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Seasonal variability in the population structure of a habitat-forming kelp and a conspicuous gastropod grazer: do blue-rayed limpets (*Patella pellucida*) exert top-down pressure on *Laminaria digitata* populations?

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Abstract

Kelp forests dominate wave-exposed rocky reefs along mid-to-high latitude coastlines. The distribution and structure of kelp forests is determined by a range of physical and biological processes operating across varying spatial and temporal scales. Many kelp forest systems are strongly influenced by herbivory, and overgrazing by urchins, in particular, is a recognised driver of kelp forest distribution and structure. The ecological significance of herbivory by kelp-associated limpets, however, has received far less attention. We quantified seasonal population dynamics of *Laminaria digitata* and the blue-rayed limpet *Patella pellucida* on two rocky shores in North Devon, UK. For the kelp, we quantified density, percent cover, morphology, standing biomass, elongation and erosion rates, and C:N and phenol content. For the limpet, we measured abundance, biomass, and morphology, and for the limpet-kelp interaction we recorded observable grazing damage on the blade. Both populations exhibited typical seasonality with kelp growth rates peaking in spring, maximum standing biomass observed in summer and increased erosion rates in autumn. Blue-rayed limpets, which were recorded within kelp holdfasts as well as on stipes and blades, recruited in spring and peaked in abundance in late summer, with length and biomass generally increasing through the year. The area of kelp blade damaged by limpet grazing was low (a maximum of ~ 4 %) and relatively consistent throughout the year, and the number and size of grazing scars exhibited limited seasonality. Survey data from other *L. digitata* populations in the UK suggested that the limpet abundances recorded in North Devon were comparable with other sites in the region. Although the impact of *P. pellucida* grazing on kelp blade tissue appears to be minimal, further research into cavity grazing by limpets on the stipe and in the holdfast is needed to formerly assess the impact these cavities have on dislodgement and fracture rates, especially when increased occupancy and grazing coincides with periods of intense wave action. We conclude that while herbivory is an important processes acting upon many kelp populations globally, the grazing pressure exerted by *P. pellucida* on *L. digitata* is unlikely to strongly influence population structure on UK rocky shores.

Key Words

Temperate reefs; Northeast Atlantic; Macroalgal beds; Laminariales; Grazers; Herbivory

Highlights

- Typical seasonality in *Laminaria digitata* and *Patella pellucida* population dynamics.
- Despite high limpet abundances, little evidence of significant grazing effects.
- Limpet grazing unlikely to impact *L. digitata* population structure in southwest UK.

1. Introduction

Kelp forests are widely distributed across wave-exposed coasts at mid-to-high latitude regions in both hemispheres (Dayton, 1985; Kain, 1979; Teagle et al., 2017). Kelps function as ecosystem engineers by altering environmental conditions and providing food and habitat for associated organisms (Dayton, 1985; Kain, 1979; Smale et al., 2013; Steneck et al., 2002; Teagle et al., 2017). The distribution, extent, structure and productivity of kelp forests is influenced by a range of physical and biological processes (Dayton et al., 1984; Smale et al., 2016; Wernberg et al., 2011), the importance of which vary considerably across spatial and temporal scales. For example, strong top-down control on kelp populations, through intense herbivory, has been recorded in eastern Canada (Bernstein et al., 1981; Mann, 1977; Scheibling et al., 1999), Iceland (Hjorleifsson et al., 1995), northern Norway (Leinaas and Christie, 1996), parts of South Africa (Bustamante et al., 1995), eastern Australia (Andrew and Underwood, 1993; Fletcher, 1987), and New Zealand (Shears and Babcock, 2002). In contrast, some kelp populations appear to be far less influenced by herbivory, including those in Western Australia (Fowler-Walker and Connell, 2002; Vanderklift and Kendrick, 2004), other parts of South Africa (Day and Branch, 2002; Velimirov et al., 1977), Argentina (Barrales and Lobban, 1975), Chile (Vasquez et al., 2006) and potentially those in the British Isles (Hargrave et al., 2017; Smale et al., 2013). The majority of studies pertaining to grazing pressure have focussed on sea urchins, which can overgraze kelp forests and drive phase shifts to urchin barrens (Filbee-Dexter and Scheibling, 2014; Law and Morton, 1993; Ling et al., 2014; Paine and Levin, 1981).

Non-urchin grazers may also exert top-down control over kelp populations but have received far less research attention. A number of studies have identified grazing by molluscs, crustaceans and fish as a key process within kelp forests (e.g. Krumhansl and Scheibling, 2011), although major knowledge gaps pertaining to the role of non-urchin grazers within many systems still persist. For example, in the northeast Atlantic, only a handful of studies have examined the role of limpet grazing on natural kelp populations (e.g. Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). More generally, studies on kelp-grazer interactions have been concentrated within a few geographic regions, including eastern Canada (e.g. Scheibling et al., 1999), eastern Australia (e.g. Andrew, 1993), California (e.g. Harrold and Reed, 1985) and Norway (e.g. Hagen, 1983). To add to our understanding of limpet-kelp interactions, we adopted the North Atlantic canopy forming kelp *Laminaria digitata* and the blue-rayed limpet *Patella pellucida* as a model system to examine the influence of a non-urchin grazer on kelp forest structure.

Laminaria digitata is a perennial species, reaching maturity between one and two years and surviving for up to six years (Smale et al., 2013). Kain and Jones (1975) found adult *L. digitata* to be fertile between August and December with spores appearing to settle throughout most of the year, but less so during mid-winter. In addition, it can grow throughout the year (Schaffelke and Lüning, 1994), but exhibits seasonality in growth rates, with peak elongation and growth occurring in late spring (May-June in the northern hemisphere) (Kain, 1979; Parke, 1948; Perez, 1969). Further to these growth-rate fluctuations, the biochemical content of kelp tissue also changes seasonally (Hargrave et al., 2017), which is likely in part to be influenced by the availability of nutrients in the water (Arnold and Targett, 2003; Black, 1950; Dayton, 1985; Gevaert et al., 2008; Hay and Fenical, 1988; Jormalainen and Honkanen, 2008; Targett and Arnold, 1998). This seasonal fluctuation also possibly reduces the palatability of the tissue for the associated grazers (Graham and Fretter, 1947; McGrath, 1992; Norderhaug et al., 2006).

Kelp tissue loss also occurs seasonally, as dislodgement of the whole or part of the plant or the substrate beneath the holdfast, or as erosion of the blade (de Bettignies et al., 2013; Mann, 1972). Chronic erosion of blade (or ‘lamina’) tissue may occur year-round, although many species exhibit periodic peaks in erosion rates, leading to a seasonal pulse of detritus production (Krumhansl and Scheibling, 2012). Dislodgement can occur throughout the year (de Bettignies et al., 2013; Krumhansl and Scheibling, 2012) but may increase during extreme storm events (Filbee-Dexter and Scheibling, 2012; Smale and Vance, 2015). Alongside this seasonal tissue loss, kelp-derived material is also consumed by a wide range of organisms, either as living material or as kelp detritus (Krumhansl and Scheibling, 2012; Vanderklift and Wernberg, 2008). If live kelp tissue is overgrazed, for example by fish or invertebrate herbivores, it can drive widespread kelp biomass loss (Dayton, 1985; Krumhansl and Scheibling, 2012; Orr et al., 2005; Smale et al., 2013; Steneck et al., 2002). This grazing-related biomass loss can occur directly through the consumption of kelp plants (e.g. Steneck et al., 2002), and/or indirectly, through weakening of kelp tissue and consequent increases in kelp plant fracturing and/or dislodgement (Black, 1976; Choat and Black, 1979; Muñoz and Santelices, 1989).

Of the various kelp-associated gastropods, at least five limpets have been identified as almost exclusively feeding on one or a few kelp species and, once settled as larvae, all but one spend most of their life on kelp (*Discurria* insessa, *Cymbula compressa*, *Scutellastra argenvillei*, *Scurria scurra* and *Patella pellucida*) (Black, 1976; Branch, 1975; Kain and Svendsen, 1969; McGrath, 1992; Toth and Pavia, 2002a). Of these species the only one to be found in the northeast Atlantic is the blue-rayed limpet *Patella pellucida* (Graham and Fretter, 1947; Leblanc et al., 2011; Steneck and Watling, 1982; Toth and Pavia, 2002a), which is distributed from Portugal polewards to Norway and Iceland (Fretter and Graham, 1976; Vahl, 1971). It can reproduce throughout the year but recruitment tends to peak during the spring; most individuals exhibit an annual life cycle as few survive more than a year, although those inhabiting kelp holdfasts may overwinter (Fretter and Graham, 1976; Vahl, 1971). Recently-settled *P. pellucida* individuals found on kelp blades and stipes are typically 0.1 - 0.3 cm in length, and may attain a maximum length of ~ 1 cm (McGrath, 1992) whilst individuals over-wintering within kelp holdfasts can reach 2 cm in length (Fretter and Graham, 1976). Limited research has been conducted on *Laminaria* spp. and *P. pellucida* interactions and, consequently, the importance of limpet grazing remains largely unexplored (Hargrave et al., 2017; Kain and Svendsen, 1969; Toth and Pavia, 2002a).

