symposium, pp. 1-5. From: 12th International Coral Reef Symposium, 9-13 July 2012, Cairns, QLD, Australia.

Cappo M, Stowar M, Syms C, Johansson C, Cooper T. (2011) Fish-habitat associations in the region offshore from James Price Point – a rapid assessment using Baited Remote Underwater Video Stations (BRUVS). Journal of the Royal Society of Western Australia, 94. 303-321. Kimberley Special Issue.

Castro-Sanguino C, Bozec YM, Dempsey A, Samaniego BR, Lubarsky K, Andrews S, Komyakova V, Ortiz JC, Robbins WD, Renaud PG, Mumby PJ. (2017) Detecting conservation benefits of marine reserves on remote reefs of the northern GBR. *PLoS One* 12:e0186146

Ceccarelli, DM, Richards ZT, Pratchett MS, Cvitanovic C. (2011) Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. *Marine and Freshwater Research* 62:1214-1220.

Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R. (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93-102.

Cheal AJ, Emslie MJ. (2018) Synopsis of current coral reef monitoring on the Great Barrier Reef. Supplementary Report S3 to Final Report of the Coral Reef Expert Group. Report provided to GBRMPA.

Cheal A, Emslie M, Miller I, Sweatman H. (2012) The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology* 159(5):1143-54.

Coker DJ, Wilson SK, Pratchett MS. (2014) Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries* 24:89-126.

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9:286-307.

Courtial L, Roberty S, Shick J, Houlbrèque F and Ferrier-Pagès C (2017), Interactive effects of ultraviolet radiation and thermal stress on two reef-building corals. *Limnology and. Oceanography* 62: 1000-1013.

Dajka J-C, Wilson SK, Robinson JPW, Chong-Seng KM, Harris A, Graham NAJ. (2019) Uncovering drivers of juvenile coral density following mass bleaching. *Coral Reefs*. https://doi.org/10.1007/s00338-019-01785-w

De'ath G, Fabricius KE. (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-3192.

De'ath G. (2002) Multivariate regression trees: A new technique for modeling species-environment relationships. *Ecology* 83:1105-1117.

De'ath G. (2007) Boosted trees for ecological modeling and prediction. *Ecology* 88:243-251.

De'ath G, Fabricius K, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 17995–17999.

Doropoulos C, Roff G, Bozec YM, Zupan M, Werminghausen J, Mumby PJ. (2016) Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. *Ecological Monographs* 86:20-44.

Dufrêne M, Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366

Elith J, Leathwick JR, Hastie T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802-813.

Emslie MJ, Pratchett MS, Cheal AJ, Osborne K. (2010) Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs* 29(3):705-15.

Emslie MJ, Logan M, Ceccarelli DM, Cheal AJ, Hoey AS, Miller I, Sweatman HP. (2012) Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology* 159(6):1293-304.

Emslie MJ, Logan M, Williamson DH, Ayling AM, MacNeil MA, Ceccarelli D, Cheal AJ, Evans RD, Johns KA, Jonker MJ, Miller IR, Osborne K, Russ GR, Sweatman HPA. (2015) Expectations and Outcomes of Reserve Network Performance following Re-zoning of the Great Barrier Reef Marine Park. Current Biology 25:983-992.

Emslie MJ, Cheal AJ, Logan M. (2017) The distribution and abundance of reef-associated predatory fishes on the Great Barrier Reef. *Coral Reefs*. 36(3):829-46.

Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HP (2018) Reef fish communities are spooked by scuba surveys and may take hours to recover. PeerJ. 2018 May 24;6:e4886.

Emslie MJ, Cheal AJ (2018) Visual census of reef fish. Australian Institute of Marine Science, Townsville, Australia.

Emslie MJ, Logan M, Cheal AJ. (2019) The Distribution of Planktivorous Damselfishes (Pomacentridae) on the Great Barrier Reef and the Relative Influences of Habitat and Predation. *Diversity* 11:33.

Emslie MJ, Logan M, Bray P, Cheal AJ, Hughes TP, Johns KA, Jonker MJ, Kerry J, Mellin C, Miller IR, Osborne K, Puotinen M, Sweatman HP. (Submitted) Increasing disturbance frequency undermines coral reef recovery. *Proceedings of the National Academy of Science USA.*

Fabricius KE, De'Ath G, Puotinen ML, Done T, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography* 53: 690-704

Fernandes L, Day J, Kerrigan B, Breen D, De'ath G, Mapstone B, Coles R, Done T, Marsh H, Poiner I, Ward T (2009) A process to design a network of marine no-take areas: Lessons from the Great Barrier Reef. *Ocean & Coastal Management*. 8:439-47.

Ferrari R, McKinnon D, He H, Smith NR, Corke P, González-Rivero M, Mumby PJ, Upcroft B. (2016) Quantifying Multiscale Habitat Structural Complexity: A Cost-Effective Framework for Underwater 3D Modelling. *Remote Sensing* 8: 113.

Figueira W, Ferrari R, Weatherby E, Porter A, Hawes S, Byrne M. (2015) Accuracy and precision of habitat structural complexity metrics derived from underwater photogrammetry. *Remote Sensing* 7:16883-16900.

Figueiredo J, Baird AH, Connolly SR. (2013) Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. *Ecology* 94:650-659.

Friedman A, Pizarro O, Williams SB, Johnson-Roberson M. (2012) Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions. *Plos One* 7:e50440.

Fukunaga A, Burns JH, Craig BK, Kosaki RK. (2019) Integrating Three-Dimensional Benthic Habitat Characterization Techniques into Ecological Monitoring of Coral Reefs. *Journal of Marine Science and Engineering* 7:27.

Gallagher C, Doropoulos C. (2017) Spatial refugia mediate juvenile coral survival during coral–predator interactions. *Coral Reefs* 36:51-61.

Geoffrey PJ, Lara S, Laurence J. M. (2006) Resource use and impact of three herbivorous damselfishes on coral reef communities. *Marine Ecology Progress Series* 328:215-224.

Gilmour, J. (1999) Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* 135:451-462.

Gleason DF, Edmunds PJ, Gates RD. (2006) Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral Porites astreoides. *Marine Biology* 148:503-512.

González-Rivero M, Rodriguez-Ramirez A, Tonk L, Puotinen M, Heron S, Skirving W, Kennedy E, Ridgeway T, Hoegh-Guldberg O. (2017a) The effect of cumulative stress on reef slope coral communities in the far northern and northern Great Barrier Reef: 2012 to 2016. Report to the Department of Environment and Energy.

González-Rivero M, Harborne AR, Herrera-Reveles A, Bozec YM, Rogers A, Friedman A, Ganase A, Hoegh-Guldberg O. (2017b) Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports* 7:13965.

González-Rivero, M., C. Roelfsema, S. Lopez-Marcano, C. Castro-Sanguino, T. Bridge, R. Babcock. (2018) Novel technologies in coral reef monitoring. Supplementary Report S6 to Final Report of the Reef 2050 Integrated Monitoring and Reporting Program (RIMReP) Coral Reef Expert Group. Report provided to GBRMPA.

Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation* 30:200-208.

Graham NAJ, Nash KL. (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315-326.

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK. (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518(7537):94.

Great Barrier Reef Marine Park Authority 2017, Final report: (2016) coral bleaching event on the Great Barrier Reef, GBRMPA, Townsville. http://elibrary.gbrmpa.gov.au/jspui/bitstream/11017/3206/1/Final-report-2016-coral-bleaching-GBR.pdf

Gust N, Choat JH, McCormick MI. (2001) Spatial variability in reef fish distribution, abundance, size and biomass: a multi scale analysis. *Marine Ecology Progress Series* 214:237-51.

