

Title	Biodiversity of shallow subtidal, under-rock invertebrates in Europe's first marine reserve: effects of physical factors and scientific sampling
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Publication date	2016-12-27
Original Citation	Trowbridge, C. D., Kachmarik, K., Plowman, C. Q., Little, C., Stirling, P. and McAllen, R. (2017) 'Biodiversity of shallow subtidal, under-rock invertebrates in Europe's first marine reserve: Effects of physical factors and scientific sampling', Estuarine, Coastal and Shelf Science, 187, pp. 43-52. doi:10.1016/j.ecss.2016.12.022
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1016/j.ecss.2016.12.022
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Download date	2025-04-18 04:14:57
Item downloaded from	https://hdl.handle.net/10468/3968



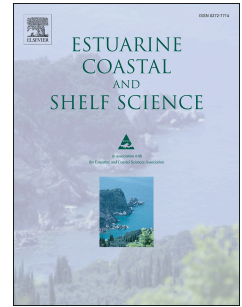
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PII: S0272-7714(16)30787-9

DOI: [10.1016/j.ecss.2016.12.022](https://doi.org/10.1016/j.ecss.2016.12.022)

Reference: YECSS 5352

To appear in: *Estuarine, Coastal and Shelf Science*

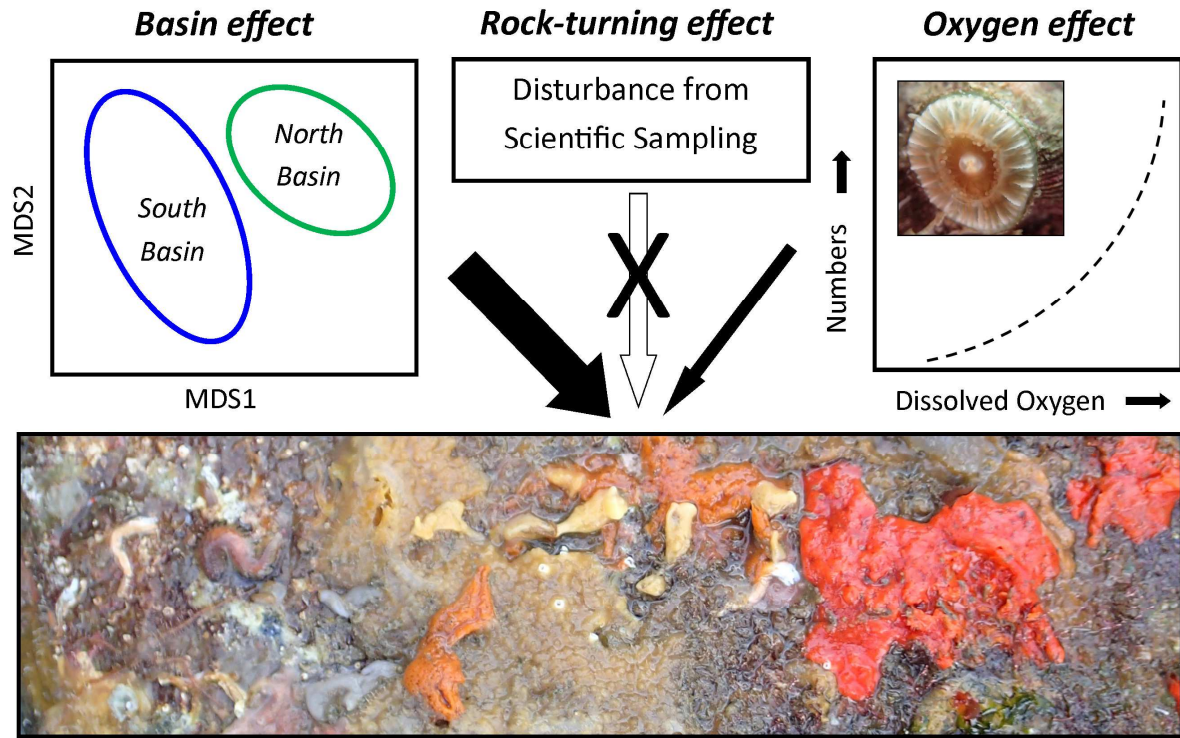
Received Date: 3 March 2016

Revised Date: 23 December 2016

Accepted Date: 26 December 2016

Please cite this article as: Trowbridge, C.D., Kachmarik, K., Plowman, C.Q., Little, C., Stirling, P., McAllen, R., Biodiversity of shallow subtidal, under-rock invertebrates in Europe's first marine reserve: Effects of physical factors and scientific sampling, *Estuarine, Coastal and Shelf Science* (2017), doi: 10.1016/j.ecss.2016.12.022.

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**Biodiversity of shallow subtidal, under-rock invertebrates in Europe's first marine reserve:
effects of physical factors and scientific sampling**

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Abstract

At Lough Hyne Marine Reserve in SW Ireland, shallow subtidal, under-rock biodiversity was investigated to assess (i) any deleterious effects of scientific sampling and (ii) quantitative baseline community patterns. Comparisons were made between 10 sites with annual rock-turning disturbance and 10 with multi-decadal (historical) disturbance. At each site, shallow subtidal rocks (N=1289 total) were lifted, organisms recorded, and rocks replaced in their original position. Biodiversity indices were calculated to evaluate how diversity varied with location within the lough, frequency of sampling disturbance, degree of hypoxia/anoxia, dissolved oxygen (DO) concentration, and number of rocks turned. The richness of solitary invertebrates surveyed *in situ* averaged 21 taxa per site with significantly more in the South Basin (near the lough's connection to the ocean) than in the North Basin. The Shannon-Wiener Index did not differ significantly with variables investigated. However, evenness was higher at annually disturbed sites than at historical ones where anemones with algal symbionts often dominated. Several sites were hypoxic to anoxic under the shallow subtidal rocks. Cup corals were most abundant in the South Basin; DO was a crucial explanatory variable of these sensitive species. Solitary ascidians were most abundant at South-Basin annual sites with DO levels being a highly significant explanatory variable.

Keywords: Epilithic invertebrates; Dissolved oxygen; Lough Hyne; Marine reserve; Ireland; Shallow subtidal

1. Introduction

Marine protected areas (MPAs) are designated to protect and conserve select species, communities, habitats, or ecosystems. They represent a crucial tool in the arsenal of coastal biotic protection. Some MPAs are selected to conserve an outstanding area whereas others are selected to enhance closely situated non-reserve areas by exporting larvae, algal propagules, and food outside reserve boundaries (Lubchenco et al., 2003). To evaluate the effectiveness of a marine reserve or a MPA, it would be ideal to survey (1) before and after protection, (2) inside and outside the area, and (3) through long periods of time (e.g. Lester and Halpern, 2008; Lester et al., 2009; Soykan and Lewison, 2015). These comparisons would help to elucidate the role of food web alteration due to increased predatory fishes, anthropogenic disturbance (trampling, nutrient enhancement, etc.), and climatic change. However, these conservation ideals cannot always be met, particularly in the earliest MPAs that were selected for their outstanding and even unique attributes. How can coastal improvement or degradation be assessed in these situations? Comprehensive scientific monitoring through time is needed to assess community-level changes. But at what point does scientific sampling itself become a physical disturbance? In our study of Europe's first marine reserve, there was the unprecedented opportunity to evaluate the biodiversity patterns within the fully marine lough at the end of a two-decade, rocky shore monitoring program but also to evaluate the potential disturbance inherent in scientific sampling of under-rock invertebrate communities.

