

Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales

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ABSTRACT: The role of limpet grazing in preventing the development of algal canopies is a recurrent theme in intertidal ecology. Less is known about interactions of limpets with the long-term dynamics of established canopies. Aerial photographs indicate that intertidal canopy cover has declined over the past 44 yr in Strangford Lough, Northern Ireland. There has been a loss of the previously continuous cover of *Ascophyllum nodosum* (L.) Le Jolis in the mid-shore. A barnacle-dominated assemblage now fills gaps in the *A. nodosum* canopy. The rates at which barnacle patches become established and grow have increased since 1990. Changes in canopy cover have been accompanied by increases in limpet densities since the 1980s. Measurements between 2003 and 2004 showed no increase in length of *A. nodosum* fronds when limpets *Patella vulgata* had access to the algal holdfasts. In contrast, when limpets were experimentally excluded from the holdfasts, there was net frond growth. In the Isle of Man, which is climatically similar to Strangford Lough but has fewer limpets, growth occurred regardless of limpet grazing. The breaking force for *A. nodosum* declined with increasing local densities of limpets. *A. nodosum* is a sheltered shore species, potentially vulnerable to changes in wave exposure. There is no evidence, however, that Strangford Lough has become windier over the past 3 decades. Variation in wave exposure among locations within the lough was not related to rates of barnacle patch creation or expansion. Limpet population density has increased following a series of mild winters. Climate change may have a role in causing canopy loss, not by direct effects on the growth of fucoids, but by increasing the severity of grazing through changes to limpet populations.

KEY WORDS: Limpets · *Ascophyllum nodosum* · *Patella vulgata* · Grazing · Climate · Canopy loss · Fucoid

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INTRODUCTION

A canopy of fucoid algae is frequently seen as the defining characteristic of sheltered rocky shores (Lewis 1964). Fucoids often act as foundation species, creating habitat and modulating the flow of resources to other organisms (Dudgeon & Petraitis 2005). A particularly striking example of such a foundation species is *Ascophyllum nodosum* (L.) Le Jolis, a mid-shore dominant along sheltered coasts of the North Atlantic. *A. nodosum* canopies may have a high biomass (Cousens 1984), and can influence biodiversity by facilitating other species (Jenkins et al. 1999). *A. nodo-*

sum is relatively long-lived, with estimated holdfast ages exceeding 50 yr (Åberg 1992a,b). Given this longevity, it is perhaps unsurprising that the temporal dynamics of *A. nodosum* stands are not well understood. The majority of temporal work consists of studying the responses to catastrophic disturbances, whereby patches of mature plants are removed completely from the shore (e.g. by scraping and/or burning; Keser & Larson 1984, Jenkins et al. 1999, Dudgeon & Petraitis 2001, Bertness et al. 2004). While these experiments can define the recovery time of canopies, they do not necessarily reflect the dynamics of *A. nodosum* in areas where large-scale removal is rare

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or absent, such as the ice-free shores of the NE Atlantic.

In general, long-term time series studies of intertidal communities are a rarity, leaving ecologists to infer community dynamics on the basis of relatively short-term experiments (Underwood 2000, but see Dye 1998). Where longer-term observations have been made, it is still difficult to assess drivers of ecosystem change. For example, in a 17 yr study of a shore in the Severn Estuary, England, Little & Kitching (1996) identified wave action and limpet grazing as possible factors involved in the loss of a fucoid canopy. It has long been known that experimental removal of limpets leads to proliferation of fucoids (e.g. Jones 1946, 1948). Such experiments have contributed to a consensus that patellid limpets are the dominant grazers on NE Atlantic shores (e.g. Hawkins & Hartnoll 1983). Removing limpets commonly results in a bloom of ephemeral green algae, followed by a dense coverage of fucoid species. Hence much research has emphasized the role of grazing in preventing establishment of canopy-forming *Fucus* spp. (e.g. Southward 1964, Southward & Southward 1978, Hawkins 1981, Hawkins & Hartnoll 1983, Jenkins et al. 1999, Thompson et al. 2004, Jonsson et al. 2006). In contrast to cases involving the grazing of juvenile algae or recruits, the loss of established canopies has been less studied, and it is not clear what role grazing may play. Furthermore, relatively few studies have recorded patellid grazing in *Ascophyllum nodosum*-dominated areas (but see Jenkins et al. 1999). Loss of adult plants is usually attributed to changes in physical disturbance (Little & Kitching 1996) and has been observed as part of the recovery of limpet densities following oil spills and related impacts (Southward & Southward 1978). Limpet grazing on established *A. nodosum* canopies has been observed sporadically on NE Atlantic shores (Fischer-Piette 1948, Southward 1964). It is therefore possible that limpets may play a role in the long-term dynamics of *A. nodosum* canopies by damaging or removing established adult algae.

For shores around the coast of Northern Ireland, preliminary observations suggested a trend of decreases in *Ascophyllum nodosum* canopy cover over the last decade. We were able to use aerial photographs of the intertidal zone in Strangford Lough (Northern Ireland) taken at various times between 1962 and 2002 to assess this suggested change in canopy cover. The possibility that grazing is associated with this loss could be assessed using survey data on limpet *Patella vulgata* L. densities between 1979 and 2004. Given these historical data, 2 potential hypotheses were tested as explanations for the observations of *A. nodosum* canopy loss (1) a change in environmental conditions (increased wave exposure, Little & Kitching 1996) has resulted in

the loss of adult plants; (2) a change in strength of the grazing effect of limpets on adult *A. nodosum* has increased the loss rate of adult plants. The 2 hypotheses are not mutually exclusive and *A. nodosum* loss may result from an interaction between environmental and trophic processes. To further quantify the potential role of limpets we manipulated grazing in 2 regions with similar climatic conditions but different densities of limpets. The relationship between limpet density and the breaking force for adult fronds was also estimated.

