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The ecology of sponges in Lough Hyne Marine Nature Reserve (south-west Ireland): past, present and future perspectives

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Lough Hyne was Europe's first Marine Nature Reserve and is a well known biodiversity hotspot that supports extensive sponge assemblages. The unusual, but predictable, flow and sedimentation regimes have important impacts on the sponge assemblages at the species and assemblage levels. Here I present a review of recent sponge research at Lough Hyne, which covers: (1) a description of the sponge-dominated habitats; (2) the biological and physical factors controlling sponge biodiversity and abundance; (3) sponge species and assemblage level morphological variability; and (4) the relationship between sponge morphological, species and functional diversity. It appears that physical factors are primarily responsible for the sponge diversity and abundance patterns found in Lough Hyne, although the importance of intra- and interphyletic (particularly with algae) competitive interactions requires further investigation. Although our knowledge of how sponges respond and adapt to environmental variability has increased substantially because of the research conducted at Lough Hyne, I have highlighted a number of future research areas in the context of Lough Hyne sponge assemblages, which are relevant to understanding structuring processes across the globe.

INTRODUCTION

Lough Hyne was Europe's first Marine Nature Reserve (established 1981) and is known globally as a biodiversity hotspot. Although there is some debate as to whether or not this recognition as a biodiversity hotspot is a function of the intensive sampling within Lough Hyne over the past 80 years (Bell & Shaw, 2002), it certainly supports a diverse range of habitats within a very small area (approximately 0.6 km^2); this probably accounts for the high faunal and floral diversity (e.g. Holmes & O'Connor, 1991; Rogers, 1991; Bell & Barnes, 2000a). Habitats within the reserve area include: submarine cliffs, experiencing a range of flow and sedimentation regimes; soft sediment basins; extensive boulder fields; sea grass beds; and a submarine cave. One of the common features of all these habitats (with the notable exception of the sea grass beds) is the presence of abundant and rich sponge assemblages (for species lists see Lilly et al., 1953; van Soest & Weinberg, 1980; van Soest et al., 1981; Picton, 1991; Bell & Barnes, 2000a). In fact, for a standardized sampling area, Lough Hyne has comparable species richness to many other tropical, polar and temperate sites from where comparable data are available (Table 1).

LOUGH HYNE MARINE NATURE RESERVE

Formation and hydrology

Lough Hyne is a fully marine sea lough located on the south-west coast of county Cork, Ireland (51°30'N 9°18'W). The lough is roughly rectangular, being approximately 1 km long and 0.5 km wide, which is thought to have formed by glacial erosion during previous ice ages (Holland, 1991). This small isolated sea lough is thought to have undergone a marine transgression from a freshwater basin approximately 4000 years ago (Holland, 1991). The lough is divided into

Table 1. *Global values for sponge species richness. All values shown are taken from a depth of 12–18 m over similar sized sampling areas on hard substrata (updated from Bell & Barnes, 2000a). Please note that although other sponge richness figures are available within the literature they are not directly comparable due to large differences in sampling effort or habitat type.*

Location	Species richness	Source
Hoga Island (Indonesia)	100	Bell & Smith (2004)
New South Wales (Australia)	82	Roberts et al. (2006a)
Cuba (Havana)	80	Alcolado (1990)
Ireland (Lough Hyne)	77	Bell & Barnes (2000a)
Mozambique (Quirimba)	73	Bell & Barnes (2000a)
Skomer Island (Wales, UK)	57	Bell et al. (2006)
Southern Florida (USA)	43	Schmahl (1990)
Kenya	25	Barnes & Bell (2002)
Red Sea (Sharm el Sheik)	21	Bell (unpublished data)
Antarctica (Signy)	19	Bell & Barnes (2000a)
Panama (San Blas)	17	Bell & Barnes (2000a)
Ireland (Cork)	13	Bell & Barnes (2000a)
Britain (Sussex)	12	Bell & Barnes (2000a)
Cape Verde (Sal)	9	Bell & Barnes (2000a)
Britain (Cornwall)	6	Bell & Barnes (2000a)
Venezuela	15	Diaz et al. (1990)

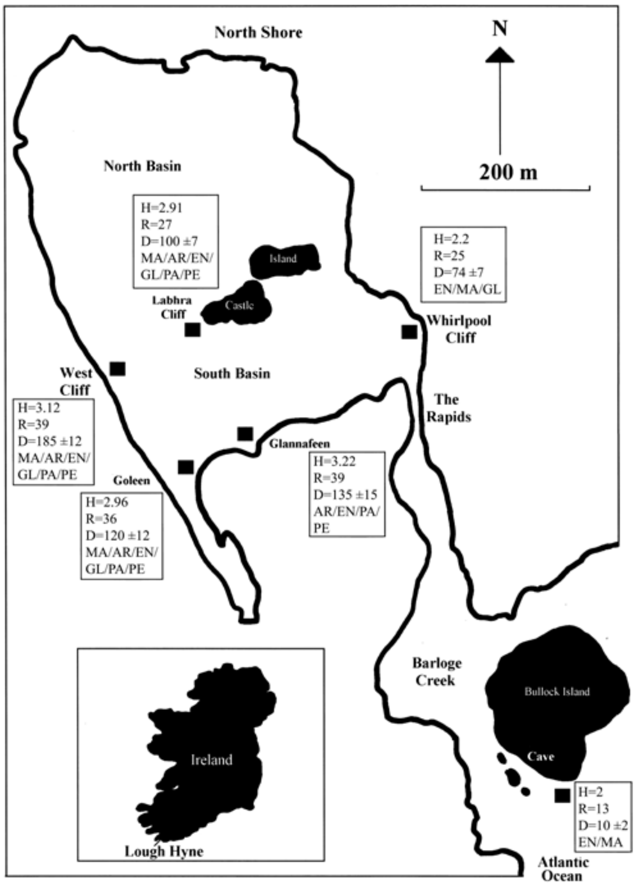

Figure 1. Lough Hyne Marine Nature Reserve. (H) Diversity (Shannon); (R) species richness (total number of species); and (D) density (sponges m^{-2}). Morphology definitions: EN, encrusting; MA, massive; AR, arborescent; PE, pedunculate; PA, papillate; and GL, globulose. All figures at each site are from 18 m.

the north and south basins, separated by Castle Island, with the water depth exceeding more than 50 m in the western trough (Figure 1). Although the lough is more than 50 m deep, its connection with the open Atlantic coast is much shallower, which combined with the unusual topography of this connecting channel creates an unusual flow regime, which strongly impacts the marine fauna inside Lough Hyne. The lough is sheltered from all sides and wave heights rarely exceed 1 m even during the strongest winter storms. There is very little freshwater input into Lough Hyne, with the exception of two small streams; one in the south-west corner, the other in the north-west corner.

The narrow channel connecting Lough Hyne to the open Atlantic Ocean, known as the Rapids, is approximately 25 m wide and only 3 m deep at high tide. This contrasts with the depth inside the lough, and has a strong influence on Lough Hyne's tidally generated flow regime. The Rapids is approximately 100 m long and has a raised sill that runs perpendicular to the shore and across the channel. This restricts water flow into and out of the lough, such that the incoming tide must reach the level of the sill before it can flow in, resulting in delayed tides compared with the Atlantic coast. Inflow of water into Lough Hyne lasts approximately four hours, while outflow lasts eight hours (over a normal semi-diurnal tidal cycle). Not only do these delayed tides have important implications for current and sedimentation regimes inside the lough, but they also result in a reduced tidal range (only 1–1.5 m), compared with the open Atlantic coast (3–4 m).

