

Long-term fluctuations in epibiotic bryozoan and hydroid abundances in an Irish sea lough

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ABSTRACT

Recent declines in coastal water quality in SW Ireland have led to changes in the abundance of algal-associated bryozoans and a hydroid. These common North Atlantic species offer considerable potential as indicator species for reduced oxygen conditions due to habitat degradation. Annual monitoring for over more than two decades (1994–2016) at 10 rocky shore sites within Lough Hyne Marine Reserve, SW Ireland revealed a significant reduction in abundance of the ctenostome bryozoan, *Flustrellidra hispida*, through time, coincident with the development of daily, extreme, shallow water oxygen fluctuations (hyperoxia and hypoxia) due to eutrophication. In contrast, the ctenostome, *Alcyonidium* species-complex, increased significantly during the two-decade period. The thecate hydroid, *Dynamena pumila*, did not show any significant decadal-scale pattern but temporal variability in abundance increased since 2010. Abundances of *F. hispida* and *D. pumila* were positively correlated with estimates of water flow. *F. hispida* inhabited a variety of algal hosts but appeared most sensitive (of the taxa surveyed) to variation in habitat quality, especially experimentally reduced levels of dissolved oxygen (<4 mg L⁻¹). Such sensitivity indicates *F. hispida* could be useful as an indicator of environmental change, whereas *D. pumila* was more robust in response to reduced oxygen with 38.6% of the hydroid zooids being able to survive under hypoxic conditions as compared to only 0.2% of the bryozoan zooids. Given the widespread European distribution of these species, they offer the opportunity to act as important bioindicators of water quality and hence environmental degradation in north temperate intertidal systems.

Keywords: Long-term, Bryozoa, Hydrozoa, Algal epifauna, Ireland, Intertidal

1. Introduction

Coastal areas worldwide are being subjected to intense anthropogenic pressures, from nutrient enhancement and resource extraction to recreational activities and climatic changes. According to Mockler et al. (2017: 326), “More than half of surface water bodies in Europe are at *less than good* [emphasis added] ecological status”; about 33% of Irish coastal waters surveyed by the Environmental Protection Agency are in this category (Bradley et al., 2015). Agriculture is the primary source of nitrogen enhancement in Irish coastal waters (Hartnett et al., 2011; O’Boyle et al., 2016; Mockler et al., 2017) which contributes towards ephemeral, macroalgal blooms (Hartnett et al., 2011; Ní Longphuirt et al., 2016) which have been shown to significantly impact marine community structure and function all around the world (Lyons et al., 2014; O’Boyle et al., 2017).

Small, epifaunal suspension feeders respond to a variety of natural and anthropogenic environmental stresses. Bryozoans, for example, are typically not found in eutrophic environments preferring well-oxygenated habitats such as ‘rapids’, sheltered habitats with large tidal flow and hence fast moving waters (e.g. Ryland and Haywood, 1977), although there are notable exceptions in both freshwater and marine environments (e.g., Hartikainen et al., 2009). Scholz (1990) reported that bryozoan communities in a eutrophic harbour in the Philippines exhibited a significant decrease in larval settlement during the start of monsoon-associated changes in environmental conditions (with wind-generated water movements) whereas communities on a nearby oligotrophic coral reef did not. As a result, Scholz proposed that bryozoans are excellent indicators of environmental stress although the causal nature of the stress impact (low salinity, elevated nutrients, high pollutants, unusual siltation, etc.) cannot always be ascertained. Cooper and Burris (1984) also suggested that freshwater bryozoans may be indicators of habitat quality and, from the fossil record, several assessments of marine cheilostome bryozoans have been used to infer unfavourable conditions before the mass extinction at the Cretaceous-Tertiary boundary (O’Dea et al., 2011).

Many bryozoans and hydroids are sensitive to hypoxia, exhibiting mortality (Cuffey, 1970; Vaquer-Sunyer and Duarte 2008) or reduced growth and feeding rates (Sagasti et al., 2001). Since both bryozoans and hydroids are major components of epibiotic communities, hypoxia may thus act indirectly to influence the composition of these communities, by altering the competitive ability of the component species. Furthermore, calcareous bryozoans have been advocated as sensitive indicators, providing early warning of ocean acidification or other adverse environmental conditions (Smith, 2009, 2014). According to this view, bryozoans and hydroids would appear to be appropriate candidates to monitor long-term habitat change. However, recent authors have stressed the high metabolic flexibility of bryozoans (Barnes and Peck, 2005), their resistance to ocean acidification (Saderne and Wahl, 2013), and their ability to maintain equal growth efficiencies across a wide range of treatments including high CO₂, low temperature and low food availability (Swezey et al., 2017).

To test the validity of these two opposing views, we used long-term studies to determine the reactions of bryozoan and hydroid epibionts to changing environmental conditions. We focused on the

well-studied taxa associated with intertidal brown algae. Extensive work in the United Kingdom and Ireland has focused on algal host-specificity, population dynamics, and species interactions of four common taxa found throughout the North Atlantic on intertidal fucoid algae: the thecate hydroid, *Dynamena pumila* (Linnaeus, 1758), the cheilostome bryozoan, *Electra pilosa* (Linnaeus, 1767), and ctenostome bryozoans, *Flustrellidra hispida* (Fabricius, 1780), and the *Alcyonidium hirsutum* (Fleming, 1828)/*A. gelatinosum* (Linnaeus, 1761) species complex (Stebbing, 1973; Boaden et al., 1975; Ryland and Nelson-Smith, 1975; O'Connor et al., 1980; Seed and Harris, 1980; Seed and O'Connor, 1981a, b; Seed and Wood, 1994; Orlov, 1996; Ryland and Porter, 2006; references therein). While there are several other genera of bryozoans and hydroids that occur on brown algae (e.g., Boaden et al., 1975; O'Connor et al., 1979), *F. hispida*, *E. pilosa* and *Alcyonidium* spp. are typically the most frequent species on serrated wrack, *Fucus serratus* (L.) and *D. pumila* the most frequent hydroid on *Ascophyllum nodosum* (L.) (e.g., Wood and Seed, 1992; Williams, 1996). These three species of bryozoan, together with *Membranipora membranacea*, are frequently so abundant on fucoid fronds that intense competition for space occurs (O'Connor et al., 1980). These epibionts can also occur on other algal hosts (e.g., fucalean and laminarian taxa: Boaden et al., 1975; Ryland and Nelson-Smith, 1975; Seed and Harris, 1980; Seed and O'Connor, 1981a; Orlov, 1996), and *E. pilosa* is frequently recorded on a wide variety of algae and hard substrata (Ryland and Hayward, 1977).

