Can sponge morphologies act as environmental proxies to biophysical factors in the Great Barrier Reef, Australia?

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ABSTRACT

Sponges play a vital role in the world's most complex and vulnerable marine ecosystems. Various *in situ* studies have suggested that sponge morphologies (developed from exposure to a range of biophysical factors) can be considered as ecological indicators to current detrimental environmental changes such as climate change, overfishing, pollution and dredging for coastal development. Regional and long-term taxonomic data on sponges within each geographic range is not always available, especially from the Great Barrier Reef (GBR), due to dearth of sponge research. In this study, to understand large-scale variation and advance sponge research and knowledge, morphological characteristics were adopted as a rapid practical way to identify sponges from photo-transect images of a long-term dataset from the GBR. Biennial surveys were carried out in 2008 to 2014 from 28 pairs of take and no-take zones of the GBR. To evaluate the temporal changes in sponge morphology and correlation between abiotic factors, remote-sensed data such as chlorophyll *a*, current, wave height and sea surface temperature (SST) during the survey period were analyzed. Results showed sponges were ubiquitous in all six surveyed locations and their distribution was spatially heterogeneous. Encrusting forms were dominant followed by upright, massive, cups and tabular growth forms. Sponges were more prevalent in Innisfail, Pompey and Townsville compared to Cairns, Swain and Capricorn Bunker. Biennial observations showed greater sponge coverage in 2010 and 2014, especially in the central GBR, which may be related to the geomorphology and habitat of reefs along with its influence by wind and wave action. Also, the aftermath of Cyclone Hamish (2009) and Yasi (2011) would have triggered suspended particulate matter that are beneficial to sponge growth. Geostrophic current showed a weak relationship on encrusting, upright and massive forms, whereas, chl-a, wave height and SST appeared to have no effect on sponge morphology, suggesting sponges may be resilient to adverse conditions in the GBR. Whilst selected sponge morphologies can act as environmental proxies to monitor adverse conditions, further *in situ* research on other environmental parameters such as turbidity, sedimentation, cyclone, tides are required to bring substantial conclusions on sponge morphologies as ecological indicators.

Keywords
Sponge, Great Barrier Reef, Australia, GBRMPA, morphology, environmental indicators, biophysical factors, marine protected areas, current, chlorophyll *a*, sea surface temperature, wave height

1. Introduction

Sponges are dominate in some coral reef habitats and practically absent in others. The importance of sponges is widely known with their vast microbial fauna which provides dissolved organic matter that play pivotal role to any coral reef ecosystem (De Goeij et al. 2013). Sponges also have varied functional roles (Wulff 2001; Bell 2008) in supporting the marine resources by creating three-dimensional habitat and biomass, water purification by constant filtering, nutrient recycling, bioerosion and reef consolidation (Powell et al. 2010). Despite being the simplest group (Phylum Porifera) of multicellular animals, sponge research is still a conundrum for spongologists because of their survival success in varied habitats (from shallow to the abyssal marine and freshwater systems) and adverse conditions (Bell et al. 2013); high species diversity (Van Soest et al. 2012); wide-range of symbiotic associations (De Goeij et al. 2013); and enormous bioactive properties (Thomas et al. 2010).

Apart from this, sponge morphologies are plastic and exhibit different bauplans like encrusting, branching, foliaceous, massive, tabular etc. and studies show that the structure and functional roles of sponges are highly associated with their morphologies (Bell 2017). For instance, burrowing sponges break down substrate and support reef consolidation, while upright sponges have a greater ability to reduce current flow compared to low-profile forms, which can influence the downstream feeding nature of other organisms (Bell 2007). Whilst sponges are highly susceptible and can act as agents to biophysical disturbance like predation, competition etc. (Wulff 2006), damage or change in sponge morphology can act as a proxy to help identify some important ecological characteristics (Schönberg and Fromont 2014).

Alterations in sponge species diversity, distribution, abundance and morphology were found to be induced by various biophysical environmental factors (McArthur et al. 2010; Cleary et al. 2016) such as: wave action and current (Kaandrop 1999), light intensity (Wilkinson and Trott 1985; Cheshire and Wilkinson 1991; Duckworth and Wolff 2007), angle of substrate and offshore distance (Bell and Barnes 2002; Powell et al. 2010), phytoplankton biomass, water flow and depth (Wilkinson and Evans 1989; Robert and Davis 1996; Duckworth et al. 2004), salinity (Barnes

1999), sediment grains (Bannister et al. 2012) and sedimentation (Duckworth 2015; Pineda et al. 2016). Whilst research on the impact of these complex and synergistic abiotic factors on sponge morphology and its adaptations is paramount, it is still in its infancy.

Besides sponges across the globe are poorly quantified and challenge the spongologists in systematics due to their complex mineral skeletal structure and myriad spicule categories. This reflects the poor update of periodic sponge taxonomic checklists with qualitative overviews of long-term spatial shifts in relative abundance from specific geographic locations including the Great Barrier Reef (GBR). The 2,300 km long GBR in northeast Australia with over 3,000 reefs is influenced by each of its position to the continental shelf, edge of shelf, distance from coast, latitude and distance from equator and temperate waters to the south (Fernandes et al. 2010). GBR with its complex array of biophysical parameters are likely to influence sponge cover by fluctuations of sedimentation, current shear, chlorophyll concentrations, turbidity, benthic irradiance, depth and nutrients (Pitcher et al. 2007; Brodie et al. 2007). All these factors are likely to influence sponge morphology, either individually or synergistically. Notable studies in the GBR are large-scale spatial comparison of sponges (Hooper et al. 2002) and the pre-2004 rezoning to investigate the biological diversity and substrates to identify biotypes (Pitcher et al. 2007). Recent studies showed natural (cyclones, floods) and anthropogenic climate change stressors (urban run offs, dredging, temperature rise etc.) including suspended sediments (Bell et al. 2015) and overfishing impacts on the reefs have a significant effect on benthic assemblages (Hughes et al. 2012) whilst proper investigation and periodic monitoring is limited for sponges especially in the GBR.

Based on studies pertaining to monitoring specific sponge morphological variation (Bell et al. 2017), we expect that continual change of environmental factors such as phytoplankton abundance, currents, wave height, rainfall, tides, cyclones and sea surface temperature will affect reef resilience. The greatest impact on sponges are likely near shorelines *i.e*., biophysical factors are likely to have a strong impact on inshore sponges compared to outer reef communities. Since, sponge morphologies are reliable as diagnostic characters for taxonomic purposes due to their considerable intraspecific variation, we propose in this study that morphological identification could greatly aid in rapid update and modest classification of sponges. Moreover, we predict that certain biophysical factors such as waves, currents, Sea Surface Temperature (SST), turbidity and chlorophyll can lead to certain changes on sponge growth forms which is given in Table 1. Hence, in this study, we aim to determine the impacts of sponge distribution in the GBR marine parks and examine whether sponge morphology can be used as environmental proxies, by using a dataset from the Long-Term Monitoring Program (LTMP) of the Australian Institute of Marine Science (AIMS), Townsville. The LTMP dataset consists of photo-transect images where identification of sponges was aimed based on morphology (growth-forms) and analyse the common and long-term trajectories of sponge morphologies and correlate sponge growth forms with selected biophysical factors along the GBR.

Table 1: Predicted sponge morphology changes due to biophysical factors

Biophysical factors	Sponge growth form prophecies
Wave height/wave action	Horizontal laminar, upright, foliaceous and massive forms can be transformed to encrusting and tabular forms with impact of high intensity wave action while low intensity waves can lead to branching forms.
Currents	Upright and horizontal laminar and massive forms can be transformed to encrusting and sheet-like foliaceous forms due to high intensity currents while low intensity currents can lead to branching and tabular forms.
Sea Surface Temperature (SST)	High SST can lead to sponge bleaching with decrease in overall sponge abundance and it is expected that massive forms can be transformed to branching forms while encrusting forms can lead to finger-like digitates. Low SST with suspended particulate matter if available can favour sponge proliferation of any forms, especially foliaceous, laminar and branching forms.
Turbidity (caused by river runoff, cyclone, tides and rainfall)	Due to the absence of light, stressed sponges tend to acquire more suspended particles. Hence massive/cups/tabular forms are expected by forming more surface area.
Chlorophyll	All forms expected with greater sponge proliferation due to increased phytoplankton biomass.
Clear water with moderate waves and currents	Sponges with symbiotic algae can proliferate in all growth forms due to availability of light and suspended particulate matter

2. Survey Locations and Methodology

The LTMP dataset was obtained from 56 reefs (28 pairs from take and no-take zones) in the Great Barrier Reef (Fig. 1) during biennial surveys conducted in June and July between 2008 to 2014. Each pair of reefs was located close to each other in the mid and outer-shelf regions of Cairns, Innisfail, Townsville, Pompey, Swain and Capricorn Bunker. In the LTMP, only mid-shelf reefs were selected in Pompey and only outer-shelf reefs were included in Capricorn Bunker (Sweatman et al. 2008) (Appendix A: Supplementary data, Table I). On each reef, three sites parallel to the reef crest were sampled using five replicates of permanently marked 50 m line intercept photo-transects at a depth of 6 to 11 m. Using the Reefmon program (Image Analysis Software) designed by AIMS (Sweatman et al. 2008), the five 'red' points from each photo-transect image (Fig. 2) were identified for sponges to distinguish from other benthic groups such as ascidians, hard corals, soft corals etc. based on morphology and reclassified based on morphology following Schönberg and Fromont (2014). We included an additional tabular growth-form because of the abundant tabular forms in the photo-transect images from the GBR while Schönberg and Fromont (2014) functional growth-form classification includes more West and North Australian sponges in addition to GBR sponges. Thus, the sampling protocol is based on the 5 points per 10,567 images from 168 sites. Sponge codes were reclassified to 12 growth-forms (Fig. 3) which were then condensed to five major hierarchical groupings (Table 2) for simplified analytical purpose. The point-data count was then estimated to percent cover of sponges per transect, averaged per reef per year and the results were shown as mean (X_m) percent cover. The measure of variance of mean values is one standard error (SE) in the results and discussion section.

Remote-sensed, point-series biophysical data for geostrophic currents, wave height, chlorophyll *a* (chl-*a*), and SST was obtained from the Australian Ocean Data Network (AODN for currents), European Centre for Medium-Range Weather Forecasts (ECMWF for wave height), Moderate-Resolution Imaging Spectroradiometer (MODIS for chl-*a*) and the Integrated Marine Observing System (IMOS for SST).

2.1. Statistical analysis

The statistical variation in sponge community composition among year, location and coral reef types was tested for significance using ANOSIM by R-Studio (R-software, vegan data package), based on the Bray-Curtis similarity index. The results of ANOSIM analysis were presented in addition to Non-Multidimensional Scale Plot (N-MDS) ordinated based on the Bray-Curtis similarity index using PAST-3.0, MAC Version. The impact of environmental parameters on sponge abundance and distribution in coral reefs were studied using Spearman correlation. For exploratory analysis of sponge distribution and its correlation with selected biophysical factors, the clustering or ordination of sponge samples with continuous environmental variables was carried out using Bray-Curtis resemblance matrix (similarity, dissimilarity or distance), Distance-based Redundancy Analysis (dbRDA) and Distance-based linear modeling (DISTLM) using PRIMER Version 7 (Clarke et al. 2014).