Harborne AR, Jelks HL, Smith-Vaniz WF, Rocha LA. (2012a) Abiotic and biotic controls of cryptobenthic fish assemblages across a Caribbean seascape. *Coral Reefs* 31:977-990.

Harborne AR, Mumby PJ, Ferrari R. (2012b) The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes* 94:431-442.

Harmelin-Vivien ML. (1994) The effects of storms and cyclones on coral reefs: a review. *Journal of Coastal Research* 211-231.

Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, Van Herwerden L, Planes S, Srinivasan M, Berumen ML. (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology*. 11:1023-8.

Heyward AJ, Negri AP. (2010) Plasticity of larval pre-competency in response to temperature: Observations on multiple broadcast spawning coral species. *Coral Reefs* 29: 631–636.

Highsmith RC, Riggs AC, D'Antonio CM. (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* 3:322-9.

Hoey AS, Bellwood DR. (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27(1):37-47.

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, et al. (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543: 373.

Hughes TP, Kerry JT, Simpson T. (2018a) Large-scale bleaching of corals on the Great Barrier Reef. *Ecology* 99:501-501.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears R, Pratchett MS, Skirving WJ, Stella JS, Torda G. (2018b) Global warming transforms coral reef assemblages. *Nature* 556: 492.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, Hill T, Hoey AH, Hoogenboom MO, Jacobson M, Kerswell A, Madin JS, Mieog A, Paley AS, Pratchett MS, Torda G, Woods RM. (2019) Global warming impairs stock-recruitment dynamics of corals. *Nature* 7752:387 https://doi.org/10.1038/s41586-019-1081-y

Johns KA, Emslie MJ, Hoey AS, Osborne K, Jonker MJ, Cheal AJ. (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. *Ecosphere* 9:e02349.

Johnson GB, Taylor BM, Robbins WD, Franklin EC, Toonen R, Bowen B, Choat JH. (2019) Diversity and Structure of Parrotfish Assemblages across the Northern Great Barrier Reef. *Diversity* 11(1):14.

Jonker M, Johns K, Osborne K. (2008) Surveys of benthic reef communities using underwater digital photography and counts of juvenile corals. Long-term Monitoring of the Great Barrier Reef. Standard Operational Procedure Number 10. 2008. Australian Institute of Marine Science, Townsville, Australia.

Jonker MJ, Thompson AA, Menedez P, Osborne K. (2019) Cross-shelf variation among Juvenile and Adult Coral Assemblages on Australia's Great Barrier Reef. *Diversity* 11:85 doi.org/10.3390/d11060085

Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E. (2018) Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (Platygyra daedalea) of the Arabian/Persian Gulf. *Molecular Ecology* 27(24):5180-5194.

Klumpp DD, McKinnon D. A. (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Marine Ecology Progress Series* 86:77-89.

Klumpp DW, Polunin NVC. (1989) Partitioning among grazers of food resources within damselfish territories on a coral reef. *Journal of Experimental Marine Biology and Ecology* 125:145-169.

Legendre P, Anderson MJ. (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*. 69(1):1-24.

Legendre P, Gallagher ED. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.

Madin JS, Connolly SR. (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444:477-480.

Magel JMT, Burns JHR, Gates RD, Baum JK. (2019) Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Scientific Reports* 9:2512.

Matley JK, Tobin AJ, Lédée EJI, Heupel MR, Simpfendorfer CA. (2016) Contrasting patterns of vertical and horizontal space use of two exploited and sympatric coral reef fish. *Marine Biology* 163:253.

Matley JK, Tobin AJ, Simpfendorfer CA, Fisk AT, Heupel MR. (2017) Trophic niche and spatio-temporal changes in the feeding ecology of two sympatric species of coral trout (Plectropomus leopardus and P. laevis). *Marine Ecology Progress Series* 563:197-210.

Mellin C, Aaron MacNeil M, Cheal AJ, Emslie MJ, Julian Caley M (2016) Marine protected areas increase resilience among coral reef communities. *Ecology Letters* 19:629-637.

Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH, Fordham DA. (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. *Global Change Biology* 22.

Miller IR, Jonker M, Coleman G (2009) Crown-of-thorns seastars and coral surveys using the manta tow and SCUBA Search techniques. Long-term Monitoring of the Great Barrier Reef Standard Operational Procedure Number 9, Edition 3. Australian Institute of Marine Science, Townsville.

Miller IR, Logan M, Johns KA, Jonker MJ, Osborne K, Sweatman HPA (2013) Determining background levels and defining outbreaks of crustose coralline algae disease on the Great Barrier Reef. Marine and Freshwater Research 64(11): 1022-1028.

Moore C, Cappo M, Radford B, Heyward A. (2017). Submerged oceanic shoals of north Western Australia are a major reservoir of marine biodiversity. *Coral Reefs* 36(3):719-734.

Mumby PJ, Steneck RS, Adjeroud M, Arnold SN. (2016) High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. *Oikos* 125:644-655.

Nakagawa S, Schielzeth H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133-142.

Nordborg FM, Flores F, Brinkman DL, Agustí S, Negri AP. (2018) Phototoxic effects of two common marine fuels on the settlement success of the coral Acropora tenuis. *Scientific Reports* 8:8635.

Osborne K, Thompson AA, Cheal AJ, Emslie MJ, Johns KA, Jonker MJ, Logan M, Miller IR, Sweatman HP. (2017) Delayed coral recovery in a warming ocean. *Global Change Biology* 9:3869-81.

Puotinen M, Maynard JA, Beeden R, Radford B, Williams GJ. (2016) A robust operational model for predicting where tropical cyclone waves damage coral reefs. *Scientific Reports* 6:26009.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/doc/manuals/refman.pdf.

Randall CJ, Szmant AM. (2009) Elevated temperature affects development, survivorship, and settlement of the elkhorn coral, Acropora palmata (Lamarck 1816). *Biological Bulletin* 217: 269–282.

Remondino F, Fraser C. (2006) Digital camera calibration methods: considerations and comparisons. *International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences* 36:266-272.

Ridgeway G. (2007) gbm: Generalized Boosted Regression Models. URL: http://wwwi-pensiericom/gregr/gbmshtml

Risk, MJ. (1972) Fish diversity on a coral reef in the Virgin Islands. Smithsonian Institution.

Russ G. (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series* 20(1):23-34.

Russ GR, Alcala AC (2011) Enhanced biodiversity beyond marine reserve boundaries: the cup spilleth over. *Ecological Applications* 21:241-250.

Russ GR, Cheal AJ, Dolman AM, Emslie MJ, Evans RD, Miller I, Sweatman H, Williamson, DH (2008) Rapid increase in fish numbers follows creation of world’s largest marine reserve network. *Current Biology*, 18:514-515.

Schaffelke B, Anthony K, Babcock R, Bridge T, Carlos E, Diaz-Pulido G, Gonzalez-Rivero M, Gooch M, Hoey A, Horne D, Kane K, McKenzie C, Merida F, Molloy F, Moon S, Mumby P, Ortiz JC, Pears R, Phinn S, Ridgway T, Roelfsema C, Singleton G, Thompson A. (2018) Monitoring coral reefs within the Reef 2050 Integrated Monitoring and Reporting Program. Final report of the Coral Reef Expert Group. Report provided to GBRMPA.

Schobernd ZH, Bacheler NM, Conn PB. (2014) Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 71(3):464-471.

Snaydon R. (1987) Population responses to environmental disturbance. pp15-31. Disturbance in Grasslands. Springer.