We examined the population dynamics of *L. digitata* and *P. pellucida* at two intertidal reef sites in the southwest of the UK. Specifically, we examined the seasonal patterns of (i) kelp density, biomass, length, elongation, erosion, dislodgement and biochemical composition; (ii) limpet abundance and morphology and; (iii) evidence of grazing damage on kelp blades. Our overall aims were to benchmark seasonal population dynamics for these critically under-studied kelp and limpet species and to determine whether grazing pressure by *P. pellucida* may exert top down control over *L. digitata* populations.

2. Methods

2.1. Study Sites

The study was conducted at two sites, Lynmouth Bay and Wringcliff Bay in North Devon, UK (Fig. 1). Both are open-coast rocky reef sites comprising of a mix of boulders and bedrock, and experience typical mid-latitude seasonality in key environmental variables (Fig. 1). Both sites sit within Exmoor National Park, mid-way along the Bristol Channel and within the Bideford to Foreland Point Marine Conservation Zone. Preliminary observations indicated that these sites support fairly extensive stands of *Laminaria digitata* and associated fauna, including *Patella pellucida* (Fig. 1).

2.2. Field Surveys

All surveys were conducted in the low intertidal zone (~ 0.8 m above chart datum), within stands of *L. digitata* exposed during spring low tides. At each site, three fixed points parallel to the low tide line and ~ 10 m apart were established using GPS and marked by drilling a bolt with a fluorescent tag into the bedrock. The density of mature canopy-forming *L. digitata* plants (i.e. fully formed thalli with stipe length > 10 cm) was quantified by haphazardly placing four 0.25 m^2 quadrats within 3 m of each of the fixed points. Quadrat surveys were completed monthly from March 2016 to March 2017 (excluding July and August 2016 at both sites, November 2016 and January 2017 at Lynmouth and June 2016 and March 2017 at Wringcliff due to a limited tidal window). To determine kelp elongation rates, 20 mature canopy-forming *L. digitata* plants were randomly selected from areas between the fixed points at Lynmouth Bay and tagged (with fluorescent tubes on cable ties) during the spring low tides of March 2016. Plants were revisited monthly (March 2016 to March 2017) and blade length and elongation were measured in the field. Monthly blade elongation was determined following the hole punch method, whereby the blade was punctured at distances of 5 and 10 cm from the stipe/meristem junction and re-measured on return (Parke 1948). The erosion rate of the blades was calculated using the blade length and elongation rate data in the equation:

$$\text{Erosion (cm day}^{-1}\text{)} = \frac{\text{((blade length month1 + elongation during month1) - blade length month2)}}{\text{Number of days between month1 and month2}}$$

Kelp standing crop biomass values were obtained by randomly harvesting 10 mature *L. digitata* plants per site per month outside the immediate vicinity but adjacent to the fixed points at the same tidal height on the shore at both sites. These were returned to the laboratory to determine stipe and blade length (± 0.5 cm) (later combined for the total length of each plant) and stipe/holdfast and blade biomass (± 1 g). Harvested biomass data and density estimates were then used to calculate estimated standing crop biomass. To determine dislodgement rates of *L. digitata* over the winter, a further three fixed points were established per site (~ 0.8 m a.c.d.), each > 5 m apart from one another. Within a 3 m radius of each point, 10 mature *L. digitata* plants were tagged with fluorescent tubing and cable ties during the October 2016 (Wringcliff Bay) and November 2016 (Lynmouth Bay) spring low tides. These were revisited in March 2017, when the number of tagged plants remaining was quantified.

The harvested kelp plants were also used to examine the population structure of associated *P. pellucida*. Any limpets attached to the kelp plants were removed and retained in 70% Industrial Methylated Spirits (IMS). The length and fresh-weight biomass of *P. pellucida* were then quantified. To determine the total area of each kelp blade, the area of grazed tissue, the number and size of grazing scars and a measure of relative grazing damage, a digital image of each side of each kelp blade was taken by placing the blades between two pieces of acrylic sheet. These images were later analysed with ImageJ software (National Institutes of Health, USA); the total area of the blade and the total area of grazed tissue were used to calculate the total percentage of each blade damaged by limpet grazing. In addition, to assess the grazing pressure on new growth tissue per month an index of relative grazing damage was calculated for a randomly selected sub-set (n=5) of Lynmouth Bay blades, using the formula:

$$\text{Relative grazing damage} = \frac{\text{average area new growth for that month (cm}^2\text{)}}{\text{total area new tissue grazed (cm}^2\text{)}}$$

The average area of new growth for that month was identified in ImageJ using the monthly elongation rate averages from the tagged kelp plants. Within this area of new tissue, the total area of grazed tissue was also calculated.

Finally, in order to place our *P. pellucida* density values in a broader regional context, we collated exiting unpublished data on limpet abundances associated with intertidal *L. digitata* populations in the UK. Data were collected in the same manner as described above, and comparisons between our main study sites and these additional survey sites were made for corresponding months.

2.3. Biochemical Analysis

To assess seasonality in the biochemical composition of *L. digitata*, samples of basal and distal sections of blade (> 20 cm^2) were collected from the harvested kelp plants (10 plants were harvested per site per month). The samples were cut (basal = immediately above the stipe-blade/meristem junction; distal = from ~ 5 cm below the tips of the blade), externally cleaned using deionised water, blotted dry, placed in pre-labelled bags and put on ice, before being transferred to a freezer for storage. Samples were then freeze-dried (Lablyo Freezedrier, Frozen in Time Ltd) for at least 48 hours before being ground to a 250 μm powder. To represent the seasonal biochemical content of *L. digitata* at both sites, four months were selected to reflect each season (March for winter, June for spring, September for summer and December for autumn; Gevaert et al., 2008); within each month five or six samples were randomly selected to represent basal and distal tissues. Both basal and distal samples were analysed in an Elemental Microanalysis CHN Analyser (EA1110, CE Instruments Ltd, Wigan) for carbon, hydrogen and nitrogen content following Gevaert et al. (2008) but using cyclohexanone-2,4-dinitrophenylhydrazone as the standard and L-cystine as the Certified Reference Material. The Certified Reference Material was replicated in triplicate and each basal/distal sample was sub-sampled in duplicate to account for machine error. The powdered samples were also analysed for phenols following methods based upon Van Alstyne (1988) and Hargrave et al. (2017). Each basal/distal sample was sub-sampled twice and each sub-sample was assayed in triplicate to eliminate machine error; resulting data were averaged for use in statistical analysis. For each sub-sample, a measured mass (100 mg ± 10 mg) of powder was added to 1 ml of 50 % aqueous methanol in a 1.5 ml Eppendorf tube. Each tube was vortexed for 30 seconds and then extracted in a fridge (4 °C) for 24 hours. Samples were then vortexed again and centrifuged for two minutes at 13000 rpm. 0.5 ml of the supernatant was decanted into another 1.5 ml Eppendorf tube and diluted with 0.5 ml of deionised water. 0.48 ml of this solution was transferred into another 1.5 ml Eppendorf tube and combined with 60 µl of Folin Ciocalteau reagent. After five minutes incubation at room temperature, 30 µl of 1.5 Molar sodium carbonate was added. Samples were then sealed and vortexed and left to stabilise in the fridge (4 °C) for a further 24 hours to ensure the plateau of absorbance was reached. Subsequently, samples were centrifuged again and triplicate samples of the supernatant were loaded into multiwell plates and the absorbance was read at 765 nm on a SpectraMax 190 microplate reader. Absorbances were then converted to soluble phenolic equivalents per unit mass by reference to a phloroglucinol (Sigma-Aldrich, Gillingham) standard curve.

2.4. Statistical analysis

Variability in the various population-level metrics between sampling months and sites for *Laminaria digitata* and *Patella pellucida* were visualised plotting mean values (± SE) across time. Comparisons of dislodgement rates at both sites were analysed using a Mann-Whitney *U* test in R (R Core Team, 2016) due to the small data set. Variability between seasons and sites in the biochemical composition of *L. digitata* (i.e. C:N values and phenol content) was examined using univariate permutational analysis of variance (PERMANOVA; Anderson et al., 2008) in PRIMER v.7 software (Primer-E Ltd, Plymouth). Basal and distal sections were analysed separately using a two-factor model with Season and Site as fixed factors. Tests were conducted using a similarity matrix based on Euclidean distances between untransformed data, and 4999 permutations were conducted under a reduced model. Where main factors or interactions were significant (at $p < 0.05$), further pairwise tests were conducted. Variability in grazing metrics (i.e. total percentage blade area grazed, total number of grazing scars and average size of grazing scars) was examined in a similar manner. Finally, variability between months in relative grazing pressure at Lynmouth was examined with a one-factor model. Univariate PERMANOVA was used as opposed to other statistical approaches as it is more robust to heterogeneity in variance and does not assume normal distributions. Even so, differences in within-group dispersion between treatments can influence main tests. As such, the PERMDISP routine was used to examine differences in within-group dispersion between levels of the treatments and, where significant, a more conservative *p*-value of 0.01 was adopted to accept significance from the univariate PERMANOVA tests.

