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Contrasting patterns of decadal stability for shallow water sponge boulder assemblages and subtidal rocky cliffs at Lough Hyne, Ireland

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Research Article

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Abstract

Lough Hyne (LH) Marine Nature Reserve in Ireland is a globally recognised biodiversity hotspot that hosts mesophotic-like communities in shallow water, however, major changes have occurred to most of the rocky cliff (>6 m) communities in one or more events between 2010 and 2015. To provide insights into these changes, we compared the sponge assemblage composition on the undersides of different sized, shallow (<1 m) subtidal boulders between 2000 and 2022 at two sites in LH. We also measured sponge species richness at seven sites in 2018. We found that unlike earlier reports from the deeper subtidal reef sponge assemblages, there was no evidence for changes in sponge assemblage composition on the undersides of boulders at either site. We also found high levels of sponge species richness at all seven sites sampled in 2018. We did find differences in sponge assemblages between sites and for different boulder sizes, which we propose is a result of site-specific environmental conditions and disturbance and size–area relationships. Since we found no changes in the shallow subtidal sponge assemblages between 2000 and 2022, our results support the hypothesis that changes to the deeper subtidal sponge assemblages at LH are driven by local processes associated with deeper water in LH, potentially related to the seasonal oxythermocline that forms within LH. Given the national and global importance of LH, understanding the drivers of change is critical to determine if management actions can prevent any future alterations to the LH sponge assemblages and support wider mesophotic community management.

Introduction

Determining the drivers of change and natural patterns of environmental variability are critical to support effective marine management, since it enables anthropogenic impacts to be distinguished from natural changes. However, for most marine ecosystems monitoring is either spatially restricted, or has at best only been conducted for decades (e.g. Edwards *et al.*, 2010; Borja *et al.*, 2016), and therefore started after the Anthropocene era began around the mid-20th century (Waters and Turner, 2022). This means that it is often very difficult to conclusively identify drivers of change in marine systems and take appropriate management actions, since we have an incomplete picture of patterns of natural variability.

Lough Hyne (LH) Marine Nature Reserve (51°29’N, 9°18’W) is a small, semi-enclosed sea lough on the southwest coast of Ireland, which is known globally as a biodiversity hotspot and has been studied extensively for over 100 years (Minchin, 1991). While in the past the rocky subtidal communities in LH have been considered highly unusual as they differ from those found at corresponding depths on the open Atlantic coast (Bell and Barnes, 2000a), more recently they have been considered similar to deeper water so-called temperate mesophotic ecosystems found elsewhere (Micaroni, 2022; Micaroni *et al.*, submitted). Mesophotic communities are those that exist at the limit of light for photosynthesis and are animal-dominated (see Bell *et al.*, 2022 for review). Therefore, LH represents an opportunity to study mesophotic communities in shallower water.

While many changes have been reported in LH over the last 50 years (e.g. Little *et al.*, 1992, 2018; Trowbridge *et al.*, 2013, 2018, 2019), most recently there has been a massive loss of sponges (>90% in some locations) on all but one of the subtidal cliffs (Micaroni *et al.*, 2021). The exact cause of this change remains unknown, but based on long-term casual observations and quantitative data, we know it occurred in one or more events between 2010 and 2015 (Micaroni *et al.*, 2021). While many species of sponge were impacted during this event, branching, massive and papillate forms declined the most. Prior to this change, direct SCUBA diver observations from various sources (authors observations, personal communication, Bernard Picton, John Turner, Declan O’Donnell) confirm that these sponge assemblages have been stable for many decades and possibly much longer. Importantly, these changes appear to only have occurred in LH and not on the wider Atlantic coast, and only at sites within LH that experience low water currents and high sedimentation rates (Micaroni *et al.*, 2021).

Several hypotheses have been proposed to explain the sponge loss, including extreme temperature events, disease outbreaks and changes in sedimentation and water quality (see Micaroni *et al.*, 2021 for a full discussion). However, the cause or causes remain unresolved, and most of potential drivers have low likelihood of being the cause. One of the interesting oceanographic features of LH is a seasonal oxythermocline that forms in the deeper (>50 m) western part of the lough (Kitching *et al.*, 1976; Johnson, 2006). Calm conditions inside LH typically support the development of a colder, oxygen-poor layer in the deeper areas from northern hemisphere spring, with full development by summer, and breakdown during autumn. The low-oxygen layer is thought to have a strong influence on the ecology and biology of organisms in the deeper areas of the lough (Kitching *et al.*, 1976; Ballard and Myers, 1997), with a marked decline in the biodiversity of sponges and other organisms below approximately 25 m (Bell and Barnes, 2000a). This deeper layer is also thought to contain hydrogen sulphide, although this has not been explicitly measured to date (authors personal observation). One proposed explanation for the sponge decline could be an unusual or rapid breakdown of this thermocline, effectivity 'bathing' sponges in this low oxygen water. However, explicit testing of LH sponge oxygen tolerance found sponges to be resilient to short-term oxygen stress (Micaroni *et al.*, 2022), with the focus now being on the presence of hydrogen sulphide as the main driver of change.

