Fish and benthic communities in an offshore and well-managed coral reef after bleaching disturbance in the Philippines

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Research Article

Abstract

Climate change is perhaps the greatest threat to coral reefs worldwide. However, there is spatial variation in the extent and severity of this disturbance, with offshore and well-managed reefs presumed to minimize the consequences. In this study, fish and benthic communities at the offshore and well-managed reefs of Apo Reef Natural Park, Philippines was examined during (2016), 2 years (2018) and 3 years (2019) after bleaching disturbance. Fish and benthic surveys were conducted on scuba at 5 sites at depths of 8-10m. Results showed that benthic communities varied more strongly with year attributed to changes in the benthic cover of coral. These changes were also influenced by site, with some sites experiencing coral loss of 41–48%, while at other sites there were minimal changes. These site differences were associated with the cover of coral pre-bleaching, with higher cover prior to the disturbance contributing to larger losses. Fish communities varied more with sites associated with differences in the predominant benthos among sites. The stability of fish communities with year despite coral loss may be attributed to the variable loss of coral cover among sites. For sites that experienced high losses of coral cover, the presence of alternative and/or deeper habitats may have provided shelter and food for fishes maintaining taxonomic composition within sites. This study shows that bleaching disturbance circumvents localized protection, but impacts are variable even at small (≤ 3km) spatial scales. Community composition pre-bleaching and alternative habitats seem to buffer against the consequences of bleaching disturbance.

Introduction

Coral reefs are one of the most biodiverse yet vulnerable ecosystems on the planet. Stressors affecting coral reef ecosystems can be localized (e.g., eutrophication and overfishing) or global (e.g., climate change and ocean acidification) influencing coral reef processes at varying spatial scales from a few meters to hundreds of kilometers (Jackson et al.; D'Angelo and Wiedenmann 2014; Hoey et al. 2016; Roche et al. 2018). Of these stressors, climate change-induced thermal stress that cause mass coral bleaching and coral mortality may perhaps be the greatest threat that coral reefs presently face due to its large spatial coverage (Hughes et al. 2017). To date, most of the world's reefs have been affected by three global bleaching events (i.e., 1983–1984, 1997–1998 and 2014–2017), although the magnitude of coral bleaching and coral mortality varied among reefs, geographic locations, and bleaching events (Heron et al. 2016; Eakin et al. 2019). For example, during the recent 2014–2017 coral bleaching events, there was location-dependent heterogeneity in the recorded range of coral bleaching prevalence, coral mortality, and/or coral recovery at various reefs from the Atlantic to the Indo-Pacific (Gintert et al. 2018; Harrison et al. 2019; Banha et al. 2020; Ng et al. 2020; Quimpo et al. 2020; Xie et al. 2020). For some of these reefs' annual variation in coral bleaching prevalence and coral loss was also recorded (Harrison et al. 2019). While corals experience the immediate effects of thermal stress with a potential increase in mortality and decline in population, the indirect loss of corals and the habitat they provide may also negatively affect associated fauna, such as coral reef fishes.

There are 4000 estimated coral reef fishes in the world, with ~ 320 species from 39 families known to use live corals as habitats for a portion of or throughout their life spans (Coker et al. 2014). These tight associations between reef fishes and corals are attributed to corals providing nutrition for a suite of reef fishes (Cole et al. 2011), the high structural complexity of corals that can mitigate competition and predation (Almany 2004; Coker et al. 2014), serve as settlement and recruitment habitats(Jones et al. 2004) and reducing energetic demands in high-water flow environments (Johansen et al. 2008). The reliance of reef fishes on corals suggests that any major changes in coral cover and coral assemblages can have negative consequences for reef fishes. Indeed, fish species diversity and abundance have been shown to decline in accordance with coral loss due to large-scale disturbances(e.g., Cheal et al. 2002; Wilson et al. 2006) including thermal stress and coral bleaching (Munday et al. 2008; Pratchett et al. 2008, 2011, 2018). However, the effects of coral loss on reef fishes are not homogenous, as different trophic groups and fish families vary in their responses to changes in coral cover. For example, corallivores (Chaetodontidae) and residential planktivores (Pomacentridae) are generally severely affected by coral bleaching and decline in densities or experience sub-lethal consequences due to the loss of their main source of nutrition and/or habitat (Pratchett et al. 2004; Graham et al. 2006, 2008). In contrast, other groups, such as invertebrate feeders (Mullidae), roving herbivores (Labridae: Scarinae) and detritivores (Acanthuridae), respond positively to the loss of coral cover attributed to the increase of their foraging areas and/or food items (Russ et al. 2015a, 2015b, 2015c, 2018).

Although coral loss has been shown to reduce fish diversity and abundance, the magnitude of such loss is influenced by the severity of coral cover decline. Coral loss and associated changes in fish assemblages are largely heterogenous and varies across wide geographic spatial scales (Graham et al. 2008). Geographic locations that are offshore, isolated, managed and protected, and away from nearby human settlements are presumed to buffer against significant coral loss from environmental disturbances(Bellwood et al. 2003; Graham et al. 2008; Halford and Caley 2009) as confounding localized stressors (e.g., pollution and overexploitation) are reduced or non-existent (Sandin et al. 2008). While some studies show that these reefs seem to be robust against coral loss (e.g., Graham et al. 2008; Harrison et al. 2019), others have shown great changes in coral and fish communities (Graham et al. 2006), or documented an initial decline in corals and reef fishes before communities recovered after some time (Halford and Caley 2009; Gilmour et al. 2013). The diversity of these outcomes perhaps suggests that numerous variables nested within these offshore reefs influence their ability to minimize the negative consequences of coral loss.

In this study, fish and benthic communities at Apo Reef Natural Park (ARNP), central west Philippines were examined at 3 time periods (during, 2 years and 3 years after a coral bleaching event). ARNP is an offshore reef that has been properly managed and protected for 26 years and provides an opportunity to examine the effects of coral bleaching in the general absence of localized stressors. Specifically, investigation on potential changes in fish (species richness, abundance, and trophic group composition) and benthic communities (benthic identity and cover) at 5 reef sites at the ARNP from years 2016, 2018 and 2019 were conducted. This study expands local coral reef research that are predominantly conducted in inshore reefs(e.g., Gomez et al. 1994; Nañola et al. 2011; Go et al. 2015; for exceptions see Nacorda et

al. 2017; Quimpo et al. 2018, 2019) and more importantly contributes to our understanding on the response of offshore and well-managed reefs to large-scale environmental perturbations.