3. Results

The structure of *L. digitata* populations, which was similar across both sites, exhibited distinct seasonality (Fig. 2). The density of mature plants ranged from 4 inds. m^{-2} (at Wringcliff in December) to 20 inds. m^{-2} (at Wringcliff in March 2016), while standing biomass ranged from 422 g m^{-2} (at Wringcliff in December) to 2116 g m^{-2} (at Lynmouth in September). However, in general, densities were moderately consistent at ~ 10 inds. m^{-2} (Fig. 2A). This was reflected in the percent cover of *L. digitata*, which ranged from 14 % (at Lynmouth in October) to 55 % (at Lynmouth in June) but was averaged ~ 30 - 40 % through most of the year (Fig. 2B). The mean biomass of individual plants did exhibit a degree of seasonality, with values generally increasing through spring and summer before decreasing sharply in winter (Fig. 2C). The mean length of plants meanwhile varied little through the year, although greatest values were recorded in spring (Fig. 2D).

Total standing biomass was comparable at both sites and fairly stable through the year, with the exception of a marked decline in biomass at Wringcliff in winter (Fig. 2E). Data from Lynmouth indicated marked seasonality in patterns of blade growth and erosion, with maximal elongation values recorded in spring/early summer and negligible elongation observed through summer and autumn (Fig. 2F). Erosion exhibited a contrasting pattern, with peak erosion rates observed in autumn and winter (Fig. 2F). The winter dislodgement rates did not differ significantly between sites ($U = 0$, $n = 6$, $p = 0.174$); nevertheless, Lynmouth had a lower rate of dislodgement (~ 10 - 20 %) whereas the maximum dislodgment was found at Wringcliff, where almost 40 % of tagged individuals were lost (Fig. 2G).

C:N values in basal and distal tissue did not vary significantly between sites but exhibited marked variability between seasons (Table 1; Fig. 3A&B). Specifically, C:N values were significantly higher in summer/autumn compared with winter/spring (Fig. 3A&B, Table 1; post-hoc tests $p < 0.05$). In addition, a significant Site x Season interaction was detected for distal tissue, with post-hoc tests showing that differences between sites were only significant in autumn ($p < 0.05$). For phenol concentrations in basal tissue a significant Site x Season interaction was detected, as variability between sites was only significant in autumn (Fig. 3C, Table 1). The phenol content of distal tissue was consistent across sites and between seasons, with no significant variability detected (Fig. 3D, Table 1).

Across the study *P. pellucida* individuals were frequently recorded on *L. digitata* plants, specifically, one or more *P. pellucida* were observed on 50 % of blade samples, 13 % of stipes and within 30 % of holdfasts. The abundance of *P. pellucida* associated with kelp plants exhibited strong seasonality, with maximum densities observed during summer and autumn (Fig. 4A-C). The maximum observed abundance was on kelp blades with 47 limpets recorded at Wringcliff Bay in September (Fig. 4A). However on average, ~ 10 limpets per plant blade were observed at both sites during summer (Fig. 4A), whereas average limpet abundances on stipes and within holdfasts were consistently less than one per plant and more temporally consistent across the year (Fig. 4 B&C). In general *P. pellucida* became larger and increased in biomass from an initial period of recruitment in May through to the end of the year (Fig. 4D-I). An exception was a single large individual sampled on a kelp blade at Wringcliff in April 2016 (Fig. 4D&G), which had presumably over-wintered. The habitat preference of *P. pellucida* also exhibited seasonality (Fig. 5), where *P. pellucida* were almost exclusively recorded on the central and distal portions of blade surfaces through the summer months (i.e. June-August), after which the relative abundance of *P. pellucida* found on the basal meristematic area of the blade increased (Fig. 5). However, through winter (i.e. November to February), *P. pellucida* were predominantly recorded on stipes and within holdfasts (Fig. 5).

The total area of *L. digitata* blades grazed by *P. pellucida* varied significantly between both months and sites (Fig. 6A, Table 2). Post-hoc tests indicated that, overall, grazing was higher at Wringliff and that grazing damage was greater in April 2016 compared with other months. Indeed, grazing damage reached ~ 4 % at Wringcliff in April 2016, whereas typical grazing damage was ~ 1 - 2 % of kelp blade surfaces across all other months (Fig. 6A). For the Lynmouth population (where elongation rates were recorded), we observed no significant variability in the area of newly-formed tissue grazed by *P. pellucida* between months ($F_{11,59} = 0.94$, $p = 0.387$), although a marked peak of ~ 6 % of newly formed tissue was recorded in September (Fig. 6B). The number of grazing scars on *L. digitata* blades was not significantly different between sites but varied significantly between months (Fig. 6C,

Table 2), with lowest values recorded in May and highest in September (Fig. 6C). Finally, the average size of grazing scars was highly variable between plants but did not vary significantly between sites or months (Fig. 6D, Table 2). The densities of *P. pellucida* we recorded at our study sites were, on the whole, comparable to survey data collected from other sites in the southwest of the UK, with the exception of a single study site near Plymouth (Fig. 7).

4. Discussion

The structure of *L. digitata* populations was similar across both sites and several characteristics varied seasonally in agreement with previous studies (Kain, 1979; Kain and Jones, 1975; Parke, 1948; Perez, 1969). Specifically, we recorded spring-time peaks in density and percentage cover (Chapman, 1984), total length (slightly later than previously recorded, likely due to continued stipe growth after peak blade growth ended) (Delebecq et al., 2016; Kain, 1979; Schaffelke and Lüning, 1994), elongation rates (Kain, 1979; Parke, 1948; Perez, 1969), nitrogen levels (in winter/spring compared with summer/autumn) (Chapman and Craigie, 1978; Gagné et al., 1982; Gevaert et al., 2008; Young et al., 2007) and phenols in the distal blade tissue (Adams et al., 2011; Connan et al., 2004; Leblanc et al., 2011). These spring peaks are likely influenced by increasing light levels (Dayton, 1985; Leblanc et al., 2011) and high concentrations of nutrients in the water column (Dayton, 1985; Gagné et al., 1982; Targett and Arnold, 1998). Meanwhile, low elongation rates recorded during the summer were inversely related to the seawater temperature (Delebecq et al., 2016; Kain, 1979; Raybaud et al., 2013; Wilson et al., 2015; Yesson et al., 2015). Plant biomass and standing crop tended to peak in summer/autumn, as expected given the timing of peak growth and winter storm-induced blade erosion and dislodgement (Black, 1950; Kain, 1979; Schaffelke and Lüning, 1994). Carbon content (as shown by C:N) also increased in summer/autumn, likely due to increased photosynthate storage (Celis-Plá et al., 2015; Gevaert et al., 2008; Young et al., 2007). In contrast to these other seasonal patterns, we observed peaks in erosion rates in the winter, coinciding with a period of increased storminess and wave action, which likely resulted in increased fragmentation and tissue loss (Krumhansl and Scheibling, 2012; Lüning, 1979; Mann, 1972). Increased wave action during winter also led to the loss of entire kelp plants, as seen in the dislodgement rates discussed below.

The population structure of *P. pellucida* also exhibited marked seasonality, largely similar to that observed in other parts of its range (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). For example, peak recruitment occurred in May/June and maximum abundance in September, in keeping with previous studies on *P. pellucida* populations in the northeast Atlantic (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). Limpet abundances on kelp blades decreased markedly after September, most likely due to dislodgement (Vahl, 1971), predation (Norderhaug et al., 2005), or migration towards the stipe and holdfast (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). Measurements of *P. pellucida* biomass and shell length were used to infer the age of individuals sampled in spring (McGrath, 1997, 1992) and confirmed that *P. pellucida* can and do overwinter (Fretter and Graham, 1976; Kain and Svendsen, 1969; McGrath, 1992); the low abundances of adults recorded during the spring months, however, suggest that most individuals persist for < 1 year (Fretter and Graham, 1976; Vahl, 1971).