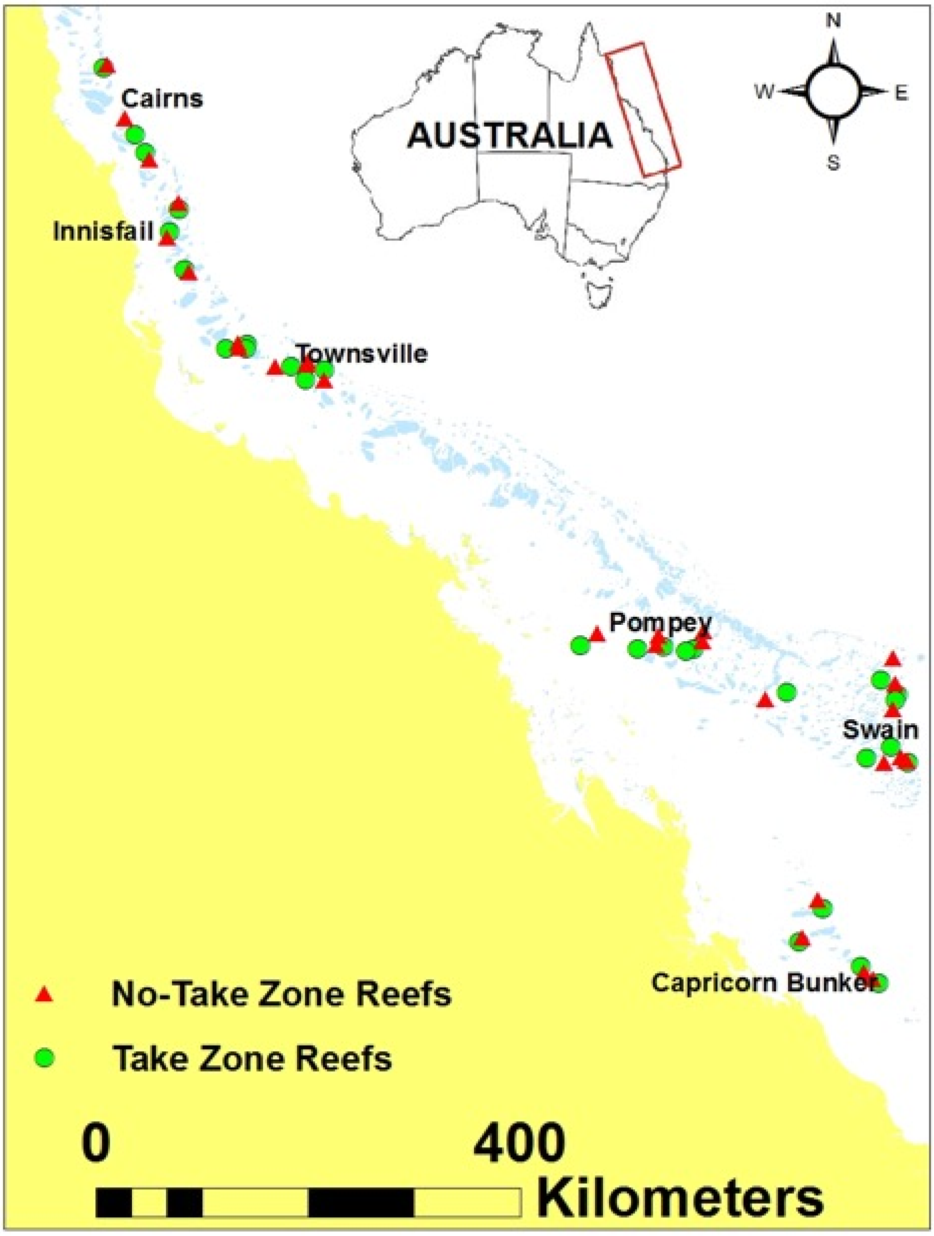


Figure 1: Map of survey locations in the take and no-take zones of the Great Barrier Reef, Australia

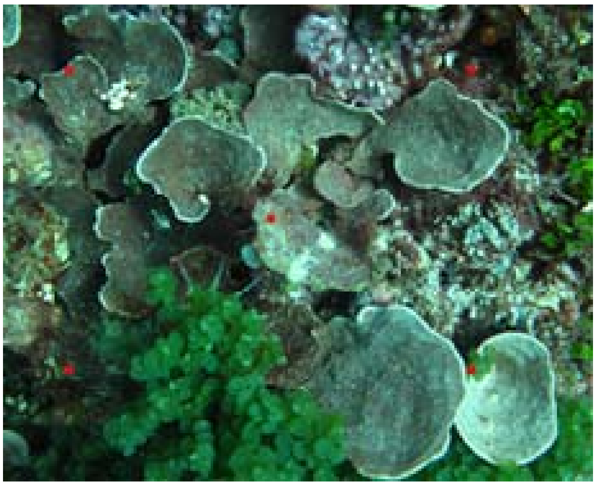


Figure 2: Five point photo-transect image which was used to identify the sponges from other groups of benthic organisms

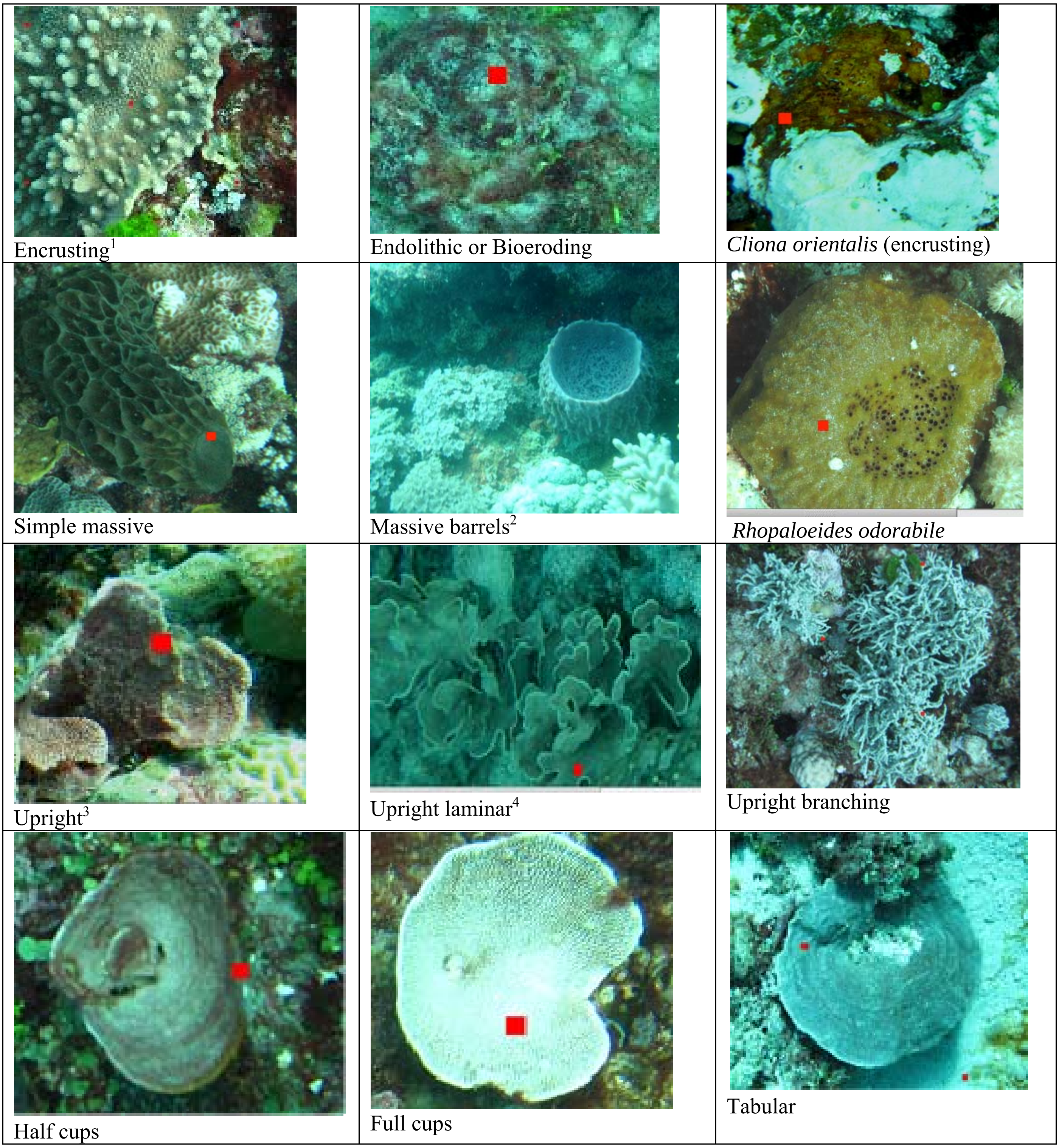


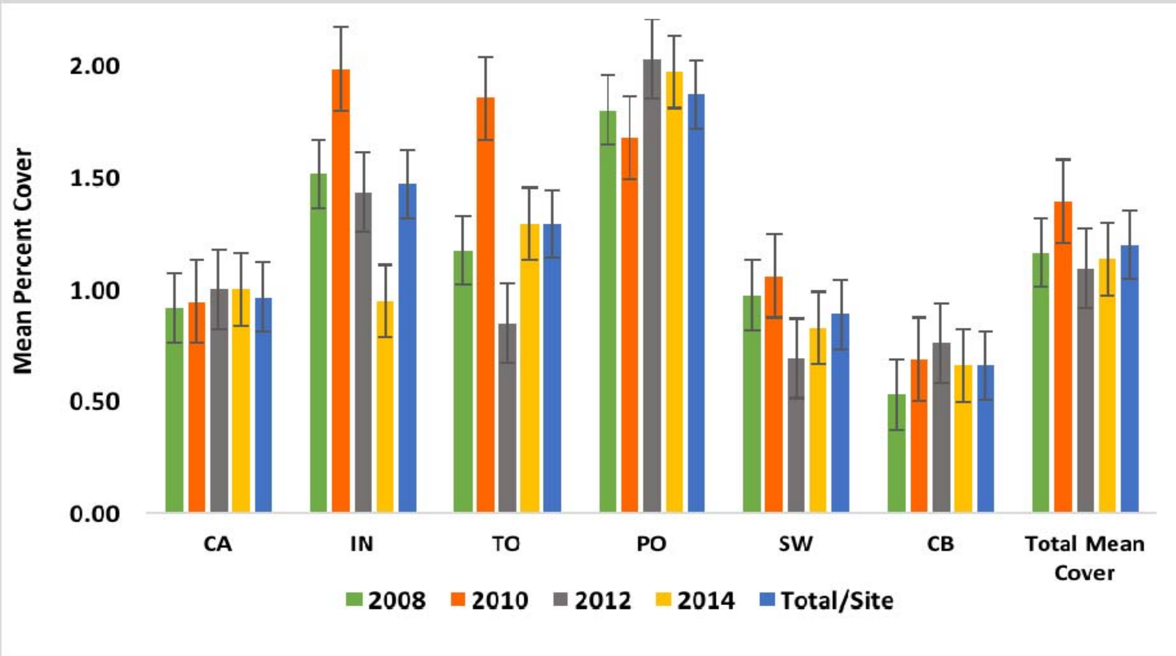
Fig. 3: Different sponge morphologies and associated characteristics (red points/squares indicates sponges) 1. Thickly or thinly encrusted forms showing substrate contours and minor erect or papillate parts; 2. Bigger, lumpy with smooth or serrated surface; inhalants and exhalants scattered or concentrated in one side; 3. Upright simple: erect and flattened, wider morphology with two dimensional parts and 4. Upright laminar: arranged in layers of thin plates or scales