There are very few long-term ecological studies of marine bryozoans—or even physiological studies—despite their purported significance as bioindicators. Indeed, there are remarkably few long-term studies of rocky-shore communities (but see Bishop, 2003 for a notable exception) despite Mieszkowska et al. (2014) and similar studies emphasizing the scientific importance of sustained observations. In the present study, we conducted annual surveys for two decades of the abundance of *F. hispida*, *Alcyonidium* spp. and *D. pumila* on rocky shores in Lough Hyne, and in 2015 we expanded the survey to include *E. pilosa*. Lough Hyne is a marine lough in southern Ireland that was designated as a Marine Reserve in 1981, partly at least, because of its pristine quality, but which has seen a significant decline in environmental conditions in recent years (nutrient enhancement and extreme oxygen fluctuations: Jessopp et al., 2011; Trowbridge et al., 2017a).

As a result of this decline in environmental conditions, we had two general predictions. First, we hypothesized that the abundance of the bryozoan and/or hydroid species would decrease with declining habitat quality within the lough, and therefore would be an effective bioindicator of water quality. Based on dissolved oxygen levels in shallow water and proliferation of ephemeral algae (ectocarpoids and ulvoids), the decline in environmental/habitat quality started in 2010 (e.g. Trowbridge et al., 2011, 2013, 2017a,b), with slight improvements observed in 2015 and 2016. The species that was most sensitive to recent changes would be considered the best indicator species.

Second, since the mass mortality of purple urchins (*Paracentrotus lividus*) in the lough (Trowbridge et al., 2011) and the concomitant expansion of many brown algae into the lough's North Basin (Trowbridge et al., 2013), we predicted that the algal-associated epibionts might also expand

their distribution into the North Basin of the lough on the newly available algal hosts. Although these two changes might counteract each other to some degree, the contrasting effects (an overall reduction due to eutrophication vs a northward expansion due to broader host distribution) should be distinguishable.

In addition to these two general predictions, based on past studies (e.g. Rossi et al., 2000), we predicted there would be (1) positive correlations of the epibionts with increased water flow and (2) negative correlations with shore slope (fewer furoid host thalli on steeper than on flatter shores).

2. Materials and methods

2.1. Site description

Lough Hyne is a semi-enclosed sea-lough in southwest Ireland (Fig. 1A), which is connected to the sea by narrow ‘Rapids’ (Bassindale et al., 1948). It was designated as Europe’s first Marine Reserve in 1981. In area it measures only approximately 1 km², and consequent upon the small fetch, all its shores are relatively sheltered. Because of the restricted inflow at the Rapids, the tidal cycle is asymmetrical, and the tidal rise and fall is restricted to about 1 m, so the intertidal zones are compressed (Rees, 1931, 1935; Bassindale et al., 1948; Little, 1991). Much of the intertidal is either bedrock or shingle, and varies from nearly vertical to shallow slopes (Ebling et al., 1960). There are several areas where small freshwater flows or seeps enter the lough and locally dilute the surface water (Rees, 1935). However, there is almost no dilution of the main body of the lough below a salinity of ca. 34 (Kitching, 1987). At times of exceptionally high rainfall, a localised thin freshwater lens may form at the surface (Little, pers. obs.).

2.2. Study sites

The fauna and flora of the rocky intertidal zone were first quantitatively surveyed in 1955 by Ebling et al. (1960). The researchers defined 20 monitoring sites around the lough and recorded the location of these photographically. The sites were resurveyed in 1990 and 1991 by Little et al. (1992).

Ten monitoring sites (‘annual sites’) were selected for annual monitoring (Fig. 1B), out of the 20 initially surveyed by Ebling et al. (1960). Each site consisted of a 10-m length of rocky shore marked at each end with a stainless steel plate to enable exact recognition at future sampling times. Each site was subdivided into five 2-m-long sections ($\Sigma_N = 10 \text{ sites} \times 5 \text{ sections} = 50$). Surveys were carried out from 1994 to 2016 at the same time of year, in the last week of August and first week of September.

Additional surveys, including the remaining 10 sites originally surveyed by Ebling et al. (1960) (‘historical sites’), as well as the ‘annual sites’ (i.e. the total defined 20 monitoring sites) were carried out in August/September 2015. These 20 sites provided a total of 100 sections and allowed comparison with two earlier surveys (Ebling et al., 1960; Little et al., 1992).

Finally, to provide a more detailed view of epibiont distribution patterns, a survey of the entire shoreline of the lough (above the Rapids) was carried out in September 2016 to detect the presence/absence of target species in the 108 sectors (Fig. 1B) originally assigned by Renouf (1931).

2.3. Epibionts

For the 23-year survey (1994 to 2016), the hydroid *Dynamena pumila* and the algal-associated bryozoans *Flustrellidra hispida* and *Alcyonidium* spp. were recorded (present vs. absent) in each section at the 10 sites. We first examined the low intertidal furoid *Fucus serratus* for the bryozoans, and the mid intertidal furoid *Ascophyllum nodosum* for the hydroid, searching all available thalli. If the epibionts were not present on these algae, we then checked other intertidal fucoids (e.g., *Fucus vesiculosus*) within each section. In 2015, the same procedure was carried out with two additions: surveying at all 20 monitoring sites (annual and historical sites) and including an additional specific search for *Electra pilosa*. In 2016, similar procedures were carried out in the 108 Renouf sectors, when all abundant perennial algal species were searched, and host algae for *F. hispida* and *E. pilosa* were recorded.