Materials And Methods

Study sites

Five coral reef sites were surveyed at the Apo Reef Natural Park (ARNP) central west Philippines (Fig. 1). ARNP is an offshore coral reef ecosystem within the West Philippine Sea biogeographic region. This region has been documented to have one of the highest fish species richness in the country (Nañola et al. 2011). It is ~ 45 km away from mainland Occidental Mindoro and is one of the largest (11,667 ha) and well-protected Marine Protected Areas (MPAs) in the country (Cabral et al. 2014). ARNP receives little terrestrial influx from the mainland (Cabaitan et al. 2019) and fishing has been banned throughout the entire MPA since 1996 till the present. ARNP has few human inhabitants (≤ 10 people), with these being the managers that enforce the protection of the MPA. Tourist and research visitors may temporarily increase the human inhabitants at the island, but these are thoroughly regulated by the managers with the number of people barely exceeding 50/day. The lack of localized stressors, together with the implementation of good management and governance, at the ARNP perhaps contributed to the maintenance of high coral cover, fish abundance and fish biomass, and the presence of rare fauna (e.g., bumphead parrotfish *Bolbometopon muricatum* and humphead wrasse *Cheilinus undulatus*) that have disappeared from reefs elsewhere in the country (Nañola et al. 2011; Lavides et al. 2016; Quimpo et al. 2018a, b, 2019; Dumalagan et al. 2019).

Occurrence Of Thermal Stress, And Reef Fish And Benthic Assemblage Surveys

ARNP temperature and Degree Heating Weeks (DHW) data from 2014 to 2019 were obtained from the National Oceanic Atmospheric Administration (NOAA Coral Reef Watch 2016). NOAA data revealed that Max Monthly Mean Sea Surface Temperatures (MMM-SST) at ARNP ranged from 29 to 30°C with coral bleaching threshold estimated at 31°C (SFig 1). ARNP experienced thermally stressful conditions annually from 2014 to 2017 during the months of May to June, albeit the duration of the heat stress varied per year (SFig 1). The 2014 heat stress lasted longer at approximately 10-weeks, whereas the 2015 and 2016 heat stress were shorter at about 4- and 6-weeks, respectively (SFig 1). Reconnaissance surveys in 2015 and instrument deployment and retrieval activities in 2016 and 2017 affirmed that coral communities at ARNP did bleach (SFig 2), but the extent of coral bleaching was not assessed due to logistics.

Reef fish and benthic community surveys were conducted in March 2016 (2 months before coral bleaching occurred) and in October 2018 and 2019 (2 and 3 years after the coral bleaching event). In each coral reef site, three 25m transect tapes were laid at the reef crest at a depth of approximately 8 to

10 m. Each transect tape was spaced 5m apart from one another with tape orientation parallel to the shore. Underwater Visual Census (UVC) was used to survey all fish species encountered within the 25m x 5m (125 m^2) area. Encountered fish individuals were identified to species level and counted, with care taken to minimize recounting of individuals. Fishes recorded were assigned to family and trophic groups based on www.fishbase.org (Froese and Pauly 2022). Benthic communities were assessed using photo-quadrat surveys. Within each transect tape, 1m x 1m quadrats were placed atop the benthos, with images of the benthos taken ~ 1m above the substratum. Images were taken for each meter of the transect tape, which yielded a total of 25 images per transect tape. Images were analyzed using Coral Point Count with excel Extension(CPCe; Kohler and Gill 2006) software. For each image, 10-points were randomly overlaid, with the observer identifying the benthos that intercepted the points. Benthic categories were classified as scleractinian coral (C), octocoral (OCT), soft coral (SC), macroalgae (MA), turf algae (TA), other (OT) organisms (i.e., anemones, ascidians, bryozoans, mollusks, clams, and urchins), dead coral with algae (DCA), coralline algae (CA) and sand/rubble (SA_RB). Benthos identified as scleractinian corals were further classified according to genus (with reference to Richards 2018) and morphology.

Statistical Analyses

To examine spatial and temporal variation in reef fish communities when constrained by *a priori* defined explanatory variables, distance-based redundancy (DBRDA) on square-root transformed fish data with Bray-Curtis dissimilarity distance was used. Constraints used were site (Aladin, Ego Wall, Mabuti, Shark Airport and South Corner), year (2016, 2018, 2019) and benthic categories (coral, octocoral, soft coral, macroalgae, turf algae, other organisms, dead coral with algae, coralline algae, and sand/rubble). To avoid overfitting the DBRDA model, the most influential constraints were identified with the aid of stepwise permutation tests using function "ordR2step" in the R package vegan (Oksanen et al. 2022). This method added or dropped constraints until a model with the "best" adjusted R2 was identified. To identify fish species that contributed to the dissimilarities among communities, the two main axes of the DBRDA ordination was correlated with the fish community data using function "envfit" in vegan. Influential (p < 0.01) fish species were identified through 5000 permutation tests. These influential fish species were then displayed on the ordination as vectors, where the direction and length of the arrow corresponds to the location and magnitude of change, respectively. DBRDA was also used to examine compositional variation in benthic community data when constrained by site and year. Benthic data was square-root transformed prior to analysis, with the Euclidian distance matrix used. Influential (< 0.01) benthic categories that contributed to the dissimilarities among communities was also identified using "envfit", with 5000 permutations and vectors superimposed unto the DBRDA ordination.

To examine variation in fish abundance among sites, years, and trophic groups (benthic invertivore, corallivore, detritivore, herbivore, omnivore, piscivore and planktivore), generalized linear models (GLMs) were used. Data was initially fitted with a poisson distribution and log link function, but model diagnostics suggested overdispersion. To address overdispersion, a negative binomial distribution was used. To examine variation in benthic cover among sites, years, and benthic categories (coral, octocoral,

soft coral, macroalgae, turf algae, other organisms, dead coral with algae, coralline algae, and sand/rubble), a binomial GLM with logit function was used. For both models, model diagnostics (e.g., residuals vs fitted, qqplot) were done using DHARMa (Hartig 2022) package in R. Model selection used Akaike Information Criteria (AIC), where we compared the interactive (site * year * trophic group/benthic category) and additive model (site + year + trophic group/benthic category), with the model with the least AIC score chosen as the "best" model. R2 values for both fish and benthic models were identified using the function "r.squaredLR" in the R package MuMIn (Barton 2022). Pairwise comparisons using Tukey's was also conducted to determine which groups within and among variables were statistically significant. All analyses were done in R statistical software version 4.2.2 (R Core Team 2022).