Steinberg C. (2007) Impacts of climate change on the physical oceanography of the Great Barrier Reef, pp 51-74. In Johnson JE and Marshall PA [eds.], Climate Change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority & Australian Greenhouse Office. Available at http://www.gbrmpa.gov.au/outlook-for-the-reef/climate-change/how-climate-change-can-affect-the-reef/great-barrier-reef-vulnerability-assessment (accessed 15 Oct, 2017).

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ. (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* 560:92–96.

Thompson A, Costello P, Davidson J, Logan M, Coleman G, Gunn K, Schaffelke B. (2016) Marine Monitoring Program. Annual Report for inshore coral reef monitoring: 2014 to 2015. Report for the Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville.133 pp.

Udyawer V, Cappo M, Simpfendorfer CA, Heupel MR Lukoschek V. (2014) Distribution of sea snakes in the Great Barrier Reef Marine Park: observations from 10 yrs of baited remote underwater video station (BRUVS) sampling. *Coral Reefs* 33:777-791.

Wen CKC, Pratchett MS, Almany GR, Jones GP. (2013) Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. *Coral Reefs* 32:389-398.

Wickham H. (2009) ggplot2: Elegant graphics for data analysis. Springer, New York, USA.

Williams DM, Hatcher AI. (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer-shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* 10(3):239-50.

Williams ID, Polunin NVC, Hendrick VJ. (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187-196.

Williamson DH, Ceccarelli DM, Evans RD, Jones GP, Russ GR (2014) Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. *Ecology and Evolution* 4:337-354.

Willis TJ, Millar RB, Babcock RC. (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* 198: 249-260.

Wolanski E. (1994). Physical oceanographic processes of the Great Barrier Reef. Florida: CRC Press.

Yearsley GK, Last PR, Morris GB. (1997) Codes for Australian Aquatic Biota (CAAB): An upgraded and expanded species coding system for Australian fisheries databases, CSIRO, Australia, Hobart, Tasmania.

9 APPENDICIES

Table S1: List of fish species for underwater visual census from fixed site surveys.

Family	Species
Acanthuridae	*Acanthurus albipectoralis*
Acanthuridae	*Acanthurus auranticavus*
Acanthuridae	*Acanthurus bariene*
Acanthuridae	*Acanthurus blochii*
Acanthuridae	*Acanthurus dussumieri*
Acanthuridae	*Acanthurus grammoptilus*
Acanthuridae	*Acanthurus lineatus*
Acanthuridae	*Acanthurus maculiceps*
Acanthuridae	*Acanthurus mata*
Acanthuridae	*Acanthurus nigricans*
Acanthuridae	*Acanthurus nigricauda*
Acanthuridae	*Acanthurus nigrofuscus*
Acanthuridae	*Acanthurus nigroris*
Acanthuridae	*Acanthurus olivaceus*
Acanthuridae	*Acanthurus pyroferus*
Acanthuridae	*Acanthurus thompsoni*
Acanthuridae	*Acanthurus triostegus*
Acanthuridae	*Acanthurus xanthopterus*
Acanthuridae	*Ctenochaetus spp*
Acanthuridae	*Naso lituratus*
Acanthuridae	*Naso tuberosus*
Acanthuridae	*Naso unicornis*
Acanthuridae	*Paracanthurus hepatus*
Acanthuridae	*Zebrasoma scopas*
Acanthuridae	*Zebrasoma veliferum*
Chaetodontidae	*Chaetodon aureofasciatus*
Chaetodontidae	*Chaetodon auriga*
Chaetodontidae	*Chaetodon baronessa*
Chaetodontidae	*Chaetodon bennetti*
Chaetodontidae	*Chaetodon citrinellus*
Chaetodontidae	*Chaetodon ephippium*
Chaetodontidae	*Chaetodon flavirostris*
Chaetodontidae	*Chaetodon kleinii*
Chaetodontidae	*Chaetodon lineolatus*
Chaetodontidae	*Chaetodon lunula*
Chaetodontidae	*Chaetodon melannotus*
Chaetodontidae	*Chaetodon mertensii*
Chaetodontidae	*Chaetodon meyeri*
Chaetodontidae	*Chaetodon ornatissimus*
Chaetodontidae	*Chaetodon oxycephalus*

Family	Species
Chaetodontidae	*Chaetodon pelewensis*
Chaetodontidae	*Chaetodon plebeius*
Chaetodontidae	*Chaetodon punctatofasciatus*
Chaetodontidae	*Chaetodon rafflesii*
Chaetodontidae	*Chaetodon rainfordi*
Chaetodontidae	*Chaetodon reticulatus*
Chaetodontidae	*Chaetodon speculum*
Chaetodontidae	*Chaetodon trifascialis*
Chaetodontidae	*Chaetodon trifasciatus*
Chaetodontidae	*Chaetodon ulietensis*
Chaetodontidae	*Chaetodon unimaculatus*
Chaetodontidae	*Chaetodon vagabundus*
Chaetodontidae	*Chelmon rostratus*
Chaetodontidae	*Forcipiger flavissimus*
Chaetodontidae	*Forcipiger longirostris*
Chaetodontidae	*Hemitaurichthys polylepis*
Labridae	*Cheilinus fasciatus*
Labridae	*Cheilinus undulatus*
Labridae	*Choerodon fasciatus*
Labridae	*Coris gaimard*
Labridae	*Epibulus insidiator*
Labridae	*Gomphosus varius*
Labridae	*Halichoeres hortulanus*
Labridae	*Hemigymnus fasciatus*
Labridae	*Hemigymnus melapterus*
Lethrinidae	*Lethrinus atkinsoni*
Labridae tribe Scarinae	*Bolbometopon muricatum*
Labridae tribe Scarinae	*Calotomus carolinus*
Labridae tribe Scarinae	*Cetoscarus ocellatus*
Labridae tribe Scarinae	*Chlorurus bleekeri*
Labridae tribe Scarinae	*Chlorurus japanensis*
Labridae tribe Scarinae	*Chlorurus microrhinos*
Labridae tribe Scarinae	*Chlorurus sordidus*
Labridae tribe Scarinae	*Hipposcarus longiceps*
Labridae tribe Scarinae	*Scarus altipinnis*
Labridae tribe Scarinae	*Scarus chameleon*
Labridae tribe Scarinae	*Scarus dimidiatus*
Labridae tribe Scarinae	*Scarus flavipectoralis*
Labridae tribe Scarinae	*Scarus forsteni*
Labridae tribe Scarinae	*Scarus frenatus*
Labridae tribe Scarinae	*Scarus ghobban*
Labridae tribe Scarinae	*Scarus globiceps*
Labridae tribe Scarinae	*Scarus longipinnis*