While *Patella pellucida* were conspicuous, common and at times abundant, there was limited evidence of ecologically-significant grazing damage on the blade. This is in contrast to other kelp-associated limpets, such as *Discurria insessa* (Black, 1976; Choat and Black, 1979) and *Scurria scurra* (Muñoz and Santelices, 1989), which can cause significant damage to kelp blades and stipes and consequent increases in erosion and defoliation. Or in comparison to the littorinid gastropod *Lacuna vincta*, a common kelp-associated grazer in the Northern Hemisphere, which has also been shown to induce tissue weakening and fragmentation through grazing activity (Chenelot and Konar, 2007; Egan and Yarish, 1999; Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and Pavia, 2002a). In contrast to these, *P. pellucida* scrapes the surface tissue of kelp blades and causes only superficial damage that may be less likely to increase breakage and erosion, particularly when compared to species that create excavations and perforations, such as *L. vincta* (Krumhansl and Scheibling, 2011; Toth and Pavia, 2002b). As such, although the total area of tissue damage associated with *Patella pellucida* grazing was similar to that of *L. vincta* in previous studies (Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and Pavia, 2002a), the impact is likely to be less. *Patella pellucida* individuals are markedly smaller than most other kelp-associated limpets (e.g. *Discurria insessa* and *Scurria scurra*, see Muñoz and Santelices, 1989) and, consequently, may consume less kelp material and cause less direct grazing damage. Similarly, the maximum densities of *P. pellucida* recorded here were 47 per plant or approximately 200 m^{-2}, whereas previous studies focussing on *L. vincta* have reported densities of up to 300 individuals per plant and > 4500 m^{-2} (Johnson and Mann, 1986). The higher densities recorded for other kelp-associated gastropods could indicate stronger grazing pressure exerted by these species.

The limited blade grazing damage we observed varied markedly through the year. Grazing pressure was low from late spring to late summer, coinciding with the period of peak kelp growth and the generally small sizes of limpet recruits. Both absolute and relative grazing damage increased slightly into autumn and winter, corresponding with a reduction in kelp growth rates and an increase in limpet size. Even so, the total area of grazed tissue was < 1.5 % through most of the year, with the exception being April 2016 when grazing damage peaked at ~ 4.5 %. These values are considerably lower than the percentage area of grazing damage caused by *L. vincta* on *L. digitata* populations in Helgoland, Germany (Molis et al., 2010), and lower than the observed grazing pressure of *P. pellucida* on subtidal populations of *Saccorhiza polyschides* in Ireland (Ebling et al., 1948). This is consistent with the conclusion that top-down control by *P. pellucida* on *L. digitata* blades within the current study region is limited. Interestingly, we did observe notable mobility in limpet grazers across sections of the plant and, probably, between plants. Limpets tended to congregate on the central and distal parts of the blade in summer, before migrating down to the base of the blade and then to the stipe and holdfast. This has previously been shown to occur on *L. hyperborea* (Kain and Svendsen, 1969) but not for *L. digitata*. The explanation is most likely related to limpets seeking shelter from increased water motion and blade erosion during autumn and winter, as holdfasts and stipes are more physically stable and offer more protection from hydrodynamic forces (Vahl, 1972), rather than any changes in factors such as plant palatability. Moreover, observations from a pilot experiment conducted at the same sites in which limpets were actively removed from kelp plants each month (authors' unpublished data), suggested that mature limpets recolonised plants fairly rapidly and moved between kelp individuals. This level of intra- and inter- plant mobility, postulated previously (McGrath, 1997) and corroborated by our observations, suggests that *P. pellucida* exhibits far less host-fidelity than other kelp-associated limpets (e.g. *Discurria insessa*, Choat and Black 1979, and *Scurria scurra*, Munoz and Santelices 1989).

While the impact of *P. pellucida* grazing on the blade appears to be minimal, the increase in stipe and holdfast *P. pellucida* abundance and percentage occupancy during the winter months would likely lead to an increase in grazing scars in these parts of the algae (Graham and Fretter, 1947; McGrath, 1992; Toth and Pavia, 2002a). Although water movement is an important factor in determining kelp dislodgement, it is often aided by prior weakening of the blade, stipe and/or holdfast by grazing scars (Duggins et al., 2001; Krumhansl and Scheibling, 2012). Given the relatively high rates of winter kelp loss we observed and the sustained winter occupancy of *P. pellucida* within holdfasts and on stipes, it is possible that dislodgement of whole plants and stipe breakage may be exacerbated by tissue weakening from grazing damage (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). Cavity grazing by *P. pellucida* has previously been speculated as a cause of *L. hyperborea* dislodgement (Kain and Svendsen, 1969) and has similarly been found for other kelp grazers, including urchins (Tegner et al., 1995). Alternatively, grazing activity may decrease in winter during periods of lower water temperatures and relative dormancy (Thompson et al., 2000). As such, it is currently unknown whether cavity grazing by limpets infesting kelp holdfasts increases the likelihood of dislodgement during periods of intense wave action, and further research into the importance of this process is needed.

Our study suggests that grazing by *P. pellucida* does not exert strong top-down control on *L. digitata* populations in the UK. The abundance patterns of *P. pellucida* observed at our main study sites were broadly comparable to limpet abundances recorded elsewhere in the southwest of the UK. It should be noted that our study was purely mensurative, and without controlled manipulations of grazer density (i.e. limpet removals/exclusions) it is not possible to conclude that grazing is not ecologically significant in shaping kelp dynamics in this system. However, the relatively low density, small size and superficial grazing action of *P. pellucida* on the blade, combined with high growth rates of *L. digitata* at certain times of the year, strongly suggest that top-down pressure from limpets is not a key driver.

Other kelp-associated grazers, meanwhile, could induce top-down control of kelp populations in the UK through direct consumption. Grazing by *L. vincta*, as discussed above, has been shown to increase fragmentation and erosion of kelp tissue, leading to canopy loss (Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and Pavia, 2002a). However, this species has a distinctly northern distribution and is more prevalent in kelp-dominated habitats around Scotland (Smale, pers. obs.), being uncommon in southern regions of the UK. Its potential grazing impacts in the UK are poorly known, and while research conducted elsewhere indicates that it could be locally important (Johnson and Mann 1986; Toth and Pavia 2002b; Krumhansl and Scheibling 2011), anecdotal evidence suggests that densities are generally low and unlikely to cause significant defoliation (Smale, pers. obs.).

Sea urchins are keystone species within many kelp forest ecosystems (e.g. Steneck et al., 2002), and three urchin species are common within shallow subtidal habitats around the UK and Ireland (Jones and Kain, 1967; Kitching and Thain, 1983). Of these, *Strongylocentrotus droebachiensis* is at its southern range edge in northern Scotland, where it is patchily distributed and is unlikely to form extensive barrens, as it has done further north along the Norwegian coastline (Hagen, 1983; Sivertsen, 2006). *Paracentrotus lividus* is also found in coastal waters surrounding the UK and Ireland but, populations are patchy and, with isolated exceptions, densities would not be high enough to induce barren formation (Kitching and Thain, 1983; O'Sullivan and Emmerson, 2011). Finally, while *Echinus esculentus* is widely distributed and at times common, it tends to feed on drift algae and exhibit omnivorous feeding habits, rather than consuming mature kelp plants and forming extensive barrens (Leclerc et al., 2015; Sjøtun et al., 2006). As such, kelp populations in coastal waters in the UK appear to be less structured by top-down processes compared with those in many other regions (e.g. eastern Canada (Mann, 1977), Iceland (Hjorleifsson et al., 1995), northern Norway (Leinaas and Christie, 1996), parts of South Africa (Bustamante et al., 1995), eastern Australia (Andrew and Underwood, 1993), and New Zealand (Shears and Babcock, 2002). Rather, other factors such as intense wave action (Burrows, 2012; Smale and Vance, 2015), localised nutrient and pollutant inputs (Moy and Christie, 2012; Sheppard et al., 1980), light availability (Burrows, 2012; Smale et al., 2016) and sea temperature (Smale et al., 2015; Smale and Moore, 2017) are likely to be more important in structuring these kelp populations and their associated communities.

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Table 1. Results of univariate PERMANOVAs to examine the effects of Season (fixed), Site (fixed) and the Season x Site interaction on C:N values and phenol concentrations in both basal and distal blade tissue. Degrees of freedom associated with each factor are shown in parentheses. An asterisk (*) with an F value indicates that PERMDISP detected significant differences in within-group dispersion between levels of that factor and significance of PERMANOVA was reduced to P<0.01.

