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Temporal variability in temperate mesophotic ecosystems revealed with over a decade of monitoring with an autonomous underwater vehicle

Nicholas R. Perkins [*], Jacquomo Monk, Rachel H.X. Wong, Neville S. Barrett

Institute for Marine and Antarctic Studies, University of Tasmania, Australia

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A B S T R A C T

Rocky reef temperate mesophotic ecosystems (TMEs) are increasingly recognised for their spatial extent and high biodiversity. Platforms such as autonomous underwater vehicles (AUVs) allow large-scale collection of benthic imagery, facilitating descriptions of TMEs, but these efforts currently remain geographically restricted. Furthermore, descriptions of temporal changes in TMEs are extremely rare and typically limited to a single site with few repeated surveys, leaving critical gaps in our understanding of ecosystem variability. Here, we report on temporal changes in abundance and size structure of sessile biota across TMEs in three Australian Marine Parks (AMPs) across decadal time scales, using AUV-collected benthic imagery, enhanced with AI tools for estimating biota size. Our results challenge the common assumption of TME stability, revealing significant fluctuations in key biota over 2–13-year periods. At the phyla-level, cnidaria exhibited threefold changes and bryozoa fivefold changes at individual sites over ~5 years. Some individual morphospecies also showed more than twofold change over ~5 years. We found that higher-level taxonomic/morphological groupings could track changes in dominant taxa, but often masked significant trends at the morphospecies level. Size structure data offer important insights into the population dynamics that abundance or cover data alone could not capture, particularly in terms of recruitment events and size shifts. Our findings highlight that mesophotic ecosystems are dynamic and underscore the need for ongoing monitoring to better understand the temporal changes within TMEs and to inform the development of effective indicators. Coupling image-based surveys with physical data collection such as temperature data should be a priority in future monitoring to better link biotic changes to environmental drivers.

1. Introduction

Rocky reef temperate mesophotic ecosystems (TMEs) are increasingly acknowledged globally for their spatial extent, high biodiversity values, and potential provision of refugia from climate change impacts (Rossi et al., 2017; Bell et al., 2024a). These ecosystems, found at depths below the primary photic zone, are characterised by a decline in macroalgal cover and an increase in invertebrates such as sponges, ascidians, bryozoans, and corals. Currently, there is paucity of knowledge about the ecology and function of TMEs, and the spatial distribution of the species and communities that inhabit them (Turner, 2019; Bell et al., 2024a), hindering the capacity to identify and prioritise conservation areas and management plans (Campoy et al., 2023). This knowledge gap is primarily due to historic technical difficulties in surveying deeper marine habitats. However, technological improvements, particularly the lower cost of image-based survey approaches, have facilitated rapid expansion of data collection across TMEs in recent years (Bongaerts et al., 2019). Existing image-based surveys reveal that TMEs are highly diverse, featuring distinct assemblages from adjacent shallower reef communities (Adams et al., 2023; Enrichetti et al., 2023), with potentially significant variations in diversity and across depth profiles (e.g., Harris et al., 2021). Despite these efforts, many regions remain unsurveyed, and basic knowledge of the extent of rocky reef habitats in mesophotic depths is still lacking. Studies describing the rates of temporal change in benthic communities within TMEs are even rarer. As anthropogenic impacts on marine ecosystems continue to rise there is a pressing need to understand how TMEs are changing, focusing on spatial scales relevant to specific pressures like climate change.

Understanding the temporal stability of TMEs is a key research priority (Bell et al., 2024a). Evidence from tropical mesophotic ecosystems shows that trajectories of change and responses to disturbances can vary between mesophotic ecosystems and their adjacent shallow water

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[*] Corresponding author. Institute for Marine and Antarctic Studies, 15-21 Nubeena Crescent, Taroona, Tasmania, 7053, Australia.
E-mail address: Nicholas.Perkins@utas.edu.au (N.R. Perkins).

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counterparts, emphasizing the need for long-term monitoring at mesophotic depths (Hernandez-Agreda et al., 2022; Diaz et al., 2023). Although TMEs are often assumed to be more stable than shallower ecosystems in the same region (e.g., Cerrano et al., 2019), this assumption is rarely formally assessed. Limited evidence to date shows that TMEs may be more vulnerable to short term disturbances than previously thought, particularly sponges, which show susceptibility to eutrophication, temperature, toxicity (Micaroni et al., 2021), and marine heatwave events (Bell et al., 2024b; Perkins et al., 2022b). For example, within depth-generalist species, individuals found at greater depths may also be more susceptible to extreme thermal stress due to the lack of acclimatisation to varying temperatures (Pivotto et al., 2015). This underscores the critical role of long-term monitoring in understanding natural variability and accurately assessing the impacts of stressors, such as climate change.

The limited knowledge of natural variability, impacts of stressors on different taxonomic groups, and the low abundance of most species (or morphospecies), with cover typically less than 2 % (Monk et al., 2018; Perkins et al., 2022a), make selecting appropriate indicators for monitoring TMEs challenging. The relative rarity of many potential target indicators requires extensive sampling to precisely quantify cover or other abundance metrics. This is further complicated by the fact that many taxa in TMEs are not identified to species-level, constraining imagery annotation to the “morphospecies” resolution - visually distinct taxa identified based on morphology and colour. Given the challenge of achieving adequate statistical power to monitor changes in individual morphospecies, grouping them into broader taxonomic groups may provide a viable alternative for creating relevant indicators for change (Bevilacqua et al., 2009; Kallimanis et al., 2012, Brind’Amour et al., 2014). Broader groupings based on functional traits or morphological characteristics may be useful for tracking specific pressures as larger sample sizes can be achieved using this approach. Furthermore, phyla-based grouping, such kelp cover, coral cover, or sponge cover, are also often of interest to marine management bodies.

Monitoring the temporal change in population size structure of target indicator species may also offer valuable insights into disturbance histories and can reveal future population trajectories, providing added value beyond assessing abundance only (e.g., Riegl et al., 2012; Dietzel et al., 2020; Perkins et al., 2022a). Shift in population size structure can have direct and indirect implications for the reef ecosystems (Graham, 2014; Kerry and Bellwood, 2014). For example, lower mortality rates among adult populations may temporarily protect against population decline and recruitment failure but can mask the decline in population viability if the loss of juveniles and recruits, which is crucial for future population growth, is overlooked (Hughes and Tanner, 2000; Sommer et al., 2024). Understanding population dynamics is particularly important for TMEs, where long-term temporal and large-scale spatial data are disproportionately lacking compared to tropical shallow systems.

The south-east marine park network (SEMPN) is part of a nation-wide network of Australian Marine Parks (AMPs) in offshore Commonwealth waters established in 2007. A benthic cross shelf monitoring program utilizing an autonomous underwater vehicle (AUV) was established under the federal government funded Integrated Marine Observing System (IMOS) program to collect benthic imagery from shortly after the SEMPN establishment. Multibeam mapping of shelf areas within these AMPs were used to target AUV surveys on sites containing rocky reef ecosystems, with initial AUV surveys providing the first descriptions of TME benthic communities in each AMP. In some of the AMPs in the SEMPN, up to four spatially replicated repeat surveys have now been conducted, spanning up to 13 years of survey data. Here, we utilise this extensive dataset of benthic imagery to (i) quantify the temporal changes that have occurred in the abundance and size structure of a range of potential indicators ranging from phyla to individual morphospecies in three AMPs spanning a latitude of >350 km, and (ii) highlight some of the lessons learnt from over a decade of monitoring TMEs in the SEMPN.