The restricted water flow into Lough Hyne has important implications for the flow regime inside the lough. Once the incoming tide reaches the top of the sill it flows into the lough very quickly with current speeds reaching in excess of 300 cm s^{-1} (Bell & Barnes, 2002a). However, because the Rapids is shallow, compared to the depth of the lough, water speeds decrease rapidly both with depth and moving from east to west. This reduction in flow rate is so rapid that current speeds have not been recorded (detectable limit using a Valeport flowmeter <3.9 cm s^{-1}) in the northern parts of the lough during inflow. Bell & Barnes (2002a) reported a large difference between the flow rates at spring and neap tides and organisms living on the western side of the lough may only experience significant water movement during spring tides. During the outflow of water (lasting 8 h), current flow has only been detected in the Rapids itself, since water is skimmed from the shallow waters at the top of the Rapids. At the sites where current flow is found, it decreases rapidly with increasing depth. For example, at Whirlpool Cliff (see Figure 1 for locations), current speeds decrease from 250 cm s^{-1} at 6 m to 150 cm s^{-1} at 18 m, while at Glannafeen current speed decreases from 60 to 20 cm s^{-1} between 6 and 18 m (at spring tides). The inflowing water is directed towards Whirlpool Cliff, and then onto Glannafeen and towards Goleen, where it is then deflected northward between Castle Island and West Cliff. Goleen and West Cliff do experience some water current flow during inflow, but only for approximately 10 min during peak spring tide inflow; current speeds reach approximately 20 cm s^{-1} at Goleen and 15 cm s^{-1} at West Cliff (at 6 m). No detectable current flow has been reported (<3.9 cm s^{-1} was the lowest rate detectable using the flow meter) at Labhra Cliff or in the North Basin.

Sedimentation

It is important to distinguish between sediment accumulation and sediment settlement, as the way they affect benthic organisms, including sponges, may be different. The variation in current flow rates across Lough Hyne creates a sedimentation gradient from east to west, as current speeds decrease; there is also an increase in gross sedimentation rates with depth. Submarine cliff surfaces on the eastern side of the lough are devoid of sediment (e.g. Whirlpool Cliff), while areas only 500 m away are covered in a thick layer of sediment (e.g. West Cliff). Although Whirlpool Cliff has no sediment accumulation on cliff surfaces, the short-term deployment of sediment traps (J.J. Bell, unpublished data) does indicate that sediment settles on the benthos during outflow, when there is no current, however, this is quickly washed away when inflow begins and hence there is no net sediment accumulation. As water flow rates decrease across the lough, sediment begins to settle from suspension. Interestingly, Bell & Barnes (2002a) found the highest sedimentation rates (for any given depth) at the site experiencing moderate levels of current flow (Glannafeen), while the lowest sedimentation rates (with the exception of

Whirlpool Cliff) are found in the areas considered to have the lowest current movement (North Basin). This can be explained by the largest sediment particles settling from suspension first (current flow must reach some critical, currently undetermined, level), with only the finer particles (mainly silt) being carried to the western and northern parts of the lough. It seems unlikely that any major sediment re-suspension occurs inside Lough Hyne (because of its depth and sheltered nature), and it probably acts as a sediment sink. Sedimentation rates also vary seasonally, with considerably higher sediment settlement during the winter months (November to February), compared with the summer months, although the organic content of the sediment is higher during the spring and summer (Bell & Barnes, 2002a). Unfortunately, there is no detailed quantitative information on the sediment types and sizes at the different sites, although the proportion of silt collected in traps increases substantially from east to west across the lough and with increasing depth.

Seasonal stratification

Like many semi-enclosed water basins, Lough Hyne experiences seasonal stratification, and a thermocline forms between 20 and 30 m during summer months, with a cold, virtually anoxic layer (oxygen content of the deeper layer is <5% of the surface layer) lying below the warmer surface waters (Kitching et al., 1976). Although this thermocline was thought to be a reasonably static feature of the lough in the past (Bell & Barnes, 2002a), recent work by Johnson (2006) has shown that this thermocline moves up and down with the spring–neap tidal cycle. The influence of this thermocline is dramatic, and although earlier observations (Kitching et al., 1976) suggested that the thermocline kills all the organisms below 25 m in the western trough during summer months, some sponges (including *Paratimea constellata* and *Eurypon* spp.) have been reported on the cliffs at 35 m (see below) all year round.

LOUGH HYNE SPONGE ASSEMBLAGES

Sponges are associated with three major habitats in Lough Hyne MNR: submarine cliffs; subtidal boulders; and the submarine cave. There are also some free-living sponges associated with the soft sediment habitats including *Suberites* sp. and *Hymeniacidon perlevis* (Montagu, 1818), which also occur attached to scallop shells (Bell & Barnes, 2002b).

Submarine cliffs

The highest sponge diversity is associated with the five submarine cliff sites (Figure 1); Whirlpool Cliff, Glannafeen, Goleen, West Cliff and Labhra Cliff. Whirlpool Cliff (Figure 1) is characterized by fast flowing water conditions (>250 cm s^{-1}), with very little sediment accumulation. The diversity and richness of sponges at Whirlpool Cliff is the lowest of the five main submarine cliff sites inside the lough, although the diversity (but not abundance) of sponges does increase with depth (Bell & Barnes, 2000a). The shallow waters of this site are dominated by algae including *Laminaria digitata* L. and a rich turf layer. This site is characterized by high cover of *Cliona celata* Grant, 1826, which exhibits different gross morphologies, compared with other areas outside, and inside the lough (Bell et al., 2002). The cliff extends to approximately 18 m where current speeds decrease to approximately 150 cm s^{-1}. The common sponge species at 18 m include *Cliona celata*, *Iophon ingalli* (Bowerbank, 1866) = *I. hyndmani* (Bowerbank, 1858), *Axinella dissimilis* (Bowerbank, 1866) and *Dysidea fragilis* (Montagu, 1818) (Bell & Barnes, 2000b,c). The fast flowing conditions and clear water at Whirlpool Cliff support rich benthic communities, including anthozoans, hydroids, bryozoans, and turf algae (Picton, 1991), which are usually absent, or restricted to vertical or overhanging surfaces at the lower-energy sites.

Despite Glannafeen only being approximately 250 m from Whirlpool Cliff, the site is very different. The slower water currents (<50 cm s^{-1}, although only detectable for 2.5 h of inflow) result in the settlement of large sediment particles from suspension, with this site experiencing the highest sediment settlement rates (for any given depth) within Lough Hyne (although accumulation rates are higher in western and northern parts of the lough). This cliff is composed of a single steeply inclined rock platform with a boulder scree environment to its north side. This site has the highest sponge diversity in Lough Hyne (Bell & Barnes, 2000a). *Polymastia* spp. are particularly important, in terms of both numerical abundance and species richness (Picton, 1991). Branched sponge species are also abundant at Glannafeen including *Raspailia ramosa* (Montagu, 1818), *Stelligera stuposa* (Ellis & Solander, 1786), *S. rigida* (Montagu, 1818) and *Axinella dissimilis*, as they are well suited to this sedimented environment (Bell & Barnes, 2002d). The pedunculate shaped sponge *Suberites carnosus* (Johnston, 1842) is also abundant at Glannafeen.