	Season (3)			Site (1)			Season x Site (3)			Residual (33)
Response	MS	F	*P*(perm)	MS	F	*P*(perm)	MS	F	*P*(perm)	MS
Basal C:N	656.64	217.68	**0.001**	5.58	1.85	0.186	2.07	0.68	0.545	3.01
Distal C:N	373.48	93.89	**0.001**	2.56	0.64	0.420	13.07	3.28	**0.033**	3.97
Basal phenol	0.007	5.28*	**0.007**	0.006	4.46*	0.050	0.004	3.11	**0.038**	0.001
Distal phenol	0.005	1.43	0.253	0.001	0.30*	0.618	0.001	0.084	0.976	0.003

Table 2. Results of univariate PERMANOVAs to examine the effects of Month (fixed), Site (fixed) and the Month x Site interaction on the total percentage area of grazing scars, total number of grazing scars and average size of grazing scars on *Laminaria digitata* blades grazed by *Patella pellucida*. Degrees of freedom associated with each factor are shown in parentheses. F values marked with an asterisk (*) indicates that PERMDISP detected significant differences in within-group dispersion between levels of that factor and significance of PERMANOVA was reduced to P<0.01.

	Month (11)			Site (1)			Month x Site (11)			Residual (215)
Response	MS	F	*P*(perm)	MS	F	*P*(perm)	MS	F	*P*(perm)	MS
Tot. % area grazed	15.73	9.69*	**0.001**	13.94	8.58*	**0.002**	0.98	0.60	0.836	1.62
Tot. no. scars	776.22	7.78*	**0.001**	17.04	0.17	0.703	47.22	0.47	0.928	99.74
Av. size scars	2.09	1.83	**0.044**	0.21	0.18	0.675	1.63	1.43	0.132	1.14

Figure Legends

Figure 1. (A) Location of main study sites within the UK, with top inset indicating specific locations of Lynmouth Bay (blue star) and Wringcliff Bay (green star) on the North Devon coastline and bottom inset depicting the blue rayed limpet *Patella pellucida* and the kelp *Laminaria digitata*, which were the focus of the current study. (B) *In situ* temperature (Lynmouth = black line, Wringcliff = orange line) and light availability (Lynmouth = blue line, Wringcliff = green line) data for the period March 2016-March 2017 at both study sites. Measurements were obtained with a 'Hobo Tidbit' logger and a 'Hobo light and temperature pendant' logger, which were attached to the rocky substratum at each site and recorded hourly measurements. (C) Also shown are average daily significant wave height obtained for Bideford Bay (data courtesy of Channel Coastal Observatory, www.channelcoast.org) (January 2016 – March 2017) and monthly total sunshine hours obtained for Bude (Met Office, June 2017) (January 2016 – March 2017).

Figure 2. *Laminaria digitata* population dynamics in North Devon, UK. Plots show seasonal trends in (A) density (n = 10), (B) percentage cover (n = 12), (C) plant length (n = 10), (D) plant biomass (n = 10) and (E) standing biomass (n = 12). Where n = per site, per month. Additionally, at Lynmouth Bay only, seasonal trends in (F) elongation and erosion rates were measured. The number labels on plots indicate the number of replicate kelp individuals. At both sites, (G) winter dislodgement rates were quantified. NB. Black * = no data collected at both sites, Orange * = no data collected at one site.

Figure 3. Biochemical analysis of *Laminaria digitata* blades collected from the two study sites (Lynmouth Bay and Wringcliff Bay) in North Devon, UK. C:N ratio in (A) basal and (B) distal blade tissue and phenol content in (C) basal and (D) distal tissue for the four seasons of observation (n = 5 for all sampling events and sites).

Figure 4. *Patella pellucida* population dynamics in North Devon, UK. Plots indicate limpet abundances associated with the (A) blade, (B) stipe and (C) holdfast. Also shown are the length of limpets associated with the (D) blade, (E) stipe and (F) holdfast (F) and biomass (fresh weight) of limpets associated with the (G) blade, (H) stipe and (I) holdfast. All values are mean averages (± SE). NB: Numbers refer to the number of individual *P. pellucida* measured, "0" = no limpets found in the area of the kelp for that month (colour coded to the sites).

Figure 5. Micro-habitat preference of *Patella pellucida* associated with *Laminaria digitata.* Stacked bars indicate the relative occurrence of limpets on each section of the kelp plants,

for each survey month. Data from both sites pooled; numbers refer to the total number of individual *P. pellucida* found across the kelp plant.

Figure 6. Evidence of grazing on *Laminaria digitata* by *Patella pellucida* in North Devon, UK. (A) average total area grazed (as a percentage of blade area), (B) average area of newly-formed tissue grazed, (C) average number of grazing scars and (D) average grazing scar size. All values are mean averages (± SE).

Figure 7. (A) Map of southwest UK indicating additional survey sites (with insets a&b showing specific locations of North Devon and Plymouth sites). The abundances of *Patella pellucida* on *Laminaria digitata* blades at the two main sites in North Devon were compared with: (B) routine monthly surveys at two sites in south Devon; (C) autumn survey data from three sites along the south coasts of Devon and Cornwall; and (D) summer survey data from one site in Aberystwyth, Wales. The number of replicate kelp blades examined per site/month ranged from 8 to >50.

