Taking a deeper look at the biodiversity on temperate mesophotic reefs to inform adaptive management of impacts in Storm Bay, Tasmania

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ABSTRACT

Mesophotic reef assemblages in south-eastern Australia remain poorly described despite their growing vulnerability due to new pressures from expanding offshore industries such as aquaculture and renewable energy. To address this knowledge gap, imagery from Automated Underwater Vehicles offers an efficient method of obtaining initial baseline inventories and tracking changes in these under-studied mesophotic benthic ecosystems. Here, we characterise the composition of sessile epibenthic communities across a depth gradient (24 – 55 m) on three distinct offshore reef systems in western Storm Bay, Tasmania, a large embayment subject to increasing anthropogenic pressures. We sampled at two time points (2015 and 2020) and quantify components of variance to help select candidate indicator morphospecies. The shallower communities (<30 m) were dominated by macroalgae, mostly *Caulerpa* spp., while deeper communities (>30 m) were dominated by encrusting sponges and fine turfing biological matrices. From 2015 to 2020, there was a reduction in overall morphospecies diversity between depth zones across all three reefs, except in the shallowest zone. This was matched by declining Caulerpa depth range and cover. Further, there was a general decline in the cover of morphospecies groups with depth, as abundance became more concentrated on a few morphospecies, primarily matrix groups. Simulation-based power analysis showed that for most individual morphospecies, change in cover of +/- 50 % or less was not detectable with sufficient power, unless the survey design incorporated sampling across all three reefs. This was primarily because in our study system few individual morphospecies reached > 2 % cover, and hence greater sampling effort was required for adequate description. The prevalence of sparse morphospecies and generally low cover underscores the necessity for pilot studies to ascertain the required sampling effort for accurate quantification of biodiversity changes on mesophotic reefs.

1. Introduction

Coastal benthic ecosystems are some of the most productive and important biomes on the planet evidenced by their biodiversity and human reliance on the resources they provide (Waddington et al, 2010; Harris et al, 2021; Micaroni et al, 2021). However, traditionally, marine research has been focussed on shallow areas due to the logistical and economic constraints in accessing deeper coastal waters. Despite this, improved understanding of temperate mesophotic ecosystems (TMEs), particularly rocky reefs, is becoming more urgent as these important shelf systems face increasing anthropogenic pressures, including offshore expansion of renewable energy and intensive agriculture under the blue economy (Nelson et al, 2015; Cerrano et al, 2019; Turner et al, 2019; Strain et al, 2020).

Natural gradients, such as depth, encompass changes in environmental factors closely linked to the physiological performance of organisms (Roberts et al, 2019). The mesophotic zone is located between the shallower euphotic and deeper aphotic zones and hosts highly diverse and often endemic benthic assemblages (Bridge et al, 2011). The depth of the mesophotic zone and the organisms within this zone can vary greatly based on a range of biotic and abiotic factors, including but not limited to light incidence, energy availability and presence or absence of competitive taxa such as zooxanthellates or turf algae (Cerrano et al, 2019; Soares et al, 2020). Therefore, quantifying the occurrence of these transitions within systems and understanding the factors influencing them in each distinctive TMEs is crucial.

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Benthic communities in TMEs are typically subject to more stable environmental conditions than shallower ecosystems, allowing longer-lived, slow growing and often fragile sessile invertebrate species to thrive and create living three dimensional structures (Magalhães et al, 2015; Cerrano et al, 2019). The lower light availability reduces the abundance of algal species as depth increases, providing opportunity for other shallow water competitors, such as sponges to increase in cover (Cardenas et al, 2012; Harris et al, 2021). Accordingly, the function that sessile invertebrate species perform may be increasingly important with depth in TMEs when compared with shallow ecosystems (Keesing et al, 2012; Harris et al, 2021). These assemblages also play a major role in the processing and filtering of the water column, by removing particulate and dissolved organic matter, including carbon, creating a strong link between benthic and pelagic ecosystems as well as supporting a range of commercially important species via enhanced productivity (De Goeij et al, 2013; Heyns et al, 2016; James et al, 2017; Bell et al, 2020).

Here we undertake a case study focussed on TMEs in Storm Bay, Tasmania, a large estuarine and ocean influenced system subject to a range of natural physical drivers as well as anthropogenic influences including offshore expansion of intensive salmon aquaculture and nutrients and sediment loads associated with the Derwent River, a major river system entering the bay (Edgar et al, 2010). The expansion of offshore infrastructure into the deeper waters of Storm Bay and elsewhere is relatively new and there is very little guidance on the potential interaction with nearby reef systems and the design of appropriate monitoring programs. Hence, there is a pressing need to characterise community structure of mesophotic reef ecosystems both in this particular system and elsewhere.

Selecting indicator taxa to monitor the impacts of anthropogenic activities on TMEs is hampered by the limited baseline knowledge regarding the responses of many mesophotic taxa to such pressures. However, knowledge gained from monitoring shallower ecosystem responses can provide guidance for a theoretical framework of how TMEs may respond (Oh et al, 2015; Strain et al, 2020). Ideally the response of any potential indicator should also be consistent over time and space so that small changes can be detected (Australian and New Zealand Environment and Conservation Council (ANZECC), 2000; Canovas-Molina et al., 2016). For example, at intermediate distances from salmon farms species such as ascidians and sponges could increase in abundance due to increased food supply (Strain et al, 2020). On the other hand, closer to salmon farms the stimulation of phytoplankton growth and opportunistic taxa is likely to reduce the abundances of green and brown algae due to declines in light and/or increased competition (Holmer 2010; Price et al, 2015; Strain et al, 2020). These impacts have been well studied in shallow waters (Oh et al, 2015; MacLeod et al, 2016; Valentine et al, 2016) but to date there is limited understanding of the effects of aquaculture on benthic community composition of TMEs in Storm Bay, or indeed other anthropogenic influences in the area.

Visual survey tools are the typical sampling platform of choice for benthic communities at depths below diving range, with Autonomous Underwater Vehicles (AUVs) being increasingly favoured for biodiversity assessments and monitoring projects focussed on sessile species in TMEs (Monk et al, 2020). This is due to their ability to collect a large amount of seabed imagery over a relatively large spatial extent with a consistent image footprint as well as their ability to conduct relatively spatially precise repeated surveys through time. To enable consistent and accurate description of the biota present in the immense amount of imagery collected by AUVs and other visual survey platforms, a nationally standardised approach to image classification has been developed in Australia through the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) project (Althaus et al, 2015). With the development of this technology and classification hierarchy, we can provide detailed quantitative descriptions of biota and habitats in TMEs, including candidate indicator species for long-term monitoring.

Here we use repeated AUV-derived imagery surveys collected as part of a TME (~24 – 55 m) monitoring program to provide a quantitative assessment of the sessile benthic communities on three offshore reef systems spanning a scale of 30 km in Storm Bay, Tasmania. Our approach integrates quantitative data with a theoretical framework to assess likely indicator taxa that could be used to monitor the effects of nutrient enrichment and sedimentation from sources such as salmon farms and other inputs for TME in Storm Bay. We aimed to 1) identify and quantify the epibenthic biodiversity, 2) assess spatial and temporal variation in the epibenthic biodiversity and 3) identify potential indicator species or morphospecies for ongoing monitoring of TMEs in Storm Bay.

2. Methods

2.1. Study area

The survey focused on three isolated TME rocky reefs located off North-east Bruny Island in Storm Bay, Tasmania (Fig. 1). The north reef is located off the coast of Trumpeter Bay (43°9′36″S, 147°27′0″E) and ranges in depth from 24 to 40 m. The central reef (43°12′36″S, 147°28′48″E), ranging in depth from 30 to 50 m. The south reef was the deepest and most isolated reef surveyed, located out from Cape Queen Elizabeth (43°16′12″S, 147°30′36″E) and ranges in depth from 40 to 55 m.

The surveys conducted in 2015 and 2020 were the first quantitative surveys of TMEs in this area. The three reefs selected for this survey covered a depth gradient in western Storm Bay, and a gradient in distance from the nearest in-use salmon farming leases. At the time of survey, YB1, SB1, SB2 and SB3 were active leases while SB4 was being built (Fig. 1).

2.2. Survey design and data collection

Imagery was collected through the IMOS (Integrated Marine Observing System) AUV-based long term reef monitoring program. The AUVs *Sirius,* and later *Nimbus,* collected high resolution geo-referenced still images using artificial light, with initial surveys being completed in February 2015 and repeat surveys being completed in January 2020.