Table 2: Sponge categorization into five major groups based on differing morphology

Major growth-forms	Different identified growth-forms that are combined to major growth-form
Encrusting	Encrusting, endolithic/bioeroding including *Cliona orientalis*
Massive	Simple massive, massive barrels including *Rhopaloeides odorabile*
Upright	Upright simple, upright laminar, digitate/branching (e.g. *Ianthella basta*)
Cups	Half cups and full cups (e.g. *Ircinia campana, Cymbastela coralliophila*)
Tabular	Tabular (e.g. *Spheciospongia areolata*)

3. Results and Discussion

Sponge coverage was highest in Pompey (m=1.9% SE ±0.08) and the similarity matrix of total sponge distribution showed significant difference between locations (R_{ANOSIM} = 0.167, p = 0.001) and lowest in Capricorn Bunker (0.7% SE ±0.05 of the four surveyed years) (Fig. 4a and 4b). The similarity matrix of total sponge distribution in all the 56 reefs from six locations varied significantly (R_{ANOSIM} = 0.064, p = 0.001) between four different surveyed years (2008, 2010, 2012 and 2014) where higher coverage was observed in 2010, slightly lower in 2012 and moderately similar during 2008 and 2014 (Fig. 4c). The five major sponge morphologies showed only a meagre difference at the regional scale as follows: Encrusting forms were ubiquitous and dominant with the highest coverage recorded in Innisfail (m=1.01% SE ±0.1) and lowest in Swain and Capricorn Bunker (m=0.6%); upright forms had significantly greater coverage in Pompey (0.9% SE ±0.08), particularly in 2010 (p <0.0005), whilst cup and tabular forms were absent in Capricorn Bunker during the entire surveyed period (Fig. 5a). Biennial differences showed encrusting forms had greater coverage (m=0.9% SE ±0.1) in 2010 with lowest coverage (m= 0.7% SE ± 0.1) in 2008, 2012 and 2014 respectively (Appendix A: Fig. II). The similarity matrix of sponge distribution was significantly different between reefs (R_{ANOSIM} = 0.618, p =0.001) and were not significant between open and closed zones (R_{ANOSIM} = -0.003, p < 0.69) (Figs. 6a & b; Appendix A: Table III, Spearman's Correlation and Fig. IV). Moreover, the heterogeneity of sponge distribution in this study corresponds with the major Seabed Biodiversity Project (SBD), where encrusting sponges are the common growth forms in the inter-reefal areas of the GBR (Pitcher et al. 2007).


2.00
1.50
1.00
0.50
0.00
Mean Percent Cover
CA
IN
TO
PO
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CB
Total Mean Cover
2008
2010
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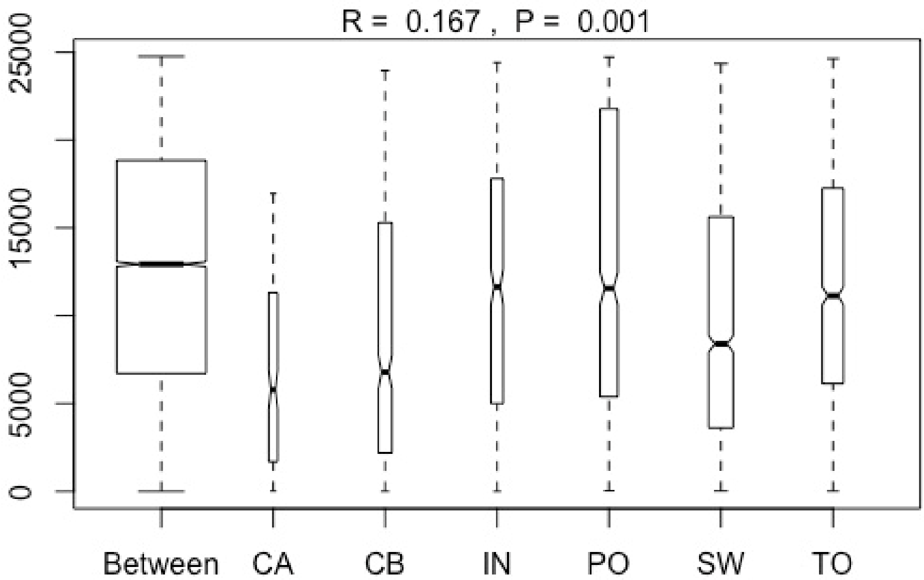
2014
Total/Site

(a)


R = 0.167 , P = 0.001
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Between
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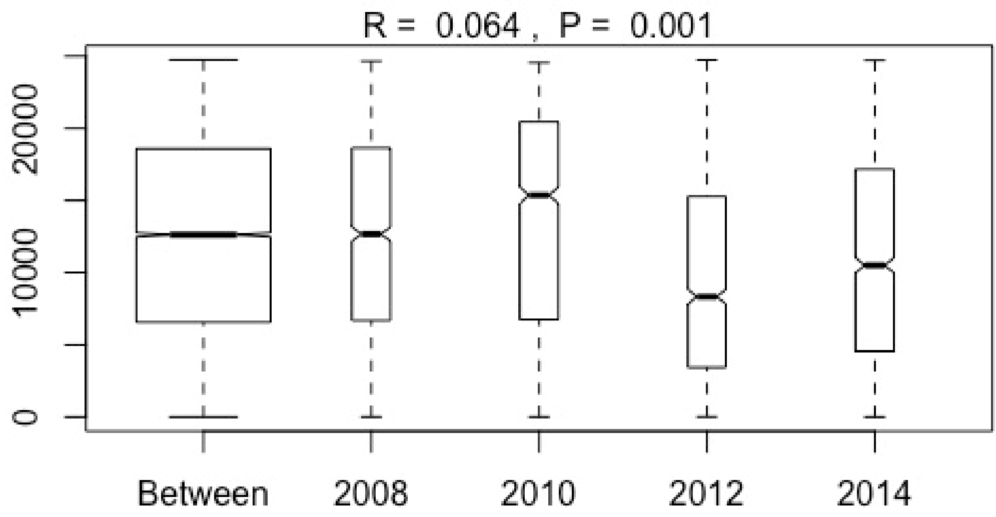
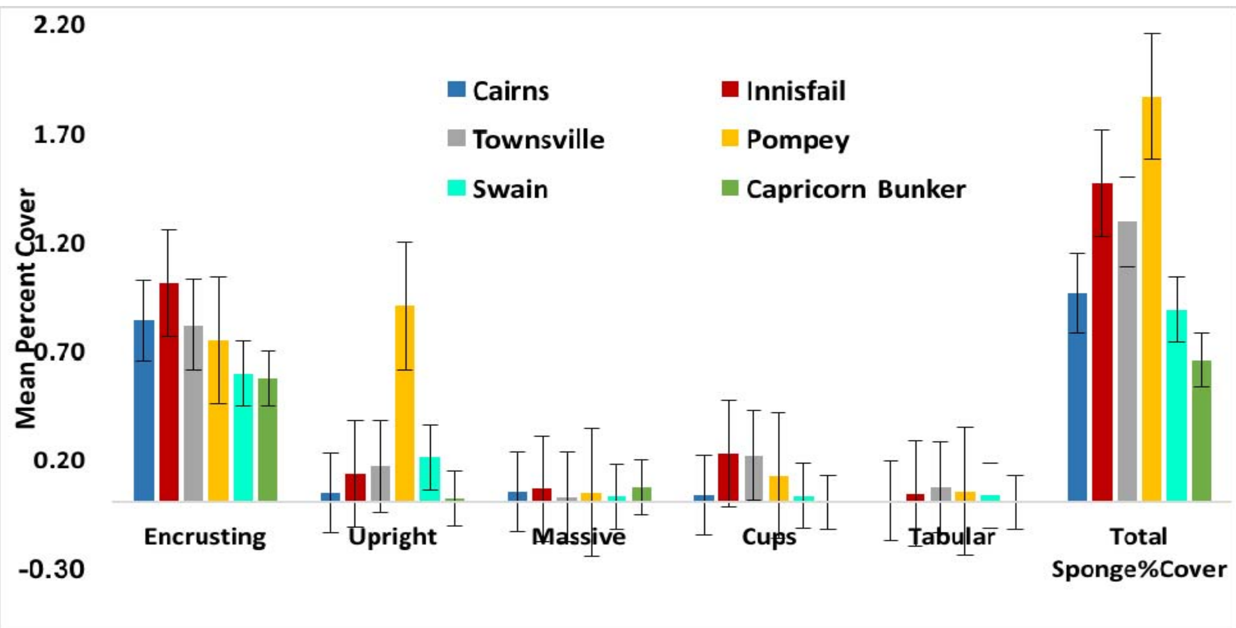
(b)



(c)

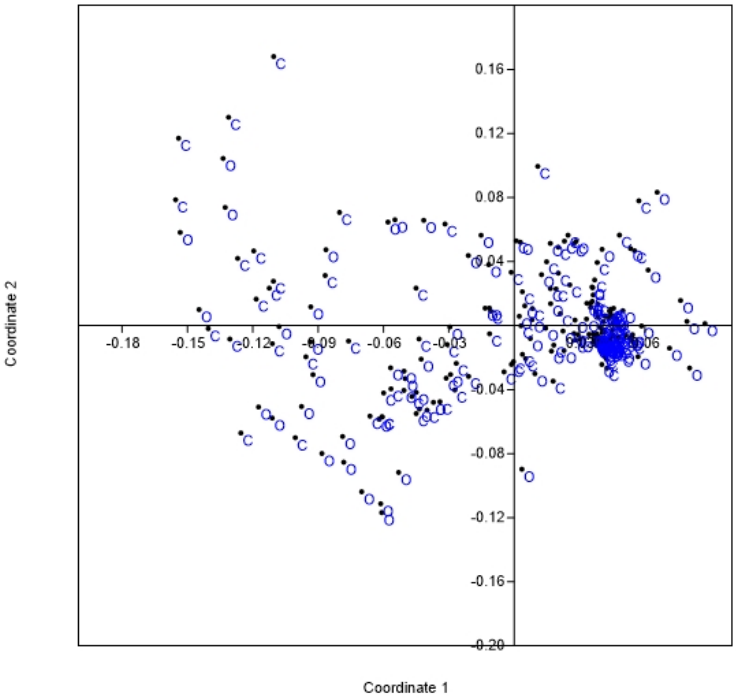
Figure 4: a) Total mean sponge cover changes across six locations in the Great Barrier Reef (CA-Cairns, IN-Innisfail, TO-Townsville, PO-Pompey, SW-Swain and CB-Capricorn Bunker); b) Similarity matrix differences between sponge morphologies and the six survey locations showed significant difference (CA-Cairns, CB-Capricorn Bunker, IN-Innisfail, PO-Pompey, SW-Swain and TO-Townsville); c) Similarity matrix differences between sponges from the six locations showing significant difference during and the biennial survey period (2008 to 2012)