Results

Reef fish communities

The DBRDA results revealed that there was variation in fish communities when constrained by sites, years, and benthic categories. Of the constraints fitted, the "best" model only included sites, years, and the benthic categories: other organisms and turf algae. Together these constraints explained 48.73% of the observed variation among fish communities (Fig. 2). Of the constraints, sites seem to be more influential with Aladdin and Shark Airport dissimilar from the communities of Ego Wall, Mabuti and South Corner. Year had a comparatively minor influence on fish communities, except for Mabuti where communities in 2019 were dissimilar from communities in 2016 and 2018. The benthic constraints other organisms and turf algae were associated with the fish communities of Shark Airport and Mabuti 2019. Nineteen fish species were identified to have contributed to the dissimilarity among fish communities (Fig. 2). Ten of these fish species (*Amblyglyphidodon aureus*, *Chaetodon baronessa*, *Pomacentrus moluccensis*, *Chaetodon auriga*, *Cephalopholis argus*, *Chromis viridis*, *Chromis retrofasciata*, *Neoniphon samara*, *Cheilodripterus quinquelineatus* and *Dascyllus reticulatus*) were associated with Aladdin, while 9 (*Chaetodon kleinii*, *Pomacentrus vaiuli*, *Pomacentrus coelestis*, *Parupeneus multifasciatus*, *Scolopsis bilineata*, *Sufflamen bursa*, *Acanthurus japonicus*, *Ctenochaetus striatus* and *Oxycheilinus unifasciatus*) were associated with Shark Airport and Mabuti 2019.

Fish species richness at the ARNP ranged from 42 to 85 species, varying among sites and years (Fig. 3). Aladdin did not show changes in species richness among sites and years, while Shark Airport showed a slight increase only in 2019. In contrast, Ego Wall, Mabuti and South Corner had a slight decline during 2018, but richness increased afterwards and mirrored richness in 2016. There were differences in fish abundance at the ARNP (Fig. 4) and these were attributed to the interaction between sites, years, and trophic groups. The full interactive GLM that contained all these terms explained 50.98% of the observed variation. This suggests that the magnitude of changes in the abundance of reef fishes were heavily dependent on the trophic group of the fish, the sampling site and year. For example, two of the most notable differences were changes in the abundance of herbivores and planktivores among years and sites. Pairwise comparisons for herbivores; revealed that changes in Aladdin were attributed to differences in 2016–2018 (39% increase); 2016–2018 and 2018–2019 in Shark Airport (65 and 51%

increase, respectively) and South Corner (86 and 87% increase, respectively); 2016 vs 2018 and 2019 in Ego Wall (95 and 202% decline, respectively); and among all pairs in Mabuti (78–258% decline). For planktivores, Mabuti did not show changes in fish abundance with years and sites; pairs between 2016 and 2019 in Ego Wall (66%) and Shark Airport (85%) showed increases in planktivores; while Aladdin and South Corner had differences between pairs in 2016 and 2018 (66 and 70% increase, respectively) and 2016 and 2019 (49 and 81% increase, respectively).

Benthic Communities

The DBRDA results suggests that there was variation in the benthic communities when constrained by sites and years at the ARNP (Fig. 5). These two constraints explained 95.56% of the variation. Benthic communities were more strongly clustered according to year, with communities in 2016 dissimilar from 2018 and 2019. However, the extent of dissimilarity within communities were also dependent on site. For example, there were greater multidimensional distances in communities in Mabuti and Ego Wall when compared with Shark Airport. The benthic categories that contributed to the dissimilarity among communities were coral, turf algae, coralline algae, and dead coral with algae. Coral cover was associated with communities in Aladdin and Mabuti in 2016; turf algae was associated with Ego Wall 2016 and South Corner 2016, 2019; dead coral with algae was associated with Shark Airport and Ego Wall 2018; and coralline algae was associated with Ego Wall 2019.

There were differences in the cover of benthic categories at the ARNP and these were influenced by site, year, and identity of the benthos (Fig. 6). The interaction between these three terms explained 57.36% of the observed variation. Of the benthos, notable differences in dead coral with algae and coral cover were recorded, with the extent of these changes varying among sites and years. Dead coral with algae increased in cover at four sites (Aladdin, Shark Airport, Ego Wall and Mabuti). At Aladdin dead coral with algae covered increased by 21% from 2016 to 2019, while at Shark Airport it increased by 22% from 2016 to 2018. At Ego Wall and Mabuti, dead coral with algae also increased from 2016 to 2019, ranging from 20–44% in the former and 20–50% in the latter. Coral cover decreased only in two sites, Ego Wall and Mabuti, with the rate of decline 41% for the former and 18–48% for the latter. Majority of the coral loss at these sites were of the abundant genera *Acropora*, *Porites* and *Seriatopora*, with the branching morphology predominantly affected (SFig. 3–4).

Discussion

Sea surface temperatures that were conducive to coral bleaching was experienced at the ARNP, an offshore and well-managed coral reef ecosystem in the Philippines. The impact of this large-scale disturbance at the ARNP varied among taxonomic communities. Benthic communities were more strongly dissimilar among years than among sites, with variation among years attributed to the increase in dead coral and the decrease in coral cover. While the influence of site in benthic communities was comparatively minor, two (i.e., Ego Wall and Mabuti) of the five sites experienced more drastic declines

(41–48%) in coral cover over others. The higher coral loss at these sites correlates with their comparatively higher coral cover pre-bleaching. This suggests that small-scale (≤ 3km) variability in the composition of benthic communities influence the impact of bleaching disturbance. In contrast, fish communities were more strongly dissimilar among sites than years. This suggests that despite the large-scale disturbance, there were little changes in the fish communities. The site variation in the fish communities was likely associated with the predominant benthos in each site, which supports a different suite of fishes. Indeed, at two sites (i.e., Aladdin and Shark Airport) with different predominant benthos (i.e., coral in Aladdin and other organisms and turf algae at Shark Airport), the associated fishes were different. Coral-associated damselfishes, cardinalfishes and butterflyfishes were associated with Aladdin, while benthic invertivores and herbivores/detritivores were associated with Shark Airport. Although, the influence of year in fish communities was small, one site in particular (Mabuti) had dissimilar communities in 2019 when compared to 2016 and 2018. This suggests that fish communities at the ARNP were minimally affected by the bleaching disturbance. This minimal effect was perhaps influenced by the availability of alternative and deeper habitats that provided shelter and food for reef fishes, maintaining taxonomic composition. These results suggests that localized protection does not safeguard against bleaching disturbance, but small-scale variation in benthic composition and availability of alternative and/or deeper habitats may alleviate the negative consequences.

Benthic communities at the ARNP varied more strongly among years than among sites. These yearly differences were attributed predominantly to changes in the benthic composition at Ego Wall and Mabuti. In these two sites, there were pronounced differences in coral and dead coral cover among years. Coral cover decreased by 41–48% at both sites in 2019, while dead coral cover increased by 44–50%. This loss in coral cover may be attributed to 3 coral genera (*Acropora*, *Porites* and *Seriatopora*) of branching morphology. Previous studies have shown the vulnerability of branching *Acropora*, *Porites* and *Seriatopora* to bleaching disturbance (Loya et al. 2001; van Woesik et al. 2011). Furthermore, coral cover prior to the bleaching disturbance may have been associated with the severity of coral loss as Ego Wall and Mabuti had higher coral cover compared to the other sites. Higher coral cover is associated with larger sized colonies or number of individual colonies thereby increasing the likelihood of colonies being affected by bleaching disturbance when compared to sites with smaller sized colonies or lower number of individuals (Bena and van Woesik 2004; Lafratta et al. 2017; Kim et al. 2019; Quimpo et al. 2020). Indeed, at South Corner and Shark Airport, where coral cover was comparatively lower, there were no changes in coral cover among years. Interestingly, Aladdin had high *Acropora* cover that remained relatively unchanged throughout the years. This was perhaps associated with water flow as the direction of currents pushes water from Aladdin southward (Cabaitan et al. 2019). The potentially high flow environment in Aladdin likely minimized the effects of bleaching disturbance (Fabricius 2006; Bayraktarov et al. 2013).