Multibeam echo sounder (MBES) mapping was collated from a range of sources, including the Marine National Facility, prior to the surveys allowing identification of areas of hard bottom substrata for targeted AUV transects. This also allowed the pre-programed transects to traverse the reefs in a way that captured the different depth gradients present and provide adequate spatial coverage to complete the initial surveys in 2015, and subsequent replicate surveys in 2020 (Fig. 1; Table 1). Both AUVs fly at an altitude of approximately 2 m above the sea floor, using onboard sensors, taking still photographs that cover $\sim$ 2.5 m^2. AUV *Sirius* flies at a speed of $\sim$ 0.5 m s^{-1} while AUV *Nimbus* moved at a faster pace $\sim$ 1m s^{-1}.

A subset of imagery based on every 40th image from 2015 transects and every 135th image from 2020 transects, were used for annotation. This image interval was chosen so annotated images would provide good spatial coverage with ~20 m distance between images for both 2015 and 2020. Images were annotated in Squidle+ (https://squidle.org/, Greybits Engineering), with 25 random points superimposed on each image. The image subset replication and number of points annotated per image were chosen based on previous research that suggest this would be sufficient to provide high precision in estimates of cover for the morphospecies of interest that are not too rare (Perkins et al, 2016, 2017). Each point was annotated to morphospecies level based on the Australian Morphospecies Catalogue, which is an extended version of the classification framework CATAMI (Althaus et al, 2015).

2.3. Data processing

Variation in benthic morphospecies were initially described based on
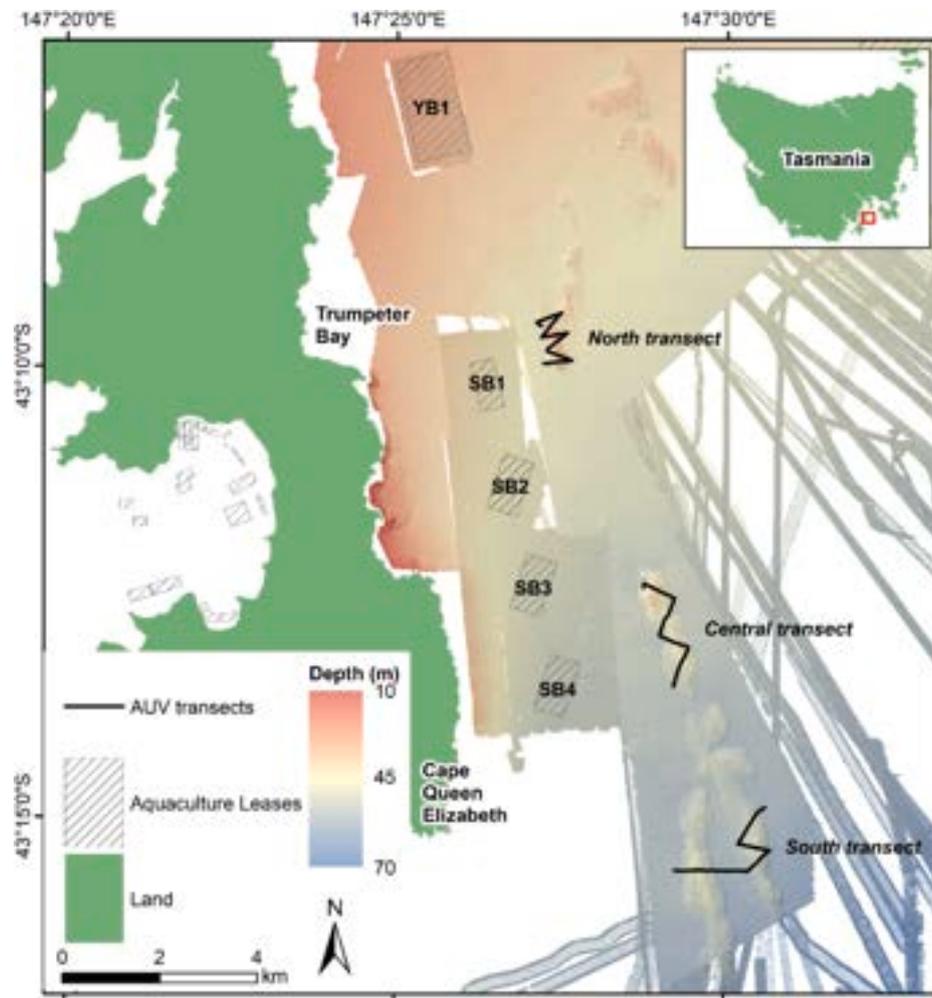
Fig. 1. Location of remote reef features mapped by multibeam sonar and photographically sampled by Autonomous Underwater Vehicles off the coast of North-east Bruny Island, Storm Bay, Tasmania. (YB1- Yellow Bluff 1; SB1-4 – Storm Bay 1–4).

Table 1
Summary of transects, including depth range, length and number of still images captured.

		Depth (m)	Length (m)	Total number of still images	Number of images annotated
2015	North	26 – 42	3680	7965	203
	Central	32 – 51	3231	6622	152
	South	41 – 57	3857	7896	143
2020	North	26– 42	3594	10,479	166
	Central	32 – 51	3070	9271	114

percentage cover data. After the annotations were completed, the images from each transect were grouped into depth zones (20 – 30 m, 30 – 40 m, 40 – 50 m, and 50 – 60 m), based on the overlap of depth across each of the transects before percentage cover was calculated. Unscorable annotations (due to lighting), mobile species, and images with 20 or more points scored as soft sediment substrata were removed prior to percentage cover estimates. Patchy reef and reef covered in sediment tended to occur on reef margins, which may be important ecotones. A cut-off of 20 points was used to ensure that images from these areas were include in analysis. All soft sediment substrata points were removed from the analyses after percentage cover was calculated, to ensure the focus was on the hard substrata reef community assemblage.

Due to the low cover of the majority of morphospecies, cover was also aggregated to higher levels within the CATAMI hierarchy to allow sufficient quantitative data for further analysis. This higher level is referred to as "Broad morphospecies" throughout the analysis. Matrix morphospecies are typically composed of turfing mixed bryozoa/cnidarian/hydrozoan/sponge/macroalgae associations that are too difficult to differentiate to a lower taxonomic resolution in image analysis. Therefore, we have aggregated the three matrix groups into a new label, Biological Matrix, with the intention that "Biological" is representative of any organism. The percentage cover analysis was completed using and R v4.0.4 (http://www.R-project.org/, R Foundation for Statistical Computing, 2021).

2.3.1. Multivariate analysis of assemblages

The variation in sessile assemblages through time, between reefs and across depth zones were analysed in PRIMER v6 with PERMANOVA + add-on. A Bray-Curtis similarity matrix was computed across all samples for the total species assemblage, treating each image as a separate sample. Reef and depth zone were then used as grouping factors in the PERMANOVA. A dummy variable of one was added to reduce the effect of sparse data (some samples, i.e. images, did not contain any biological morphospecies) on the similarity measure (Clarke et al, 2006). Inspection of the Shepherds diagram indicated that standardisation and transformation were not required for this data set.

A multi-dimensional scaling plot (MDS) was used to visualise how assemblages differed in taxa composition across time, reef and depth surveyed. Distances among centroids were calculated for the nMDS plot to aid in interpretation of the graph and to reduce stress. A three factor PERMANOVA (time, reef, and depth) and their interactions were used to

test the null hypothesis that the community composition was not significantly different across depth, time, and reef. Pairwise tests were undertaken on significant interaction terms within the PERMANOVA, to better understand source of variation. A distance-based test for homogeneity of multivariate dispersions (PERMDISP) routine was run to assess the dispersion assumption for the PERMANOVA, with no strong dispersion differences detected between distance categories. Calculation of the Pseudo-F ratio and P value ($\alpha = 0.05$) were based on 9999 permutations of residuals under a reduced model. A Similarity Percentage Analysis (SIMPER) was used to identify morphospecies that contributed most to the average similarity within a reef, depth zone and across survey years. DIVERSE was also applied to the data to calculate morphospecies diversity indices for each depth, time, and reef.

