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Article

Cross-Shelf Differences in the Response of Herbivorous Fish Assemblages to Severe Environmental Disturbances

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Abstract: Cross-shelf differences in coral reef benthic and fish assemblages are common, yet it is unknown whether these assemblages respond uniformly to environmental disturbances or whether local conditions result in differential responses of assemblages at different shelf positions. Here, we compare changes in the taxonomic and functional composition, and associated traits, of herbivorous reef fish assemblages across a continental shelf, five years before and six months after two severe cyclones and a thermal bleaching event that resulted in substantial and widespread loss of live hard coral cover. Each shelf position maintained a distinct taxonomic assemblage of fishes after disturbances, but the assemblages shared fewer species among shelf positions. There was a substantial loss of species richness following disturbances within each shelf position. Total biomass of the herbivorous fish assemblage increased after disturbances on mid- and outer-shelf reefs, but not on inner-shelf reefs. Using trait-based analyses, we found there was a loss of trait richness at each shelf position, but trait specialisation and originality increased on inner-shelf reefs. This study highlights the pervasiveness of extreme environmental disturbances on ecological assemblages. Whilst distinct cross-shelf assemblages can remain following environmental disturbances, assemblages have reduced richness and are potentially more vulnerable to chronic localised stresses.

Keywords: coral reefs; environmental gradients; cyclones; coral bleaching; inshore; offshore; runoff; trait richness; diversity

1. Introduction

Environmental gradients across small spatial scales produce distinct assemblages of species. For example, plant and animal assemblages have been shown to vary with altitudinal gradients [1–3], with salinity gradients [4], and with water quality and wave energy gradients [5–10]. Maintaining these spatially distinct species assemblages enhances overall biological and ecological diversity, and contributes to economic and social prosperity [11,12]. While the biophysical drivers that maintain these assemblages over small spatial scales are increasingly understood, we do not fully appreciate how distinct assemblages along large-scale environmental gradients respond to environmental disturbances. This is concerning because many species, habitats, and assemblages occur at the extremes of environmental gradients, making them more vulnerable to change [13]. This is particularly pertinent to tropical coral reefs spanning continental shelves.

Differences in assemblages of species across continental shelves produce some of the most pronounced spatial variability among coral reefs. Indeed, cross-shelf differences in species abundance and community structure are often more distinct than latitudinal or temporal differences [7,14–17]. Environmental gradients of improving water quality and increasing wave energy contribute to the distinct assemblages of corals, algae, and fishes on inner-, mid-, and outer-shelf reefs of Australia's Great Barrier Reef [6,7,10,14–16,18–22]. Nearshore, or inner-shelf, reef habitats are typically characterised by sediment-tolerant coral species and morphologies such as massive *Porites* and by a high cover of macroalgae such as *Sargassum* [6,23]. In contrast, outer-shelf reef habitats are generally characterised by higher coral cover but low macroalgal cover [7,15,20]. These environmental and habitat characteristics lead to distinct cross-shelf differences in coral reef fish assemblages.

Coral reefs are becoming increasingly subjected to a wide range of environmental stressors. Localised environmental disturbances (e.g., terrigenous runoff), and more spatially extensive disturbances (e.g., thermal stress and severe cyclones) are intensifying with climate change [24]. Such disturbances potentially threaten the distinct patterns of coral reef assemblages across continental shelves. Thermal bleaching events can cause widespread loss of live coral cover, while severe tropical storms can remove both live coral cover and the underlying physical structure, leading to the loss of taxa that are dependent on live coral and/or the physical structure that they provide [25]. While many reef fish species experience deleterious effects of environmental disturbances that cause benthic habitat change, others can benefit from such habitat change, at least in the short term [25–29]. Coral reefs subject to severe environmental disturbances often become more suitable to rubble specialists, such as some damselfishes (Pomacentridae), goatfishes (Mullidae), and wrasses (Labridae), and fish that feed on algae or utilize hard reef pavement platforms, such as nominally herbivorous parrotfishes (Scarinae) and surgeonfishes (Acanthuridae) [26,28–33]. However, if environmental disturbances are large enough to affect coral reefs across entire continental shelves, it is not known whether local environmental conditions at each shelf position continue to maintain distinct assemblages post-disturbance or whether severe environmental disturbances reduce or even eliminate differences in cross-shelf assemblages.