Figures

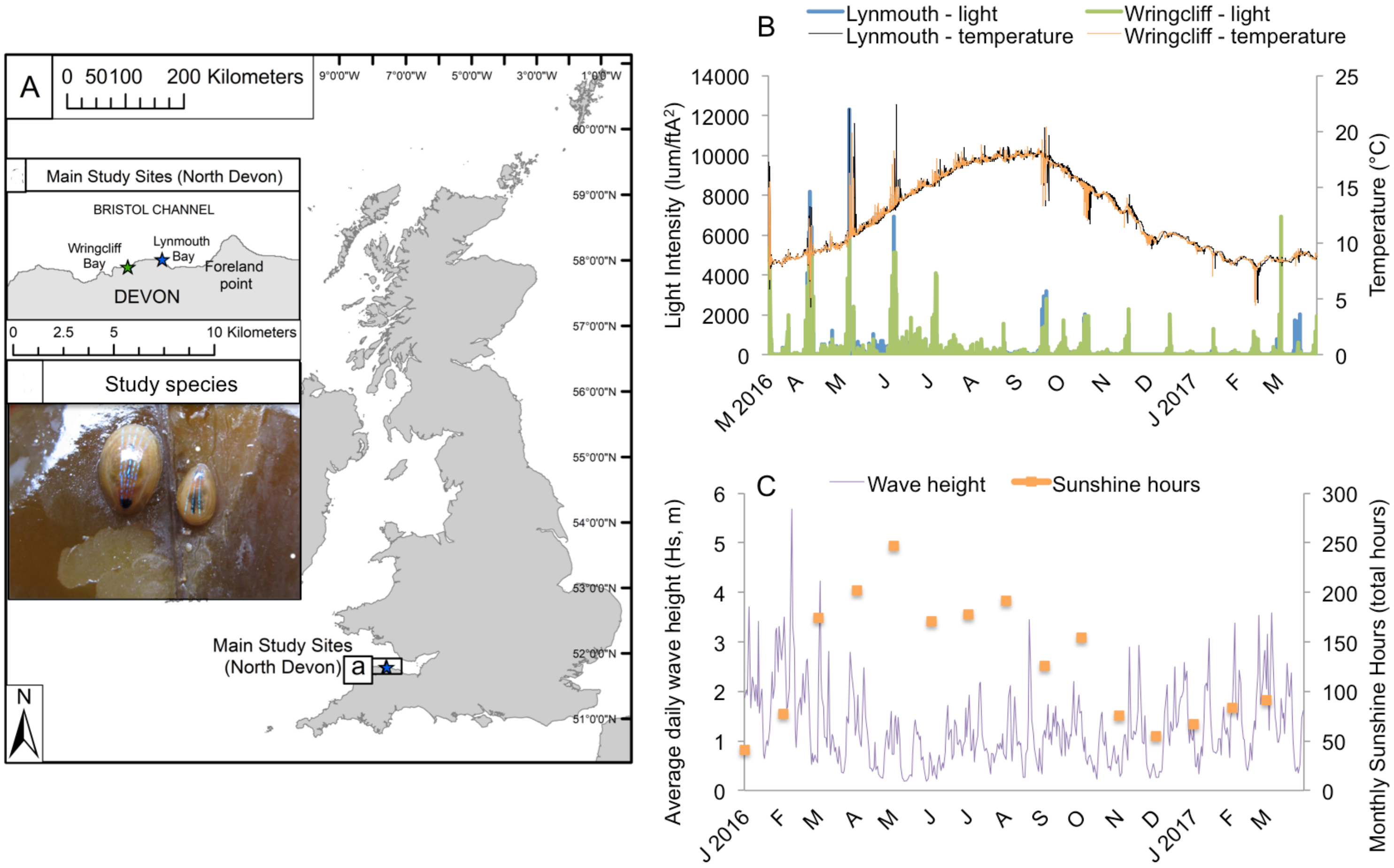

Fig. 1

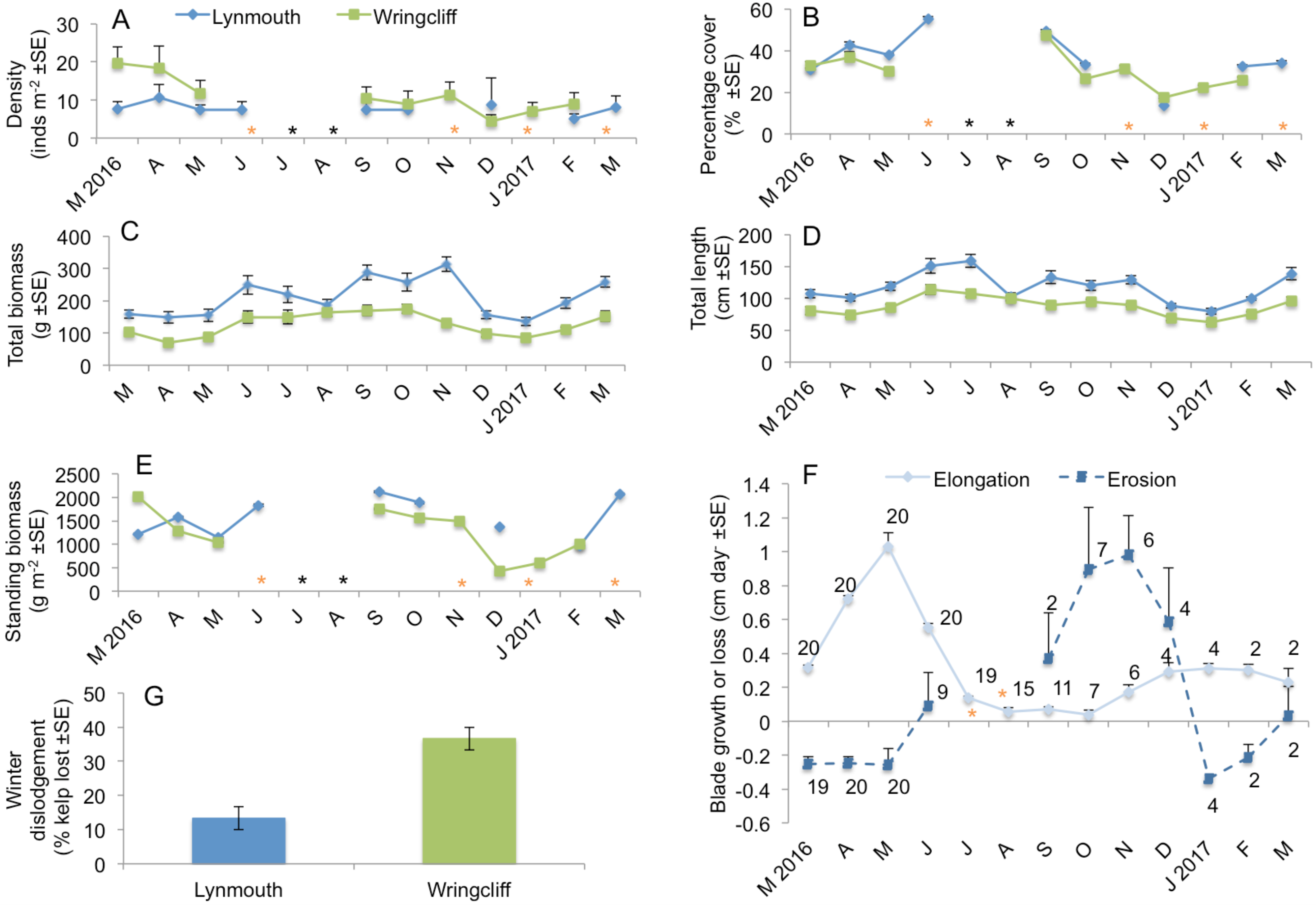
A
Lynmouth
Wringcliff
Density (inds m-2 ±SE)
30
20
10
0
M 2016
A
M
J
J
A
S
O
N
D
J 2017
F
M
B
Percentage cover (% ±SE)
60
40
20
0
C
Total biomass (g ±SE)
400
300
200
100
0
D
Total length (cm ±SE)
200
150
100
50
0
E
Standing biomass (g m-2 ±SE)
2500
2000
1500
1000
500
0
F
Elongation
Erosion
Blade growth or loss (cm day- ±SE)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
G
Winter dislodgement (% kelp lost ±SE)
50
40
30
20
10
0
Lynmouth
Wringcliff

Fig. 2

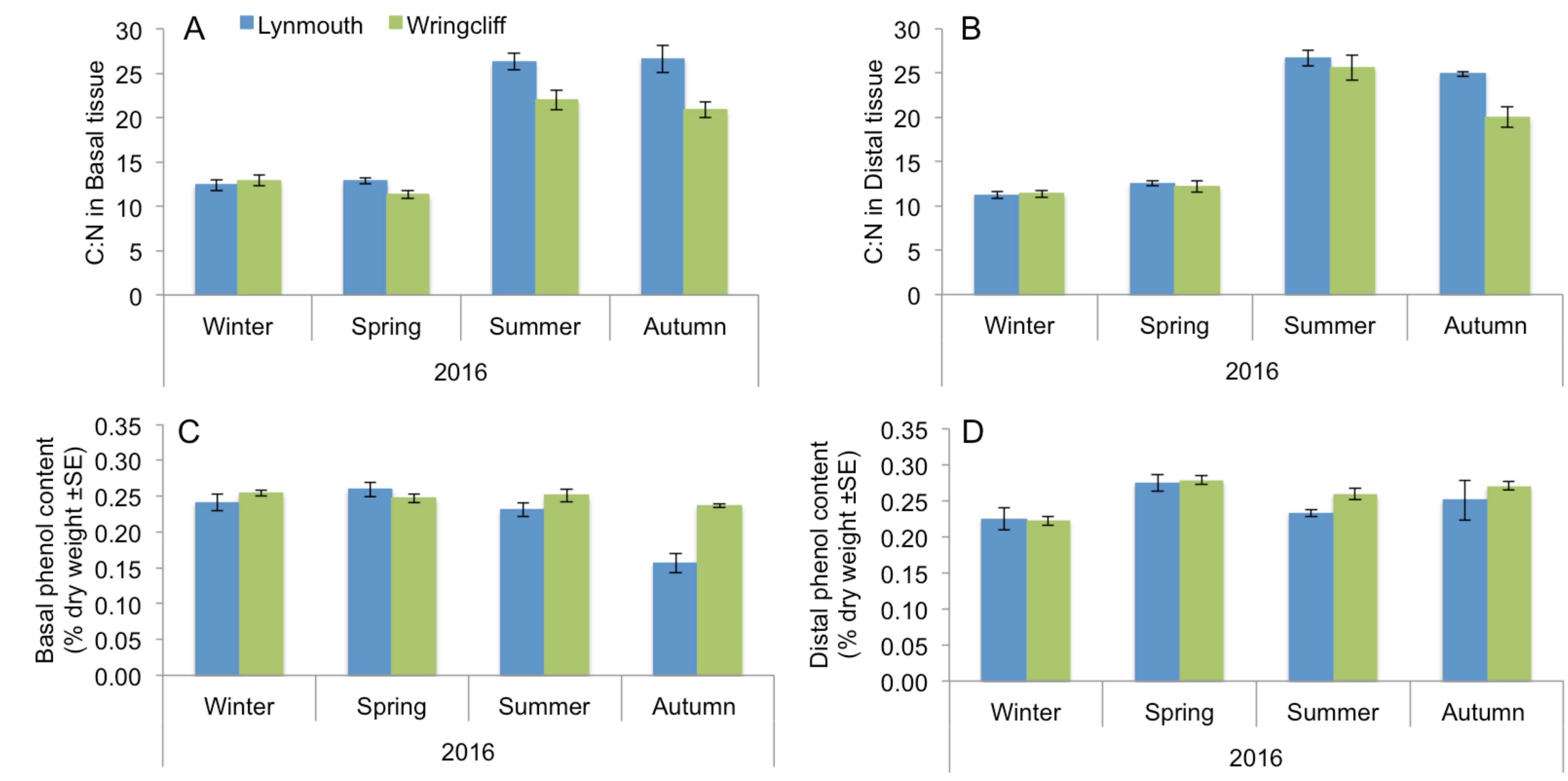
A
🟦 Lynmouth
🟩 Wringcliff
C:N in Basal tissue
30
25
20
15
10
5
0
Winter
Spring
Summer
Autumn
2016
B
C:N in Distal tissue
30
25
20
15
10
5
0
Winter
Spring
Summer
Autumn
2016
C
Basal phenol content
(% dry weight ±SE)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Winter
Spring
Summer
Autumn
2016
D
Distal phenol content
(% dry weight ±SE)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Winter
Spring
Summer
Autumn
2016