2. Methods

2.1. Survey sites and data collection

AUV surveys began in the SEMPN in 2009 in the Huon marine park, subsequently expanding to other marine parks in the network, with repeat surveys conducted on 1–5-year intervals (Fig. 1 and Table 1). The AUV transects at each site were pre-planned based on prior multibeam mapping within each marine park and designed to primarily target reef features identified on the continental shelf regions in mesophotic to rariphotic depths (~40–200 m depth).

The Western Boundary site is relatively low-profile limestone platform reef that is often sand inundated with occasional ledge features which drop-off ~ 2m. Joe’s Reef is a high-profile granite outcropping reef, rising 15–20 m from surrounding soft sediment. The Huon 13 site consists of relatively high-profile basalt reef in shallower sections, with occasional boulders. In deeper sections (below ~ 70 m) the reef profile lessens, and areas of reef are interspersed with soft sediment.

The AUV navigates the pre-planned transect lines which are in a grid pattern (see Fig. 1) covering linear lengths of ~3.5 km (Western Boundary), ~3.5 km (Joe’s Reef), and ~3.5 km–2.8 km (Huon_13). Note that the initial survey (2009) at the Huon_13 site covered a larger area than later surveys which were more focussed due to seafloor mapping being available. Our spatial modelling approach (see below) provides a means for accounting for these differences in spatial coverage.

While multiple sites have been surveyed within each AMP, we focus on a single site with at least 3 surveys (Table 1). The included sites are ‘core’ monitoring sites that have been included from the initial survey and thus have the longest time-series, whereas other sites have been added subsequently or not surveyed as regularly. Our aim is to focus on temporal changes at these sites rather than provide a comprehensive overview of all morphospecies and habitats surveyed in each AMP. Hereafter, for brevity, we refer to the site surveyed by the AMP names (i.e., Flinders, Freycinet, and Huon).

2.2. Image sampling and annotation

A typical deployment will collect between 5000 and 12000 overlapping images. Therefore, subsampling of images is usually undertaken due to the large amount of time taken for human annotation. All image sampling and annotation was completed with Squidle+ (https://squidle.org/), an online image annotation platform that provides access to the imagery data sets as well as tools for image subsampling and annotation. Depending on the annotation approach (see below) the desired number of reef images was subsampled by selecting images systematically along the transect. This avoids issues with inadvertently selecting overlapping images and ensures a spatial spread of images across the transect. A set quantity of reef images were targeted as most of the sessile organisms that are the focus of monitoring require reef substrata for attachment.

Annotation was completed to the morphospecies level, with visually distinct biota classified under broader taxonomic groups (e.g., sponge, ascidian, etc.) and then further defined in terms of morphological and colour characteristics. We used the Australian Morphospecies Catalogue (AMC), a purpose-built classification system for morphospecies identified across Australian imagery data sets. It uses a hierarchical classification scheme, utilizing the CATAMI approach, whereby the finest taxonomic units (species or morphospecies) are nested under broader taxonomic and morphological groupings, allowing aggregation to higher taxonomic levels and a standardised approach that allows cross-study comparison (Althaus et al., 2015).

Two approaches were taken when annotating all imagery data sets: (i) ‘Biodiversity annotation’, and (ii) ‘Targeted morphospecies annotation’.

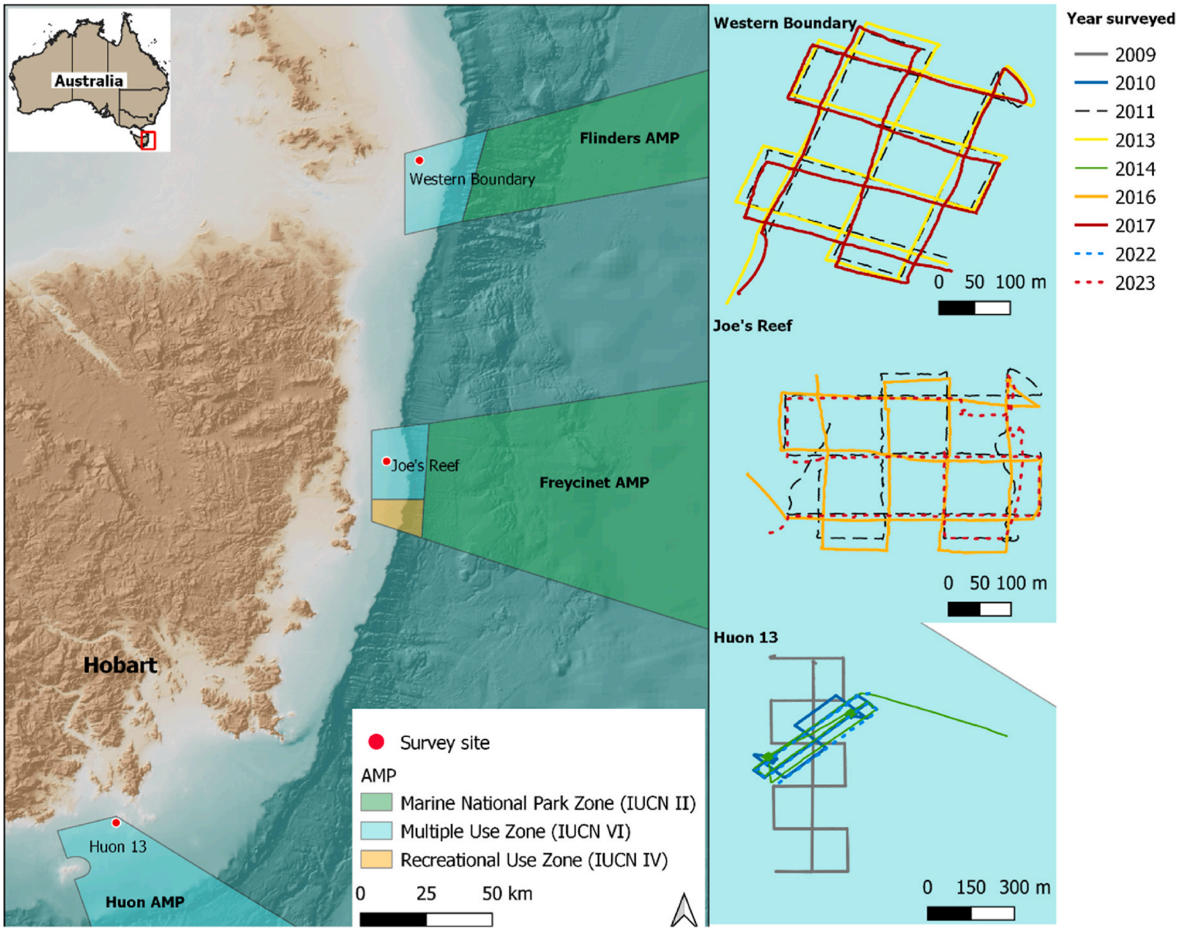

Fig. 1. Map showing the Australian Marine Parks (AMP) surveyed by autonomous underwater vehicle used in the study. Red dots show the location of AUV survey sites. Cut-aways show the repeated AUV transects at each site and the years surveyed. Legend shows the current zoning present in each AMP.