Family	Species
Labridae tribe Scarinae	*Scarus niger*
Labridae tribe Scarinae	*Scarus oviceps*
Labridae tribe Scarinae	*Scarus psittacus*
Labridae tribe Scarinae	*Scarus rivulatus*
Labridae tribe Scarinae	*Scarus rubroviolaceus*
Labridae tribe Scarinae	*Scarus schlegeli*
Labridae tribe Scarinae	*Scarus spinus*
Lethrinidae	*Lethrinus erythracanthus*
Lethrinidae	*Lethrinus harak*
Lethrinidae	*Lethrinus laticaudis*
Lethrinidae	*Lethrinus lentjan*
Lethrinidae	*Lethrinus miniatus*
Lethrinidae	*Lethrinus nebulosus*
Lethrinidae	*Lethrinus obsoletus*
Lethrinidae	*Lethrinus olivaceus*
Lethrinidae	*Lethrinus ornatus*
Lethrinidae	*Lethrinus rubrioperculatus*
Lethrinidae	*Lethrinus semicinctus*
Lethrinidae	*Lethrinus xanthochilus*
Lethrinidae	*Monotaxis grandoculis*
Lutjanidae	*Lutjanus adetii*
Lutjanidae	*Lutjanus argentimaculatus*
Lutjanidae	*Lutjanus biguttatus*
Lutjanidae	*Lutjanus bohar*
Lutjanidae	*Lutjanus boutton*
Lutjanidae	*Lutjanus carponotatus*
Lutjanidae	*Lutjanus fulviflamma*
Lutjanidae	*Lutjanus fulvus*
Lutjanidae	*Lutjanus gibbus*
Lutjanidae	*Lutjanus kasmira*
Lutjanidae	*Lutjanus lemniscatus*
Lutjanidae	*Lutjanus lutjanus*
Lutjanidae	*Lutjanus monostigma*
Lutjanidae	*Lutjanus quinquelineatus*
Lutjanidae	*Lutjanus rivulatus*
Lutjanidae	*Lutjanus rufolineatus*
Lutjanidae	*Lutjanus russellii*
Lutjanidae	*Lutjanus sebae*
Lutjanidae	*Lutjanus semicinctus*
Lutjanidae	*Lutjanus vitta*
Lutjanidae	*Macolor spp*
Pomacentridae	*Acanthochromis polyacanthus*
Pomacentridae	*Amblyglyphidodon aureus*

Family	Species
Pomacentridae	*Amblyglyphidodon curacao*
Pomacentridae	*Amblyglyphidodon leucogaster*
Pomacentridae	*Amphiprion akindynos*
Pomacentridae	*Amphiprion chrysopterus*
Pomacentridae	*Amphiprion clarkii*
Pomacentridae	*Amphiprion melanopus*
Pomacentridae	*Amphiprion percula*
Pomacentridae	*Amphiprion perideraion*
Pomacentridae	*Cheiloprion labiatus*
Pomacentridae	*Chromis acares*
Pomacentridae	*Chromis agilis*
Pomacentridae	*Chromis amboinensis*
Pomacentridae	*Chromis atripectoralis*
Pomacentridae	*Chromis atripes*
Pomacentridae	*Chromis chrysura*
Pomacentridae	*Chromis flavomaculata*
Pomacentridae	*Chromis iomelas*
Pomacentridae	*Chromis lepidolepis*
Pomacentridae	*Chromis lineata*
Pomacentridae	*Chromis margaritifer*
Pomacentridae	*Chromis nitida*
Pomacentridae	*Chromis retrofasciata*
Pomacentridae	*Chromis ternatensis*
Pomacentridae	*Chromis vanderbilti*
Pomacentridae	*Chromis viridis*
Pomacentridae	*Chromis weberi*
Pomacentridae	*Chromis xanthochira*
Pomacentridae	*Chromis xanthura*
Pomacentridae	*Chrysiptera biocellata*
Pomacentridae	*Chrysiptera flavipinnis*
Pomacentridae	*Chrysiptera rex*
Pomacentridae	*Chrysiptera rollandi*
Pomacentridae	*Chrysiptera talboti*
Pomacentridae	*Dascyllus aruanus*
Pomacentridae	*Dascyllus melanurus*
Pomacentridae	*Dascyllus reticulatus*
Pomacentridae	*Dascyllus trimaculatus*
Pomacentridae	*Dischistodus melanotus*
Pomacentridae	*Dischistodus perspicillatus*
Pomacentridae	*Dischistodus prosopotaenia*
Pomacentridae	*Dischistodus pseudochrysopoecilus*
Pomacentridae	*Hemiglyphidodon plagiometopon*
Pomacentridae	*Neoglyphidodon melas*

Family	Species
Pomacentridae	*Neoglyphidodon nigroris*
Pomacentridae	*Neoglyphidodon polyacanthus*
Pomacentridae	*Neopomacentrus azysron*
Pomacentridae	*Neopomacentrus bankieri*
Pomacentridae	*Neopomacentrus cyanomos*
Pomacentridae	*Plectroglyphidodon dickii*
Pomacentridae	*Plectroglyphidodon johnstonianus*
Pomacentridae	*Plectroglyphidodon lacrymatus*
Pomacentridae	*Pomacentrus adelus*
Pomacentridae	*Pomacentrus amboinensis*
Pomacentridae	*Pomacentrus australis*
Pomacentridae	*Pomacentrus bankanensis*
Pomacentridae	*Pomacentrus brachialis*
Pomacentridae	*Pomacentrus chrysurus*
Pomacentridae	*Pomacentrus coelestis*
Pomacentridae	*Pomacentrus grammorhynchus*
Pomacentridae	*Pomacentrus imitator*
Pomacentridae	*Pomacentrus lepidogenys*
Pomacentridae	*Pomacentrus moluccensis*
Pomacentridae	*Pomacentrus nagasakiensis*
Pomacentridae	*Pomacentrus nigromarginatus*
Pomacentridae	*Pomacentrus philippinus*
Pomacentridae	*Pomacentrus reidi*
Pomacentridae	*Pomacentrus tripunctatus*
Pomacentridae	*Pomacentrus vaiuli*
Pomacentridae	*Pomacentrus wardi*
Pomacentridae	*Pomachromis richardsoni*
Pomacentridae	*Premnas biaculeatus*
Pomacentridae	*Stegastes apicalis*
Pomacentridae	*Stegastes fasciolatus*
Pomacentridae	*Stegastes gascoynei*
Pomacentridae	*Stegastes nigricans*
Serranidae	*Aethaloperca rogaa*
Serranidae	*Anyperodon leucogrammicus*
Serranidae	*Cephalopholis argus*
Serranidae	*Cephalopholis boenak*
Serranidae	*Cephalopholis cyanostigma*
Serranidae	*Cephalopholis microprion*
Serranidae	*Cephalopholis miniata*
Serranidae	*Cephalopholis sexmaculata*
Serranidae	*Cephalopholis urodeta*
Serranidae	*Epinephelus coioides*
Serranidae	*Epinephelus cyanopodus*

Family	Species
Serranidae	*Epinephelus fasciatus*
Serranidae	*Epinephelus fuscoguttatus*
Serranidae	*Epinephelus hexagonatus*
Serranidae	*Epinephelus howlandi*
Serranidae	*Epinephelus lanceolatus*
Serranidae	*Epinephelus macrospilos*
Serranidae	*Epinephelus merra*
Serranidae	*Epinephelus ongus*
Serranidae	*Epinephelus polyphekadion*
Serranidae	*Epinephelus quoyanus*
Serranidae	*Epinephelus sexfasciatus*
Serranidae	*Epinephelus spilotoceps*
Serranidae	*Epinephelus tauvina*
Serranidae	*Epinephelus undulatostriatus*
Serranidae	*Plectropomus areolatus*
Serranidae	*Plectropomus laevis*
Serranidae	*Plectropomus leopardus*
Serranidae	*Plectropomus maculatus*
Serranidae	*Variola albimarginata*
Serranidae	*Variola louti*
Siganidae	*Siganus argenteus*
Siganidae	*Siganus corallinus*
Siganidae	*Siganus doliatus*
Siganidae	*Siganus fuscescens*
Siganidae	*Siganus javus*
Siganidae	*Siganus lineatus*
Siganidae	*Siganus puellus*
Siganidae	*Siganus punctatissimus*
Siganidae	*Siganus punctatus*
Siganidae	*Siganus spinus*
Siganidae	*Siganus vulpinus*
Zanclidae	*Zanclus cornutus*

Table S2: Summary of each taxonomic Order recorded on 129 BRUVS samples from seven reefs in the northern GBRMP, in decreasing order of diversity.