Goleen and West Cliff are very similar sites, experiencing very low current flow rates, which have only been detected during peak inflow. Although sediment settlement rates are not as high as found at Glannafeen (for any given depth), sediment accumulation is much higher (Bell & Turner, 2000). Labhra Cliff is also similar to Goleen and West Cliff in terms of sediment accumulation rates, although no water currents have been detected at Labhra Cliff. These four cliffs extend to different depths: Goleen extends to 21 m; West Cliff extends to 24 m; and Labhra Cliff extends to more than 40 m. Of these three sites, only Labhra Cliff (below 25 m) is influenced by the seasonal thermocline. The cliffs at these three sites are composed of vertical, horizontal, inclined and overhanging surfaces (but predominantly vertical and overhanging surfaces). The high sediment loading in the water at these sites limits algal development, and shallow (<6 m) cliff surfaces are covered in calcareous algae (*Lithothamnion* sp.), while macroalgae are rare. These algal populations decline quickly below 6 m, where the community is dominated by sponges. Encrusting species, including *Paratimea constellata* (Topsent, 1893), *Hymeraphia stellifera* (Bowerbank, 1866) and *Halicnemia patera* Bowerbank, 1862 are common at these sites, as are *Polymastia* spp. However, the most abundant encrusting group are the *Eurypon* spp. This genus is more typical of deep-water communities, but there are at least eight species of this genus recognized to date inside Lough Hyne, and according to Bernard Picton (Ulster Museum, Belfast) several of these appear to be undescribed from other habitats. The deeper water is several degrees lower than the surface water during the formation of the seasonal thermocline (Bassinadale et al., 1957; Johnson, 2006). Very few organisms are found below the thermocline, with the exception of *Paratimea constellata* and *Eurypon* spp. It is unclear how these species survive this summer stress and it is possible that they form some type of resistant stage (see Gaino et al., 1996).

Bullock Island (Figure 1) and the area on the coast immediately outside Lough Hyne have frequently been used as a comparative site, as the area is typical of exposed Atlantic Ocean communities in southern Ireland. The subtidal habitats along this coastline experience high levels of wave exposure, particularly during the winter months. The infralittoral zone extends deeper than inside Lough Hyne and the sponge diversity and abundance is much lower (Bell & Barnes, 2000a). Conspicuous members of the sponge assemblage at Bullock Island include *Cliona celata*, *Hemimycale columella* (Bowerbank, 1874) (which is rare inside Lough Hyne) and *Tethya* sp.

Boulder habitats

In most areas where sublittoral cliffs are found, boulder habitats are also present. Despite the differences in environmental characteristics between different parts of the lough, surprisingly similar sponge assemblages have been found on the undersides of shallow boulders (<1 m), irrespective of location. For example, approximately 90% of sponge species are shared between boulder habitats (at depth of 1 m) at Whirlpool Cliff (fast flow), West Cliff (very slow flow) and in the North Basin (very little or no flow) (Bell & Shaw, 2002). The sponge fauna inhabiting boulders differs considerably to that found on cliffs (Bell & Barnes, 2003a). Sponge boulder assemblages are dominated by encrusting and low profile species including *Haliclona* spp., *Aplysilla rosea* (Barrois, 1876), *A. sulfurea* Schulze, 1878, *Chelonaplysilla noevus* (Carter, 1876), *Leucosolenia complicata* (Montagu, 1818) and *Plakortis simplex* Schulze, 1880. Most of the sponges found growing on boulders are restricted to their undersides, and sponge diversity is generally very low on the uppersides of boulders (particularly in shallow waters). Above 3 m, only *Hymeniacidon perlevis*, *Haliclona* sp. and *Halichondria bowerbanki* Burton, 1930 have been found on the upper surfaces of boulders.

Bullock Island cave

The final habitat where sponges dominate is the cave at Bullock Island. Although this cave is not within Lough Hyne itself, it does occur within the reserve boundary and is an important sponge-dominated environment. The cave measures 97 m in length, and 68 m of the cave floor remains covered at low water spring tide. Earlier studies of this cave by Norton et al. (1971) only reported two species of sponge, *Clathrina coriacea* (Montagu, 1818) and *Pachymatisma johnstonia* (Bowerbank, 1842), but Bell (2002a, 2003) reported considerably higher sponge species richness (>30 species). The most common species in this cave are *Pseudosuberites sulphureus* (Bean, 1866), *Oscarella lobularis* (Schmidt, 1862), *C. coriacea*, *Aplysilla sulfurea*, *P. johnstonia* and *Aplysilla rosacea* (Bell, 2003). Sponge diversity and richness increase from 0 to 10 m horizontal distance from the entrance of the cave, but then decrease with further increasing horizontal distance.

PHYSICAL FACTORS INFLUENCING SPONGE BIODIVERSITY AND ABUNDANCE

Sedimentation, current flow and surface inclination

Research since 2000 has identified sedimentation, flow rate/regime and substratum angle to be the primary physical factors that influence sponge assemblages on the submarine cliffs at Lough Hyne, although these three factors are not independent of each other (Bell, 2001). Water flow regime has a direct influence on sediment settlement rates and accumulation, as does water depth (Bell & Barnes, 2002a), while the nature of the substrate (particularly orientation) also determines how these factors influence sponges.

One of the most interesting aspects of sponge ecology at Lough Hyne is that sponge biodiversity and abundance is greatest in the areas experiencing the highest sediment settlement rates (Bell & Barnes, 2000a), and is contrary to the still widely held belief (e.g. Preciado & Maldonado, 2005) that sedimentation and silt are detrimental to sponges (Gerrodette & Flechsig, 1979). Bell et al. (2006) also reported rich sponge assemblages in sediment rich habitats at Skomer Island (Wales, UK), while Bell & Smith (2004) found rich sponge assemblages in sedimented habitats in Indonesia (although not as high as non-sedimented areas). The generalized conception that sedimentation has negative impacts on sponge assemblages may be incorrect, with specially adapted sponge fauna being found in sedimented habitats (e.g. Bell, 2004). However, Bell (2002b) did find that regeneration rates of *Cliona celata* were reduced in sedimented environments compared with Whirlpool Cliff, which suggests that sedimented habitats may be more difficult for sponge survival compared to high flow areas.

One important aspect that should be emphasized when sampling sponge fauna (particularly with photographic methods) is that sediment must be fully removed in order that encrusting and low profile forms are not missed (Bell et al., 2006). For example, at the most sedimented sites in Lough Hyne over 50% of the sponges are encrusting or low profile forms that live beneath a layer of sediment (Bell & Barnes, 2000d), and are only visible once the sediment is removed. It remains unclear whether living beneath sediment offers any adaptive advantage to sponges, such as protection from predators or UV exposure, or the potential to exploit microbial communities as a food source from the sediment, but whatever the mechanism or advantage gained, sponges seem to be able to thrive in sedimented environments.

Whirlpool Cliff supports the lowest sponge abundance and diversity in Lough Hyne, which can potentially be explained by a number of complex interacting factors. The overall community diversity at Whirlpool Cliff is high and competition for space with algae and other organisms (e.g. cnidarians and ascidians) is likely to be intense (see below for a discussion of the potential for algae to limit the distribution and abundance of sponges), since conditions are considered to be suitable for a range of suspension feeding organisms (Hiscock, 1983). However, the most likely reason for the overall lower diversity and reduced sponge abundance at this site is the strong tidally generated flow rate. Although this hypothesis remains untested experimentally, the proposed environmental restriction of many sponge species (e.g. arborescent forms are rare) is supported by the low morphological diversity at Whirlpool Cliff, and high proportions of robust encrusting and massive forms (Bell & Barnes, 2000d).