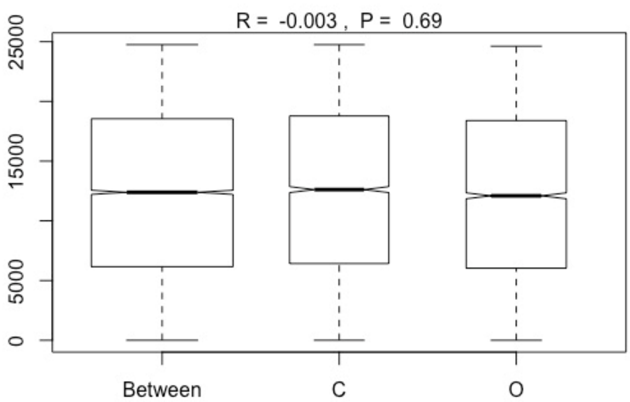
(a)

Figure 5a: Mean percent cover of sponge morphologies per location during biennial surveys 2008 to 2014

The N-MDS analysis showed far off points in some reefs of Pompey, Swain, Innisfail and Townsville while Cairns and Capricorn Bunker reefs showed a distinct accumulation of nearby points indicating a similar sponge distribution pattern (Fig.7). This variance probably could be due to the distinction of reefs in geomorphology and habitat (Cairns located closer to the shore compared to others) and the influence of wind and wave action based on its location. Since the midshelf and outershelf reefs were not equally nominated in the Long-Term Monitoring Program of AIMS (Appendix A: Table 1), the results were biased to a considerable extent.



(a)



(b)

Figure 6: a) MDS plot showing similar distribution patterns of Open (O) and Closed (C) zones in the Great Barrier Reef during the survey period; b) Similarity matrix between Open and Closed zones does not show any significant differences (R_{ANOSIM} = -0.003, P = 0.69)

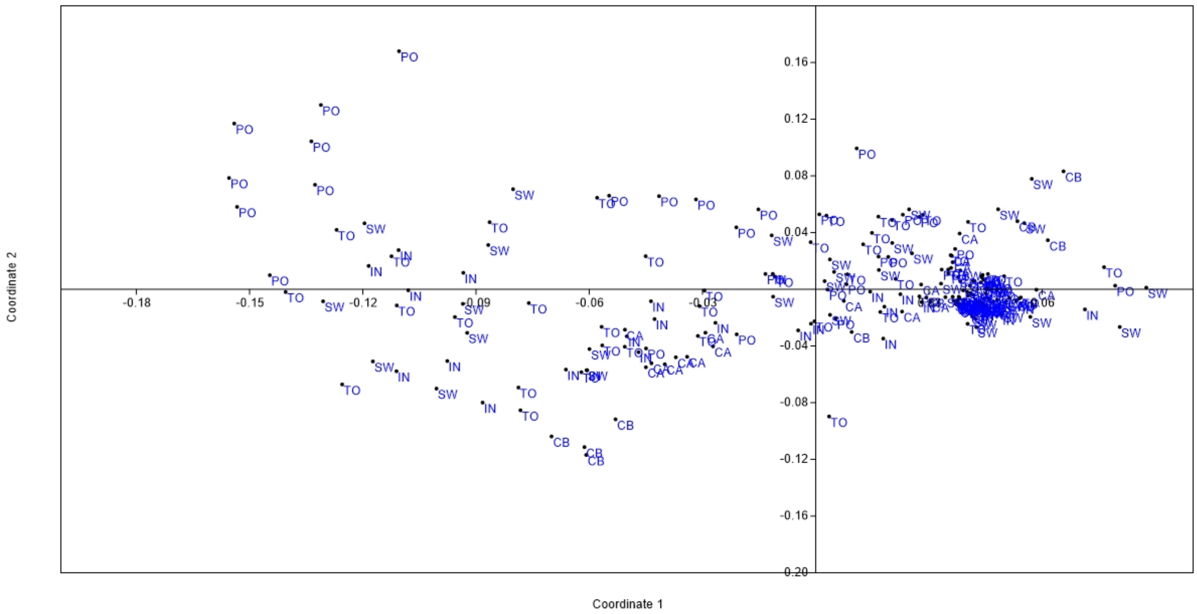


Figure 7: PCA showing different levels of sponge distribution variations in locations where Pompey, Swain and Townsville reefs showing far apart points while Cairns and Innisfail reefs showing similar patterns of sponge distribution across the four distinct blocks (CA-Cairns, CB-Capricorn Bunker, IN-Innisfail, PO-Pompey, SW-Swain and TO-Townsville)

Spatial and temporal trends for biophysical factors: chl-*a*, geostrophic current, wave height and SST varied between locations. Based on distance-based linear model (DISTLM), chl-*a*, waveheight and current showed moderate impacts on the annual variations of sponge cover at a regional scale while SST showed no signs of impact on sponges (Fig. 8). The analysis of specific sponge morphologies like encrusting, upright, massive and cup forms demonstrated a significantly but weak affinity towards only the biophysical factor, current ($P=<0.05$; Fig. 9; Spearman's Correlation). Whilst chl-*a* showed faint relationship with upright, massive, cups and tabular forms, it is interesting to note that tabular forms with their plate-like morphology does not show any impact with current, waveheight and SST (Fig. 9). In this variable model, the relative strength of individual relationships of SST > wave height > chl-*a* > current can be observed with low R^2 values ~0.02 which suggests that although significant, those relationships are too weak to show a reasonable difference in separation in dbRDA.

Chl-*a* was consistently higher in selected reefs of Pompey, Swain and Capricorn Bunker while it was lower in Innisfail (m=0.4 μgL^{-1}) across all four sampling years; peaks (m=0.98μgL^{-1}) were also observed in Cairns during 2008, 2010 and 2014 and in Townsville during 2010, 2012 and 2014 (Appendix A: Fig.Va). Chl-*a* concentrations derived from phytoplankton biomass are an indicator of enhanced nutrient input (Spencer 1985) while blooms can prevent light penetration and impact the ecosystem and nutrient cycle dynamics (Devlin et al. 2013). River run-off in 2011 from flood and cyclone events that led to elevated turbidity, nutrients and pollutants contributed considerably to natural environmental gradients in the GBR (De'ath and Fabricius 2008; Devlin and Brodie 2005; Devlin et al. 2013). The impacts of nutrient enrichment and potential eutrophication of the GBR has been studied in corals, seagrass and phytoplankton communities (Fabricius 2005; Brodie et al. 2011, 2012; Devlin et al. 2013), but not on sponges. Whilst, sponge morphologies can respond to sedimentation stress (Bell et al. 2015; Pineda et al. 2016) and substrate impacts (Duckworth 2015), no evidence has been presented on nutrient enrichment impacts on sponge population dynamics in the GBR. Whereas studies on boring sponges showed bioerosion rates correlates with eutrophication on *Cliona orientalis* (Holmes et al, 2009) and sediment impacts on Mexican sponges showed encrusting forms were able to survive in perturbed conditions, particularly boring species like *Cliona* (Bautista-Guerrero 2006). In this study, the remote-sensed chl-*a* data used are calculated as an average across the year which leads to bias as some locations may have been subjected to algal blooms skewing the datum. Therefore, it is impractical to use this data to correlate with sponge morphology research. Nonetheless, these findings highlight the need for further research on sponge morphologies in response to nutrient inputs and chl-*a* concentrations on a seasonal basis with a more regional focus.

