

## **Vulnerability of Temperate Mesophotic Ecosystems (TMEs) to environmental impacts: Rapid ecosystem changes at Lough Hyne Marine Nature Reserve, Ireland**

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# Vulnerability of Temperate Mesophotic Ecosystems (TMEs) to environmental impacts: Rapid ecosystem changes at Lough Hyne Marine Nature Reserve, Ireland

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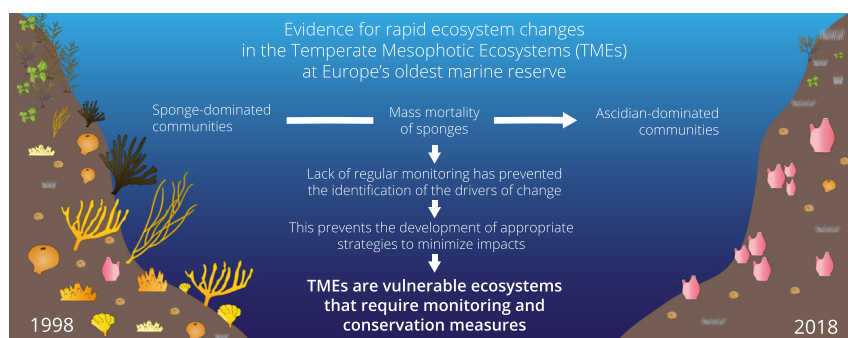
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## ABSTRACT

Temperate Mesophotic Ecosystems (TMEs) are stable habitats, usually dominated by slow-growing, long-lived sessile invertebrates and sciaphilous algae. Organisms inhabiting TMEs can form complex three-dimensional structures and support many commercially important species. However, TMEs have been poorly studied, with little known about their vulnerability to environmental impacts. Lough Hyne Marine Nature Reserve (Ireland) supports TMEs in shallower waters (12–40 m) compared with other locations (30–150+ m) as a result of the unusual hydrodynamic conditions. Here, we report changes that have occurred on the sponge-dominated cliffs at Lough Hyne between 1990 and 2019, providing insights into TME long-term stability and vulnerability to environmental impacts. Our main finding was a marked decline in most three-dimensional sponges at the internal sites of the lough. This was likely the result of one or more mass mortality events that occurred between 2010 and 2015. We also found an increase in ascidians, which might have been more tolerant and benefited from the space freed by the sponge mortality. Finally, in the most recent surveys, we found a high abundance of sponge recruits, indicating that a natural recovery may be underway. The possible factors involved in these community changes include eutrophication, increased temperature, and a toxic event due to an anomaly in the oxycline breakdown. However, the absence of comprehensive monitoring of biotic and abiotic variables makes it impossible to identify the cause with certainty. Our Lough Hyne example shows the potential vulnerability of TMEs to short-term disturbance events, highlighting the importance of monitoring these habitats globally to ensure they are appropriately conserved.

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## 1. Introduction

Coastal ecosystems are among the most important biomes on the planet because of the reliance of human populations on the resources they provide (Costanza et al., 2014). However, many coastal ecosystems remain poorly studied. Mesophotic ecosystems lie between the shallow euphotic waters and the aphotic deep-sea. While these ecosystems have been relatively well-studied in tropical regions, termed mesophotic coral ecosystems (MCEs), the importance of temperate mesophotic ecosystems (TMEs) has only recently been recognised (see Cerrano et al., 2019; Turner et al., 2019).

TMEs extend from the lower limit of the euphotic zone ( $<1\%$  of the surface irradiance,  $\sim 20\text{--}30\text{ m}$ ) to the limit of benthic primary production ( $150\text{--}300\text{ m}$ ) (Cerrano et al., 2019). These ecosystems host rich and diverse communities typically dominated by invertebrates, including sponges, cnidarians, bryozoans, and ascidians, or by shade-adapted (sciaphilous) algae (Rossi et al., 2017; Turner et al., 2019). TMEs provide important ecosystem services, including supporting commercial fisheries, providing raw materials (e.g. pharmaceuticals), genetic resources, and a range of cultural and recreational values (e.g. SCUBA diving and angling) (Tonin, 2018). To date, only 20% of studies on mesophotic ecosystems are from temperate seas. Of those, 67% are from the Mediterranean Sea and temperate Australasia, with little known about TMEs in other regions (Bongaerts et al., 2019).

Importantly, like shallow-water ecosystems, TMEs are also threatened by a wide range of anthropogenic stressors, including ocean warming, ocean acidification, urbanisation, the arrival of non-indigenous species, and fishing activity including trawling (Gennaro and Piazzini, 2011; Cerrano et al., 2013; Bo et al., 2014; Rossi et al., 2017; Ferrigno et al., 2018; Marzloff et al., 2018; Enrichetti et al., 2019; Turner et al., 2019; Betti et al., 2020). Nonetheless, there have been only a few reports of changes in TME communities, which have been linked to wastewater discharge (Hong, 1983; Roberts et al., 1998), heatwaves (Cerrano et al., 2000; Garrabou et al., 2009), shifts in species distribution patterns due to climate change (Perkins et al., 2020) and aquaculture-related eutrophication (Haeussermann et al., 2013). However, as TMEs are challenging to access, many changes may have gone unnoticed due to limited baseline data. Furthermore, there is very little information on TME species and community ecology and how these organisms respond to anthropogenic stressors (Turner et al., 2019).

In recent decades, legislative efforts by governments to protect TMEs have increased substantially. In Europe, under the EU Marine Strategy Framework Directive 2008/56/EC, important mesophotic habitats, including coralligenous reefs, coral gardens (e.g. gorgonian and alcyonarian forests) and deep-sea sponge aggregations have been formally given special protection (OSPAR, 2008; UNEP-MAP-RAC/SPA, 2008). To date, very few countries have implemented long-term monitoring programmes in mesophotic habitats. The best examples are the coralligenous assemblage monitoring in the Mediterranean Sea (UNEP-MAP-RAC/SPA, 2008) and the Automated Underwater Video benthic monitoring program run by Australia's Integrated Marine Observing System (IMOS) (Williams et al., 2010; Pizarro et al., 2013). However, for most TMEs, there is still a lack of baseline data, inhibiting our ability to distinguish between population fluctuations and anthropogenic impacts (Thurstan et al., 2017).

Lough Hyne Marine Nature Reserve (est. 1981) is a fully marine semi-enclosed lough in southwest Ireland, one of the most well studied marine environments in the world (Lawson et al., 2004). Lough Hyne hosts many rare species and contains a very high number of habitats within a small area ( $\sim 0.5\text{ km}^2$ ) and has been highlighted as a globally important biodiversity hotspot (Kitching, 1987; Bell and Barnes, 2000a; Bell, 2007). Lough Hyne is particularly well-known for its rich and abundant mesophotic cliff communities, which occur in much shallower water than other areas in the Atlantic because of the elevated water turbidity and sheltered conditions (Picton, 1990). These

communities were dominated by sponges, including many three-dimensional forms that provided habitat complexity to the subtidal cliffs and formed extensive sponge gardens (Picton, 1990; Bell and Barnes, 2000a). Similar ecosystems are only found in a few other areas in the world, for example, Bathurst Channel in Tasmania, Fiordland in New Zealand, and on the southwest coast of Chile (Schiel and Hickford, 2001; Barrett et al., 2010; Försterra et al., 2017). Because of the environmental conditions, the high level of endemism, and highly restricted distribution patterns, these ecosystems are considered among the most threatened on earth (Barrett and Edgar, 2010).

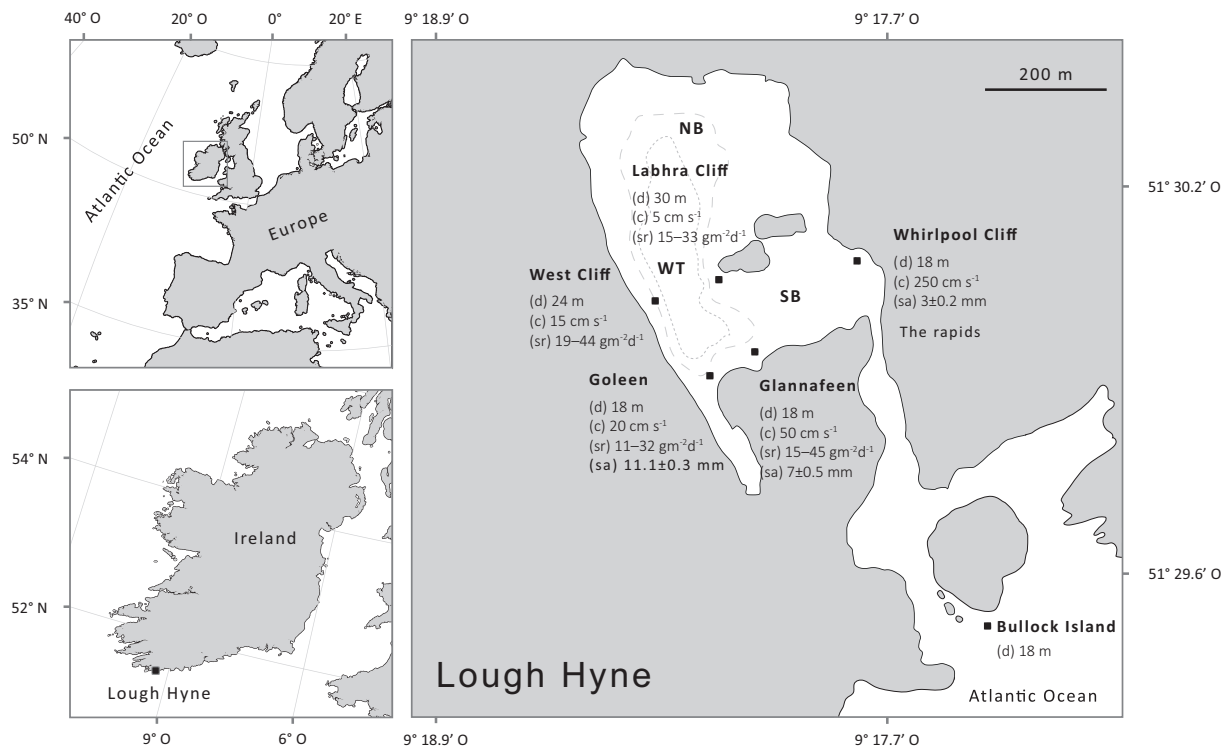
In recent years, major community changes have occurred at Lough Hyne in intertidal and shallow-subtidal ( $<1\text{ m}$ ) habitats, suggesting some large-scale environmental impact (Trowbridge et al., 2013; Little et al., 2018). These include shifts in algal assemblages (Trowbridge et al., 2011; Trowbridge et al., 2013), invasions by non-indigenous species (Salvaterra et al., 2013; Gallagher et al., 2017), and changes in the abundance and composition of many intertidal and shallow subtidal invertebrates, such as echinoderms, bryozoans, hydrozoans, and molluscs (Trowbridge et al., 2011; O'Sullivan and Emmerson, 2011; Little et al., 2018, 2020; Trowbridge et al., 2018). Moreover, some authors have reported the occurrence of algal blooms, that appear to be increasing in frequency (Jessopp et al., 2011). While anecdotal reports have suggested changes have also occurred on deeper subtidal rocky cliffs, this has never been quantified as no long-term monitoring programme exists (unlike for the intertidal and shallow subtidal habitats; see Trowbridge et al., 2013; Little et al., 2018).