Small-scale habitat differences can have important influences on marine assemblages and communities (Lilley et al., 1953; Sousa, 1979; Bell & Barnes, 2000b,c; Knott et al., 2004; Preciado & Maldonado, 2005). Organisms living on substrata with different inclinations will experience different light, flow, UV and sedimentation regimes, which in turn will influence the environmental characteristics and the potential suite of sponge competitors. For example, organisms inhabiting overhanging cliff surfaces will experience lower light and sedimentation levels, compared with horizontal surfaces. On the cliffs in Lough Hyne there are marked differences in sponge assemblages inhabiting vertical and inclined cliff surfaces (Bell & Barnes, 2000a,b,c,d). Contrastingly, at wave exposed sites on the open Atlantic coast, little difference is found between surface angles and depth, as wave action appears to be the most important factor controlling sponge biodiversity and abundance (Bell & Barnes, 2000a). Higher sponge diversity and abundance has been reported on vertical, compared with inclined surfaces at Glannafeen, Goleen and Whirlpool Cliff, but not at Labhra and West Cliffs, where diversity is similar irrespective of substratum angle. There are several possible explanations for these differences, which are likely to depend on local-scale environmental characteristics. At Glannafeen and Goleen differences between surface types probably relate to the rates of sediment settlement on the different surface types, particularly at Glannafeen since it has the highest sedimentation rates (for any given depth). Increased sediment has been shown to reduce sponge water pumping rates, which is likely to be detrimental to the animal (Gerrodette & Flechsig, 1979), however, this single-species study may not be representative of the phyla. Other direct and indirect effects of sediment on sponges are poorly described, but sediment may influence feeding, oxygen acquisition, waste removal, and larval settlement potential (Hiscock, 1983). Furthermore, and perhaps most importantly, sediment has the potential to clog the inhalant pores and channels of sponges.

No significant differences in species diversity were found between vertical and inclined surfaces at Labhra or West Cliff. The reason for this is unclear, but may relate to differences in the type, rather than amount, of sediment falling on cliff surfaces at different sites. Labhra and West Cliffs are further along the sedimentation gradient than Glannafeen and Goleen, meaning larger particles will have already fallen from suspension by the time inflowing water reaches West and Labhra Cliffs. Smaller more cohesive particles may be falling out of suspension at West Cliff and Labhra Cliff, and settling on vertical, as well as inclined surfaces making sedimentation accumulation rates similar (or just very high) on both surface types. However, this hypothesis remains untested, but is supported by both surface types at these two sites being covered in a thick layer (5–10 mm) of fine silt.

Physical factors also influence sponge boulder assemblages. Although sponge assemblage composition differs very little between boulder sites within Lough Hyne, the total abundance of sponges varies considerably. Higher numbers of sponges (per unit surface area) have been found on the undersides of boulders at West Cliff than at either Whirlpool Cliff or in the North Basin (Bell, 2001). This reduced abundance at Whirlpool Cliff is probably due to increased competition with members of other phyla, as the overall community diversity is much higher, particularly cnidarians, which are one of the few groups that are not overgrown by sponges (Bell & Barnes, 2003b). However, reduced sponge abundance at North Basin sites probably results from reduced water currents making conditions less suitable for sponges (Bell, 2001).

Light and salinity

The direct effects of light and salinity on sponges have not been considered within Lough Hyne. There are only small inputs of freshwater into the lough from the small streams in the north-west and south-west corners, while the local freshwater catchment is small. Therefore the effect of freshwater on sponges is probably very minor, since it is unlikely to reach the major sponge habitats. The direct impact of light on sponges is difficult to assess, since it is related to other physical factors, particularly the amount of suspended material in the water column. Indirect effects (e.g. on algal as potential sponge competitors—see below) of light may be more important, than direct light exposure. In the past sponges have been considered more characteristic of shaded (e.g. vertical and overhanging surfaces) than un-shaded habitats, which has been explained by competitive exclusions, particularly by algae (Witman & Sebens, 1990; Bell & Barnes, 2000a), but also by silt and UV radiation avoidance (i.e. unrelated to algal abundance) (Preciado & Maldonado, 2005). However, the high diversity of sponges at highly sedimented sites (even on inclined surfaces) (Bell & Barnes, 2000a), the range of potential UV-B protector compounds that have been reported from sponges (e.g. Mackarchenko & Utkina, 2006), and the recent work of Preciado & Maldonado (2005) does not support any of these explanations for sponges being restricted to shaded habitats in the presence of macroalgae. In fact, there are still very few experimental investigations (but see Roberts et al., 2006b) examining the effects of light (particularly UV) and silt on sponges, particularly at the assemblage level.

There is further evidence that light influences some sponge species directly. There are two sponges known to contain high quantities of photo-symbionts within Lough Hyne, *Haliclona* sp. and *Halichondria panicea*, although it seems likely that many other cyanobacterial–sponge relationships occur. There is some evidence for the dependence of these two species on their photosynthetic symbionts since both are mainly restricted to shallow subtidal environments in Lough Hyne (Bell & Barnes, 2000c,d) and decrease in abundance with depth.

Physical processes in the sea cave

The sponge zonation patterns at the Bullock Island sea cave have been explained with respect to a complex of biotic (competition) and abiotic factors (e.g. flow rate, light, humidity and disturbance). Although horizontal zonation patterns into the cave have been considered analogous to vertical distribution patterns for algae (Norton et al., 1971), this is not the case for sponge assemblages (Bell, 2002a, 2003). This could be viewed as further evidence that negative associations between algae and sponges are not the result of algal–sponge competition (Preciado & Maldonado, 2005; Wulff, 2006a). The community composition in this cave is very different to the cliffs outside (and inside Lough Hyne), which may mean the cave fauna is specially adapted to this habitat type, but cannot colonize the entrance of the cave because of the presence of algae. Sponge diversity increases between 0 to 10 m horizontal distance into the cave. Beyond 10 m horizontal distance, sponge species diversity begins to decrease, although the maximum sponge abundance is found approximately 30 m from the entrance of the cave, which is much further than the algae extends. This increase coincides with the presence of extensive intertidal sponge assemblages, so is probably a result of increased habitat suitability (e.g. particularly higher humidity and possibly reduced UV radiation), rather than reduced competition with algae. The increased sponge abundance, correlated with decreasing algal abundance with increasing distance into the cave is consistent with studies of sponge fauna from elsewhere (e.g. Sarà, 1958, 1961a,b; Corriero et al., 2000) and demonstrates the consistency of these relationships at large geographical scales. Vertical zonation patterns are also found on the cave walls, with decreases in sponge richness and abundance when approaching the cave floor, which was also reported by Sarà (1962b). Such decreases have been attributed to the disturbance associated with the cobble substrate, which probably mechanically damages sponges and prevents settlement as water surges through the cave (Bell, 2002a). Resolving which physical factors are primarily responsible for the underlying structure of sponges in this cave will be difficult, but should be a focus of future research.

The effect of disturbance on sponge assemblages

The intermediate disturbance hypothesis (IDH—Connell, 1978; Sousa, 1979) predicts reduced diversity at high and low levels of disturbance, due to the complex interaction of biological and physical processes. The effect of several disturbance gradients on sponge assemblages have been investigated at Lough Hyne, particularly on boulders. Since both boulder size (Sousa, 1979; Maughan & Barnes, 2000a) and sampling site (e.g. Whirlpool Cliff compared with West Cliff) represent different potential surrogates of disturbance we would expect the lowest diversity of sponges to occur on large boulders at the least disturbed site, and small boulders at the most disturbed site. However, there is relatively little difference in sponge diversity between boulders at Whirlpool Cliff, North Basin and West Cliff. Furthermore, decreases in richness are not reported at higher boulder sizes (Bell, 2001), with sponge assemblages following typical species–area relationships (Connor & McCoy, 1979; McGuinness, 1987, 1994), rather than supporting the IDH. There are several interrelated reasons that may explain these results. Most importantly, boulder size may not necessarily represent different surrogates of disturbance as suggested by Sousa (1979), where smaller boulders are more likely to be moved than larger boulders. In fact, in the majority of boulder fields, boulders are overlying, where smaller boulders are held in place by larger ones, which means the probability of a small boulder moving is dependent on that of larger boulders. Therefore, in the majority of circumstances boulder size may not be a good surrogate of disturbance. Furthermore, although current flow is fast at Whirlpool Cliff, it is predictable and the boulder matrix is stable, hence disturbance levels at the Whirlpool Cliff boulder field are similar to those in other areas of the lough (although scour may be greater). Therefore boulder size (and the area available), rather than disturbance is the primary factor controlling sponge diversity on the undersides of boulders.