2.3.2. Power analysis of candidate indicator species

Finally, a power analysis was undertaken for several key morphospecies. The objective of the power analyses was to quantify the number of images required to detect predetermined changes in percentage cover (25 %, 50 %, and 75 %) of selected indicator cover in subsequent surveys. The method used here was a simulation-based approach similar to that outlined in Perkins et al. (2017) and Bolker (2008). In short, this approach uses model-based estimates of cover from the initial surveys and simulates pre-determined levels of change and the data gathering process i.e., image subsampling and point scoring approaches). Power is then determined as the proportion of simulations where the change is detected. Further details are given below. This was completed using the sjmisc package (v 2.8.10, Lüdecke, 2018) in R (v4.04, R Foundation for Statistical Computing, 2021).

Model-based estimates of cover from the 2015 survey at each reef were used for the basis of the power simulations, as they are a pre-farm baseline. To complete this power analysis, all image locations from the 2015 transects on each reef were compiled. From these potential image locations for subsequent surveys, only images from within the depth range found in the empirical data were used for the simulation models to avoid predictions outside the bounds of the data used in the current model. Image sampling efforts between 50 and 250 (at 25 image intervals) were used to test a range of sampling effort, both more and less than were used in this project. Simulated within image sampling was kept at 25 points to mimic sampling effort used in this project. A random starting point between 1 and the given sampling effort was used to make a systematic random selection of new images for analysing in each simulation. Predictions of the binomial probability of success (i.e., probability that a point would land on the target morphospecies) were then made using the model at each randomly selected image location in the simulation, with depth treated as a covariate.

The selection of morphospecies for the power analysis was from a range of broad taxonomic groups, to provide an outline of sampling effort for potential candidate monitoring morphospecies. Individual morphospecies were selected based on theoretical expectations of considerable responses to impacts (Strain et al, 2020). Morphospecies with higher abundance or presence across each of the systems were identified, as they would be indicators that are regionally relevant and provide sufficient cover to detect change. The directional shift in abundance was chosen based on the predicted hypothetical responses due to the impact of interest, salmon farming (Strain et al, 2020). Opportunistic algae and turfing matrices are more likely to increase (MacLeod et al, 2016), so the simulated within image binomial probability for these morphospecies was increased by 25 %, 50 % and 75 %. On the other hand, other algae and invertebrate morphospecies would be more likely to decrease under increasing pressure (Oh et al, 2015; Strain et al, 2020), and so the within image binomial probability was adjusted to produce a reduction of 25 %, 50 %, and 75 %.

Using this adjusted binomial probability, 25 random binomial draws were then taken representing the use of 25 random points, and thus simulating the binomial variability of point sampling. Models were then refit using the empirical data from the 2015 survey and the simulated

data from the following survey, including a time effect. A total of 1000 simulations were used for each scenario, and the proportion of times that a significant time effect was detected was used as a measure of power. Typically, high statistical power is achieved at 80 % with a significance (alpha) level of 0.05. Therefore, in a simulation framework this equates to the proportion (ideally > 80 %) of simulations where the simulated change is detected with a P-value of 0.05.

3. Results

Across the three reef systems, a total of 300 individual morphospecies were identified in 778 images, including bryozoa, cnidaria, echinoderms, macroalgae, mollusc, sponges, and invertebrate turfing matrices (Supplementary S1, Fig. 2).

Broad morphospecies groups, in which fine level morphospecies are grouped into higher level CATAMI classes, were utilised to graph assemblage composition, as percentage cover for most individual morphospecies were too low (i.e. less than 2 %) to be appropriately presented visually (Table 2; Figs. 3 – 5).

3.1. Epibenthic community composition across the depth gradient

There was no clear pattern across the depth gradient for morphospecies diversity or evenness, except for 20–30 m depth zone which consistently had the lowest diversity and evenness in percentage cover (Table 2).

The north reef 20–30 m depth zone was the only depth zone extending shallower than 30 m in the study system and was dominated by fine branching algae in both 2015 and 2020, with encrusting algae, filamentous/filiform algae, encrusting sponges, and biological matrix individually contributing up to 10 % of the total cover in each survey period.

Within the 30–40 m depth zone, a zone shared across the northern and central reefs, the dominant morphospecies varied between reefs and survey year, although biological matrix typically dominated (Figs. 3 & 4). Macroalgal groups had varied cover but were overall higher in cover than invertebrate groups. Erect fine branching algae was most abundant on the north reef, while filamentous/filiform was more dominant on the central reef. Aside from matrices and macroalgal dominance, sponge groups had a higher percentage cover on central reef compared to the north reef.

The 40–50 m zone was the only depth zone found across all three reef systems (Figs. 3 – 5). Biological matrix dominated this depth zone, followed by turf/silt/sediment matrix on all three reefs. Macroalgal groups still had a strong presence in this depth zone, particularly filamentous/filiform algae, and encrusting algae. Encrusting sponges dominated the invertebrate groups but still had less cover than macroalgae. Between 30–40 m and 40–50 m depth zone, macroalgal cover varied much more than sponge groups which appear to remain stable in their cover. Interestingly, zoanthids increased in this depth zone.

The south reef was the only site with reefs extending into the 50 – 60 m depth zone, it was found that this zone typically had generally lower percentage cover of all morphospecies groups (Fig. 5). Biological matrix was the group with the highest cover, followed by turf/silt/sediment matrix with and encrusting macroalgae (Fig. 5). Erect forms and encrusting sponge and zoanthids all had higher cover in this depth band compared to 40 – 50 m depth.

3.2. Epibenthic community composition through time

There was a clear negative relationship between survey year and diversity indices for all reefs and depth zones, excluding the shallowest depth (Table 2). Most notably, morphospecies richness in the 40–50 m depth zone virtually halved for north and central.

In the 20–30 m depth zone, erect fine branching algae, the most dominant group, decreased in percentage cover between 2015 (89.20 %,
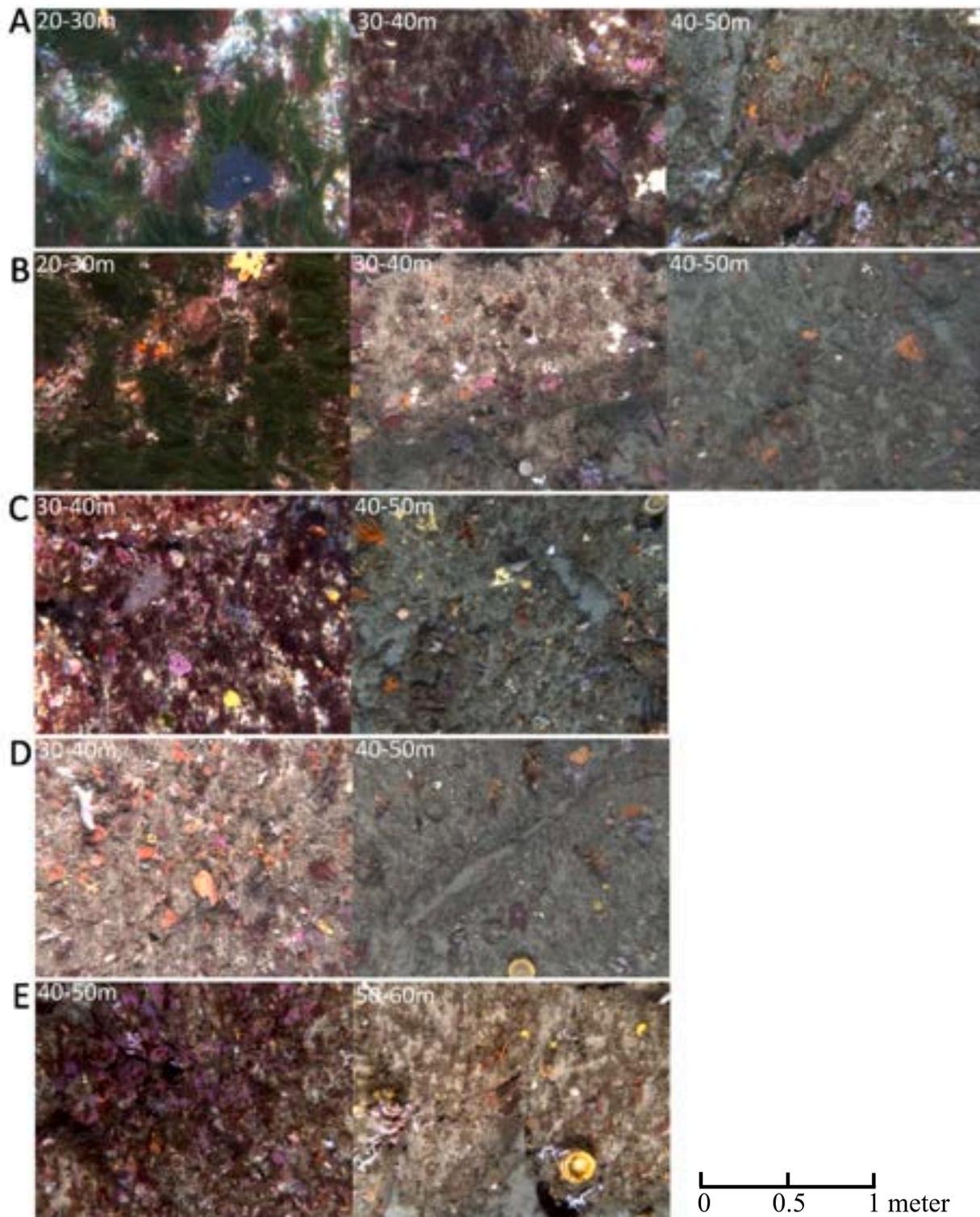
Fig. 2. Example images from each of the transects and depth bands used for analysis. A) North 2015 – Macroalgae (*Caulerpa* spp.) more common in shallower depth, sponges common in most photos, biological matrix common in deeper depth bands; B) North 2020 – Macroalgae (*Caulerpa* spp.) more common in shallower depth, sponges common in most photos, increasing occurrence of in biological matrix in deeper depth bands; C) Central 2015 – Macroalgae (Rhodophyta) common in shallower depth band, biological matrix interspersed with sponges increasing in deeper depth band; D) Central 2020 – Macroalgae (Rhodophyta) and soft corals common in shallower depth band, biological matrix increasing in deeper depth band; E) South 2015 – Macroalgae (Rhodophyta) common in shallower depth band, biological matrix interspersed with sponges increasing in deeper depth band.