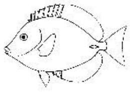
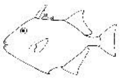
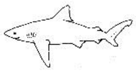
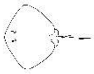
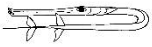
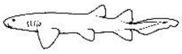
	Order	**Common Name**	***n* families**	***n* genera**	***n* species**	***n* individuals**
	Perciformes	Perch-like fishes	31	120	372	11071
	Tetraodontiformes	Puffers and triggerfish	5	12	18	215
	Carcharhiniformes	Sharks	1	4	5	139
	Myliobatiformes	Rays	2	5	6	16
	Gasterosteiformes	Flutemouths	2	2	2	14
	Anguilliformes	Moray eels	1	1	1	14
	Beryciformes	squirrelfish	1	2	5	12
	Orectolobiformes	Wobbegong sharks	2	2	2	7
	Aulopiformes	Lizardfish	1	1	2	7

Table S3: The Dufrene-Legendre indices (DLI) for each of the 290 species analysed as the multivariate response in Figure 29. The DLI species, and their values, are shown for each node of the tree. These nodes include the hierarchical branches, and the terminal nodes comprising the 7 fish assemblages (in bold italics).

Node name	Tree node	Dufrene-Legendre Index (%)
All	1	*Plectropomus leopardus (60), Ctenochaetus striatus (56), Thalassoma lunare (53), Labroides dimidiatus (49), Chaetodon vagabundus (41), Pomacanthus sexstriatus (40), Parupeneus multifasciatus (39), Acanthurus nigricauda (34), Parupeneus barberinus (33), Lethrinus atkinsoni (33), Oxycheilinus digrammus (25), Balistoides viridescens (21), Centropyge bicolor (20), Coris batuensis (20), Scarus flavipectoralis (19), Sufflamen chrysopterum (16), Zebrasoma veliferum (15), Epinephelus fuscoguttatus (11), Acanthurus xanthopterus (9), Chromis atripectoralis (8), Platax orbicularis (8), Pomacentrus chrysurus (7)*
Mid-shelf reefs	2	*Scolopsis monogramma (51), Carangoides fulvoguttatus (37), Lethrinus obsoletus (27), Gnathanodon speciosus (11), Choerodon anchorago (8), Sphyraena jello (4)*
Outer-shelf - edge reefs	3	*Grammatorcynus bilineatus (88), Naso brevirostris (82), Amblyglyphidodon leucogaster (80), Naso unicornis (72), Oxycheilinus orientalis (72), Lethrinus erythracanthus (71), Scarus schlegeli (68), Pterocaesio marri (67), Dascyllus reticulatus (67), Scarus frenatus (65), Pomacentrus amboinensis (56), Lutjanus bohar (56), Acanthochromis polyacanthus (55), Chlorurus sordidus (54), Plectropomus laevis (49), Triaenodon obesus (46), Caesio cuning (44), Cheilinus undulatus (39), Macolor niger (28), Scarus altipinnis (26), Monotaxis grandoculis (26), Variola louti (25), Scarus chameleon (22), Epinephelus polyphekadion (18), Scarus psittacus (17), Thalassoma nigrofasciatum (14), Carangoides plagiotaenia (13), Zanclus cornutus (13), Stethojulis bandanensis (13), Acanthurus olivaceus (13), Kyphosus vaigiensis (11), Pseudochromis fuscus (10), Chaetodon mertensii (9), Lutjanus rivulatus (9), Dascyllus trimaculatus (8), Scarus rubroviolaceus (8), Chromis lepidolepis (7), Halichoeres scapularis (5), Balistoides conspicillum (4)*
Princess Charlotte Bay mid-shelf	4	*Lutjanus sebae (87), Dischistodus perspicillatus (44), Meiacanthus atrodorsalis (42), Platax pinnatus (42), Choerodon vitta (38), Gymnothorax javanicus (31), Siganus puellus (27), Cephalopholis boenak (27), Caranx ignobilis (20), Lethrinus harak (12)*
Cape Grenville mid-shelf	***5***	*Choerodon cyanodus (85), Choerodon schoenleinii (82), Lethrinus laticaudis (82), Chaetodontoplus duboulayi (79), Scarus rivulatus (73), Siganus virgatus (69), Siganus argenteus (69), Lutjanus carponotatus (68), Hemigymnus melapterus (61), Cheilinus fasciatus (48), Cephalopholis cyanostigma (48), Abudefduf bengalensis (45), Chelmon marginalis (45), Echeneis naucrates (44), Chaetodon aureofasciatus (43), Carcharhinus amblyrhynchos (38), Siganus punctatus (37), Choerodon fasciatus (35), Chaetodon rainfordi (33), Acanthurus grammoptilus (33), Chaetodon auriga (30), Chlorurus microrhinos (29), Pomacentrus wardi (28), Abudefduf whitleyi (27), Neoglyphidodon nigroris (27), Plectorhinchus multivittatus (27), Chaetodon lineolatus (26), Novaculichthys taeniourus (26), Scarus ghobban (25), Diagramma pictum (23), Coradion chrysozonus (23), Pseudocheilinus evanidus (22), Halichoeres melanurus (22), Chaetodon ephippium (22), Siganus corallinus (21), Carcharhinus melanopterus (21), Acanthurus blochii (21), Scolopsis margaritifer (18), Scarus globiceps (18), Dischistodus prosopotaenia (16), Diploprion bifasciatum (16), Naso annulatus (15), Parupeneus barberinoides (12), Cheilinus oxycephalus (12), Stegastes nigricans (11), Pomacentrus bankanensis (10), Chlorurus bleekeri (7), Hemiglyphidodon plagiometopon (6), Lutjanus monostigma (6), Lutjanus*