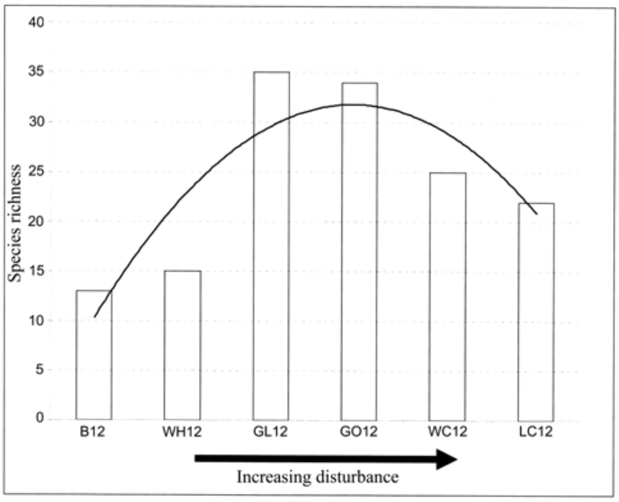

Figure 2. The relationship between increasing disturbance (water flow regime) and total species richness reported from vertical surfaces on submarine cliffs at 12 m at sites inside Lough Hyne (sampling area=2.5 m^2 at each site). B, Bullock Island; WH, Whirlpool Cliff; GL, Glannafeen; GO, Goleen; WC, West Cliff; and LC, Labhra Cliff. Polynomial second order trend line has been fitted (in Excel), R-squared=0.74.

Although boulder habitats do not conform to the IDH, there is evidence that the highest diversity does occur at moderate levels of disturbance on the submarine cliffs, although this does depend on the type of disturbance considered. Figure 2 shows the relationship between species richness and water flow rate at 12 m on vertical cliff surfaces (data adapted from Bell & Barnes, 2000a). Similar relationships (graphs not shown) are also found at 6 and 18 m, and on inclined surfaces. The highest sponge species richness occurs at moderate levels of disturbance (Glannafeen), with reduced diversity at the sites experiencing the highest (Bullock Island) and lowest (Labhra Cliff) disturbance. However, this relationship only exists when water flow regime is considered as the disturbance measure, and even though sedimentation can also be considered as a form of disturbance, this does not correlate with the diversity levels that would be predicted under the IDH, as the highest sponge richness occurs at the most sedimented site.

Sponge diversity appears to be effected by different measures of disturbance in different ways, which supports the hypothesis that a combination of sedimentation and current flow are important in determining sponge diversity in Lough Hyne, rather than any single factor.

BIOLOGICAL FACTORS INFLUENCING SPONGE BIODIVERSITY AND ABUNDANCE

Competition

Although physical factors are thought to be primarily responsible for the distribution and abundance of sponges within Lough Hyne, inter- and intra-phyletic competitive interactions certainly occur between sponges, particularly for space. Given that sponge abundance is so high in boulder areas and cliff habitats (Bell & Barnes, 2000a), sponges frequently come into contact with each other. Understanding and quantifying competitive interactions between sponges is difficult since interactions are complex (for review see Wulff, 2006a). Past research on sponge spatial competition at Lough Hyne has focused on instantaneous observations (Bell & Barnes, 2003b), particularly focusing on boulder assemblages. Although time-series observations have been considered most appropriate for examining competitive interactions between sponges, instantaneous observations have been widely used across several phyla (e.g. bryozoans and ascidians) to investigate assemblage level structuring, rather than for sub-sets of species or single species interactions. The main problem with instantaneous observations is the potential for incorrectly reporting tied competitive outcomes (Quin, 1982; Russ, 1982). These are interactions where the edges of two sponges are growing next to each other, without one overgrowing the other, which may not necessarily mean neither sponge is winning the interaction. The outcome of such interactions may only be fully realized through temporal sampling; in fact these may not even be competitive interactions as sponge relationships may also be mutalistic (Wulff, 1997). With respect to competitive interactions, it may be important to distinguish between overgrowth interactions (where one species physically overgrows another) and those where space is acquired by one species from another by bulldozing or chemical warfare, since these are different types of interactions. The latter can be considered direct competition for space, at the expense of the losing species, while the former results in the winner having great access to food resources at the expense of the loser, but both essentially share the primary space (and the loser persists). The significance of these different interactions remains unknown and may be mediated through seasonal regression and growth of tissues in space-limited habitats, allowing species co-existence.

Instantaneous observations have been made of the competitive interactions between sponges on the undersides of boulders at Whirlpool Cliff and West Cliff, and in this case the assumption was made that interactions where the edges of two sponges met, but neither species overgrew the other, were considered stand-off interactions (neither species is winning) (Bell & Barnes, 2003b). This assumption is supported by the high levels of sponge diversity found on boulders (Bell & Barnes, 2003a), particularly in areas which experience very low levels of disturbance. The IDH requires that communities or assemblages are hierarchically structured (i.e. species A overgrows species B, species B overgrows species C etc.), such that in the absence of disturbance the top competitor will eventually dominate the community and diversity will be reduced (Russ, 1982). In such systems, the top competitor is prevented from dominating the community by some form of disturbance (thereby maintaining the poorer competitors). However, high diversity and species co-existence can also be maintained in the absence of disturbance through the persistence of so called 'network' structuring (Russ, 1982; Quin, 1982), through tied interactions, backloops and indeterminate competitor pairings. Since I consider that all boulders experience relatively similar, low levels of disturbance in Lough Hyne (see above), with sponge biodiversity being controlled by typical species–area relationships, rather than the intermediate disturbance hypothesis (see above), sponges are not thought to be structured hierarchically, and the high diversity must be maintained by a high degree of tied interactions.

Bell & Barnes (2003b) found a high degree of tied interactions (>70%) between sponges on boulders, with few sponges being found to overgrow the tissues of other sponges. The most superior competitor varied somewhat depending on the ranking method used. When species were ranked based on the total interactions they won, as a proportion of the total interactions they were involved in, the top five spatial competitors were *Leucosolenia complicata*, *Haliclona fistulosa* (Bowerbank, 1866), *Plakortis simplex*, *Haliclona rosea* (Bowerbank, 1866) and *Haliclona simulans* (Johnston, 1842). Despite sponge–boulder assemblages being dominated by thin encrusting sponges, the top competitors had non-encrusting morphologies. *Plakortis simplex* was the exception, although it is encrusting it has a different morphology to typical encrusting species, as it is very loosely attached to the substratum, which may give it greater ability to more easily overgrow other species.

Sponge abundance on the subtidal cliffs at Lough Hyne varies with site (Bell & Barnes, 2000a), and there is little available bare space at any of the sites due to changes in overall community composition; there is approximately 20–30% bare space at most of the subtidal cliff sites in Lough Hyne. The high abundance of sponges, particularly at the low energy sites means that sponge–sponge interactions are common, and linearly correlated with sponge abundance (J.J. Bell, unpublished data). In fact the number of interactions can exceed 50 per m^2. Recent studies of the competitive interactions of the subtidal sponges at Labhra and West Cliffs have found very high levels of stand-off interactions (>90%), with observations made over a 1-y period showing no significant changes in the patch size (corresponding to a decrease in another species) of the ten most common species (J.J. Bell, unpublished data). This further supports our assumption that interactions (at least in temperate regions), where the edge of one sponge comes into contact with another, are most commonly tied-interactions in Lough Hyne, where neither species win, and is also consistent with Ayling (1983), who found little change in the area occupied by encrusting temperate sponges over a 9-month period. It is also noteworthy that few potential examples of mutualisms were observed for the boulder or subtidal sponge species (Rützler, 1970; Sarà, 1970; Wulff, 1997), since there were no particularly common species–pair interactions.