±1.72 SE) and 2020 (58.72 %, ±2.20 SE) (Fig. 3). By contrast, most other broad morphospecies groups increased in percentage cover between the 2015 and 2020 surveys in this depth zone (Table 2; Fig. 3). This included the cover of biological matrix (2015 0.31 %, ±0.31 SE;

2020 10.02 %, ±1.34 SE) and octocorals (2015 0.31 %, ±0.31 SE; 2020 3.41 %, ±0.81 SE) (Fig. 3).

In the 30–40 m depth zone, biological matrix became increasingly abundant from 2015 to 2020 on both reefs covering 4.75 % (±0.36 SE)

Table 2
Summary of data used for analysis and diversity for each group of factors.

		Number of images (points included in analysis)	Number of broad morpho-species (>2% cover*)	Number of morpho-species (>2% cover**)	Species Richness	Shannon's index	Simpson's index
20–30 m							
2015	North	13 (319)	11 (2)	23 (2)	3.186	0.8544	0.687
2020	North	20 (496)	14 (7)	39 (6)	6.123	1.972	0.2963
30–40 m							
2015	North	137 (3056)	20 (9)	134 (7)	16.57	2.654	0.1748
	Central	31 (727)	19 (10)	103 (6)	15.48	3.189	0.1077
2020	North	110 (2465)	21 (6)	80 (6)	10.12	2.108	0.2385
	Central	33 (749)	16 (9)	76 (6)	11.33	2.65	0.1346
40–50 m							
2015	North	53 (1079)	20 (8)	87 (6)	12.31	2.738	0.1231
	Central	121 (2262)	21 (7)	166 (5)	21.36	3.032	0.1194
	South	81 (1716)	18 (8)	132 (6)	17.59	2.57	0.1854
2020	North	36 (705)	14 (6)	39 (7)	5.794	2.014	0.2398
	Central	81 (1557)	17 (6)	96 (3)	12.92	1.914	0.3262
50–60 m							
2015	South	62 (993)	19 (7)	120 (5)	17.24	2.735	0.1719

*The portion of broad morphospecies that have > 2 % cover within each transect, is written within the brackets.
** The portion of individual morphospecies that have > 2 % cover within each transect, is written within the brackets.
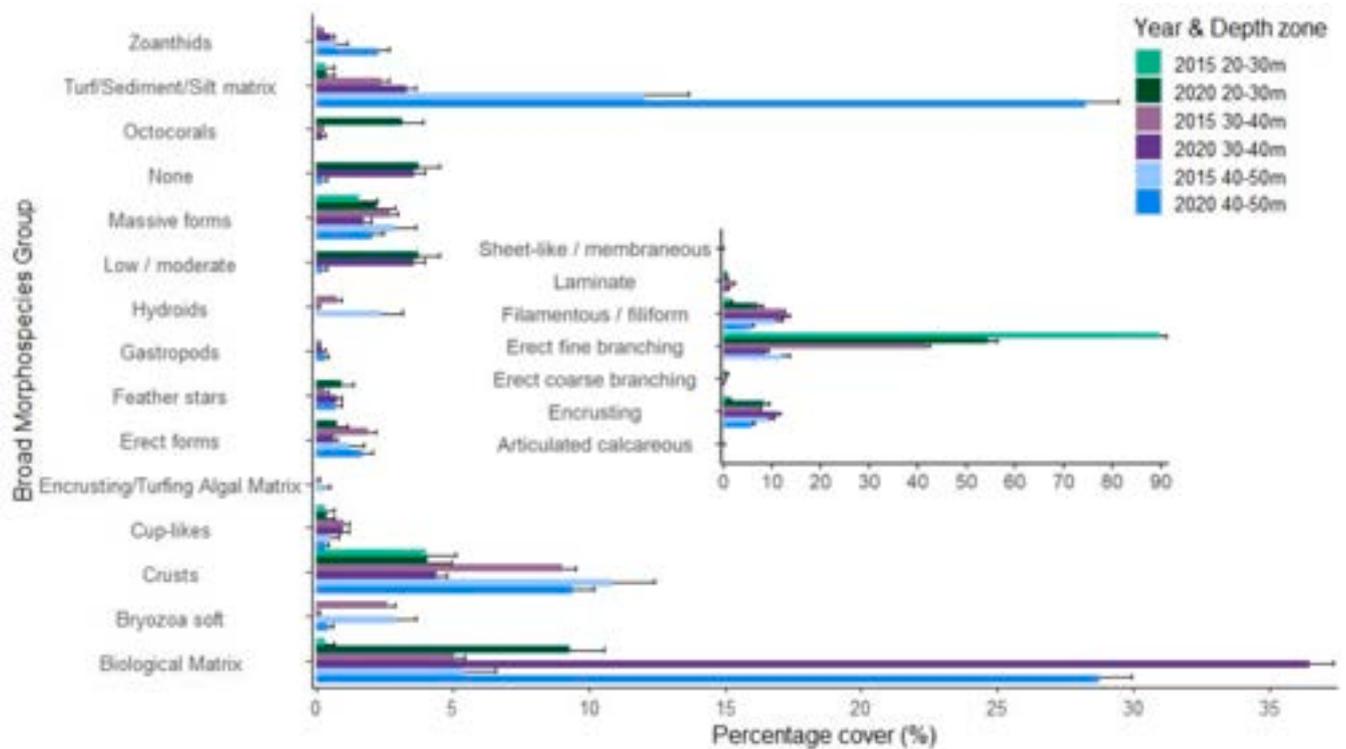
Fig. 3. Percentage cover, of benthic morphospecies groups on each AUV transect on the north reef, subset into depth zones. Values are mean ± SE. Inset plot shows algal groups for ease of interpretation. Note: x-axis is on different scales for invertebrate and algal groups.

in 2015 and 39.57 % (±0.93 SE) in 2020 on the north reef and 8.79 % (±1.02 SE) in 2015 and 24.51 % (±1.50 SE) in 2020 on the central reef (Figs. 3 & 4). Algae was still a prominent feature in this depth zone. On the north reefs there was a shift from erect to low profile algae between surveys, where erect fine branching algae covered 41.67 % (±0.84 SE) in 2015 and filamentous/filiform algae covered 14.22 % (±0.67 SE) in 2020 (Fig. 3). A similar pattern was seen on central reef, however encrusting algae had higher cover then filamentous/filiform algae in