Biodiversity patterns on intertidal and subtidal rocks relate to community and rock stability, disturbance, successional changes, and species-area relationships (e.g., Osman, 1977; Sousa, 1979; Smith and Otway, 1997; references therein). Classical experimental work by Sousa (1979) on marine epilithic biota strongly supported the intermediate disturbance hypothesis (Connell, 1978): (1) small rocks, disturbed frequently by water movement, supported depauperate communities of early successional species, (2) large rocks, disturbed infrequently, supported low diversity communities of competitive dominants, and (3) intermediate-sized rocks had the greatest diversity. Thus, rock size, disturbance regime, larval settlement patterns, interspecific interactions (competition for space and predation), and functional group (sessile vs. mobile fauna) are all salient factors in determining patterns of community structure (Osman, 1977; Connell, 1978; Sousa, 1979; McGuinness and

Underwood, 1986; McGuinness, 1988; Chapman and Underwood, 1996; Smith and Otway, 1997; Chapman, 2002, 2003).

There are some apparent exceptions to the pattern of unimodal diversity vs. disturbance regime, depending particularly on the scale of investigation and the spectrum of disturbance in the system (e.g. Lake, 2000; Death, 2010). In bays, estuaries, and sea loughs, the turbulence required to turn or flip rocks is often missing due to limited fetch of the basin. Thus, the ways in which the disturbances or stresses impinging on species in wave-sheltered habitats affect biodiversity patterns require investigation.

Clearly rock size is important in contributing to disturbance (e.g., rock shifting and/or flipping) as well as larval recruitment and adult colonization (e.g., McGuinness, 1988) and even body size (Smith and Otway, 1997). However, biodiversity patterns at a larger spatial scale than individual rocks—meters to 100s of meters—are also crucial in terms of conservation and habitat management in MPAs. Thus, current flows, sedimentation, and dissolved oxygen could be consequential. Tolerances of individual species to these factors, and to sampling-induced disturbance, have been evaluated by experimentally transplanting rocks and quantifying species survivorship (e.g. Muntz et al., 1972; Sousa, 1979; Chapman and Underwood, 1996; Smith and Otway, 1997). Maughan and Barnes (2000) reported that epilithic diversity was greatest at intermediate current flows in 3 intermediate-depth subtidal habitats in Lough Hyne, Ireland; at high flow, community coverage or occupancy was high, particularly by bryozoans. At low flow, high sedimentation, extreme oxygen levels, and other stresses occur (e.g., Bell and Barnes, 2000b, 2002; Bell and Turner, 2000; Bell, 2002).

As part of the mandate to characterize and maintain MPAs, scientific sampling is necessary. McGuinness (1988), Chapman and Underwood (1996), and Smith and Otway (1997) focused on community responses to disturbance, particularly short and long-term responses to the requisite disturbance associated with scientific sampling, even non-destructive survey sampling. Many scientists assume that replacement of sampled rocks, boulders, and other loose substrata would not be a disturbance in its own right, especially if the researchers carefully resettled the rocks back into their original position and orientation on the shore. However, (1) mobile fauna often fall off (passively or actively) the boulders during visual examination; (2) light and temperature may negatively affect

epilithic species when rocks are lifted out of seawater or even induce gamete or larval release; (3) water circulation among the rocks may be altered after rock replacement; (4) finally, resettling rocks on the benthos may damage fragile taxa (e.g., ophiuroids and echinoids). The frequency and timing of scientific disturbance and the care of rock replacement, thus, may have short and/or long-term consequences (Chapman and Underwood, 1996; Smith and Otway, 1997).

The biodiversity patterns within Europe's first marine reserve, Lough Hyne, were investigated as well as the potential contributory role community sampling may have on these patterns. Epilithic rock communities at Lough Hyne, particularly the under-rock communities, are diverse in terms of species and phyletic richness (Lilly et al., 1953; Ebling et al., 1960; Maughan and Barnes, 2000). For example, Maughan and Barnes (2000) reported 114 taxa from 378 subtidal rocks surveyed in the 1990s. Sessile fauna (bryozoans, cnidarians, sponges, ascidians, tube worms, bivalves, and barnacles) as well as associated mobile consumers (e.g., snails, chitons, flatworms, ribbon worms, and segmented worms) formed highly diverse invertebrate assemblages. The wealth of the sessile suspension feeders (Bell and Barnes, 2000a; Bell and Shaw, 2002) is one of the reasons that Lough Hyne was designated a marine reserve in 1981: to protect these significant invertebrate communities and habitats. There has, in fact, been a long history of scientific investigation in the lough before 1981, particularly of the benthos (e.g. Kitching, 1987).

In the past few decades, there have been large-scale phase shifts at the lough due to population fluctuations of ecologically significant species, large nutrient enhancements, warm-water species incursions and/or proliferations, and invasive species arrivals (Little et al., 1992; Jessopp et al., 2011; Trowbridge et al., 2011, 2013a,b; Little and Trowbridge, 2014). Whether these are altered stable states or sliding baselines is not clear, but the decline of the purple sea urchin *Paracentrotus lividus* and an increase in dissolved nutrients has led to the explosive seasonal proliferation of ephemeral algae. Consequently, shallow waters are hyperoxic during the day and hypoxic to anoxic at night (Trowbridge et al., submitted ms). Such conditions may be lethal to shallow-water invertebrates (reviewed by Levin et al., 2006), particularly those living underneath rocks where water flow is limited.

The goal of our research was to document the biodiversity of the under-rock communities in the shallow subtidal zone around the lough and to determine the potential role of sampling disturbance and environmental variables in the structure of invertebrate communities. Comprehensive spatial comparisons were made for 10 long-term monitoring sites that were disturbed annually during surveys and 10 further sites that were surveyed 25 years earlier by Little et al. (1992). O'Sullivan and Emmerson (2011) subsampled a few of these marked sites in 2010 though the extent of their disturbance was unclear. We made three major predictions. (1) There would be significant differences in biotic communities between the shallow North Basin sites and deeper South Basin sites with greater biodiversity in the latter (due to the proximity to the Atlantic Ocean). (2) The historically disturbed sites would be more diverse than the annually disturbed ones because of lower sampling-induced disturbance, despite our care in replacing rocks. (3) Dissolved oxygen concentrations in late summer would be limiting for many sensitive sessile species including scleractinian corals.

2. Materials and Methods

2.1 Study site

Lough Hyne Marine Reserve (51°30' N, 9°17' W) is a semi-enclosed, fully marine sea lough in Co. Cork, southwest Ireland. The lough is ~0.8 km long and ~0.5 km wide and is connected to the Atlantic Ocean by a shallow, narrow (25 m wide at high tide, 12 m at low tide) channel called the Tidal Rapids (Fig. 1). The tidal range within the lough is about a meter (Bassindale et al., 1957).

Renouf (1931) designated 108 sectors of shoreline (Fig. 1) corresponding to discrete topographical units; these marked sectors are still used because GPS devices have difficulty obtaining satellite signals in several areas of the lough. The lough's shoreline was also considered as belonging to two different basins (Fig. 1). The South Basin was nearest the tidal rapids where seawater entered and exited the lough whereas the North Basin was partially separated from the south by an island consisting of two well-defined halves. The inflowing current on a rising tide moves in an anti-clockwise pattern in the eastern half of the South Basin and clockwise in the western half (Bassindale et al., 1957, fig. 9). The North Basin has generally low current flow.

2.2 Monitoring sites

The under-rock communities in Lough Hyne were investigated in August and September 2014 at 20 long-term monitoring sites (Fig. 1). Ten sites were “historical” monitoring sites that were sampled in the early 1990s (Little et al., 1992) and ten sites were “annual” monitoring sites that have been looked at every year since the early 1990s (Little and Trowbridge, 2014). Seven of the historical sites were in the South Basin and three in the North Basin; six of the annual sites were in the South Basin and four in the North Basin (Table 1, Fig. 1). The unbalanced sampling design was a product of rocky shore distribution within the lough coupled with historical decisions of study site selection by Ebling et al. (1960) and Little et al. (1992). The statistical software Systat handles unbalanced designs automatically.