Inter-phyletic interactions between sponges are common on boulders and competitive interactions have been recorded between molluscs, serpulid worms, barnacles, bryozoans and ascidians (colonial and solitary) (Bell & Barnes, 2003b). In most cases all sponges overgrew serpulids, barnacles and bryozoans, resulting in their death, although in some cases barnacles were found surrounded by sponge, with only the opercular plates or feeding cirri being visible. Interactions with cnidarians (including anemones, solitary corals and soft corals) mostly resulted in tied interactions, while colonial ascidians were commonly reported to overgrow sponges. The inter-phyletic competitive interactions in Lough Hyne appear to be similar to those reported elsewhere (see Wulff, 2006 for a review), with sponges being one of the top spatial competitors in temperate regions.

Bell & Barnes (2000a) considered that the higher diversity on vertical surfaces at Whirlpool Cliff probably results from decreased algal populations, compared with inclined surfaces, relating to reduced light intensity. However, the underlying interaction between sponges and algae that accounts for this pattern remains unclear although several potential explanations exist; algae may out-compete sponges for space (Palumbi, 1985; Witman & Sebens, 1990); algae may inhibit the settlement of sponge larvae by sweeping frond action (see Jenkins et al., 1999); or sponge abundance and diversity may be independent of algal populations (Preciado & Maldonado, 2005). Negative associations between sponges and algae have been commonly reported (both between sites and with depth), although direct interactions between sponges and algae, which result in the exclusion of sponge species from algal-dominated habitats have been rarely reported. Palumbi (1985) found that the coralline alga *Corallina vancouveriensis* Yendo could outcompete *Halichondria panicea*, but only in the absence of natural chiton grazing, which reduces the abundance of the macroalgae. It is possible that these negative associations with algae are the result of sponges simply dominating in areas that are unsuitable/less suitable for algae, or that they are specifically adapted to these supposedly less suitable habitats, rather than being prevented from inhabiting the surfaces where algae are most abundant. Preciado & Maldonado (2005) found that substratum angle rather than algal abundance (or potentially related competition) explained most of the variability in a study on the North Atlantic coast of Spain, suggesting that competition with algae may not necessarily restrict the distribution and abundance of sponges, instead sponges may be restricted to more suitable habitats (e.g. overhangs where UV and silting are reduced). However, this assumes sponges are more likely to inhabit overhangs to avoid sedimentation (and UV exposure), as this is a more suitable habitat, but such an assumption contrasts with the high diversity found in sedimented habitats within Lough Hyne. The difference in sponge diversity between surface angles at Whirlpool Cliff supports the conclusions of Preciado & Maldonado (2005), since although diversity is higher on vertical surfaces, abundance is actually higher on inclined surfaces (although lower than other sites inside Lough Hyne), where algal abundance is also highest.

Reproduction, recruitment and dispersal

Despite there having been numerous recruitment studies at Lough Hyne using artificial substrata (Maughan & Barnes, 2000b; Maughan, 2001; Bell & Barnes, 2003a; Watson & Barnes, 2004a,b) only four sponge species have been recorded on settlement panels: *Halichondria panicea* (Pallas, 1766), *Sycon ciliatum* (Fabricius), *Leucosolenia complicata* and *Amphilectus fucorum* (Esper, 1794). Further artificial substrata placed at 20 m at Labhra Cliff for four months by the author in 1999 (unpublished data), did recover large numbers of *Haliclona urceolus* (Rathke & Vahl, 1806), which must have grown rapidly as individuals were >6 cm in length when the panels were removed. However, no further sponges were reported on these panels. Maughan (2000b) monitored artificial substrata for two years in Lough Hyne and found very few sponges on settlement panels. There are several potential explanations for these results. It is possible that for some reason sponges do not recruit to artificial substrata, or that sponges are late colonizers of marine communities (Dayton, 1971). I believe the latter is probably the case for most sponges in Lough Hyne, since some fast growing species did colonize the artificial substrata. There is little evidence for reproduction and recruitment events for most sponge species in Lough Hyne, mainly due to the lack of long-term data sets and species-specific studies. Asexual reproduction has been observed in *Tethya* sp., but information is not available for other species (J.J. Bell, personal observation). Since the majority of sponges are not found commonly on the coastline immediately outside the lough, potential sources of gene flow are not obvious for many sponge species.

Predation

Although sponge predators are thought to include opistobranch molluscs, asteroid and echinoid echinoderms, crustaceans and fish (Guida, 1976; Battershill & Bergquist, 1990; Witman & Sebens, 1990; Dunlap & Pawlick, 1996; Wulff, 2005), few observations of sponge predation have been reported from Lough Hyne. This is perhaps surprising since Lough Hyne supports over 50 species of opisthobranchs (Picton, 1981), and over 70 species of fish, representing over 50% of the coastal fish fauna of the British Isles (Rogers, 1991). Some species-specific predation has been observed. For example, large dorid nudibranchs can often be found feeding on *Suberities domuncula*, but widespread sponge predation by opisthobranchs has not been reported. However, since many species of nudibranchs within Lough Hyne are small, cryptic and possibly nocturnal, their predatory effects may remain mostly undetected. Widespread direct predation of sponges by fish has not been reported at Lough Hyne, although fish nest building and feeding activities are thought to cause indirect damage to sponges (Bell et al., 2003), resulting in their removal from cliff surfaces. The only direct fish feeding on sponges that I have observed in Lough Hyne was by wrasse that were seen feeding on the tips of exhalent chimneys of *Cliona celata*.

THE RESTRICTION OF SPONGES TO THE UNDERSIDES OF BOULDERS

Sponge–boulder biodiversity at Lough Hyne is primarily controlled by physical factors (boulder size) and the locally available species pool, however, in the absence of disturbance the high diversity of sponges is probably maintained through a high degree of tied interactions. There is a marked contrast between the diversity of sponges on the upper and lower surfaces of boulders, with only a few species being reported from the upper surfaces, but over 45 species on the undersides of boulders (Bell & Shaw, 2001). There are a number of potential explanations for this discrepancy: (1) sponges inhabiting the undersides of boulders may be restricted from inhabiting the upper surfaces of boulders (at least in shallow waters) because of potential damage from UV exposure; (2) sponges may be out-competed by the abundant algae on the upper surfaces of boulders; or (3) sponges may be restricted to the undersides of boulders in order to avoid predation from fish and other predators. It remains unclear which of these explanations (or possibly others) account for the differences between the upper and lower surfaces on boulders. Preliminary qualitative observations indicate that sponges quickly disappear from boulders that are overturned and not replaced. The short time-scale before sponges are removed from overturned boulders probably means the reduced sponge biodiversity on the upper-sides of boulders is not the result of interactions with algae, but may be niche specialization to avoid predators or exposure to UV. I have observed increased fish activity in the vicinity of boulders that have been overturned, while sponges remaining on boulders a few days after they have been overturned do look bleached of their colour, which suggests potential impacts from UV exposure (boulders at a depth of 1 m).

SPONGE MORPHOLOGICAL VARIATION

Assemblage level and gross morphological variation

Sponges are well known to exhibit considerable macro- and micro-morphological variation, which has been considered as an adaptive mechanism to environmental variability (Palumbi, 1984, 1986; Gaino et al., 1995; Hill & Hill, 2002; Meroz-Fine et al., 2005). My early work at Lough Hyne (Bell & Barnes, 2000d) examined the distribution of gross sponge morphologies in relation to the different environmental conditions. There were clear patterns, with low profile (massive and encrusting) morphologies dominating in the higher energy sites (Whirlpool Cliff and Bullock Island), while upright forms (including arborescent, pedunculate and tubular forms) were more abundant at the low energy sites.