Table 1
Details of the survey sites including site name, depth range, years surveyed, number of images annotated in each survey and morphospecies used in targeted annotation at selected long-term monitoring sites. Morphospecies marked with an * were also annotated for size structure by delineating individuals with polygons.

AMP	Site	Depth range (m)	Years surveyed	Number of reef images annotated in each year of biodiversity annotation	Number of images annotated each year of targeted annotation	Morphospecies scored in targeted annotation
Flinders	Western Boundary	43–52	2011	206	381	Cup Black Smooth Sponge*
			2013	215	348	Cup Red Smooth Sponge*
			2017	202	354	Fan Pink Sponge *
						Massive Purple Sponge *
						Bramble Coral
Freycinet	Joe's Reef	53–83	2011	194	1465	Cup Black Smooth Sponge
			2014	251	1450	Cup Red Smooth Sponge
			2016	200	2210	Cup Yellow Sponge
			2023	214	335	Fan Pink Sponge
						Massive Purple Sponge
Huon	Huon 13	52–81	2009	125	200	Cup Black Smooth Sponge
			2010	205	250	Cup Red Smooth Sponge
			2014	202	241	Cup Yellow Sponge
			2022	230	223	Fan Pink Sponge
						Massive Purple Sponge

2.2.1. *Biodiversity annotation*

Biodiversity annotation was undertaken to annotate random points within images to the finest taxonomic resolution possible, thereby capturing the biodiversity across each site. The aim was to annotate a minimum of 100 reef images from each site and year with 25 random points used within each image. This level of sampling has been shown to provide sufficient statistical power to detect significant changes in the cover of benthic biota that are not too rare or sparsely distributed (see Perkins et al., 2016; Perkins et al., 2022a). Each of the 25 random points within each image was labelled to the finest taxonomic resolution possible (i.e., typically morphospecies).

2.2.2. *Targeted morphospecies annotation*

Targeted morphospecies annotation was undertaken for pre-selected target morphospecies across images, where every individual of each target morphospecies was labelled with a point, allowing counts per image. The aim was to annotate at least 200 reef images from each site (see Perkins et al., 2022a), with all targeted morphospecies annotated in each image (see Table 1 and Supplementary Figs. 1–3 for examples). We annotated four sponge morphospecies (i) cup black smooth sponge, a typically large (up to 30 cm in diameter) black sponge, (ii) cup red smooth sponge, a large (up to 60 cm diameter) maroon/red sponge that sometimes shows bleaching, (iii) fan pink sponge, a stalked pink/grey sponge that has a morphology ranging between cup and fan-like, often curled over, and attaining up to 40 cm in diameter, and (iv) massive purple sponge, a large (up to 38 cm in diameter) purple ball-like to elongate massive sponge with oscula on top (see examples in Supplementary Figs. 1–3). We also annotated bramble coral at the Flinders site, which is a small (<20 cm tall) octocoral of the order *Alcyonacea* (see example in Supp. Fig. 2). Previous annotation effort at Joe's Reef for another project yielded over 1400 images scored between 2011 and 2016 (Table 1). In 2023, a smaller subset of imagery was scored at Joe's Reef due to technical issues with the AUV, resulting in some images displaying colour fringing. However, 335 images were annotated and considered sufficient based on previous power analyses (Perkins et al., 2022a).

Targeted morphospecies were selected for their distinctive morphologies and colours, facilitating easy identification in the imagery and potential segmentation (see Size-structure analysis section below). Additionally, these morphospecies were present in sufficient abundance for analysis across all three sites (except for yellow cup sponges, which were too scarce in Flinders, and bramble coral was only annotated in Flinders), allowing for comparisons of trends across sites.

2.2.3. *Size-structure analysis*

Four targeted morphospecies - cup red smooth, cup black smooth, fan pink and massive purple sponges - were selected at the Flinders Western Boundary site to examine population size structure. Bramble coral was excluded due to poor performance of the segmentation approach for this morphospecies. The "segmentBOT" tool, an artificial intelligence (AI) tool within the Squidle + online annotation platform, was used to generate polygon segments around each target and determine its surface area within a known image footprint. The segmentBOT utilises the segment anything model (SAM; Kirillov et al., 2023) to generate segments from points placed on the targeted morphospecies. All generated polygons were reviewed, with erroneous ones deleted and redrawn manually. The area of each polygon in mm^2 was then calculated by converting the area in pixels using the formula:

$$area\ (mm^2) = number\ of\ pixels * \left(\frac{altitude*1000}{focal\ length}\right)$$

where the focal length was 1730 mm, calculated from prior calibration of the AUV Sirius camera and the altitude (in metres) recorded for each image from the sensor data during AUV deployment. Changes in size structure over time were explored visually using density plots.

Additionally, the area occupied by each targeted morphospecies within an image was aggregated to determine percent coverage, calculated as the total area of occupied by a given species divided by the total image footprint, which is based on the image resolution of 1024 by 1360 pixels. This is metric will be referred to as 'percent area coverage' hereafter.

2.3. *Statistical analyses*

To explore potential indicators across the time-series we chose to analyse changes in: (i) community composition, (ii) cover of phyla-level taxonomic groups, (iii) cover of "phyla-morph" level groupings where distinctive morphologies within phyla were aggregated, (iv) targeted annotation data of counts for specific selected morphospecies, and (v) size structure and cover data from polygons created for morphospecies in the targeted annotations (see Table 1). Based on exploratory analysis of the dominant biota present, univariate analysis of trends in cover were conducted on the cover of all grouped phyla (and bare substrate), and the dominant phyla-morphs which had sufficient cover for analysis.

2.3.1. *Multivariate analyses*

Multivariate analysis was conducted using generalized linear latent variable models (GLLVMs; Niku et al., 2019). GLLVMs are a multivariate extension of generalized linear models (GLMs) that can provide ordinations and visualizations of trends in multivariate species distributions as well as assessments of species driving community differences. We chose these models as they take into account the error distribution of the data as well as accounting for correlation in species abundances and environmental covariates such as depth. For this analysis images were treated as samples with presence-absence of each morphospecies within an image treated as the response. Survey year was treated as a categorical variable, with the first survey treated as the reference year against which subsequent surveys were compared. Morphospecies which occurred in less than five images across the time series at a site were excluded from analysis to minimise the influence of rare morphospecies. The depth of each image was treated as a continuous covariate to account for depth effects. The spatial correlation between images was modelled using an exponentially decaying correlation structure based on the distance between images using the '*corEXP*' argument within the *gllvm* function. Morphospecies driving differences between years were plotted using the '*coefplot*' function. Significance was assessed by finding morphospecies whose confidence intervals for year estimates did not overlap zero.

2.3.2. *Univariate analyses*

For univariate analyses, a generalized linear modelling approach was used which treated the response as the binomial probability of a point landing on a given morphospecies within an image given the number of points annotated (i.e. 25 points). For the targeted annotation data, the response was modelled as a count, with the negative binomial distribution used to account for any overdispersion present. For the cover data estimated from the size structure polygons a beta distribution was used. As zeros and ones cannot be modelled in a beta regression, cover data was first transformed using the transformation outlined in Smithson and Verkuilen (2006):

$$x' = \frac{x(N-1)+s}{N}$$

where N was the sample size of images, and s was set at 0.5 as recommended in Smithson and Verkuilen (2006).