MATERIALS AND METHODS

Aerial photography. Aerial photographic surveys of Strangford Lough (Fig. 1) were made in 1969, 1994, 1997, 2001 and 2002 by the Environment and Heritage Service, Northern Ireland, and in 1962 and 1988 by the Ordnance Survey, Northern Ireland. Eleven locations photographed at more than one time were identified from these surveys (Table 1). Analysis was restricted to areas of bedrock as changes in cover on boulder shores were difficult to

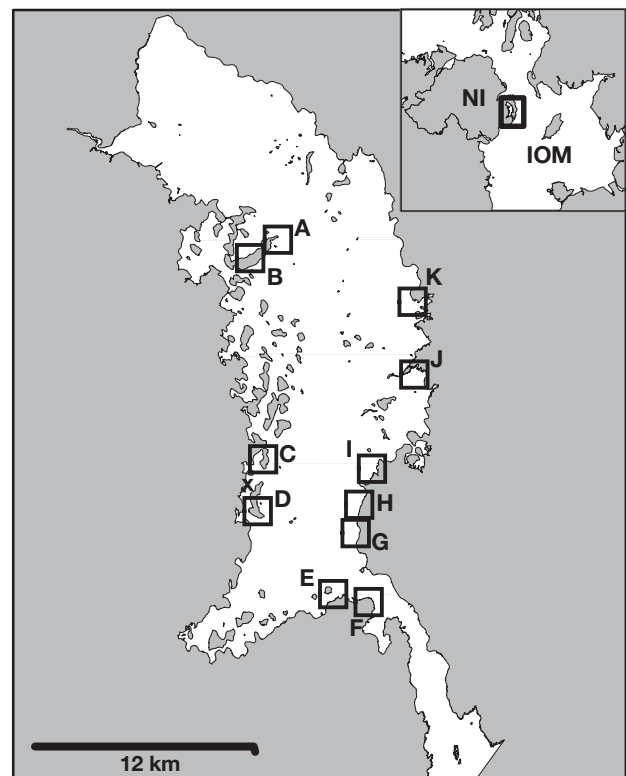


Fig. 1. Strangford Lough and photographed locations (X = Rathcunningham site; other abbreviations as in Table 1). Inset shows locations of Strangford Lough (box), Northern Ireland (NI) and Isle of Man (IOM)

Table 1. Algal and mean barnacle cover estimates for each available shore photograph for Strangford Lough. Estimated area of furoid cover (Fuc. cover) in first photograph of each series was standardised to 100% cover to allow comparisons of sites where fraction of intertidal varied (as a proportion of the georeferenced 100 ha areas used to overlay photographs in the GIS)

Site	Year	Fuc. cover (%)	Barnacle patches n	Size (m ²)
A: Mahee Island N	1962	100	0	0
	1969	100	0	0
	1988	98.7	14	73.5
	1994	97.6	9	211.6
	1997	98.3	10	135.5
	2001	94.7	14	293.0
B: Mahee Island S	2002	95.3	23	158.7
	1994	100	16	114.8
	2001	95.9	24	130.2
C: Ringdufferin	2002	93.7	31	122.6
	1994	100	9	94.3
D: Taggart Island	2001	99.0	18	128.2
	1969	100	0	0
E: Chapel Island	1994	98.9	26	56.4
	2001	95.7	37	149.4
	1994	100	4	91.9
F: Audley's Castle	2001	99.9	5	113.9
	1994	100	44	72.2
G: Marlfield Bay	2001	97.0	28	148.4
	1994	100	27	40.2
H: Priest Town	2001	90.2	48	86.0
	1994	100	40	95.7
I: Lady's Port	2001	94.0	56	116.8
	1994	100	13	55.5
J: Black Neb	2001	99.2	11	172.4
	1994	100	27	81.1
K: Kircubbin	2001	99.5	28	95.0
	1994	100	6	2.3
	1994	99.3	23	32.7
	2001	97.4	27	99.9

quantify in photographs. A fixed 100 ha area was marked out in photographs for each location using a geographical information system (GIS, ArcInfo). This provided a means for standardising comparison of photographs among different dates. Between 5 and 10 control points per location were identified for georeferencing areas in photographs from different dates (Caloz & Collet 1997) and recorded in the field during 2001 and 2002 using geographical positioning systems (GPS).

Areas of furoid canopy in photographs contrast sharply with the barnacle cover that dominates in the absence of macroalgae. Although it was not possible to distinguish the *Ascophyllum nodosum* canopy from other furoids in photographs, the majority of mid-shore areas in Strangford Lough are dominated by *A. nodosum* (Brown 1990). The presence of pale white or grey barnacle patches against the darker algal-dominated

mid-shore therefore facilitates automated identification of gaps in canopy cover (Ekebom & Erkkila 2003). This approach was ground-truthed using GPS to trace the outlines of 7 barnacle patches during 2001. In the field an average area of 404.04 m² (SE = 145.8) was recorded. The same patches were identified in aerial photographs from 2001. An average patch area of 351.06 m² (SE = 108.7) was recorded (error = 13 %). For each photograph, individual barnacle patches were extrapolated into polygon shapefiles to measure patch surface area (total area of barnacle patches in each photographed location) and frequency (number of barnacle patches at each photographed location). The initial cover of algal canopy was measured for the first photograph at each site to provide a baseline to estimate canopy loss. The annual rates of change for barnacle and furoid cover were estimated from successive pairs of photographs at each site, with data plotted at the mid point of the 2 years used to estimate the rate of change.