Herbivorous reef fishes are a critical group that through their feeding activities help maintain a healthy balance between corals and macroalgae [31,34]. Cross-shelf assemblages of herbivorous reef fishes are often distinct in taxonomic structure [18,22,33,35–38], as well as being highly diverse in diet, feeding mode, and behaviour [39], often collectively referred to as 'function' (but see [40]). Nominally herbivorous reef fishes are typically categorised into two groups based on the substrata they bite; macroalgal 'browsers' that typically bite erect or fleshy macroalgae and 'grazers' that bite surfaces covered with algal turfs and associated infauna and microbes. Within grazers, groups can be further described as scrapers, excavators, algal croppers, and detrital feeders, based on jaw morphology and observed feeding behaviour [39]. Macroalgal browsers have the capacity to remove macroalgal biomass [41], scrapers and excavators contribute to the turn-over and distribution of carbonate in coral reef systems (bioerosion) (in [42]) while targeting protein-rich epilithic and endolithic micro-organisms [43], and algal croppers and detrital feeders contribute to the turn-over of productivity on coral reefs [15,44]. Such diversity and functional variation of herbivorous fishes may allow for rapid detection of ecosystem change through trait-based approaches that capture more nuanced variation than approaches based on broad functional groupings alone [45]. However, it remains unknown how cross-shelf differences in diversity (be it taxonomic, trait, or functional) are affected by shelf-wide environmental disturbances and thus what the implications are for maintenance of trophic interactions.

Given the widespread distribution and importance of herbivorous fishes to coral reefs globally, this study investigates the response of assemblages of herbivorous reef fish across a continental shelf gradient to severe environmental disturbance events. Specifically, we sought to understand 1. the cross-shelf variation in benthic cover and the herbivorous fish assemblage structure five years before and six months after two severe cyclones and a severe bleaching event, 2. the overall impact of severe environmental disturbances on the taxonomic and trait-based composition, and on biomass of herbivorous fish across the continental shelf, 3. whether inner-, mid-, and outer-shelf benthic and reef fish assemblages respond differently to environmental disturbance events given the differences in prevailing local environmental conditions at each shelf position. We then discuss the potential of recovery for inner-, mid-, or outer-shelf coral reef assemblages, considering local environmental conditions.

2. Materials and Methods

2.1. Study Area

This study took place in the northern section of the Great Barrier Reef (approx. 14°41′ S, 145°27′ E). Six coral reefs were selected to span the continental shelf including two inner-shelf reefs (located in the Turtle Island Group), two mid-shelf reefs (Lizard Island and MacGillivray reef), and two outer-shelf reefs (Hicks and Day reefs) (Figure 1). Within each of these six reefs, the reef crest habitat was selected to compare cross-shelf changes in benthic biota and herbivorous fish species before and after the impacts of two category 4 cyclones (Ita, April 2014, and Nathan, March 2015), and a severe coral bleaching event (March–April 2016) [24,46]. Benthic and herbivorous fish assemblages were surveyed twice at all reefs; once approximately five years 'before' the first disturbance event in the Austral summer of 2008/09 and once six months 'after' the last disturbance event in October–November 2016.

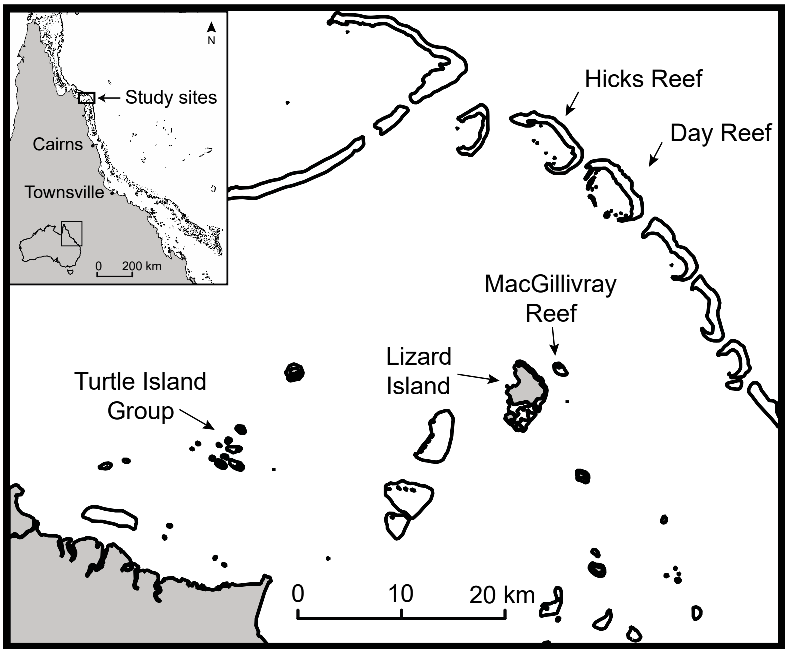

Figure 1. Map of the study area (modified from [23]).