All twenty sites were 10-m along the shore and the sampling area started from below the low intertidal portion of the fucoid zone to approximately a meter depth offshore. The area sampled and the number of rocks turned was a function of low tide level, light levels, and weather. There were 3 crucial aspects of the sampling. (1) This 2014 study was linked to a 2-decade data set for which there was extensive information (Little et al., unpubl. data). (2) Our approach was nondestructive due to marine reserve conservation issues and long-term sampling. (3) The 10 sites selected to be annual monitoring sites were not randomly selected from the original 20 sites: they were selected 2-decades ago (by Little and Stirling), in large part, on feasibility of logistical sampling. Thus, differences in biotic communities could be due to annual vs. multidecadal rock-turning disturbances and/or inherent differences between these two groups of sites.

While the latter issue cannot be discarded, the issue was evaluated in 2011 by comparing 10 monitoring sites to 8 other areas of rocky shores in the lough. We compared the abundance of 12 species of animals (4 echinoderm, 1 nemertean, 5 molluscan, and 1 vertebrate species). Because there was no significant difference in under-rock abundance of any of the 12 species, there was no clear evidence of bias of the 10 selected annual monitoring sites.

2.3 Shallow subtidal rocks

Lough Hyne is in the region of the Lower Old Red Sandstone formation (Ebling et al. 1960). The shallow subtidal rocks are primarily schists, slates, and sandstone slabs. For the historical sites, rocks larger than 6 cm (max. length) were turned, the solitary organisms (both mobile and sessile) were

counted, the underside of each rock was photographed, and the rock was replaced carefully in its original position. All specimens that fell from a rock during sampling were collected, recorded, and returned to the under-rock habitat after the rock was replaced. For the annual sites, the same general methods were used, but all rocks were turned and observed regardless of size. Rocks at two sites (Boundary Bay and East Goleen) could not be photographed due to logistical issues (sheer drop-off into deep water for the former site and poor water clarity due to mud for the latter site). For all sites, the largest rock slabs (*ca.* 1 m diameter) lifted, turned, and observed were limited by the number of people present to turn the rock (usually 2-3 individuals). At all monitoring sites the number of rocks turned was counted and any signs of anoxia were noted.

The methodological discrepancy (not sampling small rocks at historical sites) was considered to be not a major issue for three reasons. First, rocks <6 cm rarely had many attached invertebrates. Second, we still were sampling >90% of the area at each site. Third, species richness approached an asymptote long before we sampled the entire 10-m stretch of shoreline.

Biodiversity indices including species richness (S), Shannon-Wiener (H'), and Pielou's evenness index (J) were calculated to analyze the under-rock communities based on *in situ* count data. In addition to the *in situ* counts, colonial and clonal species were identified from photographs to the lowest operational taxonomic unit (OTU); condensation in the lens of the underwater cameras (Olympus TG3) prevented us from making a full field vs. photo count comparison.

2.4 Dissolved oxygen and other physical variables

During daytime low tides in August and September 2014, dissolved oxygen (DO) concentrations in seawater were measured at each location. Small holes or gaps under rocks were located and an optical YSI ProODO™ probe was used to measure the DO under the rock. For logistical reasons (too much trampling on non-disturbance sites and time lag necessary for probe to stabilize), the DO concentrations were measured under 10 rocks adjacent to the monitoring sites rather than under each rock for which invertebrate communities were recorded. The mean of 10 values was used in statistical analyses as a site attribute. The state of anoxia at each site was characterized by recording the number of rocks that showed signs of anoxia (black discoloration and/or sulfide smell).

Finally, a series of other physical factors were recorded for each site including shore slope, aspect, fetch, relative water flow, dissolved oxygen levels under rocks, etc. (see Table 1 for the temporally constant attributes). Slope was measured with a plumbers' level across the shallow subtidal shoreline (in the subtidal boulder habitat). Aspect was determined by averaging the compass reading at either end of each site as well as in the center. Fetch was determined as the linear distance (perpendicular to the shore) to the nearest shoreline, using satellite imagery and measuring tools in the software program Garmin BaseCamp (ver. 4.4.6). Water flow was evaluated using gypsum (Plaster of Paris) semi-spherical flow blocks deployed at each site for 3 days in March 2015; the weight loss of each block (and still-water controls) was measured to determine relative current flow at the 20 sites. This latter method has been widely used since Muus (1968) and Doty (1971).

2.5 Statistical analyses

The monitoring sites (10-m of shoreline, ~1 m offshore) were considered the statistical replicates. For all these analyses, 3 sites were excluded from the analyses (Rookery Nook, North Island, and Whirlpool Point) as they had few rocks (4-7 per 10-m shoreline) and the focus herein was to characterize the under-rock invertebrate communities.

Potential univariate correlations were investigated between the abundance of a species and a site-level environmental variable, using Pearson's correlation analysis (Systat ver. 9). To investigate the role of lough basin and disturbance, 2-way factorial ANCOVAs (analyses of covariance) were run, with number of rocks and dissolved oxygen concentrations as the covariates. Data were transformed (typically $\log(x+1)$) as needed to meet the parametric assumptions of homogeneity of variance and normality of data.

To evaluate if there were major differences in community structure between the lough basins, annual vs historical monitoring sites, and other environmental factors, non-parametric, assumption-free analyses were conducted using the software program Primer (ver. 7). Bray-Curtis dissimilarities were calculated from fourth-root transformed count data of 84 taxa at 17 sites; the transformation enhanced the information value of species with low abundances (and was not used to meet any statistical assumptions). The resulting community-level patterns were illustrated using a nMDS (non-metric Multi-Dimensional Scaling) plot; an Analysis of Similarities (ANOSIM) routine was

conducted and statistically different groups of sites were designated by different symbols. Based on one-way SIMPER analysis, species contributing the most to each group were listed along with their percentage contributions. Primer's BEST routine (with 999 permutations) was used to evaluate which environmental variables best explained variations in biotic community structure.

3. Results

3.1 Taxonomic richness

For the field surveys, 84 animal taxa (in 12 phyla) were counted and recorded *in situ* (Appendix 1); for photographic analyses, about twice that number of observable taxa was recorded with many categorized as operational taxonomic units (OTUs). The species richness of the under-rock community averaged 20–25 taxa recorded per site ($N = 17$ sites) in the field (Fig. 2) and 68 taxa (particularly sponges and bryozoans) from photographs ($N = 7$ sites). These data indicated field surveys failed to capture about half of the species present, particularly the small and/or cryptic taxa, but were highly correlated to richness estimates from examination of digital photographs (Pearson correlation, $r = 0.934$, $p = 0.002$). ANCOVA indicated that the number of species counted in the field was a good predictor of overall richness whereas the number of rocks examined (excluding the 3 sites with few rocks) was not significant.

3.2 Biodiversity indices

Based on ANCOVAs, species richness was not significantly affected by most factors investigated, including disturbance history, dissolved oxygen, numbers of rocks turned, etc. (Table 1). The only factor that was statistically significant was lough basin (ANCOVA: $F = 6.268$, $p = 0.029$): there were more benthic species at South Basin sites than North Basin ones (Fig. 2A). The average Shannon-Wiener value ($N = 17$ sites) was $H' = 3.23$ and the average evenness value was $J = 0.71$. H' values were not significantly affected by basin, disturbance, or other factors evaluated (Table 1). J values were significantly higher at annual sites ($F = 6.086$, $p = 0.031$) than historical ones. For both Shannon-Wiener and evenness indices, the North-Basin historical sites had, on average, lower values than the other sites (Fig. 2B-C).

To investigate possible causes of the reduced H' and J values, the data were reanalyzed in three ways. First, the anemone *Anthopleura ballii* was removed from the dataset and the analyses repeated.