Fish community dissimilarity at the ARNP was more strongly influenced by sites than by years. This site variation was attributed to the predominant benthos at each site, perhaps supporting different suites of reef fishes. Indeed, at Aladdin, where corals were abundant, majority of the fishes were coral-associated damselfishes (*Amblyglyphidodon aureus*, *Pomacentrus moluccensis*, *Chromis viridis*, *C. retrofasciata* and

Dascyllus reticulatus), cardinalfishes (*Cheilodipterus quinquelineatus* and *Neoniphon samara*) and butterflyfishes (*Chaetodon baronessa* and *C. auriga*) (Coker et al. 2014). In contrast, in Shark Airport, where other organisms and turf algae were abundant, the associated fishes were benthic invertivores (*Oxycheilinus unifasciatus*, *Sufflamen bursa*, *Scolopsis bilineata* and *Parupeneus multifasciatus*) and herbivores/detritivores (*Acanthurus japonicus* and *Ctenochaetus striatus*). These site differences in fish communities likely reflect the differential dietary and habitat requirements of fish species. While the influence of year on fish communities at the ARNP was minor, communities in 2019 at Mabuti were dissimilar in the multidimensional space when compared to communities in 2016 and 2018. It is currently unknown why only Mabuti experienced shifts in fish communities at the ARNP.

The relative stability of the fish communities among years despite changes in the benthos, particularly coral cover (upwards of 40% loss at two sites), may be attributed to the availability of alternative habitats that were unaffected by the bleaching disturbance (Graham et al. 2008). These habitats perhaps sustained the dietary and shelter requirements of most fishes at the ARNP. While this study only examined depths of 8-10m, previous works have revealed that coral reefs at the ARNP are expansive spanning multiple depths from 0 to 150 m (Cabaitan et al. 2019), with broadly comparable coral cover at depths of 10 to 30 m (Dumalagan et al. 2019; Albelda et al. 2020). Depths of 30m have been documented to reduce the impacts of bleaching disturbance (Bridge et al. 2013; Crosbie et al. 2019). Furthermore, environmental variables until 30m are not dissimilar enough from shallow reefs perhaps allowing movement of some fishes among depth gradients (Slattery et al. 2011). Studies in Hawaii (Walsh 1983) and Australia (Lewis 1997; Crosbie et al. 2019) similarly documented no changes in fish communities despite substantial (> 30%) coral loss. In contrast, other studies have documented declines in fish species richness and shifts towards alternative fish communities following coral loss of greater than 10% cover (Graham et al. 2006; Wilson et al. 2006; Richardson et al. 2018). These contrasting results reinforce the spatially variable impacts of bleaching disturbance on benthic and fish communities.

There were differences in the abundance of reef fishes at the ARNP attributed to the interaction between sites, years, and functional groups. Contrary to our expectations, we did not detect changes in corallivores at the ARNP. Previous studies have shown the sensitivity of corallivores to coral loss due to their reliance on corals as food (Graham et al. 2008; Pratchett et al. 2008). This lack of change was attributed to (1) three sites (i.e., Aladdin, Shark Airport and South Corner) not experiencing drastic changes in coral cover and (2) the potential alternative food sources at the two other sites (i.e., Ego Wall and Mabuti) that experienced heavy coral loss. At Ego Wall and Mabuti, other potential food sources such as *Pocillopora* and *Montipora* (to a lesser degree) (Pratchett 2007) showed rather stable percentage cover at the ARNP. In contrast, herbivores are presumed to positively respond to coral loss as the demise of corals frees up substrate for algae to occupy (Russ et al. 2015a, b, 2018; Taylor et al. 2020). At the ARNP, however, the response of herbivores was site-dependent, where abundance at Ego Wall and Mabuti declined, while it increased at the other three sites. The cause of this decline at Ego Wall and Mabuti was probably the loss of corals at these sites because even if herbivores are not entirely dependent on corals, some species are still highly associated (Coker et al. 2014). At the other three sites, the reason for the increase in herbivores is unknown as there were no noticeable changes in turf and macroalgae. This suggests that other

variables aside from food availability may be shaping the herbivores at the ARNP. Planktivores increased in abundance at the ARNP in all sites surveyed. Interestingly, this increase was also recorded in Ego Wall and Mabuti where coral cover declined, even though coral loss has been associated with reduction in planktivore abundance (Russ et al. 2017). The persistence and increase of planktivores despite coral loss at the ARNP may be attributed to the presence of deeper habitats (Quimpo et al. 2018b; Dumalagan et al. 2019; Albelda et al. 2020) and/or the documented upwelling events (Cabaitan et al. 2019) that move nutrient-rich water to the surface.

The coral loss experienced at the ARNP for some sites were broadly comparable to other offshore reefs in the country that experienced bleaching disturbance, but much lower than offshore reefs at other geographic locations. In 1998, thermal stress and mass coral bleaching was documented in the Philippines, with ~ 45% decrease in coral cover recorded at one offshore location (Tubbataha; Arceo et al. 2001). This large decline in coral cover following bleaching was associated with high (~ 60%) coral cover pre-bleaching (Arceo et al. 2001). In contrast, more recent studies from the 2014–2017 bleaching event showed minimal effects of thermal stress on corals at 3 fringing reef sites in the Philippines because of cold water influx (Keith et al. 2018), turbidity (Valino et al. 2021) and preponderance of heat tolerant corals (Quimpo et al. 2020). This suggests that within the country, offshore reefs may be more vulnerable to increases in sea surface temperatures than fringing reefs. When contrasted with coral loss of other offshore reefs in the Seychelles (Graham et al. 2006) and northwestern Australia (Gilmour et al. 2013), coral loss at the ARNP was 30–50% lower. The presence of deeper habitats and proximity to cooler waters at the ARNP (Cabaitan et al. 2019; Dumalagan et al. 2019; Albelda et al. 2020) may have reduced the impacts of the bleaching disturbance as similarly documented in offshore reefs at Chagos (Graham et al. 2008) and Australia (Harrison et al. 2019).

