Long-term fluctuations in intertidal communities in an Irish sea-lough: Limpet-fucoid cycles

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ARTICLE INFO

ABSTRACT

Long-term cyclical changes in rocky shore community structure were documented over two decades at sheltered shores in Lough Hyne Marine Reserve, County Cork, Ireland. Three peaks of abundance were recorded for the limpet, *Patella vulgata* (1990-5, 2002-6 and 2010-14) with oscillations that varied in amplitude and frequency among sites. The cover of the fucoid *Fucus vesiculosus* varied inversely with limpet abundance and showed the strongest negative correlation with a lag time of 0–2 years. The species complex *Fucus spiralis/guiryi* showed a weaker correlation with a lag time of 1–2 years. Two other fucoid species showed no such negative correlations despite their close proximity to limpets within the lough's compressed tidal range. There was no relationship between overall barnacle cover (dominated by *Austrominius modestus*) and the limpet-fucoid cycles, suggesting that the shelter provided by *A. modestus* for algae to escape from limpet grazing pressure may not be necessary for these cycles to occur on wave-sheltered shores.

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1. Introduction

Spatial and temporal cycles in community structure have been repeatedly recognized in marine, freshwater and terrestrial systems (e.g. Reise, 1991; Scheffer, 2009; Petraitis, 2013). Ecological theories of multiple community 'states', 'phases', 'catastrophes' and 'regime shifts' have been proposed to account for communities and/or ecosystems that shift to alternate configurations (Johnson and Mann, 1988; Petraitis and Latham, 1999; Steneck et al., 2002; Scheffer and van Nes, 2004; deYoung et al., 2008; Lauzon-Guay et al., 2009; Petraitis and Dudgeon, 2005, 2015a,b). At least four commonly cited examples of such patterns exist in the marine literature, including: (i) the temporal cycle between N Pacific and N Atlantic kelp beds and urchin barrens (Johnson and Mann, 1988; Steneck et al., 2002); (ii) Caribbean coral reef communities oscillating between coral assemblages and those overgrown by perennial seaweeds and/or algal turfs (reviewed by Jackson et al., 2014); (iii) alternation between NW Atlantic *Ascophyllum* beds and mussel or *Fucus* beds (Petraitis and Dudgeon, 1999, 2005, 2015a,b; Menge et al., 2017); and (iv) European fucoid communities (*F. spiralis* and *F. vesiculosus*) alternating with limpets and barnacles (Southward and Southward, 1978; Hawkins and Hartnoll, 1983a,b; Hawkins and Southward, 1992; Burrows and Hawkins, 1998).

Mechanisms controlling the transitions or shifts in these communities are less well understood, and the scale of the changes can vary from local (cm to m) to regional (e.g. for regime shifts). Along with spatial patterns of variation, temporal fluctuations of such cycles are also important to our understanding of the mechanisms that may drive community changes. Given the time scale needed to observe changes in community patterns, however, there are relatively few studies which have been able to document true alternations between community 'states' as often such studies require long term (>10 years) data series that can encompass the life cycles

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of the species involved. However, Menge et al. (2017) have followed a change from an *Ascophyllum*-dominated community to one comprising mainly *Fucus* spp. which has remained stable over a period of 4 decades. Here the controlling factors may mainly involve the differences in recruitment between the two species.

Gastropod molluscs have been shown to play an important community regulating role as grazers on shores worldwide (Underwood and Chapman, 1995; Menge and Branch, 2001; Poore et al., 2012), particularly on European shores (Coleman et al., 2006). Since the classic experimental studies of Jones (1948) on the Isle of Man, in which the removal of limpets, *Patella vulgata*, from a strip of intertidal shore initially resulted in extensive growth of the fucoids, *Fucus vesiculosus* and *F. serratus*, it has been accepted that limpets are a major force controlling the abundance and distribution of intertidal fucoid algae on European shores (see reviews by Branch, 1981; Hawkins, 1981a, b; Hawkins and Hartnoll, 1983a; Hartnoll and Hawkins, 1985; Jenkins et al., 2005; Coleman et al., 2006; Moore et al., 2007; Poore et al., 2012). This influence is not, however, static but involves a complex series of species interactions as described by Southward and Southward (1978) following the resultant changes in species composition on rocky shores after the *Torrey Canyon* oil spill: oil and detergents caused limpet mortality which resulted in fucoid algae becoming dominant, with a later recovery to limpets and barnacles. This pattern varies with season (Hawkins, 1981a), and with wave exposure, such that on more wave-exposed shores, the cycle favours limpets and barnacles whilst with increasing shelter it favours fucoids (Hawkins and Hartnoll, 1983b; Jonsson et al., 2006). On moderately exposed shores, however, the fucoid cover and the limpet density cycle over periods of years (e.g. Thompson, 1980).

