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

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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.

Keywords

grazing cycles; rocky shores; limpets; herbivory; fucoids
Ireland, County Cork, Lough Hyne Marine Reserve

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 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 involve mainly 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

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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 'snap-shot' 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 ~1km^2, and with a consequent small fetch (<1km, 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 ~1m 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 1990/1, selecting 10 out of the original 20 (Fig. 1; Ebling et al., 1960; Little et al., 1992). Each site consists of a 10m length of rocky shore marked at each end with a stainless steel plate to enable exact relocation. For the monitoring surveys, each site was subdivided into five, 2m-long sections to aid visual quantification of algal cover. The sites were considered the replicates, not the sections. Analyses were conducted with site-level data (averaged across sections). Non-destructive surveys were carried out in the last week of August and first week of September from 1994 to 2014. Two researchers surveyed the shore at low tide, from the top of the high-shore *Pelvetia* to the bottom of the low shore *F. serratus*. We use these biologically defined terms because tidally defined heights (e.g. MHWN) are not well determined in the lough and are not generalizable to those found outside the lough, due to the asymmetric tidal pattern experienced inside.

2.2 Macroalgae

To ensure the data collected could be compared with earlier surveys (Ebling et al., 1960; Little et al., 1992), the original sampling protocols were employed. Within each of the 2m-wide sections, algal cover was assessed by a pair of experienced researchers who cross-tabulated their assessments. To be consistent with methods of Ebling et al. (1960), visual estimates were made for the appropriate vertical band (from the highest to the lowest individual) of each target species (*Pelvetia canaliculata*, *Fucus spiralis/guiryi*, *Ascophyllum nodosum* and *Fucus vesiculosus*). The fucoid *F. guiryi* was only described by Zardi et al. (2011) and is found in Lough Hyne (CDT, pers. obs.). As we could not retrospectively distinguish the morphologically similar congeners, the *F. spiralis* 'taxon' was used to include both species. Observations in 2013 and 2014 indicated that *F. guiryi* predominated, but that both species were present, so we refer to the known species complex as *F. spiralis/guiryi*.

2.3 Macrofauna

Within the lough, the vast majority of intertidal limpets are *Patella vulgata* whilst the congener *P. ulyssiponensis* occurs on shallow subtidal rocks (Ebling et al., 1960) and at extreme low water (Little, pers. obs.). *P. vulgata* abundances were assessed using a 5-point ACFOR abundance scale (see Crisp

and Southward, 1958), in their zone of maximum abundance (five points were 0, <10, <50, <100 and >100 individuals /m^2). For plotting and analysis, these points were converted to numbers approximately in the mid-point of each level on the scale (represented as 0, 5, 30, 75, and 100). When numbers were >100/m^2, exact counts were also made to determine maximum density.

The total percentage cover of acorn barnacles (including *Chthamalus stellatus*, *C. montagui*, *Austrominius modestus* and *Semibalanus balanoides*) was assessed by eye by two trained researchers in each section. Although we did determine the relative abundance of each barnacle species, those results are presented elsewhere.

2.4 Statistical Analysis

Temporal biplot patterns of limpet and fucoid abundances, by site, as well as temporal trajectories of abundant species were used to characterize the mid-shore communities, using average values for each site. To determine any relationships between species, we compared (i) limpet and fucoid abundances and (ii) limpet and barnacle abundances, using Spearman's rank correlations. In both cases, we evaluated the relationships with 0 to 5 year time lags, as previous studies have shown that differences between peaks of individual species with time usually occur after transitional periods (Hartnoll and Hawkins, 1985; Hawkins and Hartnoll, 1983a; Hawkins and Jones, 1992).

To ascertain whether the spatial variation in limpet and fucoid abundances were due to specific site attributes, the shore slope, aspect, fetch, and water flow of the different sites were quantified to incorporate into a non-metric Multi-Dimensional Scaling (nMDS) plot, using Primer (ver. 7). Slope was measured with a clinometer (with a 0.5-m base) at 5 locations (with limpets) per 2-m section across the 10-m broad monitoring sites (25 slope values were averaged per site). Aspect was determined by averaging the compass reading at either end of each site. For the Primer analysis, the aspect angles (in degrees) were converted into radians, the two-dimension locations of each angle (theta) determined with cosine (theta) and sine (theta) functions, and the two values were linked (merged) for the BEST and RELATE analysis (K.R. Clarke and M. Anderson, PRIMER, pers. comm. 2016). Fetch was determined as the linear distance (perpendicular to the shore) to the nearest shoreline, using a protractor and Ordnance Survey map (1:7500 scale); 5 values were measured to the nearest 10 m for each site and averaged. Water flow was evaluated using gypsum (Plaster of Paris) semi-spherical flow blocks deployed at each site for 3 days in March 2015; we measured the weight loss of each block (and still-water controls) to determine relative current flow at the 10 sites. Limpet abundance data were square-root transformed and fucoid percent cover data were log transformed [log (x+1)] before calculating a Bray-Curtis similarity matrix among sites. The second stage analysis of the Bray-Curtis similarity matrix was conducted with the biological and physical variables, using the BEST and RELATE routine (with 999 permutations) in Primer: the latter determines whether biotic and environmental factors (individually or collectively) were 'congruent' (Primer's terminology) and, thus, could be explanatory variables for the biological patterns.