Our study provides an example of how to investigate spatial and temporal variability in TME communities in the absence of long-term monitoring, with data from a range of quantitative and qualitative sources. We collated 30 years (1990–2019) of scientific surveys and opportunistic observations on the subtidal communities of Lough Hyne to gain insights on the long-term stability and vulnerability of TMEs. We then explored the available environmental data and considered the possible causes of the changes observed. Finally, we discussed the limits of the methodology used and the importance of regular monitoring of biotic and abiotic variables for TME conservation globally.

## 2. Materials and methods

### 2.1. Area of study

Lough Hyne is a small ( $\sim 0.5\text{ km}^2$ ), fully marine (salinity 34.3–34.9) semi-enclosed lough on the southwest coast of Ireland (Fig. 1) consisting of a shallow North and South Basin (maximum depth  $\sim 25\text{ m}$ ) that are joined by a deeper Western Trough ( $\sim 50\text{ m}$  deep). The lough is connected to the adjacent Atlantic coast by a narrow ( $\sim 25\text{ m}$  wide) channel called the Rapids. Water-flow into the lough is essentially unidirectional due to a sill (maximum depth  $3\text{ m}$ ) in the Rapids, meaning the incoming tide must reach the level of the sill before the water inflow can begin (Kitching, 1987). As a result, water flows in for 4 h, with currents reaching  $>300\text{ cm s}^{-1}$  and flows out for 8 h when currents are low ( $<5\text{ cm s}^{-1}$ ) in all parts of the lough, except in the Rapids. Current speed decreases rapidly as in-flowing water moves across the lough resulting in an east-west sedimentation gradient (Bell and Barnes, 2002). A seasonal thermocline also develops in the Western Trough ( $20\text{--}30\text{ m}$ ) over the summer months (Kitching, 1987), although there is inter-annual variation in its duration. In general, the thermocline starts forming in April, reaching maximum intensity in August/September and then dissipates between September/November, depending on the temperature and storm activity (McAllen et al., 2009; Sullivan et al., 2013). This stratification leads to a hypoxic/anoxic deeper layer that becomes isolated from the surface water mass for several months (McAllen et al., 2009). When the thermo-oxycline begins forming, the oxygen content decreases progressively from  $15\text{--}20\text{ m}$  to the bottom of the Western Trough (Fig. 1). During the summer months, the oxycline becomes steeper,



**Fig. 1.** Lough Hyne map showing its position in the North-East Atlantic (top left corner) and Ireland (bottom left corner). NB, North Basin; SB, South Basin; WT, Western Trough. For each site, the maximum depth (d), maximum current speed (c, from Bell and Barnes, 2002), sedimentation rate (sr, from Bell and Barnes, 2002) and accumulated sediment on surfaces (sa, from Bell and Turner, 2000) are shown. Inside Lough Hyne, the 25 and 35 m bathymetric contours around the Western Trough are indicated by the short-dashed and dotted line, respectively (from Sullivan et al., 2013).

and the oxygen concentration of the water changes from 100% air saturation (a.s.) at 15–25 m to 0% a.s. at 25–35 m (Kitching, 1987). Hydrogen sulphide has also been recorded (but not quantified) in the deeper anoxic water (Kitching, 1987).

The presence of multiple environmental gradients results in considerable habitat heterogeneity at the different sites and explains the high biological diversity reported from Lough Hyne (Picton, 1990; Bell and Barnes, 2000a,b,c). Previous studies in Lough Hyne recognised water flow, sedimentation, light, and oxygen as the main factors structuring the biological communities (Bassindale et al., 1957; Kitching, 1987; Bell and Barnes, 2000a, b, c; Bell and Turner, 2000; Maughan and Barnes, 2000).

## 2.2. Study sites

Our study focused on six sites within the boundaries of Lough Hyne Marine Nature Reserve, five of them located inside the lough and one located on the adjacent Atlantic coast (Fig. 1).

Among the sites inside the lough, the four internal sites (Glannafeen, Labhra Cliff, Goleen and West Cliff) share similar environmental conditions, which is reflected in the similar biological communities found at these sites (Picton, 1990; Bell and Barnes, 2000a, b, c). During the incoming tide, the internal sites experience low to moderate current flow (5–50 cm s<sup>-1</sup>), and most of the time, there is little or no water movement at all (Bell and Barnes, 2002). These internal sites are characterised by high sedimentation rates and considerable sediment accumulation upon cliff surfaces (7–11 mm) (Bell and Turner, 2000; see Fig. 1 for more details). Shallow cliff areas are characterised by coralline algae and other macroalgae, although algae quickly decline below 6–10 m, where the substrate becomes dominated by sponges and turf algae (Bell, 2007).

The site at the entrance of the lough (Whirlpool Cliff) is subjected to strong flow conditions (up to 250 cm s<sup>-1</sup> during in-flow) and negligible

sediment accumulation on rocky surfaces (3 ± 0.2 mm) (Bell and Barnes, 2002; Fig. 1). The deeper areas of Whirlpool Cliff are dominated by suspension-feeders (cnidarians and sponges), while macroalgae, including the kelp *Laminaria*, mostly dominate the shallower parts (<12–15 m).

Our final site (Bullock Island) is located outside the lough and contrasts with the other sites as it is subjected to strong oceanic wave action, with waves exceeding 10 m during storms. The benthic communities of this site are characteristic of the open Atlantic coast, with the kelp *Laminaria* dominating to 10–12 m depth, and encrusting filter feeders, coralline algae and turf algae dominating in the deeper areas (Kitching, 1987; Bell, 2007).

## 2.3. Spatial variation and temporal changes in benthic communities and sponge assemblages

Our study focused on the communities of the subtidal cliffs of Lough Hyne and the adjacent Atlantic coast. We used the same sampling design for investigating spatial variation and temporal changes between 1998 and 2018 for both the overall benthic communities and sponge assemblages. Abundance data of sponge taxa and benthic organisms were collected in July/August 1998 and July 2018 at the six sites described above (Fig. 1). Each site was sampled at 6 m intervals, from 6 to 18, 24 or 30 m depth depending on the maximum depth of each site (see Fig. 1 for maximum depths). Data from 1998 at Glannafeen 12 m was missing, and therefore could not be included in the analysis. At each site, five replicate photoquadrats (0.25 m<sup>2</sup>) were recorded on vertical (~90°) and inclined (~40–50°) surfaces. This distinction was necessary since substrate inclination has been shown to structure sponge assemblages and benthic communities at Lough Hyne (Bell, 2007) and other mesophotic reefs (Bridge et al., 2011). In 1998, photographs were taken on slide film using a Sea and Sea Motormarine II and YS-50 Strobe, while a Sony Rx100 I digital camera



with two 12,000 lm photo lights (Diving Torches Powerpro 100w) was used in 2018. Sediment was wafted from surfaces prior to taking photographs in both 1998 and 2018 as many sponges are buried beneath this layer.

The abundance of the dominant sessile organisms was estimated from the photoquadrats using a random point count method in Coral Point Count with Excel extensions (CPCe; Kohler and Gill, 2006). This software randomly allocates points over a picture, and the user manually identifies the organism beneath each point. For each photograph, 120 randomly generated points (480 points/m<sup>2</sup>) were used. Preliminary trials indicated that this number of points was appropriate to estimate the benthic cover accurately. The benthic categories used were: macroalgae, sponges, bryozoans, anthozoans, hydrozoans, ascidians, polychaetes, barnacles, turf-forming organisms (i.e. turf-forming algae and small invertebrates, as hydroids and bryozoans) and bare substrate.

For the sponge assemblages, photoquadrats were analysed using the area/length analysis tool in CPCe. Every sponge was manually outlined using a freehand drawing tool to measure the planar area occupied by the sponge in the photo. Each sponge was assigned to a taxon/operational taxonomic unit (OTU) group and a morphological type. Additional close-up photos and voucher specimens were also used for the identification of species and morphological types. Due to technological differences in the photographic equipment used between years, particularly the lower resolution of photoquadrats in 1998, measures were taken to make the data comparable. A minimum cut-off sponge size of 1 cm<sup>2</sup> was used, a slightly higher value than the minimum 1998 detection limit. Furthermore, all the photographs from 1998 and 2018 were analysed to a common taxonomic resolution. When possible, sponges were identified to species level. However, due to the indistinguishable external morphology of some specimens (especially in photos from 1998), some species were combined into OTUs that included multiple species. OTUs as are known to be generally effective for identifying patterns of distribution of benthic invertebrates (Brind'Amour et al., 2014), and marine sponges (Strano et al., 2020), at the same time avoiding the need for destructive sampling in concerned habitats. The list of OTUs/taxa and associated species is provided in Table A1.