2.2. Assessment of Benthic and Fish Assemblages

The benthic assemblage was assessed along point-intercept transects at each reef, both before (December 2008–January 2009) and after disturbances (October–November 2016). In 2008/9, benthic composition was quantified along six replicate 10 m transects at each of two sites on each of the six reefs. The substratum immediately under, and 1 m either side of a transect tape, was recorded at 1 m intervals (following [23]). In 2016, benthic composition was quantified along four replicate 50 m transects at each site, with the substratum immediately under the transect recorded at 50 cm intervals (following [47]). Both benthic surveys used point-intercept methods and the haphazard placement of transects within each site, and as such the estimates from the different benthic survey methods were comparable. Benthic categories were recorded as sand, rubble, dead coral, reef pavement, live hard coral, soft coral, macroalgae, or 'other' benthic organisms. Hard coral was identified to the highest taxonomic classification possible (usually genus) and further categorized by life forms of massive, branching, tabulate, digitate, encrusting, and foliose. Algae was identified to genus where possible but otherwise classified as fleshy macroalgae, filamentous turf algae, or calcareous. Transects were standardized by expressing each benthic category as a percent benthic cover.

The abundance of all diurnally active, nominally herbivorous roving fishes (families Acanthuridae, Ephippidae, Kyphosidae, and Siganidae and subfamily Scarinae (in Labridae) excluding *Bolbometopon muricatum* due to the highly mobile and aggregated nature of this species), was recorded at each of the 12 sites in both years. In 2009, the surveyor (ASH) performed four replicate 10 min timed swim transects at each site, counting all herbivorous fishes greater than 10 cm total length (TL) within a 5 m belt along the reef crest, from the benthos to the water's surface (following [23]). The length covered by each transect was, on average, 117 m (±27.7 SE). In 2016, the surveyors (A.S.H., E.C.M.) performed four replicate 50 × 5 m belt transects (following [47]), whereby a transect tape was simultaneously laid while surveying to reduce any potential diver-related disturbance to fishes. The two fish census methods employed in this study to collect data before (2008/2009) and after (2016) environmental disturbances are considered comparable to one another. They have similar diver effects on fish, in contrast to methods that lay transect tapes prior to survey, which are more likely to impact the accuracy of fish density estimates [48]. Furthermore, the width of transects was the same between years (5 m) and the difference in distance covered by each survey method was comparable to previous studies that found no effect on the detectability of fishes when transect lengths varied from 110 to 400 m [19]. In both years, fish were identified to species level and placed into 5 cm length categories. Abundance estimates were converted to biomass using published species length–weight relationships [49] and standardized per hectare (kg ha^{-1}). Species were categorized into functional groups based on their diet (and/or feeding substrata) and feeding mode [26,39,50,51]. Here we use the term 'function' to refer to the process of feeding a species rather than any ecological 'service' provided by that feeding process [40,52].

Species traits are often used as a proxy for their function, but direct links between traits and function are rarely established (see [40,52]). To assess cross-shelf differences in the trait structure of roving herbivore assemblages in 2008/9 and 2016, all surveyed species were classified according to six traits: diet (macroalgal browsers, scrapers, excavators, algal croppers, detritivores, omnivores) maximum reported body-size (TL; 10 cm size classes), social grouping, position in the water column, mobility within/between reefs, and time of activity (diurnal, nocturnal) based on published literature [26,39,51] (ESM Table S1). Fish visual surveys were conducted in accordance with animal ethics approvals (Ethics Approval Number A2253).

2.3. Statistical Analyses

Cross-shelf differences in the taxonomic composition of herbivorous fish assemblages were assessed across years using a PERMANOVA (maximum permutations = 9999) with shelf position and year (fixed) as well as site (random, nested in shelf) as factors. Monte Carlo sampling was used when there were insufficient unique permutations for *P*-value estimation (<100 permutations; [53]). These differences were then visualised using a non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity of data at the transect level. Percentage similarity analysis (SIMPER) was used to identify the mean similarity within, and the dissimilarity among, herbivore assemblages found in the inner-, mid-, and outer shelf in each year, and species identified that consistently contributed to within-group similarity (with similarity/SD ratio $\geq$2; Table S2) [53]. This was supported by multivariate dispersion analysis (MVDISP) to quantify differences in assemblage composition both within and among shelf groups in 2008/9 and 2016. Cross-shelf variation in species dominance patterns across years was tested with a two-way crossed analysis of similarity (ANOSIM) using shelf position and year as fixed factors, based on a dissimilarity matrix of log-weighted species rank (with DOMDIS). Pairwise comparisons of species dominance over time (pre- and post-disturbance) were assessed within each individual shelf position. All multivariate analyses were performed on fourth root-transformed transect level data.