Limpet abundances. Several different sets of survey data were collated to estimate the extent of change in limpet abundance over time. Information on limpet density for each aerial photograph location was collected from 20 haphazardly thrown quadrats (0.25 m²) in the intertidal during summer 2002. At Rathcunningham Quay, Strangford Lough (Fig. 1, Site X), the abundance of limpets (*Patella vulgata*) boulder⁻¹ (n = 232) had been surveyed in 1979 (Boaden & Dring 1980) and the same methodology (Boaden & Dring 1980) was replicated in 2000 (n = 10) and 2004 (n = 58) to remain consistent with earlier counts in 1979. Limpets were counted on boulders with a horizontal circumference of approximately 1 m. In each case, all boulders of the target size were examined, as encountered, along a transect in the mid shore at the Rathcunningham site.

At Taggart Island, Strangford Lough (Fig. 1: Site D) limpet data were available from both the 1986 Northern Ireland Littoral Survey (Wilkinson et al. 1988) and the 2003 Strangford Lough Ecological Change Survey (Roberts et al. 2004). Both surveys used the same methodology. Densities were estimated in 0.25 m² quadrats (1986, n = 16; 2003, n = 35), but converted into an 8-point categorical scale to describe the mean abundance of species within the vertical height limits in which they were found. As the raw data were not available, categorical estimates were back-transformed to estimates of population density by taking the log mid point of each category (thus, a category indicating abundances between 10 and 99 limpets has a mid point of 55 or log mid point of 3.45, see Burrows et al. 2002). The loss of information during this process is more likely to have obscured differences between surveys than to have created artefactual changes in abundance.

Physical factors. A cartographic method was used to estimate temporal changes in wave exposure concurrent with the aerial photograph time series. The exposure index was calculated on an annual basis for 400 locations spaced at 0.5 km intervals along the shoreline of Strangford Lough. As the lough has a narrow connection to the Irish Sea, waves are determined by local winds without any influence from open water swells. The model was based upon 2 factors, fetch distance and consensus wind speed. Using a GIS routine, fetch distances for each of the locations were calculated as the distance of open water along 36 compass bearings at 10° intervals.

Daily wind records consisting of wind speed and wind direction spanning 1972 to 2003 were obtained from 3 local wind stations situated around the lough (<2 km from the shoreline). Data from each wind station were transformed to a mean speed of zero with unit standard deviation to allow records from sites with different mean speeds to be averaged. The consensus wind speeds took into account variable wind speed and direction recorded at different sites as a result of modification by the surrounding topography (Klaic et al. 2002). Therefore, they were considered to be a more reliable basis for extrapolation of wave exposure than records from any single site.

Relative wave exposure was estimated by multiplying the square of average consensus wind speed by the fetch distance along each 10° bearing (modified after Thomas 1986). To avoid confounding changes in location with time, estimates of the mean exposure and change in exposure were estimated for 1994 to 2001 for each location. These dates provided the highest number of paired photographs ($n = 11$) for comparison over the same time period. The short-term change in exposure at each location was calculated as the rank correlation between annual relative exposure and year. Hence a positive trend in exposure indicates that wind speeds have been increasing between 1994 and 2001 and/or winds along relatively longer fetches are becoming more common for a particular location. In addition to mean relative exposure the variance of the time series was used as a measure of the potential for relatively extreme years to affect algal cover. The 8 yr summaries (mean, variance and trend) were used as predictor variables for the change in patch frequency or area between 1994 and 2001 at the 11 photographed locations. Longer timescale trends in wind speed were analysed using regression to determine whether mean wind speed had decreased or increased over the 1972 to 2003 time period. In case mean wind speed was not a good indicator of the potential for algal loss in storms, the overall trend in records of strong winds to gales (annual proportion of records $>12 \text{ m s}^{-1}$) was also examined between 1972 and 2003.

Manipulative experiments. To determine the effect of limpets on the frond length of adult *Ascophyllum nodosum* a hierarchical experimental design was employed. Experiments were carried out in 2 regions, Strangford Lough and the Isle of Man. The Isle of Man lies 70 km to the SE of Strangford Lough. It was selected as a second region because previous studies have shown it to have a lower density of limpets, yet it is both climatically and biologically similar to Strangford Lough. At the sites used for experiments, the average density of limpets was 29 m^{-2} at sites in the Isle of Man compared to 115 m^{-2} in Strangford Lough (0.25 m^2 quadrats, $n = 20 \text{ site}^{-1}$). Two sites were randomly chosen from those available in each region that exhibited $>50\%$ cover of *A. nodosum* interspersed with *Patella vulgata*. At each site, there were 7 replicates of each of 3 treatments. The 3 experimental treatments were (1) square enclosures of $30 \times 30 \text{ cm}$ surrounded by 1 cm mesh rabbit-wire fences to prevent limpet access (exclusions), (2) partial fences with a gap of 5 cm in the middle of each side as a procedural control and (3) an open treatment, marked only with screws (controls). Each treatment was centred on an individual adult *A. nodosum* plant, randomly allocated to 1 of the experimental treatments. There was a minimum spacing of 1 m between experimental replicates. All enclosures and controls were initially cleared of grazers (in May 2002) and frond length of the *A. nodosum* plant standardised to 25 cm. Frond length for each *A. nodosum* individual was recorded at approximately 2 mo intervals for 14 mo. Prior to analysis using a mixed-model ANOVA, data were examined for heteroscedasticity ('cage type' and 'region' as fixed factors, 'site' as random factor, nested within 'region').