2020 with 16.87 % (±1.30 SE) (Fig. 4). Aside from the algal and biological matrix groups, encrusting sponge has the highest percentage cover on the north reef, covering 9.21 % (±0.50 SE) in 2015 and 4.60 % (±0.40 SE) in 2020 (Fig. 3). On the central reef however, encrusting sponge was the next most abundant in 2015 only with 15.50 % (±1.30 SE) while turf/silt/sediment matrix became more dominant in 2020 with 14.20 % (±1.22 SE) cover (Fig. 4). On both reefs sponge groups decreased in percentage cover between 2015 and 2020 (Figs. 3 & 4).
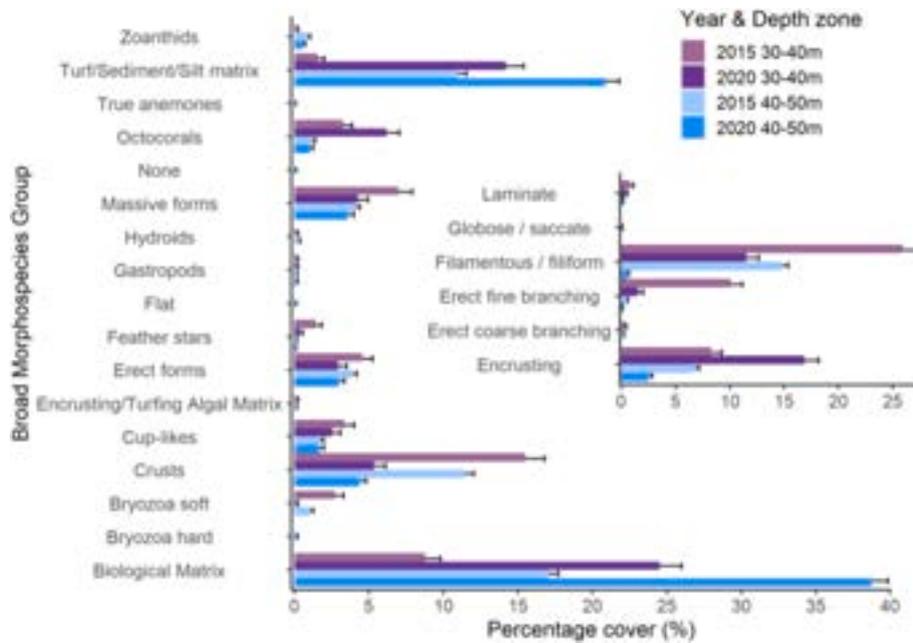
Fig. 4. Percentage cover of benthic morphospecies groups on each AUV transect on the central reef, subset into depth zones. Values are mean ± SE. Invertebrate and algal groups have been separated for ease of interpretation. Note: x-axis is on different scales.
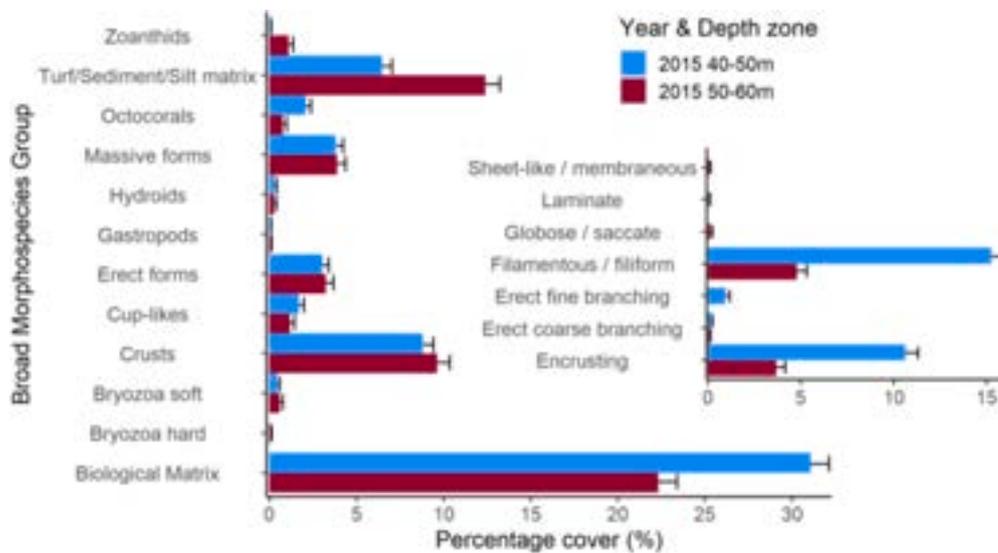
Fig. 5. Percentage cover of benthic morphospecies groups on the AUV transect on the south reef, subset into depth zones. Values are mean ± SE. Invertebrate and algal groups have been separated for ease of interpretation. Note: y-axis is on different scales.

Table 3
PERMANOVA based on Bray-Curtis similarities of the relative abundance of 315 morphospecies in response to reef location (Reef), survey year (Time) and depth zone (Depth) and their interactions.

Source	Degrees of freedom	Sum of Squares	Mean Square	Pseudo-F ratio	P- value (By permutation)	Unique permutations
Time	1	27,967	27,967	15.744	0.0001	9925
Reef	2	43,201	21,600	2.7417	0.0001	9895
Depth	3	202,310	67,437	30.12	0.0001	9896
Reef x Time	1	12,632	12,632	7.3828	0.0001	9933
Time x Depth	2	31,456	15,728	10.023	0.0001	9909
Reef x Depth	1	23,907	23,907	5.8307	0.0001	9928
Reef x Time x Depth	1	12,479	12,479	3.2853	0.0001	9924
Res	766	1,360,700	1776.4			
Total	777	1,961,100				

Other broad morphospecies groups did not follow any trend, but octo-corals had a large increase in percentage cover on the central reef (2015 3.36 %, ±0.65; 2020 6.19 % ±0.84).

In the 40–50 m depth zone, again biological matrix had the highest percentage cover on all transects, except for north reef in 2015 (North 2015 12.75 %, ±0.91 SE; Central 2015 16.94 %, ±0.68 SE; South 2015 31.09 %, ±1.03 SE; North 2020 28.79 %, ±1.51 SE; Central 2020 38.76 %, ±1.09 SE) (Figs. 3 – 5). In 2015, filamentous algae were the dominant morphospecies on the north reef with 18.42 % (±1.06 SE) cover. On the other hand, turf/silt/sediment matrix was the next most prevalent morphospecies on the reefs in 2020, with 24.44 % (±1.44 SE) cover on the north and 20.92 % (±0.91 SE) on central (Figs. 3 & 4). There was a general trend of decreasing percentage cover between 2015 and 2020 in broad morphospecies groups. Interestingly, on the north reef zoanthids (2015 1.26 %, ±0.31; 2020 2.34 %, ±0.51) and feather stars (2015 0.07 %, ±0.07 SE; 2020 0.67 %, 0.27 SE) groups both increased within this depth zone through time (Fig. 3).

3.3. Variation in epibenthic community

PERMANOVA revealed significant differences in the cover and structure of epibenthic biota assemblages between each of the variables and their interactions; reef, survey year, and depth zone (Table 3). This is supported by the nMDS ordination plot which displays a clear change in assemblages along the depth gradient and the differences in assemblages appearing to be greatest in the shallow depth zones in 2015 (Fig. 5). All combinations of depth bands, reefs and year indicated statistically significant differences for all pairwise comparisons.

The particularly community found in the 20–30 m depth zone is a result of high cover of erect fine branching macroalgae. SIMPER analysis indicated that *Caulerpa* spp. was the morphospecies contributing most to the dissimilarity between this depth zone and all other depth zones across reef and years.

There was also a difference between 30–40 m on the north and central reef in 2015 and all other depth zones across surveys. SIMPER analysis indicated that this difference is largely caused by the stark increase in biological matrix and changes in the cover of individual macroalgae morphospecies. Other invertebrate morphospecies remained relatively similar, although gorgonian red and various encrusting sponge morphospecies made small contributions to the dissimilarity.

At 40 – 50 m depth zone the assemblages were most dissimilar between south and the other reefs in 2015, the only year where all three reefs were surveyed (Fig. 6). The 40–50 m depth zone for south 2015 was found to be more like 30–40 m depth zone for the north and central 2020 survey. Further, the 50–60 m depth zone for 2015 was most similar to 40–50 m depth zone on the north reef in 2020 (Fig. 6). SIMPER analysis indicated that the community differences in these depth zones across the surveys was mostly due to dissimilarities in the cover of biological matrix, filamentous/filiform red and turf/silt/sediment matrix. These three morphospecies groupings accounted for ~ 50 % of dissimilarity between 40–50 m depth zone and each of the interactions mentioned above.