In addition to the well-described sponge fauna on the subtidal cliffs at LH, extensive and diverse sponge assemblages can be found on the undersides of boulders in the shallow (<1–3 m) sublittoral zone (Bell and Barnes, 2003). These boulders are overlying each other and are mostly very stable (Maughan and Barnes, 2000), with the sponge assemblages being dominated by low profile encrusting, massive and repent forms, because of the two-dimensional habitat. These boulders also support many sponges, including species that are not common on the deeper subtidal cliffs (Bell and Barnes, 2003). Although the changes in the LH cliff fauna have been recently described, to date there has been no assessment of whether these shallow subtidal underside boulder sponge assemblages have also changed. Understanding the temporal dynamics of these boulder-associated sponges may provide important insights into the cause of change on the deeper subtidal cliffs, especially if they show different dynamics. Importantly, some recent changes have been reported in the very shallow water communities in LH (<2 m; Trowbridge *et al.*, 2013, 2018, 2019; Little *et al.*, 2018), which have been linked to oxygen stress and eutrophication (Trowbridge *et al.*, 2017a, 2017b), but no explicit examination of the sponge fauna has been made. Furthermore, there has been very limited study on the fauna inhabiting the undersides of the boulders more generally and the accessible boulder fields at LH provide a rare opportunity to study changes in under-boulder fauna through time.

The aim of this study was to compare the sponge boulder assemblages at two sites in LH at 1–2 m depth between 2000 and 2022 (incorporating the period when the subtidal sponge assemblages declined) to assess if there is any evidence for change or a decline in sponges. One site was at the entrance to the lough (Whirlpool Cliff), where the deeper (max 18 m) subtidal cliff sponge assemblages have not changed over the last 20 years, and the other at one of the locations where the subtidal cliff sponge fauna has been most impacted (West Cliff). We propose that if the shallow subtidal (<1 m) sponge assemblages have remained stable through time, this lends support to the hypothesis that an unusual breakdown of the thermocline may have caused the change in the deeper subtidal cliff sponge fauna in LH.

Materials and methods

Study sites

LH Marine Nature Reserve is a small semi-enclosed sea lough on the southwest coast of Ireland. LH is characterised by an unusually high number of ecological niches within a localised area (0.5 km^2) largely because of flow and sedimentation gradients from east to west (Bell and Barnes, 2002). LH is extremely sheltered in comparison to the adjacent Atlantic coastline, with slight wave action only being experienced inside the lough during the strongest winds (>50–70 mph). The lough is connected to the Atlantic Ocean by a narrow (25 m wide) tidal rapids that has a raised sill running across it, which leads to an unusual tidal regime (Bassindale *et al.*, 1957). The tidal inflow lasts only 4 h, with currents in the eastern part of the lough being very fast (>200 cm s^{-1}). However, the outflow of water lasts for more than 8 h and the water currents are slight in all parts of the lough, with the exception of the rapids. The sponge fauna on the undersides of boulders was examined: (1) at two sites within LH in 2000 and 2022 (Figure 1) to assess temporal stability in sponge assemblages; and (2) at seven sites in 2018 (Figure 1) to assess spatial variation in sponge species richness. Whirlpool Cliff was the first site sampled in 2000 and 2022, and is characterised by fast (>200 cm s^{-1} at 0–6 m), unidirectional water flow during the incoming tide. Although sedimentation rates are likely to be high, accumulation rates are negligible as material is moved back into suspension during the incoming tide. West Cliff was the second site sampled in 2000 and 2022. This site experiences only slight currents (5–10 cm s^{-1}) during peak spring tide inflow (lasting only 15–30 min) (Bell and Barnes, 2002). These conditions result in high rates of sediment settlement and accumulation rates. However, in the first 1–2 m, wind-induced currents are likely to create some water circulation around boulder communities at West Cliff. For the wider species richness survey in 2018, sites that experience a range of different environmental conditions, from high flow in the Rapids to low flow at the North Basin were examined (Figure 1).