Linear mixed-effects models were used to assess cross-shelf differences in total cover of coral (hard coral and *Millepora* spp.) and macroalgae over time, and assess the trait structure of herbivorous fish assemblages (trait richness; trait specialisation; trait originality; total log transformed herbivore biomass; and biomass of individual functional groups: browsers, croppers, scrapers, detrital feeders, and excavators) and taxonomic diversity (Shannon diversity, H) over time. All models included shelf position, year, and their interaction (fixed effects) as well as site (random effect), fit within a Gaussian structure due to normal residual distributions, followed by planned comparisons (if interaction detected) or Tukey's multiple comparisons (no interaction) post hoc to identify where differences occurred. Model assumptions of homogeneity of variance, normality, and independence were validated with visual assessments of Pearson residual diagnostic plots. Where heterogeneity of variance occurred among shelf positions (the total cover of macroalgae, log-transformed total herbivore biomass, the biomass of each herbivore functional group, trait specialisation, and trait originality) or across years (total hard coral cover), models were fit with a constant variance structure.

The trait richness of the herbivorous fish assemblages was calculated for each transect by constructing a principal coordinates analysis (PCoA) of species positioned in multidimensional trait-space based on a Gower distance matrix of species pairs and a square root correction for negative eigenvectors [54]. Scores from the first four PCoA axes summarising species distributions in trait-space were combined with species biomass to calculate three complementary indices of trait diversity: trait richness, trait specialisation, and trait originality [45,55]. Trait richness represents the range of unique trait entities and was calculated as the proportional convex hull volume occupied by species present in the trait space. The average trait specialisation of an assemblage (i.e. species close to the periphery of trait space) was calculated as the biomass-weighted relative distance of a species from the centroid of trait space. Trait originality indicates the isolation of species in trait space and is calculated as the mean pairwise distance of biomass-weighted species present. Three transects were omitted for the calculation of trait diversity (from 2016 surveys of site Turtle North 1) due to minimum trait entity requirements to compute convex hulls.

Multivariate analyses of the taxonomic composition of herbivore assemblages were performed in Primer v6 with PERMANOVA+ [53,56]. All other analyses were performed in R [57], with the packages *lme4*, *nlme*, *multcomp*, *MumIn*, *ape*, *cluster*, *geometry*, *rcdd*, *vegan*, *ade4*, and *FD* (*FDchange*).

3. Results

The best model of total hard coral cover included shelf position, year, and their interaction. Total hard coral cover was highest on outer-shelf reefs, and lowest on inner-shelf reefs in both 2008/9 and 2016 (Figure 2a). Macroalgal cover was highest on inner-shelf reefs and almost non-existent on mid- and outer-shelf reefs (Figure 2b). These patterns did not change with environmental disturbance, despite significant declines in hard coral cover across the shelf and significant increases in macroalgal cover on the inner shelf (Figure 2; Table S3).

Assemblage structure of herbivorous reef fish was distinct among shelf positions both before and after environmental disturbances (PERMANOVA, Psuedo-F = 3.86, df = 2, 65, $P = 0.001$, unique permutations = 9950; Figure 3; Table S2). Assemblage structure changed at all shelf positions following disturbances, and significantly so on the inner and outer shelf (PERMANOVA, pairwise comparisons: both $P = 0.03$). Following disturbances, fish assemblages became more distinct among shelf positions but more variable within shelf positions, with environmental disturbances increasing the cross-shelf assemblage differences in multivariate space (Figure 3; Table S2). Across the shelf, increased assemblage differences were characterised by a marked decrease in species richness at all shelf positions (ANOSIM, Inner: Global-R = 0.82, $P = 0.03$; Mid: Global-R = 0.90, $P = 0.005$; Outer: Global-R = 0.99, $P = 0.03$). On inner-shelf reefs four characteristic species decreased to one (*Scarus rivulatus*), on mid-shelf reefs eight characteristic species decreased to one (*Acanthurus nigrofuscus*), and on outer-shelf reefs eight characteristic species decreased to two (*Acanthurus lineatus* and *Ctenochaetus striatus*) (SIMPER: simm/SD ≥ 2; Table S2).