3.4. Power analysis

A simulation-based power analysis for an increase in the percentage cover filamentous/filiform red algae indicated a 25 % or more increase could be detected with high power (80 %) by scoring 50 images on individual reefs and all reef combined (Fig. 7). Increases in erect fine branching red algae of 25 % or more was also detectable with high power by sampling 50 images per reef for all reefs, as well as all reefs combined. However, 150 images were required detect a 25 % increase in the central reef and there was insufficient power to detect changes in the south reef (Fig. 7). The central, south and all reef analysis was omitted from the *Caulerpa* spp. simulations, as this morphospecies was only found on the North reef. High power was achieved in detecting a 25 % decrease in cover with only 50 images (Fig. 7).

High power could be achieved when there was a stimulated 25 % decline in cover for only a few morphospecies used in the analysis. This was achieved for calcareous red macroalgae within 75 images across all reefs and 200 images on the north reef. High power was also achieved within 225 images for Bryozoa soft (merged) and 150 images for orange encrusting sponge, when sampling across all reefs (Fig. 8).

A decrease of 50 % cover of all morphospecies in the power analysis could be detected, when sampling all reefs, by sampling between 50 and 125 images in total for all three reefs. Further, a 50 % decline in cover of calcareous and encrusting orange sponge could be detected with high power in 50–175 images across each individual reef (Fig. 8).

Finally, a 75 % decline in cover could be detected with high power across most individual reefs and all reefs by sampling 50–200 images depending on the morphospecies (Fig. 8). However, this was not detectable with sufficient power for simple white rough and gorgonian red on the north reef and hydroids on the south reef (Fig. 8).
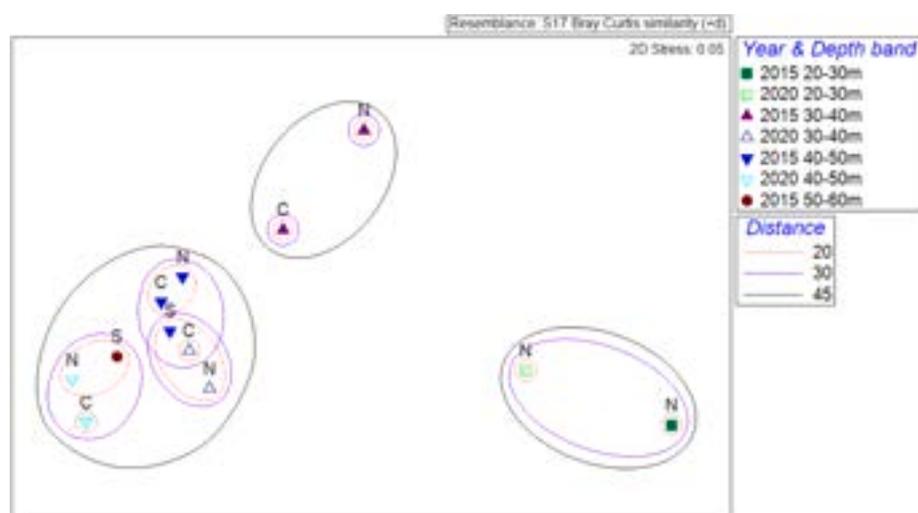
Fig. 6. Multi-dimensional scaling (MDS) plot of all AUV transects, showing depth zones, reefs, and time surveyed. Substrata categories and mobile species were excluded from assemblages. Analysis based on Bray-Curtis similarity matrix of count data. Clusters are based on resemblance levels at 20% (red), 30% (blue) and 45% (black).
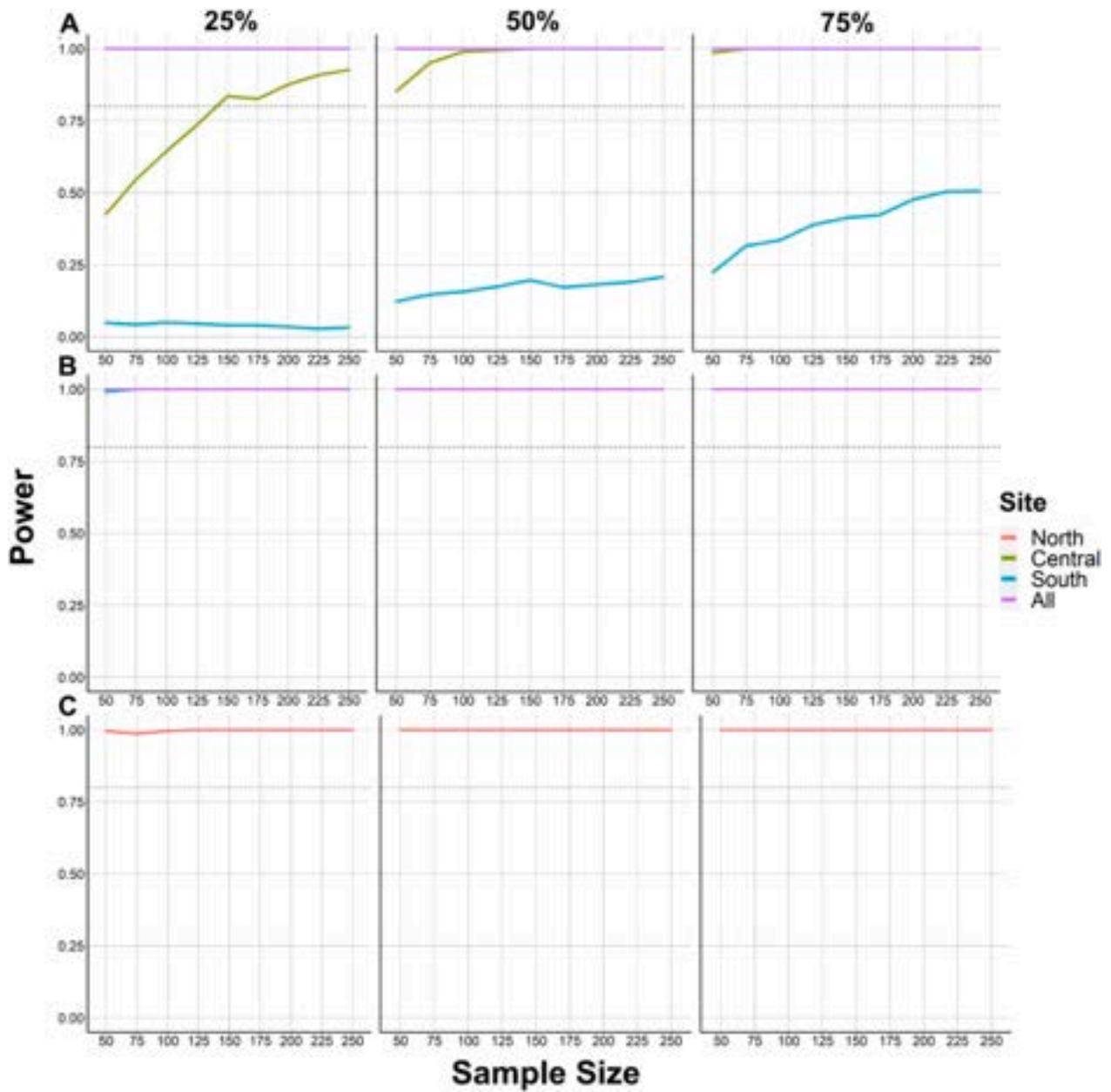
Fig. 7. Power analysis to detect a simulated 25%, 50% and 75% increase of A) Erect fine branching red algae B) Filamentous/filiform red algae and C) *Caulerpa* spp. – only north reef is presented this graph. Sample size is number of images being annotated. The dashed line is at 80% power.
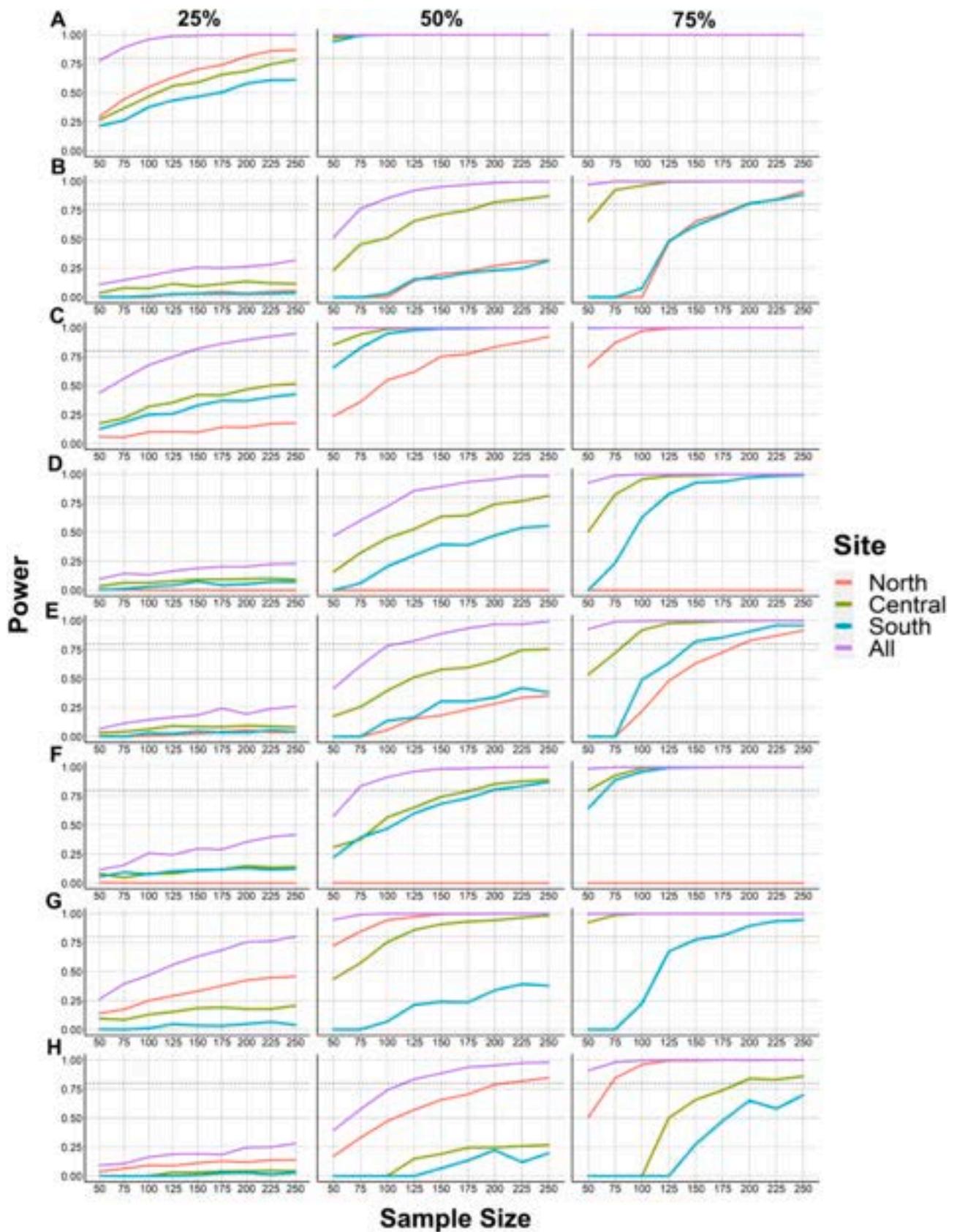
Fig. 8. Power analysis to detect a simulated 25%, 50% and 75% decrease in A) Calcareous red macroalgae; B) Cup red sponge; C) Orange encrusting sponge; D) Simple white rough sponge; E) Parazoanthid sp.; F) Gorgonian Red; G) Bryozoa (Merged) and H) Hydroids (Merged). Sample size is number of images being annotated. The dashed line is at 80% power.