In all models, the depth of each image was treated as a covariate to account for any depth effect, with a quadratic term (depth^2) also included to address any non-linear effects. Models also included spatial random effects, which models the spatial dependence between images (i.e., spatial autocorrelation) that is not accounted for by the depth covariates. Thus, these models take into account the different spatial sampling locations of images across sampling years. This modelling approach is therefore particularly important for the Huon_13 site which covered a larger spatial extent in the first year of surveys (2009 – see Fig. 1). All modelling was conducted using the integrated nested Laplace approximation (INLA; Rue et al., 2009) approach using the R-INLA package. Bayesian priors were set for the spatial parameters using penalised complexity priors (Fuglstad et al., 2019), with the probability that the spatial range was <10 m set to 0.1, and the probability that the spatial standard deviation was >1 set to 0.1.

Mean covers (and counts per image for targeted morphospecies) and the associated uncertainties for each taxonomic grouping in each year were obtained by taking 5000 joint posterior draws from the fitted models. Means and 95 % credible intervals were calculated at the mean depth of each site and setting the spatial random effects to zero. Model-based estimates for each year were back-transformed to the response scale. Estimates that did not include zero in the 95 % credible intervals of the posterior were considered significant. Plots were produced for each grouping/site combination and plotted on combined plots to allow trajectories to be compared across each marine park. All plots include the 95 % credible intervals, with estimates for any given year that were significantly different to the first year of survey indicated on the plots.

3. Results

3.1. Multivariate analysis of temporal change in morphospecies

Analysis of community composition through time at each long-term monitoring site showed that a large number of individual morphospecies had undergone significant shifts in abundance over the survey period (Supp. Figs. 5–7; significance is determined where 95 % confidence intervals do not overlap zero). For Flinders, 28 of the 80 morphospecies (35 %) modelled showed significant differences to the initial survey on at least one subsequent survey over a 6-year survey period. For Freycinet, 70 of the 166 morphospecies (42 %) modelled showed significant differences during at least one subsequent survey over a 13-year survey period. For Huon, 48 out of the 89 morphospecies (54 %) showed significant differences over a 13-year survey period. Some morphospecies appeared to undergo trajectories of increase over the survey period (e.g. palmate orange flat sponges at Flinders, yellow smooth ball sponges in Freycinet, and arborescent orange sponges at Huon; Supp. Figs. 5–7); others fluctuated significantly across the survey period (e.g., branching grey stumpy sponges at Huon, Supp. Fig. 6); and some showed trajectories of decline (e.g., branching beige spindles sponge at Flinders and gorgonian red Pteronisis like at Freycinet, Supp. Figs. 5 and 6).

3.2. Phyla analysis of cover

Model-based estimates indicated significant fluctuations in phyla cover over 6 to 13-year timescales, with trends varying across AMPs (Fig. 2). Significant differences for a given survey year were made in comparison to the initial survey year at each site, based on coefficient estimates in the model-based analysis not containing zero in their 95 % credible intervals (see Supplementary materials for model summaries). Significant differences for a given survey year are indicated with triangles in the figures. Certain sponge morphologies exhibited significant changes that often mirrored phyla-level trends due to their dominance within the phyla (Fig. 5). The trajectory in the cover of corals (Fig. 3) also closely reflected that of overall cnidaria cover (Fig. 2), as the estimated coral cover was the predominant component of cnidaria across the AMPs. Coral morphospecies were predominantly soft corals of the order *Alcyonacea*, with small gorgonian fans in the genus *Pteronisis* being particularly prevalent. The only stony corals of the order *Scleractinia* present were small solitary cup corals that typically made up < 0.1 % of the cover. Similarly to cnidaria/corals, the trajectories for soft bryozoa cover (Fig. 3) paralleled those of overall bryozoa (Fig. 2), with soft bryozoa of a variety of morphospecies comprising the majority of overall bryozoa cover.

3.2.1. Sponges

Sponge cover fluctuated around 10 % over the time series, with approximately 10 % increases observed at Huon from 2009 to 2010 and at Freycinet from 2011 to 2014. These early increases were primarily due to encrusting and massive sponge morphologies (Fig. 3). However, from 2014 onwards at Huon, encrusting sponge cover declined and was replaced by an increase in massive sponges.

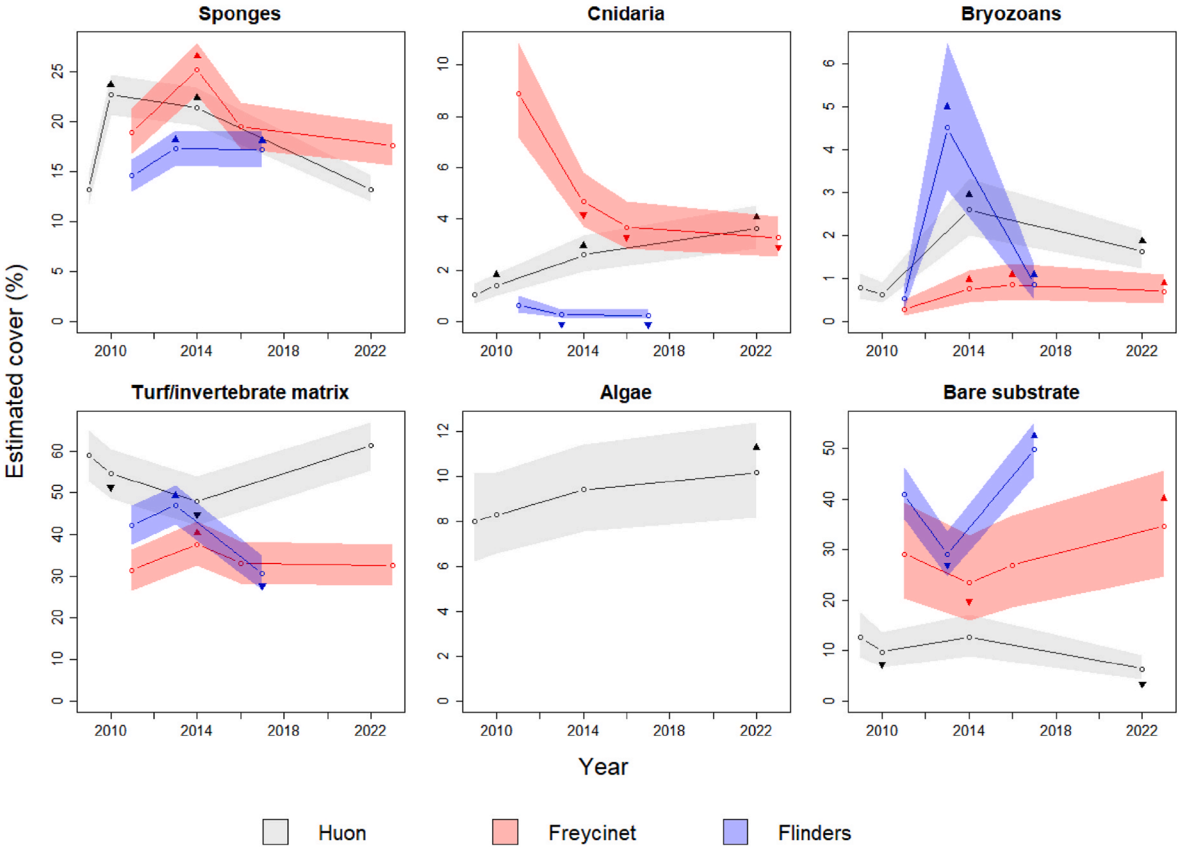

Fig. 2. Model-based estimates of cover of phyla and bare substrate across the time-series of AUV surreys within the long-term monitoring site within each AMP. Solid lines show the mean trend estimated within each site with shaded areas showing the 95 % credible intervals. Upward triangles signify statistically significant increases, and downward triangles indicate significant decreases from the initial survey year. All estimates were made at the mean depth within the associated site and setting spatial random effects to zero. Note the differing y-axis scales.