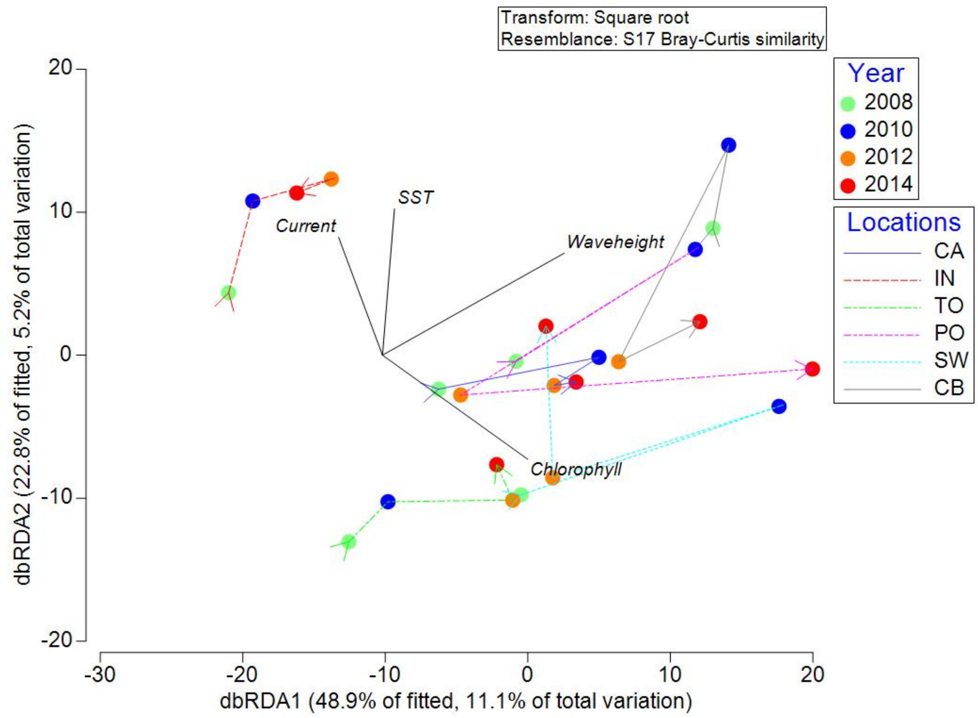
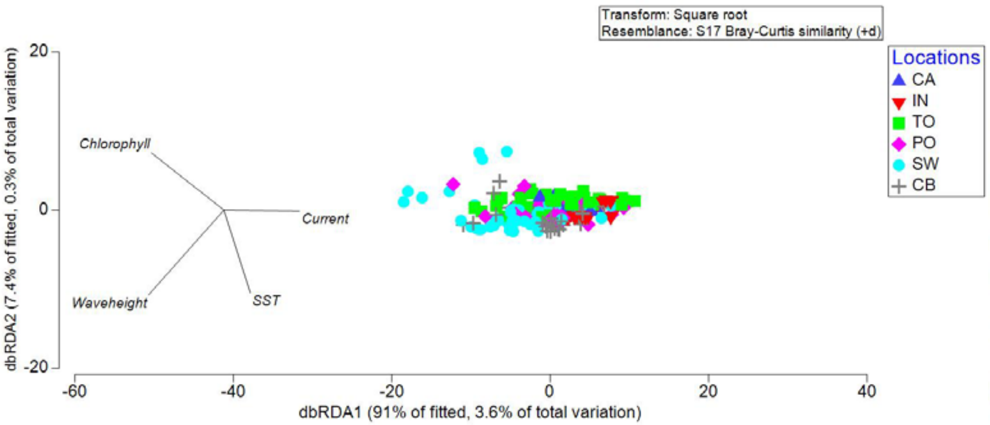
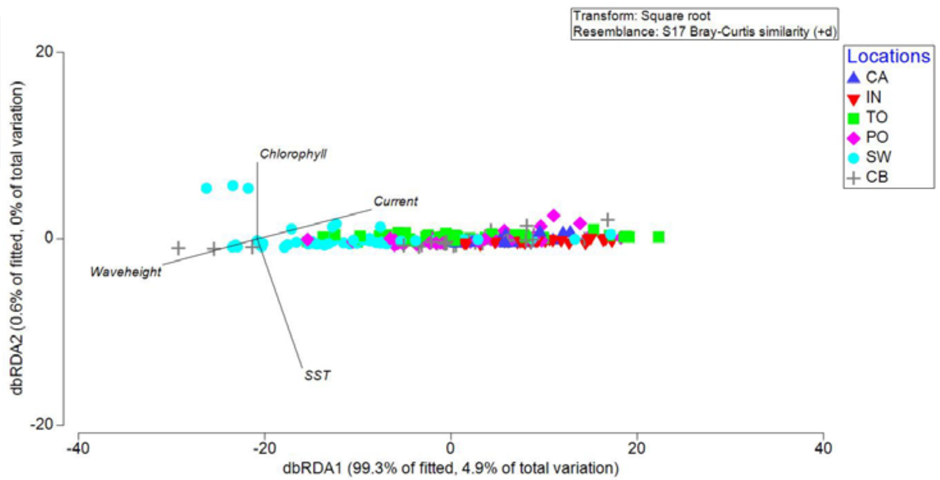
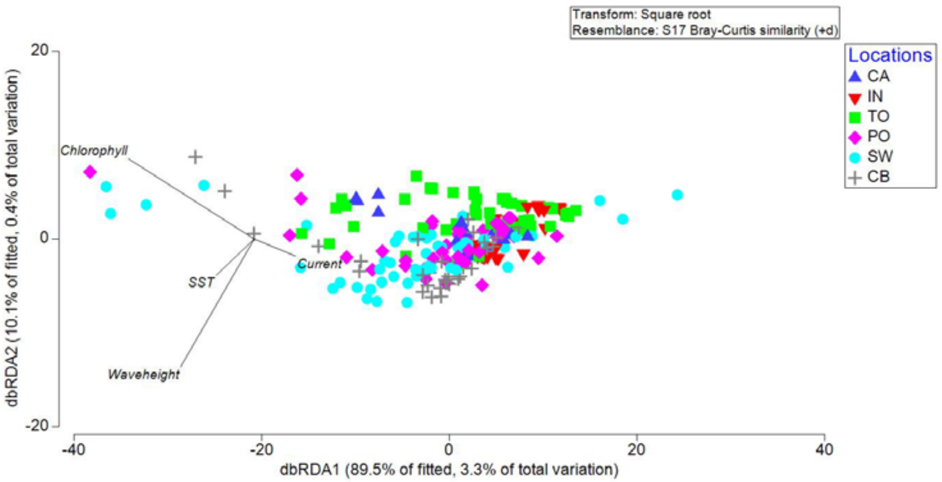


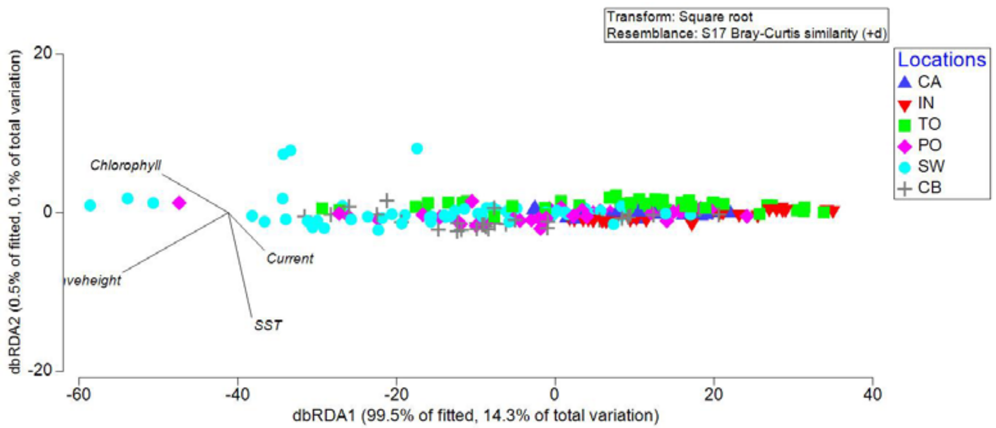
Figure 8: Distance-based Redundancy Analysis (dbRDA) biplot showing variations in the four biophysical factors (Current, SST, Waveheight and Chl *a*) in relation to locations and surveyed years. (CA-Cairns, CB-Capricorn Bunker, IN-Innisfail, PO-Pompey, SW-Swain and TO-Townsville). (Averaged Bray-Curtis resemblance matrix with no dummy variables used)



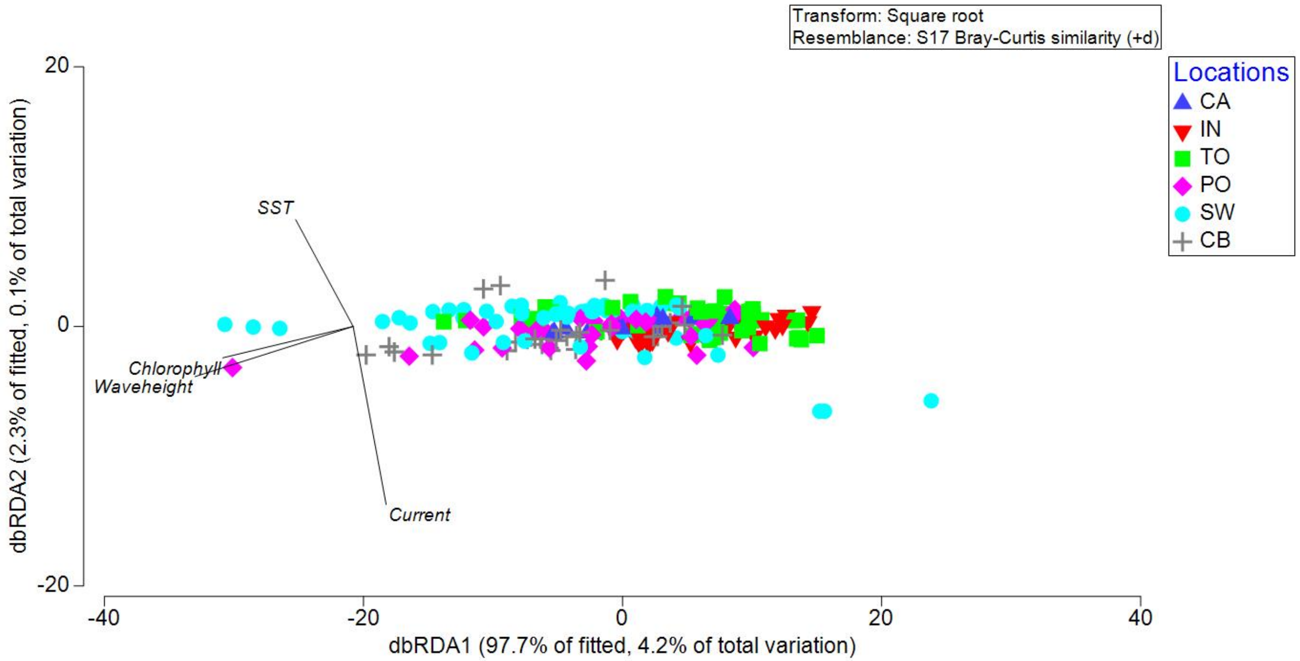


Encrusting **Massive**





Upright **Cup**



Tabular

Figure 9: Different sponge growth forms (Encrusting, Massive, Upright, Cup and Tabular) and their relation to selected environmental factors (chl-*a*, current, wave height, SST) shown by clustering of reefs in six surveyed locations (CA-Cairns, CB-Capricorn Bunker, IN-Innisfail, PO-Pompey, SW-Swain and TO-Townsville)

Geostrophic currents were consistently higher (m=0.3Sv) in selected reefs of Innisfail, Townsville, Pompey and Capricorn Bunker during the surveyed period while Capricorn Bunker showed a moderate (m=0.2Sv) and lower currents (m=0.1Sv) was observed in some reefs of Townsville and Swain (Appendix A: Fig.Vb). Similarly, wave heights were generally highest (m=3.9m SE±0.3) at Pompey, Swain and Capricorn Bunker in 2010 and 2014 while lowest (m=2.8m SE±0.2) in all other locations. Current analysis indicates geostrophic currents showed a meagre effect on encrusting, massive, upright and cup forms while no impact was observed on tabular forms (Fig. 9) which calls for *in situ* studies to support our predictions (Table 1). Studies from northern Australia showed sponges at a right angle to current flow may favour upright and cup forms that are stalked and can withstand the force of water movement (Kelly and Przeslawski 2012).