Methods

For the surveys at the two sites sampled in 2000 and 2022, boulders were haphazardly selected for examination in June each year. The surface area of lower boulder surfaces was measured by laying a transparent cloth marked in square centimetres over the boulders in 2000 and by taking a photograph of each boulder with an iPhone 13 with scale in each picture in 2022 followed by image analysis in Image J (Schneider *et al.*, 2012). A total surface area of approximately 35,000 cm^2 was examined at each site. All boulders were examined *in situ* to prevent excessive drying of material in 2000 and to build a visual database of sponge species and from photographs in 2022. The number of each sponge (number of patches) species on each boulder was recorded. Samples were taken for spicule analysis in the laboratory to allow positive identification where necessary. While we would have preferred to have compared the sponge assemblages using both number of patches and area occupied data, only number of patches data were available from previous surveys in 2000 (see Bell *et al.*, 2017 for further discussion on the use of number of patches *vs* area occupied). For the wider survey of sponge species richness in 2018, 20 boulders ranging in size from

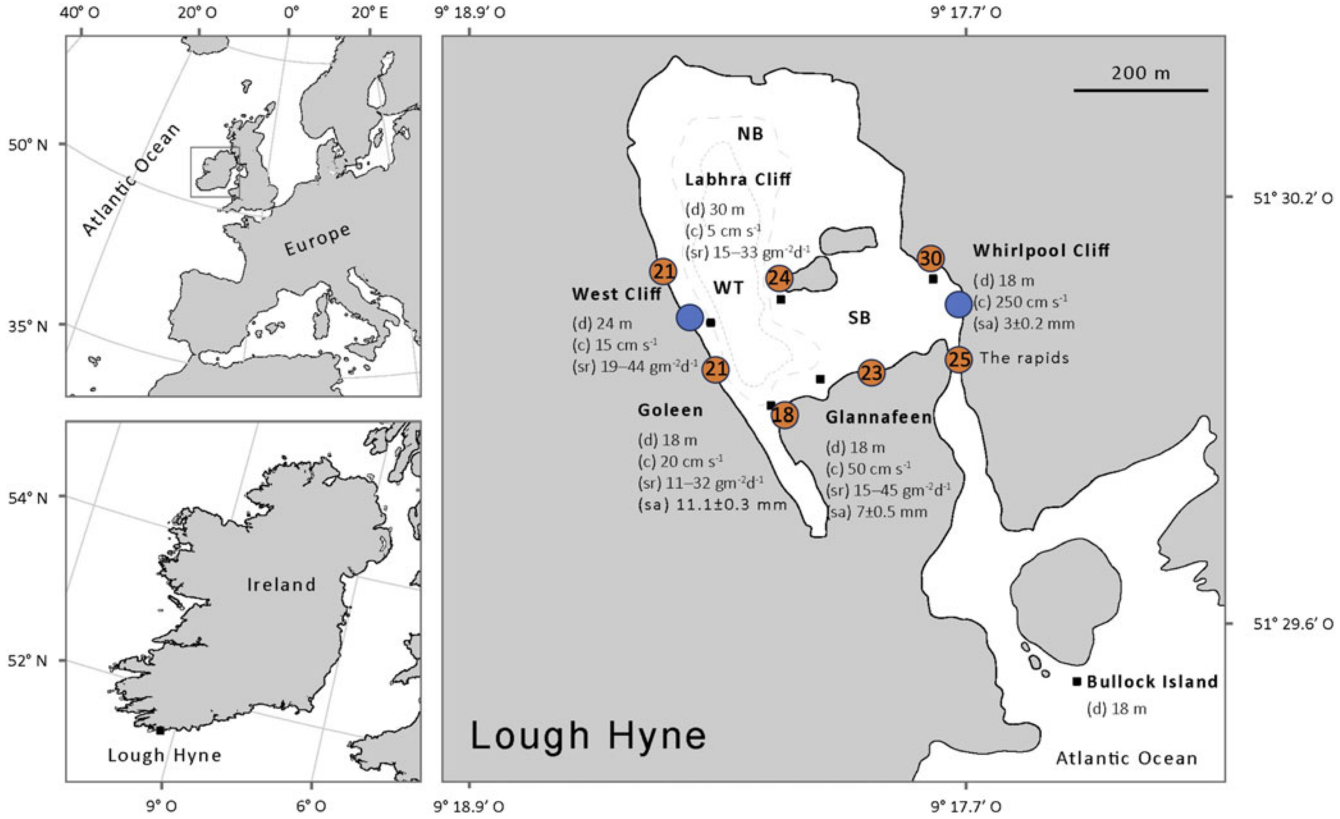

Figure 1. Location of Lough Hyne Marine Nature Reserve showing the location of the subtidal cliffs (squares) and the environmental conditions (d = depth, c = current speed, sa = sediment accumulation of rocks, sr = sedimentation settlement rate). Blue circles indicate the sites sampled for sponge boulder assemblages in 2000 and 2022, while the orange circles are the locations where sponge boulder assemblages were sampled in 2018. The numbers in the orange circles are the sponge species richness at each location.

approximately 50 to 600 cm^2 were haphazardly selected at the seven sites and the total species richness across all those boulders recorded.