3. Results
3.1 Bimodal Fucoid Patterns

The shores varied greatly in their algal cover and hence in their appearance over the two-decade period of the surveys. For most shores, this appearance was determined by the abundance of two taxa, *Fucus spiralis* and *F. vesiculosus* (Fig. 2). In the early 1990s, cover of these species was low (~10%), and rock surfaces were dominated by barnacles and limpets. Algal cover increased in the late 1990s to reach 40% or more, decreased in the early 2000s, then rose again between 2007-12 before falling in the period 2013-4. There were thus two clear fucoid 'peaks' (cover > 40%), separated by a 'trough' (cover <15%), over the 21-year period.

The oscillations were highly variable among sites. For example, *Fucus spiralis* was common at most sites (Fig. 3) except the southward-facing SE Labhra and Boundary Bay. The fucoid complex showed two peaks of abundance at most sites (particularly at North Island), although the peaks differed in magnitude (Fig. 3). The pattern was less clear at Graveyard and Codium Bay, where there were irregular fluctuations in cover from ~10 to ~50%. Cover of *F. vesiculosus* varied from low values of <10% to >60% (Fig. 4). A pattern of two peaks (1997-9 and 2008-11) and two troughs (1994-6 and 2002-6) was, however, very pronounced, and there was close synchronicity (Fig. 4) in algal cover at several sites (e.g., North Island, Boundary Bay and Codium Bay), although the pattern was less clear at East Castle, and the initial peak appeared to be absent at SE Labhra and Westwood South.

3.2 *Patella vulgata*

Densities of *Patella vulgata* varied from <10/m^2 up to 50/m^2 and occasionally even >200/m^2, when there were large numbers of juveniles (<10mm in shell length). Periods of low limpet densities (20-30/m^2) in the late 1990s and 2008-10 were separated by periods of high densities (50-100/m^2) in the early 2000s and 2010-14 (Fig. 2), and there was some synchronicity among sites (Fig. 3-4).

Overall, there were significant rank correlations between *P. vulgata* abundance and cover of the mid-shore fucoids (Figs. 3-4, Table 2). Initially, limpet–*F. spiralis* relationships showed a negative slope (Table 2), but with relatively low r_s values. When a time lag of 1-2 years (i.e. fucoid abundance lagging behind limpet counts) was introduced (Table 2), significant negative correlations were seen, and with a 5 year lag, a positive correlation was found. For the limpet–*F. vesiculosus* relationship, there was a highly significant inverse relationship with no lag or a one or two-year lag (Table 2) and a significant positive correlation with a 5-year lag.

Temporal trajectories illustrated that there were oscillations between (i) high fucoid cover and low limpet densities and (ii) low fucoid cover and high limpet densities (Fig. 2). However, the cycles varied considerably with fucoid species (Fig. 5), time, and site (Fig. 6). The most distinctive cycles were at sites with vertical to steeply sloping mid-shore surfaces with some degree of wave exposure (e.g. North Island and North Labhra, see Table 1).

3.3 *Non-Bimodal Patterns*

In marked contrast to the mid-shore *F. spiralis* and *F. vesiculosus*, the other intertidal fucoids did not exhibit any clear oscillating pattern (Fig. 7). The high shore *Pelvetia canaliculata* did, however, exhibit this pattern when pooled across sites, but not at the individual site level (Fig. 7). At seven sites, this alga formed a fringe with up to 60% cover but was sparse at Boundary Bay and SE Labhra, on

near-vertical south facing cliffs where only small sprigs of *P. canaliculata*, particularly in tufts of the high shore lichen *Lichina pygmaea*, could be found.