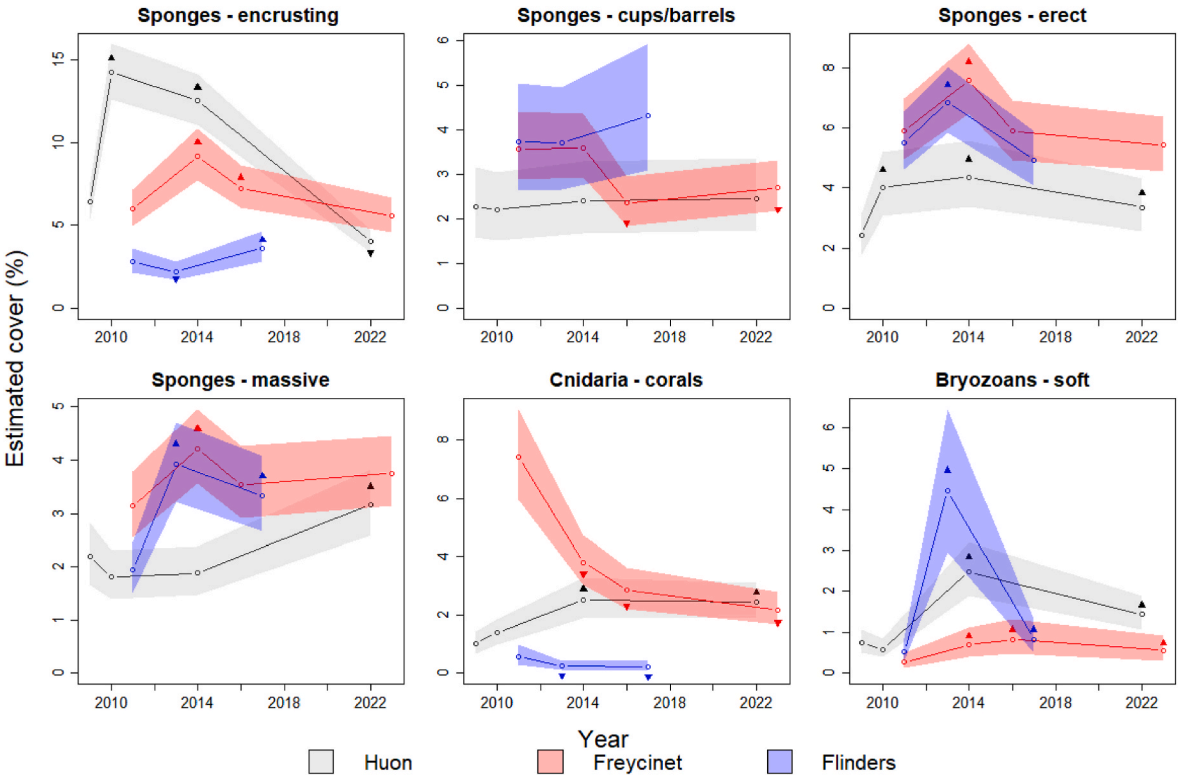

Fig. 3. Model-based estimates of cover of the dominant "phyla-morphs" (morphological groups within phyla) across the time-series of AUV surveys within the long-term monitoring site within each AMP. Solid lines show the mean trend estimated within each site with shaded areas showing the 95 % credible intervals. Upward triangles signify statistically significant increases, and downward triangles indicate significant decreases from the initial survey year. All estimates were made at the mean depth within the associated site and setting spatial random effects to zero. Note the differing y-axis scales.

At Flinders, the initial rise in sponge cover from 2011 to 2013 were driven by increases in erect and massive morphologies (Fig. 3). While overall cover remained relatively stable between 2013 and 2023, encrusting and massive morphologies have continued to rise, whereas erect morphologies have declined. Cup/barrel sponges remained relatively stable throughout the time-series at Flinders and Huon, although a significant decline was observed at Freycinet.

3.2.2. *Cnidaria*

Cnidaria cover declined at Flinders and Freycinet, while Huon exhibited an approximate threefold increase in cover from 2009 (~1 % cover) to 2022 (~3 % cover). The decline in Freycinet was dramatic, with cover halving from approximately 9 % in 2011 to less than 4 % in 2023. The largest decline (approximately 4 % total cover) occurring between 2011 and 2014.

3.2.3. *Bryozoa*

Bryozoa cover increased significantly across all sites compared to initial surveys, but with considerable fluctuations in cover through time. At Flinders, cover rose ninefold from 0.5 % to 4.5 % between 2011 and 2013 before dropping back to 0.5 % in 2017. At Huon, the cover tripled from under 1 %–2.5 % between 2009/10 and 2014. In Freycinet, bryozoans increased over time but remained low, staying below 1 % across the surveys.

3.2.4. *Turf/invertebrate matrix*

Turf/invertebrate matrix (a matrix of indeterminant invertebrates) remained the dominant cover at all sites, fluctuating around 10 % at Huon and Freycinet. At Flinders, a 10 % increase in cover occurred between 2011 and 2013, followed by a 20 % drop to 30 % in 2017, falling below the levels of the first survey.

3.2.5. *Algae and bare substrate*

Algae was only present in sufficient cover to model at Huon, where it gradually increased from ~8 % to ~10 % between 2009 and 2022. Bare substrate remained relatively stable around 10 % cover at Huon but increased at Freycinet and Flinders, with a sharp rise at Flinders from 30 % to 50 % between 2013 and 2017.

3.3. *Analysis of temporal change in targeted morphospecies*

Model-based estimates of the count per image for targeted morphospecies through time revealed divergent trajectories across sites, with some morphospecies remaining stable or decreasing at one site while increasing elsewhere (Fig. 4). Once again, significant differences for a given survey year were made in comparison to the initial survey year at each site, based on coefficient estimates in the model-based analysis not containing zero in their 95 % credible intervals (see Supplementary materials for model summaries). Significant differences for a given survey year are indicated with triangles in the figures. Cup red smooth sponges exhibited stability in abundance through time at Freycinet and Flinders, but at Huon, their abundance approximately doubled between 2014 and 2022. Massive purple sponges declined strongly at Flinders, halving in abundance between 2011 and 2017, and also decreased at Freycinet between 2014 and 2023. In contrast, at Huon, massive purple sponges showed an upward trajectory, with an approximate threefold increase in abundance between 2010 and 2022.

