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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 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.

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 Hayward, 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

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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 CO_2, 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 responses 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 fucoid 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 km^2, 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 (Σ_N = 10 sites x 5 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).