Breaking force for *Ascophyllum nodosum*. The breaking force for *A. nodosum* fronds ($n = 94$) was estimated from haphazardly selected individuals close to the experimental and survey sites. Around the base of each individual, local limpet densities were recorded within an 0.25 m^2 quadrat centred on the plant. Breaking force was estimated for 1 randomly selected frond by attaching a grommet below the basal internode (McEachreon & Thomas 1987). A spring scale (0 to 2500 g) with a maximum force recorder was hooked to the grommet and steadily pulled vertically; if the frond did not break, the procedure was repeated on the same frond using a 0 to 10000 g spring scale. If the breaking force of the second pull did not exceed that of the first pull, weakening of the frond was assumed and the frond omitted from analysis. Broken fronds were retained to record the number of limpet grazing marks (defined as rasped areas formed by the characteristic sweeping movements of limpets per centimetre of frond).

RESULTS

Temporal change in barnacle patches and limpet abundances

There has been a change in algal cover since 1962, when the photographed shores were almost totally covered in algae, to a canopy interspersed with patches of barnacles (Fig. 2). From the predominantly mid-shore development of patches and from examination of locations, it is clear that most of the lost canopy consisted of *Ascophyllum nodosum*. The rate of patch formation was estimated for successive pairs of photographs at each location. Since 1962, the average annual barnacle patch formation rate at each location has been 1.43 yr^{-1} (SE 0.595, significantly greater than zero in a Student's *t*-test, $p < 0.05$). Only 3 changes in patch frequency were negative (i.e. a decrease in patches between photos, Fig. 3). For these 3 cases, the corresponding change in barnacle patch area was positive, implying coalescence and expansion of existing patches. The correlation between year and change in patch frequency was positive, implying that the rate of patch formation has increased over time (Spearman's $r_s = 0.714$, $p < 0.05$). This pattern does not seem to have resulted from changes in the locations used at different times. Individual locations all showed a net increase in patch formation over time (Locations A, B, D and K all increased in rate overall).

As with the patch formation rate, the estimated rate of loss of canopy cover appears to be increasing (Fig. 4). The correlation between rate of change in percentage cover and year was negative, indicating that the loss rate of furoid cover has increased over time ($r_s = 0.479$, $p < 0.05$). There was an average estimated reduction of 3 % of canopy between 1994 and 2001 (the years for which most data exist). This loss represents a 1.7 ha decrease in algal cover within the lough.

The available data on limpet density imply large increases in limpet density at the surveyed sites. Limpet numbers were greater in recent surveys at both Rathcunningham and Taggart Island (1-way ANOVAs, Rathcunningham: $F_{2,299} = 230.59$, $p < 0.05$; Taggart Island: $F_{1,50} = 51.27$, $p < 0.05$, Fig. 5).

Barnacle patch and limpet densities in relation to physical factors

There were no clear changes in wind speeds in the consensus data for Strangford Lough over the 1972 to 2003 period. Linear regressions of mean annual wind speed and frequency of strong winds to gales (speeds $> 12 \text{ m s}^{-1}$) were not significant (mean wind speed [negative slope]: $r^2 = 0.140$, $p = 0.551$; frequency of

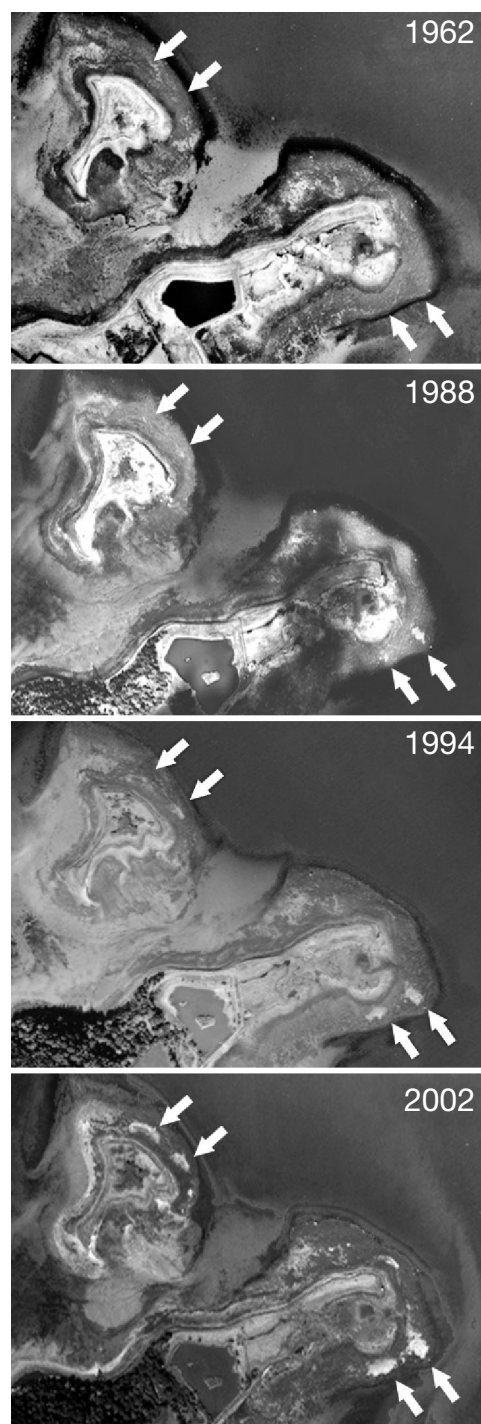


Fig. 2. Development of barnacle patches over time (arrowed) in the intertidal zone of Mahee Island, Strangford Lough. Spacing within pairs of arrows is approximately 50 m

strong winds to gales [negative slope]: $r^2 = 0.086$, $p = 0.109$).