Cup black smooth sponges remained relatively stable in abundance at Flinders and showed a slight trajectory of decline at Freycinet but increased about fourfold at Huon from 2010 to 2022. Fan pink sponges showed relatively low cover at Freycinet over the survey period but had strong increases at both Flinders and Huon, nearly doubling at Flinders between 2011 and 2017, and increasing approximately fivefold at Huon between 2014 and 2022.

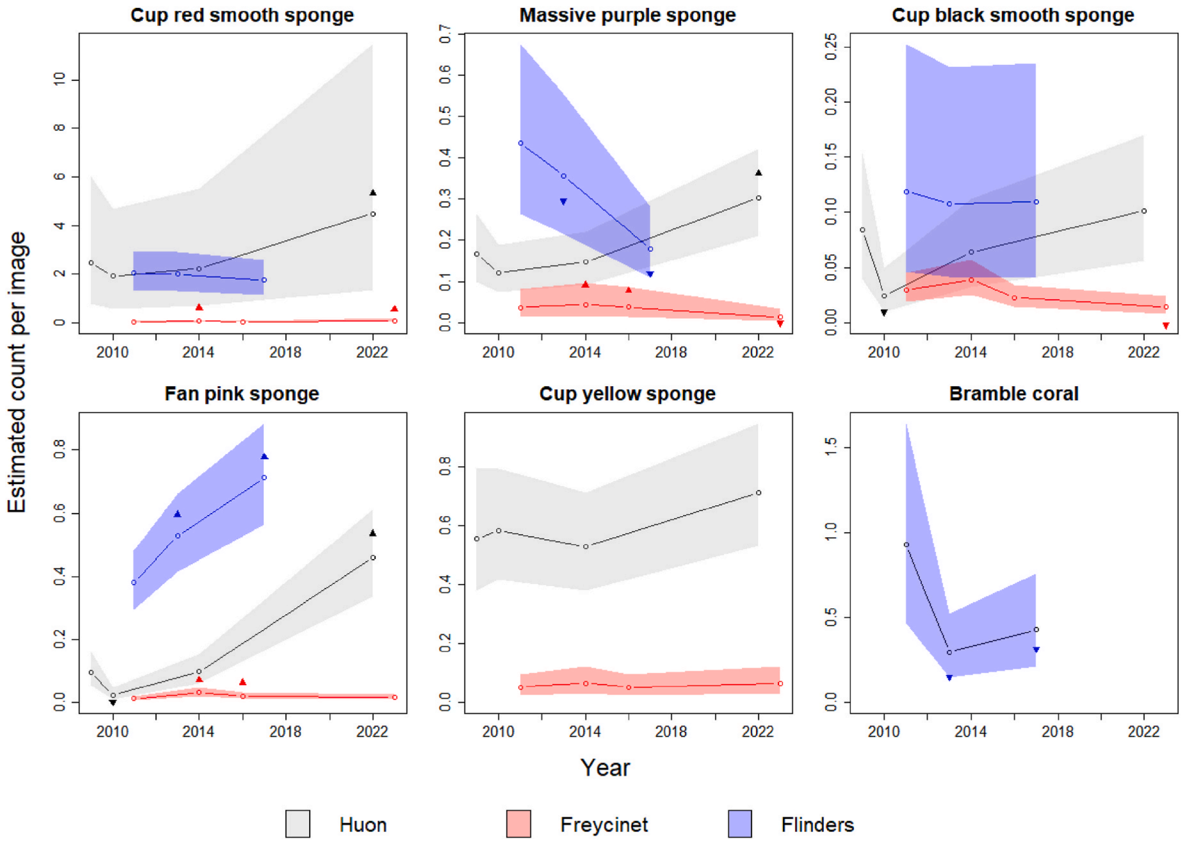

Fig. 4. Model-based estimates of the counts per image of targeted morphospecies across the time-series of AUV surveys within the long-term monitoring site within each AMP. Solid lines show the mean trend estimated within each site with shaded areas showing the 95 % credible intervals. Upward triangles signify statistically significant increases, and downward triangles indicate significant decreases from the initial survey year. All estimates were made at the mean depth within the associated site and setting spatial random effects to zero. Note the differing y-axis scales.

Bramble coral experienced a sharp decline in abundance in Flinders, more than halving between 2011 and 2013, followed by a slight recovery from 2013 to 2017. Cup yellow sponges maintained relatively stable cover throughout the time series at both Huon and Freycinet.

3.4. Analysis of size structure and percent area coverage at Flinders western boundary site

The segmentBOT algorithm provided high accuracy in generating polygons around individual morphospecies that were annotated with a point (see Supp. Materials Fig. 4 for an example). Over 85 % of individuals had polygons generated that were deemed acceptable after initial segmentation. Incorrect polygons were manually corrected in Squidle+.

Cup black smooth sponges had similar size distribution across the time series at the Flinders western boundary site, with a small increase in the proportion of smaller individuals evident in 2017 indicating recruitment was likely to have occurred between 2013 and 2017 (Fig. 5). Cup red smooth sponges showed no signs of recruitment, and a gradual increase in the size distribution across the time series. Fan pink sponges showed an increase in the proportion of smaller sponges in 2013 and again in 2017, indicating that at least two recruitment events were likely to have occurred across the time series. Massive purple sponges showed similar size distribution between 2011 and 2013, followed by a large decrease in density around the mean size class in 2017 and a small increase in smaller size classes.

Model-based estimates of the temporal trends in percent area coverage revealed significant increases in cup red smooth sponges and significant declines in massive purple sponges in 2017 compared to 2011 (Fig. 6). The mean cover of cup red smooth sponges increased from ~1.75 % in 2011 to ~2.1 % in 2017. In contrast, the mean cover of massive purple sponges decreased from approximately 0.4 % in 2011 to around 0.32 % in 2017. No statistically significant changes were found in the cover of cup black smooth sponges or fan pink sponges during this period.

4. Discussion

Here we report on the temporal trends of sessile biota in TMEs within Australia's SEMPN across a 13-year monitoring time-series, highlighting that TMEs are dynamic across the region, with significant changes in cover, abundance, and size structure of many taxa. Notably, the cnidarian and bryozoan phyla exhibited biologically significant changes in abundance (2–5 folds) within these timeframes. We demonstrate that careful consideration should be given to the taxonomic level that is tracked as well as the metrics collected when monitoring TMEs. Trends at higher taxonomic levels such as phyla tracked lower levels when those lower levels were dominated by few taxa but could mask differing trajectories in individual morphospecies which may differ markedly. This has important implications for indicator selection, which requires an understanding of natural variability combined with knowledge of how indicators are likely to respond to pressures of interest. Finally, we show that a more complete picture is provided through a combination of abundance and size metrics which reveal growth, mortality, and recruitment dynamics which cannot be tracked with cover alone.