Analyses

Boulders sampled in 2000 and 2022 were grouped according to size into small (<150 cm^2), medium (151–400 cm^2), large (401–750 cm^2) and very large boulders (>750 cm^2), since boulder size has been shown to impact sponge boulder assemblages at LH and elsewhere (Bell and Carballo, 2008). Thirty boulders of each size class were sampled at each site (120 in total for each site; 240 in total across both sites). Differences in sponge assemblage composition between the two sites, for the 2 years and the different boulder sizes were analysed using permutational multivariate analysis of variance (PERMANOVA). Three-way PERMANOVAs included year (2 levels), site (2 levels) and boulder size (4 levels) as factors. Year and site were treated as random factors, while boulder size was treated as a fixed factor. The analysis was based on Bray–Curtis dissimilarities and models were run using 9999 unrestricted permutations of raw data. Data were log (x + 1) transformed to reduce the influence of the most abundant and rare sponges and standardised based on the overall sponge abundance to account for the different overall numbers of patches on differing boulder sizes. Differences in multivariate assemblages were graphically displayed using non-metric multidimensional scaling based on Bray–Curtis dissimilarities. SIMPER analyses were used to determine which species contributed most to any significant differences observed. All analyses were conducted using PRIMER V6 + PERMANOVA.

Results

In total, we found 43 sponge species (37 Demospongiae, 5 Calcarea and 1 Homosleromorpha) inhabiting the undersides of boulders across 2000 and 2022 (Table 1). These 43 species were represented by a total of 12,011 and 12,770 individual patches in 2000 and 2022, respectively. All species found in 2000 were also found in 2022. There were 38 and 40 unidentified patches in 2000 and 2022 respectively, which may represent some additional species. In 2000, only four of the 43 species (*Leuconia nivea*, *Clathria (Microciona) fallax*, *Mycale (Aegogropila) contarenii* and *Mycale (Carmia) macilenta*) were exclusively found at West Cliff, while only *Grantia compressa* was found exclusively at Whirlpool Cliff. In 2022, *Grantia compessa*, *Clathria (Microciona) strepsitoxa* and *Pseudosuberites sulphureus* were exclusively found at Whirlpool Cliff, while *Halichondria (Halichondria) bowerbanki*, *Iophon hyndmani*, *L. nivea*, *C. (Microciona) fallax*, *M. (Aegogropila) contarenii* and *M. (Carmia) macilenta* were only found at West Cliff. However, the abundance of all these exclusive species was low, with abundances less than 0.8% of the total number of sponge patches observed, and often these species were represented by a single patch (see Supplementary Table 1). In both 2000 and 2022, we found that species richness generally increased with boulder size (Table 1), although there was less difference between large and very large boulders, compared to small *vs* large and very large boulders. For examples of sponge boulder communities, see Supplementary Figure 1.

PERMANOVA (Table 2) showed no significant effect of time ($P = 0.379$) on the sponge boulder assemblages. However, there was a significant effect ($P = 0.001$ in each case) of both site and boulder size on sponge boulder assemblages, and for the

Table 1. Sponge species reported from the undersides of boulders found at two sites at Lough Hyne for small (S < 150 cm^2), medium (M, 151–400 cm^2), large (L, 401–750 cm^2) and very large boulders (VL > 750 cm^2) across both 2000 and 2022