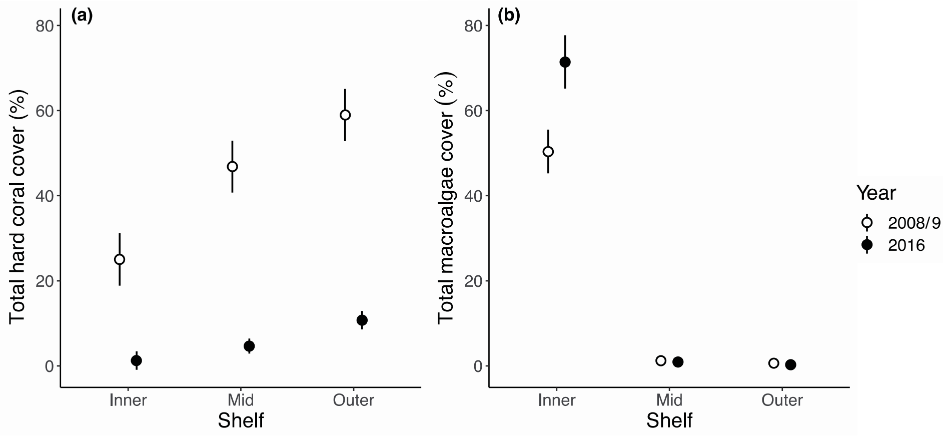

Figure 2. Cross-shelf differences (fitted values 95% confidence intervals) in (**a**) total hard coral cover (%) and (**b**) total macroalgal cover (%) in 2008/9 (white) and 2016 (black).

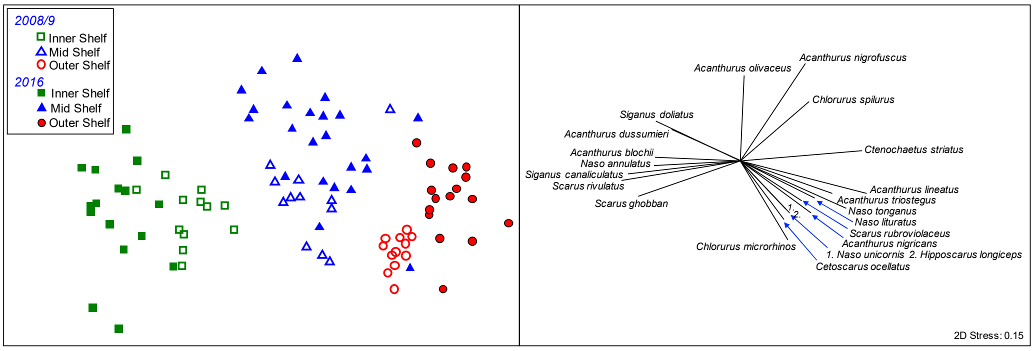

Figure 3. Non-metric multidimensional scaling analysis showing cross-shelf differences in assemblage structure of herbivorous reef fish (green square: inner-shelf; blue triangle: mid-shelf; red circle: outer-shelf) in 2008/9 (open) and 2016 (filled), using transect-level fourth root transformed data. The relative contributions of species to the observed variation in composition are illustrated (>0.4 Pearson correlation).

Prior to environmental disturbance, total biomass of all roving herbivorous fishes was highest on outer-shelf reefs and not significantly different between mid- and inner-shelf reefs. Following disturbances, total biomass increased significantly on mid- and outer-shelf reefs but did not change significantly on inner-shelf reefs (Figure 4a; Table S3). Increased biomass on the mid- and outer-shelf reefs was driven by significant increases in biomass of algal croppers and detrital feeders (Figure 4b,c; Table S3). Concurrently, there were slight declines in biomass of excavators, macroalgal browsers, and scrapers across the shelf (Figure 4d–f; Table S3).

The four PCoA axes used to describe fish species distribution in trait space cumulatively explained 61.23% of the variability. Analysis of cross-shelf variation in herbivorous fish assemblage structure revealed changes in taxonomic (Shannon, H, and total log biomass) and trait characteristics (trait richness, specialisation, and originality) in response to disturbances. However, the nature and extent of the changes varied with metric and, in some instances, with shelf position (Figure 5, Table S3). Trait richness (Figure 5a) and taxonomic diversity (Shannon, H) (Table S3) declined significantly across the entire shelf following disturbance. However, patterns of cross-shelf differences in both metrics were maintained, with greater trait richness and taxonomic diversity (H) of assemblages on the mid-shelf than the inner- and outer-shelf reefs in both 2008/9 and 2016 (Figure 5; Table S3).

Responses to environmental disturbance in trait specialisation and originality of herbivore assemblage structure did vary with shelf position. Trait specialisation and originality of herbivore assemblages increased significantly on the inner shelf, indicating an increase in biomass of 'specialist' species positions towards the periphery of trait space, and a potential loss of redundancy, respectively

(Figure 5; Table S3). Conversely, the trait specialisation of assemblages decreased on the mid-shelf reefs indicating a loss of biomass of 'specialist' species. Neither trait specialisation nor originality of assemblages changed on outer-shelf reefs with disturbance (Figure 5; Table S3).