Anemones with symbiotic microalgae were particularly common at a few sites in the North Basin and East Goleen that exhibited low DO levels. There were still significant basin effects on species richness ($p = 0.029$) but no longer any disturbance effects with evenness (Table 1). Second, photos of rocks were examined to determine empirically whether space was limiting (an assumption requisite to invoke interspecific competition for space). If one or a few species dominated limited space, then inferior competitors could be excluded, thus reducing evenness values. However, most rocks had considerable bare space available for additional species establishment. Third, a subset of the data was analyzed—just mobile species (57 taxa) which would be expected to be most affected by disturbance. The species richness was significantly greater in the South Basin than the North ($F_{1, 13} = 8.844$, $p = 0.011$), but there was no significant disturbance effect ($p = 0.771$) or interaction effect ($p = 0.174$). H' and J indices of mobile species did not vary significantly with basin, disturbance, or their interaction.

3.3 Anoxia and dissolved oxygen (DO)

The extent of anoxia (black discoloration and sulfide smell) per site averaged 20.6% of the rocks surveyed (ranged from 0 at 8 sites to 88% at East Goleen). There was no significant difference in extent of anoxia between basins irrespective of whether East Goleen (a statistical and biological outlier) was included in the analysis or not (Student's t -tests, $t = 0.101$, $p = 0.921$ and $t = 1.121$, $p = 0.280$, respectively). The percent of rocks showing signs of anoxia beneath them did not significantly affect biodiversity estimates. For example, there was no significant correlation between anoxia and species richness (Pearson correlation, $r = -0.226$, $p = 0.400$). Furthermore, the DO values were not significantly correlated with occurrence of anoxia ($r = -0.468$, $p = 0.068$). The mean DO under shallow subtidal rocks during daytime low tides ranged from 3 to almost 9 mg O₂ L⁻¹ at the monitoring sites in 2014; the site with the lowest mean, East Goleen, had values that ranged from 0.3 (hypoxic) to 7.7 O₂ mg L⁻¹ (normoxic). DO concentrations did vary significantly with lough basin, irrespective of whether East Goleen was included or not ($t = 2.202$, $p = 0.041$ or $t = 3.716$, $p = 0.002$, respectively): the South Basin sites had significantly higher DOs than the North Basin ones.

3.4 Sensitive anthozoans

There were several taxonomic groups including cup corals, octocorals, prosobranch and heterobranch gastropods, bryozoans, and sponges that were more abundant in the South Basin than

the North Basin. Because many of the cnidarians are sensitive to environmental or anthropogenic stress, their spatial distributions within the lough were documented. Additional details on other taxa will be presented elsewhere.

The abundance of Devonshire cup corals (*Caryophyllia smithii*) on shallow subtidal boulders increased logarithmically with increased dissolved oxygen and this pattern was highly significant statistically ($r^2 = 0.443$, $F = 14.3$, $p = 0.001$) (Fig. 3A). The jewel anemones or corallimorphs (*Corynactis viridis*) were also extremely abundant at many sites in the South Basin. Therefore, counts were made of the number of occupied rocks (up to 88% of shallow subtidal rocks surveyed) rather than the hundreds to thousands of these corallimorphs. Their abundance increased logarithmically with increased DO and this pattern was highly significant statistically ($r^2 = 0.269$, $p = 0.033$) (Fig. 3B).

Of these cnidarian species, few were recorded at sites with DO levels $<5 \text{ mg O}_2 \text{ L}^{-1}$ although one individual cup coral was attached under a rock at East Goleen, a site with mean DO of $3 \text{ mg O}_2 \text{ L}^{-1}$ and a few specimens were found at sites with mean DO of $4\text{--}5 \text{ mg O}_2 \text{ L}^{-1}$ (Fig. 3). In marked contrast to these 3 aposymbiotic species, the symbiont-containing anemone *Anthopleura ballii* was most abundant at sites with low DO ($3\text{--}7 \text{ mg O}_2 \text{ L}^{-1}$) (Fig. 3C). This anemone was clearly prevalent at low-oxygen sites ($r^2 = 0.244$, $p = 0.044$).

3.5 Solitary ascidians

For logistical reasons (tide-related time limitations), ascidians were recorded in 3 consolidated categories: (1) *Ascidia/Ascidiella* spp., (2) *Ciona* and allies, and (3) *Pyura/Styela* spp. In the North Basin, *Pyura tessellata* predominated whereas in the South Basin, *Ascidia mentula* predominated; both are native species. Overall (Fig. 4), there were highly significant differences in ascidian abundance between annual and historical sites (ANCOVA, $F_{1,12} = 8.621$, $p = 0.012$) and basin \times disturbance interaction effects ($F_{1,12} = 9.187$, $p = 0.010$); the covariate, dissolved oxygen, was also highly significant ($F_{1,12} = 20.084$, $p = 0.001$). The first two categories of ascidians exhibited this general pattern; the third taxon, however, did not differ with basin or disturbance, and the dissolved oxygen significance was marginal ($F_{1,12} = 4.545$, $p = 0.054$). Three sites had particularly high ascidian densities (146–163 per 10 m of shoreline): Westwood South, SE Labhra, and Codium Bay.

3.6 Multivariate patterns

The patterns of community analysis indicate that the epilithic invertebrate communities are fairly distinct between North and South Basins (Fig. 5). Non-metric multidimensional scaling (nMDS) analysis showed a separation of North and South Basin sites with the exception of two sites: East Goleen (EG) and Westwood North (WWN). The environmental attributes and biotic communities of East Goleen, a shallow, low-flow site almost mid-way down the dead-end armlet of the lough, were more similar to North Basin sites than South Basin ones. Westwood North was similar to Westwood South in terms of substratum, aspect, water flow, and biotic communities; the Westwood sites were both dissimilar to the intervening West Concrete (WC) site which had fewer rocks and a North Basin type of community.

Analysis of similarities (ANOSIM) indicated that there were highly significant differences among the sites ($R = 0.725$, $p = 0.001$). Post-hoc comparisons revealed that South Castle (SC in Fig. 5) did not differ from either cluster of sites ($p > 0.140$), but the other North and South Basin clusters were significantly different ($R = 0.728$, $p = 0.001$).

Based on one-way SIMPER analysis, the taxa contributing the most to the distinctive South Basin under-rock communities were (1) the ascidians *Ascidia/Ascidiella* species (10.2%), *Ciona* and allies (9.7%), *Pyura/Styela* species (8.3%); (2) the sea star *Marthasterias glacialis* (8.5%); (3) polynoid polychaetes (7.7%); and cup coral *Caryophyllia smithii* (7.5%). The taxa contributing the most to the North-Basin communities were the anemone *Anthopleura ballii* (16.8%), porcelain crabs (2 species, 7.9%), the bivalve *Anomia ephippium* (7.4%) and the strawberry terebellid (7.2%).

Primer's biotic/environmental matching routine, using Spearman rank correlations, indicated that anoxia was the single most important variable ($r_s = 0.501$) and the number of rocks plus anoxia were the best pair of variables ($r_s = 0.789$) explaining biotic community structure. The Global BEST routine found that the inclusion of four variables (anoxia, rocks, slope, and water flow) were significantly related to invertebrate communities ($Rho = 0.81$, $p = 0.001$). The inclusion of current DO conditions under rocks at each site did not improve the correlation coefficients.