4. Discussion

Our study provides an exemplary pathway and methodology for conducting baseline assessments of TMEs in regions with limited prior research or facing increasing anthropogenic pressures. The insights gained aim to inform future environmental monitoring programs. We characterised the identity and relative cover of morphospecies that may be present and, the extent that they vary with depth, in space and in time. Overall, we found a clear shift in the benthic assemblage across the depth gradient sampled. The shallower communities (<30 m) were dominated by macroalgae, mostly *Caulerpa* spp. while deeper communities (>30 m) were dominated by encrusting sponges and turfing matrices of unidentifiable invertebrates, with a transitional zone between 30–40 m. Notably, while the algal zone on shallower reefs often constituted algal morphospecies that could exceed 20 % cover, except for turfing invertebrate matrices, the invertebrate morphospecies on deeper reefs rarely exceeded 2 % cover. This variation has significant implications for monitoring and annotation of imagery and for selecting potential indicator species or morphospecies to ensure sampling power is adequate to detect meaningful changes.

A key finding of the study was that during the five-year period between surveys, there were some marked changes in assemblage structure that, despite reef-to-reef variability, were relatively consistent across the reefs sampled. These changes include an increase of dominance in the communities, with fewer but more abundant morphospecies, except in the 20–30 m depth band, suggesting a response to changing environmental conditions had occurred (Edgar et al, 2010; Micaroni et al, 2021). In 2020 the shallower depth zones on the north reef while still significantly different, had similarities to deeper depths on the south reef in 2015. This suggests that the changes observed during that period included a transition to biota more typical of deeper systems potentially influenced by altered light penetration. For ongoing monitoring of such changes in these systems our power analysis suggested that to detect change of 50 % or more in overall cover for most individual morphospecies we would need to sample at a similar intensity to that undertaken in this study, with sampling across all reefs to provide generality and sufficient replication.

4.1. Epibenthic biodiversity and distribution

Detailed taxonomic descriptions of the vast majority of mesophotic species in our study region are currently lacking. Therefore, we are currently reliant on the description of taxa to the morphospecies level, based on a combination of taxonomy, and distinctive morphological traits and colour. However, it is likely, particularly for sponges, that some morphospecies represent different morphologies (or colours) of the same species (e.g., Schonberg 2021). We do not suggest that this morphospecies list reflects actual species diversity but is using a cost effective and non-destructive approach over a broad spatial and temporal scale to provide insight into the nature and extent of the fauna, which is standard practice for marine image-based studies (Balata et al, 2011; Althaus et al, 2015; Monk et al, 2016; Harris et al, 2021).

As expected, macroalgae gradually declined in cover and structural complexity with depth, until 50 m where it was no longer a key component of the assemblage, as reported on temperate rocky reef in New Zealand (Harris et al, 2021) and tropical rocky reefs in Brail (Magalhães et al, 2015). Typically, species of the green algal genera *Caulerpa* dominated reef area shallower than 30 m before declining rapidly below 30 m and being replaced by red algae as the dominant group. In the temperate waters of New Zealand, Nelson et al. (2014) demonstrated with increasing depth there was a taxonomic shift in algae from Chlorophyta to Rhodophyta, as well as from branched to prostrate forms and crustose coralline algae, as seen in this study. Below 30 m, as invertebrate groups became increasingly prominent, unlike the macroalgae, no single group or morphospecies was dominant with most morphospecies having less than 2 % cover, a pattern found throughout mesophotic reef species in this region (Perkins et al, 2021). Despite this, fine invertebrate turfing matrices tended to dominate the substrate cover at these depths. Encrusting sponges remained stable across depths on the central and south reef, while they increased with depth on the north reef. This stability in percentage cover on the central and south reefs could be due these reefs having typically lower profile than the northern reef, allowing settlement of encrusting sponges and beneficial organic matter (Bell et al, 2015). This increase in matrices groups and some invertebrate morphospecies groups with depth could be reflective of varied responses or life-history adaptations of the different morphological forms to disturbances and environmental factors (Bell et al, 2015; James et al, 2017; Cummings et al, 2020).

A key finding of the temporal analysis between survey years were that erect fine branching algae (primarily *Caulerpa* spp.) decreased markedly in the 20–30 m depth zone, while other broad groups in that zone followed an increasing trend and the biotic assemblage shifted to represent that previously found in deeper depth zones. The marked decrease in the cover of *Caulerpa* spp. and concurrent shift in epibenthic assemblages could be due to a variety of disturbance regimes. One distinct possibility is that a reduction in light levels (resulting from increased siltation or abundances of phytoplankton) can create an environment in shallow reefs more like that of a deeper TME, allowing an increase in abundance of morphospecies groups more adapted to those conditions, such as sponges and octocorals, and decrease a in light-dependent macroalgae (Bokn et al, 2003; Burfeind and Udy, 2009; Harris et al, 2021; EPA, 2024). Alternatively, increases in temperature due to climate drivers can also reduce macroalgal cover, and facilitate spatial competition with other benthic invertebrates (Cardenas et al, 2012; Harris et al, 2021; Soler et al, 2022). Without longer-term surveys and the associated environmental data, it is hard to determine the cause of this shift at this stage.