Flustrellidra hispida seasonally recruits to its algal hosts from June to August (Seed et al., 1981; Seed and Wood, 1994) and *Dynamena pumila* from April to August (Cornelius, 1995), so both were expected to be abundant during our August/September sampling. *Alcyonidium hirsutum* seasonally recruits in the autumn and/or winter (Seed et al., 1981; Seed and Wood, 1994; Ryland and Porter, 2006) but the adult colonies would still be present in late summer. *Electra pilosa* also recruits in late summer and autumn. Although cyphonautes larvae are present in the plankton all year round, colonies contain eggs and sperm in August and September (Ryland and Hayward, 1977). As there is known intra- and inter-thallus variation in recruitment (Seed and Wood, 1994) as well as site-specific differences related to water flow, we felt that the large-scale view (2-m sections at 10-m wide sites) would detect major changes in epifaunal populations. To determine if there were changes in temporal abundance of the taxa through the survey time, Pearson's correlations were used when data were normally distributed (based on the Shapiro-Wilks test); otherwise, Spearman rank correlations were calculated. Likelihood ratio chi-square tests were used to compare the frequency of occurrence of the bryozoans and hydroids from 1955 (Ebling et al., 1960), 1990 (Little et al., 1992), and 2015 (this study). We first compared all three dates and when the results were significant, we then conducted pairwise comparisons. As the 1955 vs. 1990 comparison has already been published (Little et al., 1992), we focused herein on 1955 vs. 2015 and 1990 vs. 2015.

Finally, to evaluate if low host availability in the North Basin constrained epibiont occurrence, we conducted a field transplant experiment of *F. serratus* to 7 North Basin sites (WWN, NL, NWC, NC, EC, RN, and sector N1) and 1 South Basin site (WL). Specifically, we attached 16 epibiont-free fronds of *F. serratus* to 0.25-m² quadrat frames and transplanted these frames to shallow subtidal habitats from June to September 2017; we expected settlement of *F. hispida* (if algal host availability

was the limiting factor) as the summer was the species' reported recruitment period (Seed et al., 1981; Seed and Wood, 1994).

2.4. *Physical factors*

In March 2015, we measured the relative water flow, aspect, and fetch at each of the 10 sites. For flow, we made hemispherical plaster of Paris (gypsum) blocks (Muus, 1968; Doty, 1971; Seed and Hughes, 1992) that were dried, attached to bricks and transplanted at each site for three days to measure weight loss of plaster as a relative measure of water flow; three control blocks were set in buckets of seawater to measure weight loss without current flow. Aspect was measured by the compass direction (in degrees) of each end of the site relative to a north bearing and the two values averaged for a site attribute. Fetch (in metres) 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). Slope (at the low-tide level of the epibionts) was measured in September 2016 using a clinometer ($\pm 5^\circ$), with a 0.5-m base. Five measurements were made in each 2-m sector, i.e. 25 measurements per site. Most of the site-specific physical factors are summarized by Trowbridge et al. (2017b) so are not shown here.

Because most of the data were not normally distributed, we analysed the three algal-associated taxa in two ways. First, we conducted a multivariate analysis of the epibiont assemblage, using Primer ver. 7. Specifically, we conducted non-metric MDS (multi-dimensional scaling) of Bray-Curtis similarities of fourth-root transformed abundance data. The biotic resemblance matrix was then compared to the environmentally derived one (based on flow, slope, aspect, and fetch of sites). Because aspect (compass direction) was a circular variable rather than a linear one, we broke down the two-dimensional component of each angle, using cosine and sine function of the angle (in radians, not degrees); the two functions were selected together, using an indicator variable, in Primer's BEST routine. Second, for each of the four taxa, we calculated the relationship with each physical factor, using non-parametric Spearman rank correlations (Systat ver. 9) because data were not normally distributed. In all tests, as we had specific predictions (e.g. increased epibionts with increased water flow), we used 1-way probabilities.

2.5. *Ephemeral algal mats and dissolved oxygen*

From 2011 to 2014, we surveyed the relative abundance of the ephemeral algal mats which were composed of ulvoids, ectocarpoids, etc. at the 10 sites. In 2015 and 2016, we also deployed Onset HOBO sensors (U26-001) to measure dissolved oxygen levels within algal mats and open areas or large (>1 metre in diameter) 'gaps' in the mats (within metres to tens of metres of each other along the shoreline). Two sensors were deployed (1 in an algal mat and 1 in a gap) in 2015; in 2016, we had 5 sensors (3 in algal mats and 2 in gaps). The sensors recorded dissolved oxygen levels every 15 min for

6 days on the North Shore (in Renouf sector N2) in September 2015 and for 5 days on the West Shore (sectors W16 and W17) in August-September 2016.

2.6. Experimental determination of low-oxygen tolerance

In September 2017, we conducted two laboratory experiments to evaluate epibiont tolerance to reduced dissolved oxygen levels. For the first experiment, we used a 1 cm x 1 cm piece of the bryozoan *Flustrellidra* (attached to its algal host *Fucus serratus*). For the second, we used 20 upright colonies of the hydroid *Dynamena* with approximately 20 zooids per colony. We did not test *Alcyonidium* because it was a species complex with at least three recognized species (see Ryland and Porter, 2006) recorded by us in 2017 as present in the lough: *A. hirsutum*, *A. gelatinosum*, and *A. polyoum*.