Fig. 3

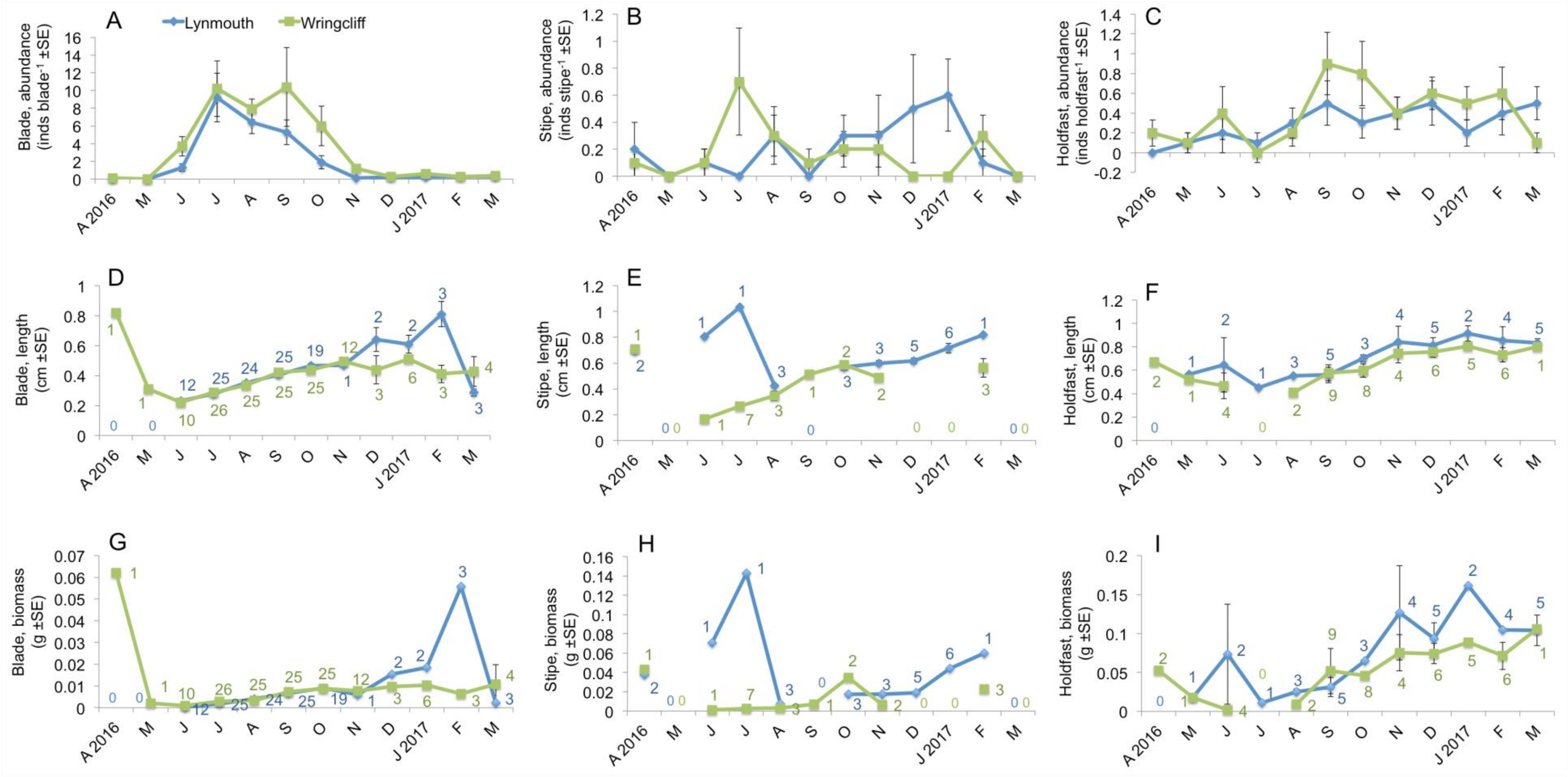
A
Lynmouth
Wringcliff
Blade, abundance (inds blade⁻¹ ±SE)
B
Stipe, abundance (inds stipe⁻¹ ±SE)
C
Holdfast, abundance (inds holdfast⁻¹ ±SE)
D
Blade, length (cm ±SE)
E
Stipe, length (cm ±SE)
F
Holdfast, length (cm ±SE)
G
Blade, biomass (g ±SE)
H
Stipe, biomass (g ±SE)
I
Holdfast, biomass (g ±SE)
A 2016
M
J
J
A
S
O
N
D
J 2017
F
M

Fig. 4

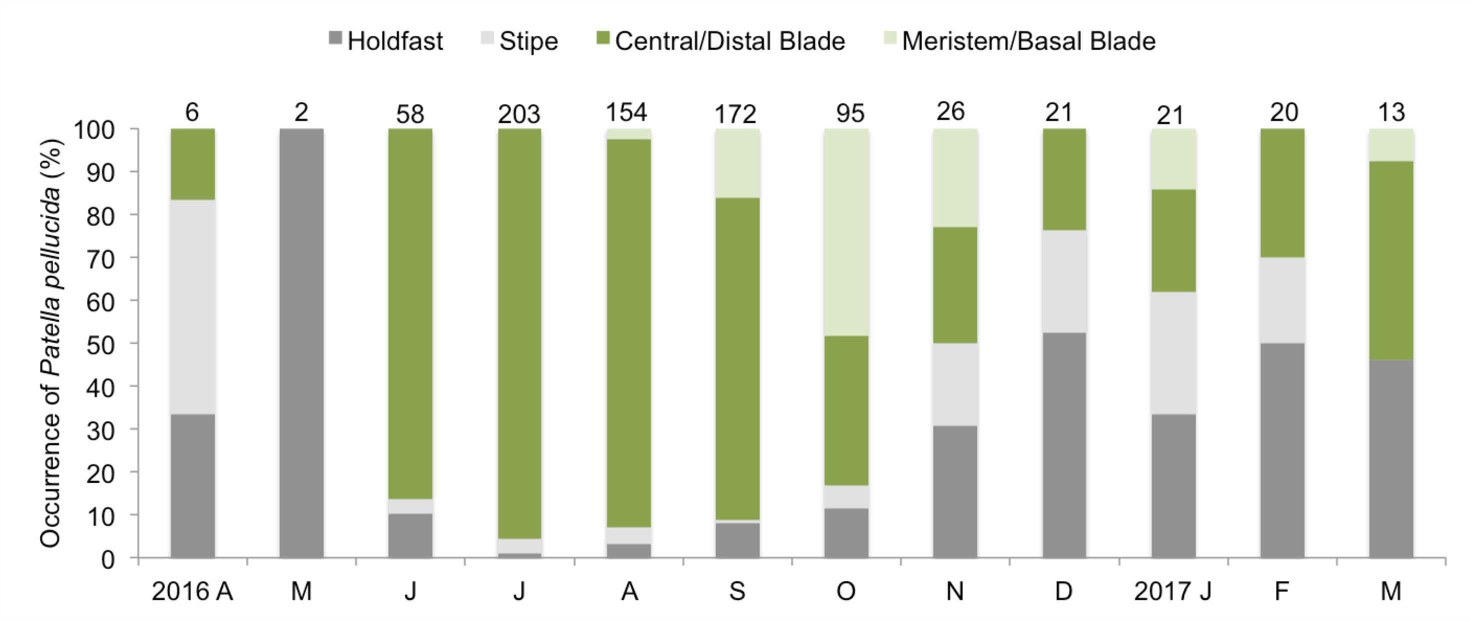
Holdfast
Stipe
Central/Distal Blade
Meristem/Basal Blade
Occurrence of *Patella pellucida* (%)
0
10
20
30
40
50
60
70
80
90
100
6
2
58
203
154
172
95
26
21
21
20
13
2016 A
M
J
J
A
S
O
N
D
2017 J
F
M