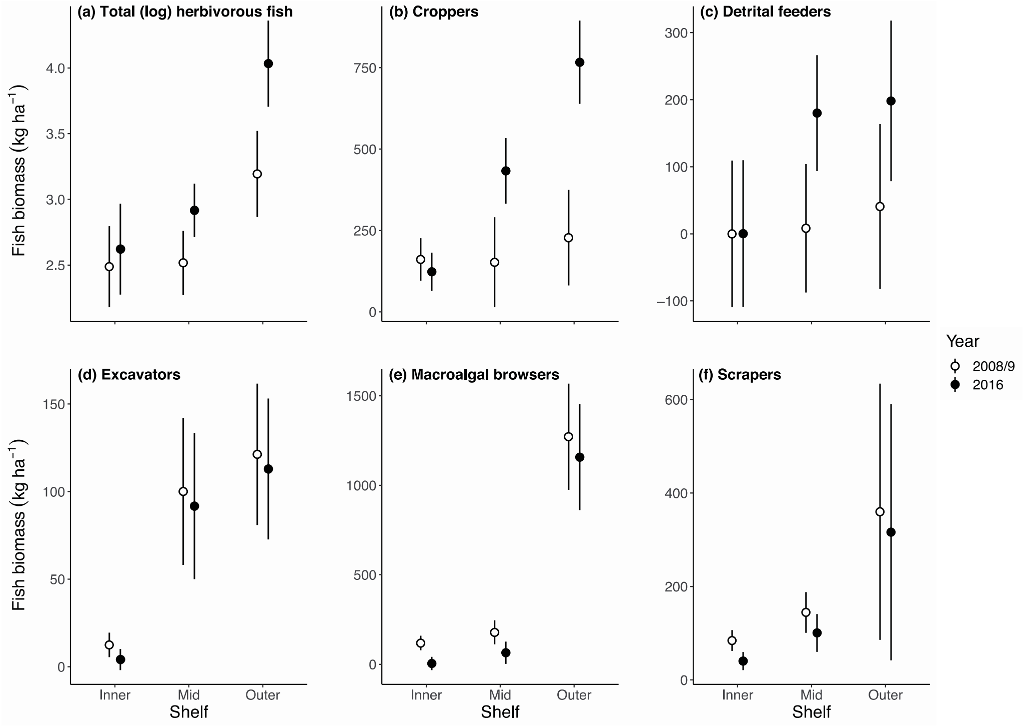

Figure 4. Cross-shelf differences (fitted values 95% confidence intervals) in biomass (kg/ha) of (**a**) the total herbivorous fish assemblage (log transformed), (**b**) algal croppers, (**c**) detrital feeders, (**d**) excavators (less Bolbometopon), (**e**) macroalgal browsers, and (**f**) scrapers, in 2008/9 (white) and 2016 (black).

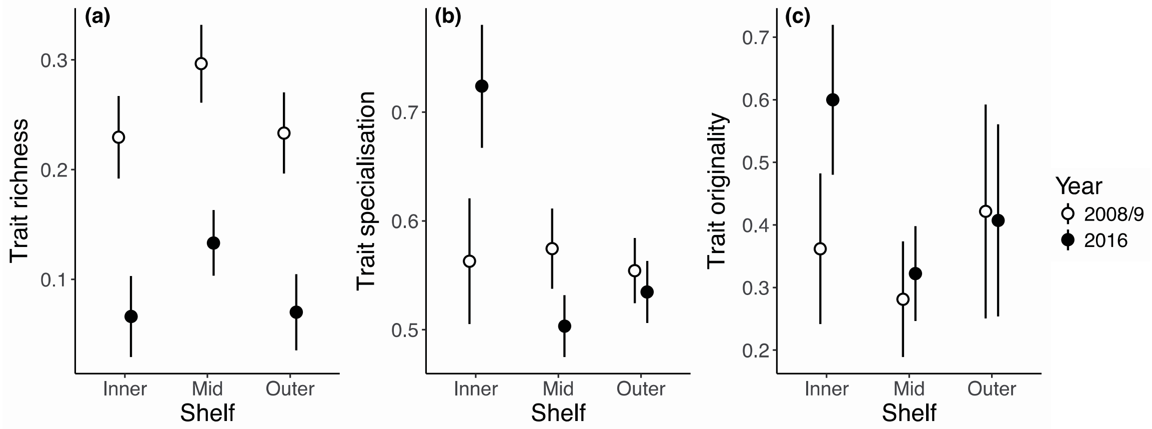

Figure 5. Cross-shelf differences (fitted values 95% confidence intervals) in (**a**) trait richness, (**b**) trait specialisation, and (**c**) trait originality, in 2008/9 (white) and 2016 (black).