For each experiment, we used 1.0-L jars filled with filtered seawater; we lowered the dissolved oxygen (DO) levels in each experimental jar by bubbling down with nitrogen gas and then measured the starting DO values in each jar. Our four treatments were ‘normoxic’ water (unmanipulated control: ca. 8 mg O₂ L⁻¹), ‘suboxic’ (ca. 4 mg L⁻¹), ‘hypoxic’ (<2 mg L⁻¹), and ‘anoxic’ (<0.2 mg L⁻¹) with five replicates per DO treatment. All 20 jars were placed in a water bath with the temperature maintained close to that in the lough (15-17°C). After 24 hours, we added neutral red dye to each jar (final dye concentration was 1:100,000 as used by Jessopp, 2007); the dye stains lysosomes in living animal tissue bright red but not in dead tissue (Crippen and Perrier, 1974) and is widely used in determining lethal environmental stress in invertebrates (e.g. Svendsen and Weeks, 1995). After 6 hours, the final DO levels were determined as well as the number of zooids that were alive vs. dead in each jar. After checking the survivorship data for normality and homogeneity of variances, the data were analysed with non-parametric Kruskal-Wallis tests, followed by *post-hoc* multiple comparisons with the Tukey-like analogue following Zar (1984).

3. Results

3.1. The bryozoan *Flustrellidra hispida*

The distribution of the ctenostome bryozoan, *Flustrellidra hispida*, differed significantly when we compared 1955, 1990, and 2015 data (Fig. 2, Likelihood ratio chi-square test, $G = 11.6$, 2 df, $N = 60$, $P = 0.003$). The 2015 distribution was similar to that in 1990 (Fig. 2, $G = 0.1$, 1 df, $N = 40$, $P = 0.751$). However, prior to this in 1955, the bryozoan had a much wider distribution, occupying 18 of 20 sites (fig. 45 in Ebling et al., 1960), including several sites in the North Basin. The 1955 vs 2015 distributions differed significantly with a wider distribution in 1955 than in 2015 ($G = 9.918$, 1 df, $N = 40$, $P = 0.002$). The bryozoan thus suffered a significant and protracted contraction in distribution, especially in the North Basin, at some time after 1955 but before 1990. Since 1990 there has apparently been no significant change in overall distribution.

From 1994 to 2016, *F. hispida* was present every year at five sites in the South Basin of the lough: Westwood South, SE Labhra, Boundary Bay, Codium Bay and Graveyard (Fig. 3A-B); the bryozoan never occurred at East Goleen, a site where the shallow subtidal habitat was typically hypoxic to anoxic with a strong odour of hydrogen sulphide. Occasionally the species occurred in the North Basin at North Labhra and Westwood North. Until 2011 presence of the bryozoan varied between 15 to 29 of the 2-m wide sections at the monitoring sites (30-58% of 50 sections Fig. 3A). Subsequently, its frequency of occurrence within sites declined abruptly such that in 2013 and 2014 the bryozoan was recorded in only 9 out of 50 sections (18% of sections). In 2015 this rose to 14 sections, but fell again in 2016 to 11 sections. There was a significant decline over the two-decades (Pearson correlation, $r = -0.528$, $N = 23$, $P = 0.01$).

The detailed distribution of *F. hispida* in 2016 showed this species to occur in 45 out of the 108 Renouf sectors (~42%) but it was absent from much of the Goleen and scarce in most of the North Basin, though dense populations were recorded in sector E5 (Fig. S1). *Flustrellidra hispida* showed a varying relationship with its host algae (Fig. S2). Near the Rapids, it was very common on its usual primary host, *F. serratus*, but was also often found on *A. nodosum* and *F. vesiculosus*. Further from the Rapids (on the Island and parts of the East and West shores) it was found mostly on *A. nodosum*, particularly at the very bases of stipes where the algae were clumped on the rock surface. At some sites around Castle Island and in E4 it was abundant on the long bare stipes (i.e., no remaining lateral blades) of *F. vesiculosus* but was absent from the dense bushy clusters of fronds. The penetration of *F. hispida* into the North Basin on the East shore also coincided with the presence of *F. serratus* in E4 and E5 (Fig. S1-2), but at other sites where *F. serratus* was absent, the bryozoan occurred on *F. vesiculosus*.

3.2. The bryozoan *Alcyonidium* spp.

The distribution of *Alcyonidium* species-complex differed significantly among the three surveys (Fig. 2, Likelihood ratio chi-square test, $G = 39.187$, 2 df, $N = 59$, $P < 0.001$). In 1955, records for *Alcyonidium* showed a very restricted distribution (Ebling et al., 1960, fig. 44) compared to the 2015 distribution ($G = 33.1$, 1 df, $N = 39$, $P < 0.001$). The wide distribution of *Alcyonidium* in 2015 (Fig. 2) was, however, similar to that in 1990 ($G = 1.2$, 1 df, $N = 40$, $P = 0.282$).

After an apparent rise in abundance from 1994 to 1996, the distribution of *Alcyonidium* spp. was relatively constant from 1996 to 2015 (Fig. 3C). Over the whole period, the total number of 2-m sections at which *Alcyonidium* was present varied from 32 to 50 and it was present in all 50 sections in 2010 and 2011. There was a significant increase of this taxon over the two-decades (Pearson's correlation, $r = 0.531$, $N = 23$, $P = 0.009$).

Alcyonidium species complex was found on *Fucus vesiculosus*, *F. serratus* and *Ascophyllum nodosum*. It was more widely distributed than *Flustrellidra hispida*, being present in 106 out of 108

(>98%) Renouf sectors in 2016 (Fig. S1A). In June 2017, we recorded three congeners present at three sites (Goleen, Codium Bay, and Bohane Harbour): *A. hirsutum*, *A. gelatinosum*, and *A. polyoum*.

3.3. The thecate hydroid *Dynamena pumila*

The distribution of the hydroid *Dynamena pumila* decreased slightly between 1955 and 1990 (Fig. 2), but increased again by 2015 although these temporal trends were not statistically significant ($G = 2.2$, 2 df, $N = 60$, $P = 0.329$).