#### 2.4. Statistical analysis

Differences in benthic community and sponge assemblage structure were analysed using permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) based on Bray-Curtis dissimilarities. The models were run using 9999 unrestricted permutations of raw data. When the number of unique permutations was lower than 100, Monte Carlo *p*-values were used instead of permutation *p*-values. Because of the difference in the number of levels for the depth factor among sites, both 3 and 4-way PERMANOVAs were performed. Four-way PERMANOVAs included the factors year, site, depth (only the depths common for all the sites: 6 m and 18 m) and inclination. Three-way PERMANOVAs were then conducted separately for each site and included the factors year, depth (including all the levels available), and inclination. Year and site were treated as random factors, while depth and inclination were treated as fixed factors. Cover data of both the benthic organisms and sponges were Log transformed to reduce the influence of the most abundant groups. We conducted pairwise comparisons of significant multivariate differences between years. *P*-values for the pairwise analyses were corrected using the Benjamini-Hochberg procedure to reduce the chance of type I errors (Benjamini and Hochberg, 1995). Effect size (omega squared,  $\omega^2$ ) was calculated for PERMANOVA tests made for each combination of site and depth, with data from vertical and inclined surfaces pooled (Lakens, 2013). Differences in multivariate assemblages were graphically displayed using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities and Principal Component Analysis (PCA). All the multivariate analyses were performed by the software PRIMER v6 (with the PERMANOVA+ add-on).

Differences in the abundance and richness of the main benthic organisms and sponge morphologies (following Bell and Barnes, 2001) between 1998 and 2018 were analysed using an unequal variance *t*-test on ranked data. This test was chosen due to the unequal variance and non-normal distribution of data, even after transformation (Ruxton, 2006). The Benjamini-Hochberg procedure was used to correct for multiple comparisons for each family of analysis. *T*-tests were performed using the software IBM SPSS Statistics v26. Statistical significance was set to *p* < 0.05. All the data and the detailed results of all the statistical tests are reported in the supplementary materials.

#### 2.5. High-resolution sponge diversity comparison between 1998 and 2019

A detailed taxonomic survey was conducted involving extensive photographic sampling and sponge tissue collection to compare the species diversity before and after the changes. In 2019, 213 tissue samples and >3000 photos were collected during 15 dives (3 dives at each site, except the external site). Sponge taxa were identified through a combination of external and internal morphological characteristics. Species lists from 1998 were taken from Bell and Barnes (2001), where the authors used a similar sampling effort. However, in Lough Hyne, there are still many undescribed sponge species of the genera *Eurypon* and *Haliclona* and from the family Polymastiidae and Suberitidae. To avoid biases in the comparison, undescribed or indistinguishable members of these genera/families were combined (e.g. *Eurypon* spp., encrusting Suberitidae).

#### 2.6. Long-term sponge abundance reconstruction

To reconstruct and estimate the long-term changes that may have occurred on the subtidal cliffs at Lough Hyne, we gathered all the published and unpublished data available, along with opportunistic observations made by researchers between 1990 and 2019. These include:

- 1) Scientific surveys: twenty-five Hi8 video transects (20–35 min each), collected in 1990, 1993, 1995, 1996 and 1997 at Whirlpool Cliff, Glannafeen, Goleen, West Cliff and Labhra Cliff; in each video, the same video operator conducted transects across each cliff at 2 m depth intervals, from 18 m to the surface. Photoquadrats that were taken in 1998 and 2018 (see previous sections).
- 2) Opportunistic surveys: observations, photos and videos from researchers diving at Lough Hyne for other projects in 2005, 2010, 2012 and 2015 (material by Julia Nunn and Nick Owen), and surveys conducted by the authors in 2017 and 2019.

Due to differences in sites and species recorded, different analyses were performed on these data. For papillate (family Polymastiidae) and arborescent sponges (*Raspailia* spp., *Axinella dissimilis* and *Stelligera stuposa*) at Goleen, we were able to determine the presence of adults (> 10 cm) and recruits (<2 cm) from all the time points mentioned above. For *Raspailia ramosa* at West Cliff, we were able to determine the presence of adults and recruits from all the time points mentioned above, except 2010 and 2012. For all the other sites, we were only able to extrapolate presence data for 8 easily distinguishable sponge taxa: *Axinella damicornis*, *A. dissimilis*, *Cliona celata*, *Polymastia* spp., *Raspailia ramosa*, *Stelligera rigida* and “other branching sponges” (this latter category included *Raspailia hispida* and *Stelligera stuposa*). Data used were from the video transects 1990–1997, the scientific surveys (1998 and 2018), and opportunistic surveys conducted by the authors in 2017 and 2019.

#### 2.7. Environmental data analysis

Local environmental data (sea surface temperature, air temperature and rainfall) were analysed for any deviations from the expected

climatology to evaluate their potential contribution to the biotic changes. For further details, see Appendix A.

### 3. Results

#### 3.1. Temporal changes in benthic communities between 1998 and 2018

Benthic communities were highly variable among sites, depths and inclination. However, three main different communities could be identified: the internal sites (Glannafeen, Labhra Cliff, Goleen and West Cliff), the site at the entrance of Lough Hyne (Whirlpool Cliff) and the site outside the lough (Bullock Island) (Figs. 2a, 3; more details about the spatial variation in the benthic communities are provided in Appendix B).

We found significant temporal changes between 1998 and 2018 at all sites, but these differences were greater at the internal sites. The four-way PERMANOVA (considering all the sites) showed significant differences in benthic communities between years, sites, and depths, with significant interactions between year and site ( $p = 0.0001$ ,  $F = 10.5$ ), year, site and depth ( $p = 0.0001$ ,  $F = 5.2$ ), year, site and inclination ( $p = 0.0003$ ,  $F = 3.6$ ), and site depth and inclination ( $p = 0.0002$ ,  $F = 9.5$ ) (Table 1). These interactions indicate significant changes

between 1998 and 2018, but these changes varied between the different sites. Furthermore, within the individual sites, changes were not homogeneous for each depth and between vertical and inclined surfaces. Three-way PERMANOVAs on the individual sites showed significant changes between years at all sites, with interactions between year and depth, and depth and inclination at most sites (Table A2). Both nMDS and PCA show clear spatial gradients in benthic communities, with the internal sites separating from the site at the entrance and outside the lough (Figs. 2-3, Figs. A1-A2). However, temporal changes at the internal sites were similar and generally greater than at the entrance and outside the lough (Figs. 2-4, Figs. A1-A2). Pairwise PERMANOVA comparisons between 1998 and 2018 showed significant differences for most combinations of site, depth, and inclination, except for the site at the entrance, where significant differences were found at 6 m on vertical surfaces (Table 1).

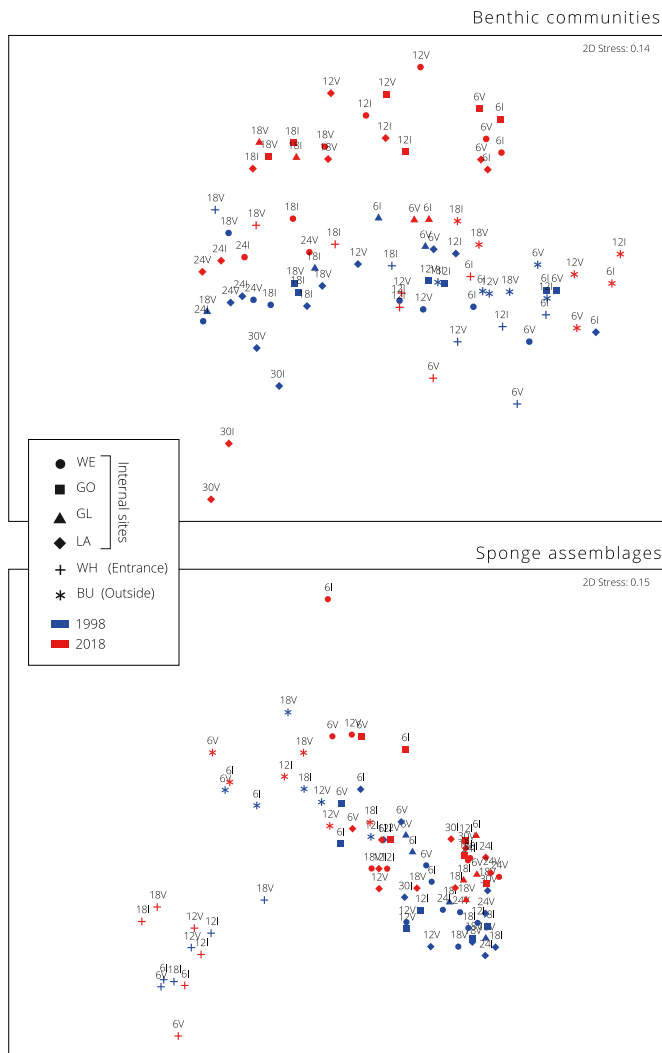
The benthic organisms that changed the most between 1998 and 2018 were sponges and ascidians, followed by turf-forming organisms and macroalgae (Fig. 5; Fig. A3). Sponge abundance generally decreased between 1998 and 2018 at the internal sites, while it increased at the entrance of the lough (Fig. 5; Fig. A3). At the internal sites, mean sponge abundance in 1998 was up to 25.3%, while in 2018, it never exceeded 12.9%. Changes were more pronounced on vertical surfaces than inclined ones and at the innermost sites (West Cliff and Goleen). No changes were found outside the lough. Ascidian abundance increased significantly at all sites, except at the entrance of the lough. At the internal sites, mean ascidian abundance changed from a maximum of 0.8% in 1998 to 19.2% in 2018 (Fig. 5; Fig. A3). Outside the lough, ascidian abundance also increased (from 0% in 1998 to 0.2–2.7% in 2018). In contrast, turf-forming organisms generally increased at the internal sites of the lough but decreased outside (Fig. 5; A3). Complete data of benthic organism abundance are provided in supplementary Table A3 and Fig. A3; univariate statistical analyses are provided in supplementary Table A4 and summarised in Fig. A3.