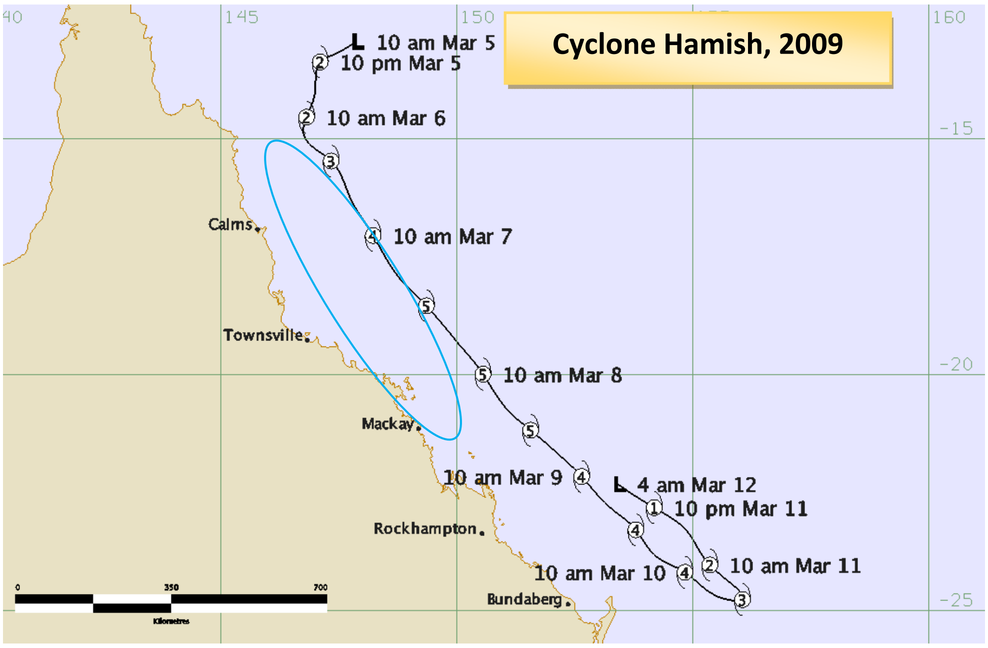
Wave height was higher (annual mean=4-4.9m) during 2010 and 2014 in all locations, while Cairns and Innisfail showed a wave height maximum of 4m (Appendix A: Fig.Vc). Multivariate statistical analysis showed wave height does not have any effect on the sponge forms (Fig. 8), yet showed slight affinity towards massive and tabular forms (Fig. 9) which calls for more data. Previous studies showed no significant impacts on sponges due to increased water flow (Wilkinson and Evans 1989; Gosling, 2005; Bannister et al. 2007; Duckworth 2015) and wave action (Gosling 2005) along the GBR. Low water movement means depletion of air and nutrients and sponges need to work vigorously due to their filter-feeding nature. Hence, high current flow, tides and wave action could have favoured the abundance of sponges during 2010 and 2014 while sponge morphological variation showed a constant trend (Appendix A: Fig. II). Moreover, in support of our hypothesis that increase in wave height can transform upright to encrusting forms due to the constant stress of crashing waves, the present findings showed that upright forms were higher during 2010 and 2014 while the dispersal of growth forms were in a direction horizontal to the substratum in the rest of the survey period.

The highest SST was recorded in Cairns (m=28.4°C SE±0.2) and lowest in Swain (m=25.7°C SE±0.5) during the total survey period. Annual variation in SST was observed during 2010 with a highest (m=27.5°C SE±0.5 of the six locations) and lowest in 2008 (m=26.8°C SE±0.5 of the six locations) (Appendix A: Fig.Vd). While stalked upright and cup forms that can access light with large surface area for their growth, current results showed no signs of impact even during high SST (>28ºC) in Cairns and Townsville. Sponges appear to be highly tolerant to both *El Nino* and *La Nina* (ENSO) conditions and are less affected by increased SST than other benthic groups (Kelmo *et al*. 2013). *In situ* experiments in New Zealand also showed no considerable change to sponge growth with increased temperature (Bell and Barnes 2002; Bell et al. 2013). Contrastingly, higher

SST (> 31°C) are lethal to *Rhophaloides odorabile* in the GBR (Massaro et al. 2012). Nonetheless, specific species-related studies on SST impacts requires further research though apparently sponges are generally a highly tolerant group of organisms to variable environmental parameters.

As expected, reefs closer to the mainland (Cairns, Innisfail and Townsville) with continual water movement and wave impact favoured more encrusting forms compared to outer reefs (Swain and Capricorn Bunker) (Appendix A: Fig. II). Pompey mid-shelf reefs in the continental shelf are at their widest and the main reefs are farthest (50 kms) from shore however, there is significant sponge proliferation, especially upright growth forms. This could be due to the high tides and strong currents (reaching up to 10 knots) that gush through numerous twisting channels between the large reef platforms (Spalding et al. 2001) which would favour consistent upwelling and downwelling that are nutrient laden. Moreover, sponges can survive in varying environments due to their rigid skeletal structure (Wilkinson and Evans 1989) and the spatial and temporal variations of chl-*a* due to run off from the catchments in the central GBR (Brodie et al. 2007; Devlin et al. 2013) could have favoured the increased sponge growth in Innisfail and Pompey. Whilst compact rather than branching forms have been observed due to these abiotic factors (Kaandrop, 1999), some studies have shown no such impact on morphology and coverage (Wilkinson and Evans 1989; Duckworth 2015). This evidently suggests that prolonged time period of observation on continual sponge morphology changes is needed as stated in the sponge monitoring review (Bell et al. 2017). The notable difference in low sponge distribution in Swain and Capricorn Bunker reefs (which are located offshore) could not be directly related to any of the environmental parameters considered in this study, as all the values showed a similar trend. Moreover, the complete absence of tabular and cup forms in Capricorn Bunker needs further research although only outer shelf reefs are considered in our data.

The high percent cover of sponges in 2010 and 2014 compared to 2008 and 2012 is likely to be linked with increased chl-*a*, wave height and stronger currents in 2010 and 2014. Regarding the temporal variation, another possible explanation for the high percent cover of sponges in 2010 in Innisfail, Townsville, and particularly high coverage in 2014 in Pompey, could be related to the aftermath of Cyclone Hamish (2009) and Yasi (2011) (Fig. 10), which affected large areas of the GBR. The recovery of sponges in the subsequent years after Cyclone Hamish (2009) and Yasi (2011) may be due to resuspension of sediments associated with decreased current flow, chl-*a* and wave action which can have a positive effect on these filter-feeders. Due to the 50 km distance from mainland, Swain and Capricorn Bunker did not appear to be impacted by the cyclone.



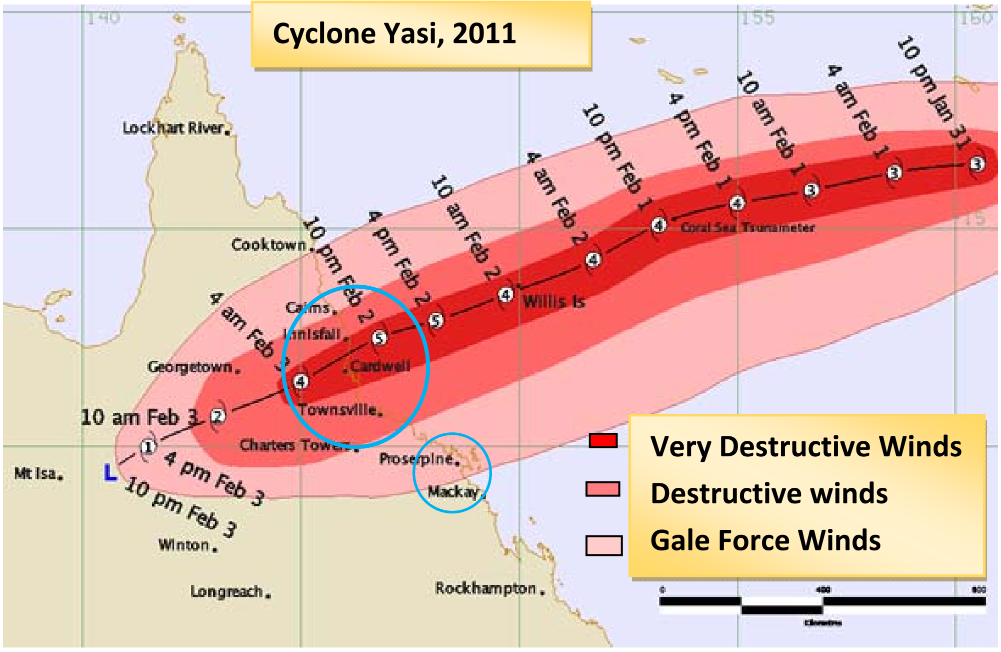


Figure 10: Track of cyclone pathways of Hamish (2009) and Yasi (2011) along the GBR. Blue circles indicate the survey sites (Picture Courtesy: Bureau of Meterology; Last assessed 22 August 2016).

Research on sponges and their biophysical interaction in the GBR are patchy and no specific focus is given to record their distribution status and ability to survive adverse environmental conditions. This study highlights that sponges can tolerate adverse temperatures, wave action and cyclone events, likely due to resuspension of increased nutrient input. Although sponges are ubiquitous in the GBR, their distribution between different reefs and locations are highly related to the microhabitat influences on sponge species (Ribeiro et al. 2003) with varied morphologies, which might be related to the geomorphology of the continental shelf of GBR (Brinkman et al. 2002).

3.1 Future Research Implications

Morpho-identification can be reliable only when there is a large dataset over large geographic range with large-scale spatial variation that could assist in avoiding identification delays in laboratory. Whilst the current morphological identification of sponges in long-term datasets like AIMS-LTMP have been updated, many of the five-point images were out of focus due to working in difficult environments (~2% visibility), leading to some possible misidentification of sponge types in the GBR. Hence, high quality images with additional biophysical details related to habitat and associated organisms would give more lucidity to the dataset. Additionally, gaps in the consistency of the survey (season/month) from the same reefs and missed surveys (due to inclement weather) from a few reefs (in Townsville and Innisfail during 2014), made compilation, comparison and analysis quite challenging.

Regarding the remote-sensed biophysical parameters, care should be taken on using government website data such as eReefs and eAtlas, as the survey locations and remote-sensed data coordinates should match. However, our survey location coordinates from AIMS-LTMP does not match with the remote-sensed data. The environmental factors (chl-*a*, waveheight, currents and SST) used in this study were collected as point-series data per hour/day and the moderate values recorded in all locations showed a uniform trend and hence could not be utilised to enhance clarity and links with sponge morphologies. There are also considerable gaps in the time-series data for some years from IMOS and ECMWF, which makes comparison efforts difficult. Hence, more predictions could be made if biophysical data are collected *in situ*. In addition, remote-sensed data cannot be relied upon in shallow waters (current data is between 6 to 11m depth) as the benthic reflectance from organisms especially corals, seagrass, algae can have considerable impact on biophysical factors especially chl-*a*. The relative importance of other biophysical factors on sponge abundance can lead to inferences that can also predict environmental disturbances. Besides with the present DISTLM analysis, the low R^2 values, indicates that more sophisticated classification and regression tree (CART) analyses are needed to specifically determine complex relationships at which levels of the environmental variables are most likely to detect changes in sponge distribution.

4. Conclusion

Whilst there are some correlations between sponge morphologies (encrusting, upright, massive and cup forms) and biophysical factors (currents, wave height and chl-*a*) to decide sponges can act as effective environmental proxies, further data is required to draw a definitive conclusion. We suggest that: 1) remote-sensed data cannot be used to determine relationships with sponge morphologies, while on-site field data collection is encouraged; 2) other environmental and water quality parameters like turbidity, sedimentation, depth, cyclone, storms and tides from study locations need to be collected over a prolonged period of time; and 3) surveys of sponges during the wet and dry seasons should be carried out to determine variation in sponge morphologies related to particulate matter influx.