In summary, this study shows that offshore and well-managed reefs are equally vulnerable to bleaching disturbance and, in the Philippine context, are more susceptible than fringing reefs of similar or less management status. While bleaching disturbance was experienced at the ARNP, the effects varied with taxonomic communities and sites. Benthic communities were altered by the bleaching disturbance, but the magnitude varied with sites. Noticeable declines in coral cover were documented for some sites where upwards of 40% coral cover was lost, while at other sites, there were minor changes in cover. The severity of coral loss was perhaps associated with the cover of coral pre-bleaching as the two most affected sites had the highest cover before the disturbance. This suggests the importance of small-scale differences in benthic composition at alleviating the impacts of bleaching disturbance. Fish communities were structured more strongly by sites due to differences in benthos and the suite of fishes they support and showed minimal change across years. This suggests that fish communities were comparatively stable after the bleaching disturbance. This stability despite high coral loss at some sites was probably influenced by the presence of alternative and deeper habitats that provided shelter and/or food (Graham et al. 2008; Quimpo et al. 2018b; Dumalagan et al. 2019; Albelda et al. 2020). While offshore and well-managed reefs may experience lower localized stressors (Sandin et al. 2008), they are still affected by large-scale global disturbances, including climate change and coral bleaching. However, reef topography,

particularly the presence of alternative and/or deeper habitats, seems to minimize the consequences of bleaching disturbance (Graham et al. 2008; Harrison et al. 2019).

Declarations

Conflict of interest

The authors have no relevant financial or non-financial interest to disclose.

Author contributions

TJQ and PCC conceptualized the study. TJQ did the statistical analyses and prepared the first draft of the manuscript. All authors contributed to the collection and preparation of data, and commented and revised previous versions of the manuscript.

Data availability

Data collected and analyzed from this study are available from the corresponding author on a reasonable request.

Ethical standards

All international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained.

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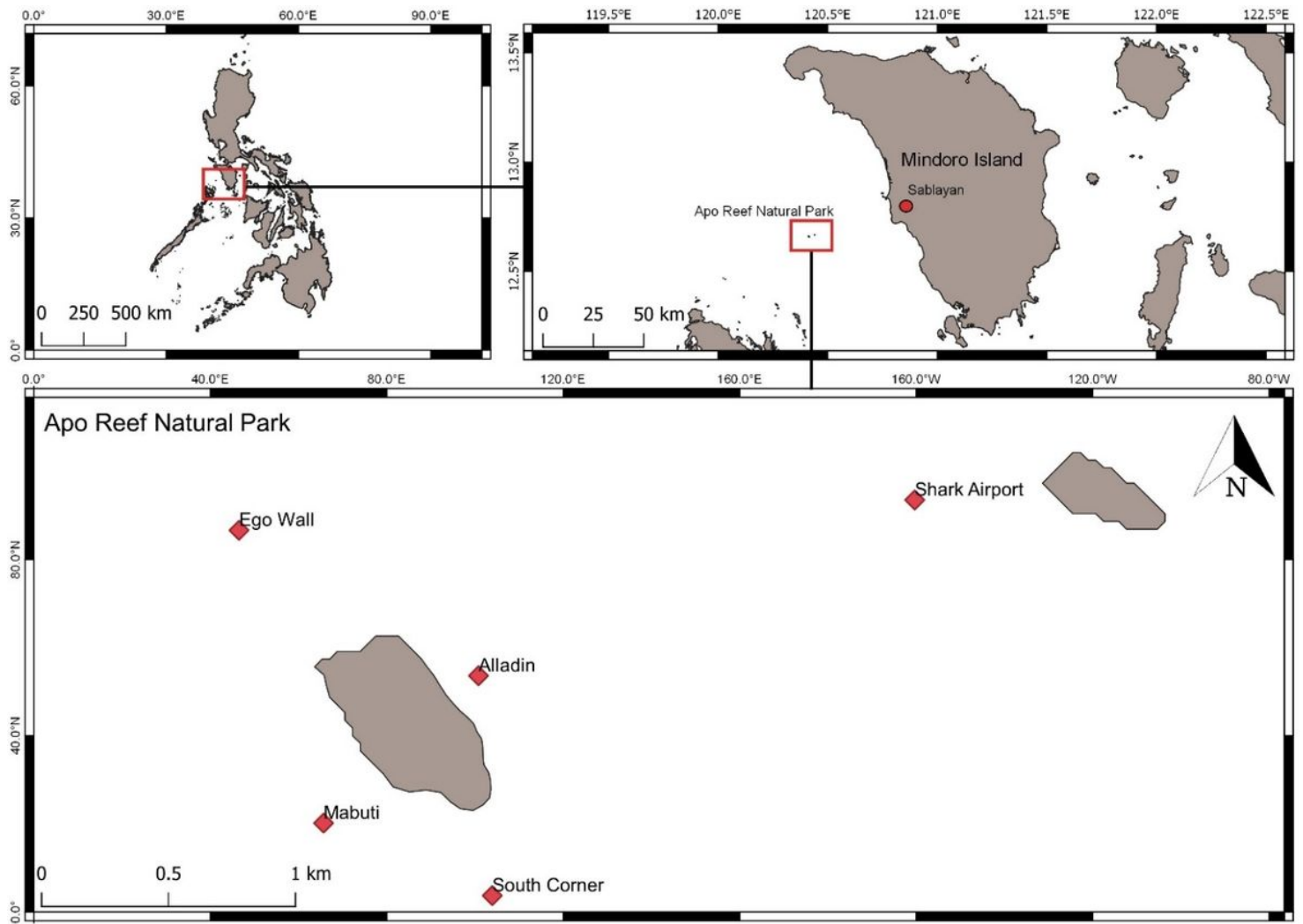
Figures