#### 3.2. Temporal changes in sponge assemblages between 1998 and 2018

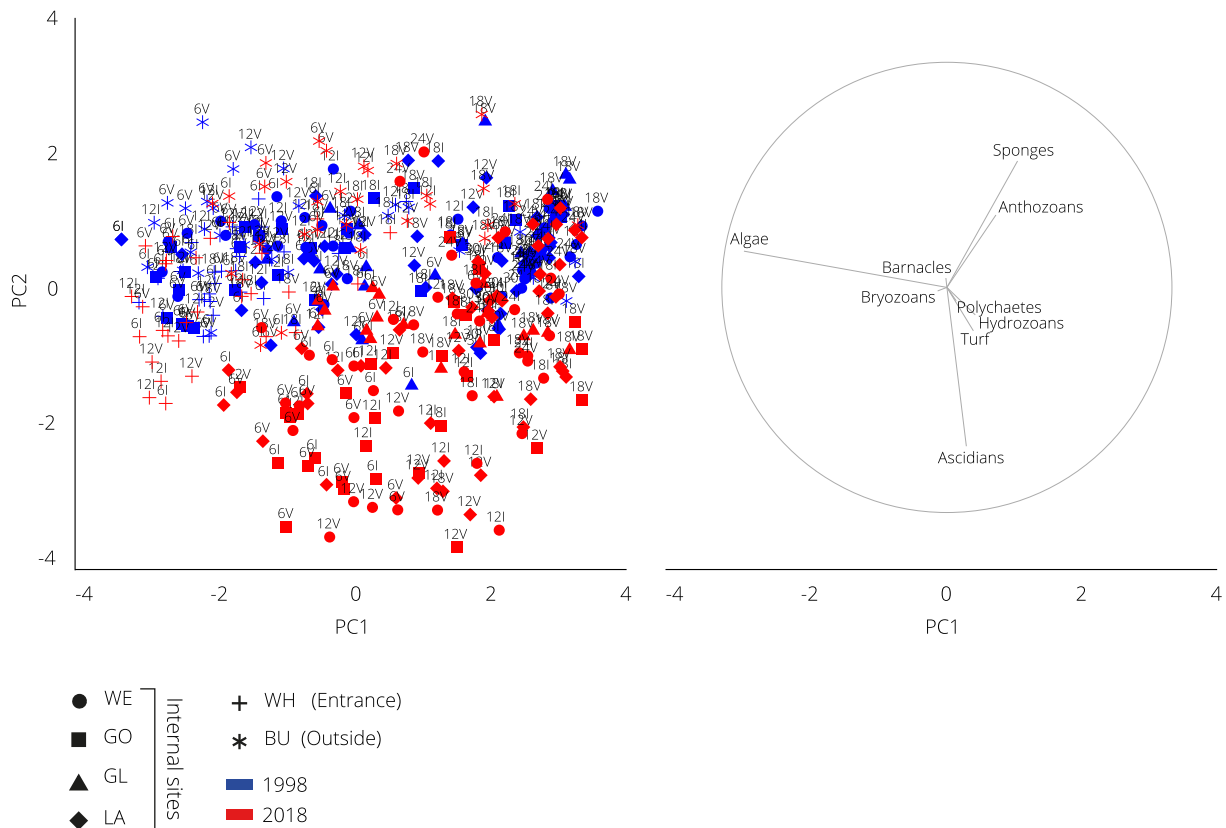
Similarly to the overall benthic communities, the sponge assemblages showed high heterogeneity among sites, depths and, to a lesser extent, inclination. The separation between internal sites, entrance and outside the lough was evident and even more marked than for the benthic communities (Fig. 2; Figs. A1-A2; see Appendix B).

Significant temporal changes between 1998 and 2018 were found at all sites in the lough (more marked at the internal sites), but not outside. The PERMANOVA test showed significant changes in sponge assemblages between sites, and significant interactions between year and site ( $p = 0.0001$ ,  $F = 4.9$ ), year and depth ( $p = 0.034$ ,  $F = 2.8$ ), year, site and depth ( $p = 0.0001$ ,  $F = 3.5$ ), year, site and inclination ( $p = 0.0008$ ,  $F = 1.9$ ) and year, site, depth and inclination ( $p = 0.0001$ ,  $F = 2.2$ ) (Table 1). These interactions suggest that changes occurred between years, but these were not homogeneous. Three-way PERMANOVAs showed significant changes at all sites, except the site outside the lough (Bullock Island). Significant interactions were also found between year and depth for all the sites inside the lough and for year and inclination at most sites inside the lough (Table A2). However, temporal changes were greater for the internal sites than at the entrance of the lough (Whirlpool Cliff) (Figs. 2, 4). Pairwise comparisons between 1998 and 2018 showed differences in sponge assemblages for most combinations of site, depth and inclination at the internal sites. At the entrance, there were significant differences only at 6 m on vertical surfaces and 18 m on inclined surfaces, while no differences were found outside the lough (Table 1).

The major change in the sponge assemblage between 1998 and 2018 was a decline in three-dimensional morphologies (papillate, arborescent, flabellate, pedunculate and massive) at the internal sites of the lough (Figs. 6-7, Fig. A4). Papillate sponges (family Polymastiidae) were one of the most affected groups. In 1998, papillate sponges were



**Fig. 2.** Non-metric multidimensional scaling (nMDS) of centroids of benthic communities (top) and sponge assemblages (bottom) for each combination of year, site, depth and inclination at all sites at Lough Hyne. Site key: WE West Cliff, GO Goleen, GL Glannafeen, LA Labhra Cliff, WH Whirlpool Cliff, BU Bullock Island.



**Fig. 3.** Principal Component Analysis (PCA) of benthic communities for each combination of year, site, depth and inclination at all sites at Lough Hyne. Site key: WE West Cliff, GO Goleen, GL Glannaheen, LA Labhra Cliff, WH Whirlpool Cliff, BU Bullock Island.

found at the internal sites with mean coverage up to 6.3%, while in 2018, the highest mean coverage (at any site/depth) was 0.2% (Fig. 6, Fig. A4). The cover of arborescent sponges has also decreased significantly at the inner sites. In 1998, arborescent sponges covered up to 2.6% of the substrate, while in 2018, they were not found at the innermost sites (West Cliff and Goleen), and their cover ranged between 0 and 0.5% at the other two internal sites (Labhra Cliff and Glannaheen) (Fig. 6, Fig. A4). Flabellate sponges virtually disappeared from the internal sites (except Glannaheen, closer to the entrance). Pedunculate sponges from the genus *Suberites* also showed a general decrease, especially at the innermost sites (Fig. 6, Fig. A4).

Pairwise comparisons of massive sponge abundance only showed some local decreases (Fig. A4). However, when pooling across depth and inclination there was a significant decrease in massive sponge cover at most of the internal sites (West Cliff;  $p < 0.0001$ ,  $t = 4.5$ ; Goleen;  $p = 0.001$ ,  $t = 3.6$ ; Labhra Cliff;  $p = 0.021$ ,  $t = 2.4$ ). Globular sponges (*Tethya citrina*) did not show any significant changes between 1998 and 2018 (Table A6).

Unlike most three-dimensional sponges, encrusting sponges were relatively abundant both in 1998 and 2018. These, however, showed some local significant decreases at most of the internal sites, except Glannaheen (Fig. A4).

Complete data of sponge abundance are provided in Table A1, A5 and Fig. A4; univariate statistical analyses are provided in Table A6 and summarised in Fig. A4.

### 3.3. High-resolution sponge diversity comparison between 1998 and 2019

From the detailed taxonomic survey, the number of sponge taxa reported in Lough Hyne decreased from 49 in 1998 to 44 in 2019 (Table A7). At the internal sites, the taxa richness decreased

by between 6 and 49%, with the innermost site (West Cliff) experiencing the greatest reduction. The total number of taxa did not change at the entrance of the lough (32 species). Ten taxa were found only in 1998, while five taxa were found only in 2019 (Table A7).

### 3.4. Long-term sponge abundance reconstruction

The available data indicate that the decline of papillate and arborescent sponges occurred between 2010 and 2015 (Figs. 8–9). At Goleen (internal site), adult individuals of papillate and arborescent sponges were commonly found during all eight surveys conducted between 1990 and October 2010 (Fig. 8). In July 2012, papillate sponge assemblage was noticeably depleted (only one adult was found), but large arborescent sponges were still present. In August 2015, no papillate and arborescent sponges were found at the innermost sites of the lough (Goleen and West Cliff), and other conspicuous sponges had almost disappeared (Nick Owen, Julia Nunn, personal communication). During surveys carried out between 2017 and 2019, we were not able to record any arborescent sponge from Goleen and West Cliff, while we recorded papillate sponges, but only small recruits. *Raspailia ramosa* at West Cliff followed a similar trend as the arborescent sponges at Goleen, but information for the 2010–2012 period was not available.

At the other sites, all the eight species investigated (*Axinella damicornis*, *A. dissimilis*, *Cliona celata*, *Polymastia* spp., *Raspailia ramosa*, *Stelligera rigida* and other branching sponges) were present every year at all sites from 1990 to 1998 (except *Axinella damicornis*, that has never been recorded at the entrance of the lough). In 2017, 2018 and 2019, these species were still present at all sites, except the innermost ones (West Cliff and Goleen). At West Cliff (innermost site), only

**Table 1**

Four-way PERMANOVA main tests and pairwise comparisons testing differences in benthic community composition and sponge assemblages between years (YE), depths (DE) and inclinations (IN) and their interactions at each site at Lough Hyne. The percentage of variance explained by each factor or combination of factors (SS/SS<sub>tot</sub>) is indicated as “% Var”. Significant *p*-values (*p* < 0.05) are given in bold and marked with an asterisk.

Four-way PERMANOVA											
Benthic communities						Sponge assemblages					
Source	df	% Var	MS	Pseudo-F	p	Source	df	% Var	MS	Pseudo-F	p
YE	1	8.5%	12,804	7.01	<b>0.0014*</b>	YE	1	1.7%	15,502	1.86	0.1434
SI	5	15.5%	4640	2.54	<b>0.0393*</b>	SI	5	25.5%	45,577	5.47	<b>0.0053*</b>
DE	1	28.9%	43,249	20.60	<b>0.0001*</b>	DE	1	5.5%	49,439	1.65	0.1245
IN	1	0.5%	788	1.49	0.2389	IN	1	1.0%	9139	1.74	0.1235
YExSI	5	6.1%	1827	10.51	<b>0.0001*</b>	YExSI	5	4.7%	8334	4.85	<b>0.0001*</b>
YExDE	1	0.0%	12	0.01	0.9864	YExDE	1	1.8%	16,439	2.75	<b>0.0338*</b>
YExIN	1	0.0%	14	0.02	0.9933	YExIN	1	0.3%	2275	0.71	0.6058
SIxDE	5	7.1%	2132	2.34	0.0719	SIxDE	5	9.5%	17,077	2.85	<b>0.0022*</b>
SIxIN	5	3.1%	931	1.50	0.2115	SIxIN	5	2.7%	4808	1.50	0.1677
DExIN	1	0.4%	562	0.93	0.5452	DExIN	1	0.4%	3188	1.18	0.3231
YExSIxDE	5	3.0%	911	5.24	<b>0.0001*</b>	YExSIxDE	5	3.3%	5982	3.48	<b>0.0001*</b>
YExSIxIN	5	2.1%	619	3.56	<b>0.0003*</b>	YExSIxIN	5	1.8%	3199	1.86	<b>0.0008*</b>
YExDExIN	1	0.0%	58	0.89	0.4503	YExDExIN	1	0.2%	1390	0.36	0.954
SIxDExIN	5	2.1%	616	9.46	<b>0.0002*</b>	SIxDExIN	5	2.5%	4560	1.18	0.309
YExSIxDExIN	5	0.2%	65	0.37	0.9786	YExSIxDExIN	5	2.2%	3856	2.24	<b>0.0001*</b>
Res	190	22.0%	174			Res	192	36.9%	1719		