Node name	Tree node	Dufrene-Legendre Index (%)
		fulviflamma (5), Lethrinus microdon (5), Pomacentrus nagasakiensis (5), Lethrinus rubrioperculatus (4)
Outer-shelf - edge reefs with mixed non-reefal substrata	***6***	*Lethrinus nebulosus (39), Symphorichthys spilurus (34), Gymnocranius grandoculis (32), Hipposcarus longiceps (26), Acanthurus dussumieri (18), Carangoides dinema (18), Pseudobalistes fuscus (18), Grammatorcynus bicarinatus (14), Caranx papuensis (14), Aprion virescens (12), Fistularia commersonii (11), Parapercis xanthozona (9), Halichoeres chrysus (8), Carangoides caeruleopinnatus (8), Bolbometopon muricatum (7), Neopomacentrus bankieri (4), Coris dorsomacula (4)*
Outer-shelf with higher reefal substrata	7	*Balistapus undulatus (55), Halichoeres hortulanus (45), Anampses neoguinaicus (44), Gomphosus varius (43), Pomacentrus brachialis (41), Chaetodon pelewensis (41), Cephalopholis urodeta (39), Labrichthys unilineatus (39), Chaetodon lunulatus (38), Scolopsis bilineata (36), Chromis ternatensis (34), Chromis margaritifer (33), Zebrasoma scopas (31), Epibulus insidiator (30), Chaetodon plebeius (28), Halichoeres prosopeion (28), Pomacentrus moluccensis (27), Centropyge bispinosa (26), Labroides bicolor (26), Acanthurus pyroferus (25), Ecsenius bicolor (24), Naso lituratus (23), Chromis weberi (21), Cetoscarus bicolor (20), Centropyge vrolikii (20), Chaetodon ulietensis (19), Chaetodon baronessa (19), Pygoplites diacanthus (18), Plectroglyphidodon lacrymatus (17), Epinephelus merra (14), Scarus spinus (14), Chaetodon trifascialis (14), Arothron nigropunctatus (10), Bodianus diana (7), Chromis amboinensis (5), Ptereleotris evides (5), Melichthys vidua (5), Plectorhinchus chaetodonoides (5)*
Princess Charlotte Bay mid-shelf reefs low live coral cover (<15%)	***8***	*Lethrinus ravus (33), Parupeneus indicus (24), Nemipterus furcosus (17), Plectropomus maculatus (17), Pentapodus aureofasciatus (15), Symphorus nematophorus (13), Halichoeres zeylonicus (12), Nebrius ferrugineus (8)*
Princess Charlotte Bay mid-shelf reefs moderate to high live coral cover (>=15%)	***9***	*Siganus doliatus (65), Chelmon rostratus (55), Neoglyphidodon melas (26), Chrysiptera rollandi (22), Chaetodon melannotus (22), Scarus niger (22), Cephalopholis microprion (21), Amblyglyphidodon curacao (19), Scarus forsteni (14), Anampses meleagrides (14), Siganus lineatus (9), Chaetodontoplus meredithi (8), Pomacentrus adelus (7), Epinephelus maculatus (4), Lutjanus fulvus (2)*
Outer-shelf reefs with mixed substrata	***14***	*Parupeneus pleurostigma (23), Parupeneus cyclostomus (22), Chaetodon citrinellus (22), Dischistodus melanotus (19), Canthigaster valentini (17), Parapercis hexophtalma (17), Halichoeres trimaculatus (16), Plagiotremus tapeinosoma (15), Pomacentrus coelestis (15), Meiacanthus grammistes (13), Valenciennea strigata (12), Pseudocheilinus hexataenia (11), Halichoeres biocellatus (10), Anampses melanurus (9), Taeniurops meyeni (9), Cheilio inermis (9), Pseudanthias squamipinnis (8), Coris gaimard (8), Aspidontus dussumieri (7), Cirrhitichthys falco (6), Dascyllus aruanus (5)*
Outer-shelf -- almost complete reefal substrata	15	*Pomacentrus lepidogenys (36), Bodianus axillaris (30), Lutjanus gibbus (28), Naso brachycentron (25), Chromis atripes (19), Paracirrhites forsteri (16), Chromis retrofasciata (16), Forcipiger longirostris (13), Hemigymnus fasciatus (12), Acanthurus mata (11), Thalassoma lutescens (9), Pterocaesio tile (9), Aulostomus chinensis (9)*

Node name	**Tree node**	**Dufrene-Legendre Index (%)**
Shallow outer-shelf -- almost complete reefal substrata	***30***	*Cephalopholis argus (42), Plectropomus areolatus (22), Thalassoma amblycephalum (22), Paracirrhites arcatus (20), Naso tonganus (20), Parupeneus crassilabris (17), Chaetodon ornatissimus (17), Plagiotremus rhinorhynchos (17), Kyphosus cinerascens (16), Lethrinus olivaceus (16), Chromis xanthura (16), Plectroglyphidodon dickii (15), Acanthurus lineatus (15), Pomacanthus xanthometopon (13), Thalassoma hardwicke (13), Chromileptes altivelis (12), Abudefduf sexfasciatus (11), Pomacanthus semicirculatus (10), Halichoeres margaritaceus (9), Scarus oviceps (8), Sargocentron caudimaculatum (7), Synodus variegatus (7), Bodianus loxozonus (7), Platax teira (6)")*
Deeper outer-shelf -- almost complete reefal substrata	***31***	*Chrysiptera talboti (26), Chaetodon kleinii (26), Genicanthus melanospilos (25), Chaetodon unimaculatus (25), Naso caesius (22), Cirrhilabrus punctatus (21), Pomacentrus reidi (18), Siganus vulpinus (15), Naso vlamingii (15), Caesio caerulaurea (15), Caranx melampygus (14), Chromis iomelas (14), Sufflamen bursa (14), Heniochus singularius (13), Cephalopholis spiloparaea (13), Myripristis kuntee (11), Scomberomorus commerson (11), Cephalopholis leopardus (10), Bodianus mesothorax (10), Lutjanus quinquelineatus (10), Aluterus scriptus (6), Lutjanus kasmira (5), Arothron stellatus (4), Arothron caeruleopunctatus (4)*