4. Discussion

4.1 Biodiversity patterns

As predicted, there were more under-rock species in the South Basin than the North Basin. This faunal difference was widely recognized in early studies (e.g., Ebling et al., 1960). Our prediction that historical sites (i.e., least-disturbed sites) would have the highest diversity was not supported. There was some evidence that scientific sampling, numerical domination by the anemone *Anthopleura ballii*, or even initial biotic differences among sites contributed to increased evenness at North Basin annual sites. One of the few cases supporting a sampling-induced increase in abundance was that of the solitary ascidians at South Basin annual sites. However, the dominance of the anemone could reflect the competitive advantage of oxygen production by the symbiotic microalgae in the oxygen-stressed North Basin. Finally, our prediction that low DO concentrations (2–7 mg O₂ L⁻¹) would strongly affect sensitive species appeared to be supported for cup corals, though laboratory experiments would be needed to confirm that oxygen was a causal rather than correlative factor.

How do our community-level diversity metrics compare with other studies within the lough? In terms of under-rock species richness, we recorded the abundance of 84 taxa *in situ* compared to 110 taxa recorded by Maughan and Barnes (2000), apparently, in the laboratory. Our study concentrated on solitary invertebrates that could be counted whereas they evaluated percentage cover of non-solitary species (sponges, hydroids, bryozoans, etc.). Furthermore, our studies differed in water depth, sampling area, and site distribution so our richness values were not expected to be comparable. Maughan and Barnes did not calculate H', J, or other diversity values but other authors have done so. Bell and Barnes (2000) reported subtidal sponge diversity H' values of 1.2 to 3.1 within the lough and refer to H'=3.6 based on their unpubl. data. Bell and Turner (2003) calculated richness values for mobile subtidal fauna along long transects in the lough: their values averaged below 20 taxa (slightly lower than ours). Although they statistically analyzed H' data, they did not show the values.

In terms of temperate rocky shores in other regions (New Zealand, Oregon, and elsewhere), researchers have frequently reported values between 2 and 4 (e.g. Schiel, 2011; Trowbridge, unpub. data), depending on how extensive the sampling may be. Vandepitte et al. (2010) reported arctic and temperate European H' values ranging from 4.0 to 5.5 for rocky shores and 2.0 to 4.8 for pelagic data.

4.2 Cup corals, corallimorphs, and anemones

The cup coral *Caryophyllia smithii* was recorded at 62.5% (10/16) of the monitoring sites in 1955 (Ebling et al., 1960). In 1990/91, it was found at 35-45% of the sites (7-9/20) (Little et al., 1992). In 2014, it was recorded from 76% of the sites (13/17), so it appears to have become more widespread recently. Hiscock and Howlett (1976) reported mean densities of 15 m⁻² at 16 m in the lough and 220 m⁻² outside the lough. The lough specimens were typically larger than oceanic ones (Hiscock and Howlett, 1976; Bell, 2002) though it was unclear if that was due to lower density of conspecifics (less intraspecific competition for space or food), lower levels of epibionts (barnacle *Boschia anglica*, boring worms, etc.), or lower mortality due to dislodgment. Our observations support Hiscock and Howlett (1976) such that the lough cup corals were not the “still-water” forms with a narrow base and fragile skeletons despite the low flow in the lough under shallow-subtidal boulders. However, there was much variation in shape of skeletons within the lough (Bell, 2002), and taller individuals were found in areas of high sediment such as the Goleen (Bell and Turner, 2000). On Whirlpool Cliff, cup corals were shown to be more common on inclined surfaces than on overhangs, as their sediment-tolerance allowed them to colonize these areas (Bell, 2001).

In contrast, the corallimorph or jewel anemone *Corynactis viridis* is sediment-intolerant (Bell, 2001), and is more common on overhangs than on inclined or vertical slopes. Ebling et al. (1960) reported the species at 25% of the sites whereas we recorded it from 47% of the sites (8/17), despite the fact that Ebling et al. worked down to 5 m and the species is more subtidal than intertidal. The polyps close when exposed to light and specimens do not inhabit unshaded shallow subtidal conditions (Muntz et al., 1972; Bell, 2001; Bell et al., 2006). Muntz et al. (1972) transplanted rocks with the species to various locations around the lough and monitored survivorship. The species persisted under rocks raised off the bottom of seawater tables but not on the shore, leading authors to speculate that “proximity of sediment, with its organic content” may be a controlling factor (Muntz et al., 1972: p. 749). We suggest that DO concentrations might be instrumental in constraining the distribution of this species. We found the species at 9 of the 11 South Basin monitoring sites and none of the North Basin ones.

The symbiotic anemone *Anthopleura ballii* is widespread in Lough Hyne (Bell and Turner, 2000; Bell, 2001). This species attained densities of 100–120 polyps m⁻² at 0 m on the south-western side of

the island (Bell, 2001). Its distribution was thought to be positively associated with light and current flow (Bell, 2001) although we found it at many sites (e.g., East Goleen) that have low flow and considerable daytime anoxia (Fig. 3B). A known predator of this anemone, the nudibranch *Aeolidia papillosa* (*sensu lato*), was not seen during our 2014 surveys although it has been recorded by us in earlier years, and reported by Nunn et al. (2006).

4.3 Solitary ascidians

Ascidia mentula, a large (up to 10-15 cm) ascidian, has been an important faunal constituent under shallow subtidal rocks in the South Basin for the past decade. This European species was reported as common elsewhere including Sweden, where it lives at least five years in exposed areas and seven in sheltered regions (Svane and Lundälv, 1981). Although these authors did not observe substantial predation on the species, in 2013 spiny sea stars (*Marthasterias glacialis*) were photographed by the first author (CDT), targeting the mussel *Modiolarca* embedded in the tunic of *A. mentula*. This caused extensive damage, often lethal, to the ascidian host. The smaller, short-lived *Ciona intestinalis* and allies were also abundant. The proliferation of *A. mentula* and perhaps other ascidians in the mid-2000s followed soon after the die-off of purple urchins in the lough's under-rock habitats (Trowbridge et al., 2011). Whether the ascidian proliferation was related to habitat availability or other factors is not known. However, Svane (1984) did report that larger urchins (*Echinus* spp.) detached *A. mentula* during their grazing activities.

4.4 Scientists as anthropogenic disturbances

With trawling, dredging, and soft-sediment cores, it is inherently obvious that scientists disturb the communities they sample, even in marine protected areas. As emphasized by Gutt (2001) in terms of Antarctic research, “the scientist has to abide by certain rules aimed at protecting the biota” and to evaluate “whether research activities harm the benthic ecosystem, which is generally seen as worth protecting, or whether their effect is insignificant.” However, with most rocky-shore studies including the two-decade monitoring surveys described herein, the extent of the damage or disturbance is unclear unless explicitly examined. Our 2014 study indicated that our long-term rock-lifting and turning (by Little, Stirling, Trowbridge, and team-members) did not significantly affect the under-rock

biota in Europe's first marine reserve. With careful methodology, nature conservation and marine reserve research can coexist as suggested by Gutt (2001).

Acknowledgments

We are grateful to D. O'Donnell and P. Graham of the National Parks and Wildlife Service for permission to carry out scientific research in the Lough Hyne Marine Reserve. We were much helped by information and assistance from T. Kearney (Skibbereen Heritage Centre) as well as L. Harman and J. Davenport (UCC colleagues). Hal Ross and the Hunrunrs provided continual encouragement and support throughout the project. We are indebted to the following colleagues for their field help: B. Dlouhy-Massengale, C. Otis, and other members of the 2014 IRES crew. We thank J. Davenport for his valuable and constructive comments on an earlier draft of this paper. CDT, KK, and CQP were supported in part by NSF grant INT-1130978 awarded to CDT. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

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Table 1. Static site characteristics of 10 long-term annually monitored sites and 10 historically monitored sites in Lough Hyne. Aspect measured in degrees from a north compass bearing, fetch measured in meters, slope measured in degrees from the horizontal and tree canopy as presence (+) or absence (-). Dynamic site attributes were also measured (but data not shown) including dissolved oxygen concentrations, presence of any signs of anoxia, number of rocks turned and relative water flow.