In the deeper depth zones, there was a general trend of decreasing percentage cover in broad morphospecies groups, other than matrix groups, and morphospecies richness between survey years in most categories. The reduction in morphospecies richness and diversity across all reefs surveyed on the western side of Storm Bay may be an indication of ecosystem wide disturbance. The development and expansion of offshore salmon farms in Storm Bay over the period of this study could be one potential driver of this shift, as nutrient enrichment and sedimentation are known to alter the ecosystem (Hamoutene et al, 2016; MacLeod et al, 2016; Strain et al, 2020). However, while the observed changes follow a pattern that may be consistent with increased disturbance, to untangle the range of potential drivers, a more extensive time-series is needed with more replicates for each of the variables explored in this paper. For example, other anthropogenic inputs may also be combined with larger ecological mechanisms, such as those highlighted in research on estuary connectivity by Wild-Allen and Andrewartha (2016), which showed a strong outflow of nitrogen into Storm Bay driven by the seasonal variation in surface river outflow from the adjacent Derwent estuary. These larger scale patterns and anthropogenic activities can have cascading effects on entire ecosystems, and we are yet to understand how or by how much they are influencing the TMEs in the survey region over multi-year scales.

While variation in community structure was observed between reefs at similar depths, overall, these patterns were less distinct than the observed changes between depth zones or across years. Macroalgae is the primary morphological group impacted by light incidence, while other factors such as reef slope, habitat microtopography and oceanography of a region can have more immediate effects on invertebrate community structure (Bridge et al, 2011; Cardenas et al, 2012). Multi-beam echo sonar seabed mapping in this region highlights the different geomorphology of each reef, while relative distance to factors such as the mouth of the adjacent Derwent River, exposure to tidal currents and oceanic swells in Storm Bay could all contribute to the slight variation in assemblage between reefs (Cherukuru et al, 2014; Strain et al, 2020).

On all the deep reef systems examined in Storm Bay there was a large amount of biological matrix cover present, and one that generally increased with depth. Notably though, there was also a significant increase in the extent of biological matrix cover scored in 2020 compared to 2015 across most reefs and depths. Monk et al. (2017) identified the clear dominance of biological matrices (typically composed of turfing mixed bryozoa/cnidarian/hydrozoan/sponge) associations in multiple offshore TMEs in Tasmania that typically increase with depth and declining wave influence. Overall, this suggests that various matrix groups form an important benthic component of TMEs generally, as the low-energy nature allows more fragile communities to thrive (Monk et al, 2016). However, some authors also suggest this can be indicative of a decline in reef health when matrix cover increases while larger growth forms decline (Balata et al, 2011; Magalhães et al, 2015; Fraser et al, 2020). The substantial increase in biological matrix noted across both reef systems over the 5-year interval covered by this study, may be an indication of significant system changes over this period, although identifying whether this is related to anthropogenic causes or periods of less disturbance will require further studies. One potential method for further assessing the components of the matrices would be to have an additional high resolution (i.e. greater than the current 2750 x 2200 on AUV *Nimbus*) camera taking photos closer to the seafloor, potentially allowing more detailed imagery of the matrices while the other camera captures images with a larger area for other analysis. However, this method presents its own challenges in matching the finer resolution data with the broader analysis. Regardless, it is suggested that recording the extent of such turfing matrix, and possibly identifying to a finer taxonomic level, would be an important component of ongoing monitoring programs.

4.2. TME monitoring

Ideally monitoring programs should be designed with sufficient statistical power to detect biologically meaningful changes from impacts such as salmonid farming, major storms or changes in adjacent ocean currents and riverine outputs (Perkins et al, 2017). Detecting a change of +/-50 % or less, particularly if outside the bounds of observed natural variability, would help to identify shifts in key indicator species before the ecosystem reaches potential tipping points beyond which resilience to undesirable phase shifts becomes reduced and recovery more difficult (Perkins et al, 2017; Turner et al, 2019). At the level of sampling undertaken in our study, there were only six morphospecies where high power was achieved to the detect changes in cover of 25 % through time and this was only on a particular reef or all reefs. This is primarily because at depth, very few broad morphospecies groups had more than 2 % cover, as such individual morphospecies had very low percentage cover, thus requiring significantly more sampling effort before enough statistical power was gained to detect meaningful change. While the underlying mechanisms are unknown, increases in some morphospecies occurring concurrently with decreases in others could indicate a balancing in the system after disturbance. For example, in the shallower zone the increase in encrusting red algae could be in response to the decline of erect fine branching algae, particularly *Caulerpa* spp. (Edgar et al, 2004) and is consistent with what may be expected if additional nutrient input into this region resulted in lower light penetration at depth (Strain et al, 2020). Likewise declines in encrusting sponge cover at depth could be a result of increasing sedimentation and formation of turfing biological matrix, an additional response anticipated under enhanced nutrient inputs over that period (Strain et al, 2020). Overall, these morphospecies, including the more abundant natural response groups such as *Caulerpa* spp. and foliose red algae satisfy some of the requirements of good indicator species/groups and may provide an example of potential indicators for a future monitoring program. However, using the current method sampling intensity, the ability to detect biologically meaningful change with sufficient power in a wider variety of morphospecies may be limited based on the typical sparsity of many

morphospecies, especially at greater depths. Hence, if acquired imagery is analysed in a similar manner to this study, future monitoring may either be restricted to the more common morphospecies, or by aggregated groupings of similar morphospecies (such as branching sponges). This may be overcome by targeted scoring or by addition of extra images within transects, particularly in depth zones that are not replicated across all reef systems (Perkins et al, 2022).

In TME, as opposed to shallower algal-dominated systems, benthic species often exhibit high diversity but with low cover even among the most common of individual morphospecies (Monk et al, 2016; Perkins et al, 2018). When monitoring programs aim to detect biologically meaningful changes in morphospecies, additional sampling or alternative data annotation approaches are likely to be required. The results from this study indicate that detecting change over time of +/- 50 % or less for individual morphospecies is likely to be challenging, even with significant sampling effort, particularly using randomised point count approaches to quantifying cover in imagery. Alternate sampling designs, such as targeted scoring of all individuals across non-overlapping images, or stratified sampling within known distribution ranges, may be more appropriate for morphospecies with < 2 % cover when considering future designs to detect changes in indicator taxa (Perkins et al, 2017; Perkins et al, 2022). The power analysis in this study serves as a starting point for selection of indicator taxa. As more AUV-based surveys or image-based sampling with similar platforms are conducted and combined with environmental data, there will be an accumulation of knowledge to guide the most appropriate indicator taxa used to match the desired sensitivity of individual monitoring programs to detect environmental impacts.

4.3. Conclusion

This study provides a baseline of the benthic flora and fauna on offshore temperate mesophotic reefs in areas subject to increasing anthropogenic pressures, and an indication of potential indicator morphospecies and groups that may be informative indicators for monitoring environmental change. It is the first biological assessment on mesophotic reefs in Storm Bay, Tasmania, allowing the benthic biota to be described and quantified, underpinning future monitoring programs in the region. We highlight the importance obtaining data from initial surveys to determine the influence of depth, and temporal, and spatial variability in a diverse range of algal and invertebrate morphospecies on reefs in this region. The extensive amount of rare invertebrate morphospecies observed highlights the importance of initial exploration of these deeper communities to document biodiversity and identify appropriate indicator morphospecies or groups with sufficient overall cover to be reliable indicators of change. There were a few key indicator groups which appeared relevant to detection significant environmental changes, including algal assemblages, particularly *Caulerpa* spp. in the upper mesophotic zone, encrusting sponges and calcareous algae and the turfing biological matrix across all depths. Together, these groups are likely to show clear responses to changes in light and siltation levels. While there was insufficient data and time-series to attribute a cause to our initial observed changes through time, the patterns observed do fit a pathway predicted under increasing nutrification of Storm Bay and additional monitoring through time is recommended to track patterns in environmental health in this productive system as human use increases.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112345.

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