Hawkins and Hartnoll (1983a) elaborated on Southward and Southward's model, suggesting larger amplitudes of change in community structure on moderately exposed shores. Hartnoll and Hawkins (1985) documented these fluctuations over seven years on the limestone ledges of Port St. Mary, the Isle of Man, and proposed that the cycle was driven by a series of mechanisms. These included the growth of barnacles, which would discourage limpet recruitment and thus form a grazing refuge, allowing increased settlement and survivorship of *F. vesiculosus*. Development of stands of *Fucus* discouraged further barnacle settlement as a result of their sweeping action (Hawkins, 1983) but promoted increased settlement and hence localized higher densities of juvenile limpets. Subsequently, recruitment of *Fucus* was reduced because germlings were grazed away by the increased limpet population. As the surviving clumps of *Fucus* grew older, thalli weakened and detached and juvenile limpets dispersed to establish home scars; consequently the shore area reverted to cover by barnacles, which were able to settle in these areas of reduced grazing pressure. The complex interactions between limpets, fucoids and barnacles thus determined the scale and timing of patchiness on moderately exposed shores (Hawkins et al., 1992).

Short-term variations in limpet-fucoid-barnacle cycles have been investigated experimentally (Hawkins and Hartnoll, 1983a; Johnson et al., 1997; Jenkins et al., 1999a, b; Mrowicki et al., 2014) to elucidate key causal mechanisms for the various stages of these cycles. However, the duration of these studies was not sufficient to investigate the long-term nature of the cycles (of the order of 5–7 years, Hartnoll and Hawkins, 1985). Studies which have been able to measure the amplitude and duration of such cycles are rare (but see the 13-year pattern illustrated in Hawkins and Jones, 1992: 117 and 17-year patterns in Burrows and Hawkins, 1998), given the long time-scales needed to document such changes. As a result, the importance of processes such as disturbance, larval supply, or local wave exposure (Southward and Southward, 1978) in driving these cycles is difficult to generalize. Intrinsic factors such as the

longevity of dominant species are also likely to be important driving forces. Fucoid seaweeds typically live 2–5 years, with the exception of the much longer-lived *Ascophyllum nodosum*. However, monitoring after the *Torrey Canyon* oil spill demonstrated that a massive pulse of *Fucus* settlement can persist from 10 to 15 years (Hawkins and Southward, 1992), and the experimental removal of *Ascophyllum* resulted in dominance by *Fucus* spp. for 38 years (Menge et al., 2017). The limpet, *Patella vulgata*, produces pelagic veliger larvae that settle in 15 days and, after a juvenile vagrant phase, form home scars that they occupy for the rest of their lives (Fretter and Graham, 1976). Growth and longevity of *P. vulgata* are directly related to habitat: limpets under the shelter of fucoids grow rapidly but may live only 2–3 years, whereas those on bare rock grow slowly but live up to 15–17 years (Lewis and Bowman, 1975; Fretter and Graham, 1976; Thompson, 1980). Such differences in life history pattern due to local environmental conditions may, therefore, drive spatial variability in the duration of such cycles.

Because of these relatively long life-spans, evidence for the generality of limpet-fucoid cycles requires surveys carried out over many years to span complete phases of these cycles. Many long-term studies on rocky shores have shown that communities are continually changing, with both rapid inter-annual fluctuations and longer-term trends. The logistical problems inherent in recording variation in intertidal assemblages over long periods of time, however, have resulted in many rocky shore studies making 'snapshot' comparisons between two sets of observations separated by a number of years. Although such surveys are useful in documenting long-term changes in communities at discrete times, they do not record cycles that occur over periods of decades or more. Time-series data such as Hawkins and Jones (1992: 117) and Bishop (2003) are notable exceptions. To address this gap, our study presents annual surveys of limpet and fucoid abundance on sheltered rocky shores, dominated by *Fucus spiralis*/*F. guiryi* and *F. vesiculosus*, in Lough Hyne, Ireland over a period of 21 years. The patterns of changes in species abundances were used to evaluate the dynamics of fucoid-limpet oscillations within the sheltered shores of the lough, and their subsequent variation with local conditions. Finally, the oscillations seen were compared with the cycles recorded on moderately exposed, oceanic, rocky shores to investigate the generality of limpet–fucoid dynamics in driving community structure on NE Atlantic rocky shores.

2. Materials and methods

2.1. Site description

Lough Hyne (Ine) is an enclosed sea-lough (Fig. 1) in southwest Ireland connected to the Atlantic Ocean by narrow 'Rapids' (Bassindale et al., 1948; Kitching, 1987) and is Europe's first and Ireland's only marine reserve. At only ~1 km², and with a consequent small fetch (<1 km, Table 1), all the shores are relatively sheltered. The tidal cycle is asymmetric as a result of the restricted inflow at the Rapids, and the tidal rise and fall is restricted to ~1 m inside the lough, so the intertidal zone is compressed (Rees, 1931, 1935; Little, 1991). Much of the intertidal zone is formed by either bedrock or shingle, and varies from nearly vertical to shallow slopes (Ebling et al., 1960; Williams et al., 1999, Table 1; present study).

Whilst the algal flora of the lough was first inventoried and its distribution described by Rees (1931, 1935), the fauna and flora of the rocky intertidal zone were first extensively quantified by Ebling et al. (1960) from 20 monitoring sites around the lough. Little et al. (1992) started re-monitoring these sites in 1990/91, selecting 10 out of the original 20 (Fig. 1; Ebling et al., 1960; Little et al., 1992). Each