The long-lived *Ascophyllum nodosum*, also inhabited the mid-shore and was common at most sites but generally absent from steep, south-facing sites (North Island and SE Labhra). *Ascophyllum* did not show any obvious temporal pattern of peaks and troughs (Fig. 7), although it did exhibit a clear increase at Westwood North from 2004-14 as well as several other areas (e.g., the north shore) not monitored during this study.

3.4 Barnacles

There was a significant decrease in barnacle cover throughout the two-decade study (Spearman's rank correlation, r_s=-0.727, n=21 years, P<0.001), but overall barnacle cover showed no obvious temporal cycles and no significant correlations with *Pelvetia*, *Fucus spiralis*, or *F. vesiculosus* abundance (r_s=0.409, 0.351, 0.147, respectively, for n=21, all P>0.05).

3.5 Multivariate Patterns

The non-metric MDS plot showed considerable spatial variation in limpet-fucoid assemblages at the 10 sites (Fig. 8); the low two-dimensional stress value (0.06) indicates that the pattern was a realistic depiction of the limpet-fucoid assemblages. The biotic patterns of limpets and fucoids were not significantly related to any of the environmental variables (slope, fetch, aspect, and flow) collectively (Primer RELATE permutation, Rho = -0.074, P = 0.658).

4. Discussion

4.1 Decadal Scale

In Lough Hyne, the peaks of abundance of *Fucus vesiculosus*, and to a lesser degree *F. spiralis*, in the late 1990s and the late 2000s coincided, at many sites, with low densities of the limpet *Patella vulgata*. These cyclical patterns appeared to be synchronous and provide evidence to support the mosaic hypothesis of Hawkins and Hartnoll (1983a), Hartnoll and Hawkins (1985), and Burrows and Hawkins (1998). Hawkins and Hartnoll (1983a) proposed that fucoid algal cover could be cyclically reduced by interactions between variation in limpet grazing and relative longevity of the algae on moderately exposed shores, resulting in a mosaic of patches at different stages of the cycle. According to this hypothesis, on sheltered shores where limpets are not such effective grazers, there would be smaller fluctuations in fucoids and limpets, and shores will be dominated by fucoids (Hartnoll and Hawkins, 1985).

In contrast to this theory, on the wave-sheltered shores of Lough Hyne, synchronous changes in algal cover and limpet abundance were recorded on a wide scale. One explanation for this difference may be that unlike extremely sheltered shores where *Ascophyllum nodosum* is dominant (Jenkins et al., 1999a, 2004), the sheltered shores in Lough Hyne are relatively steeply sloping and experience considerable tidal currents (Bassindale et al., 1957; Ebling et al., 1960). These factors may favour limpets and barnacles over fucoids. In addition, it is possible that limpets may show some degree of

larval retention within the lough, as suggested for the sacoglossan *Elysia viridis* (Trowbridge et al., 2008).

The synchronicity of peaks in abundance of limpet populations in Lough Hyne is best seen in the period 2010 to 2014 when there were high numbers of juveniles (<1cm in shell length) (see Fig. 3-4). Presumably these 'good years' for limpet settlement provide the basis for a future increase in grazing pressure. Even modest rises in limpet abundance from 2000 to 2006 were, for example, correlated with a major decrease in fucoid abundance after 3-5 years. Juvenile recruitment of limpets can differ greatly between years (Bowman, 1985; Bowman and Lewis, 1986), as shown on the west coast of Ireland by Delany et al. (1998), which will contribute to the periodicity of the cycles observed.

The lag times of up to 2 years between high limpet abundance and high fucoid cover relate to the life-cycles of the fucoids *F. spiralis/guiryi* and *F. vesiculosus* which are typically 3-5 years (MarLIN; http://www.marlin.ac.uk/). If fucoids settle when limpet densities are low, the thalli will grow to form a canopy in 1-2 years (Schonbeck and Norton, 1980; Hawkins, 1981a). Settlement and recruitment of limpets are enhanced by this canopy which offers shelter from desiccation (Hartnoll and Hawkins, 1985). Limpet growth in these conditions will be rapid (see references in Introduction), and limpet grazing will thus prevent further algal settlement in close proximity to these algal stands. Recent evidence shows that limpets can also feed on adult fucoids (Davies et al., 2007; Lorenzen, 2007; Notman et al., 2016). Further settlement of algae may then depend upon a decrease in the limpet population (and concomitant reduction in grazing pressure) as the adult individual limpets disperse or die off (Hawkins and Hartnoll, 1983a). In extreme cases, dense settlement of fucoids can maintain fucoid cover for more than a decade before limpet dominance returns (Hawkins and Southward, 1992).