Internal sites						Entrance	Outside
						Whirlpool Cliff	Bullock Island
				West Cliff	Goleen	Labhra Cliff	Glannafeen
PERMANOVA Pairwise comparisons - Benthic communities							
6 m	Inclined	<b>0.0078*</b> ( <i>t</i> = 3.36)	<b>0.0058*</b> ( <i>t</i> = 5.5)	<b>0.0169*</b> ( <i>t</i> = 2.67)	0.0981 ( <i>t</i> = 1.46)	0.1383 ( <i>t</i> = 1.45)	<b>0.0091*</b> ( <i>t</i> = 3.15)
	Vertical	<b>0.0077*</b> ( <i>t</i> = 4.82)	<b>0.0083*</b> ( <i>t</i> = 4.54)	<b>0.0082*</b> ( <i>t</i> = 2.48)	<b>0.0075*</b> ( <i>t</i> = 2.32)	<b>0.0082*</b> ( <i>t</i> = 3.8)	<b>0.0087*</b> ( <i>t</i> = 2.61)
12 m	Inclined	<b>0.0069*</b> ( <i>t</i> = 3.14)	<b>0.0082*</b> ( <i>t</i> = 3.84)	<b>0.0086*</b> ( <i>t</i> = 3.11)		0.0465 ( <i>t</i> = 1.98)	<b>0.0156*</b> ( <i>t</i> = 2.04)
	Vertical	<b>0.0079*</b> ( <i>t</i> = 4.09)	<b>0.0079*</b> ( <i>t</i> = 2.96)	<b>0.0056*</b> ( <i>t</i> = 4)		0.23 ( <i>t</i> = 1.26)	<b>0.0082*</b> ( <i>t</i> = 2.17)
18 m	Inclined	0.2634 ( <i>t</i> = 1.26)	<b>0.0101*</b> ( <i>t</i> = 2.86)	<b>0.0088*</b> ( <i>t</i> = 2.64)	<b>0.0226*</b> ( <i>t</i> = 2.17)	0.0855 ( <i>t</i> = 1.84)	0.1983 ( <i>t</i> = 1.25)
	Vertical	<b>0.0258*</b> ( <i>t</i> = 1.96)	<b>0.007*</b> ( <i>t</i> = 3.71)	<b>0.0081*</b> ( <i>t</i> = 2.08)	<b>0.0081*</b> ( <i>t</i> = 3.64)	0.039 ( <i>t</i> = 1.79)	<b>0.0091*</b> ( <i>t</i> = 3.07)
24 m	Inclined	0.4297 ( <i>t</i> = 1.01)		0.0882 ( <i>t</i> = 1.44)			
	Vertical	0.1668 ( <i>t</i> = 1.38)		<b>0.0074*</b> ( <i>t</i> = 2.55)			
30 m	Inclined			<b>0.0169*</b> ( <i>t</i> = 2.54)			
	Vertical			<b>0.0084*</b> ( <i>t</i> = 3.13)			
PERMANOVA Pairwise comparisons - Sponge Assemblages							
6 m	Inclined	<b>0.0003*</b> ( <i>t</i> = 3.94)	0.3494 ( <i>t</i> = 1.06)	0.0637 ( <i>t</i> = 1.56)	0.1353 ( <i>t</i> = 1.28)	0.6761 ( <i>t</i> = 0.62)	0.2711 ( <i>t</i> = 1.09)
	Vertical	<b>0.0082*</b> ( <i>t</i> = 2.45)	0.2859 ( <i>t</i> = 1.13)	<b>0.0163*</b> ( <i>t</i> = 1.73)	<b>0.0086*</b> ( <i>t</i> = 1.94)	<b>0.0082*</b> ( <i>t</i> = 2.82)	0.8143 ( <i>t</i> = 0.57)
12 m	Inclined	<b>0.0073*</b> ( <i>t</i> = 2.03)	<b>0.0165*</b> ( <i>t</i> = 2.2)	<b>0.0244*</b> ( <i>t</i> = 1.53)		0.1433 ( <i>t</i> = 1.45)	0.323 ( <i>t</i> = 1.1)
	Vertical	<b>0.0087*</b> ( <i>t</i> = 2.88)	<b>0.0069*</b> ( <i>t</i> = 1.93)	<b>0.0094*</b> ( <i>t</i> = 1.83)		0.0625 ( <i>t</i> = 1.36)	0.0538 ( <i>t</i> = 1.4)
18 m	Inclined	<b>0.0069*</b> ( <i>t</i> = 2.88)	<b>0.009*</b> ( <i>t</i> = 2.85)	<b>0.0102*</b> ( <i>t</i> = 3.03)	0.0556 ( <i>t</i> = 1.56)	<b>0.0067*</b> ( <i>t</i> = 3.69)	0.0417 ( <i>t</i> = 1.54)
	Vertical	<b>0.0166*</b> ( <i>t</i> = 1.98)	<b>0.0073*</b> ( <i>t</i> = 2.56)	<b>0.006*</b> ( <i>t</i> = 2.84)	<b>0.0085*</b> ( <i>t</i> = 2.55)	0.0831 ( <i>t</i> = 1.42)	0.1828 ( <i>t</i> = 1.28)
24 m	Inclined	0.0336 ( <i>t</i> = 1.89)		<b>0.0089*</b> ( <i>t</i> = 3.47)			
	Vertical	<b>0.0072*</b> ( <i>t</i> = 2.84)		<b>0.0163*</b> ( <i>t</i> = 2.56)			
30 m	Inclined			0.0538 ( <i>t</i> = 1.42)			
	Vertical			<b>0.0166*</b> ( <i>t</i> = 2.33)			

*Polymastia* spp. was recorded (only small recruits). While at Goleen (internal site), only *Polymastia* spp. (only small recruits), *S. rigida* (only small recruits), and *A. damicornis* were recorded (Table A8).

### 3.5. Environmental data analysis

From the environmental data analyses, no major heatwave, cold spell, or extreme rainfall event could be identified during the potential time frame when the biological communities are most likely to have occurred at Lough Hyne (October 2010–August 2015). For further details, see Appendix A.

## 4. Discussion

The unusual environmental conditions inside Lough Hyne support TMEs in much shallower water than other locations creating a rare opportunity to study TMEs using SCUBA. Despite early video surveys showing stability in the subtidal hard substratum communities at Lough Hyne, a major change has occurred between 1998 and 2018, characterised by a marked decline of predominantly three-

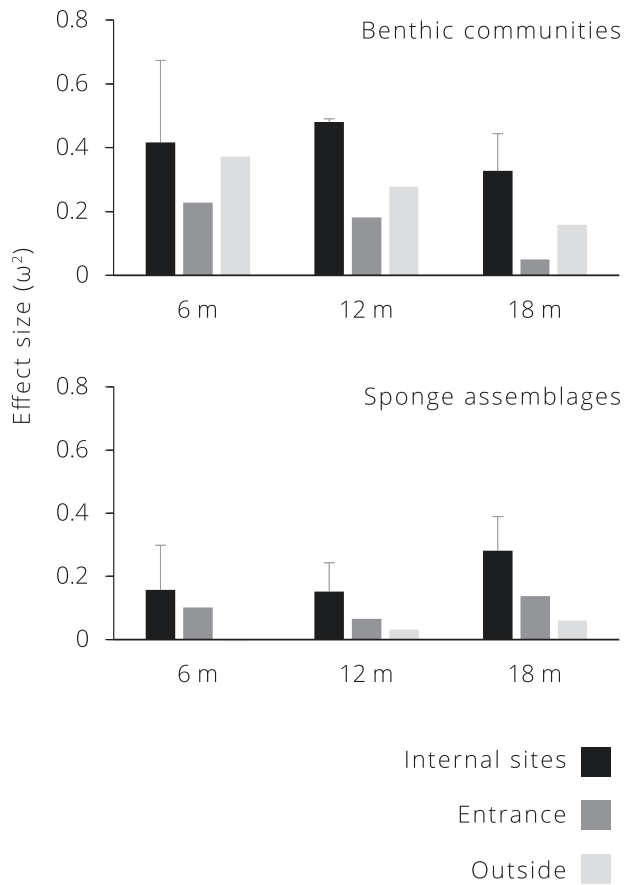
dimensional sponge species and an increase in ascidians. These changes were generally restricted to the internal sites of Lough Hyne, suggesting a localised impact. Opportunistic observations suggest that the decline of sponges mostly likely occurred between 2010 and 2015, following one or more mortality events. We explored several potential drivers, but the absence of regular monitoring has made it impossible to identify the causative factor(s) confidently.

### 4.1. Temporal changes in subtidal benthic communities

Between 1998 and 2018, we found changes in the overall biological community at all sites and sponge assemblage changes at all sites, except the site outside the lough. These changes were not consistent across the sites and mainly affected the internal sites, especially the innermost ones. Changes were also not consistent between taxa and functional groups, suggesting a differential vulnerability of TME organisms to stressful events.