	West Cliff				Whirlpool Cliff			
Species	S	M	L	VL	S	M	L	VL
Antho (Antho) inconstans (EN)	X		*X	*X	*X	*X	*X	*X
Aplysilla sulfurea (EN)	*X	*X	*X	*X	*X	*X	*X	*X
Chelonaplysilla sp. (EN)	*X	*X	*X	*X	*X	*X	*X	*X
Clathrina coriacea (CL)	*X	*X	*X	*X	*X	*X	*X	*X
Cliona celata (MA)			*	*X			*X	*X
Dercitus (Dercitus) bucklandi (MA)		*	*X	*X		*X	*X	*X
Dysidea fragilis (MA)	*X	*X	*X	*X	*X	*X	*X	*X
Dysidea pallescens (MA)			*X	*X			*X	*X
Amphilectus fucorum (RE)		*X	*X	*X		*X	*X	*X
Grantia compressa (TU)					X	X	*X	
Haliclona sp. 1 (MA)	*X	*X	*X	*X			*X	*X
Haliclona sp. 2 (RE)	*X	*X	*X	*X	*X	*X	*X	*X
Haliclona sp. 3 (RE)		*X	*X	*X	*X	*X	*X	*X
Haliclona sp. 4 (RE)	*X	*X	*X	*X	*X	*X	*X	*X
Haliclona sp. 5 (MA)	*X	*X	*X	*X	*X	*X	*X	*X
Haliclona sp. 6 (MA)	*X	*X	*X	*X	*X	*X	*X	*X
Haliclona sp. 7 (MA)		*X	*X	*X		*X	*X	*X
Haliclona sp. 8 (MA)	*X	*X	*X	*X		*X	*X	*X
Halichondria (Halichondria) bowerbanki (RE)		X	*X	*X			*	*
Hymedesmia (Stylopus) coriacea (EN)	*X	*X	*X	*X	*X	*X	*X	*X
Hymedesmia (Hymedesmia) jecusculum (EN)				*X			*	*X
Hymedesmia (Hymedesmia) pansa (EN)				*X		*X	*X	*X
Hymedesmia (Hymedesmia) paupertas (EN)		*X	*X	*X		*X	*X	*X
Hymeniacidon perlevis (MA)	*X	*X	*X	*X	*X	*X	*X	*X
Iophon hyndmani (EN)	X	X	X	*X				*
Leuconia nivea (EN)		*X	*X	*X				
Leucosolenia complicata (RE)	*X	*X	*X	*X	*X	*X	*X	*X
Clathria (Microciona) fallax (EN)		*	*X	*X				
Clathria (Microciona) strepsitoxa (EN)				*			*X	*X
Mycale (Aegogropila) contarenii (MA)		X	*X	*X				
Mycale (Carmia) macilenta (MA)		X	*X	*X				
Mycale (Aegogropila) rotalis (MA)				*X			X	*X
Myxilla (Myxilla) rosacea (MA)	*X	*X	*X	*X		*X	*X	*X
Pachymatisma johnstonia (MA)		*X	*X	*X	*X	*X	*X	*X
Plakortis simplex (EN)	*X	*X	*X	*X	*X	*X	*X	*X
Pseudosuberites sulphureus (EN)	*					X		
Sycon ciliatum (TU)	X	*X	*X	*X	X		*X	*X
Spanioplon armaturum (EN)			*X	*X		*X	X	*X
Phorbas dives (EN)	*X	*X	*X	*X	*X	*X	*X	*X
Phorbas plumosus (MA)	*X	*X	*X	*X	*X	*X	*X	*X
Suberites sp. (EN)	*X	*X	*X	*X	X	*X	*X	*X
Terpios fugax (EN)			*X	*X	X	*X	*X	*X
Tethya aurantium (GL)		*	X			X	*	

(*Continued*)

Table 1. (*Continued.*)

	West Cliff				Whirlpool Cliff			
Species	S	M	L	VL	S	M	L	VL
Total no of species	19 (21)	28 (29)	35 (36)	40 (39)	17 (21)	27 (30)	35 (34)	36 (34)

Asterisks (*) represent species found in 2000 and crosses (X) species found in 2001. The overall number of species found in 2000 and 2022 (in brackets) are shown. Sponge morphologies are also shown: EN, encrusting; CL, clathrate; MA, massive; RE, repent; TU, tubular; GL, globulose.

interaction between site and boulder size. These differences between sites and boulder size were also evident from the MDS plot (Figure 2). The significant interaction between site and boulder size was driven by the very large boulders at Whirlpool Cliff in 2022 having more similar sponge assemblages to those on medium and large boulders compared to the pattern in 2000, and for both years at West Cliff. SIMPER analyses found that many species equally contributed to the differences in sponge assemblages between both sites and boulder size (see Supplementary Table 2), with those species absent from any particular boulder size or site (Table 1), unsurprisingly, being the main species driving the differences.

The wider site survey conducted in 2018 showed some variation in sponge species richness between sites, with all the same species being found as for the 2000 and 2022 surveys (Figure 1). There was generally higher sponge species richness in the eastern parts of the lough, particularly at Whirlpool Cliff.

Discussion

The deeper (>10 m) subtidal communities at LH changed substantially between 2010 and 2015, with a major decline in sponge populations (Micaroni *et al.*, 2021). Here we aimed to assess whether similar changes had occurred in the sponge assemblages inhabiting the undersides of boulders at LH. While we found differences in the sponge assemblages between the two sites that experience different environmental conditions and for different boulder sizes, there was no significant effect of time. We propose that the boulder sponge assemblages at LH have not been impacted in the same way as the sponges inhabiting the deep-water reefs. This difference may have resulted from the boulder sponges: (1) being more resilient to the impact that the deeper sponges experienced; (2) not having experienced the impact that affected the deeper water sponges; or (3) having recovered since the impact.

Temporal stability in sponge assemblages

Despite the increasing recognition of the importance of sponges in shallow water subtidal ecosystems in temperate regions (Bell *et al.*, 2020), and particularly in temperate mesophotic ecosystems (Bell *et al.*, 2022), we still have a very poor understanding of natural patterns of sponge variability. Furthermore, there are no temporal data available for sponges inhabiting the undersides of boulders to compare with the present study. Early reports from the Atlantic region suggested that sponges were generally slow growing and long-lived, with low recruitment rates (Fowler and Laffoley, 1993; Hiscock, 1994). However, these early studies did not consider entire sponge assemblages, but only selected species (which included some species found at LH).