Over the period 1994 to 2016, the hydroid showed considerable variation, occurring at 22–36 sections (44–72%, Fig. 3E). It was common at most sites in the South Basin (except East Goleen) as well as two North Basin sites (East Castle and North Labhra, Fig. 3F). The species was occasionally found at other sites in the North Basin and at East Goleen. It did not increase at Westwood North in the last decade despite the increase of its host *A. nodosum* (Little et al., unpubl. data). In 2013 the hydroid's distribution dropped to an all-time low (22 sections, 44%), but recovered slightly in 2014, to fall again to 23 sections in 2015. There was no significant overall linear change in hydroid abundance on the 2-decade scale (Pearson's correlation, $r = 0.033$, $N = 23$, $P = 0.882$) but increased fluctuations were noted from 2009/2010 onward.

In the 2016 survey *Dynamena* was found at 75 out of the 108 Renouf sectors (~70%, Fig. S1B). It was ubiquitous in the South Basin but absent in the Goleen, where the shallow subtidal substrate was very muddy and hypoxic to anoxic with a strong odour of hydrogen sulphide. In the North Basin the hydroid was less widespread. Its major host in the lough was *A. nodosum* at the mid-tide level, unlike the bryozoan species which occurred mostly near low-tide level, but it was also recorded on *F. vesiculosus* and *F. serratus*.

3.4. The bryozoan *Electra pilosa*

The bryozoan *Electra pilosa* showed a scattered distribution around the lough. Although not followed in detail over the two-decade monitoring period, it appeared to have increased in distribution from 1955 to 1990 and again to 2015 at the 20 monitoring sites (Fig. 2). This has mostly been due to an increased occurrence at sites in the North Basin, though all the colonies recorded there were very small (5–10 mm in diameter).

Electra pilosa was widely distributed in the 2016 survey of Renouf sectors (Fig. S1C) being recorded in 82 out of 108 (76%) Renouf sectors. It was absent in the Goleen and in very sheltered bays. It was found on a variety of brown and red host algae: *Fucus serratus*, *F. vesiculosus*, *Ascophyllum nodosum* and *Chondrus crispus*.

3.5. Distributions in relation to physical factors

The assemblages of epibionts varied among sites with the North Island and East Goleen assemblages being notably different than those at the other eight sites (Fig. 4). Fetch was the best

single predictor of epibiont abundance; and fetch coupled with water flow had the highest Spearman rank correlation (0.386). Inclusion of shore slope or aspect decreased the correlation coefficient. The distributions of the species varied in relation to relative water flow (Fig. 5).

It was predicted that there would be more occurrences of hydroids and bryozoans at higher-flow than lower-flow sites and this was true for *Flustrellidra hispida* (Fig. 5A), which increased significantly with flow (Spearman's $r_s = 0.723$, $N = 10$ sites, $P < 0.05$). This distribution of *Flustrellidra* could arguably be divided into two main groups of sites: ones with reduced flow and low numbers of *Flustrellidra* (e.g., North Basin sites and East Goleen) and those with high flow and greater abundance of *Flustrellidra* (e.g. South Basin sites). In contrast *Alcyonidium* spp. occurrence (Fig. 5B) was high at all sites and did not show any variation with water flow (Spearman's $r_s = 0.472$, $N = 10$, $P > 0.05$). *Dynamena* occurrence (Fig. 5C) over the two-decade period (i.e., overall counts at each site) showed the most clear relationship with short-term estimates of water flow, increasing significantly with water flow (Spearman's rank correlation, $r_s = 0.624$, $N = 10$, 1-sided $P < 0.05$). In terms of other physical variables, the aspect of the sites was not significantly correlated with the occurrence of the three epifaunal taxa; however, the mean slope of the lower shore was negatively correlated for *Dynamena pumila* (Spearman's $r_s = -0.588$, $N = 10$ sites, $P < 0.05$) and *F. hispida* ($r_s = 0.600$, $N = 10$, $P < 0.05$).

During our two-decade study, many of the monitoring sites became progressively more degraded both in appearance, with a marked proliferation of ephemeral macroalgae (ectocarpoids and ulvoids) starting in 2010 or 2011 (Fig. 6), and in odour (hydrogen sulphide smell). From 2011 onward, the shallow-water algal mats dominated the benthic communities at many sites, particularly in the North Basin and the Goleen (Fig. 6A). High-flow sites (e.g. Boundary Bay), in contrast, had a low coverage of these ephemeral algal mats (Fig. 6). When we measured dissolved oxygen (DO) levels within the ephemeral mats vs. in closely situated bare areas and/or gaps, the amplitude of DO fluctuations was more extreme in and under algal mats than in closely situated bare areas: on the north shore in 2015 (Fig. 7A) DO was 3-4 mg L⁻¹ higher in the daytime and 5-6 mg L⁻¹ lower at night. Comparable, though less extreme, diurnal fluctuations were recorded on the west shore in 2016 (Fig. 7B).

3.6. Experimental determination of low-oxygen tolerance

The epibiont species exhibited significant reductions in survivorship with decreasing dissolved oxygen concentrations (Fig. 8). The bryozoan *F. hispida* had a highly significant reduction in survivorship of zooids (Fig. 8A, Kruskal-Wallis test, $H = 14.8$, 3 df, $P = 0.002$). In fact, mortality varied significantly between (1) the normoxic and suboxic treatments and (2) the suboxic and hypoxic levels (Fig. 8A). There was no significant difference in mortality between the two lowest DO treatments but there were few survivors in either.

The hydroid *D. pumila* also exhibited a highly significant reduction in survivorship with reduced DO levels (Fig. 8B, Kruskal-Wallis test, $H = 18.1$, 3 df, $P < 0.001$). There were no survivors in the

24-hour exposure to anoxia. Although survivorship did vary, the magnitude of the reduction was less than that exhibited by *Flustrellidra hispida*, suggesting that although both species were sensitive to short-term exposures (24 h) to reduced DO, the bryozoan was more sensitive than the hydroid.

4. Discussion

4.1. Long-term patterns and potential drivers

The four epiphytic species showed very different patterns of abundance and distribution over the six decades from 1955 to 2016. While the hydroid, *Dynamena pumila*, showed little change, the bryozoans, *Electra pilosa* and *Alcyonidium* spp., have apparently increased, and *Flustrellidra hispida* has severely decreased. Why the differential responses of the four genera? We discuss potential drivers that may be involved.