Sites	Basin	Aspect (°)	Fetch (m)	Slope (°)	Tree canopy
Annual sites					
Boundary Bay (BB)	south	182.5	214	5.7	+
Codium Bay (CB)	south	342.5	175	7.4	+
East Castle (EC)	north	60.0	54	3.6	-
East Goleen (EG)	south	247.5	34	10.8	-
Graveyard (GY)	south	345.0	312	7.5	-
North Island (NI)	north	172.5	884	41.5	-
North Labhra (NL)	north	345.0	539	8.1	-
South-East Labhra (SEL)	south	152.5	200	3.4	-
Westwood North (WWN)	north	87.5	559	9.1	+
Westwood South (WWS)	south	75.0	582	10.4	+
Historical sites					
Bohane Harbour (BH)	south	277.5	51	11.3	+
Glan Quay (GQ)	south	280.0	78	14.0	+
North Castle (NC)	north	357.5	206	4.2	-
North-West Castle (NWC)	north	347.5	415	4.9	-
Rookery Nook (RN)	north	257.5	566	30.8	+
South Castle (SC)	south	170.0	314	13.9	-
South Labhra (SL)	south	150.0	280	10.2	-
West Concrete (WC)	south	75.0	569	6.5	+
West Labhra (WL)*	south	252.5	253	16.8	-
Whirlpool Point (WP)	south	215.0	135	21.1	-

* Ebling et al. (1960) considered this a north-basin site but we considered it a south basin site based on current flow, exposure and topography.

Table 2. Results of ANCOVAs (analyses of covariance) for the effects of basin and disturbance regime on community biodiversity estimates. The number of rocks turned and dissolved oxygen concentrations under shallow subtidal rocks were covariates. Of the 20 sites surveyed, 3 sites were excluded from the analysis due to few rocks for which to evaluate epilithic communities. Sub-table A includes all taxa whereas B excluded the anemone *Anthopleura ballii* which numerically dominated at several sites.

Sub-table A	Species richness (S)			Shannon-Wiener (H')			Evenness (J)		
	Variables & Covariates	df	F	p	df	F	P	df	F
Basin	1	6.268	0.029*	1	0.431	0.525	1	0.016	0.901
Disturbance	1	0.871	0.371	1	2.797	0.123	1	6.086	0.031*
Basin × Disturbance	1	2.223	0.164	1	2.037	0.181	1	1.662	0.224
# of Rocks	1	1.238	0.290	1	0.217	0.650	1	1.086	0.320
Dissolved Oxygen	1	0.001	0.977	1	0.083	0.779	1	0.129	0.726
Error	11			11			11		

Sub-table B	Species richness (S)			Shannon-Wiener (H')			Evenness (J)		
	Variables & Covariates	df	F	p	df	F	P	df	F
Basin	1	6.295	0.029*	1	0.042	0.842	1	2.259	0.161
Disturbance	1	0.628	0.445	1	0.310	0.589	1	0.222	0.647
Basin× Disturbance	1	2.076	0.178	1	0.419	0.530	1	0.000	0.999
# of Rocks	1	1.263	0.285	1	0.691	0.423	1	0.248	0.628
Dissolved Oxygen	1	0.010	0.921	1	0.513	0.489	1	1.228	0.291
Error	11			11			11		

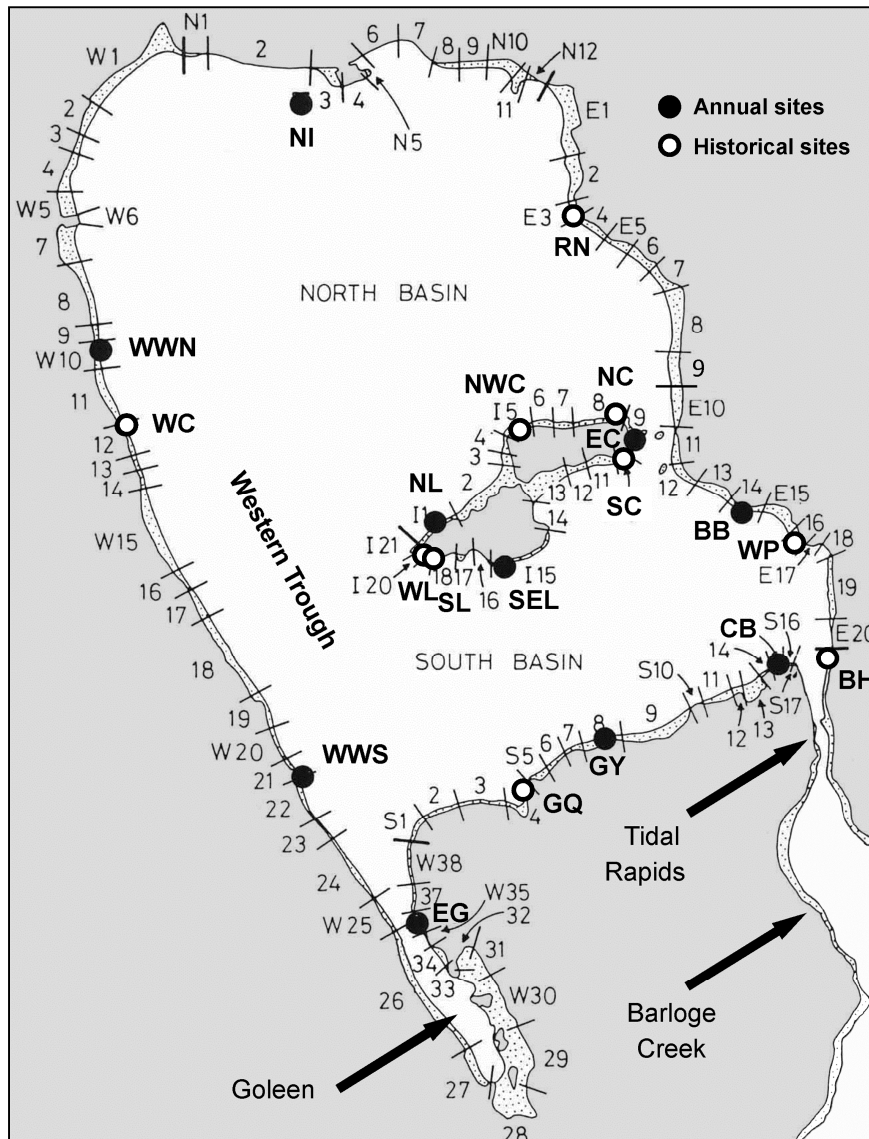


Fig. 1. Lough Hyne monitoring sites (circles), established by Ebling *et al.* (1960), are indicated by abbreviated site names: BB, Boundary Bay; BH, Bohane Harbour; CB, Codium Bay; EC, East Castle; EG, East Goleen; GQ, Glannafeen Quay; GY, Graveyard; NC, North Castle; NI, North Island; NL, North Labhra; NWC, Northwest Castle; RN, Rookery Nook; SC, South Castle; SEL, Southeast Labhra; SL, South Labhra; WC, West Concrete; WL, West Labhra; WP, Whirlpool Point; WWN, Westwood North; WWS, Westwood South. Intertidal zone (stippled) and shallow subtidal habitats are subdivided into topographically discrete units or Renouf sectors (short lines perpendicular to the shore) designated by shore (W, west; S, south; E, east, N, north; I, island) and sector number.