Figure 1

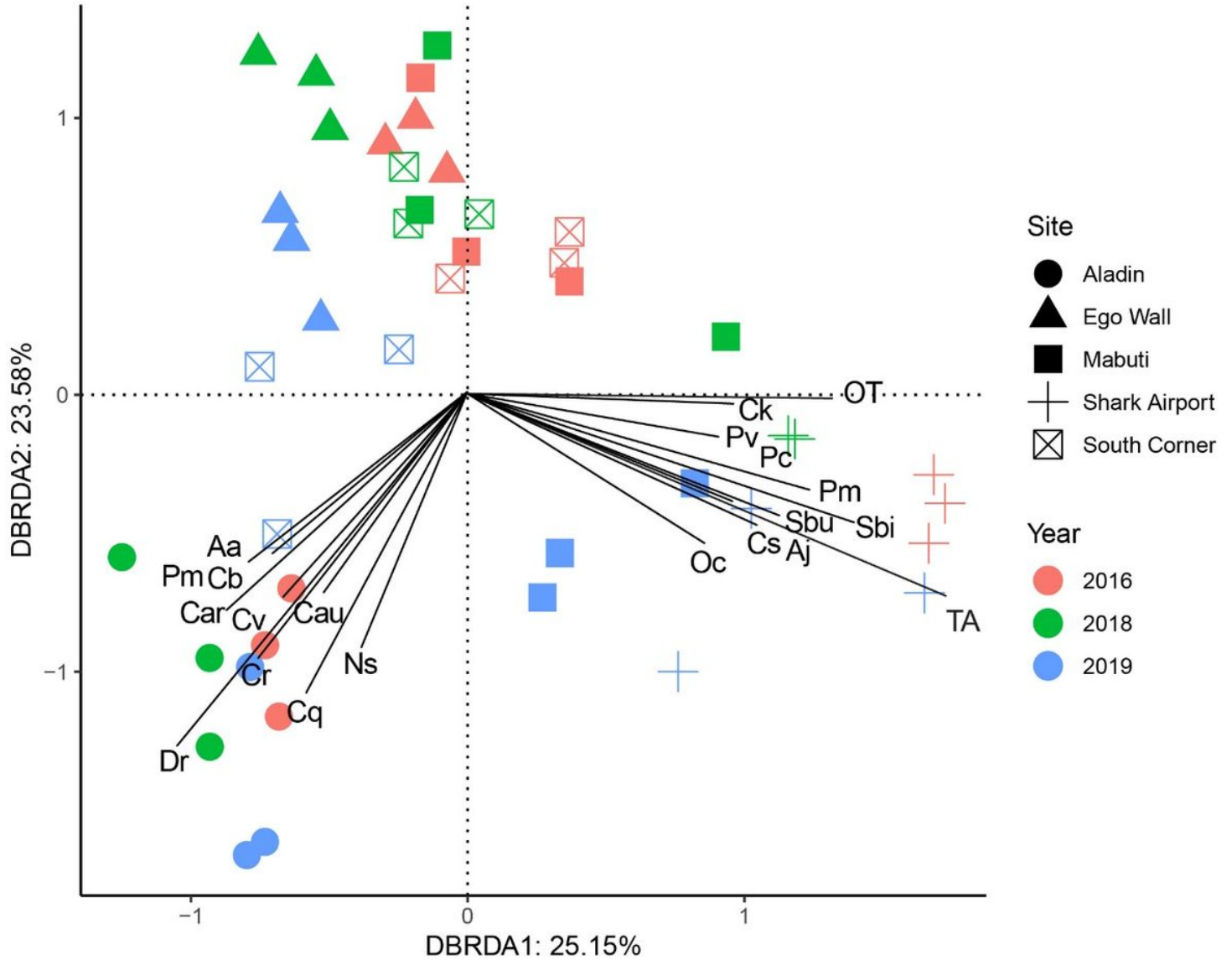Map of the study sites in the Apo Reef Natural Park, Philippines.

Figure 2

Distance-based redundancy ordination of the fish communities at the ARNP. Fish species and benthic categories that contributed (p < 0.01) to the dissimilarity among communities are overlaid as vectors. Abbreviation for fish species are: Aa: *Amblyglyphidodon aureus*, Pm: *Pomacentrus moluccensis*, Cb: *Chaetodon baronessa*, Car: *Cephalopholis argus*, Cv: *Chromis viridis*, Dr: *Dascyllus reticulatus*, Cr: *Chromis retrofasciata*, Cau: *Chaetodon auriga*, Cq: *Cheilodipterus quinquelineatus*, Ns: *Neoniphon sammmara*, Oc: *Oxycheilinus unifasciatus*, Cs*: Ctenochaetus striatus*, Aj: *Acanthurus japonicus*, Sbu:

Sufflamen bursa, Sbi*: Scolopsis bilineata*, Pm: *Parupeneus multifasciatus*, Pc*: Pomacentrus coelestis*, Pv: *Pomacentrus vaiuli,* Ck: *Chaetodon kleinii*. Abbreviation for benthic categories are: OT: Other organisms, TA: Turf algae.
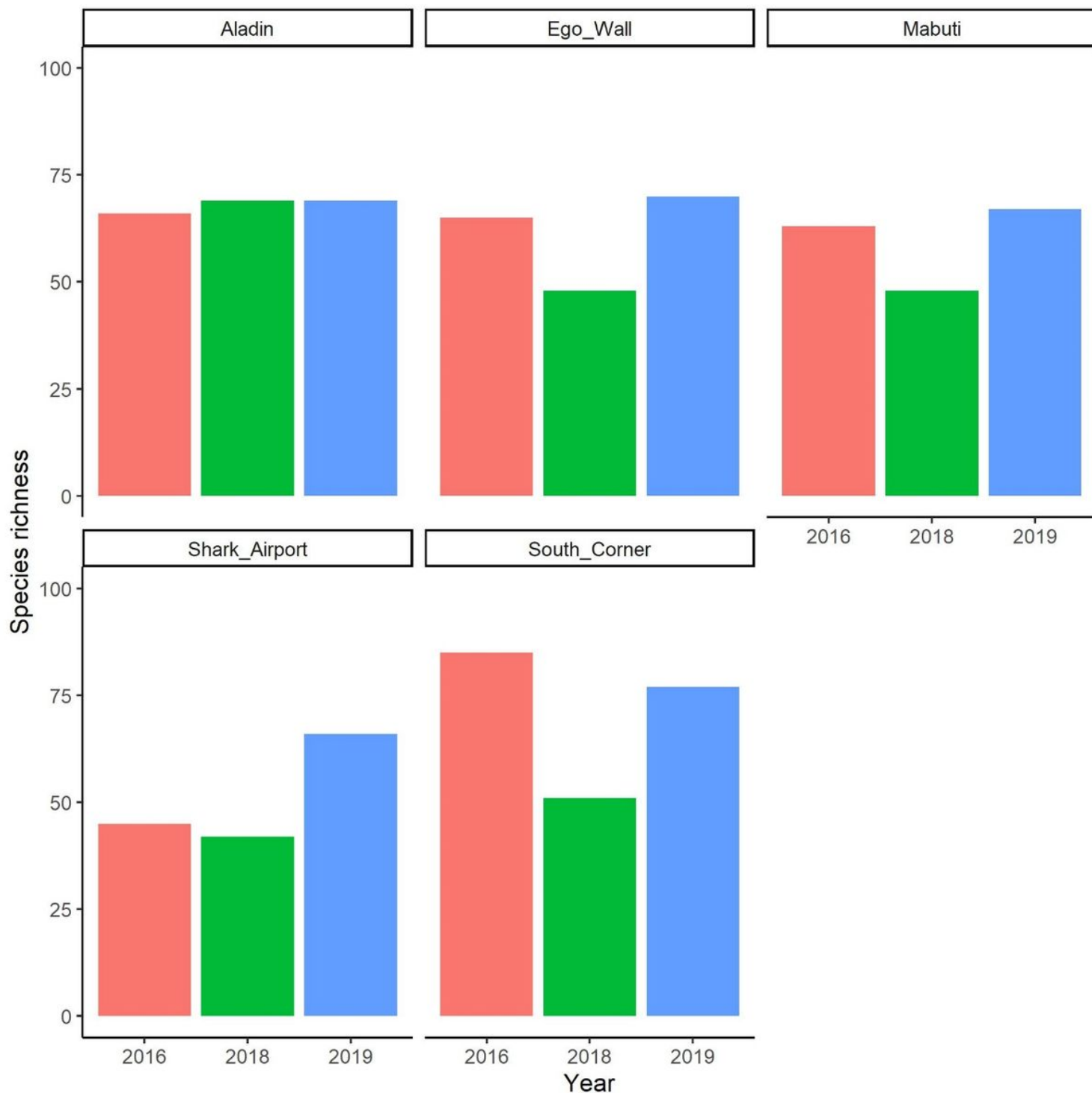