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Appendix A: SUPPLEMENTARY DATA

Table I: Survey locations with 56 reefs from take and no-take zones of the present study

Locations/Shelf	No-take Zone Reefs	Take Zone Reefs
Cairns group: Cairns		
Mid-shelf	Hastings reef	Arlington reef Thetford reef
Outer shelf	Agincourt reefs (No 1)	St Crispin reef
Innisfail		
Mid-shelf	Feather reef Moore reef, Taylor reef	Farquharson reef (No 1) McCulloch reef, Peart reef
Outer shelf	Hedley reef	-
Central group: Townsville		
Mid-shelf	Helix reef, Kelso reef Little Kelso reef Lynchs reef	Centipede reef Fore and Aft reef Grub reef (18077) Rib reef, Roxburgh reef
Outer shelf	Fork reef & Knife reef	Chicken reef
Mackay group: Pompey		
Mid-shelf	20348S, 20353S, Pompey reef (No 1), Pompey reef (No 2), Tern reef (20309)	21060S, 21062S 21064S, 21591S, Penrith reef
Swain		
Mid-shelf	21139S, 21278S, 22084S Jenkins reef Wade reef	21187S, 21245S, 21550S, Chinaman reef (22102) Small lagoon reef
Outer shelf	21296S, 21558S	21302S, East Cay reef
Capricorn Bunker		
Outer shelf	Erskine reef, Fairfax Islands reef Hoskyn Islands reefs North reef (North)	Boult reef, Broomfield reef Lady Musgrave reef Mast Head reef

Figure II: Mean percent cover of sponge morphologies per sector during biennial surveys 2008 to 2014

Table III: Distribution of sponges as in the GBRMPA zones with Mean Percent Cover (m) in survey locations

Sponge Morphologies	GBRMPA Zones		Specific GBRMPA Zones		
	Take	No-take	Marine National Parks	Habitat Protection	Conservation Parks
Encrusting	1.01± 0.3 (IN) 0.5 ±0.1 (SW)	0.9 ±0.1 (IN) 0.3 ±0.1 (CB)	**0.29 CB; 0.94 IN** P=0.002	**0.15 CB** P=0.002	**0.57 PO** **1.58 CB** P=0.002
Upright	0.8 (PO) 0 (CB)	1.0 (PO) 0 (CB)	1.04 PO	0.14 IN	0.08 CN
Massive	0.1 (PO)	0.1 (PO)	0.06 PO	0.10 IN	0.20 CB
Cup	0.4 (TO)	0.3 (TO)	0.28 TO	0.39 IN	0.05 CN
Tabular	0.1 (IN, PO)	0.1 (TO, SW)	**0.10 TO** P=0.002	**0.09 PO** P=0.002	**0.01 CN** P=0.002

Bold text highlights the significance, P=0.002; rest of the results showed no significance on distribution. Values are mean ± SE of different morphologies

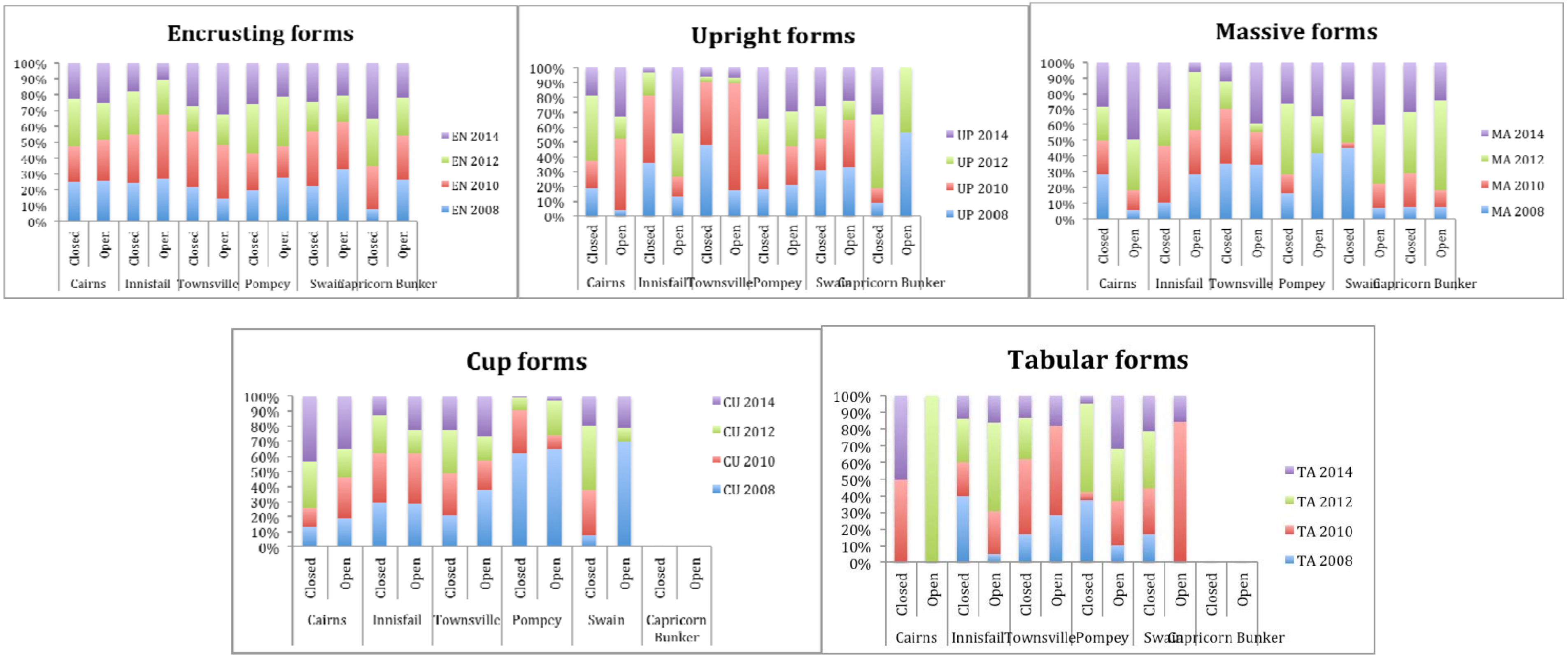

Figure IV: Mean percent cover of the five major sponge morphology trends in the biennial survey period (2008 – 2014) in the open and closed zones of the survey locations in the GBR (UP-Upright, EN-Encrusting, MA-Massive, CU-Cups, TA-Tabular; CA-Cairns, IN-Innisfail, TO-Townsville, PO-Pompey, SW-Swain, CB-Capricorn Bunker)

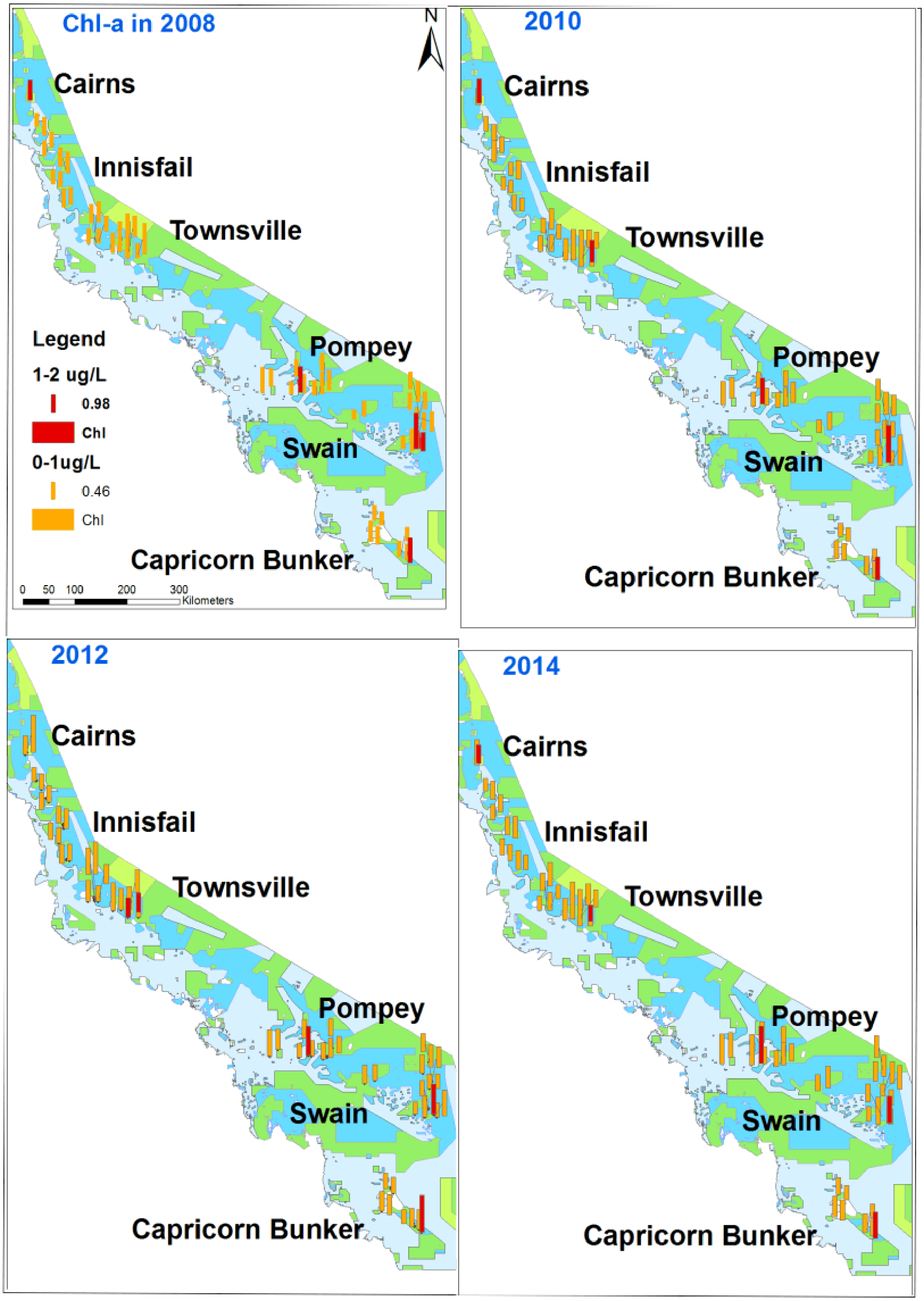

Figure Va: Annual mean variance (from January to December) of Chlorophyll *a* from all the surveyed reefs (Each bar shows each reef in their respective location)