Fig. 5

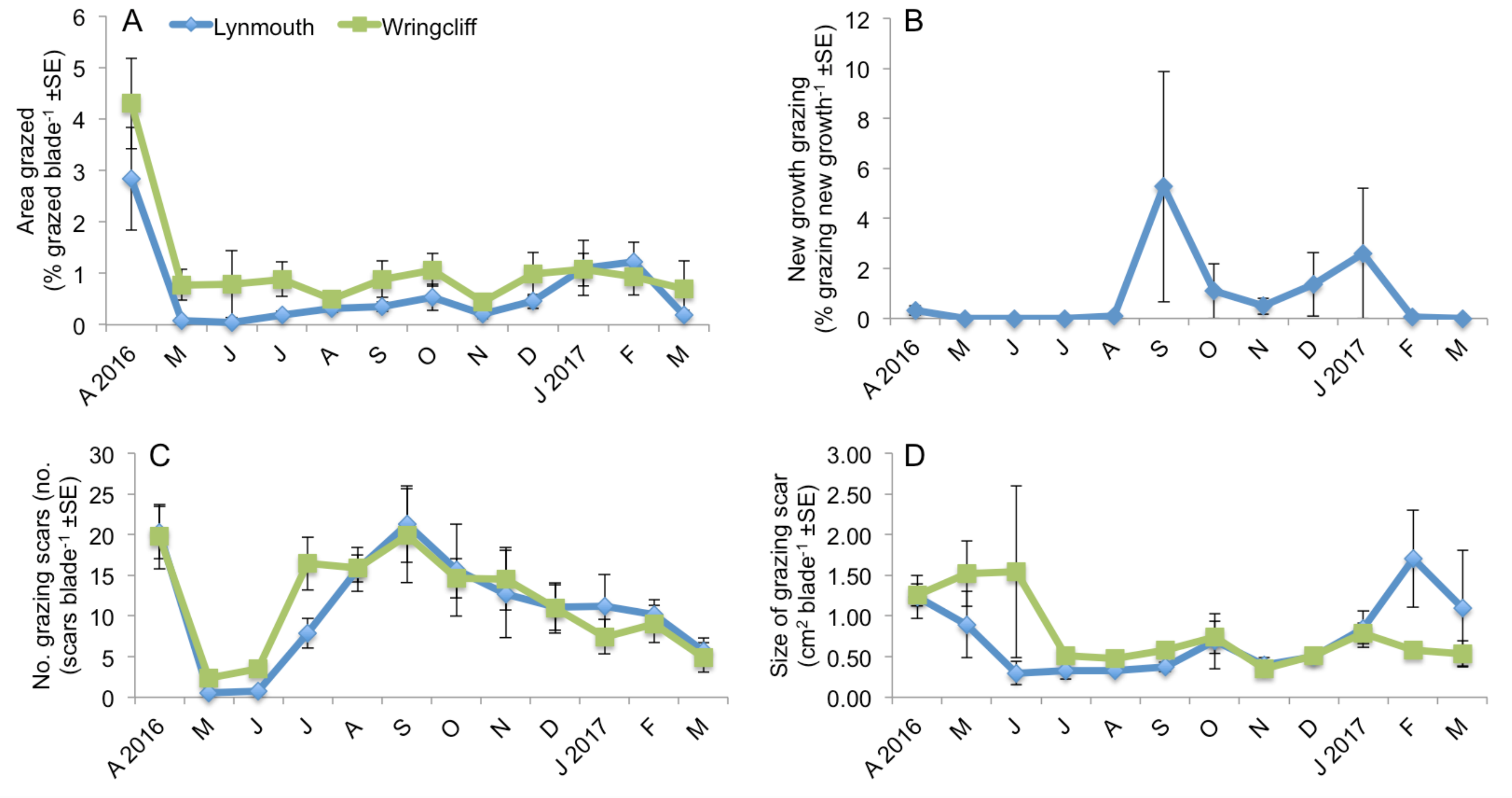
A
Lynmouth
Wringcliff
Area grazed (% grazed blade^{-1} ±SE)
0
1
2
3
4
5
6
A 2016
M
J
J
A
S
O
N
D
J 2017
F
M
B
New growth grazing (% grazing new growth^{-1} ±SE)
0
2
4
6
8
10
12
C
No. grazing scars (no. (scars blade^{-1} ±SE)
0
5
10
15
20
25
30
D
Size of grazing scar (cm^2 blade^{-1} ±SE)
0.00
0.50
1.00
1.50
2.00
2.50
3.00

Fig. 6

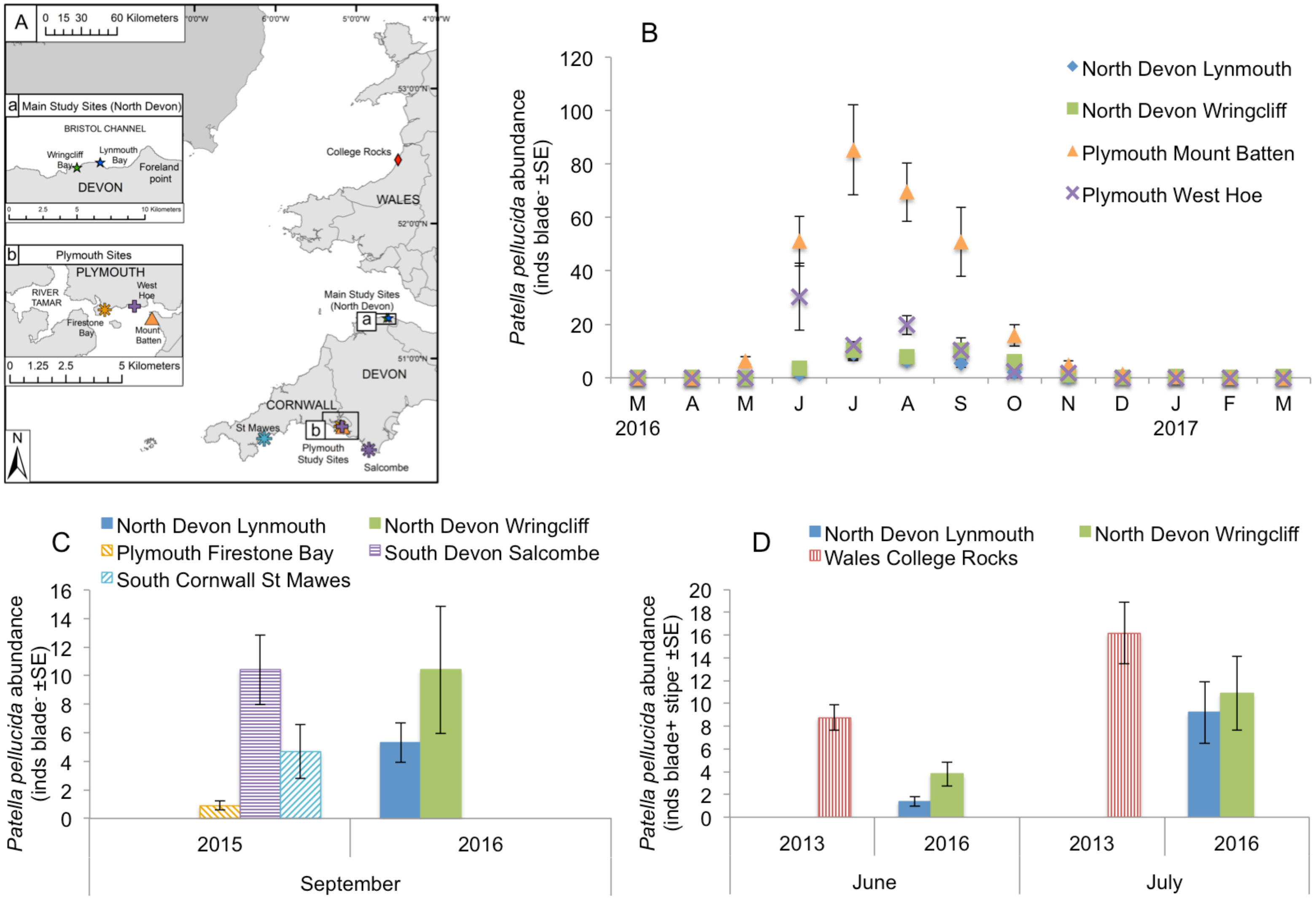
A
0 15 30 60 Kilometers
6°0'0"W
5°0'0"W
4°0'0"W
53°0'0"N
52°0'0"N
51°0'0"N
a Main Study Sites (North Devon)
BRISTOL CHANNEL
Wringcliff Bay
Lynmouth Bay
Foreland point
DEVON
0 2.5 5 10 Kilometers
b Plymouth Sites
PLYMOUTH
RIVER TAMAR
West Hoe
Firestone Bay
Mount Batten
0 1.25 2.5 5 Kilometers
College Rocks
WALES
Main Study Sites (North Devon)
a
DEVON
CORNWALL
St Mawes
b
Plymouth Study Sites
Salcombe
N
B
Patella pellucida abundance (inds blade⁻ ±SE)
0
20
40
60
80
100
120
M
A
M
J
J
A
S
O
N
D
J
F
M
2016
2017
North Devon Lynmouth
North Devon Wringcliff
Plymouth Mount Batten
Plymouth West Hoe
C
North Devon Lynmouth
North Devon Wringcliff
Plymouth Firestone Bay
South Devon Salcombe
South Cornwall St Mawes
Patella pellucida abundance (inds blade⁻ ±SE)
0
2
4
6
8
10
12
14
16
2015
2016
September
D
North Devon Lynmouth
North Devon Wringcliff
Wales College Rocks
Patella pellucida abundance (inds blade+ stipe⁻ ±SE)
0
2
4
6
8
10
12
14
16
18
20
2013
2016
2013
2016
June
July

Fig. 7