At the internal sites, the general trend was a decrease in sponges and macroalgae and an increase in ascidians and turf-forming organisms. The most significant change was the strong decline, and in some cases



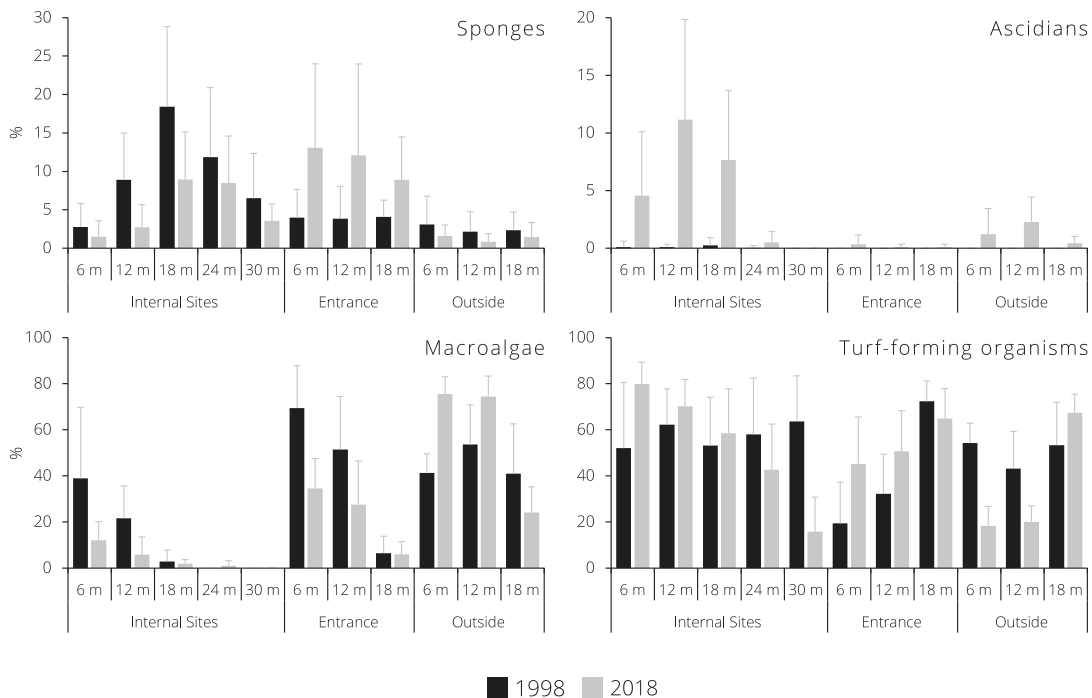


**Fig. 4.** Effect size ( $\omega^2$ ) quantifying the magnitude of temporal changes in benthic communities and sponge assemblages at 6, 12 and 18 m at the internal sites (Glannafeen, Labhra Cliff, Goleen and West Cliff pooled together), entrance (Whirlpool Cliff) and outside the lough (Bullock Island). For the internal sites, the bars indicate the mean value among sites, and the error bars indicate the standard deviation.

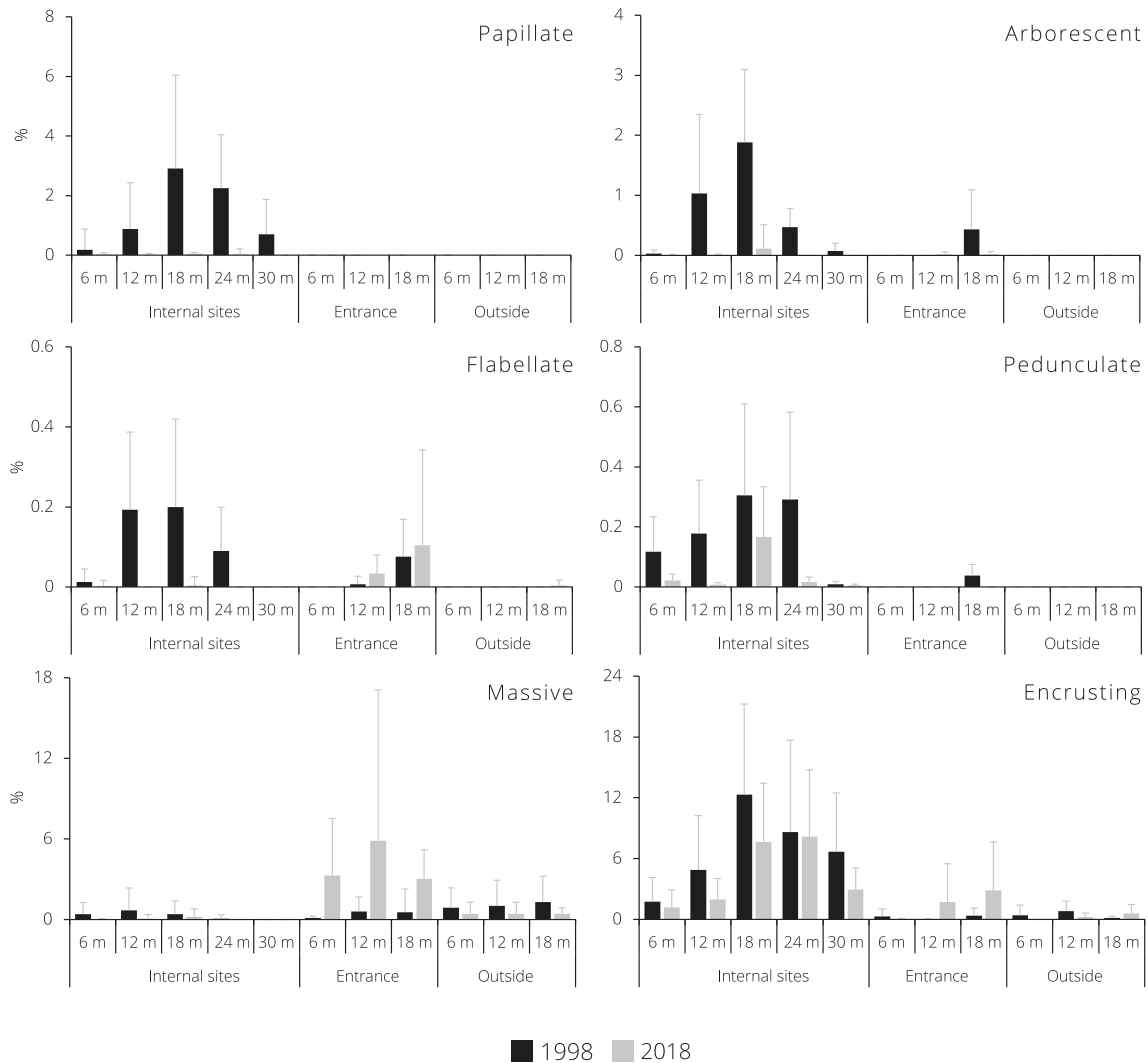
the disappearance, of most three-dimensional sponges at the inner lough sites. Papillate, arborescent and flabellate sponges that once characterised the mesophotic cliffs of Lough Hyne were the most affected. Pedunculate and massive sponges also decreased, but to a lesser extent, while globular sponges did not show any change. At present, it is unclear if different morphologies were more tolerant to the factor/s that caused the sponge declines, or their life-history traits allowed substrate recolonisation quicker than other species. In contrast to the loss of three-dimensional forms, encrusting sponges were still relatively abundant in Lough Hyne in 2018, although they also decreased at the inner sites. Given the considerable size of some of the patches of encrusting sponges (mostly *Eurypon* spp. and encrusting suberitids) found in 2018, and their very slow growth rate (Fowler and Laffoley, 1993; authors' unpublished data), it is very likely that most of these sponges were decades old and not new recruits. This differential response of sponges is consistent with previous research that found some sponge taxa to be very tolerant and others very sensitive to anthropogenic disturbance (Carballo and Naranjo, 2002).

We believe this marked decline in three-dimensional sponges is more likely the result of a mass mortality event than natural fluctuations. Although based on opportunistic observations of just a few species, our long-term sponge abundance reconstruction suggests that the sponge assemblages had been relatively stable for at least 20 years (1990–2010). Furthermore, most of the sponges that characterised the internal cliffs of Lough Hyne (including all the conspicuous species that disappeared) are long-lived and slow-growing, changing little from year to year. For example, Fowler and Laffoley (1993), in the UK, reported less than 1 cm of growth in 6 years for Axinellid sponges (the same species that drastically declined at Lough Hyne). This is also supported by Perkins et al. (2017), who found erect and massive sponge populations are reasonably stable on mesophotic temperate reefs in Australia.

Sponge abundance decreased at all depths, but changes were more evident at 18 and 24 m, than 6, 12 and 30 m, and more often on vertical surfaces than on inclined ones (except for papillate sponges that decreased more on inclined surfaces). This may result from the high level of variability of the sponge assemblages, which is supported by



**Fig. 5.** Mean percentage cover of main benthic organisms in 1998 and 2018 for each depth at the internal sites (Glannafeen, Labhra Cliff, Goleen, and West Cliff pooled together), entrance (Whirlpool Cliff) and outside Lough Hyne (Bullock Island). Error bars indicate standard deviation. Note the different y-axis scales.



**Fig. 6.** Mean percentage cover of main sponge morphologies in 1998 and 2018 for each depth at the internal sites (Glannafeen, Labhra Cliff, Goleen and West Cliff pooled together), entrance (Whirlpool Cliff) and outside Lough Hyne (Bullock Island). Error bars indicate standard deviation. Note the different y-axis scales.

the significant interaction found in most analyses. With respect to the species recorded only in 1998 or 2018, most were rare, and the differences could be explained by species being missed when sampling. None of these rare species constituted a single OTU/taxon in the quantitative analyses, so they did not influence them. In contrast, the branching sponge *Raspailia hispida* was relatively abundant in 1998 and has likely become locally extinct in the lough. The most recent surveys carried out at the lough found a high abundance of sponge recruits at most sites, which could mean that, at least for some species, natural recovery is underway.