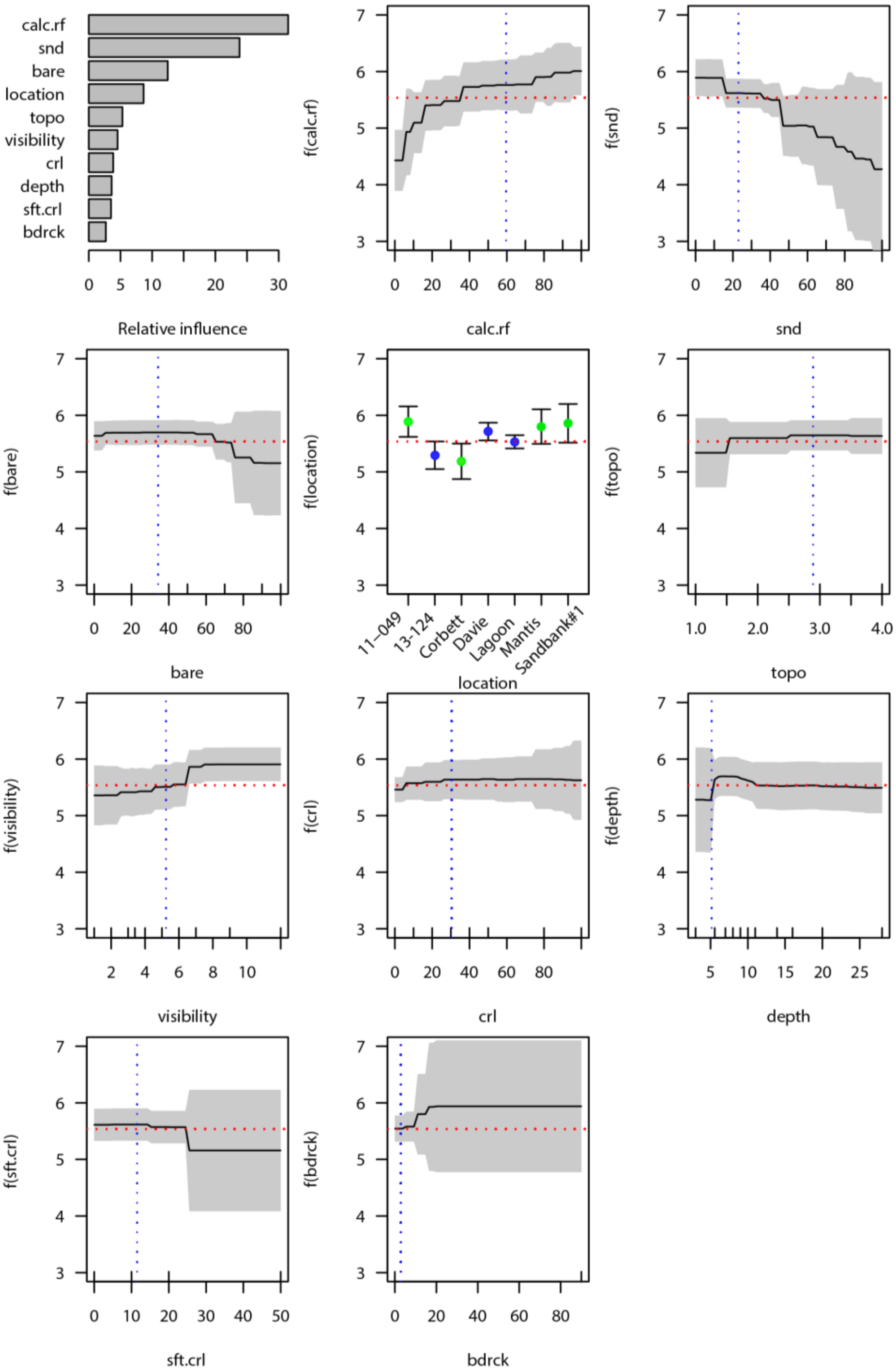


Figure S1: Partial dependency plots of the 10 major influences on transformed species richness (square root). The bar plot partitions the influences on the variation explained by the model. Horizontal dotted lines (red) show the mean richness across all BRUVS deployments. Vertical dotted lines (blue) show the mean value for each predictor. The response lines show the relationship of richness as a function of each predictor, with the influence of all other predictors held to a constant (i.e. accounted for) and shading shows ±2 standard errors.

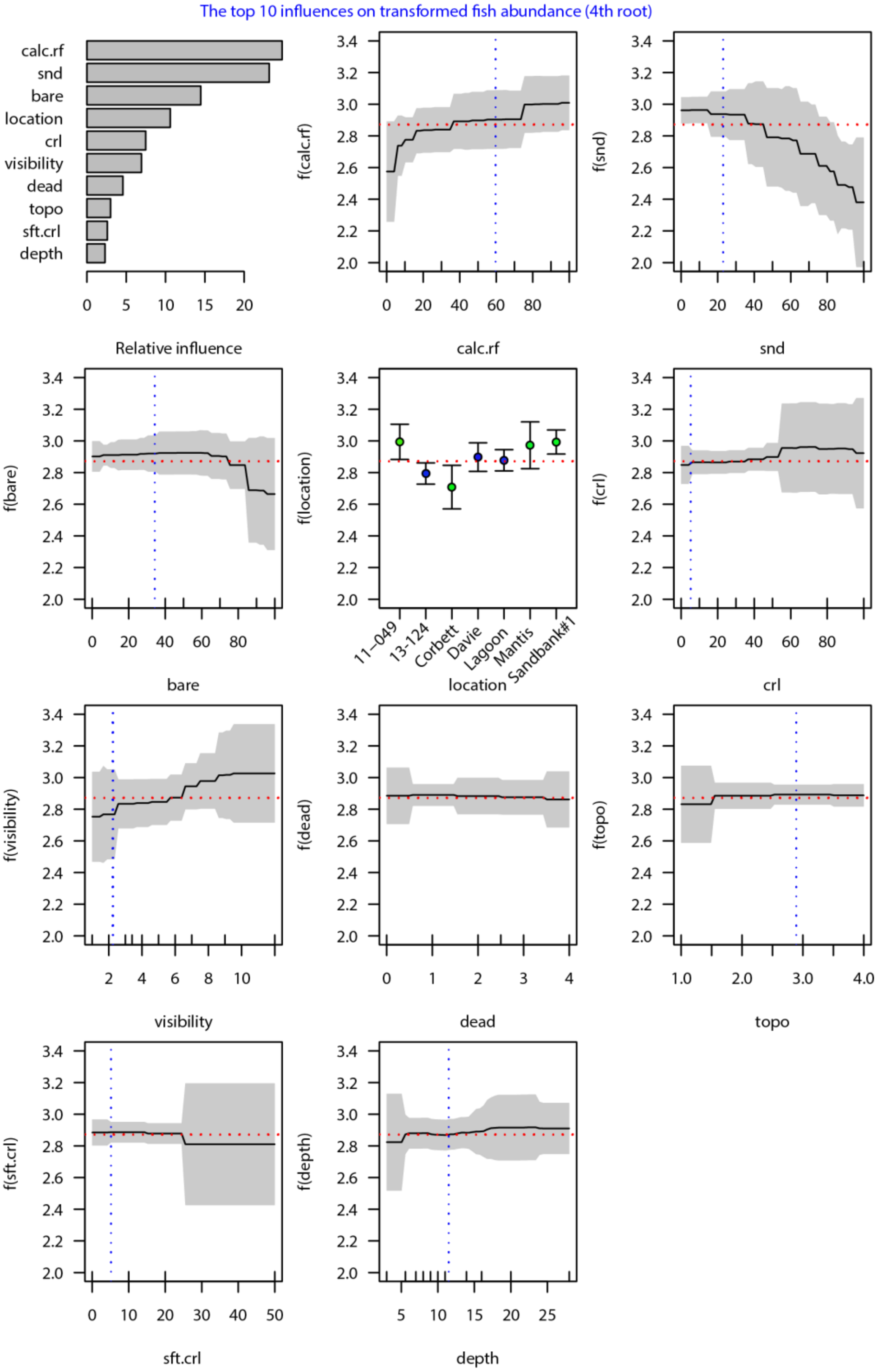


Figure S2: Partial dependency plots of the 10 major influences on total relative abundance (*MaxN* 4th root transformed). All conventions as for Figure 31.