Interactions between wind direction and fetch create variation in wave exposure among locations. This

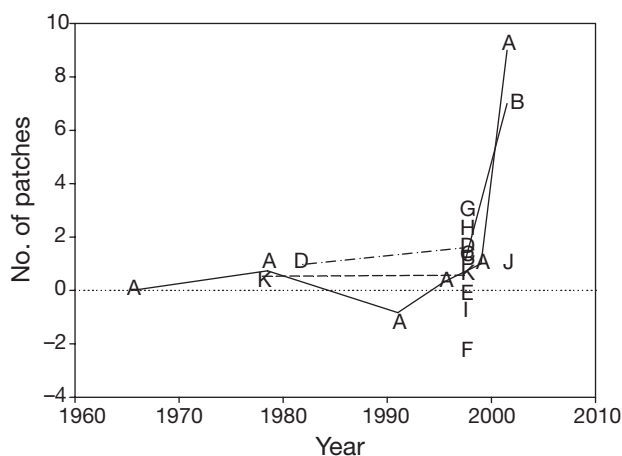


Fig. 3. Rates of change in barnacle patch numbers at each photographed location. Changes calculated as annual net change between successive dates with point plotted at the mid point of the 2 years used to estimate rate of change

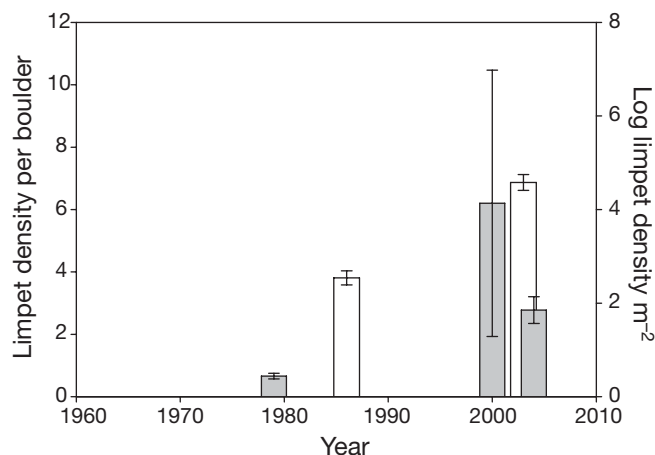


Fig. 5. *Patella vulgata*. Estimated mean (\pm SE) limpet density in different years at Rathcunningham (shaded bars, left ordinate) and Taggart Island (white bars, right ordinate)

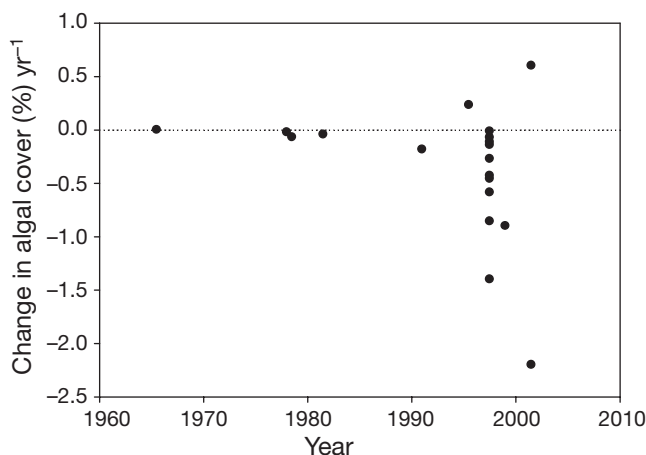


Fig. 4. *Ascophyllum nodosum*. Percentage change in algal cover between pairs of dated photographs, plotted at mid-term point between dates of photographs

variation did not, however, influence the creation of barnacle patches during the 1994 to 2001 period. There was no relationship between the mean relative exposure index, the variance or the temporal trend in the exposure index and changes in patch frequency or the total area of barnacles (Table 2). Relative exposures decreased on average over the photographed locations between 1994 and 2001 (average correlation between annual exposure and year, $r_s = -0.62$, SE 0.080, significantly different from zero, Student's $t = 7.72$, $p < 0.05$). Mean limpet densities at the photographed locations were also unrelated to exposure or patch variables.

Table 2. Correlations between potential drivers of changes in canopy cover and observed change in canopy cover at each location photographed in both 1994 and 2001 ($n = 10$). Patch frequency: number of patches in each photograph; patch area: estimated area of barnacle patches in each photograph. No correlations were significant; lowest probability associated with a coefficient was 0.16

Parameter	Relative exposure 1994–2001			Limpet count (2002)
	Mean	Variance	Trend	
Change in patch frequency	0.237	0.499	–0.482	0.315
patch area	0.110	–0.164	–0.419	0.141

Effects of limpets on *Ascophyllum nodosum*

The frond lengths of *Ascophyllum nodosum* individuals after 14 mo were similar in the Isle of Man and Strangford when limpets were prevented from grazing (Fig. 6). The regions differed when comparing across-cage designs that allowed limpets access to *A. nodosum* (significant cage type \times region interaction: $F_{2,4} = 11.9$, $p < 0.05$). Frond lengths increased regardless of grazing in the Isle of Man, but there was no net increase in frond lengths of grazed *A. nodosum* after 14 mo in Strangford. There were no differences between sites within a region (cage type \times site (region) interaction: $F_{4,59} = 0.39$, $p > 0.05$). In Strangford Lough, but not in the Isle of Man, limpets were observed to trap *A. nodosum* fronds under the shell and graze on the trapped fronds (Fig. 7a,b) and were also commonly observed aggregating around *A. nodosum* holdfasts (Fig. 7c).