More recent studies have described variation in entire temperate sponge assemblages, with some finding considerable temporal variability. However, these previous studies have generally had less than 10 years of data. For example, Bell *et al.* (2006) used a morphological approach to monitor changes in sponge assemblages over a 10-year period at Skomer Island in Wales. These authors found differences in the sponge morphological assemblages and abundance between years, but the sponge assemblages showed rapid recovery (within 1 year) to their original assemblage composition and abundance following declines. These changes were attributed to natural biological variation, rather than any anthropogenic impact as there was no correlation between any of the assemblage changes observed and environmental variables. More recently, Berman *et al.* (2013) examined seasonal and inter-annual changes at the sponge assemblage level, also at Skomer Island (using different sampling areas to Bell *et al.*, 2006), finding evidence for considerable seasonal and inter-annual variation in sponge assemblage composition and abundance. In contrast, Berman and Bell (2016) examined the temporal variation in sponge assemblages over a 2-year period in New Zealand and found significant seasonal differences in sponge abundance and assemblage composition, but no significant differences between the 2 years for any given season, suggesting the presence of cyclical seasonal variation, but low interannual variability.

Table 2. PERMANOVA main tests of log x + 1 transformed sponge abundance data for small (<150 cm^2), medium (151–400 cm^2), large (401–750 cm^2) and very large boulders (>750 cm^2) in 2000 and 2022

Source	Degrees of freedom	Sum of squares	Mean square	Pseudo-*F*	*P*	Unique permutations
Site (Si)	1	1861.7	1861.7	33.4	**0.001**	999
Year (Yr)	1	63.7	62.7	1.2	0.379	999
Boulder size (BS)	3	1944.4	648.2	11.6	**0.001**	999
Si × Yr	1	52.1	52.1	0.93	0.475	998
Si × BS	3	1258.5	419.5	7.5	**0.001**	998
Yr × BS	3	205.6	68.5	1.2	0.338	999
Residuals	3	167.2	55.7			
Total	15	5552.1				

Bray–Curtis similarity was used with 9999 permutations. Significant *P*-values are in bold.