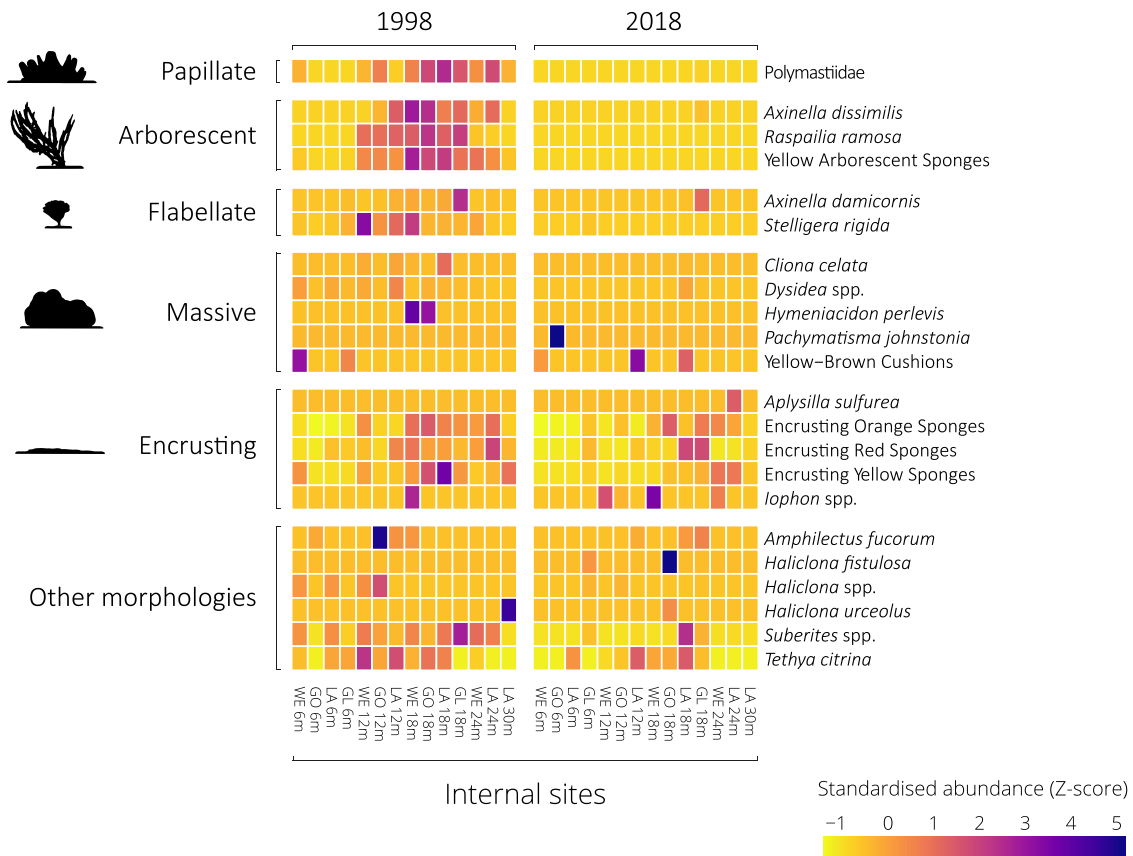
The sponge decline inside the lough correlated with a marked increase in ascidian abundance, which might be the result of the free space that became available after the sponges died. Ascians may also have a higher tolerance to stressors that affected the sponges (Naranjo et al., 1996). However, the ascidian increase could also result from their opportunistic nature and their considerable seasonal and interannual variability (Caputi et al., 2015; Lynch et al., 2016). This would be consistent with findings from the Bathurst Channel in Tasmania, where most of the species show high temporal stability, while others, including ascidians, showed considerable interannual variability (Barrett et al., 2010).

The increase in turf-forming organism abundance and the decrease in macroalgal cover inside the lough at shallow depths (6 and 12 m) is

consistent with the changes in the algal assemblages that have occurred over the last few decades in the intertidal and shallow subtidal. Trowbridge et al. (2013) reported a recent increase in ephemeral filamentous algae, potentially driven by the reduction in primary consumers and the total nitrogen increase in the area (Jessopp et al., 2011). These ephemeral algae often form continuous blankets that coat other algal species, which explains the lower cover of macroalgae found in 2018 (Trowbridge et al., 2013). Changes in spatial dominance of various foundation species to turf-forming algae are common features of degraded temperate rocky subtidal reefs globally, often caused by a complex interaction of factors including climate change and eutrophication (Strain et al., 2014; Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018).

Less clear is the reason for the increase in sponge abundance (mainly massive sponges) at the site at the entrance of the lough. We believe this more likely represents natural population fluctuations as the changes were smaller compared to the inner sites. Furthermore, some of the sponge species that increased in abundance in 2018 at this site are fast-growing and highly dynamic, particularly *Amphilectus fucorum* and *Cliona celata* (Fowler and Laffoley, 1993; Van Soest and Hajdu, 2002).

Changes in communities (but not sponge assemblages) were also found outside the lough. In this case, the main changes were an increase



**Fig. 7.** Heat map of the mean abundance of sponge taxa at the internal sites for each combination of site and depth in 1998 and 2018. Site Key: WE West Cliff, GO Goleen, LA Labhra Cliff and GL Glannafeen. Abundance data (percentage cover) are standardised (Z-score normalisation) on the taxon axes (i.e. each taxon is given equal weight). Data from vertical and inclined surfaces were pooled.

in ascidians and macroalgae, and the consequent decrease in the coverage of turf-forming organisms. These changes are more likely due to seasonal variations. Concerning ascidians, the only species found in 2018 was *Clavelina lepadiformis*, a seasonal species whose zooids disappear at the end of the summer (Berrill, 1951). It is possible that in 1998, this species was missed because all the zooids had disappeared before sampling. The same could be true for algae, as one of the most abundant algae found in 2018 was *Delesseria sanguinea*. Reports from the Normandy coasts show that this species loses its fronds in June (Nabil and Cosson, 1996); so, it might not have been recorded in 1998 because the fronds had disappeared before sampling.

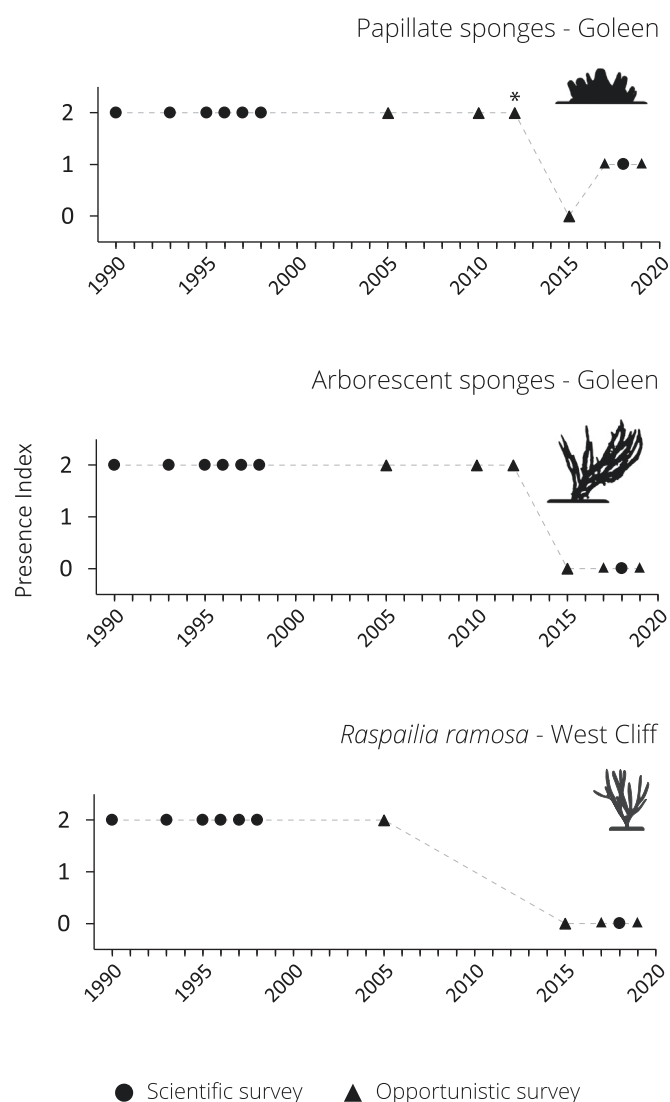
#### 4.2. Potential causes of the changes

There are many potential explanations for the changes we report at Lough Hyne (see Appendix C for a summary of the possible causes). However, the limited biological and environmental monitoring makes it very difficult to identify the exact cause or the timing. We explored available environmental data, but we could not determine with certainty any causal processes responsible for the observed mass mortality event of three-dimensional sponges.

Opportunistic observations indicate that the decline of sponges mostly likely occurred between 2010 and 2015, in one or more mortality events. This change most strongly affected the innermost sites, suggesting that the cause of the change has either originated from inside the lough or that the sheltered conditions of the Lough Hyne basin have amplified a driver originating from the surrounding coast. Similar mass mortality events in temperate waters, involving several orders of sponges, have only been reported in the Mediterranean Sea, caused by

disease outbreaks (Gaino et al., 1992), heatwaves (Garrahou et al., 2009; Di Camillo and Cerrano, 2015) and eutrophication-related anoxia (Stachowitsch, 1984), and in Australia as a result of sewage discharge (Roberts et al., 1998). Other catastrophic changes in similar environments have been reported from the Chilean Patagonian fjord region, where the cold-water coral *Desmophyllum dianthus* experienced a mass die-off in 2012 following eutrophication due to salmon farming pollution (Försterra et al., 2014). However, mass mortalities in benthic ecosystems usually remain undocumented or poorly described due to difficulties in responding rapidly to unforeseen events and a lack of baseline data, especially in remote marine systems (Jurgens et al., 2015).

Sponge mass mortalities have been often attributed to disease outbreaks, but we think this is unlikely to be the cause of the changes that occurred at Lough Hyne. Usually, pathogen outbreaks infect broad geographic areas (Webster, 2007), so we believe the effects would have likely been more uniform around the lough. Furthermore, pathogens usually affect a specific group of sponges (a species, a family or more rarely an order; Webster, 2007), while in Lough Hyne, several orders of sponges were involved. Heatwaves are also unlikely to be the main cause, considering that no significant heatwaves occurred during the period when the changes were first recognised (October 2010–July 2012; Fig. A4). In contrast, winter 2010/2011 was characterised by a moderate cold spell which probably caused the death of some intertidal gastropods at Lough Hyne (Little et al., 2020). In tropical coral reefs, cold-water events are known to be a cause of mortality of sponges and other benthic invertebrates (Colella et al., 2012). However, cold-related mortality has never been reported for temperate sponges.



**Fig. 8.** Temporal variation of papillate and arborescent sponges at Goleen, and *Raspailia ramosa* at West Cliff, between 1990 and 2019. Legend to the presence index: 0 = No sponge recorded; 1 = Only recruits recorded (<2 cm); 2 = adult recorded (>10 cm). \*only one adult was found.