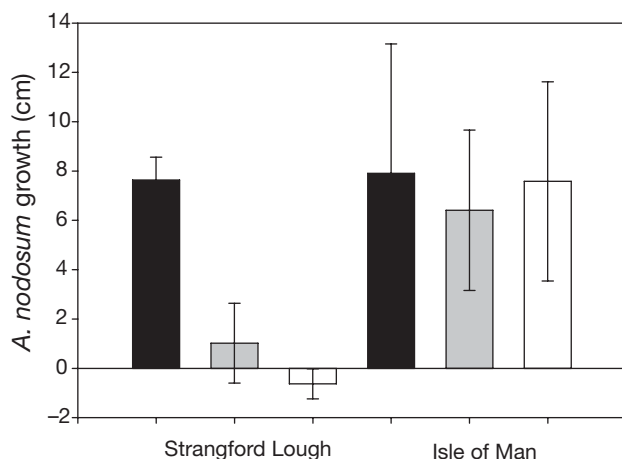


Fig. 6. *Ascophyllum nodosum*. Mean (+SE) changes in frond length in experimental treatments after 14 mo. Treatments shown as: fences to exclude limpets (black bars), partial fences as a procedural control (grey bars) and unfenced treatments (white bars)

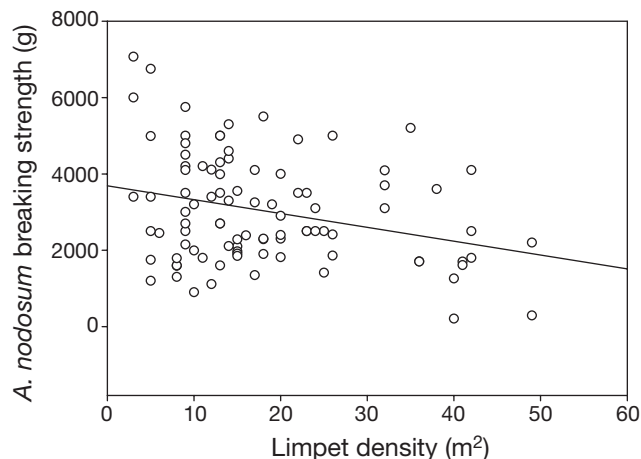


Fig. 8. *Ascophyllum nodosum*. Relationship between breaking strength and density of *Patella vulgata* adjacent to hold-fast. Fitted line is a linear regression

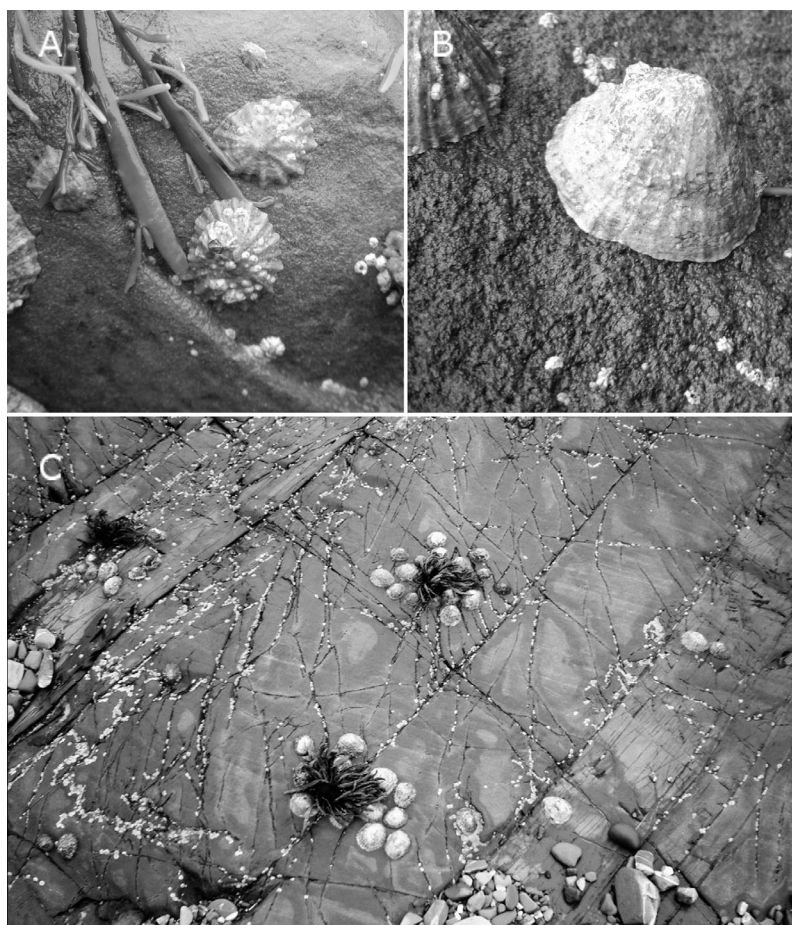


Fig. 7. *Patella vulgata*. Limpet grazing behaviour in Strangford Lough, showing *Ascophyllum nodosum* frond trapped under limpet shell at (A) Mahee Island and (B) Marlfield Bay. (C) Limpet clumping behaviour around holdfasts of solitary *A. nodosum*

Increased densities of limpets were associated with weaker *Ascophyllum nodosum* fronds (Fig. 8, $r^2 = 0.085$, $p < 0.01$). *A. nodosum* with higher densities of limpets in the immediate area had a greater frequency of grazing marks ($r = 0.239$, $p < 0.05$), structurally weakening the individual. Grazing therefore seems to increase the sensitivity of *A. nodosum* to frond breakage.