4. Discussion

Few studies have explored how coral reef assemblages across a continental shelf gradient respond to severe environmental disturbances, especially for disturbances that affect each shelf position similarly. In this study, we found that severe cyclonic and thermal impacts caused substantial loss of live hard coral cover and caused significant loss of taxonomic diversity of herbivorous reef fish assemblages across the continental shelf in the northern GBR. Prior to disturbances, there were clear differences in the taxonomic composition of roving herbivore assemblages at each shelf position. Following disturbances and loss of species richness, distinctness in shelf assemblages increased, particularly on the outer- and inner-shelf, as assemblages became less similar in their species composition. This was caused by reductions in species richness at each shelf position that resulted in dominance of biomass by a few species and functional groups common at each shelf position. The biomass of these new dominant species increased substantially on the mid- and outer-shelf reefs, enough to override biomass loss caused by reductions of other species. The biomass of herbivorous fish on the inner-shelf reefs remained stable at pre-disturbance levels, but the inner-shelf reefs had a reshuffling of species dominance to become characterised by a different suite of species following disturbance. There were significant losses of trait richness at all shelf positions. Inner-shelf reefs were the least diverse, in both species and traits, of any shelf position prior to disturbance, and appear the most vulnerable to a potential loss of redundancy, as evidenced by significant increases in trait originality and trait specialisation post-disturbance. This is particularly concerning since inner-shelf reefs are arguably subject to greater localised environmental impacts of increased sedimentation and runoff from terrestrial sources than mid- and outer-shelf reefs. Potential loss of redundancy of this important group of fishes, increased cover of macroalgae, and poor water quality may make it more difficult for these reefs to recover, especially considering the increasing threats of pervasive climate change.

Cross-shelf differences in the response of herbivorous fishes to disturbance may suggest differential susceptibility of each shelf position to disturbances. This may be influenced by the prevailing cross-shelf gradients of water-quality, particularly on inshore reefs [6,15,22], together with increasing wave action [5] and upwelling [58], particularly on outer- and mid-shelf reefs. That the inner-shelf herbivorous fish assemblage showed the lowest species richness and trait richness before disturbance, and particularly after disturbance, may indicate that inner-shelf reefs are particularly susceptible to environmental disturbances (see also [22]). However, cross-shelf differences among inner-, mid-, and outer-shelf herbivorous fish assemblages became more pronounced following disturbance, with all shelf assemblages becoming less similar to each other, diverging towards greater dominance by fewer species and greater within-shelf variability in the occurrence of species. This reduced richness of herbivorous fish within shelf positions and the increased difference in assemblages of herbivorous fish among shelf positions suggest that maintenance of ecosystem structure across the shelf may be difficult in light of predicted increases in environmental disturbance regimes [24,59].

Despite relatively uniform loss of species richness across the shelf, the biomass of all herbivores increased on mid- and outer-shelf reefs but not on inshore reefs. This was driven largely by an increase in biomass of algal croppers and detrital feeding reef fish on mid- and outer-shelf reefs. Following disturbance, inner-shelf reefs became characterised by *Scarus rivulatus* (a scraper), mid-shelf reefs became characterised by *Acanthurus nigrofuscus*, and outer-shelf reefs became characterised by *Acanthurus lineatus* and *Ctenochaetus striatus*. Increasingly we are seeing herbivorous fish assemblages respond differently to disturbance events than many other trophic groups [29]. Typically, substantial loss of live hard coral cover and structure following environmental disturbances leads to a severe loss of coral dependent species [25,26,30,60]. This may include juveniles of some herbivorous reef fish species that are reliant on live branching corals on inshore reefs for part of their life cycle (e.g., [61]). However, adults of nominally herbivorous roving species favour feeding over dead coral surfaces and may increase in abundance, biomass, and/or growth rate when coral cover is reduced, at least in the short term [27,28,62–64]. This may reinforce the importance of bottom up processes in shaping fish assemblages [28,29]. On the GBR, herbivorous fish are generally not targeted by fishers [22], nor do they respond measurably to management zoning (see [65]). Thus, our findings compliment and contrast with recent evidence for bottom-up responses of fish assemblages following disturbance events by, for the first time, providing evidence of the simultaneous response of cross-shelf herbivorous fish assemblages to disturbance.

Inner-shelf reefs showed the most distinct and possibly the most concerning response of the assemblages of herbivorous fish to disturbance. While total herbivorous fish biomass was maintained on inner-shelf reefs, trait specialisation and trait originality of the assemblage increased, indicating an increase in biomass of more 'specialist' species and a potential loss of redundancy, respectively. A loss of redundancy of traits within an assemblage reflects a reduction in the number of species contributing to particular traits and may affect the maintenance of ecological processes and thus ecosystem persistence (see [21,66]). The differential response of inner- vs. mid- and outer-shelf reefs may be due to local environmental conditions (e.g., elevated sediments and nutrients as well as reduced wave action) or the distinct herbivorous fish assemblages that are more sensitive to habitat disturbance or loss. For example, the greater impact of the disturbances on the inner-shelf reef assemblages may be related to the naturally lower coral cover and taxonomic richness of assemblages in general [6]. Nevertheless, the potential loss of redundancy on these inner-shelf reefs is concerning since they are the most vulnerable to anthropogenic stressors.