4.1.1. Host specificity

The algal-associated epibionts *Alcyonidium* spp., *E. pilosa* and *D. pumila* are all known to occur on a wide variety of algal hosts (Ryland and Hayward, 1977; Hayward, 1985; Cornelius, 1995) and, for these species, it is unlikely that distribution of algal hosts would determine the epibionts' distributions around the lough. Such a wide distribution was seen in 1990, when *Alcyonidium 'hirsutum'*, for example, was recorded at 18 of 20 sites (Little et al., 1992; Fig. 2). However, these records may have included other species in the complex, since the genus presents considerable taxonomic problems (Hayward, 1985; Ryland and Porter, 2006), and field identifications are difficult (Porter, 2012). Early records in 1955, when *A. hirsutum* was seen at only 2 of 20 sites (Ebling et al., 1960; Fig. 2), suggest that the genus was less widespread then, but again taxonomic uncertainty remains. As previously mentioned, we recorded at least three congeners in the South Basin in June 2017.

In contrast to the other three species, *F. hispida* is normally restricted to the furoid *F. serratus* and the red algae *Gigartina* and *Chondrus* (Hayward, 1985), and its distribution might be governed by the distribution of its hosts. However, in the lough, the distributions of host and epiphyte are not tightly correlated (Fig. S1). *Flustrellidra hispida* was most abundant and most consistently recorded at the five sites in the South Basin where *F. serratus* was also abundant, suggesting that its restriction to the South Basin could have been in part due to host-specificity (see Rees, 1935; Kitching, 1987; Trowbridge et al., 2013). However, Ebling et al. (1960) showed that in 1955 *F. serratus* was limited to a small area around the Rapids while *F. hispida* was widespread around the lough, evidently on another host. During our survey, the bryozoan's occasional penetration into the North Basin was not dependent upon the presence of *F. serratus* because the bryozoan then colonised *F. vesiculosus*. In fact, at the height of the bryozoan's abundance in 1955, *F. serratus* was actually less widely distributed in the lough than in 1990/91 (Little et al., 1992) or 2015. The reasons for the presence of

the bryozoan in the North Basin in 1991, 1994, 2003, 2005, 2007 and 2009 but not in other years, therefore, were probably not related to changes in the distribution of its algal hosts.

At many sites *F. hispida* attached to the furoid *F. vesiculosus*. The site where *F. hispida* was most abundant was SE Labhra, where the bryozoan formed dense accumulations on the stipes of *F. vesiculosus*. At the western end of the Island, and on parts of the East, West and South shores *F. hispida* was mostly found on *A. nodosum*. Hurlbut (1991) reported that on NW Atlantic shores, where *F. serratus* did not occur, the primary host was *A. nodosum*. Lack of appropriate algal hosts is therefore unlikely to be a limiting factor for any of the four species examined, and our prediction that expansion of hosts such as *F. serratus* into the North Basin might lead to expansion of bryozoan species there was rejected. In fact, a field experiment attaching 16 fronds of *F. serratus* to 0.25-m² quadrat frames and transplanting the frames to 7 North Basin sites (WWN, NL, NWC, NC, EC, RN) and 1 South Basin site (WL) from June to September 2017 did not result in any *F. hispida* settlement despite summer being the species' reported recruitment period (Seed et al., 1981; Seed and Wood, 1994).

4.1.2. Competition and predation

Competition between *Alcyonidium* spp., *F. hispida*, *D. pumila* and *E. pilosa* on *F. serratus* has been considered in detail by Stebbing (1973): with algal fronds being densely encrusted with epibionts indicative of limited attachment space. Competitive hierarchies for the four species we investigated have been elucidated by Wood and Seed (1980). However, most of the bryozoan and hydroid colonies in Lough Hyne were relatively sparse at the time of observation, and were mostly confined to individual species on any one algal host thallus (pers. obs.). With the exception of the *F. vesiculosus* at SE Labhra referred to above, the majority of algal stipes and fronds were free of epibionts (Little, pers. obs.), suggesting that spatial competition was not intense.

Varying levels of predation could offer an alternative interpretation of the spatial variation in hydroid and bryozoan distributions. *Dynamena pumila* may be attacked by small nudibranch molluscs such as *Doto coronata* and *Facelina dubia* which are widespread in the lough (Nunn et al., 2006). However, most of the *D. pumila* colonies were found in the mid-shore on *Ascophyllum nodosum* and would seldom be exposed to predation by *D. coronata* or *F. dubia* because these nudibranch species are usually limited to the lower shore or shallow subtidal and usually occur at low densities. Differences in predation level, therefore, probably did not affect the distribution of *D. pumila*.

The predators of all three bryozoan taxa are probably limited to some nudibranch molluscs and pycnogonids (Wyer and King, 1974; Hayward, 1985). In Wales, *Alcyonidium hirsutum* is heavily predated by *Onchidoris muricata* (Hayward and Harvey, 1974), but this nudibranch species has not been confirmed from Lough Hyne (Nunn et al., 2006). Of other nudibranch predators (Thompson and Brown, 1984), *Acanthodoris pilosa* and *Goniodoris nodosa* have been recorded in the lough (Nunn et al., 2006), but neither are usually abundant at the monitoring sites (Little and Trowbridge, pers. obs.),

and we have never recorded them on bryozoans except near the Rapids (Trowbridge, unpubl. data). Since our surveys were limited to late summer, however, we missed the spring population pulse and breeding seasons of nudibranchs, when the predators may be more abundant.