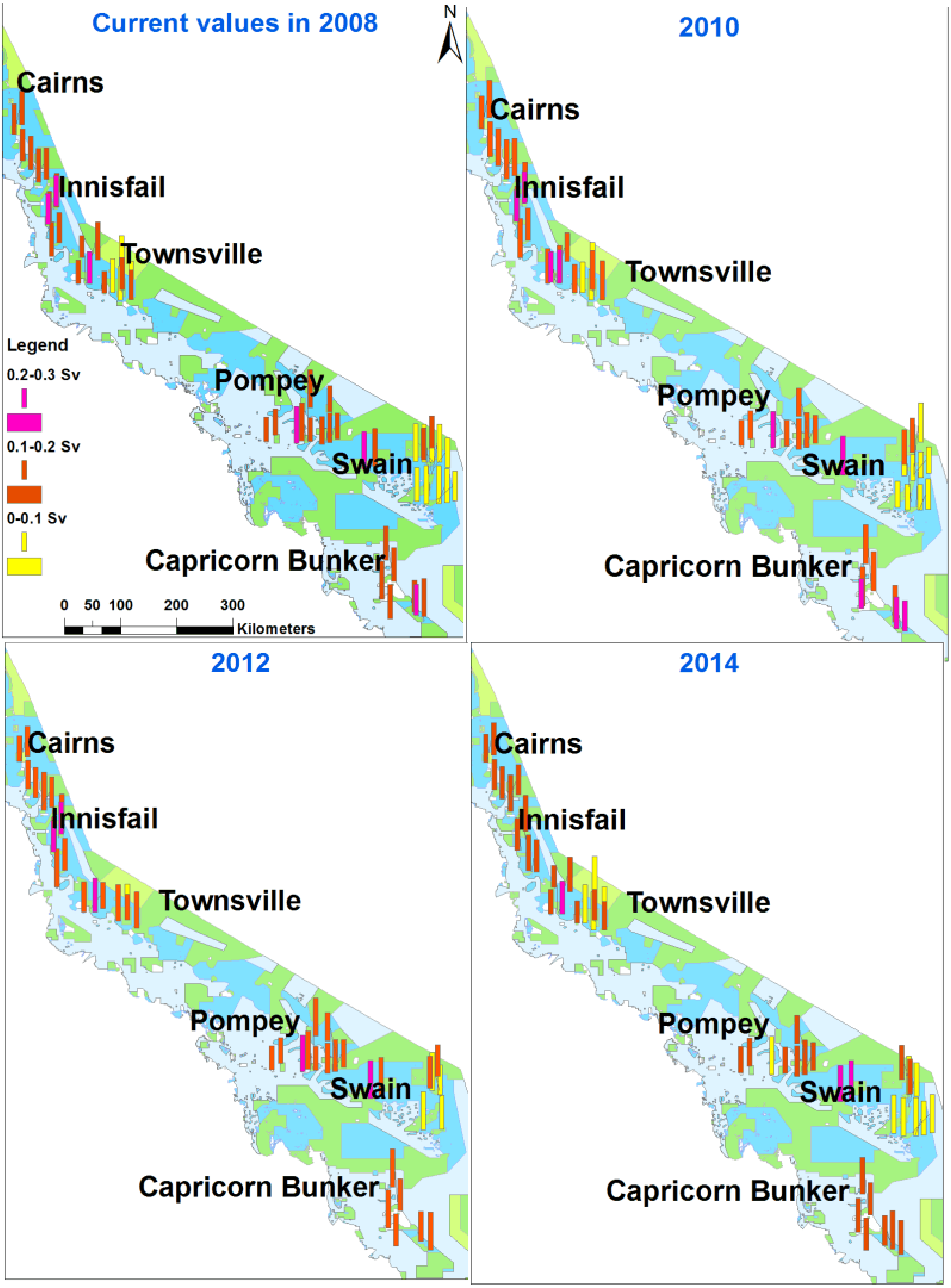

Figure Vb: Annual mean variance (from January to December) of geostrophic current from all the surveyed reefs (Each bar shows each reef in their respective location)

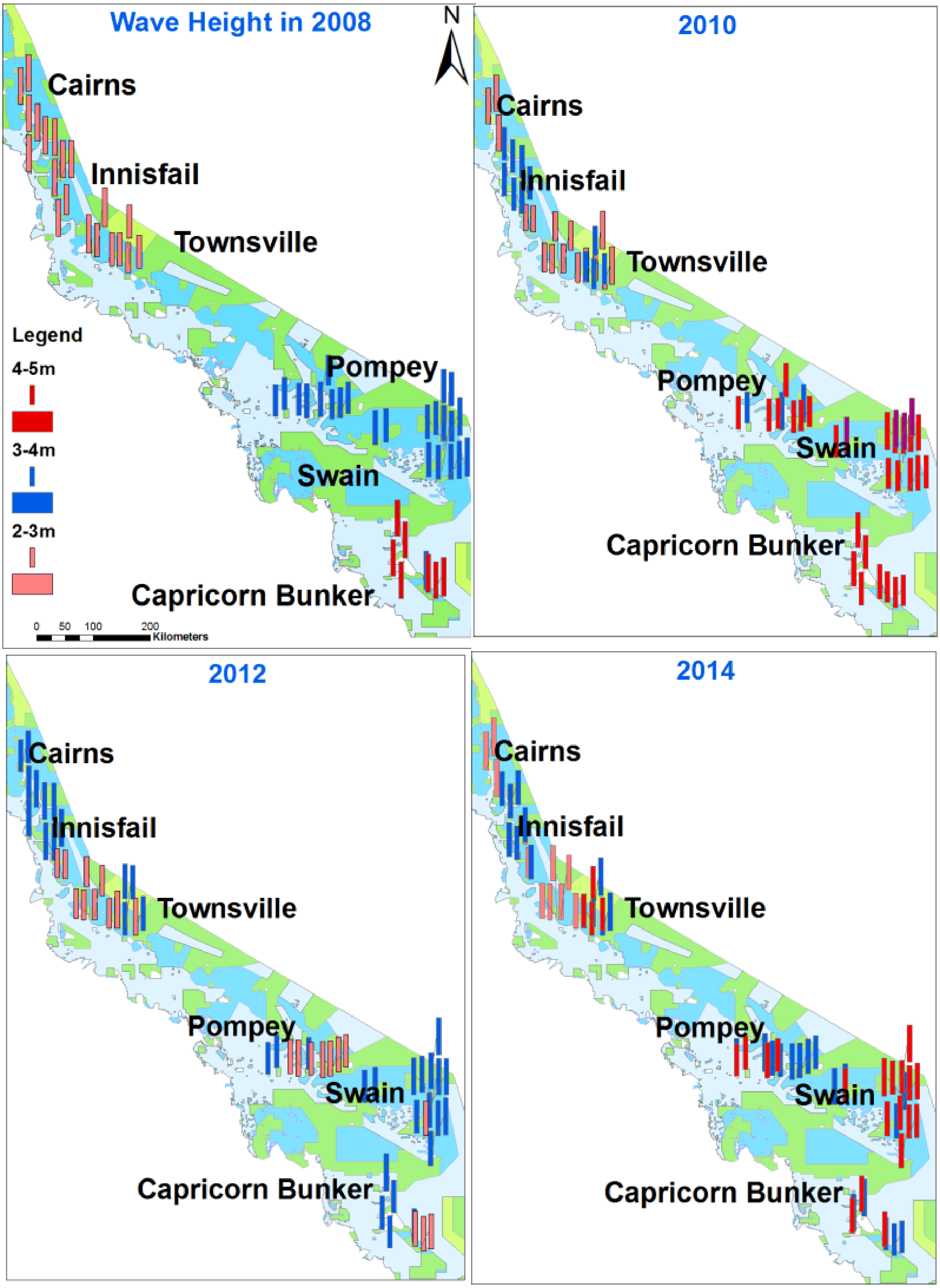

Figure Vc: Annual mean variance (from January to December) of wave height from all the surveyed reefs (Each bar shows each reef in their respective location)

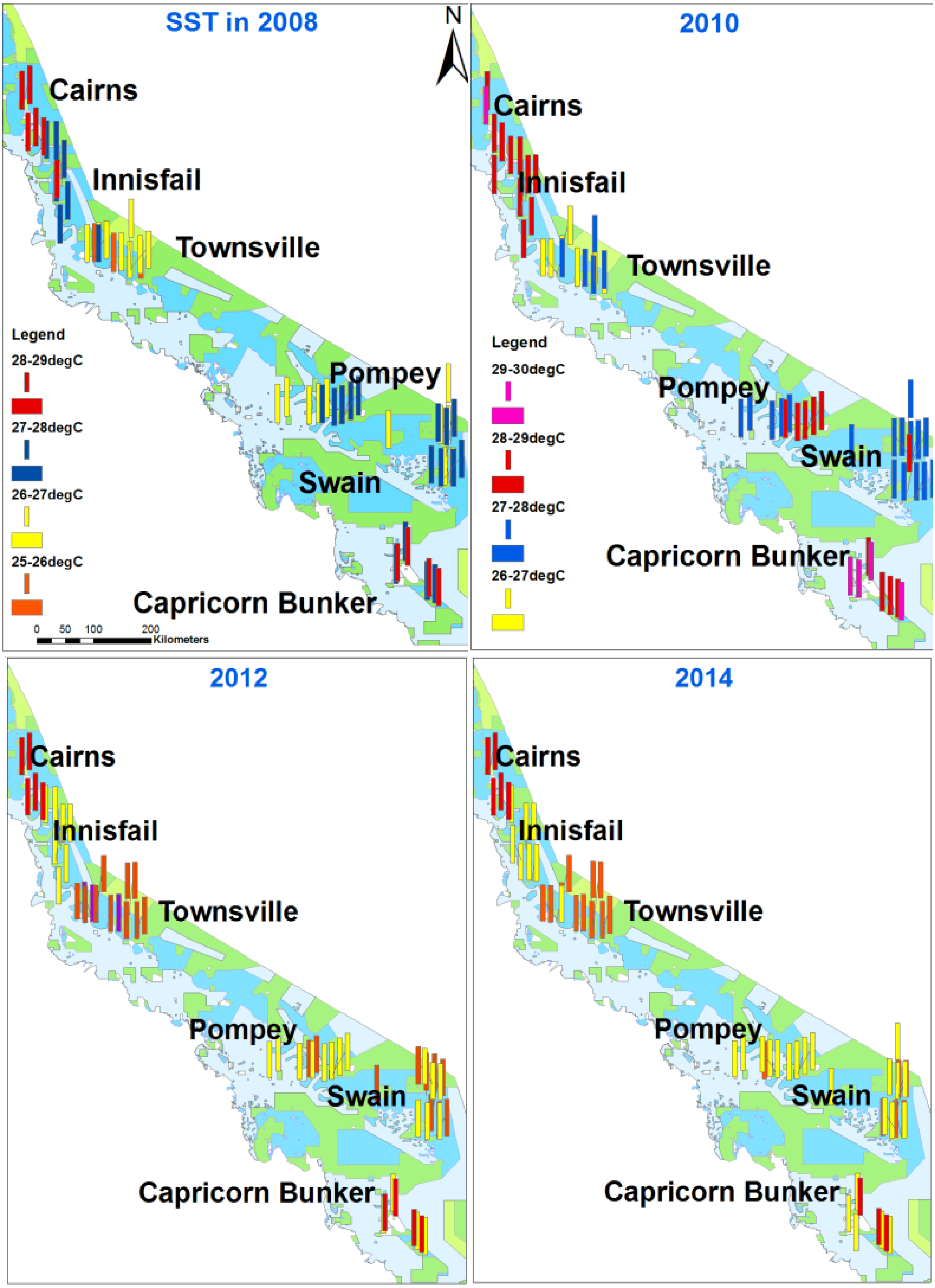

Figure Vd: Annual mean variance (from January to December) of Sea Surface Temperature (SST) from all the surveyed reefs (Each bar shows each reef in their respective location)

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