Figure 3

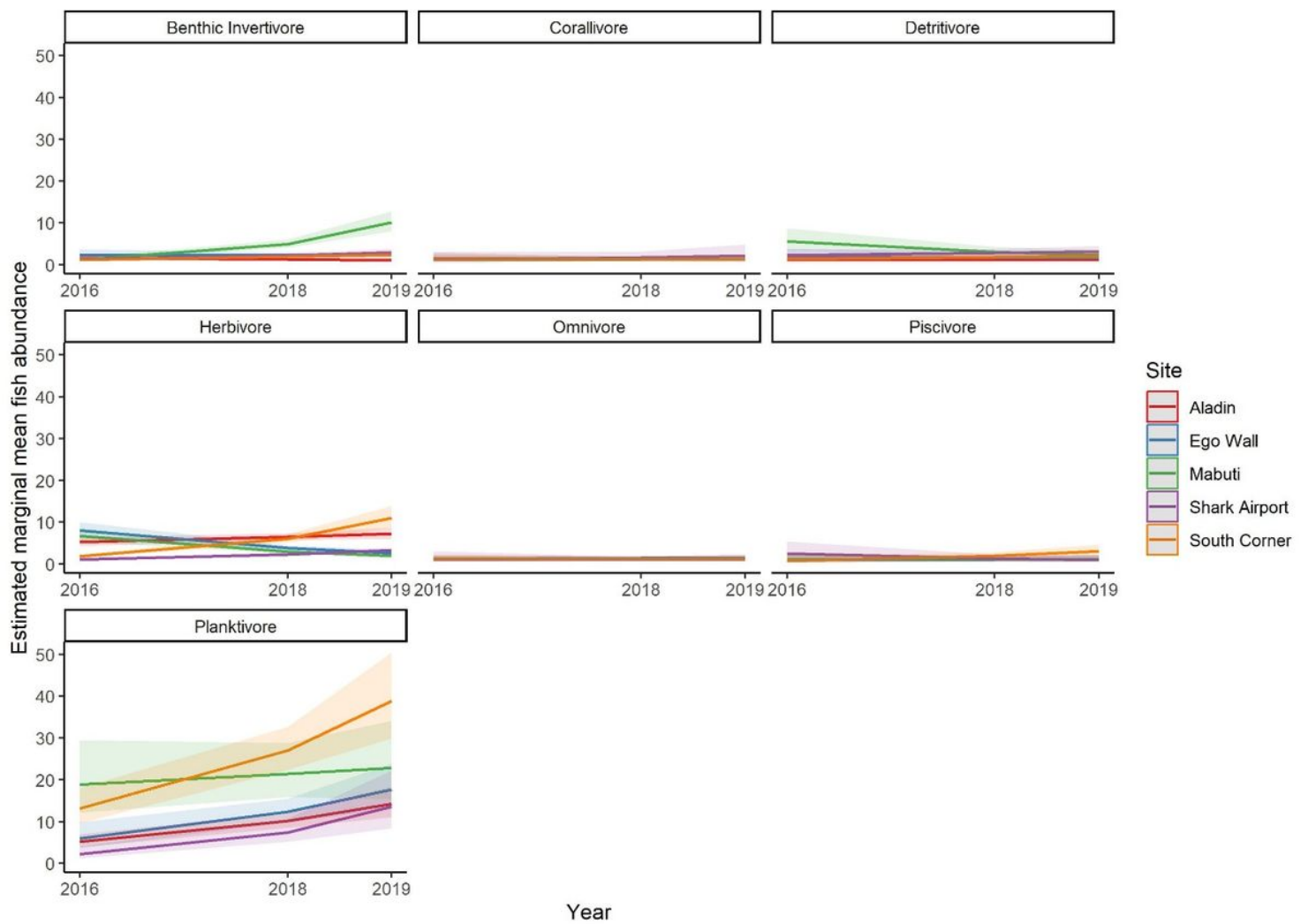Barplot of species richness among sites and years at the ARNP.