At this stage, eutrophication seems to be one of the most likely contributors to the changes. There has been a marked increase in nutrients both inside the lough and the surrounding coast in recent years. Total nitrogen inside the lough increased from a maximum monthly concentration of  $210 \text{ mg m}^{-3}$  in the 1990s (Johnson et al., 1995) to  $720 \text{ mg m}^{-3}$  in the late 2000s (Jessopp et al., 2011). Eutrophication appears to be central to the changes seen in the shallow water communities of the lough (Trowbridge et al., 2017; Plowman et al., 2020). Similarly to other coastal systems worldwide, the high nitrogen levels has stimulated the proliferation of ephemeral macroalgae (particularly ulvoids and ectocarpoids) and phytoplankton blooms (Jessopp et al., 2011; Trowbridge et al., 2011; Lyons et al., 2014). Some of these algae (e.g. *Ulva*) can produce chemicals that negatively affect benthic species (Nelson et al., 2003). When large quantities of blooming algae settle on the seafloor, they increase the organic load of the sediment, inducing anoxia and the release of hydrogen sulphide (Lyons et al., 2014). At Lough Hyne, this excess of organic matter might also influence the duration of the oxy-thermocline in the lough, promoting earlier formation and greater persistence of anoxic conditions (Diaz and Rosenberg, 2008; Jessopp et al., 2011). Furthermore, other factors, such as increased temperatures and the occurrence of a toxic event caused by an anomaly in

the oxy-thermocline break, might have contributed to the stress of the benthic communities culminating in the sponge mass mortality (see Appendix C for more information).

The small number of laboratory experiments that have tested the effects of increased nutrients on sponges have found no or little effect (Luter et al., 2014; Beepat et al., 2020; Ramsby et al., 2020). However, the effects of eutrophication on heterotrophic organisms are mainly caused by cascading effects rather than the actual nutrients themselves (Grall and Chauvaud, 2002; Gray et al., 2002). One of the most severe consequences of eutrophication is a decrease in oxygen, but, in laboratory conditions, sponges have been found to be tolerant of severe hypoxia (Mills et al., 2014; 2018; authors' unpublished data). However, the severity of hypoxia could be different in the natural environment, and threshold values can be highly influenced by temperature and the presence of hydrogen sulphide (Gamenick et al., 1996; Vaquer-Sunyer and Duarte, 2008; Vaquer-Sunyer and Duarte, 2011). For example, Stachowitsch (1984) found that during a eutrophication-related hypoxia/anoxia event sponges were among the first organisms to die.

Unfortunately, there is still very little information about TME species and community ecology, or the vulnerability of these systems to anthropogenic stressors. Basic information on life cycles, connectivity patterns, population dynamics and responses to stressors for most TMEs species is often still inferred from related shallow-water species. However, the very different environmental conditions of shallow and mesophotic waters (i.e. temperature, light, hydrodynamics, and food availability), mean the ecology and TME organisms and their response to stressors could differ (Cerrano et al., 2019). Therefore, more research is needed to understand TME ecology in the context of global and local changes, and to predict potential changes to TME species and communities.

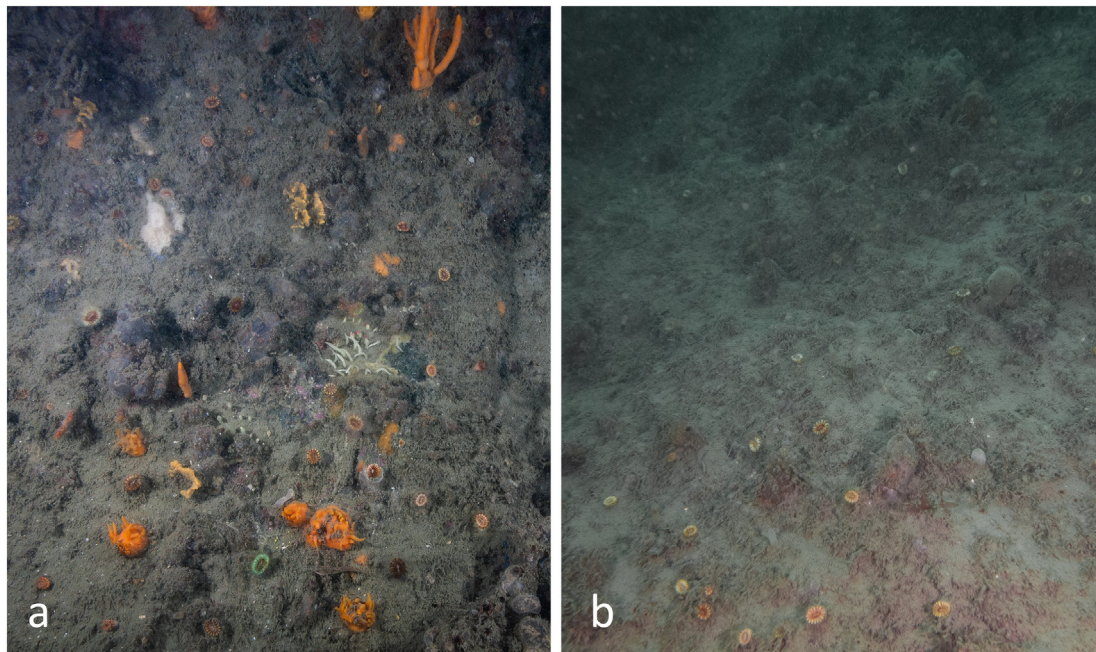
#### 4.3. Implications for the conservation of TMEs

Our study highlights the vulnerability of mesophotic habitats to environmental change, and how major changes can occur, but be easily overlooked. What has happened in Lough Hyne could also have happened or might be happening in other areas without being noticed. TMEs are comprised mainly by long-living and slow-growing organisms, which are likely to have limited resilience to human-induced impacts (Deter et al., 2012). Despite the high tolerance of some shallow-water sponges to anthropogenic disturbance, our study suggests that three-dimensional mesophotic sponges are among the most sensitive species (see also Carballo and Naranjo, 2002). Any decline in these habitat-former species will likely affect important ecosystem functions with detrimental effects on related ecosystem services (Gómez-Gras et al., 2021). Given the vulnerability and importance of TMEs, the management and conservation of these habitats should be prioritised by management agencies.

Successful management and conservation of TMEs can only be achieved through fit-for-purpose monitoring of biotic and abiotic factors, including environmental stressors (Borja, 2014). To date, TMEs are monitored in only a few regions of the world, while very little is known about them elsewhere. Furthermore, MPA management plans rarely consider TMEs and often, as in the case of Lough Hyne, protection only results from shallow MPA designation extending into deeper waters (Kitching, 1987; Turner et al., 2019). TMEs need specific consideration in current MPA monitoring programmes, and new TME monitoring schemes should be established to monitor particularly rich and vulnerable habitats and communities. Together with monitoring, current baselines need to be established, against which potential changes can be measured and evaluated in relation to natural variation in the system (Borja et al., 2012). Furthermore, historical baselines need to be reconstructed to assess if changes have already occurred as this information is critical to set future conservation targets.

Quantitative data for TMEs are rarely available, so, as in our case, it can be useful to combine scientific data with opportunistic observations to consolidate time-series and document long-term changes. Photos, videos,





**Fig. 9.** Examples of subtidal cliffs (~15 m) at Goleen in 2010 (a), the last time it was seen in a 'healthy' condition and 2018 (b). Notice the abundance and diversity of three-dimensional sponges in 2010 that are absent in 2018. Among the species present in the photo from 2010 are the branching sponges *Axinella dissimilis*, several papillate sponges of the genus *Polymastia* and *Sphaerotylus*, the flabellate sponges *Axinella damicornis* and *Stelligera rigida*. In contrast, ascidians and cup corals dominate in the photo from 2018. The photo from 2010 is courtesy of Nick Owen.

historical descriptions from all possible sources including the internet and social media (Di Camillo et al., 2018), local fishers, SCUBA divers and naturalists, can provide essential information to reconstruct earlier environmental and biological conditions (Drew, 2005; Ferretti et al., 2015; Thurstan et al., 2017). In our study, the use of opportunistic observations considerably improved our ability to reconstruct historical baselines at Lough Hyne and evaluate long-term community dynamics. However, this approach does not replace the need for long-term monitoring programmes in the assessment of environmental impacts. The absence of regular subtidal monitoring of Lough Hyne's TMEs resulted in almost a decade between the occurrence of the change and its recognition, which has significantly reduced our chances of identifying the drivers. This consequently hinders the implementation of appropriate measures aimed at restoring the original status and eliminating or minimising the impacts.

The main factors limiting the research and monitoring of TMEs globally are the depth and the availability of technology, as these ecosystems are usually out of range of conventional scientific diving (Turner et al., 2019). However, recent rapid technological advances have led to the development of a wide range of tools that can now facilitate exploring deeper ocean areas at low cost. For example, small remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs) and closed-circuit rebreathers, together with advanced acoustic and optical imaging techniques, are now available for a wide range of management and conservation applications for TMEs (e.g. UNEP-MAP-RAC/SPA, 2008; Williams et al., 2010; Pizarro et al., 2013).

If TMEs are monitored regularly in Lough Hyne Marine Reserve, then the lough could become an important reference site due to the accessibility of its TMEs, and its relative isolation from external drivers. However, the shallowness of the Lough Hyne TMEs may also contribute to their vulnerability to internal drivers, which, if monitored, could be recorded and identified relatively easily.

## 5. Conclusions

Our study at Lough Hyne demonstrates the potential fragility of TMEs and how changes can happen without being detected if adequate

monitoring is not in place. The monitoring of TMEs will contribute to our scientific understanding of these poorly-studied systems and improve our ability to make evidence-based decisions for TME management and conservation (Turner et al., 2019; Sukhotin and Berger, 2013). A better knowledge of these ecosystems will also raise the awareness of the value of TMEs among decision-makers and the general public, which is essential to ensure their conservation (Inglehart, 1995). Finally, our study is a small-scale example, that even if dramatic ecological changes happen, most species and functional groups persist, leaving space for a potential recovery (Lotze et al., 2006).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.147708>.

## CRediT authorship contribution statement

**Valerio Micaroni:** Conceptualization, Data curation, Formal analysis, Visualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Rob McAllen:** Conceptualization, Investigation, Methodology, Writing – review & editing. **John Turner:** Conceptualization, Methodology, Resources, Writing – review & editing. **Francesca Strano:** Investigation, Visualization, Methodology, Writing – review & editing. **Christine Morrow:** Investigation, Methodology, Writing – review & editing. **Bernard Picton:** Investigation, Methodology, Writing – review & editing. **Luke Harman:** Investigation, Methodology. **James J. Bell:** Supervision, Funding acquisition, Conceptualization, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing.

## 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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