Whilst frequent environmental disturbances are known to cause declines in coral cover and coral-dependent taxa, there is increasing evidence that such disturbances do not similarly impact macroalgal cover. For example, in the Caribbean, assemblages of the macroalgae *Sargassum* recovered to pre-disturbance levels one year after storm disturbance [67]. Similarly, on the GBR, *Sargassum* may be able to benefit from disturbance events via the rapid growth from holdfasts, colonization of new space through dispersion of propagules, and unpalatability of the whole plant for most species of herbivorous fishes [68]. The inner-shelf reefs in our study experienced a significant increase in macroalgal cover following environmental disturbances (including but not limited to *Sargassum*). The loss of redundancy in the herbivorous fish assemblage on inner shelf reefs of the GBR where macroalgae is abundant, including loss of fish species that can remove the biomass of some macroalgal species combined with the increase in biomass and persistence of macroalgae following disturbances, may enhance both the recovery and spread of macroalgae on these inshore reefs. This may in turn hinder coral recovery [69,70] and consequently the recovery of coral-associated fishes. The inner shelf reefs post-disturbance may therefore show a substantially different trajectory of recovery to that of mid- and outer-shelf reefs, where turf algae dominate post-disturbance benthic communities and do not similarly prevent coral recruitment and growth.

That cross-shelf structure of roving herbivorous fish assemblages was distinct at each shelf position prior to disturbances is consistent with previous studies on the GBR [5,14,18,20,22,35–37]. The differences in assemblage structure of herbivorous fish among shelf positions are likely driven by the natural variation in environmental conditions across the shelf forming distinct habitats that favour particular species [5,7,22]. These conditions include higher exposure to terrigenous sediment and nutrient fluxes inshore [6], frequent perturbation from high wave energy on outer-shelf reefs [7,19], differential settlement habitats, potential variation in the supply of larvae [15], and predation pressure [71–73]. As herbivorous fishes are not generally targeted by fishers on the GBR [10,22] (some limited recreational spearfishing occurs [74]), fishing is unlikely to influence differences in assemblage structure of herbivorous fishes across the shelf [22]. Biophysical factors other than cyclones and bleaching that likely influence differences in assemblage structure cross-shelf (e.g., wave energy and terrestrial runoff of sediments and nutrients) may have varied during our study, and their potential effects should not be discounted. However, potential change in these other environmental drivers were not quantified here. Nevertheless, our study highlights the importance of extreme environmental disturbances on distinct ecological assemblages at different shelf positions. This study also suggests that inherent conditions that make inner-shelf reefs distinct may also make them particularly vulnerable to disturbance and perhaps slower to recover. If differences in environmental conditions do cause differential shelf responses to widespread disturbance events, this will likely manifest most noticeably as the reefs recover. Our study assessed coral reef assemblages across the continental shelf just six months after the most recent disturbance event in the series. Thus, it is too soon to allow documentation of the long-term recovery trajectory of each shelf assemblage, both benthos and fish. Likely, benthic and fish assemblages at different shelf positions will remain distinct, but monitoring these different assemblages is necessary, particularly considering predicted climate change scenarios.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/2/23/s1. Table S1: Fish traits assigned to surveyed species. Trait classification based on published literature (Green and Bellwood 2009 [1]; Froese and Pauly 2018 [2]; Mouillot et al. 2013 [3]). Schooling trait categories abbreviated as follows: Small groups (SmallG); medium groups (MedG); large groups (LargeG). Table S2: Two-way nested PERMANOVA pairwise comparisons with Monte Carlo sampling estimates of taxonomic composition of herbivorous fish among shelf position and between years. Comparisons based on Bray-Curtis similarities of fourth root transformed data (shelf position and year, fixed factors; site random factor nested in shelf position; 9999 iterations). Herbivorous fish species consistently contributing to average similarity within assemblages across the shelf (grey boxes) in each year are listed (one-way SIMPER; sim/SD, dissim/SD > 2). Multivariate dispersion analysis (MVDISP) results shown with an index of multivariate dispersion (IMD).; Table S3: Pairwise comparisons (with lower and upper 95% confidence intervals: CI) of linear mixed effects models of variation in cross-shelf benthic composition and herbivorous fish assemblage structure in 2008/9 and 2016.

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