4.2 Role of Barnacles

The original hypothesis of Hartnoll and Hawkins (1985) for cycles of species mosaics on moderately-exposed shores proposed that the resurgence of algal recruitment after the algae had declined was promoted by the settlement of barnacles (see also Hawkins, 1981a; Hawkins and Hartnoll, 1983a). High densities of acorn barnacles were hypothesized to provide a refuge for algal germlings from limpet grazing: for three locations in their study, percentage cover by barnacles varied from less than 10% to more than 40%. The barnacle *Semibalanus balanoides* was also hypothesized to facilitate settlement of *Fucus* spp. by Menge et al. (2017). If this were so on the sheltered Lough Hyne shores, barnacle percentage cover would be expected to be high prior to each period of fucoid settlement and/or growth. There is no evidence, however, that this is so: barnacle percentage cover did fluctuate, with percentage cover at the different sites varying from less than 10% to more than 80% (at North Island). Some of this variation was presumably related to external drivers affecting recruitment. There was no observable relationship to the sequence of algal cycles. This lack of relationship suggests that on the sheltered shores of Lough Hyne, there may be sufficient refuges for algal germlings to escape grazing pressure regardless of barnacle density. It is also possible that the composition of the barnacle community may influence the availability of refuges; on the moderately-exposed shores examined by Hartnoll and Hawkins (1985), the dominant barnacle species was *Semibalanus balanoides*, while in Lough Hyne the dominant species was *Austrominius modestus* (Gallagher et al., 2016; Little et al., in

prep.). *A. modestus* does not grow to the tall cylindrical shapes shown by *S. balanoides* when crowded (Southward, 2008) so the two species may not be functionally equivalent. In early studies of limpet movements in Lough Hyne (Little et al., 1988), before *A. modestus* became abundant there, limpets were shown to move out of high-density barnacle areas to feed, but there have been no recent studies recording the reactions of limpets to *A. modestus*.

4.3 Spatial Asynchrony

On moderately exposed shores, there is often a mosaic of areas covered either by barnacles or by fucoid algae as the various stages of the cycle are temporally out-of-phase according to local variation in supply and subsequent abundance of limpets, barnacles and fucoids (Hawkins and Hartnoll, 1983a; Hartnoll and Hawkins, 1985). Such a 'mosaic-cycle' concept has been widened in its application to many communities, including temperate forest and marine benthic ecosystems (Reise, 1991; Remmert, 1991).

In Lough Hyne, there was some synchronicity between sites: the periods of high limpet abundance and high fucoid cover appeared to be in phase around the lough. However, the amplitude of the oscillations, as shown by their trajectories, varied among sites. In part, these variations may be related to wave exposure. Although all sites were relatively sheltered, the fetch varied from 34 to 884 m and aspect from 60° (NE) to 345° (N) (Table 1). Severe weather came mostly from the south to southwest, resulting in differential dislodgement potential for algae among sites with different aspects.

4.4 Historical Scale

The sequences of fucoid/limpet dominance in the years preceding this survey can, to some extent, be postulated from previous publications. While surveys carried out in 1955 (Ebling et al., 1960) and 1990/1991 (Little et al., 1992) used less quantitative assessments, so that direct comparisons with the present data are difficult, gross changes are still apparent, and measurements on the ACFOR scale can be compared (see e.g. Crisp and Southward, 1958; Simkanin et al., 2005). Little et al. (1992) reported a significant decrease between 1955 and 1990 in the overall abundance of *Fucus vesiculosus* and *F. spiralis* but an increase in *Patella vulgata* abundance. From the original data collected by Little et al. (1992), and from inspection of photographs of the sites taken at the time, the 10 sites were relatively free of fucoid algae in 1990/91, even East Goleen, which in 2014 still had some fucoid cover. Shores in 1990 were thus dominated by relatively 'bare' rock with *Patella*, a state that was beginning to change at the start of the present survey in 1994. This observation can therefore extend the sequence to three peaks of limpet abundance of between 4-5 year durations between 1990-95, 2002-6 and 2010-14.