4.1.3. Effects of physical conditions and seasonality

The effects of water movement and sedimentation on bryozoan and hydroid abundance and growth have been summarised by O'Connor et al. (1979), Seed and O'Connor (1981a) and Seed (1985). For both *F. hispida* and *D. pumila*, experimental transfer to areas with slow water currents and a high silt load resulted in reduced growth, but the effects were less marked for *Alcyonidium hirsutum*. Silt may also prevent settlement of *F. hispida* larvae (O'Connor et al., 1979; Seed and O'Connor, 1981a; Seed, 1985), so it could be that conditions in the less turbulent and more silt-laden North Basin at Lough Hyne often prevent epibiont settlement there. This conclusion is supported by the positive relationship between abundance of *F. hispida* and water flow. The alternation of host algae for *F. hispida* noted above may in turn be related to water flow and sedimentation: *F. serratus* away from the Rapids area often experienced heavy silt loads (and supported few bryozoans), while the basal stipes of *A. nodosum* at the same sites were clean and silt-free and had patches of *F. hispida*. Where *F. hispida* was found on *F. vesiculosus*, the alga was also clean and lacked silt, so siltation may be very important for this species. Similarly, for *D. pumila*, its partial restriction to the South Basin may be related to intolerance of silt, as suggested by the positive relationship between the abundance of this species and water flow. *Electra pilosa*, in contrast, is more tolerant of silt (Seed and O'Connor, 1981a; Seed, 1985) and would be expected to colonise the more silty sites of the North Basin, particularly due to lack of competition. It is thus surprising that *E. pilosa* was not recorded there by Ebling et al. (1960), but it may be that the small size of the colonies prevented detection. Overall, our prediction of a positive correlation between epibiont abundance and water flow can be accepted for *F. hispida* and *D. pumila*. Our prediction of a negative relationship with slope can also be accepted for these two species.

Physical conditions on the low shore have changed in the last decade, with the onset of extreme oxygen fluctuations: daytime hyperoxia (>200% air saturation) and night-time hypoxia to anoxia being found at several sites (Fig. 9, this study; Trowbridge et al., 2017a). These changes are related to the eutrophication of the lough in recent years (Jessopp et al., 2011) and the resulting growth of ephemeral algae (Trowbridge et al., 2017a, b). These types of changes have been noted on many other Irish shores (Hartnett et al., 2011).

Based on a preliminary field experiment, the bryozoans *E. pilosa* and *Membranipora membranacea* were extremely sensitive to smothering and/or oxygen fluctuation by ephemeral algae (Keats Conley et al., unpubl. data): all of the bryozoan zooids were dead after 48-hours exposure to ectocarpoid cover. Our correlation of *F. hispida* and *D. pumila* abundance with increased water flow is, thus, probably related in part to oxygen supply in the water. This result supports our hypothesis

that declining bryozoan and hydroid populations are related to declining oxygen supply (the effect of hyperoxia, namely supersaturation, has not yet been examined). The temporal increase in *Alcyonidium* spp. suggests that this taxon may be more tolerant of changing conditions. The occurrence of *Alcyonidium* spp. in the Goleen and the North Basin supports this suggestion. Overall, the greatest driver of change has probably been the eutrophication of the lough and much of coastal Ireland (Jessopp et al., 2011), which has both increased phytoplanktonic food and, by promoting growth of ephemeral algae, promoted local hypoxia.

Electra pilosa showed an apparent increase in distribution between 1955 and 1990. Colonies of this species in the North Basin were small, and this could suggest unfavourable conditions – colony size in bryozoans has been used as a measure of change in the fossil record (O’Dea et al., 2011). However, the small colony size may reflect a seasonal influence as *E. pilosa* colonies regress in winter and new colonies appear in late summer and autumn (Ryland and Hayward, 1977; Seed et al., 1981). The records of Ebling et al. (1960) for 1955 were taken in July, and so probably missed the late-settling colonies and colony re-growth, whereas our readings in 1990 were taken in September. When we repeated recordings in 1991 in July (C. Little, pers. obs.), we found very few *E. pilosa* colonies. The apparent increase of this species, in particular, between 1955 and 1990 may, thus, be an artefact of sampling date.

4.2. Bryozoans and hydroids as bioindicators

Following the suggestion that calcareous bryozoans may act as ‘canaries’ indicating environmental change (Smith, 2009), as distinct from the claims of great metabolic flexibility quoted in the Introduction, it is appropriate to ask how useful in this respect are the four epibionts we have studied.

Environmental changes in Lough Hyne have occurred mainly in the last decade (Jessopp et al., 2011; Trowbridge et al., 2011, 2013, 2017a,b), so relative abundance of the surveyed species in 2016 may give some idea of their tolerance to such changes. In terms of the number of Renouf sectors occupied (out of 108), the species ranked as follows: *Flustrellidra hispida*, 41.7%; *Dynamena pumila*, 69.4%; *Electra pilosa*, 75.9%; *Alcyonidium* spp., 98.1%. *F. hispida* was thus the most sensitive species (with fewest occurrences), with the hydroid *D. pumila* the next most sensitive. The abrupt fall in *F. hispida* abundance in recent years may be attributable to the change in available dissolved oxygen and/or smothering by the ephemeral algal mats. Its low tolerance of reduced oxygen levels in laboratory experiments (Fig. 10A) supports this conclusion. *F. hispida* may therefore be a sensitive bioindicator of change. *F. hispida* has the advantage of being a prominent species, easy to identify without requiring magnification, though its colonies regress in winter. It is widespread throughout the North Atlantic, on both European and North American shores, and so could be used as an indicator over a wide region. The hydroid *D. pumila* is also easy to identify and showed consistent distribution patterns. It lives, for the most part, higher on the shore than the other three species, and may thus not

be as readily exposed to the fluctuations from hypoxia/anoxia to hyperoxia in recent years (e.g., Trowbridge et al., 2017a). In laboratory experiments (Fig. 10B), it was not as sensitive to oxygen reduction as *F. hispida*, but it still showed declining survival with progressive hypoxia. *D. pumila* could thus be a useful bioindicator should conditions worsen, especially as its colonies persist in winter. Like *F. hispida*, it is widespread throughout the North Atlantic, so could be used as an indicator over a wide region. *E. pilosa*, on the other hand, formed very small colonies in the lough, was hard to identify in the field with certainty, and showed very patchy distributions. Although it is present in all the world's seas, its usefulness as an indicator would be limited. Finally, *Alcyonidium* spp. are difficult to identify to species *in situ*, but are also so tolerant of a range of conditions (based on the broad spatio-temporal constancy) that their usefulness as bioindicators also appears to be limited. In summary, of the four species studied, *F. hispida* and *D. pumila* show promise as bioindicators of environmental change throughout the North Atlantic, at least where this involves eutrophication and deoxygenation.