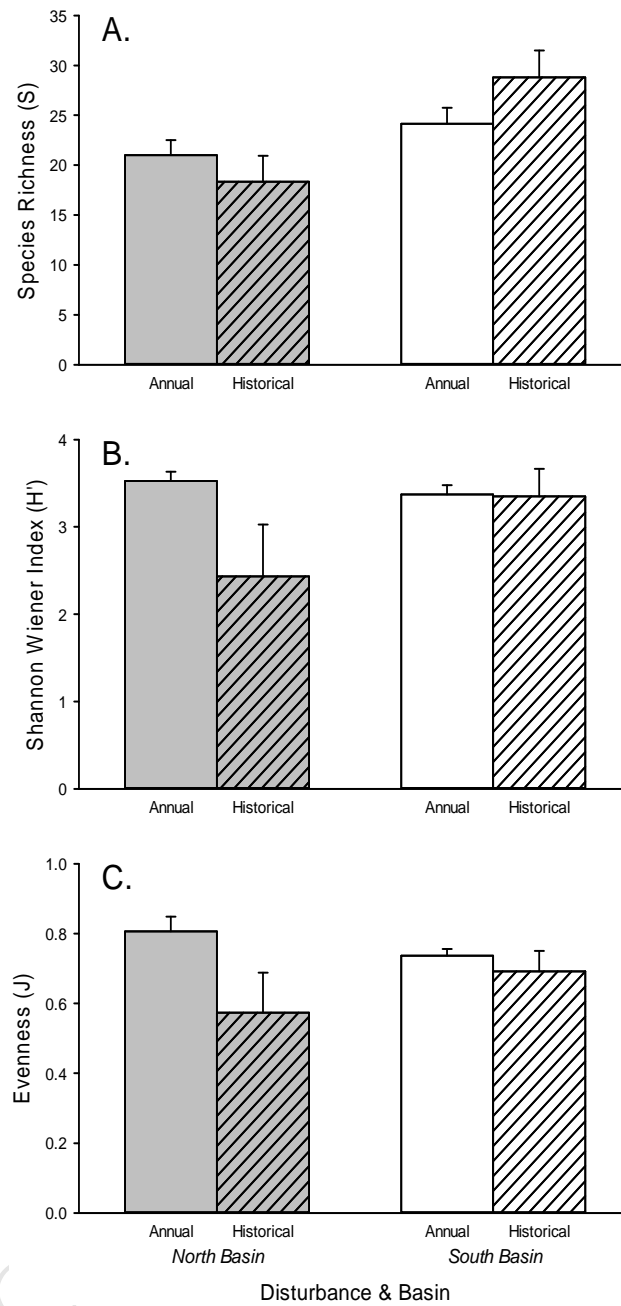


Fig. 2. Biodiversity indices of under-rock faunal communities at 17 monitoring sites in Lough Hyne in August and September 2014. Annual sites were sampled every year from 1994 to 2014 whereas historical sites were sampled only in 1955 (Ebling et al., 1960), 1990/1991 (Little et al., 1992), and 2014 (this study). Sample sizes were 3 sites per disturbance regime in the North Basin and 5-6 in the South Basin. Error bars indicate 1 SE.

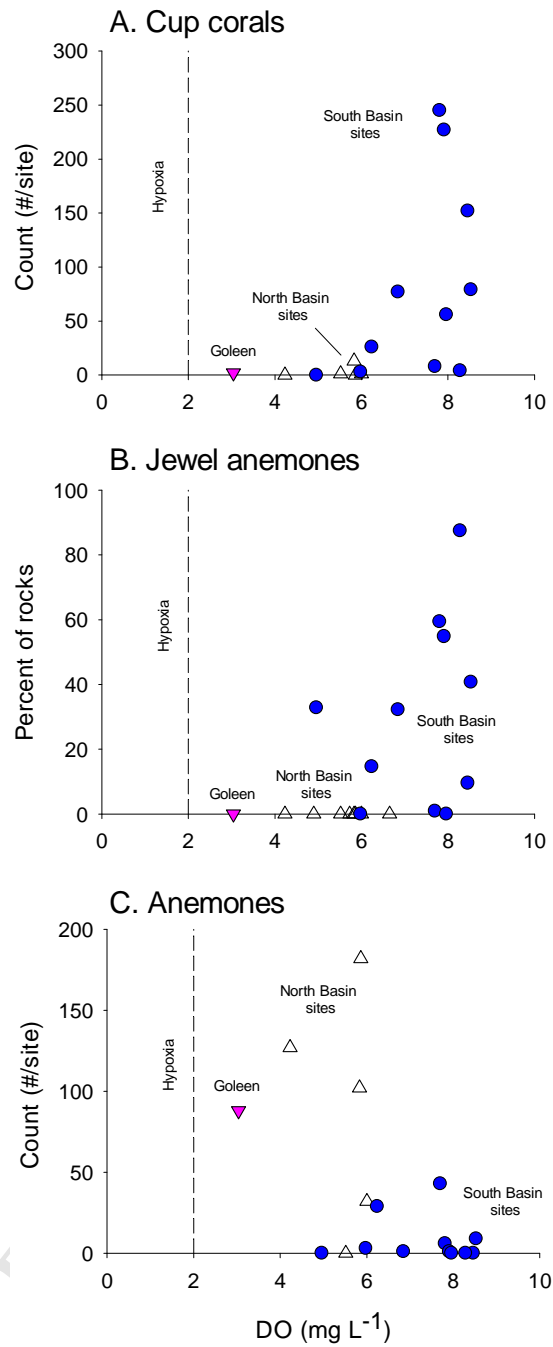


Fig. 3. Abundance of 4 species of cnidarians with respect to dissolved oxygen concentrations (mean of 10 measurements under rocks) at 17 shallow subtidal sites at Lough Hyne Marine Reserve in late summer 2014. Taxa are as follows: A. *Caryophyllia smithii*, B. *Corynactis viridis*, and C. *Anthopleura ballii*.

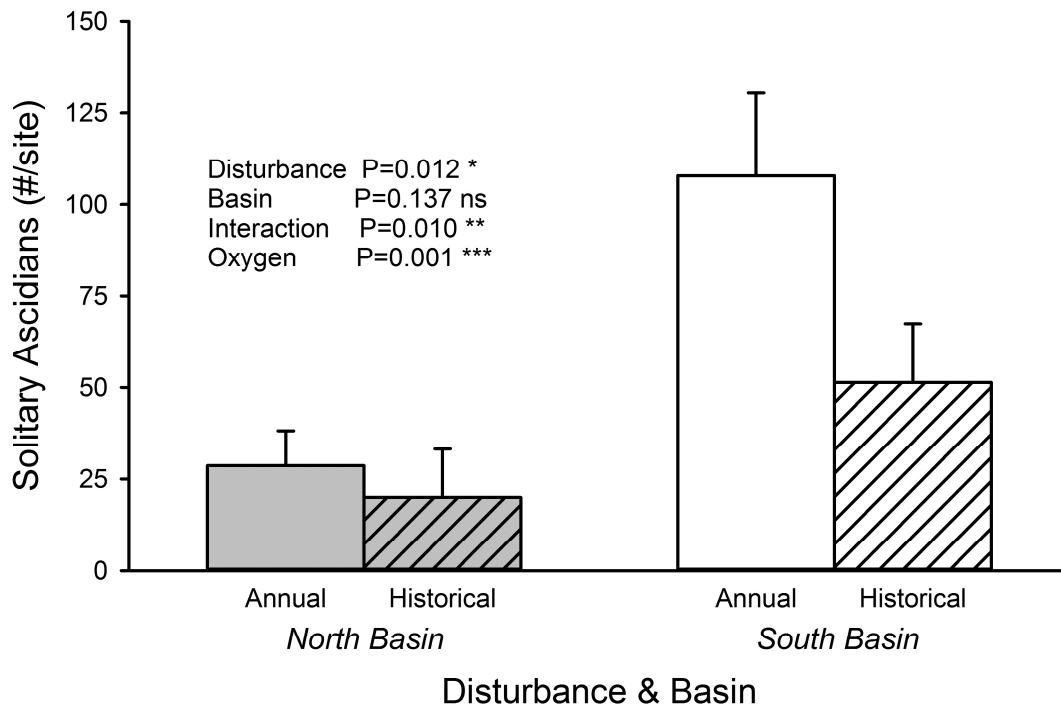


Fig. 4. Abundance of solitary ascidians at 17 shallow subtidal sites at Lough Hyne Marine Reserve in late summer 2014. Sample sizes were 3 sites per disturbance regime in the North Basin and 5-6 in the South Basin. Error bars indicate 1 SE.