Contrary to the common assumption of relative stability and slow change in TMEs compared to shallower marine ecosystems (e.g., Cerrano et al., 2019; Eyal and Pinheiro, 2020; Micaroni et al., 2021; Hernandez-Agreda et al., 2022), over a third of individual morphospecies, and all phyla at each site experienced detectable and statistically

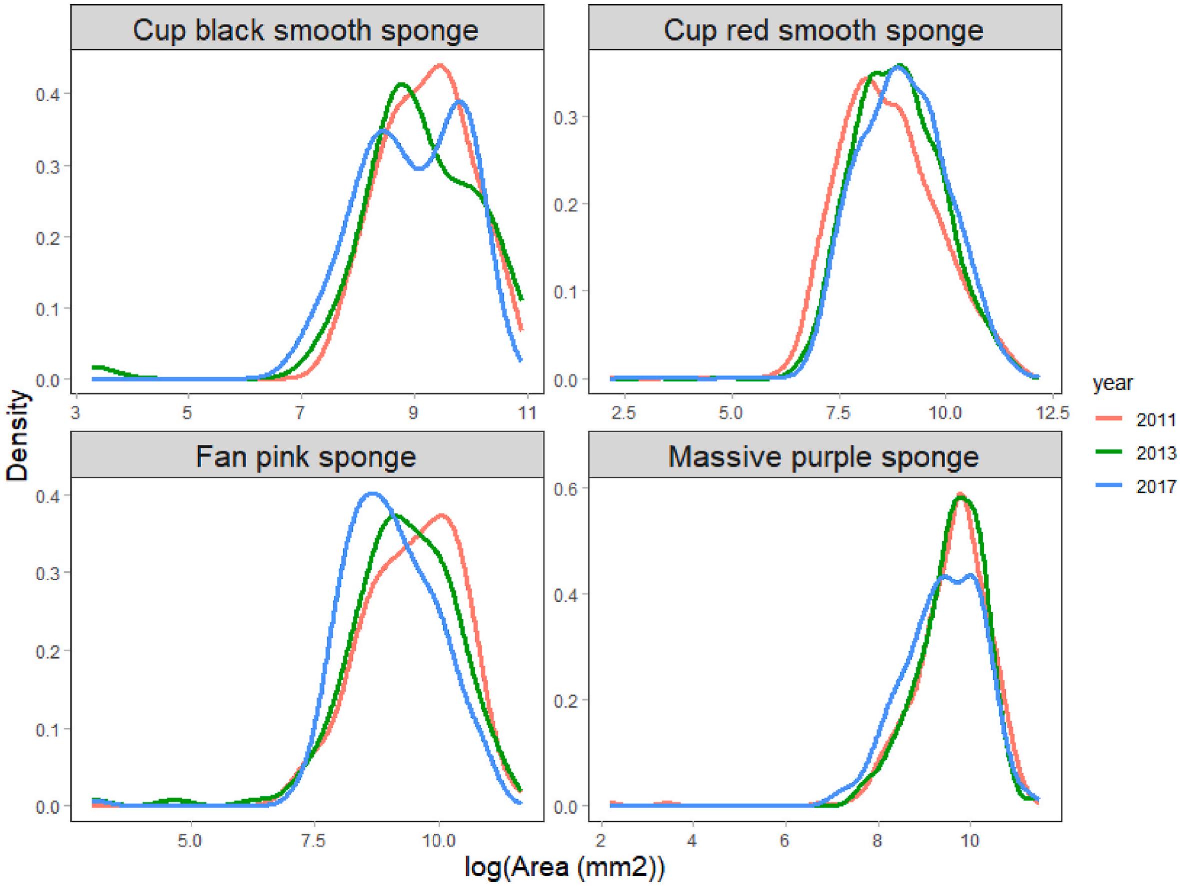

Fig. 5. Size structure density plots showing temporal trends in size distributions for four morphospecies at the Flinders Western Boundary site. Note that the x-axis has been log transformed. Note the differing y-axis scale.

significant changes in abundance over 2-to-13-year timeframes. These trends often differed within the same morphological groups and varied between sites over the same periods. This implies that site-specific pressures and population dynamics, such as recruitment events, are important in understanding overall regional trajectories. Due to funding constraints and availability of the AUV, it was not possible to conduct repeat surveys on an annual basis, and repeated surveys at a site ranged between one and seven years. Despite this, surveys closer together in time tended to have more similar levels of cover/abundance providing confidence that sampling was sufficient at each time step, and that estimated longer term trends were captured with the methodology. Improved knowledge of the variability of potential indicator morphospecies or groups can allow an assessment of the trade-offs between temporal revisits and spatial replication (see Perkins et al., 2017 for previous work).

Selecting the appropriate taxonomic resolution for monitoring is an important consideration, with some studies showing aggregation to higher levels provides “taxonomic sufficiency” to track change (e.g., Smale et al., 2010; Kallimanis et al., 2012), while others demonstrate mixed results (e.g., Bevilacqua et al., 2009). Our results reveal higher-level groupings, such as phyla or morphological groups within phyla, often show similar trends to lower-level groupings when those groupings comprise of a few dominant taxa, but in some cases may mask important trends at lower levels. For example, sponge cover displayed an increase through time at the Flinders site, but different sponge morphologies showed differing trajectories: encrusting sponges first decreased then increased, while massive and erect sponges showed the opposite trends and cup sponges remained relatively stable. At a lower taxonomic level, the massive purple sponge morphospecies declined significantly at the Flinders site, while the overall trend for massive sponges showed an increase. Therefore, careful consideration needs to be given to selecting indicators and/or aggregating to higher taxonomic levels, particular in TMEs where there is a current lack of knowledge around temporal variability. Ultimately, indicator selection must consider the specific pressures being tracked (e.g., marine heatwaves (MHWs), recovery from trawling, impacts of storm events) and the known or likely responses of a particular taxa or grouping to those pressures.

Incorporating both abundance and size structure provides a more comprehensive understanding of the population dynamics of individual taxa, especially when populations are under pressure (Lachs et al., 2021; Mueller et al., 2023; Ruhl et al., 2023). Our analysis of the size structure of four sponge morphospecies at the Flinders site provides the first such insights in our study system in a region experiencing rapid warming and increased disturbance through storm events (Oliver et al., 2018; Liu et al., 2023). Size structure information provided insights into population dynamics not evident from the abundance/cover data alone. For example, some sponge morphospecies showed no recruitment over six years while others had multiple recruitment events. These findings show all three metrics (abundance, cover and size structure) provide a more complete picture of the dynamics of each morphospecies. For example, counts of fan pink sponges increased across surveys, while cover remained relatively stable. Conversely, the cover of cup red smooth sponges increased whilst there was no change in counts. This information is critical in systems such as ours where there is currently limited knowledge concerning natural variability of populations including recruitment timing and variability, growth, and mortality. We recommend this approach should be expanded to other sites and morphospecies to test population dynamics elsewhere and potentially link these dynamics to environmental drivers.