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FIGURE CAPTIONS

Fig. 1. A. Location of Lough Hyne in SW Ireland (inset shows the Republic of Ireland and Northern Ireland for regional context). B. Map of Lough Hyne, showing 10 long-term monitoring sites that were surveyed annually in late August to early September for 21 years ('annual' sites), and 10 sites that were surveyed in 2015 to compare with older surveys ('historical' sites). Intertidal zone (stippled) and shallow subtidal habitats are subdivided into topographically discrete units (Renouf sectors, short lines perpendicular to the shore) designated by shore location (W, west; S, south; E, east; N, north; I, island) and sector number. Annual site names are abbreviated as follows: BB, Boundary Bay; CB, Codium Bay; EC, East Castle; EG, East Goleen; GY, Graveyard; NI, North Island; NL, North Labhra; SEL, SE Labhra; WVN, Westwood North; WVS, Westwood South. Historical site names are abbreviated as follows: BH, Bohane Harbour; GQ, Glan Quay; NC, North Castle; NWC, Northwest Castle; RN, Rookery Nook; SC, South Castle; SL, South Labhra; WC, West Concrete; WL, West Labhra; WP, Whirlpool Point.

Fig. 2. Comparison of bryozoan and hydroid distributions at 20 monitoring sites in 1955, 1990 and 2015. Data for 1955 (*Alcyonidium* spp. recorded as *A. hirsutum*) from Ebling et al. (1960). Data for 1990 for *F. hispida* and *Alcyonidium* spp. (recorded as *A. hirsutum*) from Little et al. (1992, with minor corrections); for *E. pilosa* and *D. pumila* from Little (pers. obs.). Data for 2015 from this study. Filled circles indicate presence and hollow circles denote absence.

Fig. 3. Number of 2m sections containing (A-B) bryozoan *Flustrellidra hispida*, (C-D) bryozoan *Alcyonidium* spp., and (E-F) hydroid *Dynamena pumila* in Aug/Sep from 1994 to 2016 at 10 monitoring sites in Lough Hyne. A, C, E: Data are pooled across sites; B, D, F: data are pooled over time. Black bars denote the South Basin and grey ones denote the North Basin. Dashed horizontal lines indicate maximum number of sections possible (50 sections over 10 sites each year; 115 sections for each site over the 23 year period). Dotted vertical line in 2010 indicates when habitat quality in lough abruptly plummeted (proliferation of subtidal ephemeral weed, extreme diurnal fluctuations of dissolved oxygen developed, etc.).

Fig. 4. Non-metric MDS plot of epibiont assemblages over the two-decade period vs. the 10 monitoring sites. Site name abbreviations as in legend of Fig. 1. Dashed lines enclose sites in North Basin vs. South Basin; the East Goleen is a biologically degraded site quite distinct from other South-Basin sites.

Fig. 5. Number of 2-m sections containing (A) bryozoan *Flustrellidra hispida*, (B) bryozoan *Alcyonidium* spp., and (C) hydroid *Dynamena pumila* in Aug/Sep from 1994 to 2014 at 10 monitoring sites in Lough Hyne vs. relative water flow. Site names abbreviated (see legend of Fig. 1).

Fig. 6. Percentage cover of ephemeral macroalgae (ulvoids and ectocarpoids) in the shallow sublittoral at 10 monitoring sites during four annual surveys from 2011 to 2014.

Fig. 7. Diurnal variation in dissolved oxygen values in shallow sublittoral areas (A) on the north shore (N2) in Sep 2015 and (B) on the west shore (W16-17) in Aug-Sep 2016. For A, there were two HOBO sensors: one in ephemeral seaweed and one in a non-weed area in close proximity. For B, there were five sensors: three in ephemeral mats and two closely situated in gaps of the mats; data shown are mean of the replicate sensors. The dashed horizontal line indicates hypoxia. Normoxia, dependent on temperature and salinity, ranged from 8 to 9 mg L⁻¹. The vertical dotted lines denote midnight.

Fig. 8. Mean survival (+1 SE) of two epibiont species: (A) *Flustrellidra hispida* and (B) *Dynamena pumila* after 24-hour exposure to experimentally produced dissolved oxygen (DO) levels. Normoxic conditions averaged about 8 mg L⁻¹ in both experiments, suboxic was ca. 4 mg L⁻¹, hypoxic <2.0 mg L⁻¹, and anoxic ca. 0.2 mg L⁻¹. Replication was 5 jars per DO treatment. *** indicates highly statistically significant between pairs at $P < 0.001$ whereas ns indicates not significant with Likelihood-ratio goodness-of-fit tests.

SUPPLEMENTARY ONLINE FIGURE CAPTIONS

Fig. S1. Distribution of *Alcyonidium*, *Dynamena* and *Electra* (and hosts) in 108 Renouf sectors within Lough Hyne (above the Rapids) in Aug/Sep 2016.

Fig. S2. Distribution of *Fucus serratus* and *Flustrellidra* (presence vs. absence) in 108 Renouf sectors on North, Island, East, and West Shores within Lough Hyne in Aug/Sep 2016. The third column indicates whether the bryozoan was present on its primary and/or secondary hosts; the small table at the bottom indicates the frequency of each of the three cases indicated to the left. Abbreviations as follows: *Fserr*, *Fucus serratus*; *Fves*, *F. vesiculosus*; *Asco*, *Ascophyllum nodosum*; *Flustr*, *Flustrellidra hispida*.