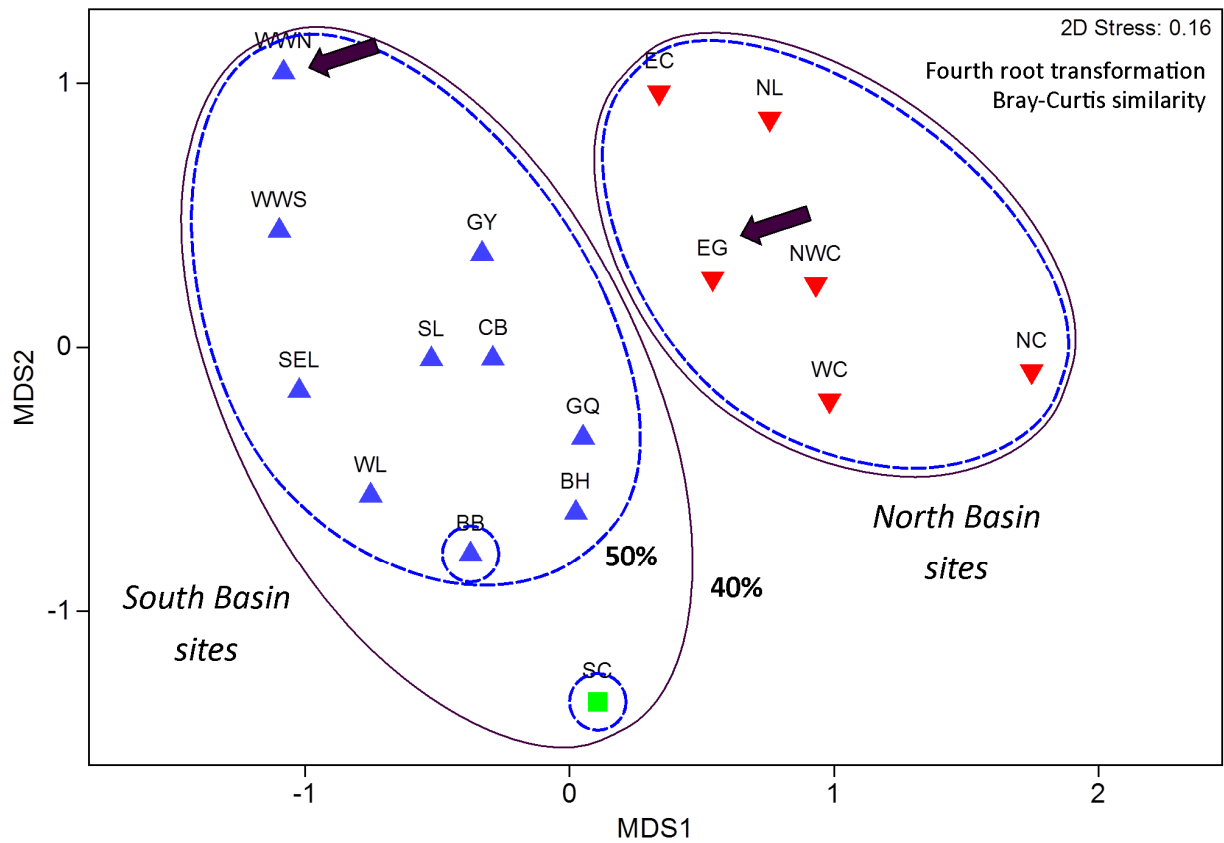


Fig. 5. Non-metric multidimensional scaling (nMDS) of under-rock fauna at 17 monitoring sites in Lough Hyne. The Primer data matrix was composed of 84 taxa. Blue and green symbols denote South Basin sites, red triangles denote North Basin, and black arrows denote two exceptions. Dashed lines indicate 50% similarity and the solid line indicates 40% similarity.

Appendix 1. Partial list of taxa surveyed under rocks *in situ* or from digital photographs at Lough Hyne.

PORIFERA

Aplysilla rosea
Aplysilla sulfurea
Clathrina
clathrus/coriacea
Clathrina rubra
Dercitus bucklandi
Dysidea fragilis
Leucosolenia sp.
Pachymatisma johnstonia
Plakina monolopha
Scyon sp.
Terpios gelatinosa
Tethya sp.
 Unknown Pea-green sponge

CNIDARIA

Scyphistoma
Caryophyllia smithii
Alcyonium hibernicum
Alcyonium glomeratum
Sarcodictyon catenatum
Anthopleura ballii
Corynactis viridis
 ?*Isozanthus* sp.
Sagartia spp.

PLATYHELMINTHES

Prostheceraeus vittatus
 Unknown flatworm

NEMERTEA

Paradrepanophorus crassus
Lineus longissimus
Tubulanus annulatus
Micrura purpurea
Micrella rufa
 Other nemerteans

MOLLUSCA**GASTROPODA**

Aeolidiella spp.
Calma gobioophaga
Doris pseudoargus
Janolus cristatus
Jorunna tomentosa
Gibbula umbilicalis
Gibbula cineraria

Lacuna sp.
 cone snail
 cerith snail
Diodora graeca
Nassarius incrassatus
 Rissoid snail
Patella spp.
Emarginula fissura
Tectura virginea
Lamellaria spp.
Nucella lapillus
Trivia spp.

BIVALVIA

Ostrea edulis
Mytilus edulis, *M. galloprovincialis*, or hybrids
Hiattella arctica
 Cockle
 Other bivalves
Anomia ephippium
Heteranomia squamula
Mimachlamys varia
Musculus subpictus

POLYPLACOPHORA

A
Acanthochitona sp.
Boreochiton rubra
Lepidochitona cinerea
Leptochiton asellus
Stenosmus albus
 Unknown chitons

ANNELIDA

Amphitrite
Dorvillea rubrivittatus
Euprosyne sp.
Filograna sp.
Metavermilia multicristata
 Mobile errant
 Nereid
 Phyllodocid
Polynoe scolopendria
 Polynoid
 Sabellid
Spirobranchus spp.

ARTHROPODA

Verruca stroemia

Balanus balanus
 Porcelain crab species
Galathea squamifera
Galathea strigosa
Carcinus maenas
Macropodia, Inachus, etc. & allies
Athanas nitescens
 Misc. shrimp
 Pycnogonid

BRYOZOA

Disporella hispida
Plagioecia patina
Schizomavella sp.
Bugula flabellata
Escaroides sp.
Crisia spp.
 Unknown white encrusting species

TUNICATA

Pyura tessellata
Ciona & allies
Ascidia, Ascidiella, & allies
 Other solitary tunicates
Clavelina lepadiformis
Dendrodoa sp.

ECHINODERMATA

Asterias rubens
Asterina gibbosa
Asterina phylactica
Marthasterias glacialis
Echinus esculentus
Paracentrotus lividus
Psammechinus miliaris
Pawsonia saxicola
 Other asteroids
 Brittle star spp.

BRACHIOPODA

Novocrania anomala

CHORDATA**VERTEBRATA**

Cling fish
 Rock goby
 Pipefish species

ACCEPTED MANUSCRIPT

- Scientific sampling did not affect invertebrate S or H' at Irish marine reserve.
- In nMDS analyses, North and South Basin sites generally clustered separately.
- Low-oxygen conditions frequently occurred, damaging under-rock communities.
- Dissolved oxygen was a crucial factor for cup corals and other species.