DISCUSSION

Aerial photographs clearly show the loss of algal canopy from mid-shore hard substrata in Strangford Lough. Over the last few decades, once-continuous canopies of *Ascophyllum nodosum* have become punctuated by barnacle-dominated patches. The rate at which these barnacle patches are created in the algal canopy appears to have increased since 1990 and at the same time the total area of these patches has also been increasing. Such changes in canopy cover, involving the replacement of primary producers with filter-feeders, will influence the ecosystem functioning of the lough, potentially altering the flows of carbon and/or nutrients between the intertidal and other coastal habitats.

Experimental manipulation of limpet grazing demonstrated that the present densities of limpets in the lough are capable of preventing the growth of established *Ascophyllum nodosum*. In addition, increased limpet density around holdfasts was associated with decreases in the breaking force of *A. nodosum* fronds. Limpets therefore increase the vulnerability of fronds to wave-induced breakage. In Strangford Lough, the observed increases in limpet densities may therefore cause loss of *A. nodosum* through direct grazing of established plants. Observations after the Torrey Canyon oil spill and in Brittany have previously suggested that extreme increases in limpet density are sufficient to cause the loss of established algal canopies (Southward & Southward 1978, Hawkins & Southward 1992, Le Roux 2005).

Demographic and environmental processes may also contribute to the loss of canopy, but there is little evidence for such factors acting in Strangford Lough. A lack of algal recruitment could potentially lead to a decline in canopy as part of an intrinsic long-term cycle, but there is little evidence to support suppression of recruitment by the established canopy. Demographic analyses of *Ascophyllum nodosum* populations indicate that population growth rate is more sensitive to changes in the survival of existing plants than to variations in recruitment (Åberg 1992a,b). The estimated lifespan of *A. nodosum* holdfasts is 50 to 60 yr in areas with sea ice and will exceed this in ice-free areas (Åberg 1992b). Given such a long lifespan, the loss of canopy during the 1990s must have resulted from an increase in the loss of established *A. nodosum*. As an alternative to a trophic interaction (grazing), *A. nodosum* may be responding to other changes in the environment of Strangford Lough. Eutrophication has been associated with decreases in fucoid cover (Vogt & Schramm 1991), but investigations during the 1990s concluded that Strangford Lough was not eutrophic (Service et al. 1996).

Climate change may affect the geographic distribution of *Ascophyllum nodosum*. In the Atlantic, fucoids are more common on shores at higher latitudes. Increases in air and sea temperatures are therefore expected to cause the ranges of fucoid algae to move northwards as shores at the southern range limits become too warm (Kendall et al. 2004). Strangford Lough, however, is not at the southern range limit of *A. nodosum* (Lüning 1990). There is recorded evidence for climate change over the last few decades in Northern Ireland. Air temperatures have increased, leading to fewer frosts, particularly since 1990 (Fig. 9). There are no continuous records of sea surface temperature for Strangford Lough. However, given the lough's estimated flushing time of 1.6 d (Service et al. 1996), temperature in the lough is expected to be close to that of

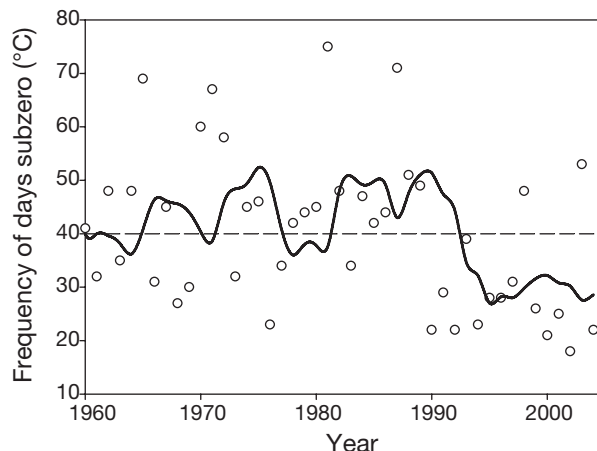


Fig. 9. Frequency of days with surface air temperatures below 0°C (Jones & Lister 2004) at Strangford Lough. Dashed line: mean of time-series; solid line: 5 yr running mean

the Irish Sea. Records from the Port Erin breakwater (Isle of Man) show an increase of approximately 1°C in average Irish Sea surface temperatures over the last 100 yr, with a current mean of approximately 11°C (Evans et al. 2003). Maximum temperatures of 15°C were recorded in intertidal areas of Strangford Lough during short-term (7 d) temperature logging in August (Strong 2003). All these temperatures seem well within the tolerance limits of *A. nodosum*, which has been shown to grow more rapidly with warming until a threshold of between 19 and 25°C is reached (Keser et al. 2005). The experimental manipulation in Strangford confirms that adult fronds are capable of growing under current environmental conditions, as long as limpets are excluded.

Ascophyllum nodosum is a sheltered-shore species and canopy loss may therefore be related to increased storm frequency (and therefore waves) as a result of changing wind climate (Thompson et al. 2002). There is no evidence for increases in wind speeds and wave exposure over the last few decades in Strangford. The rates of canopy loss showed no association with variation in mean estimated wave exposure among locations in the lough.