Upright forms can be considered adaptive to highly sedimented conditions, since the amount of sediment settling on surfaces per unit volume is reduced compared with low profile forms (Chappell, 1980). However, it still remains unclear if arborescent sponges are restricted to low-energy environments because of their small basal attachment area, compared with their size, which makes them susceptible to drag, or whether they are specifically adapted (through an evolutionary process) to sedimented habitats. In fact, for many sponge morphologies, there appears to be a problem in determining if gross morphologies, in specific environmental regimes, are the result of habitat exclusion or environmental adaptation. Bell (2004) demonstrated how the tubular forms of *Haliclona urceolus*, which is very abundant at the sedimented sites at Lough Hyne, prevents sediment settlement on its surfaces through the separation of inhalant and exhalent water flow. This species has a very small basal attachment area, so would appear unsuited to high-energy environments, however, without further reciprocal experiments resolving the relative importance of sediment and water flow rate in determining the distribution of this species will not be possible. There are other upright sponges whose morphology potentially assists in the prevention of sediment settlement including pedunculate and globulose forms (Chappell, 1980; Bell & Barnes, 2000d). The shape of such sponges is likely to aid in passive sediment settlement prevention, and this may be enhanced further when the exhalent osculum faces directly upwards, in a similar way to *Haliclona urceolus* (Bell, 2004).

The highest sponge diversity occurring at the most sedimented site has already been discussed above, but since sedimentation is thought to negatively impact suspension feeders (Hiscock, 1983), the reasons for the highest abundance and diversity of sponges in the most potentially unsuitable habitat remains paradoxical, especially since many of the morphologies that are abundant in sedimented habitats (particularly encrusting and massive forms) appear unsuited to this type of environment. For example, encrusting and massive morphologies represent up to 70% of the sponges present at Labhra Cliff, Glannafeen, West Cliff and Goleen (Bell & Barnes, 2000d). These gross morphologies would appear to be unsuited to highly sedimented environments as they are more prone to smothering, compared to upright forms (Chappell, 1980). Interestingly, many of the sponges at the sedimented sites seem to actively trap sediment on their surfaces, through protruding spicules. One possible adaptive explanation for sediment trapping, is the potential for microbial growth on the trapped sediment, although it is unclear if sponges can exploit such potential nutrient sources. A further explanation is the potential for preventing sponges being eaten by predators, or for organisms settling on their surfaces.

Species-specific micro- and macro-scale morphological variation

Several species-level morphological studies have also been conducted at Lough Hyne including research on *Cliona celata*, *Raspalia ramosa* and *Stelligera stuposa* (Bell & Barnes, 2002c; Bell et al., 2002). All three of these species show morphological variation in response to the environmental variability in Lough Hyne. Despite previous studies demonstrating that sponges show skeletal-level variation (e.g. Palumbi, 1984, 1986) and macro-morphological variation (e.g. Kaandorp & de Kluijver, 1992), Bell et al. (2002) were the first to report both types of variation within a single species. We reported six distinct morphological varieties of *Cliona celata* inside Lough Hyne and on the adjacent Atlantic coast, with different proportions of these morphologies being associated with different environmental regimes. Furthermore, skeletal-level (spicule shape) variation was also found in *Cliona celata* and despite previous studies (Palumbi, 1984, 1986) concluding that spicule variation can increase sponge strength in high-energy environments, we concluded that spicule level adaptation may also serve to make sponges more flexible, not just more robust, in high energy environments.

Species-level research (Bell & Barnes, 2002c) on *Raspailia ramosa* and *Stelligera stuposa* demonstrated that although arborescent forms are thought to be better adapted to high sediment areas (see above), at the highest levels of sedimentation (e.g. Labhra Cliff 24 m), branching complexity is reduced to very simple, single branch forms. We hypothesized that simple dichotomized sponges may be better suited to highly sedimented environments than more complex forms, although once again experimental evidence is still lacking. Morphological variation appears to be very important for sponges in their ability to adapt to different environmental regimes, and the close proximity of sites with different environmental conditions makes Lough Hyne a very useful place to study these aspects of sponge ecology.

Correlating species and morphological data

One of the most interesting relationships reported for sponges at Lough Hyne is the correlation between sponge species diversity and morphological diversity (Bell & Barnes, 2001), which has been subsequently confirmed in West Africa (Bell & Barnes, 2002d), Skomer Island MNR (Bell et al., 2006), Indonesia (Bell, 2007a), and also on the Pacific-Mexican coast (J.L. Carballo, personal communication). Two potential applications arising from the description of this relationship are biodiversity assessments and sponge monitoring. Morphological data have been successfully used to identify temporal variation in sponge assemblages at Skomer Island (Bell et al., 2006). Furthermore, this method has been adopted by the Countryside Council of Wales (CCW, UK) for monitoring sponges on the Welsh Coast, and a modified morphological approach is currently being developed and trialled by the National Institute of Water and Atmospheric Research (NIWA) in New Zealand (Michelle Kelly, personal communication) to monitor sponge-dominated habitats.

The potential for monitoring sponges using a morphological approach has received some criticism, but it is not intended to replace a taxonomic approach. Spatial and temporal monitoring of sponges is vital given their importance in benthic ecosystems, particularly with respect to their extensive functional roles (Wulff, 2001). Compared to other phyla, sponges are considered to be taxonomically complex, which coupled with the global reduction in the number of taxonomists (Giangrande, 2003) may severely limit the level of widespread species-level sponge monitoring that is likely to be achievable in the future. Although, the quality of the data collected from morphological studies will be of lower resolution than species data, we must be realistic with respect to monitoring. The design and extent of all marine monitoring programmes are driven by resource availability (e.g. funding and expertise) and practicality. A morphological approach may allow large areas of the benthos to be monitored quickly, which is particularly useful in habitats whose depth exceeds that accessible by SCUBA diving and where resources are limited. Furthermore, high quality morphological data collection is possible by volunteers with little or no taxonomic training (Bell, 2007a), and given the increase in conservation groups utilizing volunteers around the world (e.g. Sea Search, Operation Wallacea, Blue Ventures, Coral Cay, Frontier), this approach represents a possible way that sponges can be included in their monitoring and education programmes, where they would have otherwise been excluded.

Assessing sponges using a morphological approach may be an alternative approach to collecting species data, but the significance of different morphologies (in an evolutionary and adaptive context) also requires attention, as morphological diversity may also be a measure of functional diversity (Bell, 2007b). Since sponge morphologies may represent different functional roles of sponges (Pang, 1973; Rützler, 1975; Wulff & Buss, 1979; Bell, 2007b), morphological monitoring may provide a mechanism for assessing changes in the functional diversity of sponges. Such an approach may be particularly appropriate given the current focus on ecosystem-level monitoring and the importance of maintaining ecosystem functioning (rather than necessarily focusing on individual species). If sponge morphologies are a suitable indicator of sponge function then care must be exercised when applying a morphological monitoring approach to sponges, as sponge species diversity and functional diversity may not necessarily correlate (Bell, 2007b).

With the increasing interest in ecosystem-level-management to maintain ecosystem functioning (e.g. the Great Barrier Reef Marine Park Authority), understanding the functional roles that sponges play in marine ecosystems, along with the degree of functional redundancy (Micheli & Hapern, 2005), may be far more important than their species identity. Therefore, from this perspective morphological diversity may prove even more important in monitoring programmes than previously considered (Bell, 2007a,b).