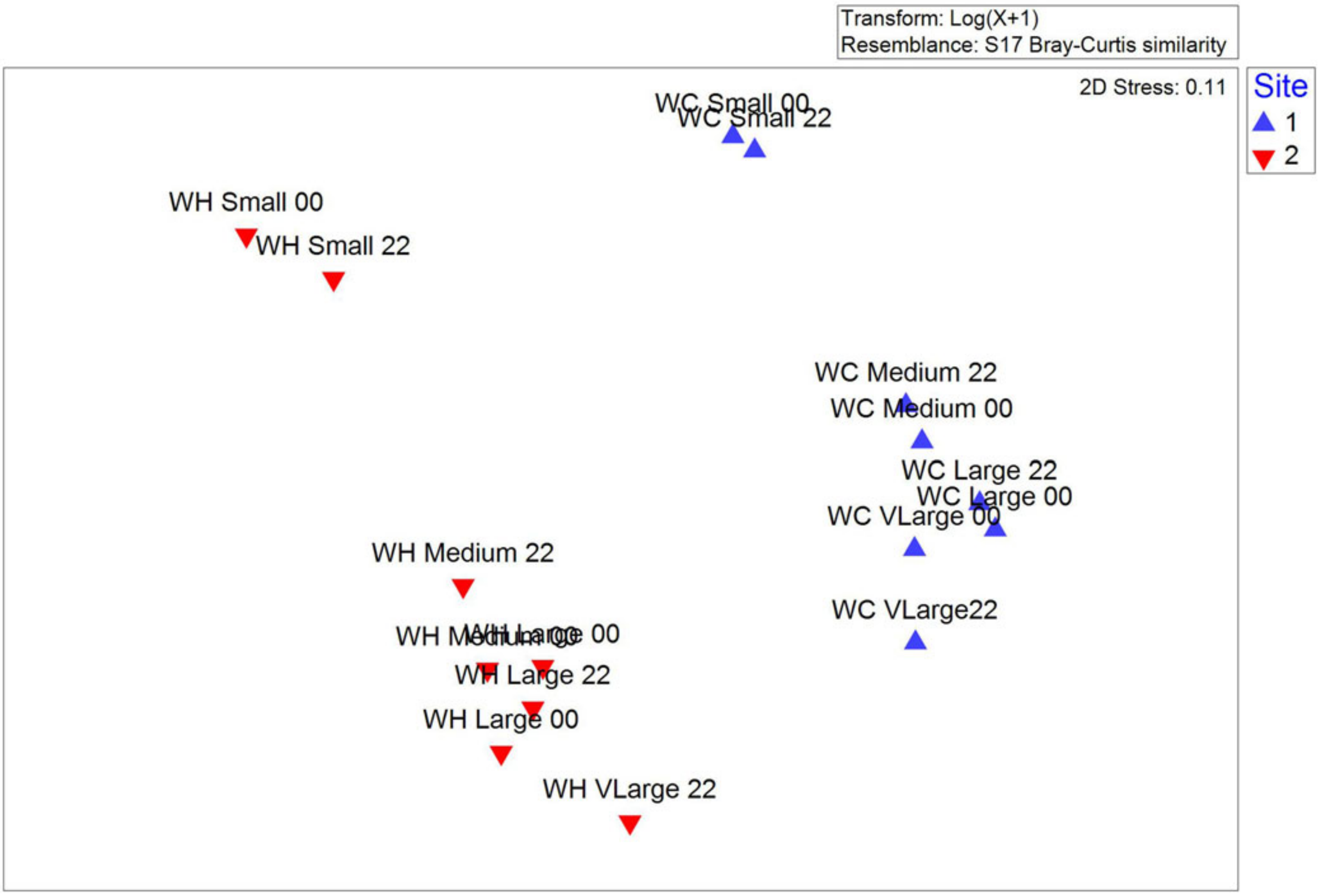

Figure 2. Non-metric multi-dimensional scaling (data log x + 1 transformed) to compare sponge assemblages found on small (Small, <150 cm^2), medium (Medium, 151–400 cm^2), large (Large, 401–750 cm^2) and very large boulders (VLarge, >750 cm^2) in both 2000 and 2022 at two sites, Whirlpool Cliff (WH, red downward-facing) and West Cliff (WC, blue upward-facing) at Lough Hyne Marine Nature Reserve, Ireland.

Combined, these studies suggest that while some sponge species are long-lived with low recruitment rates, others are highly dynamic.

To date, the longest monitoring of any cold-water temperate sponge assemblage has been described by Micaroni *et al.* (2021) from LH, which included quantitative and qualitative observations over a nearly 30-year period (noting the observations are discontinuous across this period). In contrast to the studies by Bell *et al.* (2006), Berman *et al.* (2013) and Berman and Bell (2016), these authors found evidence for very stable sponge assemblages prior to the large change that occurred at LH between 2010 and 2015. This difference likely relates to the nature of deeper LH subtidal communities, being more similar to mesophotic communities than typical shallow water assemblages, since mesophotic communities are generally thought to be stable over longer periods of time (decades), although limited data exist to support this (see Bell *et al.*, 2022 for review). However, despite this proposed stability described at LH, one of the sites where sponges declined between 2010 and 2015 has since shown rapid new recruitment of sponges (see Micaroni, 2022; Micaroni *et al.*, submitted), suggesting the potential for mesophotic communities to be highly dynamic when recovering from disturbance (noting some of deeper reefs in LH have shown no signs of recovery to date).

Unfortunately, all previous studies on temporal variation in cold-water temperate sponges have focused-on sponges that inhabit open reef areas, with very limited information generally being available for sponges inhabiting the undersides of boulders (but see Bell and Carballo, 2008). In fact, very few studies have generally considered sponges on the undersides of boulders. Our results suggest that in low-energy environments or predictable flow regimes, such as those found in LH, assemblages may be very stable over time. Importantly, in our study, we only considered two time points, with our second time point occurring at least 7 years after the estimated change that occurred in the deeper subtidal communities (Micaroni *et al.*, 2021). It is possible that the sponges inhabiting the boulders were also impacted by the same event or events that caused the decline in the deeper sponges, but they have since recovered. While we cannot completely exclude this possibility, we believe it unlikely given the very high similarity between the 2000 and 2022 sponge assemblages, and the very high overall abundance of sponges that we found. Furthermore, the deeper water sponge assemblages at West Cliff have not yet shown any sign of recovery as of 2023 (authors unpublished data).

Spatial variability and boulder size as a driver of sponge assemblage structure

We found a total of 43 sponge species on the undersides of the boulders at LH, which is substantially higher than Trowbridge *et al.* (2017a), although this is likely explained by the much larger number of boulders examined in our study. The variation in sponge assemblage structure between sites is perhaps unsurprising given the considerable differences in the environmental conditions at Whirlpool Cliff and West Cliff (Bell and Barnes, 2002; Figure 1) and is consistent with patterns for deeper subtidal communities (Bell and Barnes, 2000a, 2000b; Micaroni *et al.*, 2021).