Observations at only one site, North Quay (adjacent to North Island), made by Little et al. (1988) showed that a similar state of limpet dominance existed there in 1986. This phase may thus have lasted longer than the subsequent phases documented in this study. The lack of regularity in alternation times between fucoid and limpet dominance suggested by this extension beyond the 20 years of our study may indicate the influence of external forcing. In particular, there will have been extrinsic fluctuations in recruitment (see Hawkins and Hartnoll, 1983a, b; Hartnoll and Hawkins, 1985). Such external forcing has been emphasized by Ferreira et al. (2014, 2015) who showed the effects of physical stress

on fucoid recruitment. Limpet recruitment is also known to be extremely variable (Bowman and Lewis, 1977, Moore et al., 2011). The influence of external perturbations must therefore be considered in interpreting long-term cycles, as demonstrated in the models proposed by Burrows and Hawkins (1998) and Johnson et al. (1998).

4.5 Non-Bimodal Patterns

Despite the compressed vertical range of the intertidal zone within the lough, there was no clear relationship between *Patella* abundance and *Pelvetia canaliculata* cover over the two decades of survey. Observations have clearly shown *Patella* moving into, and above, the *P. canaliculata* zone during feeding excursions at some sites (Little et al., 1988), so this lack of correlation is surprising. On the lower shore, the lack of relationship of limpet abundance with *Ascophyllum* cover suggests that at the sites monitored, *Patella* does not attack this alga to any degree, in spite of reports that it can devastate *Ascophyllum* beds at other sites in Northern Ireland (Davies et al., 2007; Lorenzen, 2007).

Conclusions

The 21-year survey in Lough Hyne has demonstrated inverse cycles of dominance by limpets and fucoid algae over a number of sheltered shore sites. The cycles were restricted mainly to the mid shore algae, *Fucus spiralis/guiryi* and *F. vesiculosus*, and did not extend to *Pelvetia canaliculata* or *Ascophyllum nodosum*. The periodicity of these cycles within the survey period was ~12 years peak-to-peak, but the cycles may be very irregular and may last much longer than this (if our historical reconstructions are correct). The mechanism of the cycles appears to involve only the fucoids and their grazer, the limpet *Patella vulgata*, without the necessity for settlement of barnacles to provide algal refuges as has been invoked in studies to explain oscillation patterns on moderately-exposed shores. Such observations, therefore, indicate underlying similarities but important locality-specific differences in the mechanisms that drive limpet-fucoid cycles on more sheltered shores (such as sea loughs) as compared to more moderately-exposed shores.

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Figure Legends

Fig. 1. Map of Lough Hyne, showing 10 long-term monitoring sites. NI, North Island; WWN, Westwood North; WWS, Westwood South; EG, East Goleen; GY, Graveyard; CB, Codium Bay; BB, Boundary Bay; EC, East Castle; SEL, South-East Labhra; NL, North Labhra.

Fig. 2. Overall changes in percent cover of bladder wrack (*Fucus vesiculosus*), spiral wrack complex (*Fucus spiralis/F. guiryi*), limpets (*Patella vulgata*) and acorn barnacles (4 species pooled) at 10 monitoring sites in Lough Hyne, SW Ireland over a 21 year period. Data from 1986 based on Little et al. (1988); data for 1990 based on Little et al. (1992).

Fig. 3. Changes in percent cover of the spiral wrack complex (*Fucus spiralis/F. guiryi*) and the common limpet (*Patella vulgata*) at 10 monitoring sites in Lough Hyne, SW Ireland over a 21 year period.

Fig. 4. Changes in percent cover of bladder wrack (*Fucus vesiculosus*) and limpets (*Patella vulgata*) at 10 monitoring sites in Lough Hyne, SW Ireland over a 21 year period.

Fig. 5. Temporal cycles of fucoid macroalgae (two species) cover vs limpet density.in Lough Hyne, SW Ireland over a 21 year period. Each point represents an annual survey from 1994 (triangle) to 2014 (largest circle).

Fig. 6. Temporal cycles of *Fucus spiralis/guiryi* complex vs. limpet density at 10 sites in Lough Hyne, SW Ireland over a 21 year period. Each point represents an annual survey from 1994 to 2014.

Fig. 7. Changes in percent cover of the channelled wrack (*Pelvetia canaliculata*), knotted wrack (*Ascophyllum nodosum*) and serrated wrack (*Fucus serratus*) at 10 monitoring sites in Lough Hyne, SW Ireland over a 21 year period.

Fig. 8. Non-metric Multi-Dimensional Scaling plot (from Primer ver. 7) of limpet and fucoid abundances at Lough Hyne, SW Ireland. Each point is an average of 21 years at the monitoring site. Shore slope values are degrees from the horizontal. Limpet abundance data were square-root transformed whereas fucoid cover data (5 species) were log (x+1) transformed prior to analysis. Site name abbreviations as in legend of Fig. 1 and Table 1.