Figure 4

Lineplot of estimated marginal mean fish abundance with 95% confidence intervals among sites, years, and functional groups at the ARNP.
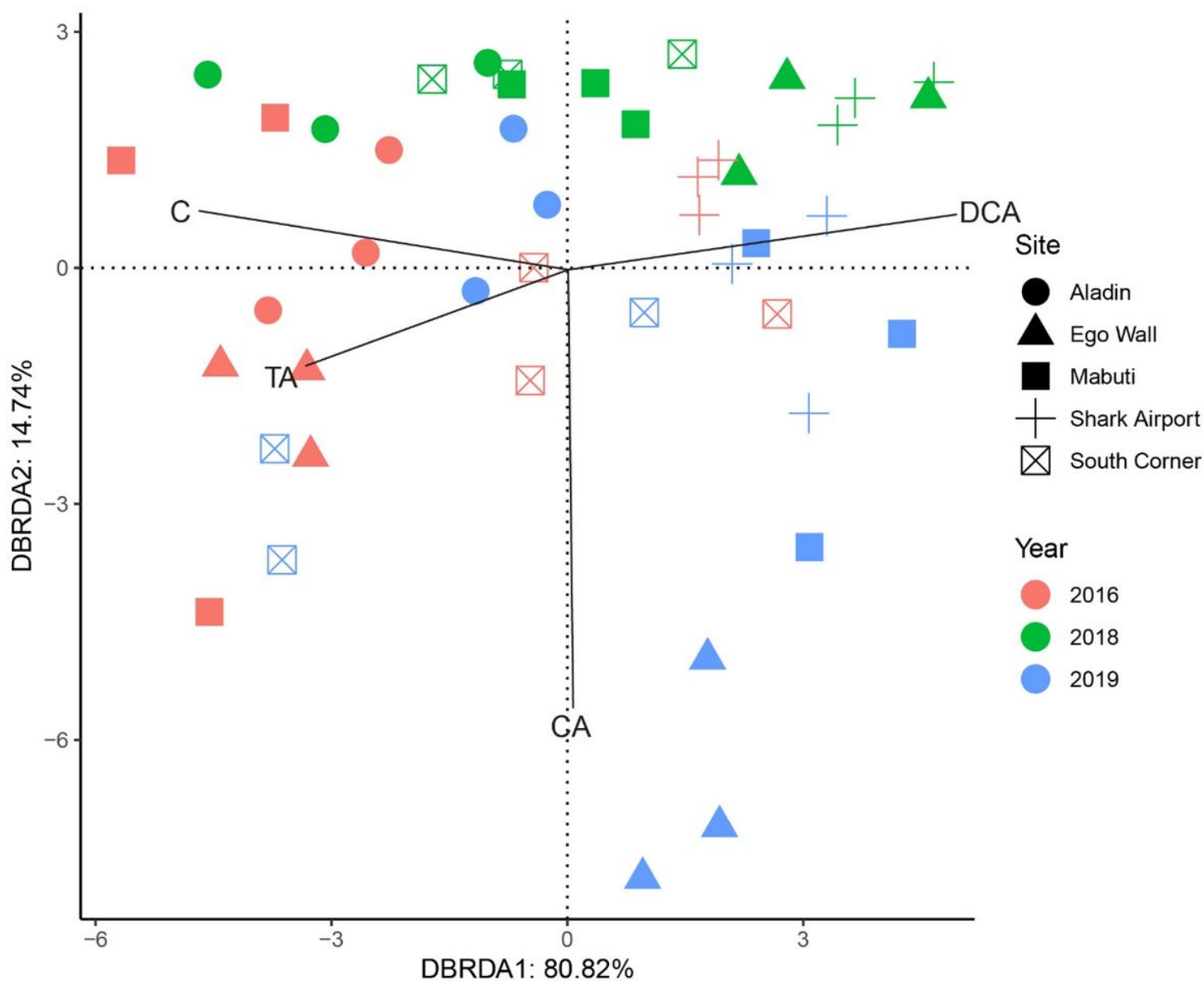
Figure 5

Distance-based redundancy ordination of the benthic communities at the ARNP. Benthic categories that contributed (p < 0.01) to the dissimilarity among communities are overlaid as vectors. Abbreviations are as follows: C: Coral, TA: Turf algae, CA: Coralline algae, DCA: Dead coral with algae.
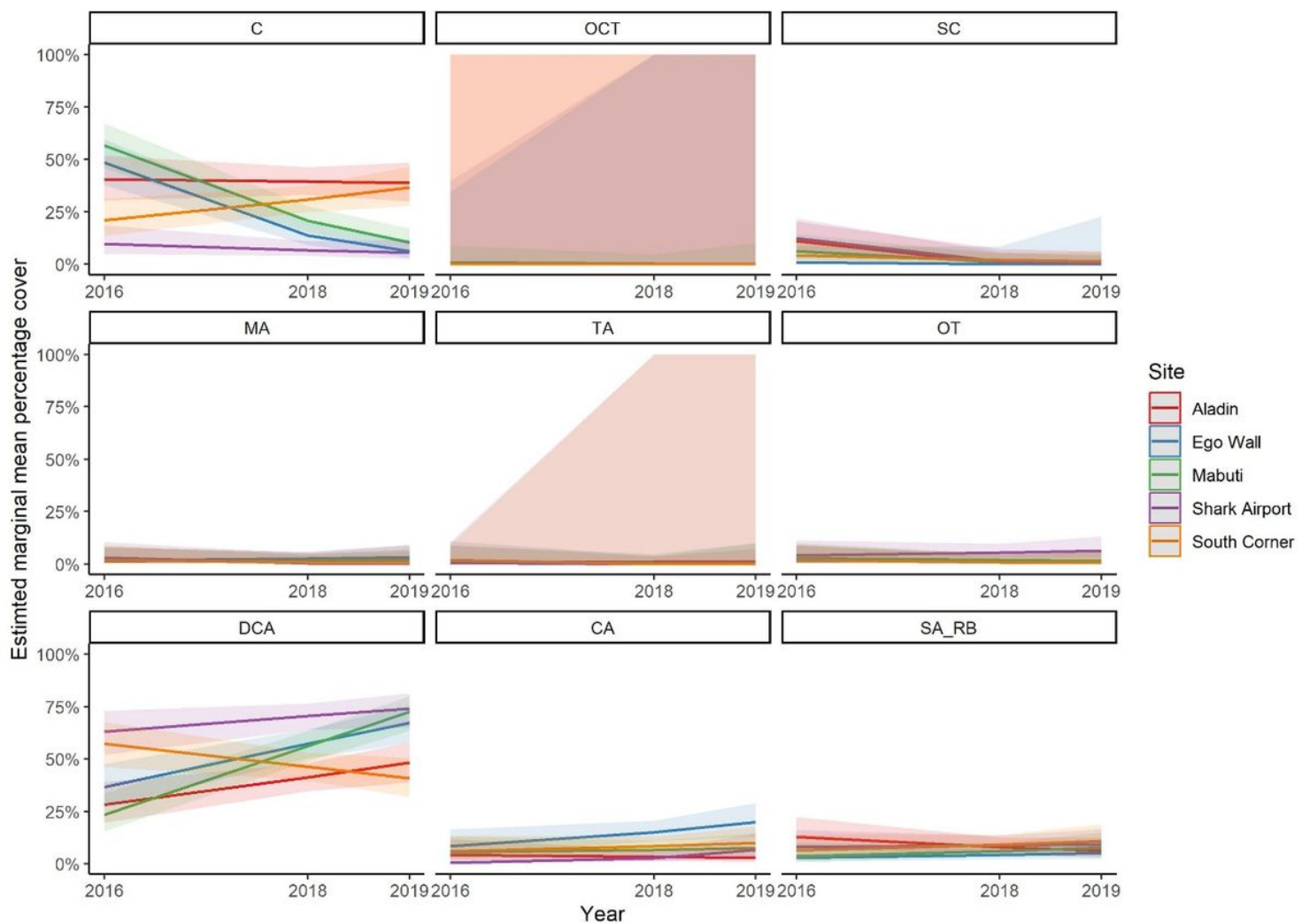
Figure 6

Lineplot of estimated marginal mean percentage cover with 95% confidence interval among sites, years, and benthic categories at the ARNP. Abbreviations of benthic categories are: C (coral), OCT (octocoral), SC (soft coral), MA (macroalgae), TA (turf algae), OT (other organisms), DCA (dead coral with algae), CA (coralline algae), SA_RB (sand/rubble).

Supplementary Files

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- SupplementaryMaterial2022Dec.docx