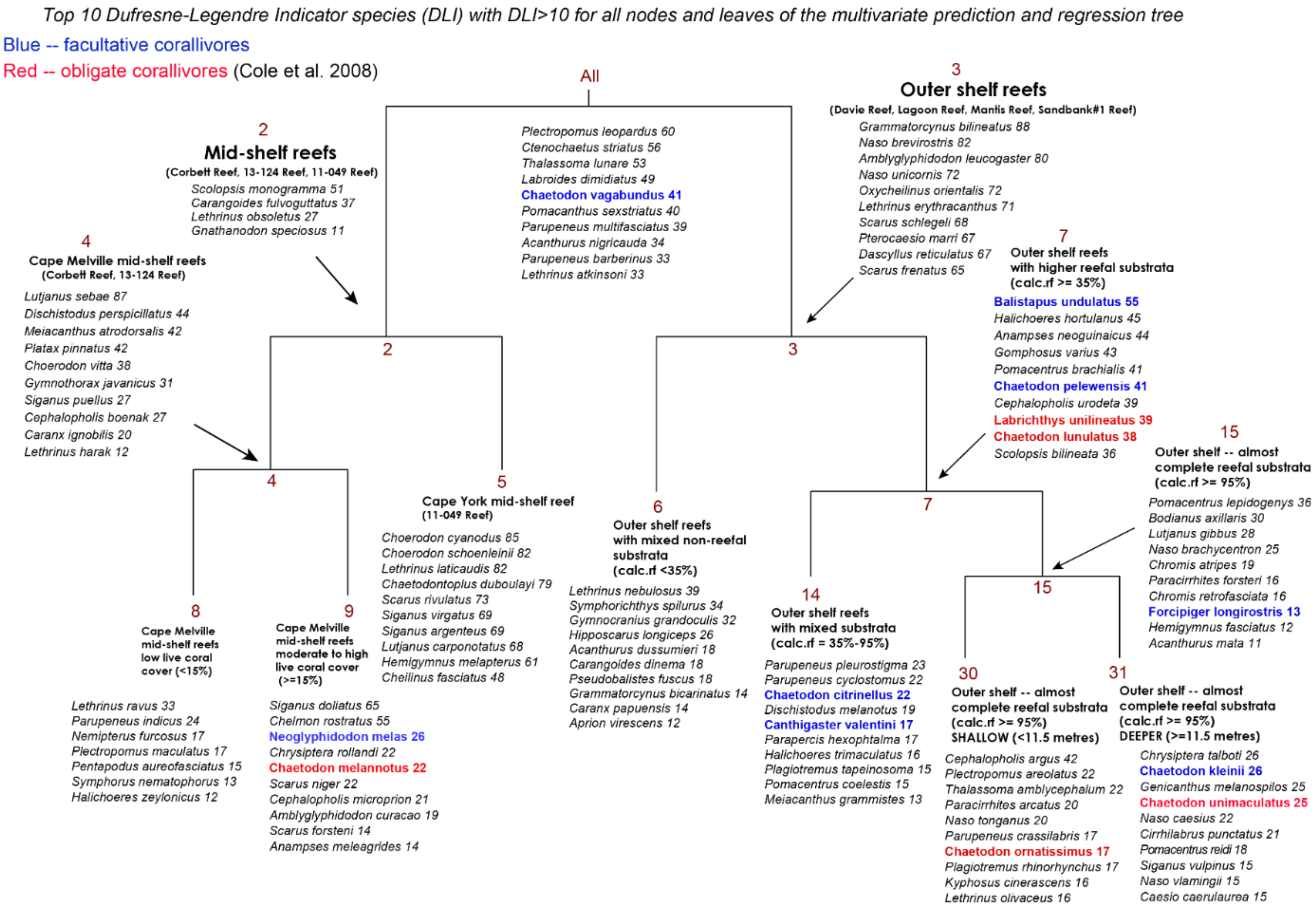
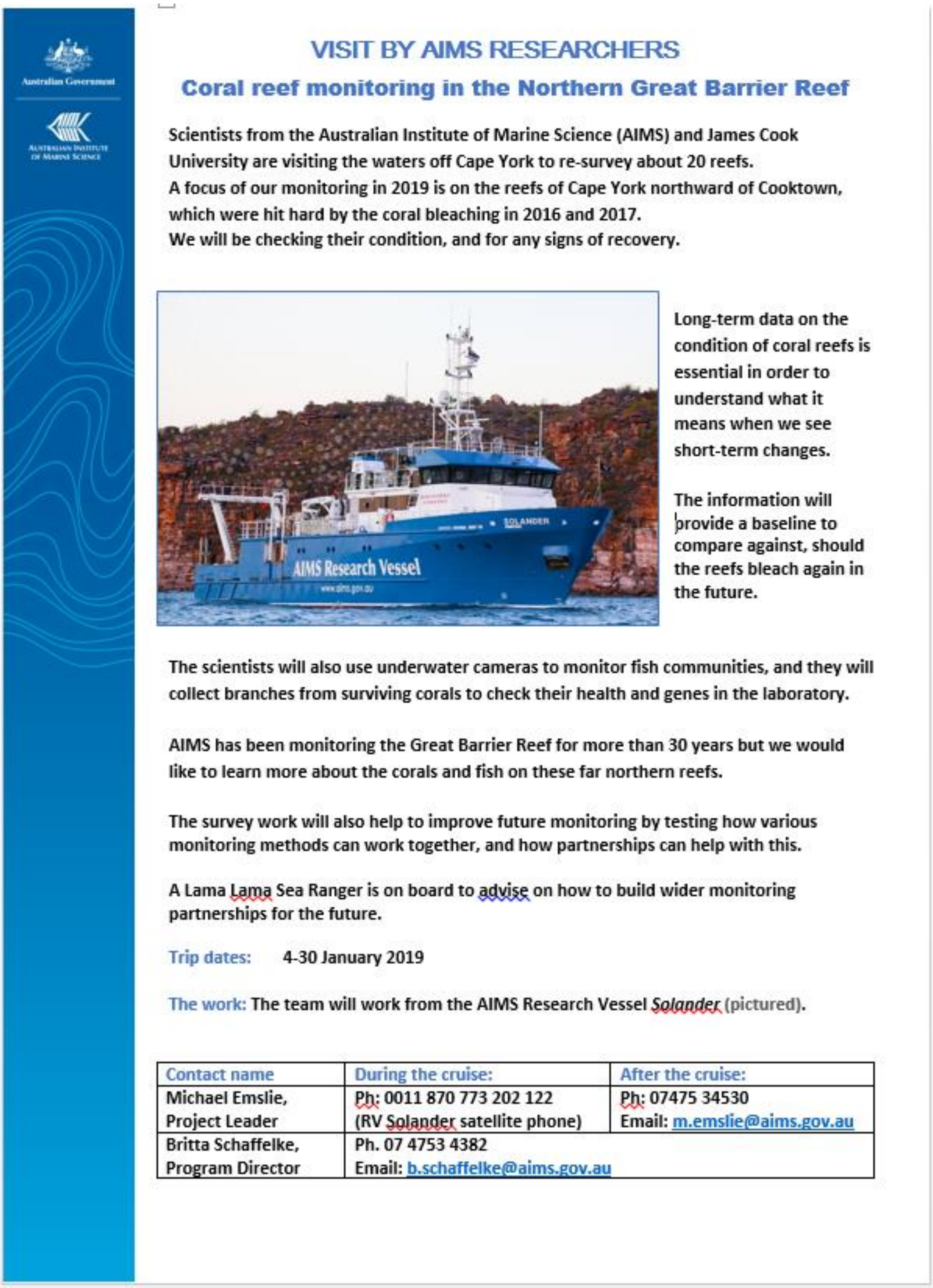


Figure S3: The Dufrene-Legendre species indicators (DLI) with DLI>10% for all nodes and leaves of the tree in Figure 33. Species reported by Cole et al. (2008) to be obligate (red) or facultative (blue) corallivores are highlighted. Species with high DLI at the tree stump (e.g. coral trout *Plectropomus leopardus*) were ubiquitous, but others with very high DLI on a leaf were largely confined to the sites in those leaves (e.g. *Choerodon cyanodus* at 11-049 Reef).



VISIT BY AIMS RESEARCHERS

Coral reef monitoring in the Northern Great Barrier Reef

Scientists from the Australian Institute of Marine Science (AIMS) and James Cook University are visiting the waters off Cape York to re-survey about 20 reefs.
A focus of our monitoring in 2019 is on the reefs of Cape York northward of Cooktown, which were hit hard by the coral bleaching in 2016 and 2017.
We will be checking their condition, and for any signs of recovery.

Long-term data on the condition of coral reefs is essential in order to understand what it means when we see short-term changes.

The information will provide a baseline to compare against, should the reefs bleach again in the future.

The scientists will also use underwater cameras to monitor fish communities, and they will collect branches from surviving corals to check their health and genes in the laboratory.

AIMS has been monitoring the Great Barrier Reef for more than 30 years but we would like to learn more about the corals and fish on these far northern reefs.

The survey work will also help to improve future monitoring by testing how various monitoring methods can work together, and how partnerships can help with this.

A Lama Lama Sea Ranger is on board to advise on how to build wider monitoring partnerships for the future.

Trip dates: 4-30 January 2019

The work: The team will work from the AIMS Research Vessel *Solander* (pictured).

Contact name	During the cruise:	After the cruise:
Michael Emslie, Project Leader	Ph: 0011 870 773 202 122 (RV Solander satellite phone)	Ph: 07475 34530 Email: m.emslie@aims.gov.au
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Figure S4. Flyer sent to Traditional Owners prior to the field trip to the far northern GBR.