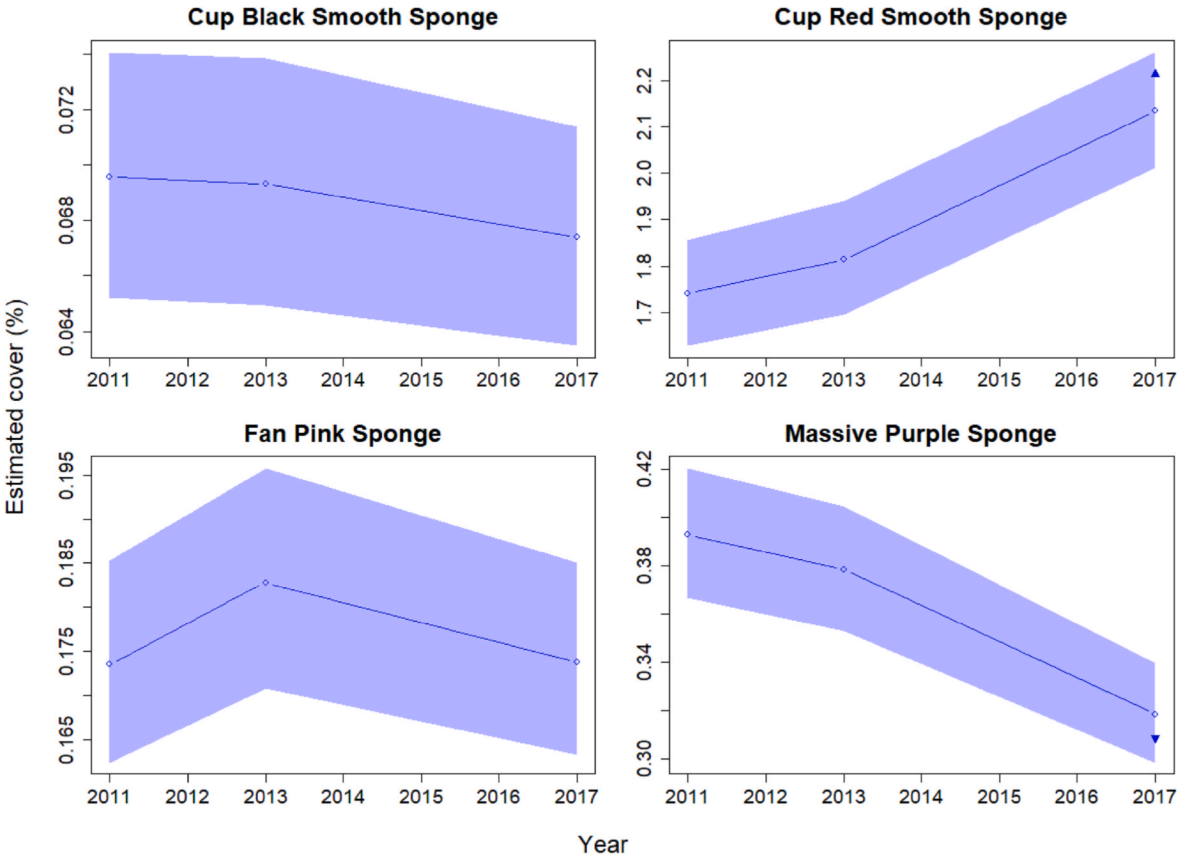

Fig. 6. Model-based estimates of the percent area coverage of targeted morphospecies across the time-series of AUV surveys at the Flinders Western Boundary site. Solid lines show the mean trend estimated within each site with shaded areas showing the 95 % credible intervals. Upward pointing triangles signify statistically significant increases from the initial survey year, downward facing triangles significant decreases. All estimates were made at the mean depth within the associated site and setting spatial random effects to zero. Note the differing y-axis scales.

Alongside a general lack of knowledge about the spatial extent and natural rates of change in TMEs, there is limited understanding and data collection on other biotic factors that are likely to influence TMEs (Wong et al., 2023). For example, data on the frequency and intensity of disturbance regimes, such as storm events or MHWs, are rarely available at appropriate temporal or spatial scales at mesophotic to rariphotic depths. Modelling has shown that there has been a regional trend for increasing wave energy over recent decades (Liu et al., 2022), particularly along the southern coastline of Tasmania (Liu et al., 2023) where the Huon site is situated. Predicted benthic disturbance regimes for the study region (see Harris and Hughes, 2012) suggest that the shelf may undergo regular influence of storm swells, but this is likely to be stronger in the southern site (Huon) compared to the eastern sites (Flinders and Freycinet). Disturbance of the benthos by storm events and increased wave energy in tropical systems has been shown to be capable of breaking off corals at mesophotic depths (Bongaerts et al., 2013) and dislodging or smothering sessile organisms (Harmelin-Vivien, 1994). Our results show that the cover of bare substrate, primarily sand, fluctuated across the time series, with a particularly dramatic increase of approximately 20 % at Flinders between 2013 and 2017. The substantial rise in sand cover during this period suggests an increase in sand inundation of previously surveyed reef areas. Concurrently, there were distinct declines in soft bryozoa, cnidaria, massive purple sponges, and large fan pink sponges. Sand and sediment inundation has been linked to declines in sessile filter and suspension feeding organisms including temperate soft coral species in Australia (Larkin et al., 2021). Whether there is an ecological link between sand inundation and decline of these groups remains to be tested. There is a need to collect in situ data about bottom velocities and temperature across the study sites in combination with follow-up surveys to test how these influence benthic fauna cover, abundance and size.

Recent work exploring the impacts of MHWs on TMEs has shown that climate change impacts can extend to mesophotic depths, with bleaching of sponges observed in both Tasmania (Perkins et al., 2022b) and New Zealand (Bell et al., 2024b). In the Mediterranean, MHWs have resulted in the mortality of gorgonians and sponges at upper mesophotic depths (Garrabou et al., 2009), with gorgonians of the same species in deeper areas more susceptible than shallower counterparts due to a lack of acclimation (Pivotto et al., 2015). Our study region is located in a global warming hotspot, and previous work has demonstrated a correlation between modelled marine heatwaves at depth in Flinders in 2014-15 and Huon marine parks in 2009-10 and 2013-14, and the subsequent bleaching in sponges (Perkins et al., 2022b). However, quantifying the effects of MHWs is currently limited to modelled data of temperature at depth, and the timing of surveys is reliant on funding and AUV availability. Thus, analysis of observed changes is largely restricted to correlations rather than causal inferences based on direct measurement of temperature and closely timed before and after surveys. Therefore, it is essential to collect environmental data such as bottom velocity and temperature at appropriate spatial and temporal resolutions alongside imagery monitoring data to better couple observed changes with environmental drivers.

Over more than a decade of monitoring TMEs in the SEMPN show these ecosystems are both biodiverse and temporally dynamic, with significant changes occurring over 6 to 13-year time scales. Contrary to the common assumption of relative stability, our results underscore the importance of long-term studies in understanding the dynamics of TMEs and highlight the need for similar studies in other regions. In our study system many observed morphospecies are rare, with even the more abundant morphospecies having low overall cover. While biodiversity scoring, such as done with our point count approach, is useful for inventory, more effort may be required for monitoring individual morphospecies. Targeted annotation of individuals can provide improved statistical power to detect change (see Perkins et al., 2022a), and with the advent of segmentation tools can also allow size structure data to be generated with little additional effort. Incorporating both abundance and size structure data provides additional insights, revealing important dynamics like recruitment events and loss of larger individuals that cover data along might not reveal. This dual approach offers a more comprehensive understanding of species trend and ecosystem health over time. Finally, our work emphasises the critical need to pair image-based surveys with the collection of physical data. Without these environmental measurements coupled with closely timed follow-up surveys, it is difficult to draw causal links between observed biotic changes and external drivers, making this integration a priority for future monitoring efforts.

CRediT authorship contribution statement

Nicholas R. Perkins: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jacquomo Monk:** Writing – review & editing, Writing – original draft, Data curation. **Rachel H.X. Wong:** Writing – review & editing, Writing – original draft, Conceptualization. **Neville S. Barrett:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107179.

Data availability

Data will be made available on request.

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