The grazing experiment indicates that the present densities of limpets in Strangford are preventing *Ascophyllum nodosum* growth by grazing, ultimately causing damage to fronds. A number of factors may have caused the recent increase in mean limpet densities to the level at which canopy cover becomes affected. Changes in climate, particularly from 1990, have led to less severe winter air (Fig. 9) and sea (Evans et al. 2003) temperatures. Limpet recruitment is lower and mortality is higher in cold winters (Crisp 1964, Bowman & Lewis 1986). The milder winters of the 1990s may therefore have reduced density-independent

restrictions on limpet populations, leading to the observed increases in population size. Such thermal limits to populations have been suggested for other molluscs (Thieltges et al. 2004). Thermal effects on grazer populations are also apparent from increased population density in response to artificial warming by power station discharges (Schiel et al. 2004). Limpet populations could also have increased due to declines in predator densities; however, evidence from bird counts suggests the opposite. Oystercatchers *Haematopus ostralegus* L. are considered to be important predators of limpets (Coleman et al. 1999). Bird counts indicate an increase in oystercatcher population size of 83% over the past 25 yr, with the steepest rises occurring in the 1990s (Maclean et al. 2005). This implies that the predation pressure on limpets may have increased during recent decades.

The trend of canopy loss seems likely to continue if limpet populations remain at their current levels within the lough. In the short term, canopy loss may accelerate as observed in the frequency of patch formation and changes in algal canopy since the 1990s. *Ascophyllum nodosum* canopy indirectly limits limpet populations by supporting an understorey of red algal turf, which is an unsuitable habitat for limpets (Jenkins et al. 1999, 2004). When the turf breaks down following canopy removal, there is often a large increase in limpet density (Jenkins et al. 2004). In Strangford Lough, these new barnacle- and limpet-dominated areas of the mid-shore may be relatively persistent. Other authors have shown that switching between assemblages can be stable and may persist for long periods. For example, Petraitis & Dudgeon (1999) have suggested that large-scale removal of *A. nodosum* from sheltered shores in New England may lead to a stable alternative assemblage dominated by mussels. Other authors have considered that the factors promoting *A. nodosum* beds are more predictable, such that any disturbed canopy will eventually revert to *A. nodosum* dominance (Bertness et al. 2002, 2004), although the period of recovery may extend over decades (Jenkins et al. 2004). As each of these studies deals with different physical habitats, a generalisation cannot be made about how shores dominated by *A. nodosum* canopies will respond to disturbance.

Ascophyllum nodosum recruits have been observed in locations within Strangford from which limpets have been removed, indicating that *A. nodosum* canopies have the potential to recover (C. A. Maggs unpubl. data). However, it is likely that any future recovery would not occur rapidly. Limpet densities would not decrease immediately with the loss of *A. nodosum* canopy, as the limpets would feed upon the microbial biofilm (Hill & Hawkins 1991, Thompson et al. 2004) and might seek alternative food supplies such as *Fucus*

spp. (Southward & Southward 1978). Such patterns were observed after the Torrey Canyon oil spill. Following periods of canopy loss resulting in food shortage, large-scale reductions in limpet density occurred (Southward & Southward 1978, Hawkins & Southward 1992). If consumption of *A. nodosum* is subsidising high limpet densities that cannot be sustained by other food sources (see Bustamante et al. 1995), a food shortage and reduction of limpet numbers seems likely if the *A. nodosum* canopy is totally lost. However, the potential benefits that limpets gain from consuming *A. nodosum* have not yet been assessed.

The loss of *Ascophyllum nodosum* in Strangford has parallels with declines in furoid canopies in the Baltic. Along with eutrophication in the Baltic, increases in grazers (mesograzers: the isopod *Idotea baltica* Pallas) following mild winters are thought to have caused reduction in algal belt widths and in percentage cover along the coasts of Sweden (Engkvist et al. 2000, Nilsson et al. 2004). The damaging level of canopy grazing observed in Brittany (Le Roux 2005) and the Baltic appears to be a regional phenomenon. It is not always clear why canopy overgrazing should be limited to particular locations. Limpets have been observed grazing on *A. nodosum* fronds in a wide range of locations (e.g. Brittany, France [Le Roux 2005]; Milford Haven, Wales; all Irish coasts; Plymouth, England and west coast of Scotland [C. A. Maggs, M. T. Burrows and S. J. Hawkins, respectively, pers. comm.]). The extent to which this grazing affects canopies may depend on limpet density. Regional variations in climate are likely to influence the density of limpets at broad scales. Local hydrography can further modify recruitment patterns (particularly in restricting grazer populations on the Isle of Man, see Norton et al. 1990 for littorinids). The diversity of observed temporal trends in limpet populations reported by Burrows et al. (2002) presumably reflects these local influences on larval supply and recruitment.

An interaction between limpets and the canopy-forming alga *Ascophyllum nodosum* has been recorded experimentally herein, for the first time. Limpets are increasing in density, perhaps driven by enhanced survivorship through recent favourable winter conditions. Analysis of canopy changes using aerial photographs has shown an accelerated loss of canopy and the continuing emergence of barnacle patches over the last 40 yr. Experimental manipulations have indicated that limpets may be responsible for the loss of established canopy. The limpet-*A. nodosum* interaction demonstrates how separate trophic levels can potentially respond differently to climate change. Assessments of climate change impacts are often made on a single-species basis with respect to the assumed climate envelope required by that species. As limpets

appear not to respond to the same climatic cues as algae, the predicted shifts in range may be influenced at small scales by mismatches between the responses of fucoids and their most important grazer. If milder winters are acting as a trigger for local increases in limpet abundance, there are likely to be more cases of *A. nodosum* canopy loss in the temperate NE Atlantic.

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