However, the drivers of deeper water sponge assemblage structure at LH are thought to be the combined effects of sedimentation and flow rates (Bell and Barnes, 2000a), which are less likely to be an important driver for sponges living on the undersides of boulders. Sponge morphological adaptation is also thought to be an important factor in the differences in sponge assemblages at different sites in LH, with more upright forms in more sedimented areas, which can passively prevent sediment settling on sponge surfaces (Bell and Barnes, 2000b). However, sponges on the undersides of boulders are not going to experience sediment settlement because of the nature of the habitat. Therefore, other factors must drive the differences between Whirlpool Cliff and West Cliff. Whirlpool Cliff experiences much stronger water currents compared to West Cliff (Figure 1), which is likely to result in greater food availability and also greater scour during the incoming tide. The greater flow rate also has the potential for more frequent disturbance of boulders (Maughan and Barnes, 2000). One or a combination of these factors may explain the site differences.

It is also unsurprising that sponge assemblages vary with boulder size, given the area effect created by larger boulders and greater potential for smaller boulders to move (noting data were standardised to account for variation in the number of sponges on smaller compared to larger boulders). Earlier work at LH by Maughan and Barnes (2000) found that small boulders are likely to be moved more at Whirlpool Cliff. Disturbance is a well-known driver of biodiversity patterns (Dayton, 1971; Osman, 1977), and smaller boulders are generally more likely to be moved more than larger boulders. However, the specific sites where we sampled in LH are generally stable over time, since the boulders are overlying and subjected to consistent (or very low in the case of West Cliff) flow regimes, so all boulder sizes are likely to see little disturbance irrespective of boulder size. Therefore, species–area relationships most likely explain the differences between sponge assemblages and boulder size at both sites.

Resilience of under-boulder sponge assemblages and implications for the changes at Lough Hyne

Changes have been reported in several components of the shallow subtidal benthic assemblages at LH in recent years (Little *et al.*, 1992, 2018; Trowbridge *et al.*, 2013, 2018, 2019), and these have been attributed to eutrophication and oxygen depletion, especially during the night (Trowbridge *et al.*, 2017b; Plowman *et al.*, 2020). However, our results suggest sponges on the undersides of boulders have been resilient to these impacts. Recent studies from LH and New Zealand have suggested that sponges are able to tolerate extremely low oxygen levels for days and even weeks (Micaroni *et al.*, 2022), which explains why sponges may have been immune to the other impacts reported for communities on the top of boulders. The changes to the subtidal cliffs in the inner parts of LH are specifically restricted to LH, as open coast Atlantic communities had not changed, suggesting the decline in sponges is highly likely a LH phenomenon.

It is also possible that the very sheltered and protected conditions experienced by sponges on the underside of boulders may account for the different response compared to deeper reefs. For example, perhaps sponges on the undersides of boulders have been protected from the impacts of predation or extreme weather events. There is no strong support for this hypothesis at present, although the impacted deep reefs are also very low energy. Predation on sponges has not been explicitly studied in LH despite the potential from the large diversity of nudibranchs (personal communication, Dr Julia Nunn). However, of all the observations made by the authors of sponges over the last 25 + years, nudibranchs have rarely been seen on sponges.

An unusual breakdown of oxythermocline that forms seasonally at LH (Kitching *et al.*, 1976) has been proposed as a potential cause of the changes to the deepwater communities at LH, and the results of present study provide some support for this theory. However, since Micaroni *et al.* (2022) showed that many LH sponges are tolerant to low oxygen levels, oxygen-stress alone is unlikely to be the driver. The formation of anoxic water masses is also associated with the production of hydrogen sulphide because of anaerobic bacterial respiration (Schunck *et al.*, 2013). A rapid breakdown of the oxythermocline could have ‘bathed’ some of the cliffs in the vicinity in this low-oxygen, hydrogen sulphide-rich water, causing the widespread sponge mortality. In contrast, the sponges living on the underside of the boulders in the immediate shallows are less likely to have been impacted by such an event as a result of the greater water mixing, driven by wind and tidally driven currents in the shallows. This hypothesis is further supported by the lack of change reported for the deeper subtidal cliffs at Whirlpool Cliff (Micaroni *et al.*, 2021), which receives high water flow from the Atlantic coast twice every day. Whatever, the cause of the change in the deep-water communities in LH, this does not appear to have impacted the very shallow water sponges in the same way.

Conclusions

We found no evidence for changes in the sponge assemblages inhabiting the undersides of shallow water boulders, but did find differences between sites at all sampling times and for different boulder sizes. Our results suggest sponge assemblage composition changes very little for these underside boulder sponge assemblages at LH over the timeframes we considered. The present study has implications for the changes reported in the deeper water communities at LH and supports the implication of the oxythermocline in the deeper water changes to sponge assemblages. Future research should focus on the potential role that hydrogen sulphide may have played in causing the deeper water changes at LH.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424000493.

Data. The data are available from the authors on request.

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