FUTURE SPONGE RESEARCH IDENTIFIED FROM STUDIES AT LOUGH HYNE

Spatial patterns of sponge biodiversity: environmental adaptation or restriction

There have been numerous studies describing the factors influencing the distribution, biodiversity and abundance patterns of sponges (e.g. Wilkinson & Evans, 1989; Alcolodao, 1990; Alvarez et al., 1990; Diaz et al., 1990; Schmahl, 1990; Wilkinson & Cheshire, 1990; Witman & Sebens, 1990; Barnes, 1999; Bell & Barnes, 2000a; Barnes & Bell, 2002; Bell & Smith, 2004; Carballo, 2006), and although we have a relatively good understanding of how different biological and physical factors correlate with the distribution patterns of sponges, the mechanisms responsible for the patterns are poorly understood, and mostly unsupported by experimental approaches and manipulations (but see Roberts et al., 2006b).

Of particular interest is the general consensus that suspension feeders are negatively impacted by sedimentation, which may not necessarily apply uniformly to sponges, with only one experimental study having investigated the impact of sediment on a single species of sponge, which found evidence for reduced sponge pumping rates in the presence of sediment (Gerrodette & Flechsig, 1979). Research at Lough Hyne has shown that sponge diversity is greatest in the most sedimented environments (Bell & Barnes, 2000a), and is consistent with rich sponge assemblages being found in highly sedimented environments at Skomer Island and in Indonesia (Bell & Smith, 2004; Bell et al., 2006). The ecological, morphological and physiological impacts of sediment settlement and accumulation across multiple sponge species should be a focus of future research to elucidate the impacts of sedimentation on sponges and how suspension feeders can tolerate this potential environmental stress, since sponges appear to be a dominant feature of sedimented environments in temperate and tropical ecosystems (see Bell & Barnes 2000a; Bell & Smith, 2004; Bell et al., 2006). Research should also focus on whether or not the sponges inhabiting these sedimented habitats are specifically adapted to survive in sedimented conditions, or if they are restricted to these potentially less suitable habitats through competition with other organisms, particularly algal assemblages (Preciado & Maldonado, 2005).

When interpreting the spatial distribution patterns of sponges there has been a tendency for biological and physical factors to be considered independently (Wulff, 1995a,b; Bell & Barnes, 2000a,b, 2003a; Carballo, 2006; Wulff, 2005), when both may potentially play an important role in determining the underlying structuring of sponge assemblages. For example, the sponge–boulder fauna in Lough Hyne is a good example of where there appears to be strong interaction between biological (predation and competition) and physical factors (boulder size and light/UV) in determining the underlying structure and nature of sponge assemblages. Despite the information available there is still some debate with respect to the relative importance of biological versus physical processes in controlling sponge biodiversity and abundance. Previously, explanations for reduced abundance of sponges at the apparently most suitable site at Lough Hyne (Whirlpool Cliff) have been explained through a combination of environmental restriction of specific morphologies, and competitive interactions with algae and other organisms (Bell & Barnes, 2000a), but this may not be the case and requires further investigation (Preciado & Maldonado, 2005). The higher abundance of sponges on inclined surfaces at Whirlpool Cliff (Bell & Barnes, 2000a) does not support the competitive exclusion of sponges by algae, although the reduced richness does. Paradoxically, a large proportion of the encrusting species, which would appear to be morphologically suited to Whirlpool Cliff, are not found there, and only occur in sedimented habitats. This suggests that physical factors may be primarily responsible for distribution patterns of sponges on submarine cliffs in Lough Hyne, although this appears more likely to have occurred through environmental adaptation to different niches, through long-term evolutionary processes, rather than being mediated by local-scale environmental restriction. The interaction (if any) between macroalgae and sponges, along with the relative roles of biological versus physical factors in influencing sponge diversity and abundance patterns should be an important and primary focus of future investigations.

Temporal variability in sponge assemblages

Although we have a relatively good understanding of the spatial variability in sponge assemblages at Lough Hyne, there is a contrastingly poor understanding of the temporal variability. Bell et al. (2003) found 20 species of sponge in nets placed at the bottom of cliffs within Lough Hyne in a study conducted over a two-year period. The loss of sponges from cliffs was seasonal, which provides evidence that some species may undergo seasonal mortality, although the loss of sponges (and other benthic organisms) was positively correlated with fish abundance, and therefore (or fragmentation) is probably an inadvertent product of the nesting and feeding behaviour of coastal fish (e.g. wrasse); these are seasonally abundant in Lough Hyne (Bell et al., 2003). Generally, we have a poor understanding of temporal variability of sponges at the assemblage level (but see Bell et al., 2006; Roberts et al., 2006a; Wulff, 2001, 2006b), and in particular the biological and physical factors that drive assemblage change. Future research needs to focus on the primary factors that control temporal variability, and measure the levels of variability in more localities to provide baseline data against which potential future change can be measured. This is particularly important at present in light of the potential for global climate change to influence marine communities including sponges.

Population connectivity and self-recruitment

Another unexplored aspect of sponge ecology at Lough Hyne is the degree that populations are dependent on self-recruitment or external larval input for population maintenance. Recent molecular analysis by Bell & Okamura (2005) has shown that populations of the direct-developing gastropod, *Nucella lapillus* L., are genetically isolated inside Lough Hyne from populations on the open Atlantic coast. Given that sponge larvae generally spend only short periods of time in the water column (Mariani et al., 2006), self-recruitment is likely to be an important part of the maintenance of sponge populations inside Lough Hyne. However, since the reserve is only thought to have undergone a marine transgression approximately 4000 years ago (Holland, 1981), it seems likely that there must be local sources of larvae, even if Lough Hyne does act as a larval sink. There is some evidence for self-recruitment, and limited larval supply from outside the lough from qualitative observations of *Axinella damicornis* (Esper, 1794). This species was harvested in Lough Hyne during the 1980s (for molecular investigations) and the populations were reduced to very low densities, which subsequently recovered very slowly, although they are now considered to be back to their original densities. Understanding the degree of sponge population dependence on self-recruitment is very important in effectively managing the sponge populations in this marine reserve and in predicting the potential for local-scale environmental perturbations (whether natural or anthropogenic) to negatively effect sponge assemblages.

Sponges and bentho-pelagic coupling

Recent research has highlighted the link between benthic and pelagic environments (e.g. Alfaro, 2006; Gili et al., 2006). The abundance of sponges in Lough Hyne and elsewhere across the globe in benthic ecosystems means that sponges must have important impacts on the pelagic environment including ultraplankton and virus removal (Pile et al., 1996; Pile, 1997; Hadas et al., 2006), and oxygen consumption (Gatti et al., 2002; Kowalke, 2002). The importance of sponges across temperate, tropical and polar ecosystems is almost certainly underestimated and substantial research effort is still required to fully demonstrate the roles sponge play in ecosystem functioning. The relatively small water volume, coupled with the high abundance of sponges on cliff faces in Lough Hyne probably means there is strong interaction between pelagic and benthic environments (e.g. oxygen and nutrient consumption), and this study site provides a model system to investigate such interactions.

CONCLUSIONS

Lough Hyne represents a very unusual marine site with predictable flow and sedimentation regimes, where the subtidal rocky substratum is dominated by sponges. Within these ecosystems sponges must be very important in ecosystem functioning given their numerical abundance and diversity. Research at Lough Hyne since 2000 has considered how a number of biological and physical factors influence sponge assemblages and populations, and it appears that physical factors are primarily responsible for sponge distribution and abundance patterns in Lough Hyne, but probably through niche specialization rather than environmental restriction. Of the potential biological factors that may influence sponge assemblages, spatial competition appears most important, particularly potential interactions with macroalgae and their role in controlling sponge vertical zonation patterns. The nature of intra-phyletic spatial interactions between sponges may also be important in maintaining species diversity in the absence of disturbance (particularly for sponge boulder assemblages). Despite the increased understanding of sponge ecology at Lough Hyne, research since 2000 has further highlighted gaps that exist in our understanding of sponge ecology relevant at both the local and global scale.

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